

# The life history and larval morphology of *Aperilampus* (Hymenoptera: Chalcidoidea: Philomidinae), with a discussion of the phylogenetic affinities of the Philomidinae

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**Abstract.** The host association and larval morphology of *Aperilampus* (Hymenoptera: Chalcidoidea: Philomidinae) are documented for the first time based on specimens collected during the excavation of ground-nesting bee nests in South Africa. *Aperilampus varians* Strand is a primary parasite of the pupa of *Halictus (Seladonia) africanus* Friese (Hymenoptera: Halictidae). The first and final-instar larvae are described and illustrated, and notes are provided on the behaviour of the first-instar larva. The first-instar larva is a planidium and synapomorphies are documented between the first-instar larva of *Aperilampus* and the planidia of Chrysolampinae, Perilampidae and Eucharitidae.

## Introduction

The Philomidinae is an enigmatic and infrequently collected group of Chalcidoidea. Two genera are generally recognized, *Philomides* Haliday and *Aperilampus* Walker. The taxonomic history of these genera consists of a few isolated descriptions and generic transfers. There has never been a comprehensive revision of these genera and only a cursory key has been published (Risbec, 1953). Diagnoses and differentiating characters for the two genera have not been published and there are several undescribed species. There is considerable variability in colour pattern which complicates the assessment of the diversity of the subfamily. A taxonomic revision of the subfamily is being undertaken by Zdenek Bouček and he estimates the world fauna at fewer than twenty species (pers. comm.). Species are restricted to the Mediterranean region (including Albania), southeast Asia, and seem to reach their maximum diversity in Africa. The biology is unknown but the host was predicted to be ground-nesting bees (Bouček, 1988: 513).

The higher classification of Philomidinae is also unresolved. Affinities with Perilampidae and Eucharitidae were noted by early authors; in fact, at least two species of *Aperilampus* were originally described in *Perilampus* including the type species of *Aperilampus* (*Perilampus discolor* Walker). More recently, affinities with both the Perilampidae (Kerrich, 1956; Peck *et al.*, 1964) and

Eucharitidae (Bouček, 1978; Prinsloo, 1980) have been suggested, based mainly on the large size and robust habitus of the adult wasps. Morphological support for the inclusion of Philomidinae in Eucharitidae centres around the extreme reduction of the size of the pronotum, which is reduced and not visible in dorsal view, a character shared with the two major subfamilies of Eucharitidae, the Oraseminae and Eucharitinae, referred to here as the Eucharitidae (*sensu stricto*). Other morphological characters of the adults are inconsistent with this hypothesis. The labrum of *Aperilampus* is among the most plesiomorphic found in the Chalcidoidea and offers no support for the view that Philomidinae is closely related to Eucharitidae and/or Perilampidae (Darling, 1988a). The most recent comprehensive treatment of the higher classification of the Chalcidoidea treats the Philomidinae as Eucharitidae (Bouček, 1988); included also are other subfamilies of uncertain affinity (Echthrodapinae and Akapalinae) that have frequently been referred to either the Eucharitidae or Perilampidae.

The current classification of the Chalcidoidea is based almost exclusively on adult characters. Life history and biological information are potentially very important in testing these hypotheses of relationships. Taxonomic congruence studies look for the concordance of hypotheses of relationships from different life history stages and are one of the strongest indications that the proposed phylogenetic relationships reflect evolutionary history. The concordance of larval and adult characters has provided many important insights into the phylogenetic relationships of many groups of Hymenoptera (e.g. Tenthredinoidea:

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Yuasa, 1922; Braconidae: Čapek, 1970; Ichneumonidae: Short, 1978; Sphecidae: Evans, 1959, 1964; Apidae: Michener, 1953, Rozen, 1965–69; Formicidae: Wheeler & Wheeler, 1976). In the Chalcidoidea studies of immature stages have been largely descriptive and focused on delimiting a number of 'types' of larvae (Clausen, 1940; Parker, 1924; Finlayson, 1987). Planidial first-instar larvae have received considerably more scrutiny (Askew, 1979; Heraty & Darling, 1984) and the occurrence of synapomorphies for the planidia of Eucharitidae, Perilampidae and Chrysolampinae (Darling & Miller, 1991) was inconsistent with one of the proposed classifications for the Chrysolampinae, viz as a subfamily of Pteromalidae (Graham, 1969).

Host information is potentially important in assessing the affinities of enigmatic taxa such as Philomidinae, Echthrodapinae and Akapalinae because all species of the subfamilies Eucharitinae and Oraseminae, the Eucharitidae (*s.s.*), with known host associations are primary parasites of ants (Heraty, 1990). In sharp contrast to the Eucharitidae, the host associations of Perilampidae are extremely diverse. At least eight orders of insects serve as hosts and both primary and secondary parasitism (hyperparasitism) occurs. Ants very rarely serve as hosts for Chalcidoidea and ant hosts in any of these enigmatic subfamilies would be evidence supporting affinities with Eucharitidae.

