

Morphology of the mesosoma of *Kapala* (Hymenoptera: Eucharitidae) with emphasis on its phylogenetic implications¹

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The skeletomusculature of the highly derived mesosoma of *Kapala* (Eucharitidae: Eucharitinae) is described with particular reference to the pronotal–prepectal complex, mesoscutum, and scutellar–axillar complex. *Orasema* (Eucharitidae: Oraseminae) was used for outgroup comparisons based on polarization of certain character states as plesiomorphic through comparisons with Perilampidae and Pteromalidae. *Dilocantha*, *Pseudochalcura*, *Schizaspidia*, and *Stilbula* were used as ingroups for analysis of structures within Eucharitinae. Several character states are discussed with regard to their use in determining relationships within Eucharitinae and a cladogram is presented for six genera. Autapomorphies discussed for the subfamily Eucharitinae are fusion of the prepectus to the pronotum, mesothoracic spiracle completely enclosed dorsally, lack of anterior ventral inflexion of the mesoscutum behind the pronotum, and transverse axillae associated with a well-developed transverse internal ridge along the scutoscutellar sulcus. Synapomorphies proposed for *Kapala* and related taxa in the New World include the reduced lateral axillar surface, internal ridge of the scutoscutellar sulcus developed as an internal phragma, posterior scutellar spines of common derivation, and structure of the internal pronotal–prepectal complex.

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On trouvera ici une description de la musculature squelettique du mésosome très évolué de *Kapala* (Eucharitidae : Eucharitinae), description orientée surtout vers l'examen du complexe pronotal–prépectal, du mésoscutum et du complexe scutellaire–axillaire. *Orasema* (Eucharitidae : Oraseminae) a été utilisé pour les comparaisons à l'aide de groupes externes, ce qui a permis de démontrer la tendance plésiomorphe de certains états de caractères par comparaison aux Perilampidae et aux Pteromalidae. *Dilocantha*, *Pseudochalcura*, *Schizaspidia* et *Stilbula* ont servi lors des comparaisons intra-groupes pour analyser les structures propres aux Eucharitinae. Plusieurs états de caractères sont examinés afin de déterminer leur valeur comme critères de détermination des relations au sein des Eucharitinae et un cladogramme de six genres est présenté. Parmi les caractéristiques autapomorphes examinées au sein de la famille des Eucharitinae, il faut mentionner la fusion du prépectus au pronotum, le stigmate mésothoracique complètement encerclé dorsalement, l'absence d'inflexion ventrale antérieure sur le mésoscutum derrière le pronotum et la présence d'axilles transverses associées à une crête interne transversale bien développée le long du sulcus scutoscutellaire. Les caractéristiques synapomorphes reconnues chez *Kapala* et chez les autres taxons apparentés du Nouveau Monde sont la surface axillaire latérale réduite, la crête interne du sulcus scutoscutellaire modifiée en phragme interne, les épines scutellaires postérieures de même origine, enfin la structure du complexe pronotal–prépectal interne.

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Introduction

The Eucharitidae is a morphologically diverse family of Chalcidoidea (Insecta: Hymenoptera). Forty-four genera are presently recognized and more than 332 described species are distributed in almost every zoogeographic region of the world (Heraty 1985). As far as is known, Eucharitidae includes only species that are specialized ant parasites (Wheeler and Wheeler 1937; Clausen 1941). Eucharitidae comprises two subfamilies: Oraseminae, which has only a few, morphologically unremarkable genera, and Eucharitinae, whose members make up the majority of the family and have radiated morphologically into many distinctive and bizarre forms (Burks 1979; Heraty 1985).

Members of the genus *Kapala* Cameron (Eucharitinae) are widespread throughout the Neotropical region; a few species extend north into the southern United States and one disjunct species is found in northeastern Africa (Heraty 1985). The generic concept of *Kapala* is based entirely on overall similarity of different species. Two characters that readily distinguish this genus and closely related genera from other Eucharitinae are the highly vaulted mesosoma (thorax +

propodeum) and presence of long posterior scutellar spines (Fig. 1). The genera that are closely related to *Kapala* have been defined entirely on phenetic similarity of species within each genus and their overall dissimilarity with *Kapala*. This has resulted in the designation of 12 New World genera, the majority of which are either monotypic or bitypic. Unfortunately, extensions of the scutellum as posterior spines are not unique to *Kapala* or other New World genera, but occur elsewhere within the Eucharitinae in apparently unrelated genera (i.e., spines are apparently convergent).

Phylogenetic systematics advocates the establishment and justification of genera as demonstrably monophyletic groups that both share the same common ancestor and contain all of the descendants of that ancestor. Demonstration of common descent is based on presence of shared, derived characters (synapomorphies) between members of taxa. Consequently, proper establishment of homology of similar character states is critical. Internal studies of the chalcidoid mesosoma have proved useful in the evaluation of homology and can provide new characters that can be used for phylogenetic analysis (Gibson 1985, 1986a). *Kapala* exhibits strong deviations from the "typical" chalcidoid form and an analysis of internal and external structure of the mesosoma was conducted to investigate the monophyly of the genus and its relationships with other taxa.

