

Comparative morphology of the planidial larvae of Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea)

JOHN M. HERATY and D. CHRISTOPHER DARLING*† Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada, and *Department of Entomology, Cornell University, Ithaca, New York, U.S.A.

ABSTRACT. The eggs and first-instar planidial larvae of *Stilbula montana*, *Kapala* sp., *Pseudometagea schwarzii*, *Orasema* sp. (Eucharitidae), *Perilampus chrysopae*, *Perilampus fulvicornis*, *Perilampus hyalinus* (Perilampidae), and *Chrysolampus thenae* (Pteromalidae: Chrysolampinae) are described. The morphological data are coordinated with the information available in the literature to develop general descriptions for the planidial larvae of *Perilampus* and the Eucharitidae. Character states were polarized with reference to a ground plan chalcidoid larva and relationships were determined cladistically. Nine synapomorphies are suggested for the planidial larvae of Perilampidae and Eucharitidae, indicating a possible sister group relationship. A re-examination of the larvae of *Chrysolampus thenae* indicates that the Chrysolampinae could be the sister group of Perilampidae + Eucharitidae.

Introduction

The higher classification of the Chalcidoidea (Hymenoptera) is in a state of confusion. There is disagreement with regard to the number of recognized families (e.g. Peck (1963) recognized twenty-one; Graham (1969) eighteen and Gordh (1979) eleven), and the associated problem of the composition of the family Pteromalidae. Putatively monophyletic taxa, such as the Perilampinae, Eucharitinae, Ormyrinae and Chalcedectinae, are referred to the Pteromalidae for unstated or unconvincing reasons, with the result that the Pteromalidae has become a repository for monophyletic groups not readily placed in other families and not considered to warrant separate family status. A high priority for a

revised classification of the Chalcidoidea is to document the monophyly of the Pteromalidae or to subdivide the polyphyletic assemblage into monophyletic taxa.

The Perilampidae and Eucharitidae (*sensu* Graham, 1969) are generally considered to be closely related. Graham (1969, p. 7) noted that a 'more mature classification' could result from the uniting of the Perilampidae with the Eucharitidae. Bouček (1956, p. 87) stated, 'the true perilampids form a specialized branch, originating at some time from pteromalids, and that Eucharitidae must be very near to them, but again more specialized'.

It is difficult to justify a sister group relationship between the Perilampidae and Eucharitidae on the basis of adult characters. The Eucharitidae and Perilampidae generally exhibit a short and high profile of the mesosoma, and have the gaster with only one or two tergites visible in dorsal view. The Eucharitinae (Eucharitidae) and the Perilampidae have the prepectus fused with the pronotum, but

Correspondence: Mr John M. Heraty, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1.

† Present address: Department of Entomology, Oregon State University, Corvallis, Oregon, U.S.A.

this sclerite is associated with the mesopleuron in Oraseminae (Eucharitidae).

Evidence of relationship between perilampids and eucharitids is based primarily on life history and on the morphology of first-instar larvae (see Clausen, 1940a; Askew, 1971). Where known, females deposit eggs away from the host, in or on leaves or buds (Smith, 1917). The first instar is an active planidium. The planidium is a very distinct larval type; in the Chalcidoidea they are characterized by heavily pigmented and sclerotized head and body segments, a pair of caudal cerci on the penultimate segment, and the last segment membranous and modified into a sucker-like organ. The active larva locates the host and attaches itself to it externally. It then either enters the haemocoel or burrows and remains just below the host cuticle. Feeding and subsequent larval development begin when the host pupates. Development is hypermetamorphic, and the second and subsequent larval instars are typically hymenopteriform.

The Perilampidae and Eucharitidae are sometimes placed as subfamilies of the Pteromalidae (e.g. Riek, 1970). The proposed relationships between Perilampidae + Eucharitidae and Pteromalidae is based, in large part, on *Chrysolampus* Spinola. Bouček (1956, 1972) considered *Chrysolampus* and allies as the tribe Chrysolampini of the Perilampidae. Graham (1969) considered *Chrysolampus* and its allies (i.e. the Chrysolampinae) as Pteromalidae. As Graham (1969) noted, the first-instar larva of *Chrysolampus* could be useful in positing relationship with the Perilampidae and Eucharitidae. Askew (1980) described the first instar of *Chrysolampus thenae* (Walker), and noted that while the larvae were not heavily sclerotized planidia, they did show some similarities with the planidia of *Perilampus*.

In this paper we present a detailed comparative analysis of the morphology of the planidial larvae of representatives of the chalcidoid families Eucharitidae and Perilampidae. Four genera of Eucharitidae, *Kapala*, *Stilbula*, *Orasema* and *Pseudometagea* and three species of *Perilampus*, representing three species groups, were examined in addition to published accounts of larval morphology. We present ground plan characters of the chalcidoid larva in order to assess synapomorphic similarities of perilampid and eucharitid plani-

dia. A cladogram of larval characters is presented.

Methods

Eggs and first-instar larvae of *Stilbula montana* Ashmead, *Kapala* sp., *Pseudometagea schwarzii* (Ashmead), *Perilampus fulvicornis* Ashmead and *Perilampus hyalinus* (Say) were obtained by various rearing methods in the laboratory. *Stilbula montana*, *Kapala* sp. and *P. schwarzii* eggs and larvae were fixed in alcoholic Bouin's solution. *Perilampus fulvicornis* and *P. hyalinus* larvae were fixed in 4% glutaraldehyde. Larvae were prepared for slide mounts by immersion in cold 10% potassium hydroxide for 1 h, dilute peroxide for 2–5 min, then rinsed in distilled water and mounted in Hoyer's medium. *Perilampus chrysopae* planidia and the exuviae of planidia were dissected from the cocoons of the host (Neuroptera: Chrysopidae) after clearing the host cocoon in warm Nesbitt's solution. The planidia and exuviae were then transferred to Hoyer's medium and mounted. All specimens used for scanning electron microscopy were critical point dried. Planidia of *Orasema* sp. were cleared and remounted from a slide in the Cornell University Insect Collection. Slides of *Chrysolampus thenae* (Walker) were obtained from Dr R. R. Askew, University of Manchester (see Askew (1980), for details of collection localities, hosts and techniques).

Voucher specimens have been deposited in the Canadian National Insect Collection, Biosystematics Research Institute, Ottawa, Canada, and consist of adults and slides of first-instar larvae. Additional specimens are in the authors' collections and in the Cornell and Guelph collections.

The morphological analysis was coordinated with data available in the literature to develop general descriptions for the planidial larvae of the Eucharitidae and Perilampidae.

There are considerable difficulties in applying a consistent terminology in the study of hymenopterous larvae. We follow the terminology of Short (1952) for the cephalic structures (Fig. 1). The small size of the first-instar larvae prevents the detailed morphological studies necessary to determine the

homologies of some cephalic structures (e.g. the labial plates and the dorsal arm of the tentorium). The terms 'pleurostomal setae' and 'pleurostomal spines' are new and are applied to the paired structures in the pleurostomal region of the cranium laterad of the mandibles (plst; Figs. 1, 10, 11). Postcephalic segments are numbered I to XIII. The modified setae associated with postcephalic segment XII have been referred to as either 'cerci' or 'stylets' by most authors. We do not consider these structures homologous with the 'cerci' of adult Chalcidoidea, but refer to the structures as 'caudal cerci', in an attempt to avoid further complicating the nomenclature. We propose the term 'tergopleural line' for the narrow desclerotized band that extends laterally along the tergites in the Eucharitidae.

The eggs and planidia of the Eucharitidae

The following description represents both the subfamilies, Eucharitinae and Oraseminae, and is based on the four species described herein and the following published accounts of sixteen species in ten genera. Oraseminae: *Orasema assectator* Kerrich (Das, 1963); *Orasema costaricensis* Wheeler and Wheeler (Wheeler

& Wheeler, 1937); *Orasema viridis* Ashmead (Wheeler, 1907; Thompson, 1915); *Orasema* sp. (Parker, 1942); *Losbanus uichancoi* Ishii (Ishii, 1932); *Losbanus laeviceps* (Gahan) (Clausen, 1940b). Eucharitinae: *Schizaspidia manipurensis* Clausen (Clausen, 1928); *Schizaspidia foveatella* (Girault), *Parapsilogastrellus montanus* (Girault) (Ishii, 1932); *Stilbula tenuicornis* Ashmead (Clausen, 1923); *Kapala* sp. (Berry, 1947); *Pseudometagea schwarzii* (Ashmead) (Ayre, 1962); *Psilogastrellus fasciiventris* Brues (Brues, 1919); *Chalcura deprivata* (Walker), *Eucharis scutellaris* Gahan (Clausen, 1940b).

The following description characterizes the ground plan of the eucharitid planidium and applies to all species studied with the exception of the species of *Orasema*.

EUCHARITID GROUND PLAN

Egg. Translucent white with smooth chorion, convex dorsally, slightly flattened ventrally. Narrow caudal stalk present, ranging in length from a quarter to twice length of body of egg.

Planidium. Length 0.12–0.20 mm; maximum width 0.04–0.07 mm. Spindle-shaped, widest medially or slightly anterior to middle (Figs. 12–15), circular in cross-section.

Cranium heavily sclerotized, without spines, setae or antennae dorsally, extending latero-ventrally posterior to the mandibles. Labrum large, semicircular, weakly sclerotized (Figs. 19, 22, 25). Prelabium circular, with sclerotized marginal rim; labial palpi reduced and located laterally on prelabium (Figs. 1, 19, 22, 25). Postlabium developed, extensible (Fig. 30). Mandibles sharply curved, comma-shaped. Labial plates present; posterior plate hatchet-shaped, narrow anteriorly, broad posteriorly (Figs. 5–7), suspended between pleurostoma and surface of postlabium. Pleurostoma heavily sclerotized, transverse, bridging cranium ventrally, not divided medially.