The biology and life history of Eucharitidae and Perilampidae are similar in many respects (Heraty & Darling, 1984). The first-instar larva is a sclerotized, active planidium and development is hypermetamorphic; the subsequent larval instars are hymenopteriform. Eggs are laid away from the host, on or in leaves, flowers or in preformed cavities in plant tissue. Oviposition in association with plant material and planidia are infrequently encountered in the Chalcidoidea and would also be evidence for phylogenetic relationships with Perilampidae and Eucharitidae.

In this paper I provide a host association for *Aperilampus varians* and illustrate and describe the larvae and pupa for the first time. Notes on the behaviour of the first-instar larva are also provided. These data are analysed from a phylogenetic perspective and the affinities of Philomidinae, Chrysolampinae, Perilampidae and Eucharitidae are discussed.

## Methods

The material available for study was collected at Sunnyside, a suburb of Pietermaritzburg, Natal, South Africa, on 15 January 1990 during the excavation of nests of *Halictus (Seladonia) africanus* Friese by Gerd Knerer, Department of Zoology, University of Toronto. All specimens were collected with bee pupae in two nests in the same aggregation (S-07, S-09). A total of ten specimens of *Aperilampus* was collected from these nests and it is extremely fortunate that a nearly complete series of life history stages was represented. Examined were four first-instar larvae, three of which were associated with the same bee pupa; a mature larva; three pupae; and nearly

completely developed male and female imagos. Both the male and female are fully sculptured and the colour pattern is apparent; only the wings are malformed. These adult voucher specimens confirm the identity of the immature stages as *Aperilampus*.

All material, including the host bee pupa associated with the first-instar larvae, are stored in alcohol except: the adult wasps are pointed, a single first-instar larva is slide-mounted (D. Chris Darling Slide No. 1483), and one first-instar larva attached to a bee pupa and one *Aperilampus* pupa are critical point dried. In addition, there are pinned voucher specimens of the F1 generation adult bees from nest S-09, which are completely developed except that the wings are not fully expanded. All material is deposited in the Department of Entomology, Royal Ontario Museum.

Terms for morphological structures follow Heraty & Darling (1984) and Darling & Miller (1991). Phylogenetic analysis was performed using HENNIG86 (version 1.5) and alternate topologies and character optimizations were investigated using CLADOS (version 1.2).

## Results

### *Biology and host association*

Approximately twenty bee immature stages, from small larvae to pigmented pupae, were collected from nest S-09 and *Aperilampus* specimens were discovered by Gerd Knerer during the examination of this material in the laboratory for parasites. In addition to *Aperilampus*, this nest had also been invaded by an unidentified species of earwig that killed all of the parental generation bees in the nest, and one of the F1 generation adult bees was parasitized by a strepsipteran (G. Knerer, pers. comm.). Six additional nests in the same aggregation were excavated and only one (S-07) contained *Aperilampus*. Apparently, parasitism is localized, which may provide some insight into the behaviour of adult females and first-instar larvae.

Oviposition was not observed. The first-instar larvae are at least initially gregarious, three were associated with a single host pupa, tucked beneath the thoracic legs (Fig. 3). A more developed bee pupa had a single engorged planidium attached to the dorsum of the mesosoma.

### *Description of the immature stages*

Eggs were not observed and only two larval instars were collected, which are regarded as the first and the final instars. This determination is based, for the first-instar larva, on the usual pattern of hypermetamorphic development (i.e. with the first-instar specialized) and for the final-instar larva, on the basis on the similarity in size with the pupa. The number of intervening larval instars, if any, is unknown.

#### *First-instar larva (Figs 1–4)*

Length about 1.2 mm, maximum width about 0.25 mm;

fusiform, oval in cross-section. Cranium and 13 body segments, I–XII pigmented and light brown in colour, XIII translucent white. Cranium sclerotized; antenna absent, indicated only as low, broad swellings on the cranium, not peg-like or papilliform; 1 pair of pleurostomal setae (plst), and 4 pairs of cranial setae (cs); pleurostoma weakly sclerotized; prelabium (prlb) circular, but without sclerotized marginal rim, labial palpi reduced and located laterad on prelabium; postlabium sac-like and probably eversible; mandibles large, curved, and rather blunt with well-developed bases, asymmetric, right mandible larger with irregular inner margin, left mandible comma-shaped.

Tergites I–XII sclerotized, I–XI strap-like and incomplete, separated ventrad by membranous areas (i.e. tergites do not completely encircle body) and III–X with narrow more weakly sclerotized region along dorsal midline; successive tergites not abutted dorsad, capable of telescoping. Setae present dorsad on I, II, III, V, VII, IX and XI; laterad on I–IX; ventrad on III; small setae ventrad on XII and XIII; only X devoid of setae. Spicules (spi) on the membranous ventral surface of I, and a single small seta on the membranous ventral region of II.

Tergites I–IV differentiated from remaining tergites, roughened, with erect triangular pustules and very short setae (visible only in slide-mounted specimens), V–XII glabrous or with weak transverse costulae. Tergites I–VII with elongate projections bearing large, flattened and multifurcate seta, on I–III these setae are directed forward over preceding segment; tergites I and II with distinct dorsal and lateral plates separated by area of weak sclerotization or membrane, on II the dorsal projections are fused to form a forward projecting v-shaped prominence which orients the setae over tergite I (Fig. 1). Spiracle (sp) present dorsad in membrane bounded by dorsal and lateral plates of II and by tergite I. Tergites I–III with more heavily sclerotized transverse ridge (sr) at ventral margin of tergites. Caudal pad present on XIII.