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The Eucharitidae, as presently defined (Oraseminae and Eucharitinae), is supported as a monophyletic group based on morphology of eggs and first-instar larvae (Heraty and Darling 1984) and on various structures of the head and mesosoma, most notable of which is the position of the pronotum beneath the mesoscutum (Graham 1969; Heraty 1985). *Orasema* Cameron (representative of Oraseminae) shares features of the mesosoma with Perilampidae and Chrysolampinae (Pteromalidae), the proposed sister groups of the Eucharitidae (Heraty and Darling 1984), and the states are therefore regarded as plesiomorphic in the Eucharitidae. The presence of an elongate mesosoma and freely articulating prepectus are shared with Chrysolampinae and most Pteromalidae, and a well-defined dorsal and lateral axillar surface, axillar carina, distinct auxillula, and frenum are shared with the Chrysolampinae and some Perilampidae. By interpreting *Orasema* as representing the plesiomorphic condition of these character states within Eucharitidae, it is possible to analyze the derivations of the mesosoma found in the Eucharitinae and, in particular, the genus *Kapala*.

This study concentrates on the structure and modifications of the mesosoma of *Kapala*, with an emphasis on the pronotal-prepectal complex, the mesoscutum, and the scutellar-axillar complex. Comparisons are made with *Orasema* (Oraseminae), *Dilocantha* Shipp, *Pseudochalcura* Ashmead, *Schizaspidia* Westwood, and *Stilbula* Spinola (all Eucharitinae). Attempts are made to determine the homology of various structures based on external and internal evidence and to evaluate the importance of certain structures in *Kapala* for determining relationships with related New World taxa.

Materials and methods

Materials

Examination of internal skeletomusculature of the mesosoma was carried out for 10 genera of Eucharitidae based upon dissections of exemplar species. Detailed descriptions are presented for five genera belonging to the Eucharitinae and one representative of the Oraseminae. Perilampidae and Chrysolampinae (Pteromalidae) have been established as outgroup taxa to the Eucharitidae based on the morphology and habits of the first-instar larvae (Heraty and Darling 1984) and four genera were used to polarize character states found in the Eucharitidae. Only one sex was available for dissection in most of the genera examined but, except in *Dilocantha*, the small amount of sexual dimorphism should not affect the present analysis or interpretation of character states. In *Dilocantha*, the male is far more similar to *Kapala* than the female and was chosen as more suitable for comparative dissections. Adult specimens and scanning electron microscope (SEM) preparations were deposited as Voucher Series No. 31 in the Insect Collection, Department of Entomology, Texas A & M University.

Descriptions of the mesosoma of *Kapala* (male) are based on individuals of an undetermined species collected from Trinidad and preserved in 70% ethanol since 1976. This species can be considered representative of *Kapala* as recently redescribed by Heraty (1985). The external structures discussed in this paper are found in all members of *Kapala*, except for posterior scutellar spines which rarely are extremely short. Other genera of Eucharitinae examined include the following: *Dilocantha* sp. (male²) (Trinidad), exemplar of a New World genus considered to be closely related to *Kapala*; *Schizaspidia* sp. (male) (Malaysia), exemplar of an Old World genus with long posterior scutellar spines that exhibit external similarity with *Kapala*,

which I initially considered a possible sister taxon to the New World group of genera; *Stilbula cynipiformis* (Rossi) (male) (Yugoslavia), exemplar of an Old World genus with short, bifurcate posterior scutellar spines, which I consider distantly related to *Kapala*; and *Pseudochalcura gibbosa* (Provancher) (female) (Ontario, Canada), exemplar of a New World genus that is considered a derived sister taxon to *Stilbula*, which has secondarily lost the scutellar spines (Heraty 1985). Material of an *Orasema* sp. (female) recently collected in Texas (U.S.A.) was examined as an exemplar of Oraseminae.

Character states analyzed for the previously mentioned taxa were verified in dissections of the following Eucharitidae: *Chalcura ?deprivata* (Walker), *Chalcura* sp. (previously in *Rhipipallus*), *Pseudometagea schwarzii* (Ashmead) (all separate lineages of Eucharitinae), and *Losbanus* sp. (Oraseminae). Character states found in outgroup taxa were represented by dissections of *Chrysolampus sisymbrii* (Ashmead) (Pteromalidae: Chrysolampinae), *Perilampus fulvicornis* Ashmead, *Perilampus hyalinus* Say, *Monacon* sp., and *Steffanolampus salicetum* (Steffan) (Perilampidae).

Methods

Ethanol-preserved *Kapala* and *Orasema* were treated according to the procedures outlined in Gibson (1985). Specimens destined for internal examination were initially dissected in 70% ethanol, including removal of head, wings, abdominal petiole, and legs. The mesosoma was then dehydrated through increasing concentrations to 99% ethanol and critical-point dried to avoid shrinkage of muscle tissue. The parts to be examined were mounted on double-sided tape on SEM stubs. Specimens were then glued to the stub using silver paint and any further dissections of the mount took place at this point. Connective tissue, dried haemolymph, and other extraneous materials were removed with adhesive collected on the end of a minuten pin dragged across the surface of Scotch® tape. Specimens were coated with gold-palladium using a Samdri-790 sputter coater and examined using a Jeol JSM 25SII scanning electron microscope. Intact *Orasema* and *Kapala* and all of the other material examined were treated by essentially the same method without initial dissection before critical-point drying.