Tergites on body segments I to XII heavily sclerotized and overlapped; tergites I and II usually fused dorsally, body appearing 11-segmented from dorsal aspect. Tergopleural line present on tergites II–IX (Figs. 12–14), present on tergite X in a few species, or reduced (Fig. 15). Ventral margins of tergites VIII and IX usually tapered to acute tips,

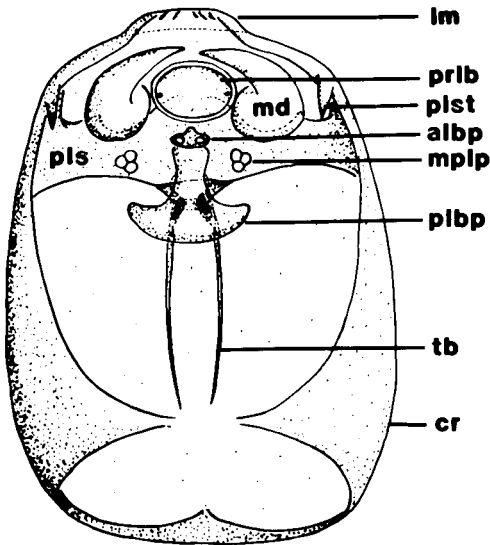
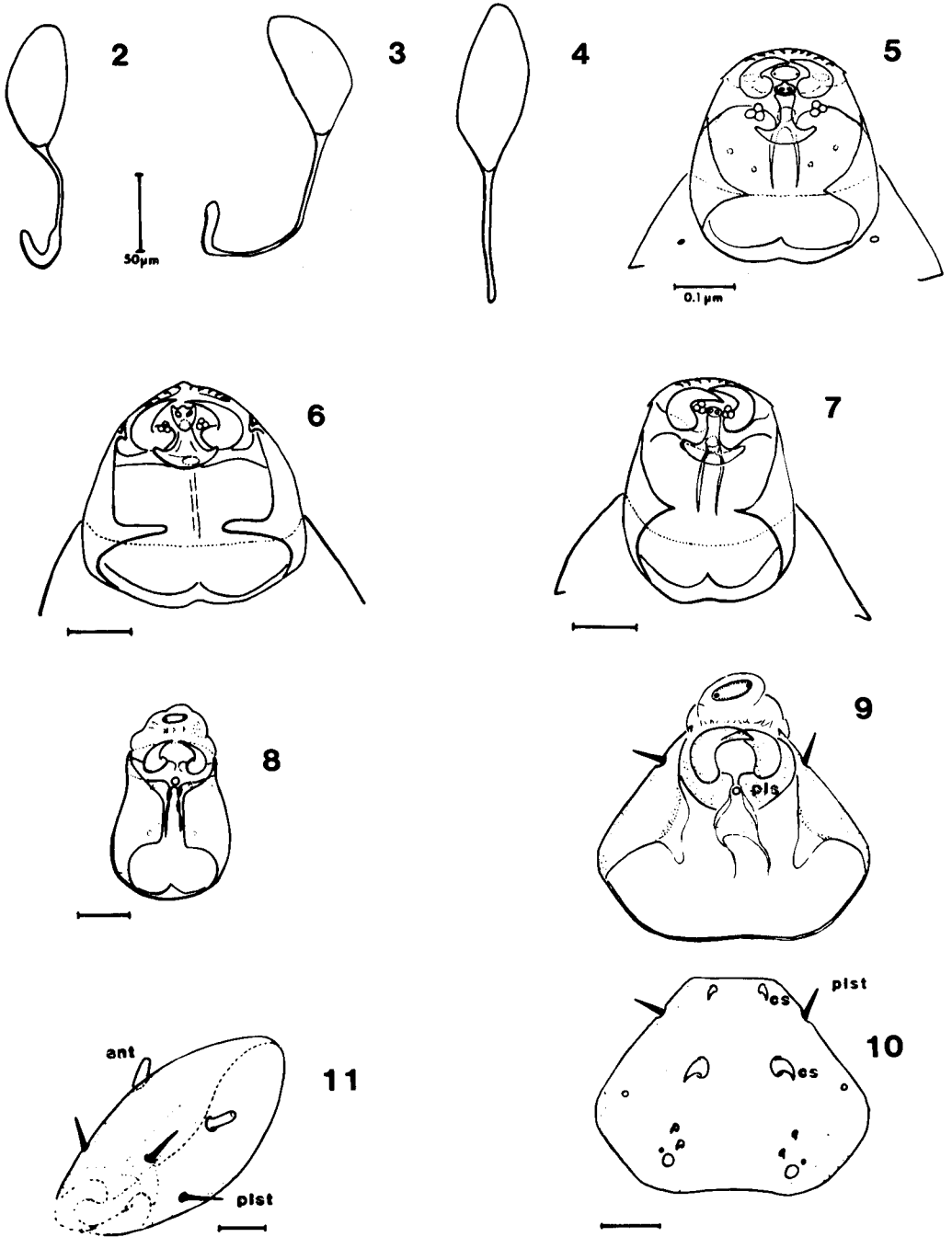


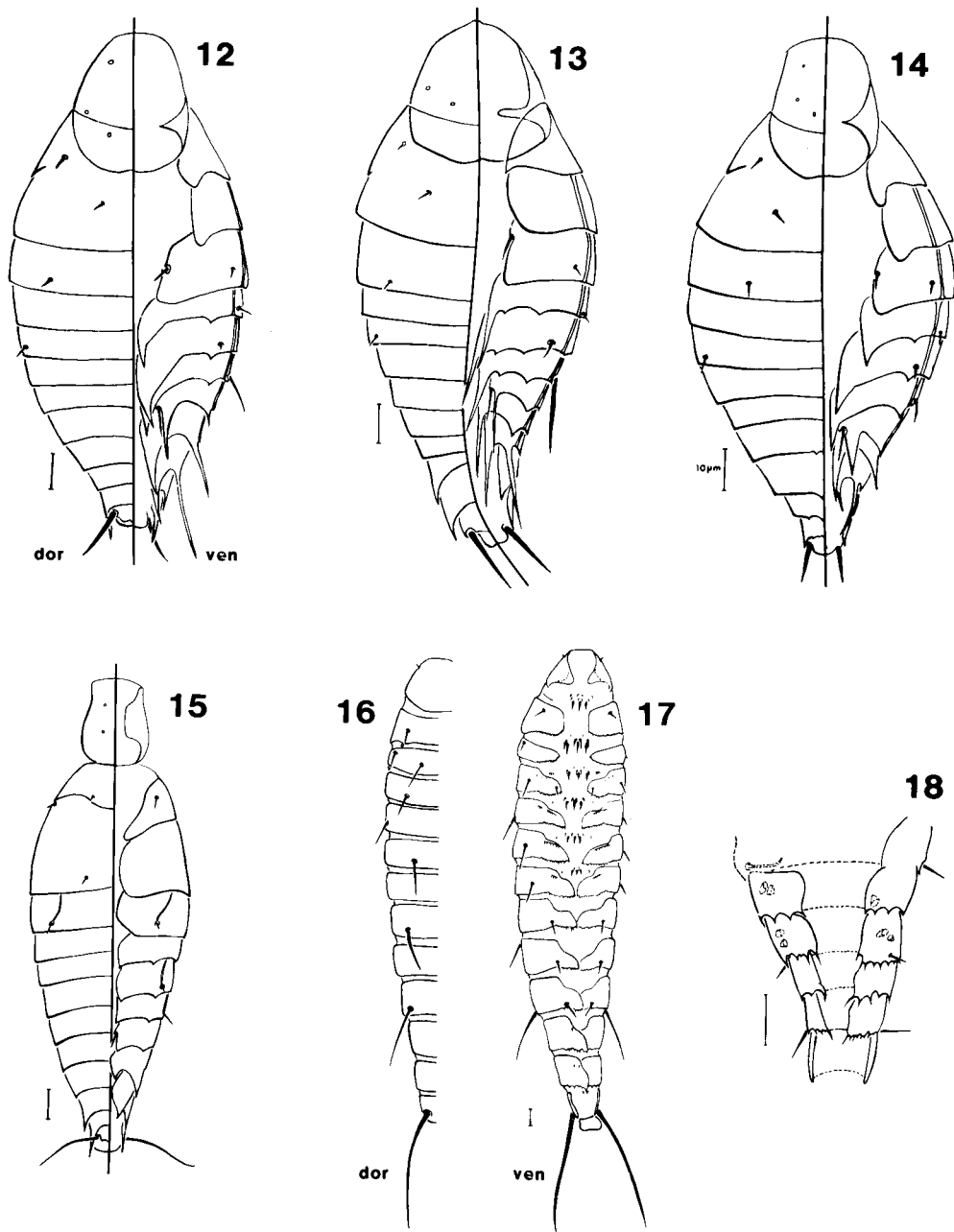
FIG. 1. Schematic ventral view of the head of a eucharitid. albp = anterior labial plate, cr = cranium, lm = labrum, md = mandible, mplp = maxillary palpus, plbp = posterior labial plate, pls = pleurostoma, plst = pleurostomal seta or spine, prlb = prelabium, tb = dorsal arm of tentorium.



FIGS. 2-11. 2-4, Eggs of Eucharitidae: 2, *Stilbula montana*; 3, *Kapala* sp.; 4, *Pseudometagea schwarzii*. 5-8, Heads of first-instar larvae: 5, *Stilbula montana*, ventral; 6, *Kapala* sp., ventral; 7, *Pseudometagea schwarzii*, ventral; 8, *Orasema* sp., ventral; 9-10, *Perilampus fulvicornis*, dorsal and ventral; 11, *Chrysolampus thenae*, dorsolateral. ant = antenna, cs = cranial spines, pls = pleurostoma, plst = pleurostomal seta.

extended posteriorly. Tergites I–II with 2–4 pairs of setae; III with 3 pairs of setae, one dorsal and two ventral; VI and in some species IV with single pair of lateral setae; V with 2 pairs of setae, dorsal and ventral; VII with a

single pair of ventral setae; VIII–XI without setae (Figs. 12–15). Ventral surface membranous, without setae or hooks. Single pair of stout, erect caudal cerci present on dorsal surface of tergite XII. Spiracles absent.



FIGS. 12–18. First-instar larvae: 12, *Stilbula montana*; 13, *Kapala* sp.; 14, *Pseudometagea schwarzii*; 15, *Orasema* sp. 16–17, *Perilampus fulvicornis*, dorsal and ventral; 18, *Chrysolampus thenae*, ventral view of apex of abdomen, dor = dorsal, ven = ventral.

SPECIES DESCRIPTIONS

Stilbula montana Ashmead*

Adult females were observed at Johnstown, Ontario, on 25.vii.1981 ovipositing through the outer bracts on flower spikelets of *Poa pratensis* (Graminae) and *Agropyron repens* (Gramineae). Egg masses consisted of between 100 and 200 eggs appressed against the inner surface of the bract. The bracts remained on the flower spikelets until after the planidia had emerged. The ant host was not located but *Lasius* sp. (Formicidae) were unusually abundant in the collection area.

Egg (Fig. 2). Caudal stalk about as long as body of egg, with terminal thickening less than one-third length of stalk, caudal stalks attached to form egg clusters (Fig. 31).