#### Final-instar larva (Fig. 5)

Length about 7 mm, maximum width about 2.5 mm; hymenopteriform. Cranium and 13 body segments membranous, not sclerotized or melanized, white in colour. Cranium reduced, mouthparts inconspicuous; mandibles widely separated, straight and sharply pointed, without teeth; antenna absent. Large spatulate setae present dorsad on I, II, III, V, VII and IX, without smaller setae. Spiracles present on II–X, spiracles II and IV larger than other spiracles.

#### Pupa (Fig. 6)

Length about 7 mm. Mesosoma with large mesothoracic (II) and propodeal spiracles (IV), the mesothoracic spiracle raised on fleshy protuberance, the propodeal spiracle very large and oval but concealed by metathoracic leg in lateral view. Mesoscutum with pair of annulate horn-like

projections, scutellum strongly vaulted over propodeum. Metasoma with spiracles on metasomal segments 2–7 (VI–XI), spiracle 7 larger and associated with modification of caudal margin of tergite. Note: there is an exact correspondence between the large spiracles in the pupa and the functional spiracles in the imago (e.g. mesothorax, propodeum and seventh metasomal tergite).

#### Cladistic analysis

A re-evaluation of the cladistic analysis of the characters of eggs and first-instar larvae (Heraty & Darling, 1984) is presented based on new information concerning the biology and immature stages of Chrysolampinae and Philomidinae and more recent information concerning the planidia of Perilampidae and Eucharitidae.

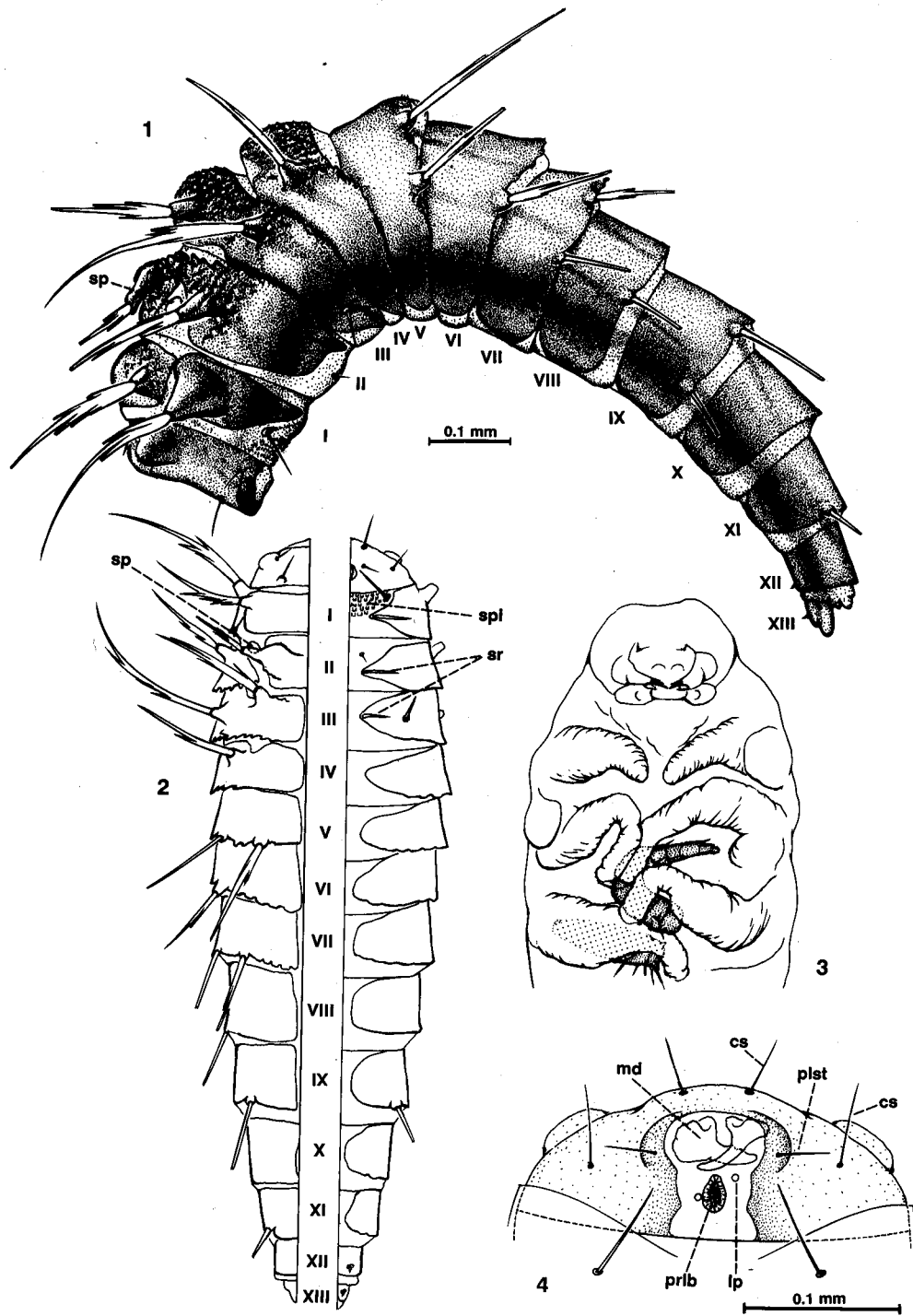
*Taxa examined.* Perilampidae and Eucharitidae (Heraty & Darling, 1984; see also Heraty, 1990; Heraty & Barber, 1990; Johnson *et al.*, 1986). Chrysolampinae (*Chrysolampus schwarzi* Crawford and *C. sisymbrii* (Ashmead); see Darling & Miller, 1991). Philomidinae, *Aperilampus varians*, this study.