Terms used for various internal and external structures follow Daly (1963, 1964) and Gibson (1985, 1986a, 1986b). Abbreviations for terms are given in the table appearing at the end of the Results section. For a detailed explanation and review of the literature on skeletomusculature in chalcidoids, the reader is referred to Gibson (1985, 1986a).

Results

Pronotal-prepectal complex

External morphology

Structure of the mesosoma in Eucharitidae is different from that of almost all other Chalcidoidea in having the pronotum (no_1) positioned ventrally to the mesoscutum ($mml + mll$, Figs. 2, 3, 5), and not or only barely visible in dorsal view (Figs. 4, 6). In *Orasema* the prepectus (pre , Fig. 5) is a free sclerite separate from the pronotum. The prepectus articulates with the pronotum, lies on a different plane, and is ventrally fused posterior to the fore coxae. In *Kapala* and other Eucharitinae, the prepectus is fused anteriorly with the pronotum on the same plane and forms a continuous sclerite, here termed the pronotal-prepectal complex. Within the outgroup taxa, a variety of character states is found corresponding to states found within Eucharitidae. In *Chrysolampus* (Pteromalidae), the prepectus articulates freely with the pronotum and lies on a different plane. In *Steffanolampus* (Perilampidae), the prepectus is on the same plane as the pronotum laterally and is closely appressed (likely immobile), but the sclerite is not fused to the pronotum and can be separated easily. In *Perilampus* and *Monacon* (Perilampidae), the prepectus is com-

²A new association of previously unknown male with female based largely on shape and peculiar modifications of the scuto-scutellar sulcus of the mesosoma.

pletely fused with the pronotum and lies in the same plane laterally. In *P. hyalinus*, an external suture separates the two sclerites, whereas in *P. fulvicornis* and *Monacon*, no external suture is visible.

There is no external indication of previous separation of prepectus and pronotum in *Kapala* and other Eucharitinae. The extent of the pronotum is identified by the relative position of the mesothoracic spiracle (*sp*, Fig. 5), which is found between the pronotum and mesoscutum in all chalcidoids (Gibson 1986a). The mesothoracic spiracle in *Kapala* and other Eucharitinae examined is found on the anterior dorso-lateral edge of the pronotal-prepectal complex (*sp*, Figs. 3, 11, 13, 15, 17) and indicates only that the fusion with the prepectus is between the spiracle and posterior margin of the sclerite.

Internal morphology

The inner surface of the prepectus (*pre*) is devoid of any muscle attachments (Figs. 21–25). The prepectus in *Orasema* is demarked by strong internal ridges (*ppr*) along the anterior and posterior margins (Fig. 21). In *Orasema* and other outgroup taxa examined, the spiracular occlusor muscle (*om*) originates medially from the anterior prepectal ridge (*ppr*) and passes at an oblique angle between the prepectus and pronotum to the base of the spiracle (Fig. 24). The anterodorsal corner of the prepectus (*pi*) in *Orasema* is elongate and extends internally beyond the mesothoracic spiracle (*sp*) but does not form a rigid attachment with the pronotum. In *Chrysolampus*, the prepectus is similar to that of *Orasema*, with the anterodorsal corner free and extending slightly beyond the spiracle internally. In *Steffanolampus*, *Monacon*, and *Perilampus*, the anterodorsal corner of the prepectus is elongated internally into a narrow rod that extends well beyond the mesothoracic spiracle. In both of these genera, the rod is free of any association with the pronotum or muscle attachment. The spiracle is not dorsally enclosed in any of the taxa mentioned above.

In *Orasema*, a large portion of the fan-shaped notopleural muscle (*pl*₁–*no*₁, Fig. 21) attaches to the dorsal margin of the pronotum anterior to the mesothoracic spiracle, and only a small section attaches to the posterior margin of the pronotum posterior to the spiracle. Exact homology of the complete musculature of the pronotum is difficult to determine and terms must be used cautiously until the anatomy is better established. In particular, *pl*₁–*no*₁ may be homologous to *pl*_e–*no*₁ of Daly (1964) but I was not able to resolve the anterior muscle attachment. The present term is used to identify the muscle in the taxa examined. The muscle has a similar attachment site along the pronotal margin in all of the outgroup taxa.

In *Kapala* and *Dilocantha*, the presumed anterior margin of the prepectus is delimited internally by a strong ridge (*ppr*, Fig. 22) that continues ventrally and fuses medially behind the fore coxae, similar to the primitive condition found in *Orasema* (Figs. 5, 21). It is evident from the position of the anterior prepectal ridge that the pronotum is not continuous between the fore coxae and that the region is entirely prepectal in origin. The spiracular occlusor muscle (*om*, Figs. 22, 25) in *Kapala* and *Dilocantha* is almost horizontal and originates from the dorsal margin of the anterior prepectal ridge, not medially as in all of the other taxa. The prepectus and pronotum are fused internally and completely enclose the mesothoracic spiracle (Fig. 25). In both genera, a broad notopleural muscle (*pl*₁–*no*₁, Figs. 22, 25) attaches to the dorsal and posterior margins of the pronotum along the anterior prepectal ridge. The attachment of *pl*₁–*no*₁, the anterior prepectal

ridge, and the occlusor muscle attachment site are useful in defining the border between the pronotum and prepectus.