Planidium (Figs. 5, 12, 19–21). Cranium with 3 pairs of dorsal campaniform-like sensilla; lateroventral processes of cranium triangular, with pair of short pleurostomal spines laterad of mandibles (Fig. 19). Maxillary palpi present as indistinct unsclerotized, trispherical structures on the postlabium (Figs. 1, 5). Pleurostoma broad, produced posteriorly around medial excavation into tentorial bars. Anterior labial plate oval, strongly sclerotized, with anterior medial nipple (Fig. 5), posterior labial plate expanded anteriorly, narrow medially.

Ventral margins of tergites IV–IX broadly tapered to acute tips, ventrolaterally with single broad tooth on posterior margin, more strongly developed on posterior segments. Posterodorsal margin of caudal tergites straight. Setal pattern of tergites as shown in Fig. 12. Caudal cerci produced from posterior invaginations in tergite XII, length equal to dorsal length of last three tergites.

Kapala sp.

Adult females were collected in the grounds of the Commonwealth Institute of Biological Control, Curepe, Trinidad, on 11.vii.1982 from *Cordia* sp. (Ehretiaceae) and exposed to undeveloped flower spikes of *Cordia*. Egg masses of 200–300 eggs were laid directly into the undeveloped flower buds. Larvae

*Species not a member of the genus *Stilbula* (s.s.) (Heraty, unpublished).

hatched within the bud and remained there until the buds were dissected.

Egg (Fig. 3). Caudal stalk about twice length of egg body, with terminal thickening about 0.2 times length of stalk.

Planidium (Figs. 6, 13, 22–24). Similar to *S. montana* except as follows: Cranium with 2 pairs of dorsal sensilla; ventral process of cranium finger-like (Fig. 6); pleurostomal spines long (Fig. 22); tentorial bars not distinct; anterior labial plate large, shield-shaped, posterior labial plate broad medially. Ventral margins of tergites IV–IX narrowly tapered. Posterodorsal margin of caudal tergites X and XI broadly concave.

Pseudometagea schwarzii (Ashmead)

In the field (Ojibway Prairie Reserve, Ontario), adult females were observed on 11.vi.1981 ovipositing in undeveloped axillary buds of *Erigeron strigosus* (Compositae). In the laboratory, oviposition took place in the terminal buds or sepals of developed flowers of *Erigeron annuus*. Adults were reared from *Lasius* sp., and the ant and plant hosts are similar to the hosts reported by Ayre (1962).

Egg (Fig. 4). Described by Ayre (1962). Caudal stalk less than length of egg body, without terminal thickening.

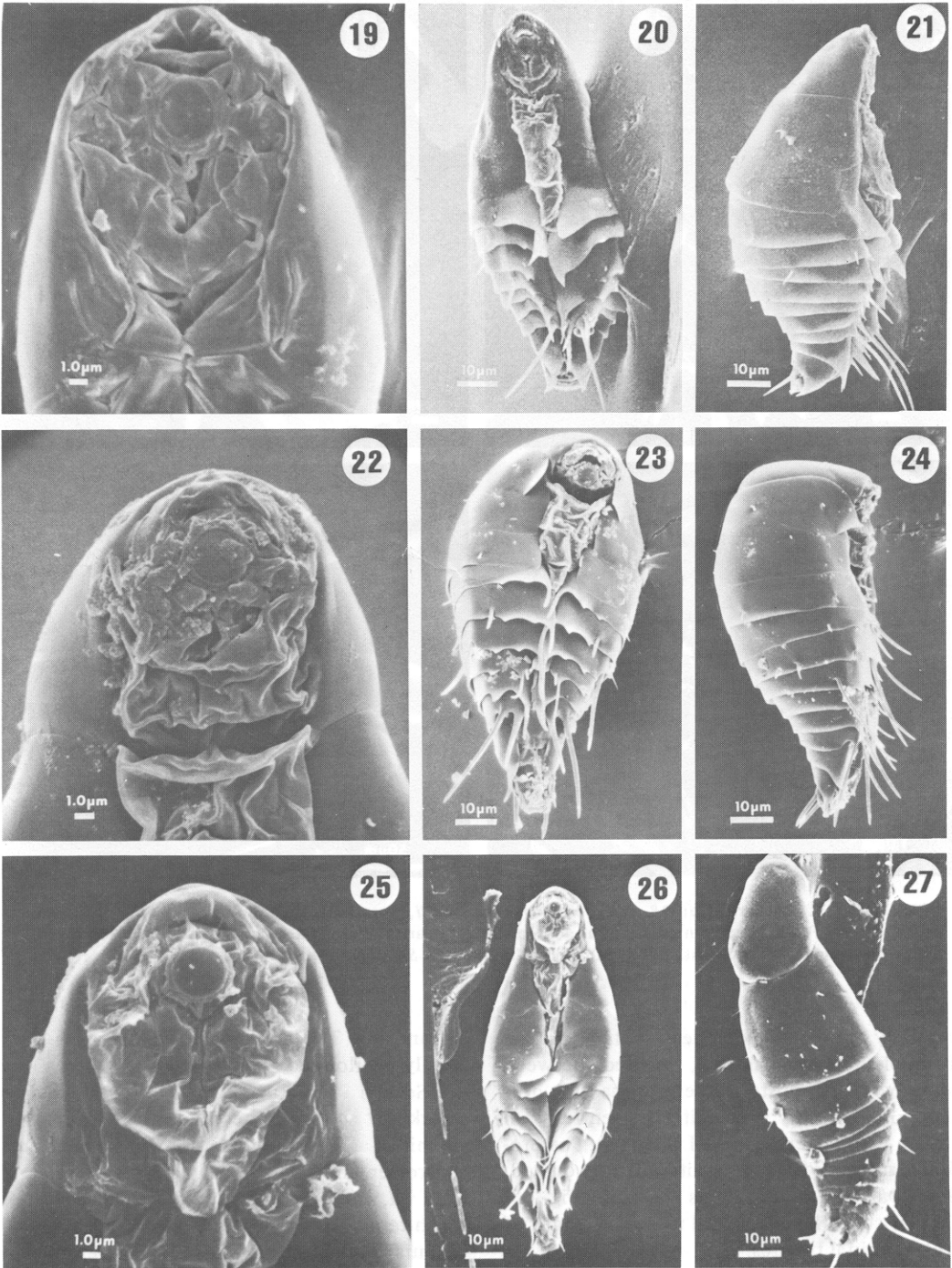
Planidium (Figs. 7, 14, 25–30). Described by Ayre (1962), similar to *S. montana* except as follows: anterior labial plates oval without anterior nipple; posterior labial plate narrow medially, not expanded anteriorly (Fig. 7); posterodorsal margin of tergites VIII to XI scalloped (Figs. 14, 28).

Orasema sp.

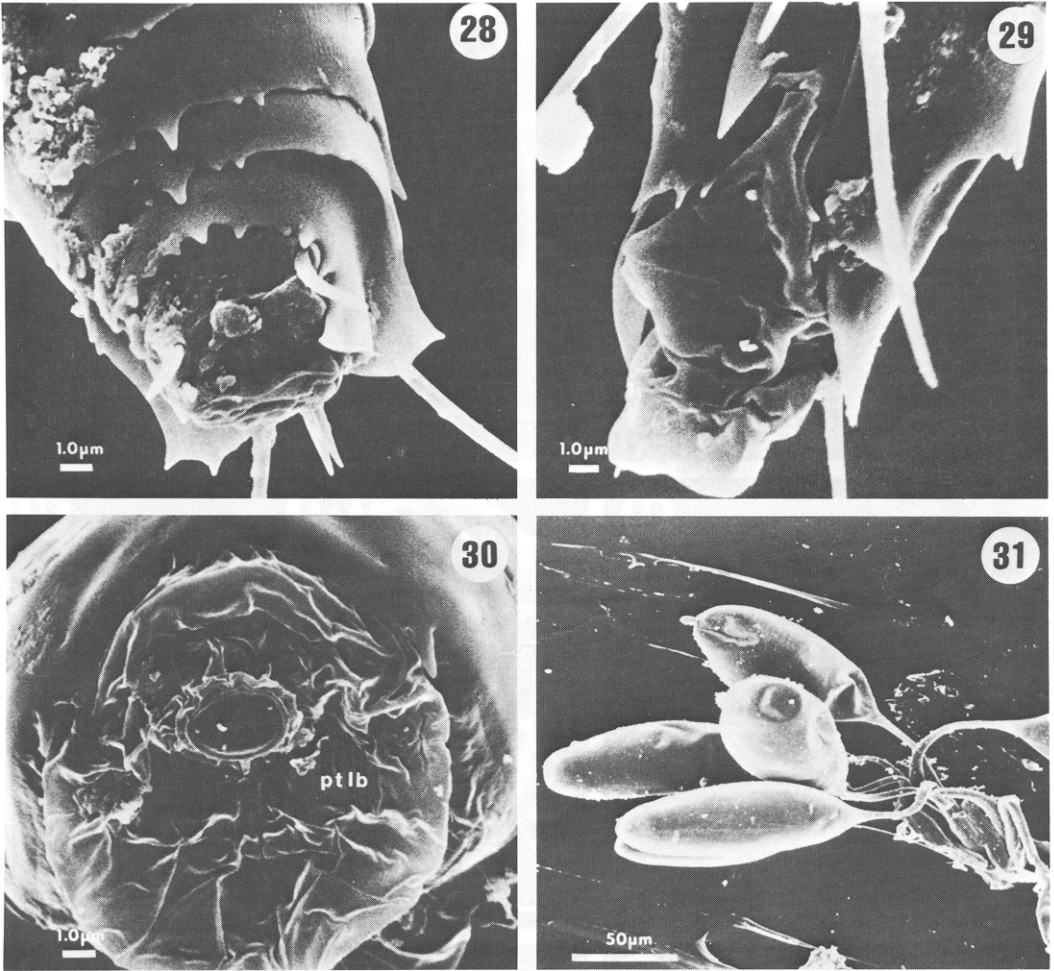
Planidia of this species (det. B. D. Burks, 1956) were collected at Coto, Costa Rica, on mango leaves by R. V. Roig on 5.iii.1956.

Planidium (Figs. 8, 15). Cranium with 2 pairs of dorsal sensilla; lateroventral processes of cranium broad, somewhat truncate; pleurostomal spines not discernible. Pleurostoma broad; tentorial bars distinct. Labial plates absent.

Tergites I and II separated dorsally. Ventral margins of tergites not tapered. Tergite IX



FIGS. 19–27. First-instar larvae of Eucharitidae: 19–21, *Stilbula montana*: 19, ventral head; 20, ventral body; 21, lateral body. 22–24, *Kapala* sp.: 22, ventral head; 23, ventral body; 24, lateral body. 25–27, *Pseudometagea schwarzii*: 25, ventral head; 26, ventral body; 27, lateral body.



