Phylogenetic implications of the mesosomal skeleton in Chalcidoidea (Hymenoptera, Apocrita) – tree searches in a jungle of homoplasy

Lars Krogmann\textsuperscript{A,C} and Lars Vilhelmsen\textsuperscript{B}

\textsuperscript{A}Zoological Institute and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany. 
\textsuperscript{B}Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. 
\textsuperscript{C}Corresponding author. Email: lak@gmx.net

Abstract. Results from a comparative anatomical study of the mesosomal skeleton of Chalcidoidea are presented. External and internal features are described and illustrated for 39 chalcidoid taxa, representing 16 families and 29 subfamilies. This is the most comprehensive morphological study ever conducted for the superfamily. The mesosa was dissected, macerated and investigated using scanning electron microscopy. The mesothorax and metathorax contributed most of the phylogenetically relevant information. The metafurca is highly variable within Chalcidoidea but seems to be relatively constant at the subfamily level. One hundred and fifty-four morphological characters were scored and analysed cladistically. Outgroup species were chosen from six apocritan superfamilies: Stephanoidea, Ceraphronoidea, Cynipoidea, Platygastroidea, Proctotrupoidea and Mymarommatoidea. Some previously suggested chalcidoid relationships were retrieved: (1) Pteromalidae: Pteromalinae + Miscogasterinae + Panstenoninae; (2) Perilampidae + Eucharitidae; (3) Chalcididae + Leucospidae + Eurytomidae; (4) Eulophidae: Eulophinae + Tetrachininae + Entedoninae; and (5) Eupelmidae + Encyrtidae. Mymarommatoidea renders Chalcidoidea paraphyletic in our analyses; however, the taxon sample is too restricted to provide a robust hypothesis. Three previously unreported putative autapomorphies of Chalcidoidea were revealed: (1) presence of an exposed, triangular or diamond-shaped prosternum; (2) presence of a percurrent mesopleural sulcus anteriorly terminating in the acropleuron; and (3) presence of paired metapetal plates lateral to the metafurca.

Additional keywords: character evolution, cladistic analysis, comparative anatomy, phylogenetic systematics.

Introduction
The superfamily Chalcidoidea is one of the most diverse groups of insects in terms of species numbers, biology and morphology. More than 22000 species have hitherto been described in 2000 genera (Noyes 2003), but worldwide far more than 100000 species may exist (Noyes 1978). A tremendous number of different lifestyles (parasitoid, phytophagous and predatory) can be found within the superfamily as reviewed in Bendel-Janssen (1977), but most species are parasitoids of other insects. Many chalcidoid species have been successfully employed in biological control programs against insect pests. The realised and potential economic importance of Chalcidoidea makes increased research in their systematics essential. Although the monophyly of the superfamily seems to be well established (Gibson 1986a), no robust phylogenetic hypothesis has been proposed. The family classification is tentative at best, and the number of recognised families has varied between 38 (classified as subfamilies in de Dalla Torre 1898) and nine (Riek 1970). Even though the number of recognised families has recently stabilised around 19 (Noyes 2003) or 20 (Bouček 1988b), only a few of these families are defined by autapomorphies (Gibson et al. 1999). Many groups are diagnosed by plesiomorphic features. The Pteromalidae is probably the least defined family and generally is regarded as the ‘rump’ of Chalcidoidea (Gibson et al. 1999; Török and Abraham 2002), i.e what remains after the distinct groups have been classified as other families. Pteromalidae derives from Dalman’s (1820) family ‘Pteromalini’, which at that time comprised the majority of today’s chalcidoid families. It was later used as a synonym for the whole superfamily (Latreille 1825). Pteromalidae is today split into 31 subfamilies (Noyes 2003), including taxa that might occupy key positions in the internal phylogeny of the Chalcidoidea.

In addition to its unresolved internal phylogeny it is also difficult to place Chalcidoidea within the Apocrita. Mymarommatoidea has been proposed as the sister-group of Chalcidoidea (Gibson 1986a). This was confirmed by cladistic analyses based on morphological data (Ronquist et al. 1999; Sharkey and Roy 2002). Until now Mymarommatoidea has not been represented in analyses of molecular data (Campbell et al. 2001; Dowton and Austin 2001; Castro and Dowton 2006).
The main reason why a robust phylogenetic hypothesis for the Chalcidoidea has so far proven elusive is the huge morphological variation within the superfamily. The current classifications (on the family, subfamily, tribal, genus or species level) are based nearly exclusively on morphological characters, but character state distribution and evolution are often unknown due to the lack of comprehensive morphological studies.