A different structure of the pronotal-prepectal complex occurs in *Schizaspidia*, *Stilbula*, and *Pseudochalcura*. The anterior prepectal ridge (*ppr*) lies very close to the posterior margin of the complex (Fig. 23), and hence the prepectus is extremely reduced. Homology of the anterior prepectal ridge is suggested by the position of the spiracular occlusor muscle (*om*) which runs obliquely from the spiracle (*sp*) to the prepectal ridge medially (Fig. 23). In *Stilbula* and *Pseudochalcura*, the mesothoracic spiracle (*sp*) is broadly enclosed dorsally by the fusion of the pronotum and prepectus (Figs. 15, 17, 23) and *pl*₁–*no*₁ attaches to the lateral surface of the pronotum, passing beneath the occlusor muscle (Fig. 23). In *Schizaspidia*, the spiracle is more narrowly enclosed dorsally (Fig. 13) and *pl*₁–*no*₁ attaches primarily to the dorsal margin of the pronotum anterior to the spiracle, with a slight lateral displacement posteriorly. This attachment is similar to the one found in the outgroup taxa.

Comparative morphology

Fusion of prepectus (character 4)—Fusion of the anterior margin of the prepectus with the pronotum (character 4, Fig. 26) is an apomorphic state for the Eucharitinae (Heraty 1985; Gibson 1986a). In association with fusion in Eucharitinae, the mesothoracic spiracle (*sp*) is completely enclosed dorsally by a narrow inflection of the anterodorsal corner of the prepectus (*pi*, Fig. 25). Within Eucharitinae, the spiracle is very narrowly enclosed in *Kapala*, *Dilocantha*, and *Schizaspidia*, but broadly enclosed (4') in *Stilbula* and *Pseudochalcura*. In Oraseminae, Chrysolampinae, and Perilampidae, the mesothoracic spiracle (and associated trachea) lies freely between the mesoscutum and the pronotum dorsally and the anterodorsal extension of the prepectus (*pi*) internally. In Perilampidae, the internal inflection of the anterodorsal corner of the prepectus is rod-like, extending into the cavity of the mesosoma, and is well separated from the pronotum. Based on the genera examined, a rod-like inflection represents a synapomorphy for Perilampidae and suggests convergent fusion of the prepectus in Eucharitinae.

Similar pronotal-prepectal complex (character 7)—The fusion of the prepectus with the pronotum creates a unique structure found in Eucharitinae. In Oraseminae and Chrysolampinae the anterior prepectal ridge (*ppr*) is associated with the margin of the free prepectus and extends to the mesothoracic spiracle (*sp*). The occlusor muscle (*om*) has an oblique attachment to the anterior prepectal ridge, and *pl*₁–*no*₁ attaches to the posterior margin of the pronotum (*no*₁) surrounding the mesothoracic spiracle. The presence of an anterior prepectal ridge that extends to the spiracle and similar placement of muscles is regarded as plesiomorphic. In *Kapala*, *Dilocantha*, *Schizaspidia*, *Stilbula*, and *Pseudochalcura*, the spiracle is displaced forward from the anterior margin of the fused prepectus based on the intermediate position of the anterior prepectal ridge (*ppr*). *Schizaspidia*, *Stilbula*, and *Pseudochalcura* share a similar structure of the pronotal-prepectal complex (character 7a) defined by a reduced, linear prepectus (*pre*) with anterior prepectal ridge (*ppr*) close to the posterior margin of the complex (Fig. 23), oblique attachment of the occlusor muscle (*om*), and *pl*₁–*no*₁ not reaching the anterior prepectal ridge. *Kapala* and *Dilocantha* share a similar structure of the internal pronotal-prepectal complex (character 7b) defined by a triangular prepectus (*pre*) with anterior prepectal ridge (*ppr*) not meet-

ing the spiracle dorsally, horizontal occlusor muscle (*om*), and broad attachment of pl_1-no_1 to anterior prepectal ridge.

Mesoscutum

Morphology

The mesoscutum comprises a mesoscutal medial lobe (*mml*) and a mesoscutal lateral lobe (*mll*, Figs. 3–6). Internally, the longitudinal flight muscles ($1ph-2ph$, Figs. 7, 9) occupy almost the entire mesosoma and attach anteriorly to the mesoscutal median lobe along the entire vertical aspect (Fig. 19) and posteriorly to the second phragma ($2ph$, Figs. 7, 20). The anterior lower attachment of the longitudinal muscle in *Orasema* is to the first phragma ($1ph$, Fig. 9), which is a downward inflection of the anterior margin of the mesoscutum that extends behind and below the dorsal margin of the pronotum. The first phragma of *Orasema* is unpigmented and not medially strengthened by a thickening of cuticle along the ventral margin. In Chrysolampinae and Perilampidae the first phragma is a well-developed, somewhat bilobed structure and forms the major anterior attachment site for the longitudinal muscle. In *Kapala* and other Eucharitinae examined, the attachment site of the longitudinal muscle is entirely above the dorsal margin of the pronotum on the vertical anterior face of the mesoscutum ($1ph-2ph$, Fig. 19). The anteroventral margin of the mesoscutum is inflected horizontally as a strong internal ridge (*mr*, Figs. 14, 16, 18, 19) so that the pronotum directly abuts the mesoscutum and an internal first phragma as found in the Oraseminae is lacking. The dorsoventral flight muscles (t_2-pl_2 , Figs. 7, 9) originate on the mesoscutal lateral lobes dorsally and the mesepisternum ventrally (*eps*₂, Figs. 3, 5).