FIGS. 28–31. Eucharitidae: 28, *Pseudometagea schwarzii*, dorsal tip of abdomen showing scalloped tergites; 29, *P. schwarzii*, ventral tip of abdomen showing partially expanded caudal pad; 30, *P. schwarzii*, head showing expanded postlabium, ptlb = postlabium; 32, *Stilbula montana*, eggs.

ventrally broadly expanded, not bifurcate. Tergopleural line narrow, located between setal base and posterior tergite margin: dorsally and ventrally on tergite III, ventrally on tergite V and laterally on VI (Fig. 15). Postero-dorsal margin of caudal tergites broadly curved. Setal pattern of tergites as shown in Fig. 15. Caudal cerci flexible, equal to dorsal length of four terminal tergites.

Notes. The first-instar larva of this species is identical to the planidium of another *Orasema* sp. (Parker, 1942), except for the pair of setae on the ventral margin of tergite VII, and the tergopleural line of tergites III,

V and VI. These characters could have been easily overlooked by Parker.

Several structures of *Orasema* deviate markedly from other described eucharitid planidia. The tergopleural line is much narrower and located only on tergites III, V and VI, and does not extend the full length of each tergite. It originates from a setal base and occurs dorsally and ventrally on tergite III.

Species of *Orasema* also lack a pair of ventral setae on tergite III, tergites I and II are not fused dorsally and the anterior and posterior labial plates are absent. The presence or absence of pleurostomal spines could not be

established from the slide-mounted material. All of the above-mentioned characters are found in the other representatives of the Eucharitidae.

The character states found in *Orasema*, except for the absence of a pair of ventral setae of tergite III, do not appear to be representative of the subfamily Oraseminae. Adult characters place *Losbanus* as the sister group of *Orasema*. Labial plates and dorsal fusion of tergites I and II were described in *L.uichancoi*. A distinct tergopleural line, which runs the entire length of the tergite, is present on tergites IX and X of *L.laeviceps* (only the posterior third of the larva was described). The character states in *Losbanus* (Oraseminae) agree with the Eucharitinae. Until more information is available, we regard the deviant character states of *Orasema* as apomorphic reductions from the ground plan of the Eucharitidae.

The eggs and planidia of the Perilampidae

The following summary diagnosis is based on the three species of *Perilampus* described herein and published accounts of five species of *Perilampus*: *P.chrysopae* Crawford (Smith, 1917; Clancy, 1946); *Perilampus hyalinus* Say (Smith, 1912; Thompson, 1915; Ford, 1922; Tripp, 1962); *P.tristis* Mayr (Parker, 1924); *P.laevifrons* Dalman (Principi, 1947); *Perilampus* 'A' (Smith, 1912; Thompson, 1915). The larvae are unknown for species in other perilampid genera.

PERILAMPID GROUND PLAN

Egg. Translucent white, heavily sculptured with intermeshing, longitudinal ridges (Figs. 32, 33); convex dorsally, slightly flattened ventrally, tapered at anterior end. Caudal stalk absent.

Planidium. Length, 0.2–0.4 mm; maximum width 0.06–0.08 mm. Shape fusiform (Fig. 17), circular in cross-section.

Cranium heavily sclerotized, extended ventrally as lightly sclerotized triangular processes; dorsally with paired setae or stout spines and sensory structures (campaniform sensilla) that appear as semi-transparent spots on cleared

slide preparations (Figs. 10, 36). Labrum large, weakly sclerotized (Figs. 34, 35). Prelabium circular, with sclerotized marginal rim; labial palpi reduced and located laterally on prelabium (Figs. 9, 34, 35). Postlabium well developed, extensible and slightly constricted medially (Fig. 9). Mandibles sharply curved, comma-shaped, bases broad and rounded. Pleurostoma heavily sclerotized, curved around base of mandibles, divided medially, not transverse.

Tergites on body segments I–XII heavily sclerotized, separated by membranous areas. Tergites entire, without tergopleural line. Tergites I, II, V, VII, IX with two pairs of setae, dorsal and ventral; IV, VI, VIII with a single pair of ventral setae; III with three pairs of setae, one dorsal and two ventral; X, XI without setae (Figs. 16, 17). Ventral surface membranous, in some species with minute setae and large, hook-like spines. Caudal cerci long and flexible, arising from dorsal sockets on tergite XII. Single pair of spiracles dorso-laterally between tergites I and II.

SPECIES DESCRIPTIONS

Perilampus fulvicornis Ashmead

Adults were reared from *Macrocentrus pallisteri* DeGant (Braconidae), a primary parasitoid of *Epiblema scudderiana* (Clemens) (Olethreutidae) collected at Guelph, Ontario, in 1982. Females were exposed to stems of *Solidago* sp. (Compositae) that contained early instar larvae of *E.scudderiana*. Gall formation by *E.scudderiana* was incomplete and only a small entrance hole, with a small accumulation of frass, indicated the presence of the larvae. *P.fulvicornis* females oviposited either directly into the entrance hole or in the vicinity. As many as six eggs were found situated inside the rim of the hole. Under non-crowded or field conditions, the preferred site for oviposition is probably into the entrance hole. *Solidago* plants without the gall-maker and older galls, in which the entrance hole was sealed with plant tissue, did not elicit an ovipositional response. Planidia of *P.fulvicornis* hatch and enter the lepidopteran host where they remain until the host is parasitized. Laing & Heraty (1981) reported four primary

parasitoids (Ichneumonidae and Braconidae) of *E. scudderiana* as hosts for *P. fulvicornis*.

Egg (Fig. 32). Sculptured, ridges broad and rounded.

Planidium (Figs. 9, 10, 32, 34). Cranium with posterior margin almost straight, dorsally with two pairs of stout recurved spines, two pairs of smaller spines and three pairs of campaniform sensilla; single pair of long pleurostomal setae; pleurostoma extended posteriorly into broadly curved or cup-shaped sclerite, produced posteriorly as tentorial bars (Fig. 9).

Tergite I truncate ventrally, II gradually tapered and III–XI obtusely angled, not extended posteriorly as long needle-like projections; tergites III–VI ventrally with row of minute spines parallel to anterior margin. Ventral membranous surface with three large spines and eight smaller spines between posterior margin of cranium and anterior margin of tergite I; segments II–VI with series of progressively smaller ventral spines. Dorsal setae longer than ventral setae, usually longer than the length of respective tergite along midline; dorsal setae IX about one-half length of caudal cerci. Caudal cerci about equal to length of four terminal segments.

Notes. We also examined planidia of *P. fulvicornis* dissected from caterpillars of *Metzneria lappella* L. (Gelechiidae). *P. fulvicornis* is hyperparasitic and attacks *Agathis malvacearum* Latreille (Braconidae), a primary parasitoid of the caterpillar (see Purrington (1979) for details of life history, as *P. similis* Crawford). These planidia agree with the description presented above.

Perilampus hyalinus Say

This species can be reared as a primary parasitoid of *Neodiprion* species (Diprionidae), and as hyperparasitoids of Lepidoptera and Orthoptera, through hymenopteran (Braconidae, Ichneumonidae) and dipteran (Sarcophagidae, Tachinidae) primary parasitoids.

There have been numerous discussions of the planidia of *P. hyalinus*, and many suggestions of host-associated differences in planidial morphology. Our purpose here is not to detail and reconcile these disparate accounts (Smith, 1912; Ford, 1922). Tripp (1962) summarizes the controversy and presents detailed

descriptions of planidia obtained from *Neodiprion* species, as primary parasitoids, and from *Melanoplus bilituratus* (Wlk.) (Acrididae), as secondary parasitoids through Sarcophagidae.

We have examined planidia of *Perilampus hyalinus* obtained from a culture (Ithaca, New York, 1982) of *Hyphantria cunea* Drury (Arctiidae). Adults were reared from tachinid puparia (*Eusisyropa blanda* (O.S.), *Blondelia hyphantriae* (Tohill) and *Mericia ampelus* (Wlk.)).

Females were isolated in petri dishes with honey water and either needles of *Pinus resinosa* or the leaves of various deciduous trees. Oviposition occurred on both substrates. Eggs were laid preferentially on the sheaths of the pine needles, and the long axes of the eggs were oriented along the long axis of the needle. Eggs were laid on the underside of the deciduous leaves, and packed along the midrib and other veins.