*Characters.* Unless discussed below, states and polarity decisions for all characters in Table 1 are as discussed in Heraty & Darling (1984).

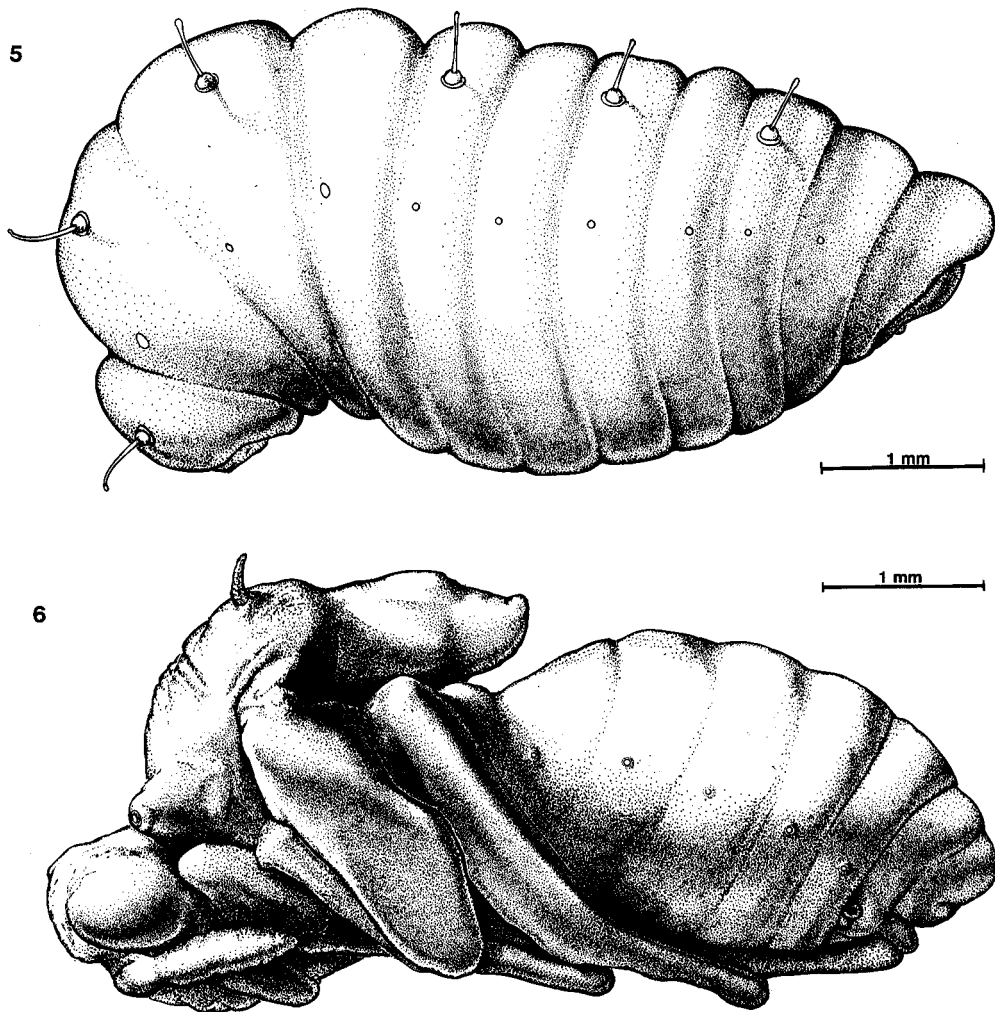
1. Egg shape. Stalked eggs were considered by Heraty & Darling (1984) as an autapomorphy of the Eucharitidae. Since then, stalked eggs have been recorded in *Chrysolampus* (Darling & Miller, 1991). Ovoid or cylindrical eggs have also been found in two genera of Eucharitidae (Oraseminae) (Heraty, 1990). However, these cylindrical eggs are regarded by Heraty (1990) as a synapomorphy of *Timioderus* and *Indosema*, which is consistent with stalked eggs as a ground plan character of the Eucharitidae.