The median and lateral lobes of the mesoscutum are separated by the notaulus (*not*, Figs. 3–6, 19), an external sulcus that extends from the anteroventral margin of the mesoscutum to the posterodorsal margin at the trans-scutal articulation (*tsa*, Figs. 4, 6). In *Orasema*, *Kapala*, and *Dilocantha*, the notaulus is narrow and sharply delineated along its entire length externally (*not*, Figs. 3, 5, 6, 11) and internally is developed as a thin ridge (*not*, Figs. 8, 10, 12, 19). In *Schizaspidia*, the notaulus is narrow but shallow and weakly developed externally (Fig. 13). In *Pseudochalcura* and *Stilbula* the notaulus is broadly and shallowly impressed and obscured anteroventrally by the reticulated sculpture of the mesoscutum (Figs. 15, 17). Internally, *Stilbula*, *Schizaspidia*, and *Pseudochalcura* have a very prominent notaular ridge (*not*, Figs. 14, 16, 18).

One further muscle attaching to the mesoscutum is the mesopleural-mesonotal muscle (pl_2-t_2c , Figs. 21, 22). In all taxa examined in this study, the muscle was very short and tubular, and originated from the dorsal region of the mesopleuron (acroleuron) and inserted to the posterolateral edge of the mesoscutum (posterior to the prepectus). A short tubular muscle was also found in *Torymus* (Torymidae) and *Elasmus* (Eulophidae) and is therefore probably plesiomorphic in the Chrysolampinae, Perilampidae, and Eucharitidae. Gibson (1986b) described this muscle as fan-shaped in chalcidoids, originating from the acroleuron, and inserting on the "process of anterolateral edge of mesoscutum." The preaxilla in eupelmids extends for almost the entire length of the mesoscutum (cf. Gibson 1986b: Figs. 5, 31), whereas this region is extremely reduced in chrysolampids, perilampids, and eucharitids. Perhaps a more correct description of the point of insertion would be to the process of the anterolateral edge of the preaxilla.

Comparative morphology

Mesoscutal ridge (character 1)—Within Chalcidoidea, the anterior attachment site for the longitudinal flight muscles is to the mesoscutum dorsally and primarily to the first phragma of the mesoscutum, a ventral projection of the mesoscutum behind the pronotum (Daly 1963; Gibson 1986b). In Eucharitidae, the pronotum is ventral to the plane of the mesoscutum and the mesoscutum forms almost the entire vertical aspect and attachment for $1ph-2ph$. Although it is difficult to distinguish the structure, the first phragma ($1ph$) in *Orasema* is a small, ventral inflection of the mesoscutum behind the pronotum which allows attachment of $1ph-2ph$ below the dorsal margin of the pronotum (Figs. 9, 10). An internal first phragma is absent in *Kapala* and other Eucharitinae examined. Apparently, it is replaced by a horizontal inflection of the anteroventral margin of the mesoscutum which forms a mesoscutal ridge (*mr*). A semicircular, flattened area of the mesoscutum ($1ph?$, Fig. 2) could be interpreted either as an exposed first phragma based on homology of the lower attachment for the longitudinal muscles ($1ph-2ph$) or as a secondary flattening of the mesoscutum. In either case, the anteroventral margin of the mesoscutum is strongly developed as an internal ridge (*mr*) and, together with the mesoscutum directly abutting the pronotum, represents a synapomorphy for the subfamily Eucharitinae.

Notaular ridge (character 5)—The fine notaular ridges (*not*) found in *Kapala* and *Dilocantha* are plesiomorphic, similar to those found in *Orasema*, Chrysolampinae, and some Perilampidae, and contribute little to the understanding of relationships within these taxa. However, in *Schizaspidia*, *Stilbula*, and *Pseudochalcura*, notaular ridges are strongly developed internally (in contrast to weak external development of the notaulus) and suggest a common origin.

Scutellar-axillar complex

External morphology

The axillae of *Orasema* are subdivided into a dorsal axillar surface (*das*) and prominent lateral axillar surface (*las*), with the latter posteriorly delimited by the axillar carina (*axc*, Figs. 5, 6). The scutoscutellar sulcus (*sss*) is diagonal in dorsal view and converges medially to the trans-scutal articulation (*tsa*), with the axillae appearing roughly triangular in dorsal view and divided medially by the scutoscutellar sulcus (Fig. 6). The scutellum (*scl*) is divided into a frenum (*fr*) posteriorly and axillula (*axa*) laterally (Figs. 5, 6). The anterior margin of the frenum is delimited by the frenal groove (*fg*) which is visible as a foveolate sulcus dorsally (*fg*, Fig. 6) and a weak, oblique ridge laterally (*fg*, Fig. 5) extending to the ventral margin of the axillar carina. The axillula (*axa*) is delimited anteriorly by the scutoscutellar sulcus (*sss*), the axillular sulcus (*axas*) dorsally, and the frenal groove posteriorly (*fg*) (Figs. 5, 6).