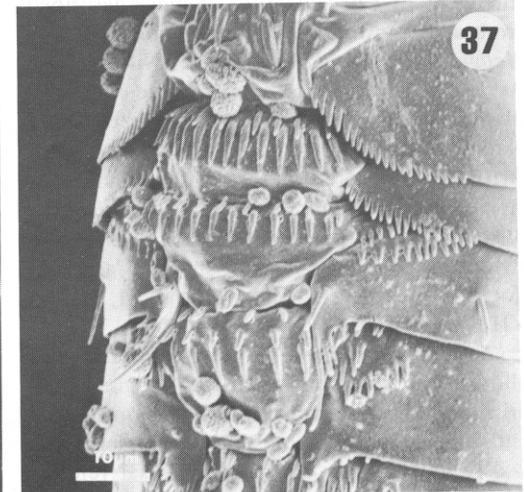
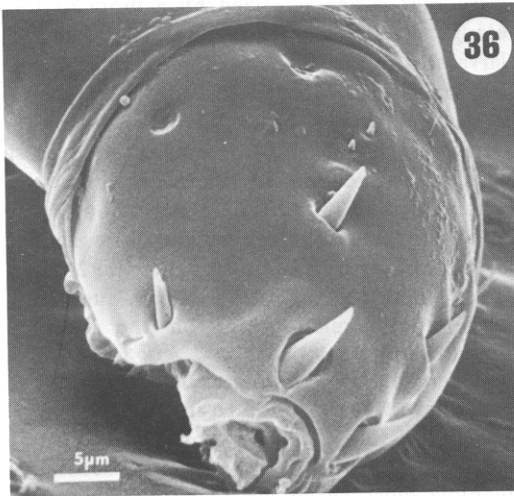
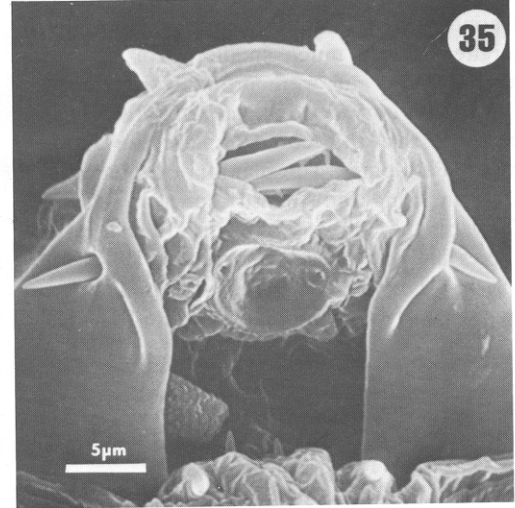
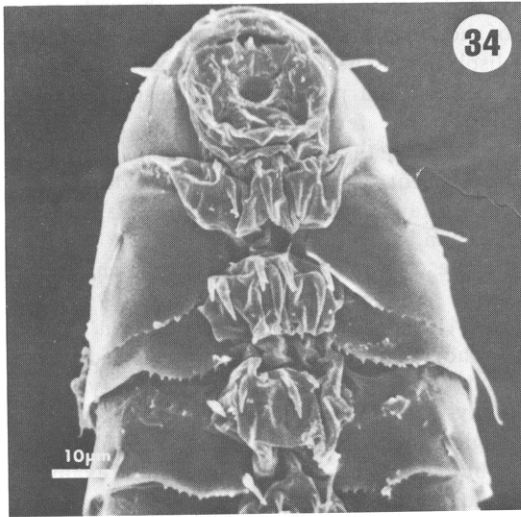
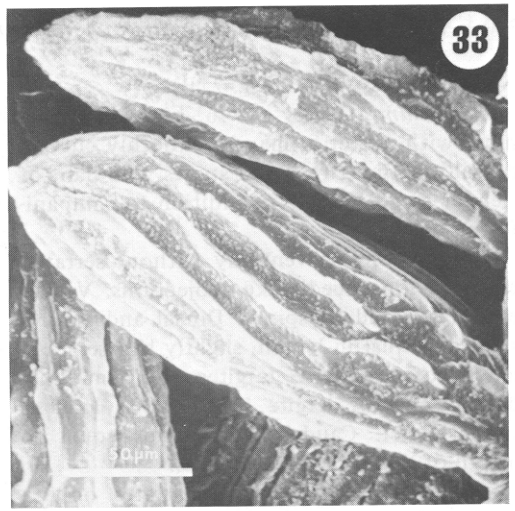
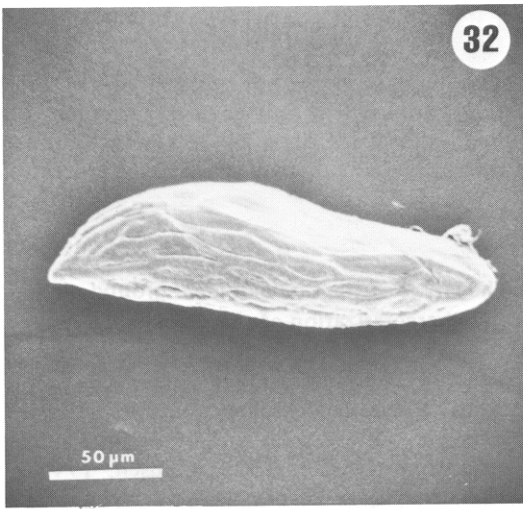
Egg (Fig. 33). Sculptured, ridges narrow and keeled.

Planidium (Figs. 35–37). Cranium very similar to *P. fulvicornis* except: posterior margin conspicuously excised medially; pleurostomal setae shorter and stouter.

Tergites similar to *P. fulvicornis* except: III–XII extended posteriorly as long needle-like projections. Venter with three very large spines and six smaller spines between anterior margin of tergite I and mouthparts; tergite II with very dense rows of ventral spines; segments III–XII with series of progressively smaller ventral spines. Dorsal setae short, equal in length to ventral setae, much shorter than length of respective tergites along midline; dorsal setae of tergite IX about one-tenth length of caudal cerci. Caudal cerci about equal to length of three terminal segments.

Perilampus chrysopae Crawford

Oviposition was not observed. Planidia were dissected from cocoons of *Chrysopa* spp. (Chrysopidae) from Uplands, California, parasitized by *P. chrysopae* in order to verify the description of the planidia provided by Clancy (1946). Scanning electron micrographs were not prepared, and details of the mouthparts are not available.



FIGS. 32–37. *Perilampus*: 32, *P. fulvicornis*, egg; 33, *P. hyalinus*, eggs; 34, *P. fulvicornis*, ventral view of first-instar larva; 35, *P. hyalinus*, ventral head; 36, *P. hyalinus*, dorsal head; 37, *P. hyalinus*, ventral view of first-instar larva.

Egg (Clancy, 1946, Fig. 21B).

Planidium (Clancy, 1946, Fig. 21C). Cranium with posterior margin smoothly curved, dorsally without recurved spines, two pairs of slender setae present in addition to campaniform sensilla.

Tergites simple ventrally without serrated edges or long needle-like projections. Venter entirely devoid of spines. Dorsal and ventral setae subequal in length, slightly shorter than length of respective tergites along midline, dorsal setae of tergite IX about as long as caudal cerci. Caudal cerci about equal to length of two terminal segments.

Notes. Clancy (1946) illustrates only a single pair of ventral setae on tergite III. The second pair of setae, on the ventral margin of tergite III, are much smaller than the more laterad setae and were probably overlooked. *Perilampus chrysopae* planidia are always ectoparasitic and this could explain the absence of cranial spines. The planidia of *P. laevifrons* Dalman, an Old World species attacking Chrysopidae, are very similar, and lack cranial spines and ventral setae (Principi, 1947, Figs. 15, 16). *Perilampus laevifrons* planidia possess two pairs of ventral setae on tergite III.

The first-instar larva of *Chrysolampus thenae*

Askew (1980) discussed the morphology of the larva of *Chrysolampus thenae*, described from slide mounted specimens associated with *Meligethes pedicularis* (Gyll.) (Nitidulidae). Askew noted the first-instar larvae are 'non-planidial', without heavily sclerotized body plates and caudal cerci. The following similarities were noted between the first-instar larvae of *Perilampus* and *Chrysolampus thenae*: (1) the presence of small spicule-like structures on the ventral surface, and (2) dorsal setae present on tergites I, II, III, V, VII, IX and XI.

A re-examination of this material has allowed us to supplement the original description. The cranium (Fig. 11) has one dorsal and one lateral pair of setae. Body segments I–XII have lightly sclerotized dorsal tergites with minutely serrate posterior margins ventrally (Fig. 18). Only the caudal tergites were easily discernible on the slides examined.

The tergites were not pigmented in these preparations. The cup-shaped structures on the tergites described by Askew (1980) are interpreted as tubercles or cuticular processes.

The larvae of the Chalcidoidea: ground plan and characterization of the planidial larva

There is a diverse array of first-instar larval types in the Chalcidoidea, but the later instars are quite similar and typically hymenopteriform (Parker, 1924; Clausen, 1940b). This diversity of first-instar larval morphology is not unexpected, considering the wide range of hosts attacked and the diverse behaviour displayed. The host's defences, both behavioural and physiological, must be circumvented and feeding must begin. In solitary parasitoids, the larvae often fight, with fatal results, for access to the host resource. The first-instar larvae are also responsible for host location in some species.

The external morphology of chalcidoid larvae was extensively reviewed by Parker (1924) and subsequently summarized (Parker & Thompson, 1925). A major focus of Parker's study was to define distinct larval types. In many cases a larval type is restricted to a single family, although some are widely distributed in the Chalcidoidea. For example, endoparasitic species often have a first-instar larva that is characterized by a more or less elongate caudal appendage. This 'caudate' larva was reported in the Pteromalidae, Chalcididae, Encyrtidae, Eulophidae and Eupelmidae. Each of these caudate larvae are 'strikingly different from even their nearest relatives, systematically speaking' (Parker & Thompson, 1925, p. 386). Both endoparasitic and ectoparasitic Pteromalidae have similar first-instar larvae (Group II, Parker, 1924). We must therefore be cautious in suggesting phylogenetic relationships on the basis of larval morphology.

There are two prerequisites to using the structure of the planidia to investigate phylogenetic relationships. Firstly, the homology of structure must be supported and, secondly, planidia must be argued to be derived larvae in the Chalcidoidea. If the planidial larva is ancestral in the Chalcidoidea, a homologous

larva in the eucharitids and perilampids would not support the hypothesis of a sister group relationship. The similarity would be plesiomorphic. It is essential, therefore, to establish ground plan characters for chalcidoid larva.

Hypotheses of ground plan characters of the chalcidoid larva are complicated by the presence of two more or less distinct larval morphologies in the ontogeny of some species (hypermetamorphosis). We assume that hypermetamorphosis is a derived condition in the Chalcidoidea, which is a result of the early instar larvae being modified in response to particular aspects of the host's biology. We base this assumption on the absence of hypermetamorphosis in the Symphyta and Aculeata and on the similarity of the Group II first-instar larvae (Parker, 1924) with the mature larvae of the majority of the Chalcidoidea. We further assume, for the present, that Group II represents the plesiomorphic first-instar larva.

Compilation of the information presented in identification keys to the larvae of the Hymenoptera (Michener, 1953), comparative studies of the head of larval Hymenoptera (Short, 1952, 1978), and the characterization of Group II larvae (Parker & Thompson, 1925) suggest the following characterization of the ground plan characters of the larvae of the Chalcidoidea:

Hymenopteriform, body spherical to spindle-shaped, with head and thirteen post-cephalic segments, without heavily pigmented (sclerotized) tergites; each segment with an anterior band of minute spines and two or three pairs of very small sensory setae; functional spiracles situated on postcephalic segments II, IV, V and VI; thoracic legs and prolegs absent; antennae short, conical and truncate; lateral eyes (stemma) absent; mouth parts without a sclerotic framework, pleurostoma and hypostoma only slightly defined, hypostoma without spur; labial and stipital sclerites absent; mandibles slender and curved, without dentition; maxillae and labium fused, not projecting as distinct and separate lobes; galea and palpi indistinct; sensilla below mouth not grouped on definitely circumscribed regions; ectoparasitic; cocoon not formed.

This characterization of the plesiomorphic chalcidoid larva allows the determination of primitive and derived similarities in the larvae of Eucharitidae and Perilampidae.