3'. Shape of tergites. A second character is coded that concerns the shape of the tergites. In *Chrysolampus*, the sclerotized tergites are ring-like and completely encircle the body, the ventral surface is not membranous. In all Perilampidae and Eucharitidae examined and in *Aperilampus* the tergites are strap-like, incomplete ventrad. The undifferentiated ring-like tergites are regarded as plesiomorphic and more similar to the uniform cuticle of the larvae of most Chalcidoidea and would result from the uniform sclerotization on the tergites. Differential sclerotization, resulting in a membranous venter, is regarded as apomorphic. An alternative transformation series, 0 – unsclerotized, 1 – partial sclerotization, venter membranous (Perilampidae, Eucharitidae, Philomidinae), 2 – complete sclerotization (Chrysolampinae) does not affect the cladistic relationships.

4. Setal pattern, tergite III. As discussed in the Heraty & Darling (1984), ventral setae, which are located at or near the margin of the tergite, are absent in Oraseminae (Eucharitidae). This has been confirmed by a more extensive analysis of the planidia of Oraseminae (Heraty, 1990), which interprets the loss of this seta as a synapomorphy of the subfamily. Hence, this seta must be regarded as a ground plan character of the Eucharitidae, as coded in Table 1.



**Figs 1–4.** First-instar larva of *Aperilampus varians*. 1. Lateral habitus drawing (sp, prothoracic spiracle). 2. Schematic drawing of dorsal (left) and ventral (right) aspect showing shape of tergites and the distribution of various types of setae; orientation of setae distorted due to slide preparation. 3. Ventral view of bee pupa showing the position and orientation of two first-instar larvae. A third larvae was attached to the venter of this host, in the vicinity of the prothoracic legs. 4. Ventral view of cranium and mouth parts (cs, cranial setae; lp, labial palp; md, mandible; plst, pleurostomal setae; prlb, prelabium). Figs 2 and 4 based on D. Chris Darling Slide No. 1483; 1 and 3 based on alcohol-preserved material.



Figs 5–6. *Aperilampus varians*. 5. Final instar larva. 6. Pupa. Both based on alcohol-preserved material.

7–8. Ventral spines and tubercles. Various types and configurations of armature are found not only in the taxa under consideration but also throughout the Chalcidoidea (Parker, 1924; see Darling & Heraty, 1984). Homology and character polarity cannot be assessed with confidence and these characters are excluded from the parsimony analysis. The tubercles and pustules of *Chrysolampus* (Darling & Miller, 1991, figs 3–5) and the spicules in *Aperilampus* (Figs 1–2) would, however, be regarded as independently derived, and as autapomorphies would not effect the cladistic relationships.

10. Tergopleural line. The presence of a tergopleural line is now regarded as a synapomorphy of the subfamily Eucharitinae (Heraty, 1990; cf. synapomorphy of Eucharitidae in Heraty & Darling, 1984). The absence of this line of desclerotization is regarded as a synapomorphy of a clade within the Eucharitinae including *Stilbula*, *Obeza* and *Pseudochalcura* (Heraty & Barber, 1990), and a reversal to the absence of a tergopleural line characteristic of the eucharitid ground plan.

12. Caudal pad. A 'sucker' or caudal pad was regarded by Heraty & Darling as a synapomorphy of Perilampidae and Eucharitidae. In these taxa the sucker is involved in the looping locomotion and erect posture of the planidia. Morphologically similar structures appear to be more widely distributed in the Chalcidoidea and may be plesiomorphic. For example, Parker (1924) illustrates a very distinct caudal pad in the first-instar larva of *Leucospis* (Leucospidae) (his fig. 51). A caudal pad is also present in Chrysolampinae and in Philomidinae, i.e. the membranous XIII segment (Fig. 1). This character is excluded from the analyses because, regardless of polarity, the caudal pad has no bearing on the relationships of the taxa under consideration.

13. Antenna. The absence of a papilliform antenna was regarded by Heraty & Darling as a synapomorphy of Perilampidae and Eucharitidae. Antennae are also absent in *Aperilampus* but there are low, broad swellings on the cranium that may indicate reduced antennae. Both possible transformation series (0→1→2 and 1←0→2)

**Table 1.** Data matrix for eggs and first-instar larvae. Character numbers, states, and polarity decisions follow Heraty & Darling (1984), except where indicated with an asterisk (\*); see text for discussion. Reduced data matrix: characters 7–8, 12 and 14–15 were deleted because of ambiguity in polarity and character 10 was deleted because it is now regarded as uninformative at the present level of analysis; see text for discussion.