The scutellar-axillar complex of *Kapala* is highly modified compared with that of *Orasema*. The axillae are formed almost entirely by the dorsal axillar surface (*das*), which is dorsally elevated and fused medially into a single transverse sclerite (Figs. 3, 4). The greatly reduced lateral axillar surface is posteriorly margined by the lateral axillar carina (*axc*, Figs. 3, 4), and is only just visible above the tegula and base of the fore wing (*wb*) (Fig. 3). The posterior margin of the dorsal axillar surface (*das*) is defined by the scutoscutellar sulcus (*sss*), which is crossed dorsally by longitudinal carinae and a series of raised cuticular nodules at the junction of each carina with the sulcus (Figs. 3, 4). The scutellum is subdivided into

an apical frenum and lateral axillula although the margins are not as clearly defined as in *Orasema*. The apex of the scutellum (*scl*) is abruptly truncate and forms an elevated ridge between the base of the paired posterior scutellar spines (*ps*), which extend from the posterior lateral margins of the scutellum (Figs. 1, 3, 4). The lateral margins of the frenum (*fr*) are defined by an oblique ridge (*fg*) extending from the base of the hind wing to the ventral margin of the posterior scutellar spine (Fig. 3). Extrapolation of the ridge (*fg*) dorsally would include the elevated ridge and spines as both originating from the frenum. However, it is equally plausible to have the frenal ridge pass ventral to the spines and therefore have the spines issue from the true scutellum (*scl*). The axillula (*axa*, Fig. 3) is poorly defined by a lateral carina (*axas*) which is contiguous with the dorsal base of the spines and forms a weak sulcus in dorsal view (*axas*, Fig. 4).

Dilocantha and *Schizaspidia* have posterior scutellar spines that extend from the apex of the scutellum (Figs. 11, 13) and are approximately as long as the mesosoma. *Stilbula* has a pair of short spines that originate posterior to the frenal groove (Fig. 15) and *Pseudochalcura* lacks any spines on the scutellum (Fig. 17). In *Dilocantha*, the spines are paired at the base, similar to those of *Kapala*, whereas in *Schizaspidia* and *Stilbula*, the spines are bifurcate apically and originate from a single point. The axillae are transverse in dorsal view in all of these genera, although deep medial pits along the scutoscuteellar suture approach the trans-scutal articulation in *Stilbula* and *Pseudochalcura*. In *Dilocantha*, the axillae are broad and the lateral axillar surface is greatly reduced as in *Kapala* (Fig. 11). In *Schizaspidia*, *Stilbula*, and *Pseudochalcura* (Figs. 13, 15), the axillar surface (*das*) is narrow and the lateral axillar surface, as defined by the axillar carina (*axc*), is prominent. The scutoscuteellar sulcus of *Dilocantha* is deeply and broadly invaginated laterally and densely packed with long, thin, hook-tipped setae (Fig. 11). In *Schizaspidia*, *Stilbula*, and *Pseudochalcura*, the sulcus (*sss*) forms a deep, crenulate furrow which is very broad in *Stilbula* and narrow in the others.

The axillular sulcus (*axas*) was visible externally in *Dilocantha* as a distinct lateral carina (Fig. 11) that ends posteriorly at the dorsal base of the posterior scutellar spine, and in *Schizaspidia* (Fig. 13) as a vague lateral carina that continues onto the lateral edge of the scutellar spines. The sulcus was visible internally as a vague longitudinal ridge in *Dilocantha* and *Schizaspidia* (Figs. 12, 14, respectively). In *Stilbula* and *Pseudochalcura*, the axillular sulcus was not visible externally or internally (Figs. 15–18).

Internal morphology

A sagittal section of the mesosoma of *Orasema* (Fig. 9) shows the well-developed longitudinal flight muscle (*1ph–2ph*) occupying almost the entire dorsal region of the mesosoma. The major muscle attachment to the inner surface of the scutellar–axillar complex (excluding ventrolateral muscle groups attaching to the ventral margin of the lateral axillar surface; cf. Gibson 1986b) is the lateral mesotergal–mesotrochanteral muscle (t_2-tr_2 , Figs. 9, 10). The muscle originates dorsally from the lateral region of the dorsal axillar surface, with an anterior expansion of the muscle onto a cuticular expansion of the axilla, the axillar phragma (*axp*), which extends anteriorly under the mesoscutal lateral lobes (as in Fig. 7). The internal V-shaped ridge (VR, Fig. 10) is only weakly developed and coincides with the external shape of the scutoscuteellar sulcus (*sss*), joining medially at the trans-scutal

articulation (*tsa*) (Figs. 6, 10). The axillular sulcus (*axas*) and frenal sulcus or ridge are barely visible internally as weak ridges (Fig. 10).