Character analysis of the eggs and planidia of the Eucharitidae and Perilampidae

A prerequisite for discussing the phylogenetic implications of larval morphology is to postulate plesiomorphic and apomorphic similarities. This character analysis is hampered by the few representatives of each family that we have been able to examine. In the Perilampidae, the immature stages are known only for *Perilampus*. Although this is the largest genus, it is clearly a derived taxon. The structure of the labrum (Darling, 1983) strongly suggests that *Monacon* is the basal extant genus. To proceed with the phylogenetic analysis of familial relationships requires that we consider the planidia of *Perilampus* as representative of the Perilampidae. This hypothesis will be refuted or corroborated with the discovery and description of the immature stages of other perilampid genera. Our analysis also assumes the validity of the current classification of the Eucharitidae, which recognizes the subfamilies Oraseminae and Eucharitinae. The planidial larva of *Orasema* is distinctive, and very different from the orasemine genus *Losbanus*. By assuming the monophyly of the Oraseminae, we conclude that the anomalous character states of *Orasema* (see Characters 6, 10 and 18) represent apomorphic modifications of the ground plan characters of the Eucharitidae.

The character analysis seeks to distinguish plesiomorphic from apomorphic similarity in the planidial larva of *Chrysolampus* by comparison with the outgroup ground plan larva of the Chalcidoidea as exemplified by the Pteromalidae. Parker (1924) discusses the first-instar larvae of nine-species of Pteromalidae and illustrates five larvae (*Dibrachys*, Figs. 96, 97; *Spalangia*, Fig. 99; *Pteromalus*, Figs. 122, 123; *Pachycrepoideus*, Fig. 124; *Nasonia* (as *Mormoniella*), Fig. 131) and Parker & Thompson (1925) republished an illustration of *Dibrachys*.

We have examined first-instar larvae of *Nasonia vitripennis* (Walker) in order to verify the characteristics of Group II larvae and to consider additional characters.

1. *Egg shape*. Stalked eggs occur in many chalcidoid families (see Parker, 1924). However, the pteromalids are characterized by an oval, unstalked egg. On the basis of outgroup comparison with the Pteromalidae, we regard

the stalked egg of the Eucharitidae (Figs. 2–4, 31) as independently derived from those in other families and as a synapomorphy of the Eucharitidae.

2. *Egg sculpture.* The plesiomorphic egg is devoid of surface sculpture. This is found in many chalcidoids, including the ectoparasitic Pteromalidae (e.g. *Nasonia vitripennis*). Tubercles and small hairs occur sporadically (Parker, 1924), but intermeshing ridges are unique to *Perilampus* (Figs. 32, 33). Only the ovarian egg has been described in *C. thenae* (fusiform with a smooth chorion), similar to the ovarian eggs of *P. chrysopae* (Clancy, 1946, Fig. 21A). It is possible that the deposited egg of *C. thenae* is ridged, and that the ridging becomes evident only after deposition, as in *Perilampus*. At this time we consider the ridged egg as an autapomorphy of *Perilampus*.

3. *Sclerotization of tergites.* The larvae of Apocrita are characterized by a lack of sclerotization (Short, 1952, 1978), and the lack of sclerotization is considered to be the plesiomorphic condition in the Chalcidoidea. In some chalcidoid larvae there is an increase in the overall degree of sclerotization (Group III larvae; Parker, 1924; Parker & Thompson, 1925), but distinct tergites have been described only in the planidial larvae and in *Chrysolampus thenae* (present study). We regard the formation of twelve distinctly sclerotized and pigmented tergites as a synapomorphy of Eucharitidae, *Perilampus*, and *Chrysolampus thenae*. The tergites extend ventrally and the lateral margins are sometimes produced as spines (Figs. 12–15, 17, 18).

4. *Setal pattern of tergite III.* In *Chrysolampus thenae* there are two pairs of setae on tergite III, one dorsal and one ventral pair (Askew, 1980). The presence of a single pair of setae dorsally and two pairs of setae ventrally is regarded as a synapomorphy of Eucharitidae and *Perilampus*. The placement of the ventral pairs of setae is the same in all species, with one lateral pair and one pair situated close to or against the ventral margin of the tergite (Figs. 12–14, 17). The marginal pair of setae are absent in *Orasema* spp. and *Losbanus uichancoi* and may be representative of the subfamily Oraseminae. The absence of the marginal pair of setae would be an opomorphic reduction, and perhaps synapomorphic in the Oraseminae.

5. *Distribution of dorsal setae.* *Chrysolampus thenae* has dorsal setae on tergites I, II, III, V, VII, IX and XI. This is regarded as a derived configuration of setae and is not found in the ground plan of the chalcidoid first-instar larva. The distribution of dorsal setae in Eucharitidae and *Perilampus* can be derived from this pattern through the loss of various setae. As noted by Askew (1980), a similar arrangement is found in *Perilampus* and in *Chrysolampus thenae*; the only difference is the absence of setae on XI in *Perilampus*. A further reduction of the setae is found in all eucharitids we have examined: dorsal setae are found only on tergites I–II, III and V. In all species of Eucharitidae and *Perilampus* examined, and in *Chrysolampus thenae*, there is a single pair of setae on tergite IV. These setae are located on the ventral or lateral aspects of the tergite and are regarded as homologous with the ventral setae of tergites III and V. A setal pattern characterized by dorsal setae on I, II, III, V but not on IV is not found in other chalcidoids (Parker, 1924; Askew, 1980) and is regarded as synapomorphic in *C. thenae*, *Perilampus* species and the Eucharitidae. We consider the absence of dorsal setae on tergite XI as synapomorphic in *Perilampus* and the Eucharitidae (character 5', Fig. 38), and the further loss of setae on VII and IX as synapomorphic in the Eucharitidae (character 5'').

6. *Dorsal fusion of tergites I and II.* The dorsal fusion of tergites I and II is synapomorphic in the Eucharitidae (Figs. 12–14). The plesiomorphic state of free tergites is found in *Perilampus* and *Chrysolampus thenae*. Within the Oraseminae, free tergites are found in *Orasema* (Fig. 15) but not in *Losbanus uichancoi*. The fusion of tergites I and II in all Eucharitinae examined suggests that free tergites are a reversal in *Orasema*. The description of separated tergites in *Kapala* sp. (Berry, 1947) is regarded as a misrepresentation.

7. *Ventral spines.* Ventral spines are absent in the Eucharitidae (Figs. 12–15). The presence of small spicule-like structures (ventral spines) in the larvae of *Chrysolampus* was regarded by Askew (1980) as 'indicative of affinity to *Perilampus*'. There are two problems with this interpretation. Firstly, ventral spines adorn the first-instar larvae of most

ectoparasitic chalcidoid larvae as ventral aspects of the continuous band around each segment (Parker, 1924; Group II, VI). The second problem is that ventral spines are present only in derived species groups of *Perilampus* (*P. hyalinus* group, *P. fulvicornis* group). Ventral spines are absent in *P. chrysopae* and the related Old World species *P. laevifrons*, both primary parasitoids of Chrysopidae (Neuroptera). We assume the absence of ventral spines as a ground plan character of the Perilampidae, and predict the absence of these spines in plesiomorphic perilampid genera (see Character 15 for further discussion of *Perilampus* species groups). The absence of ventral spines can be hypothesized as a synapomorphy of the Perilampidae and the Eucharitidae.

8. *Lateral tubercles*. The large conate tubercles on tergites II–IX of *Chrysolampus thenae* (Askew, 1980, Fig. 2) have not been described in other chalcidoid larvae. This character is autapomorphic.

9. *Spiracles*. The plesiomorphic distribution of spiracles in the Chalcidoidea is functional spiracles present on tergites II, IV, V and VI. This arrangement is found in Group II larvae (e.g. *Nasonia*) and in Group VI larvae. In *Perilampus* there is a single pair of spiracles located in the intersegmental membrane between tergites I and II (Fig. 16). The complete loss of spiracles in the Eucharitidae is regarded as a further reduction. The transformation series is suggested to be: four pairs spiracles (plesiomorphic) → one pair spiracles (character 9) → spiracles absent (character 9'). Spiracles were not reported in *C. thenae* by Askew (1980) and our re-examination of the specimens did not detect spiracles. However, the thoracic region of the specimens was very difficult to resolve. Another possibility is that the absence of spiracles is a synapomorphy of *Perilampus*, the Eucharitidae and *Chrysolampus*, and that the single pair of spiracles in *Perilampus* is a reversal. We regard this second hypothesis as less parsimonious, since it requires the re-appearance of a complex trait, a functional tracheal system.

10. *Tergopleural line*. This is a narrow, longitudinal line of desclerotization located laterally on tergites II–IX (Figs. 12–14) in the Eucharitidae. The line is visible only on slide-mounted material and is not interpreted

as a suture separating tergal and pleural sclerites. A reduced tergopleural line is found in *Orasema*, and located between the setal base and basal margin of tergites III, V and VI ventrally and tergite III dorsally (Fig. 15). We regard the tergopleural line as an autapomorphy of the Eucharitidae, and secondarily reduced in at least one species of *Orasema*.

11. *Caudal cerci*. Caudal cerci are a pair of large setae, arising on the dorsum of tergite XII. These structures are larger than the setae on other body segments. Caudal cerci are absent in *Chrysolampus thenae*. Dorsal setae are present in a homologous position in a few other chalcidoids, but in these cases the setae are not differentiated from the setae on other body segments. We regard caudal cerci as synapomorphic in the Eucharitidae and *Perilampus*.

12. *Caudal pad*. In *Perilampus* and the Eucharitidae the last segment (XIII) is membranous and expanded to form a caudal pad or 'sucker' (Fig. 29). This structure assists in locomotion and anchors the planidia in an erect position (Clausen, 1928; Tripp, 1962). In *Chrysolampus*, as in other Chalcidoidea, segment XIII is not morphologically differentiated from the preceding segments. The caudal pad is regarded as a synapomorphy of *Perilampus* and the Eucharitidae.

13. *Antennae*. The short conical antennae of *Chrysolampus thenae* are plesiomorphic (Fig. 11). The absence of a papilliform antenna in the Eucharitidae and *Perilampus* is considered synapomorphic. One of the paired sensilla on the cranium of eucharitids and perilampids could be homologous with the antennae.

14. *Cranial setae*. The presence of cranial setae is widely distributed in the Chalcidoidea and regarded as plesiomorphic. Hence the absence on the cranium is apomorphic in the Eucharitidae. There is only a single report of cranial setae in the family (*Schizaspidia foveatella*; Ishii, 1932). If not based on a misinterpretation, we could consider these setae as a subsequent modification, and not present in the eucharitid ground plan.