|                | Character |   |   |    |   |   |   |     |   |    |    |    |    |       |    |    |    |    |  |
|----------------|-----------|---|---|----|---|---|---|-----|---|----|----|----|----|-------|----|----|----|----|--|
|                | 1         | 2 | 3 | 3' | 4 | 5 | 6 | 7–8 | 9 | 10 | 11 | 12 | 13 | 14–15 | 16 | 17 | 18 | 19 |  |
| Ancestor       | 0         | 0 | 0 | 0  | 0 | 0 | 0 | 01  | 0 | 0  | 0  | 01 | 0  | 01    | 0  | 0  | 0  | 0  |  |
| Eucharitidae   | 1         | 0 | 1 | 1  | 1 | 3 | 1 | 0   | 2 | 0  | 1  | 1  | 2  | 1     | 1  | 1  | 1  | 2  |  |
| Perilampidae   | 0         | 1 | 1 | 1  | 1 | 2 | 0 | 01  | 1 | 0  | 1  | 1  | 2  | 1     | 1  | 1  | 0  | 1  |  |
| Chrysolampinae | 1         | 0 | 1 | 0  | 1 | 1 | 0 | 2   | 2 | 0  | 0  | 1  | 0  | 1     | 1  | 0  | 0  | 0  |  |
| Philomidinae   | ?         | ? | 1 | 1  | 1 | 1 | 0 | 2   | 1 | 0  | 0  | 1  | 1  | 0     | 0  | 1  | 0  | 0  |  |

Character states:

- \* Character 1. Egg shape, 0 = ovoid; 1 = stalked.
- Character 2. Egg sculpture, 0 = smooth; 1 = ridged.
- Character 3. Sclerotization of tergites. 0 = absent; 1 = present.
- \* Character 3'. Shape of tergites, 0 = completely encircling body; 1 = incomplete ventrad.
- \* Character 4. Setal pattern, tergite III, 0 = ventral setae absent; 1 = present.
- Character 5. Distribution of dorsal setae, 0 = absent; 1 = seta present on I–III, V, VII IX, XI; 2 = seta absent on XI; 3 = seta absent on VII, IX.
- Character 6. Dorsal fusion of tergites I and II. 0 = absent; 1 = present.
- \* Character 7–8. Ventral spines and tubercles. 0 = absent; 1 = tubercles; 2 = spicules.
- Character 9. Spiracles. 0 = 4 pairs; 1 = 1 pair; 2 = absent.
- \* Character 10. Tergopleural line. 0 = absent; 1 = present.
- Character 11. Cerci. 0 = absent; 1 = present.
- \* Character 12. Caudal pad. 0 = absent; 1 = present.
- \* Character 13. Antenna. 0 = present; 1 = reduced; 2 = absent.
- \* Character 14–15. Cranial setae and spines. 0 = 3–4 pairs present; 1 = reduced number.
- Character 16. Prelabium. 0 = membranous; 1 = with sclerotized marginal rim.
- \* Character 17. Postlabium. 0 = non-eversible; 1 = enlarged and eversible.
- Character 18. Labial plates. 0 = absent; 1 = present.
- Character 19. Pleurostomal setae. 0 = present; 1 = spinelike; 2 = fused spines.

produce a cladogram with the same topology and length.

14–15. Cranial setae and spines. As discussed in Heraty & Darling (1984), there is considerable uncertainty concerning the homology of these cranial structures, although both eucharitids, perilampids and chrysolampines have a reduced number of setae and/or spines. It is currently impossible to determine homology of setae and spines in *Perilampus* with any reasonable degree of certainty. In addition, cranial processes have subsequently been reported in Eucharitidae (*Orasema*, Johnson *et al.*, 1986; *Obeza*, Heraty & Barber, 1990). In *Orasema*, these processes are regarded as cranial spines and are similar to those found in *Perilampus*. In *Obeza* these processes are large but weakly sclerotized and considered by those authors to have an independent origin from the sclerotized cranial spines found in *Perilampus* (and *Orasema*?). Given these uncertainties concerning the distinction between setae and spines and the cranial armature of a ground plan first-instar larva for Chalcidoidea, these characters were excluded from the parsimony analysis.

17. Postlabium. As in Heraty & Darling (1984), an expanded and eversible postlabium is regarded by as a synapomorphy of Perilampidae and Eucharitidae. How-

ever, an expanded postlabium is also illustrated in the first-instar larva of *Leucospis* (Parker, 1924, fig. 51) and may be plesiomorphic in the Chalcidoidea. A reversal of character polarity does not change the topology of the most parsimonious cladogram.

*Cladistic relationships.* Both ordered and unordered analyses were performed on the reduced data set in Table 1 (Characters 1–6, 9, 11, 13, 16–19). In the ordered analysis, intuitive transformation series were coded for the four multistate characters (e.g. character 9; 4 pairs of spiracles [0] → 1 pair of spiracles [1] → spiracles absent [2]). Fig. 7 is the most parsimonious cladogram using the 'mhennig', 'bb' and 'ie' options (length, 22; CI, 84; RI, 70) of HENNIG86. Of the fourteen informative characters included in the analysis, homoplasy is present in only three characters: 1, egg shape, reversed in Perilampidae; 9, spiracles, independently lost in the Eucharitidae and Chrysolampinae; 16, marginal rim of prelabium, reversed in Philomidinae. The unordered analysis returned two equally parsimonious cladograms (length, 19; CI, 84; RI, 57), one with the same topology and character optimization as Fig. 7 and the other with the following topology: Chrysolampinae (Eucharitidae (Philomidinae, Perilampidae)).