A sagittal section of the mesosoma of *Kapala* (Figs. 7, 8) reveals a spacious cavity in the posterior region of the mesosoma above the longitudinal flight muscle (*1ph–2ph*) and within the scutellar–axillar complex. The lateral dorsoventral muscles (t_2-pl_2 and t_2-tr_2) are closely appressed and angled anteriorly within the mesosoma (Figs. 7, 8). The attachment of t_2-tr_2 and its relationship with t_2-pl_2 are basically similar to those found in *Orasema*, with the exception that dorsal attachment of t_2-tr_2 occupies almost the entire dorsal axillar surface in *Orasema* (Figs. 9, 10) whereas attachment in *Kapala* (Figs. 7, 8) is limited to the axillar phragma (*axp*) and anterior one-third to one-half of the axillae.

In *Kapala* (Figs. 8, 20), the dorsal cavity of the mesosoma is divided medially by a well-sclerotized V-shaped ridge that forms a transverse phragma (VR) extending down from the scutoscuteellar sulcus (*sss*). The phragma has a ventral arch, which is strengthened by a strong ridge of thick cuticle; this arch cradles the dorsal surface of the longitudinal flight muscles (Figs. 7, 20). The phragma extends ventrally to the dorsal margin of the lateral depressions of the scutellar–axillar complex, which are located above the base of the fore wing (*wb*) (Figs. 3, 20). The axillular sulcus (*axas*, Fig. 4) is visible internally as a weak, longitudinal ridge (Fig. 8). There were no internal demarcations of the frenal ridge.

In *Dilocantha* (Fig. 12), a large dorsal mesosomal cavity is divided medially by the scutoscuteellar phragma (VR) above the longitudinal flight muscles (*1ph–2ph*). The phragma is developed internally as a deep invagination of the external surface (Fig. 12) similar in placement to the phragma found in *Kapala*. Laterally, the external surface of the phragma is packed with a dense layer of short, broad setae (Fig. 12). The phragma is fused medially and narrows to a single thickness of heavily sclerotized cuticle. *Schizaspidia*, *Stilbula*, and *Pseudochalcura* all have a large dorsal cavity above *1ph–2ph* (region above broken lines, Figs. 14, 16, 18). Each has a prominent, transverse ridge that extends down from the scutoscuteellar sulcus (VR, Figs. 14, 16, 18) but lacks development of a complete phragma.

As in *Kapala*, the dorsal origin of t_2-tr_2 in *Dilocantha* is limited to the anterior region of the dorsal axillar surface and axillar phragma, and both t_2-pl_2 and t_2-tr_2 are angled forward from their ventral attachments. In *Schizaspidia*, *Stilbula*, and *Pseudochalcura*, the dorsal attachment of t_2-tr_2 occupies almost the entire dorsal axillar surface. In *Schizaspidia* and *Stilbula*, and to a lesser degree in *Pseudochalcura*, t_2-pl_2 and t_2-tr_2 are vertical within the mesosoma (Figs. 14, 16, 18) compared with the more prominent forward angle found in all of the other taxa examined.

Comparative morphology

Dorsoventral muscles (character 6)—Monophyly of *Schizaspidia*, *Stilbula*, and *Pseudochalcura* is supported by the similarity in vertical alignment of the lateral dorsoventral muscles (t_2-tr_2 , t_2-pl_2) of the mesosoma. The forward angle of these muscle groups in *Kapala*, *Dilocantha*, *Orasema*, and *Chryso-lampis* is regarded as plesiomorphic.

Lateral axillar surface (character 8)—The reduction in size of the lateral axillar surface (*las*) found in *Kapala* and *Dilocantha* is a character state shared by all of the New World taxa that I consider closely related to *Kapala* based on the presence

of long posterior scutellar spines (*Dicoelothorax* Ashmead, *Galearia* Brullé, *Isomerala* Shipp, *Lirata* Cameron, *Liratella* Girault, *Parakapala* Gemignani, *Thoracantha* Latreille, and probably also *Holcokapala* Cameron, *Pseudokapala* Gemignani, and *Lasiokapala* Ashmead, which were not available for examination). This character state reduction is not found in any of the other genera examined in this paper. A reduced lateral axillar surface, found in the Old World genus *Eucharis*, and also a broad transverse axilla, found in some closely related taxa, may indicate another lineage to be assessed as a possible sister taxon to the New World "kapaline" genera.

Axillae (characters 2 and 3)—A transverse dorsal axillar surface (character 2, *das*), as defined by the scutoscutellar sulcus (*sss*) and well-developed internal ridge (character 3, VR), was found in all Eucharitinae examined and represents a synapomorphy for the subfamily. The transverse scutoscutellar sulcus with associated V-shaped ridge developed as an internal phragma (character 3') appears to be unique for the kapaline genera based on dissections of *Kapala* and *Dilocantha*. However, caution must be exercised in postulating the homologous similarity of the internal V-shaped ridge (character 3') of *Kapala* and *Dilocantha*. The state found in *Dilocantha* could be derived from the relatively thin phragma of *Kapala* or it could be a separate derivation from an invagination of the outer cuticle and an associated fusion of the invagination medially. External appearance of the scutoscutellar sulcus as a series of nodules is found in *Kapala*, *Dicoelothorax*, *Isomerala*, *Liratella*, and *Lirata*, and the shape of the

scutellar-axillar complex suggests that a transverse internal phragma is shared between all of these taxa. The scutoscutellar sulcus in *Thoracantha* and *Galearia* lacks a nodulated appearance, but the mesosoma is extremely modified in these genera and presence of an internal phragma can only be postulated.