The most complex morphological feature of the adult wasp is the mesosoma, which is derived from the fusion of the thorax with the first abdominal tergum (propodeum). Thoracic structures have been comprehensively studied within some Hymenoptera by previous authors: prothoracic structures by Vilhelmsen (2000a), mesothoracic structures by Johnson (1988), Whitfield et al. (1989), Gibson (1993a), and the metathoracic/abdominal boundary region by Vilhelmsen (2000b). The mesosomal skeleton of Palaeomyrmex anamalum (Blood & Kryger, 1922) (Mymaromatidae) was recently examined by Vilhelmsen and Krogmann (2006). Unfortunately, there are only a few studies of the mesosomal morphology of Chalcidoidea. This is probably due to the small body size of the adult wasps (1–2 mm on average), which makes the mesosoma difficult to examine, and the daunting morphological diversity encompassed by the Chalcidoidea. Because of this, most studies have been restricted to single species (James 1926; Bucher 1948; Heraty 1989) or single families (Gibson 1989) or refer to single character systems like the mesofurca (Heraty et al. 1997). Gibson (1985, 1986a) established criteria for the evaluation of mesosomal structures in a cladistic sense, and resolved problems in the terminology used for structures.

The aims of the present study were: (1) to give a detailed morphological description of the mesosomal skeleton for a wide range of chalcidooid taxa; (2) to summarise the information in a character matrix suitable for phylogenetic analyses; and (3) to undertake a cladistic analysis of phylogenetic relationships within Chalcidoidea and compare the results with the current classification.

Materials and methods

Material

Our survey includes 39 species of Chalcidoidea, representing 16 families and 29 subfamilies, with emphasis on Pteromalidae (Appendix 1). Seven species from six apocritan superfamilies were included as outgroups in the phylogenetic analyses. Most species were collected directly in the field, primarily in central Europe. Voucher specimens of all taxa examined were deposited in the collections of the Zoological Museum Hamburg or the Zoological Museum, University of Copenhagen (Appendix 1). First choice for the morphological investigations were females, but males were also included, if available. Significant sexual dimorphism is exhibited only within Agaoniidae and Eupelmiidae (Eupelminae). Males of Agaoniidae were not included in our survey. Male characters of Eupelmus atropurpureus Dalman, 1820 (Eupelminae) were scored independently from the female and separate analyses were carried out for both sexes.

Morphological techniques

The dissections were predominantly based on material stored in 70–80% ethanol. Dried material was used in a few instances, in which case it was soaked in ethanol before dissection. The dissections were carried out with scalpels, pieces of razor blades or minutien needles. Prior to dissecting the mesosoma, the head, legs, wings, and metasoma were removed. The mesosoma was dissected into the following parts: (1) pronotum; (2) propectus (propleura, prosternum); (3) mesonotum including pro- and mesophragma; (4) mesoposts; and (5) meta-thorax–propodeum complex. The anterior part of the metasoma (i.e. the petiole) was also included in our survey. The preparations were macerated in 10% potassium hydroxide by either keeping them overnight at room temperature or in a heating cabinet at 40–50 degrees centigrade for 2–5 h, depending on the size of the specimen (the bigger the specimen, the longer and warmer the treatment). The preparations were then rinsed in demineralised water and (if necessary) cleaned in 0.1% Triton X-100. Afterwards they were transferred from 70% to 99% ethanol in an ethanol series and critical-point dried. The preparations were mounted on SEM stubs, sputter-coated with gold-platinum and observed in a JEOL JSM-6335-F or LEO 1525 SEM unit.

Cladistic analyses

The morphological data were coded as 154 discrete binary or multistate characters, which are listed in Appendix 2. A character matrix is presented in Appendix 3; missing or inapplicable data are indicated by question marks. Parsimony analyses were carried out in PAUP 4.0b10 (Swofford 1997) implementing heuristic search using the stepwise addition of 1000 random replications. All characters were equally weighted and trees rooted on Megischus (Stephanoleidae). Total Bremer support values (Bremer 1988, 1994) were calculated by implementing converse constraints with 100 random addition sequences per node. A second analysis was carried out with the same parameters, but by using Goloboff’s (1993) implied-weights criterion with k = 4.