15. *Cranial spines*. The presence of two pairs of stout spines on the cranium is a derived condition in the genus *Perilampus* (Fig. 36). In *P. chrysopae* (Smith, 1917; Clancy, 1946) and the closely related Old World species, *P. laevifrons* (Principi, 1947), spines are absent,

and long cranial setae are present in similar positions (see Character 14). *Perilampus chrysopae* never enters the haemocoel of the host, and is strictly an ectoparasite (Clancy, 1946). In contrast, *P. fulvicornis* and *P. hyalinus* enter the haemocoel of the host, and the stout recurved cranial spines are regarded as an adaptation for successful attachment and burrowing. The relative plesiomorphy of *P. chrysopae* and *P. laevifrons* is supported by other biological attributes. These species are primary parasitoids of Chrysopidae (Neuroptera), and primary parasitism characterizes the life history of the primitive perilampid genus *Monacon* Waterston. *Perilampus hyalinus* is both a primary parasitoid and hyperparasitoid and *P. fulvicornis* is known only as a hyperparasitoid. Cranial spines are considered absent in the ground plan of perilampids and of no consequence in determining family level relationships.

16. *Prelabium*. The prelabium is a circular depressed area delimited by a sclerotized rim in the first-instar larvae of the Eucharitidae (Figs. 1, 19, 22, 25) and *Perilampus* (Figs. 9, 34, 35). The reduced labial palpi are located on the lateral margins. Short (1952) notes that in the Ichneumonoidea the prelabium is delimited by a marginal sclerotization, and refers to the sclerotized area as the 'labial sclerite'. A sclerotized labial sclerite is also present in the Cynipoidea (Short, 1952), the hypothesized sister group of the Chalcidoidea (Königsmann, 1978). The absence of the labial sclerite is a key character for the mature larvae of Chalcidoidea (Short, 1952), and a circular prelabium surrounded by a labial sclerite has not been reported in the first-instar larvae of other chalcidoids (Parker, 1924). However, a circular prelabium formed by a disc of close set, short papillae was described by Arthur (1958) in uncleared first-instar larvae of *Spilochalcis side* (Walker) (Chalcididae). It is possible that the structure of the prelabium, as described here, is of more general occurrence in the first-instar larvae of Chalcidoidea. Critical point drying and SEM — techniques not available to earlier workers — facilitate examination of this region of the head without clearing the specimens and destroying unsclerotized structures. The oral region of *C. thenae* could not be clearly resolved and the prelabium, if present, was

not observed. On the basis of the ground plan analysis of chalcidoid first-instar larvae, we interpret the 'labial sclerite' of the eucharitids and perilampids as apomorphic, a reversal to the apocritan ground plan.

17. *Postlabium*. The postlabium is represented by a large, membranous, eversible sac which surrounds the prelabium in the Eucharitidae (Fig. 30) and *Perilampus* (Fig. 9). This structure may be homologous to the postlabium of the Ichneumonoidea, as illustrated by Short (1952), or may represent the fused postlabium, maxillae and hypopharynx. Clausen (1923, 1928) figures the erect or waiting stance of a eucharitid with the prelabium extended well beyond the edge of the cranium, due to the expansion of the postlabium. Similar stances are employed by *Perilampus* larvae. This complex modification of the labium of eucharitids and *Perilampus* is undoubtedly related to host location and attachment and is regarded as synapomorphic. The postlabium was not observed in *Chrysolampus thenae*.

18. *Labial plates*. The labial plates are two sclerites suspended between the pleurostoma and postlabium of Eucharitidae, and consist of an anterior plate and a posterior hatchet-shaped sclerite (Fig. 1). Ayre (1962) referred to the posterior sclerite as the 'labial plate', and did not observe the much smaller anterior plate. The labial plates are absent in *Orasema* but were described in the related orasemine, *Losbanus uichancoi* (see character 6). We regard the labial plates as present in the ground plan of the planidia of the Eucharitidae. We consider these structures as autapomorphic in the Eucharitidae and not homologous to any of the structures reported by Short (1952) for the Ichneumonoidea.

19. *Pleurostomal setae*. Setae in the pleurostomal region of the cranium are widely distributed in the first-instar larvae of the Chalcidoidea (Parker, 1924) and are also present in *Chrysolampus thenae* (Fig. 11) and *Perilampus fulvicornis* (Figs. 9, 10). The pleurostomal setae are modified into spines in *Perilampus hyalinus* (Figs. 35, 36) and in the Eucharitidae (Fig. 1). Pleurostomal setae or spines were not observed in *Orasema*. We regard the pleurostomal setae as plesiomorphic in the Chalcidoidea, and convergently developed into spines in various taxa.

Discussion

The distribution of derived characters in *Chrysolampus thenae*, *Perilampus* and the Eucharitidae is summarized in Fig. 38. The monophyly of these three groups is supported by the formation of twelve sclerotized tergites (3) and the distribution of dorsal setae (5).

The Eucharitidae and *Perilampus* are considered to share nine derived characters. The presence of caudal cerci (11) and a caudal pad or sucker (12) are definitive of the planidial larval type, and could represent convergences due to the habit of leaf oviposition and an active first-instar larva. Additionally, the first-instar larvae share a reduced number of spiracles (9), the setal pattern of tergite III (4) and the absence of antennae (13). Strong evidence of a sister group relationship between these families is the structure of the mouthparts. The prelabium (16) and postlabium (17) are

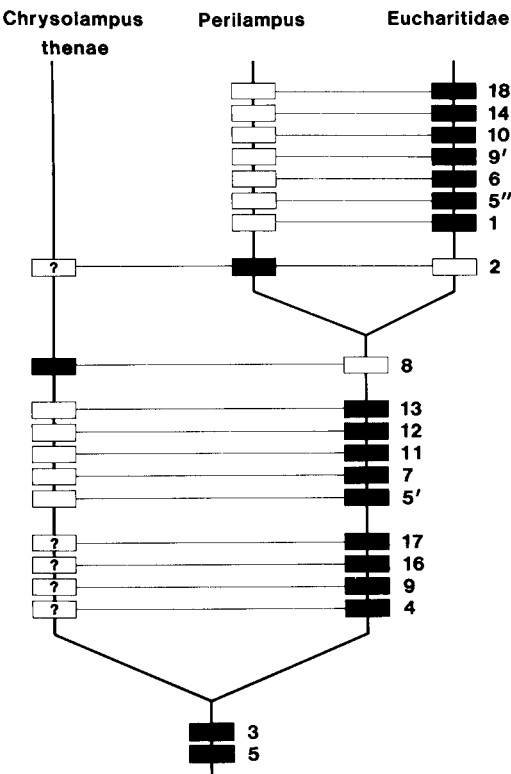


FIG. 38. Distribution of derived characters (synapomorphies) in the Eucharitidae, *Perilampus* and *Chrysolampus thenae*. See 'Character analysis' for discussion of characters and polarity decisions.

similar in fine details and argue against convergent evolution.

The planidial larvae of Perilampidae and Eucharitidae could be the result of convergence, and of no value in elucidating phylogenetic relationships between the taxa. Similar life histories, with the first-instar active in host location and attack, have evolved many times in the insects. Clausen (1940a, p. 19) summarizes the occurrence of active first-instar larvae in parasitoids (the tringulinids of Coleoptera (Rhipiphoridae, Meloidae) and Strepsiptera, and 'planidia' of Diptera (Acroceridae, Tachinidae and Sarcophagidae)) as excellent examples of convergent evolution. *Euceros frigidus* Cresson (Ichneumonidae) has convergently developed the habit of leaf oviposition and also has an active first-instar larva (Tripp, 1961). The first-instar larva of *E. frigidus* is heavily sclerotized and has distinct tergites on the thirteen body segments. It is dorsoventrally flattened and is membranous ventrally with minute spines and possesses long lateral setae. However, *E. frigidus* lacks the caudal pad, caudal cerci and modified prelabium and postlabium found in the planidia of *Perilampus* and Eucharitidae. This illustrates that convergence in larval morphology, due to similarities in oviposition and subsequent host location, need not result in the detailed structural similarities found in the Eucharitidae and *Perilampus*.

The validity of this analysis depends on the accuracy with which we have been able to determine the ground plan of the chalcidoid larvae. Two alternate possibilities must be considered. Firstly, the planidial larva of the eucharitids and perilampids is the ancestral chalcidoid larva and secondly, some other larval type, not Group II, is ancestral and should be regarded as the outgroup for the cladistic analysis.

Wheeler (1928, p. 47) presented the hypothesis that 'the remote ancestral Terebrants sought out their prey, or hosts as active larvae, since their mothers had not yet acquired the habit of laying their eggs directly on or in the larval food'. If the planidial larva is the ground plan of the chalcidoid larva, then we are not justified in suggesting that the eucharitids and perilampids are sister groups on the basis of the characters of planidia. This would be grouping by plesiomorphy.

The reduced number of spiracles characteristic of the chalcidoid planidia makes it highly unlikely that the other types of ectophagous chalcidoid first-instar larvae, all of which have four pairs of functional spiracles, were derived from an ancestor with a planidial larva. This would require an increase in the number of functional spiracles, from one pair to four pairs. It is much more likely that the number of spiracles was reduced in the common ancestor of the eucharitids and perilampids, and that planidial larvae are apomorphic in the Chalcidoidea. However, the first-instar larvae of the perilampid genera *Monacon* and *Steffanolampus* Peck are unknown. If shown to be planidial with four pairs of functional spiracles, the hypothesis that the planidial larva is the ground plan of the chalcidoid larva would be supported.

A second possible error in our analysis is that Group II is not the ground plan chalcidoid larva. Given the reasonable hypothesis that the chalcidoid larva was primitively ectophagous, the Group VI larva (Parker, 1924; Parker & Thompson, 1925) is a possible candidate. This larval type is distinguished from Group II, the basis for our ground plan analysis, by having the cranium strongly chitinized and completely fused ventrally, the mandibles more strongly curved and approximately comma-shaped, each body segment with two or three pairs of long sensory setae, and a median or submedian girdle of large and conspicuous cuticular spines. Using the Group VI larval type as the outgroup would not alter the main conclusions of our analysis. The only synapomorphy of eucharitids and perilampids that would be questioned is the caudal cerci. Group VI larvae have many long setae on all tergites including XII. The caudal cerci could then be regarded as plesiomorphic.

With either outgroup, the same conclusion follows. The eucharitid genera we have studied and *Perilampus* share derived features of the morphology of the first-instar larvae. We interpret this as evidence supporting the hypothesis that the planidial larva was derived from a common ancestor.

The implications of this analysis for the higher classification of the Chalcidoidea must be tempered because only exemplars have been examined. The synapomorphies we have discussed do strongly support the conventional

wisdom of workers in the Chalcidoidea; *Perilampus* and allies and eucharitid genera are closely related. Our results cannot, however, be used to support a sister group relationship of holophyletic taxa (Perilampidae and Eucharitidae) until data are available for other genera of Perilampidae. It is possible that recognition of the family Eucharitidae would render the Perilampidae paraphyletic. The structure of the labrum supports this conclusion (Darling, 1983). The best solution may be to recognize a single family level taxon for the genera currently placed as Eucharitidae and Perilampidae.