Posterior scutellar spines (character 9)—The relationship of the axillular sulcus (*axas*) and the frenal groove (*fg*) is useful in determining whether posterior scutellar spines are derived from the frenum or scutellum. In *Stilbula* (Fig. 15), the frenal groove is readily apparent in lateral and dorsal aspect and the spines originate from the frenum. In *Schizaspidia* (*axas*, Figs. 13, 14), the axillular sulcus appears to extend laterally along the spines. In *Kapala* (Fig. 4) and *Dilocantha* (Figs. 11, 12), the axillular sulcus extends to the dorsal base of the spines and the lateral frenal groove reaches to the ventral base of the spines. Homology of these sulci and ridges with those shown in *Orasema* is supported internally by the weak ridge associated with the axillular sulcus, but there is only a very weak ventrolateral ridge associated with the frenal groove and no dorsal demarcation. There is therefore no internal evidence to support a homologous derivation of the spines. However, external position of the lateral axillular sulcus and ventral frenal groove to the postscutellar spines is the same in all kapaline genera examined and can be used to at least postulate a similar origin for elongate spines in this group. Again, the highly modified scutellar-axillar complex of *Galearia* and *Thoracantha* makes resolution of these two characters (*axas* and *fg*) in these genera impossible.

Abbreviations in figures

<i>axa</i>	axillula	<i>2ph</i>	second phragma
<i>axas</i>	axillular sulcus	<i>1ph-2ph</i>	mesoscutellar - second phragmal (longitudinal flight) muscle
<i>axc</i>	axillar carina	<i>pi</i>	prepectal inflection
<i>axp</i>	axillar phragma	<i>pl₁-no₁</i>	notopleural muscle
<i>das</i>	dorsal axillar surface	<i>pl₂-t₂c</i>	mesopleural-mesonotal muscle
<i>eps₂</i>	mesepisternum	<i>ppr</i>	prepectal ridge
<i>fr</i>	frenum (Graham 1969; Heraty 1985)	<i>pre</i>	prepectus
<i>fg</i>	frenal groove (sulcus or ridge) (Graham 1969; Heraty 1985)	<i>pro</i>	propodeum
<i>las</i>	lateral axillar surface	<i>pss</i>	posterior scutellar spine
<i>mll</i>	mesoscutal lateral lobe	<i>scl</i>	scutellum
<i>mml</i>	mesoscutal medial lobe	<i>sp</i>	mesothoracic spiracle
<i>mr</i>	anteroventral margin of mesoscutum	<i>sss</i>	scutoscutellar sulcus
<i>no₁</i>	pronotum (pronotum + prepectus in Eucharitinae)	<i>tsa</i>	trans-scutal articulation
<i>no₃</i>	metanotum	<i>t₂-pl₂</i>	mesotergal-mesepisternal (dorsoventral flight) muscle
<i>not</i>	notaulus	<i>t₂-tr₂</i>	mesotergal-mesotrochanteral muscle
<i>om</i>	spiracular occlusor muscle	VR	V-shaped notal ridge; scutoscutellar phragma
<i>1ph</i>	first phragma	<i>wb</i>	base of fore wing

Discussion

A cladogram depicting relationships among eucharitid genera studied here is shown in Fig. 26. Hypothesized synapomorphies for the subfamily Eucharitinae include the following: strong ventral mesoscutal ridge (character 1, *mr*) and associated lack of a ventral inflection of the mesoscutum as the first phragma (*1ph*) behind the pronotum; transverse dorsal axillar surface (character 2, *das*); presence of a well-developed V-shaped ridge (character 3, VR) internally along the scutoscutellar sulcus; and prepectus fused with the pronotum (character 4), which is associated with a complete enclosure of the mesothoracic spiracle (*sp*) dorsally. Separate dissections of *Pseudometagea* and *Chalcura* (Eucharitinae)

supported all of the general character states that are attributed to the Eucharitinae.

Schizaspidia, *Stilbula*, and *Pseudochalcura* share a similar structure of the pronotal-prepectal complex (character 7a) as defined by a reduced linear prepectus (*pre*), oblique attachment of occlusor muscle (*om*), and *pl₁-no₁* not reaching anterior prepectal ridge. Notaular ridges (*not*) are well developed internally (character 5) and lateral dorsoventral muscles (*t₂-tr₂*, *t₂-pl₂*) are vertically aligned (character 6). *Stilbula* and *Pseudochalcura* share a broadly enclosed spiracle (character 4') which is regarded as a transition state from the narrowly enclosed spiracle associated with the fusion of the prepectus (character 4) in other Eucharitinae. The posterior