Results

The mesosoma of Pteromalinae (illustrated in Figs 1–4) is described in detail and serves as an introduction to chalcidooid mesosomal skeletal morphology and terminology; subsequent descriptions mainly focus on differences and provide an overview of the morphological variation that occurs within the superfamily (Figs 5–20). The descriptions are based on the species that are listed at the beginning of each section. The mesosomal regions (prothorax, mesothorax, metathorax–propodeum complex) are described from top to bottom (notum, pleuron, sternum). Selected external features of the petiole and the mesosomal–metasomal articulation are also described. The abbreviations used for the figures are listed in Table 1.
The mesosomal skeleton of Chalcidoidea

Invertebrate Systematics

Table 1. Abbreviations used in Figs 1–20.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>apodeme</td>
</tr>
<tr>
<td>ac</td>
<td>acropleuron</td>
</tr>
<tr>
<td>achr</td>
<td>acropleural ridge</td>
</tr>
<tr>
<td>acs</td>
<td>acropleural sulcus</td>
</tr>
<tr>
<td>ax</td>
<td>dorsal axillar surface</td>
</tr>
<tr>
<td>axl</td>
<td>axillula</td>
</tr>
<tr>
<td>axl</td>
<td>axillular carina</td>
</tr>
<tr>
<td>axl</td>
<td>axillar ridge</td>
</tr>
<tr>
<td>axs</td>
<td>axillar sulcus</td>
</tr>
<tr>
<td>axph</td>
<td>axillary phragma</td>
</tr>
<tr>
<td>bf</td>
<td>basal fovea</td>
</tr>
<tr>
<td>c</td>
<td>carina</td>
</tr>
<tr>
<td>clm</td>
<td>collum</td>
</tr>
<tr>
<td>clr</td>
<td>collar</td>
</tr>
<tr>
<td>co</td>
<td>costula</td>
</tr>
<tr>
<td>cx</td>
<td>procoxa</td>
</tr>
<tr>
<td>cx1</td>
<td>mesocoxa</td>
</tr>
<tr>
<td>cx3</td>
<td>mesotergum</td>
</tr>
<tr>
<td>dc1</td>
<td>prodiscrimenal line</td>
</tr>
<tr>
<td>dc2</td>
<td>mesodiscrimenal line</td>
</tr>
<tr>
<td>dc1</td>
<td>mesodiscrimenal line</td>
</tr>
<tr>
<td>dcl1</td>
<td>prodiscrimenal lamella</td>
</tr>
<tr>
<td>dcl2</td>
<td>mesodiscrimenal lamella</td>
</tr>
<tr>
<td>dcl3</td>
<td>mesodiscrimenal lamella</td>
</tr>
<tr>
<td>dcl4</td>
<td>mesodiscrimenal lamella</td>
</tr>
<tr>
<td>epc</td>
<td>epicnemial carina</td>
</tr>
<tr>
<td>epm2</td>
<td>mesepimeron</td>
</tr>
<tr>
<td>eps2</td>
<td>mesepistemum</td>
</tr>
<tr>
<td>eps3</td>
<td>metepistemum</td>
</tr>
<tr>
<td>f1</td>
<td>procura</td>
</tr>
<tr>
<td>f1a</td>
<td>profrugal arm</td>
</tr>
<tr>
<td>f1p</td>
<td>profrugal pit</td>
</tr>
<tr>
<td>f2</td>
<td>mesofurca</td>
</tr>
<tr>
<td>f2a</td>
<td>mesofurcal arm</td>
</tr>
<tr>
<td>f2p</td>
<td>mesofurcal pit</td>
</tr>
<tr>
<td>f3</td>
<td>metafurca</td>
</tr>
<tr>
<td>f3a</td>
<td>metafurcal arm</td>
</tr>
<tr>
<td>f3p</td>
<td>metafurcal pit</td>
</tr>
<tr>
<td>fx1</td>
<td>procoxal foramen</td>
</tr>
<tr>
<td>fx2</td>
<td>mesocoxoal foramen</td>
</tr>
<tr>
<td>f1</td>
<td>metapleural sulcus</td>