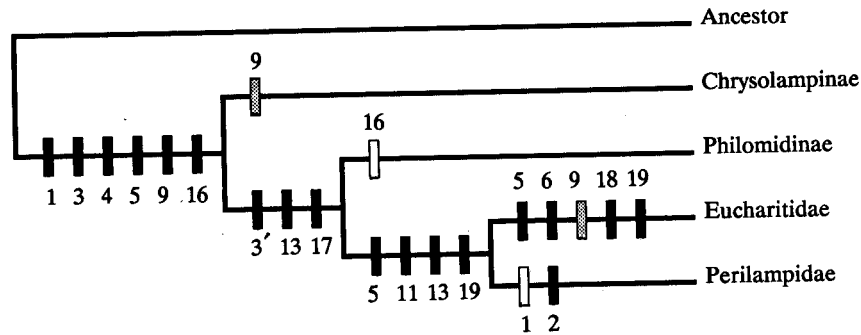


Fig. 7. Most parsimonious cladogram for the reduced data set presented in Table 1, ordered analysis. Length, 22; Consistency Index, 84. Numbers refer to characters in Table 1 and are discussed in text. Solid bars indicate non-homoplasious forward changes, stippled bars indicate homoplasious forward changes (convergence), and open bars indicate reversals.

These two cladograms only differ in their interpretation of two characters. Fig. 7 has spiracles (9) independently lost in Chrysolampinae and Eucharitidae and the other cladogram has spiracles lost and re-evolved as a synapomorphy of Perilampidae + Philomidinae. Fig. 7 interprets cerci (11) as a synapomorphy of Perilampidae + Eucharitidae and the other cladogram interprets cerci as convergent in Perilampidae and Eucharitidae. The unordered analysis that is identical in topology with Fig. 7 is preferred because the proposed transformations series are more likely on morphological grounds, i.e. do not require re-evolving a lost structure. Both ordered and unordered analyses support the cladogram in Fig. 7.

The first-instar larvae of *Aperilampus*, *Chrysolampus*, *Perilampus*, and Eucharitidae can be united on the basis of six synapomorphies, of which three are unique and unreversed: 3, presence of sclerotized tergites; 4, setal pattern on III, with a ventral seta associated with margin of tergite; and 5, distribution of dorsal setae. Three unique and unreversed characters suggests that Philomidinae is the sister group of Perilampidae + Eucharitidae: 3', tergites excised ventral; 13, reduction of antenna; and 17, postlabium eversible. Four synapomorphies remain to support the monophyly of Eucharitidae and Perilampidae: 5, distribution of dorsal setae; 11, cerci; 13, absence of antennae; and 19, spinelike pleurostomal setae.

For comparison, the next most parsimonious topology in the ordered analyses, with the Chrysolampinae as the sister group of Perilampidae + Eucharitidae, has a length of twenty-four steps (CI, 76; RI, 50). In addition to having more steps, this topology also requires character transformations that are less likely from a morphological perspective. For example, the most parsimonious cladogram suggests for character 13 that Chrysolampinae retain the plesiomorphic papilliform antenna and that reduced antenna characterize the common ancestor of Philomidinae + Perilampidae + Eucharitidae; the competing topology has the antenna lost and reevolving in the Chrysolampinae. And for character 3', the most parsimonious cladogram interprets incomplete tergites as a synapomorphy of Philomidinae + Perilampidae + Eucharitidae whereas the competing topology has the complete ring-like tergites of Chrysolampinae evolving from incomplete tergites.

## Discussion

The succession of larval instars in *Aperilampus* shows clear evidence of hypermetamorphosis; the first-instar is fundamentally different in structure from the final-instar larva. Only the first-instar larva is propneustic and adorned with diverse types of setae. The final-instar larva is hymenopteriform with six stout spatulate setae; spiracles are present on most segments.

Based on both hypermetamorphic development and the morphology of the larval stages it is appropriate to use the term 'planidium' in reference to the first-instar larva of *Aperilampus*. As discussed by Darling & Miller (1991), the definitions of a planidium are somewhat problematic and the suggestion was made to restrict this term to first-instar larvae that are synapomorphic with Perilampidae and Eucharitidae. Morphological characters of the first-instar larva of *Aperilampus* support the inclusion of *Aperilampus*, and by extension the Philomidinae, in a clade with *Chrysolampus*, *Perilampus*, and the Eucharitidae.

The mature larvae also provide corroboration for these proposed phylogenetic relationships. *Chrysolampus* (Darling & Miller, 1991, fig. 6), *Aperilampus* (Fig. 5) and *Perilampus hyalinus* (Tripp, 1962, fig. 9) all have a similar setal pattern, with dorsal setae on tergites I–III, V, VII and IX, the same distribution of setae as found in the planidia. These setae are absent in the third-instar larvae of Eucharitidae (Heraty, 1990). In *Chrysolampus* and *Aperilampus* the dorsal setae are large and modified, fluted or spatulate, respectively, and situated on distinct raised sockets. The mature or fourth-instar larva of *Chrysolampus* also has a fluted dorsal seta on XI, lateral and ventral setae that correspond to those in the planidia, and distinct peglike antenna; antennae are absent in the mature larvae of the other three taxa. Dorsal setae are very small in *Perilampus*, and there are only three larval instars. Based on these morphological characters, a plausible scenario of reductive modifications of the structure of the final-instar larvae and life history can be proposed that is consistent with the cladistic relationships in Fig. 7. Chrysolampinae is the most basal taxon, with a full complement of setae, peg-like antenna, and four instars; Philomidinae, Perilampidae and Eucharitidae have lost

the dorsal setae on XI, the lateral and ventral setae, antenna, and have only three instars (number of instars not known with certainty for Philomidinae); Perilampidae and Eucharitidae have reduced the size of the remaining dorsal setae; and Eucharitidae have lost the dorsal setae completely.