The synapomorphies of the planidial larva and the first-instar of *Chrysolampus thenae* support the inclusion of this genus in a higher taxon with Perilampidae + Eucharitidae. This relationship is also supported by the structure of the labrum (Darling, 1983). Changes in the nomenclature would be premature at this time. However, the inclusion of these groups in the Pteromalidae is also unwarranted primarily because this taxon cannot be defined (Graham, 1969).

The eucharitid planidia are more derived or apomorphic than the planidia of *Perilampus*. Monophyly of the family is suggested by seven synapomorphies: the dorsal fusion of tergites I and II (6), the complete loss of spiracles (9'), the reduction of dorsal setae (5''), and the absence of cranial setae (14) are reductions of the ancestral or plesiomorphic *Perilampus* planidia. There are, however, elaborations in the eucharitid immature stages, notably the presence of a stalked egg (1), the formation of a distinct tergopleural line (10), the labial plates (18) and parasitism of ants (Formicidae). The uniformity of the planidial larvae in all known eucharitids indicates that all species are descended from a common ancestor and provides a strong basis for uniting the morphologically distinctive subfamilies Eucharitinae and Oraseminae. Reservation is, however, expressed regarding *Orasema*, which may be the sister group of the remaining genera.

The planidia of *Perilampus* are much more diverse morphologically than the eucharitid planidia. This is all the more remarkable considering that only one genus has been examined. However, the range of hosts utilized by *Perilampus* is much greater than the single family (Formicidae) attacked by the Eucharitidae.

Primary parasitism occurs (hosts: Coleoptera, Neuroptera, Hymenoptera) as does secondary or hyperparasitism (hosts: Diptera and Hymenoptera parasitoids of Lepidoptera and Orthoptera). The functional significance of the diversity of planidial morphology in *Perilampus* is largely uninvestigated. The large recurved spines are restricted to species that penetrate the cuticle of the host. Since these structures have been regarded as apomorphic, it is reasonable to consider the cranial spines as an adaptation to entering the haemocoel of the host. The spines probably function to anchor the head in the host tissues as burrowing proceeds.

The higher classification of the Chalcidoidea has been notoriously unstable. The incorporation of larval morphology offers characters to corroborate or refute hypotheses of relationships based on adult morphology. Larval morphology becomes phylogenetically significant only when decisions regarding character polarity can be made. Further research is necessary to document the ground plan characters of chalcidoid larvae and to present detailed morphological studies of a diverse array of larvae. Continued interest in the phylogenetic analysis of diverse character systems, from as many life history stages as possible, will allow progress toward a natural classification of the Chalcidoidea.

Acknowledgments

We thank Dr R. R. Askew for providing specimens of *Chrysolampus thenae* for examination. The final version of this paper was improved by critical review by the following: K. Barber, W. L. Brown, Jr, J. M. Carpenter, G. Eickwort, G. A. P. Gibson, E. E. Grissell, N. F. Johnson, S. A. Marshall and M. Schauff. Dr D. M. Wood of Biosystematic Research Institute in Ottawa, Canada, identified the Tachinidae.

References

- Arthur, A.P. (1958) Development, behaviour and descriptions of immature stages of *Spilochalcis side* (Walk) (Hymenoptera: Chalcididae). *Canadian Entomologist*, 90, 590–595.
- Askew, R.R. (1971) *Parasitic Insects*. American Elsevier, New York.
- Askew, R.R. (1980) The biology and larval morphology of *Chrysolampus thenae* (Walker) (Hym., Pteromalidae). *Entomologist's Monthly Magazine* (1979) 115, 155–159.
- Ayre, G.L. (1962) *Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). *Canadian Journal of Zoology*, 40, 157–164.
- Berry, P.L. (1947) Oviposition habits and early stages of a eucharid (*Kapala* sp.) (Hymenoptera). *Proceedings of the Entomological Society of Washington*, 49, 77–80.
- Bouček, Z. (1956) [Notes on the Czechoslovak Perilampidae]. *Acta Faunistica Entomologica Musei Nationalis Pragae*, 1, 83–98.
- Bouček, Z. (1972) Mediterranean Perilampinae: *Euperilampus* and genera related to *Chrysomalla*. *Mitteilungen der Münchener Entomologischen Gesellschaft* (1971), 61, 90–107.
- Brues, C.T. (1919) A new chalcid-fly parasitic on the Australian bull-dog ant. *Annals of the Entomological Society of America*, 12, 13–23.
- Clancy, D.W. (1946) The insect parasites of the Chrysopidae (Neuroptera). *University of California Publications in Entomology*, 7, 403–496.
- Clausen, C.P. (1923) The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Campnotus*. *Annals of the Entomological Society of America*, 16, 195–217.
- Clausen, C.P. (1928) The manner of oviposition and the planidium of *Schizaspidia manipurensis* n.sp. (Hymen., Eucharidae). *Proceedings of the Entomological Society of Washington*, 30, 80–86.
- Clausen, C.P. (1940a) *Entomophagus Insects*. McGraw-Hill, New York.
- Clausen, C.P. (1940b) The immature stages of the Eucharidae. *Proceedings of the Entomological Society of Washington*, 42, 161–170.
- Darling, D.C. (1983) Systematic studies of the Perilampidae (Hymenoptera: Chalcidoidea). Ph.D. thesis, Cornell University, Ithaca, New York.
- Das, G.M. (1963) Preliminary studies in the biology of *Orasema assectator* Kerrich (Hym., Eucharitidae), parasitic on *Pheidole* and causing damage to leaves of tea in Assam. *Bulletin of Entomological Research*, 54, 373–378.
- Ford, N. (1922) An undescribed planidium of *Perilampus* from *Conocephalus* (Hym.). *Canadian Entomologist*, 54, 199–204.
- Gordh, G. (1979) Superfamily Chalcidoidea: in Krombein, K.V., Hurd, P.D., Jr, Smith, D.R. & Burks, B.D. *Catalog of Hymenoptera in America North of Mexico*, Vol. 1, pp. 743–1043. Smithsonian Institution Press, Washington, D.C.
- Graham, M.W.R. de V. (1969) The Pteromalidae of north-western Europe (Hymenoptera: Chalcidoidea). *Bulletin of the British Museum (Natural History) Entomology Supplement*, 16, 1–908.
- Ishii, T. (1932) Some Philippine eucharids with notes on their oviposition habits. *Bulletin of the Imperial Agricultural Experimental Station, Japan*, 3, 203–213.
- Königsmann, E. (1978) The phylogenetic system of the Hymenoptera. Part 3: 'Terebrantes' (Suborder Apocrita). *Deutsche Entomologische Zeitschrift* (N.S.), 25, 1–55.

- Laing, J.E. & Heraty, J.M. (1981) The parasite complex of the overwintering population of *Epiblema scudderiana* (Lepidoptera: Olethreutidae) in Southern Ontario. *Proceedings of the Entomological Society of Ontario*, 112, 59–66.
- Michener, C.D. (1953) Comparative morphological and systematic studies of bee larvae with a key to families of hymenopterous larvae. *University of Kansas Science Bulletin*, 35, 987–1102.
- Parker, H.L. (1924) Recherches sur les formes post-embryonnaires des chalcidiens. *Annales de la Société Entomologique de France*, 93, 261–379.
- Parker, H.L. (1942) Oviposition habits and early stages of *Orasema* sp. *Proceedings of the Entomological Society of Washington*, 44, 142–145.
- Parker, H.L. & Thompson, W.R. (1925) Notes on the larvae of the Chalcidoidea. *Annals of the Entomological Society of America*, 18, 384–395.
- Peck, O. (1963) A catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). *Canadian Entomologist, Supplement*, 30, 1–1092.
- Principi, M.M. (1947) Contributi allo studio dei Neurotteri italiani V. Ricerche su *Chrysopa formosa* Brauer e su alcuni suoi parassiti. *Bollettino dell'Istituto di Entomologia della Università delgi Studi di Bologna*, 16, 134–175.
- Purrrington, F.F. (1979) Biology of the hyperparasitic wasp *Perilampus similis* (Hymenoptera: Perilampidae). *Great Lakes Entomologist*, 12, 63–66.
- Riek, E.F. (1970) Hymenoptera. *The Insects of Australia*, pp. 867–959. Melbourne University Press, Carlton, Victoria.
- Short, J.R.T. (1952) The morphology of the head of larval Hymenoptera with special reference to the head of the Ichneumonidae, including a classification of the final instar larvae of the Braconidae. *Transactions of the Royal Entomological Society of London*, 103, 27–84.
- Short, J.R.T. (1978) The final larval instars of the Ichneumonidae. *Memoirs of the American Entomological Institute*, 25, 1–508.
- Smith, H.S. (1912) Technical results from the gypsy moth parasite laboratory. IV. The chalcidoid genus *Perilampus* and its relation to the problem of parasite introduction. *United States Bureau of Entomology, Technical Series*, 19(4), 33–68.
- Smith, H.S. (1917) The habit of leaf-oviposition among the parasitic Hymenoptera. *Psyche*, 24, 63–68.
- Thompson, W.R. (1915) Contribution à la connaissance de la larve planidium (Hymenoptera Chalcidoidea). *Bulletin Scientifique de la France et de la Belgique*, 48, 319–342.
- Tripp, H.A. (1961) The biology of a hyperparasite, *Euceros frigidus* Cress. (Ichneumonidae) and description of the planidial stage. *Canadian Entomologist*, 93, 40–58.
- Tripp, H.A. (1962) The biology of *Perilampus hyalinus* Say (Hymenoptera: Perilampidae), a primary parasite of *Neodiprion swaini* Midd. (Hymenoptera: Diprionidae) in Quebec, with descriptions of the egg and larval stages. *Canadian Entomologist*, 94, 1250–1270.
- Wheeler, G.C. & Wheeler, E.W. (1937) New hymenopterous parasites of ants (Chalcidoidea: Eucharidae). *Annals of the Entomological Society of America*, 30, 163–175.
- Wheeler, W.M. (1907) The polymorphism of ants, with an account of some singular abnormalities due to parasitism. *Bulletin of the American Museum of Natural History*, 233, 1–98.
- Wheeler, W.M. (1928) *The Social Insects. Their Origin and Evolution*. Kegan Paul, Trench, Trubner, London.

Accepted 1 October 1983