</tr>
<tr>
<td>f2</td>
<td>mesonotum</td>
</tr>
<tr>
<td>f3</td>
<td>metanotum</td>
</tr>
<tr>
<td>f1a</td>
<td>mesotegulum</td>
</tr>
<tr>
<td>f1p</td>
<td>mesotegula</td>
</tr>
<tr>
<td>f2</td>
<td>mesotegulum</td>
</tr>
<tr>
<td>f3</td>
<td>mesotegula</td>
</tr>
<tr>
<td>f1a</td>
<td>nuchal muscle</td>
</tr>
<tr>
<td>f3a</td>
<td>nuchal muscle</td>
</tr>
<tr>
<td>pcd</td>
<td>procoxal depression</td>
</tr>
<tr>
<td>pd</td>
<td>propodeum</td>
</tr>
<tr>
<td>p1</td>
<td>propleuron</td>
</tr>
<tr>
<td>p2</td>
<td>mesopleuron</td>
</tr>
<tr>
<td>p3</td>
<td>metapleural sulcus</td>
</tr>
<tr>
<td>pl1</td>
<td>mesopleural sulcus</td>
</tr>
<tr>
<td>pl2</td>
<td>mesopleural sulcus</td>
</tr>
<tr>
<td>pl3</td>
<td>lateral surface of metapleurum</td>
</tr>
<tr>
<td>pl</td>
<td>plica</td>
</tr>
<tr>
<td>pm</td>
<td>protuberance</td>
</tr>
<tr>
<td>pm</td>
<td>protuberance</td>
</tr>
<tr>
<td>pps</td>
<td>postspiracular apodeme</td>
</tr>
<tr>
<td>ppa</td>
<td>profrugal arm</td>
</tr>
<tr>
<td>pp1</td>
<td>1st phragma</td>
</tr>
<tr>
<td>pp2</td>
<td>2nd phragma</td>
</tr>
<tr>
<td>pp</td>
<td>pseudophragma</td>
</tr>
<tr>
<td>pph</td>
<td>pseudophragma</td>
</tr>
<tr>
<td>pps</td>
<td>pit correspond to prospinasternal apodeme</td>
</tr>
<tr>
<td>pre</td>
<td>prepectus</td>
</tr>
<tr>
<td>prr</td>
<td>prepectral ridge</td>
</tr>
<tr>
<td>psa</td>
<td>prosthepisternal apodeme</td>
</tr>
<tr>
<td>psc</td>
<td>paracoxal carina</td>
</tr>
<tr>
<td>psl</td>
<td>paracoxal carina</td>
</tr>
<tr>
<td>psp</td>
<td>propodeal spiral</td>
</tr>
<tr>
<td>pss</td>
<td>postspiracular apodeme</td>
</tr>
<tr>
<td>s1</td>
<td>subalar pit</td>
</tr>
<tr>
<td>s2</td>
<td>subalar pit</td>
</tr>
<tr>
<td>s</td>
<td>sulcus</td>
</tr>
<tr>
<td>ssa</td>
<td>scutellar suture</td>
</tr>
<tr>
<td>ssc</td>
<td>scutellar suture</td>
</tr>
<tr>
<td>ssc</td>
<td>scutellar suture</td>
</tr>
<tr>
<td>ssp</td>
<td>scutellar suture</td>
</tr>
<tr>
<td>p</td>
<td>tendon</td>
</tr>
<tr>
<td>temr</td>
<td>transhiperal ridge</td>
</tr>
<tr>
<td>tens</td>
<td>transhiperal ridge</td>
</tr>
<tr>
<td>tess</td>
<td>transhiperal ridge</td>
</tr>
<tr>
<td>tg</td>
<td>tegula</td>
</tr>
<tr>
<td>tsa</td>
<td>transhiperal articulation</td>
</tr>
<tr>
<td>wps</td>
<td>posterior wing process</td>
</tr>
</tbody>
</table>
nally corresponding to notaular ridge (*notr*), the ridge usually incomplete in Pteromalinae (Fig. 2F) but reaching transscutal articulation in *P. vindemmiae* (Fig. 2G); parapsidal line absent. Lateral lobe of mesoscutum (Fig. 2A) with parascutellar carina (*psc*) delimiting preaxilla (*pax*) along posterolateral edge; surface of preaxilla smooth or weakly reticulate, but mainly covered by tegula (Fig. 2A: *tg*). Prophragma (Fig. 2F: *ph*) short, medially incised, continuous with anterior mesoscutal margin.