There are also behavioural similarities between the planidia of *Aperilampus* and the planidia of *Chrysolampus*, *Perilampus* and Eucharitidae. Planidia of Eucharitidae initially attach to the dorsum of the thorax or the abdomen of the ant larvae and as the pupa begins to form, relocate and being feeding nestled in thoracic legs; three or four engorged planidia can be found aggregated on a single ant pupa (e.g. *Pseudochalcura gibbosa*, Heraty & Barber, 1990, fig. 11; see also Heraty, 1990). Multiple planidia also attack the host in *Perilampus* and *Chrysolampus* but they are never gregarious. After feeding, the planidia (*Chrysolampus*, Darling & Miller, 1991) or second-instar larva (*Perilampus hyalinus* Say: Hinks, 1971) move about the surface of the host and search out and destroy conspecific competitors. *Aperilampus* seems to combine aspects of the behaviour of Chrysolampinae, Eucharitidae, and Perilampidae: (1) the planidia are gregarious and oriented ventrad on the pupa as in at least some Eucharitidae, and (2) the observation of a single engorged *Aperilampus* planidium on the more mature bee larva (cf. three on a younger pupa) is consistent with the competitive elimination of conspecifics that is reported for *Chrysolampus* and *Perilampus*. Although oviposition has not been observed, a prediction is that eggs are deposited on flowers visited by the bees and the adults transfer the planidia to the nest. This would explain why some nests in an aggregation are heavily infested and others are not parasitized. More detailed biological information on *Aperilampus* would be extremely valuable; of particular interest is the oviposition site.

This analysis of the characters of the first-instar larvae provides the first phylogenetic evidence to support the traditional viewpoint that Philomidinae is closely related to Eucharitidae and Perilampidae. This analysis remains congruent with certain aspects of a study of the labrum and epipharynx in adult Chalcidoidea (Darling, 1988a). A digitate labrum, characteristic of Perilampidae and Eucharitidae, is not found in Philomidinae; the labrum and epipharynx of Philomidinae are the most plesiomorphic found in Chalcidoidea. The epipharynx of Chrysolampinae is also plesiomorphic; Philomidinae and Chrysolampinae are the only Chalcidoidea known to have multiple epipharyngeal setae; a single pair of stout setae are found in most Chalcidoidea, including the Perilampidae and Eucharitidae (Darling, 1988a). However, synapomorphies were suggested between the flaplike labrum of Chrysolampinae and the digitate labrum of Perilampidae + Eucharitidae. The transformation series from Chrysolampinae to Perilampidae + Eucharitidae is incongruent with the cladogram in Fig. 7, which suggests that the labrum of Chrysolampinae and Perilampidae + Eucharitidae were independently derived from a plesiomorphic labrum such as found in the Philomidinae. It should be noted that the

transformation series proposed for the labrum is congruent with the cladogram which is two steps longer. Clearly more information is needed to evaluate these competing hypotheses, in particular, behavioural data for *Aperilampus*, and information on life history and immature stages for *Philomides* and, most importantly, for other genera of Perilampidae.

Information on life history and immature stages will be extremely important in evaluating the alternative hypotheses concerning the composition of the Eucharitidae (Heraty, 1990; Bouček, 1988) and for revising the higher classification of Eucharitidae and Perilampidae. Most adult eucharitids are highly modified and apomorphic which tends to obscure patterns of relationships (Heraty, 1990). Behaviour and immature stages may be more conservative and therefore useful from a phylogenetic perspective. For example, bees are now known to serve as hosts for both Philomidinae and Echthrodapinae. *Echthrodape africana* Burks is a parasite of stem-nesting bees of the genus *Braunapis* (Anthophoridae; Xylocopinae). The mature larva of *Echthrodape* is highly modified with long hairs and pseudopods, 'curiously similar to the larva of the host', and are tended by the bees (Michener, 1969). Unfortunately, the oviposition behaviour and the first-instar larva are not known. Furthermore, nothing is known about the biology and immature stages of Akapalinae. With these data it will be possible to not only revise our notions about the relationships among Eucharitidae and Perilampidae, but also to test hypotheses concerning the evolution of host associations. For example, some species of Perilampidae are primary parasites of stem-nesting Sphecidae (e.g. *Perilampus auratus* group) and potter wasps (*Krombeinius*, Darling, 1988b) and it is possible that the evolution of perilampids and eucharitids is intertwined with the radiation of the aculeate Hymenoptera.

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