Mesoscutellar–axillar complex with scutoscutellar sulcus (Fig. 1C: *sss*) crescent-shaped, abutting transscutal articulation medially and separating axillae from mesoscutellum. Axilla (Fig. 1A) with carina separating dorsal surface (*ax*) from lateral panel of axilla (*lax*), the lateral panel having cuticular ridges. Axillula (Figs 1A, 3H: *axl*) with dorsal limit marked by shallow axillular sulcus (Fig. 3H: *axls*). Scutoscutellar sulcus and axillular sulcus internally corresponding to ridges (Fig. 2F), the scutoscutellar ridge (*ssr*)

Fig. 1. Mesosoma of Pteromalinae. A–C, Mesosoma of: *A*, Pachycrepoideus vindemmiae, lateral view (anterior to the left); *B*, Lariophagus distinguendus, ventral view (anterior to the top); *C*, Nasonia vitripennis, dorsal view (anterior to the top).
and axillar ridge \((axlr)\), the two ridges fused proximally but clearly separate distally. Mesoscutellum with smooth frenal arm (Fig. 3H: \(fra\)) posterolateral to axillula, the arms clearly evident from sculptured cuticle of mesoscutellum and sometimes connected by weak indication of punctuate frenal line \((frl)\) to delimit posterior part of mesoscutellum as inconspicuous frenum \((fr)\) (Figs 1C, 4A). Internally, axillar phragma (Figs 2F, G: \(axph\)) originating from axilla and extending along mesoscutum, the phragma at least slightly longer than broad and characterised by straight anterior margin. Mesophragma (Fig. 2G: \(ph_2\)) continuous with posterior margin of mesoscutellum, extending towards propodeum and with posterior margin deeply incised medially (Fig. 2H); anterior portion of mesophragma short, bilobed, forming

---

**Fig. 2.** Prothorax and mesonotum of Pteromalinae. *A,* Pronotum of *Cecidostiba semifascia*, lateral view (anterior to the left). *B–E,* Propectus of: *Nasonia vitripennis,* B, ventral view (anterior to the top); C, posterior view (ventral to the top); D, anterior view (ventral to the top); E, *Dibrachys cavus,* dorsal view (anterior to the top). *F–G,* Mesonotum (anterior to the left) of: *F,* *Nasonia vitripennis,* ventrolateral view; *G,* *Pachycrepoideus vindemmiae,* ventral view. *H,* Mesophragma of *Cecidostiba semifascia,* ventral view (anterior to the top).
pseudophragma (Fig. 2H: *pph*) adjacent to internal surface of mesoscutellum, its anterior margin deeply incised medially.

Prepectus (Figs 1B, 3A: *pre*) medially fused with its opposite number, separated from mesepisternum (*eps*2) by complete, flexible furrow; ventrally, fused prepecti narrow (Fig. 1B), normally hidden under procoxa; lateral surface of prepectus (Fig. 1A: *pre*) triangular, with posterior edge overlapping mesopleuron and highly mobile relative to latter. Mesepisternum in ventral view (Fig. 3A: *eps*2) with anterior margin u-shaped and with submedian incision for articulation of prepectus. Prepectus sometimes with distinct ridge along postero medial margin that fits into incision of mesepisternum (Figs 1B, 3A); internally, prepecti separated from each other by complete carina, the carina adjacent to small

---

**Fig. 3.** Mesepisternus and metathorax–propodeum complex of Pteromalinae. *A–F*, Mesepisternus of: *Nasonia vitripennis*, ventral view (anterior to the top): *A*, anterior part; *B*, posterior part; *C*, *Cecidostiba semifascia*, dorsal view (anterior to the left); *Pachycrepoideus vindemmiae*, *D*, anterior view; *E*, dorsolateral view (anterior to the top); *F*, *Lariophagus distinguendus*, anteromedian part, dorsal view (anterior to the top). *G*, *H*, Mesothorax and metathorax–propodeum complex of *Dibrachys cavus*: *G*, posterior view (ventral to the top); *H*, lateral view (anterior to the left).
mesodiscrimenal line (Fig. 1A) from which a short prospinasternal apodeme (Fig. 3F: psa) arises.

Mesoscutum forming ventral and lateral portions of mesothorax (Fig. 1A, B). Anterior margin of mesoscutum internally carinate (Fig. 3C: c). Mesopleural sulcus (Fig. 1A: mps) extending from mesocoxa (cx2) to acropleuron (ac) and dividing mesopleuron into ventral mesepisternum (eps2) and dorsal mesepimeron (epm2); sulcus weakly impressed, forming dorsal margin of slightly reticulate mesofemoral depression (Fig. 1B: mfd). Mesepimeron (Fig. 3H) divided into upper (uepm1) and lower mesepimeron (lepm1) by transepimeral sulcus (tems). Transepimeral sulci in Pteromalinae usually curved and weakly impressed, but absent in P. vindemmiae. Internally, mesepimeron characterised by weak swellings corresponding to external transepimeral sulcus and mesopleural sulcus (Fig. 3C). Upper mesepimeron often smooth and easily distinguishable from reticulate lower mesepimeron (Fig. 3H) or sometimes (P. vindemmiae) reticulate but with finer sculpture than lower mesepimeron (Fig. 1A). Acropleuron (Figs 1A, 3H: ac) a small region underneath forewing base, only ventrally delimited by acropleural sulcus (Fig. 3H: acs), and smooth (Fig. 3H) or slightly reticulate (Fig. 1A); internally, acropleural sulcus developed as arch-shaped ridge (Fig. 3C: acr) extending from anterior to posterodorsal margin of mesoscutum. Mesepisternum without transepisternal sulcus (Fig. 1A); anteroventral part of mesepisternum sometimes with shallow procoxal depression (Fig. 3A: pcd). Mesoscutum with pilosity restricted to mesepisternum, with mesodiscriminal line (Fig. 1B: dc1) developed as groove, dotted line or smooth area, and with mesofurcal pit (fps) just anterior to mesoatrochantinal plate (mtp) (Figs 1B, 3B). Mesotrochantinal plate anteriorly bordered by complete, transverse carina (Fig. 3B: c); mesotrochantinal lobe (Fig. 3B: mtl) for articulation with mesoscutum present and distinct. Mesocoxal foramen (Fig. 3G: fcx1) not completely surrounded by sclerotised cuticle, a membranous (m) strip separating foramen from metepisternum (eps3). Mesoxocaes accommodated within cavity delimited anteriorly by carina of mesoatrochantinal plate, laterally by mesopleuron, and posteriorly by anteroventral part of metepisternum (Figs 1B, 3B, G). Mesofurca (Fig. 3E: f2) y-shaped in anterior view (Fig. 3D); dorsally with anterior apodemes present, the apodemes medially fused as mesofurcal bridge (Figs 3D, E) and bridge sometimes with short median process; horizontal plate (Figs 3D, E: hp) between mesofurcal arms (Fig. 3D: fps); anteriorly extended and fused with mesodiscriminal lamella (dcl1), horizontal plate thus appearing subtriangular in anterior view, tapering proximally; mesodiscriminal lamella (Fig. 3E: dcl1) anteriorly diverging, extending to anterior margin of mesepisternum; base of mesofurca at posterior end of mesodiscriminal lamella (Fig. 3E), indicated externally as mesofurcal pit. Mesofurcal base in a few pteromalines bearing vertical ridge (Fig. 3E) at posterior end.

Metanotum (Fig. 1A: no3) articulating laterally with metepisternum and posteriorly with propodeum (pd), sometimes covered anteromedially by mesoscutellum. Metascutellum (= dorsellum) (Fig. 4A: mts) narrow, usually not extending to anterior and posterior margin of metanotum, delimited by anterior and posterior row of foveae (fov). Lateral panel of metanotum with metascutellar arm (Fig. 4A: mtsa) smooth, anteriorly delimited by broad row of foveae (Figs 4A, B).

Lateral surface of metapleuron (= lateral metepisternum) (Fig. 3H: pl2) triangular, separated from propodeum by complete metapleural sulcus (mtps); ventral surface of metapleuron (= ventral metepisternum) (Fig. 3G: eps2) with sharp, mediadly interrupted transverse carina (c) and paired metafurcal pits (fps) anterior to carina. Propodeal foramen (Figs 3G, 4C: fpd) ellipsoid, slightly larger than rounded metacoxal foramen (fcx1) and connected to latter by carina. Metadiscriminal line externally weakly developed (Fig. 4C: dc1) or indistinct (Fig. 3G); internally, metadiscrimen a short septum (= metadiscriminal lamella, Fig. 4D: dcl2) arising anterior to propodeal foramen and extending to anterior margin of metapleuron. Metafurca with arms (Fig. 4D: fps) clearly separate from each other lateral to metadiscriminal lamella, with each arm distally abruptly broadened (clavate) and partly fused with metapleural apodeme (mtpa) (only with posterior surface); additional apodeme (Fig. 4E: a) arises dorsolaterally to metapleural apodeme; metapleural plate (Figs 4D, F: mp) (see discussion) separated from metafurcal arm, the plate broad and rounded in most pteromalines (Fig. 4D) but distally elongate in P. vindemmiae (Fig. 4F).

Propodeum (Figs 4A, B) highly variable; external surface reticulate or smooth; posterior margin medially prolonged between base of mesocoxae into distinct nucha (Fig. 4A: nu), the nucha sometimes delimited anteriorly by carina (Fig. 4A); median carina (mc) usually present (Fig. 4A, B); median area laterally usually delimited by paired carinae (= plicae, Fig. 4A: pli), but only sometimes with pair of smooth anterior depressions (= basal foveae, Fig. 4B: bf), or transverse carina (= costula, Fig. 4B: co); lateral surface with long setae (Figs 4A, B). Propodeal spiracle (psp) kidney-shaped, with distinct outer margin (Figs 4A, B).

Petiole (Fig. 4H: pet) often reduced, anelliform, without sculpture, sometimes with lateral tubercle. In P. vindemmiae petiole elongate with reticulate sculpture, dorsally with median longitudinal carina, and ventrally branched by antero-laterally extended second metasomal sternite (Fig. 4G: ms2).

PTEROMALIDAE, MISCOGASTERINAE

Cytogaster vulgaris Walker, 1833

The overall mesosomal morphology is very similar to Pteromalinae and differs mainly in the following structures:
Pronotum with collar strongly reduced, without sculpture, but anterior margin with long setae; collum slightly reticulate. Mesoscutum with notaulus externally incomplete but internally complete. Prepectus medially not narrowed and with distinct pronotal depression (Fig. 10E: pnd). Metapetal plate laterally fused with metapetal arm and reduced in size. Petiole elongate with reticulate sculpture, extensions of second metasomal sternite absent.

PTEROMALIDAE, PANSTENONINAE

Panstenon oxylus (Walker, 1839)

Pronotum bell-shaped, without transverse carina. Mesoscutum with notaulus incomplete externally and internally; mesoscutellum with irregular frenal line. Prepectus reticulate, externally divided by smooth triangular area; internally, prepecti not separated by distinct carinae. Mesosdiscrinal line deep and distinct. Metepisternum with single metafurcal pit anterior to deep metadiscrinal line. Metapetal arms (Fig. 17C: f3a) medially fused on single base, metapetalura thus y-shaped, metapetal plate (mp) not fused with metapetalura. Propodeum uniformly reticulate. Petiole (Fig. 20E: pet) elongate and slightly reticulate, with short lateral tubercle and ventrally with median sulcus (s).

PTEROMALIDAE, ORMOCERINAE

Trichilogaster sp.

Mesosoma very compact, with sculpture and pilosity reduced. Pronotum reduced in size, disc-like, the separation between collum and collar indistinct. Prosternum ventrally reduced. Pronotum reduced in size, disc-like, the separation between collum and collar indistinct. Prosternum ventrally reduced. Pronotum very compact, with sculpture and pilosity reduced. Metapetal arms (Fig. 17D: f2p) fused at level of metepisternum, metapetalura thus appearing u-shaped in anterior view; metadiscrinal lamella inconspicuous, not extending to anterior margin of metepisternum, metapetal plate (mp) clearly separated from metapetal arm. Propodeum and metacoxal foramina surrounded by weakly sclerotised cuticle.

Propodeum (Fig. 15A) short, without nucha; median carina (mc) broad, plicae (pl) shifted laterally, propodeal spiracles (psp) large and circular.

Petiole (Fig. 15A: pet) reduced, anelliform, without sculpture.

PTEROMALIDAE, ASAPHINAE

Enoggera reticulata Naumann, 1991 and Asaphes vulgaris

Walker, 1834 (the prepectus and mesopleuron differ significantly between the two species and these will therefore be described separately)

Pronotum with characteristically curved lateral sulci (Fig. 5A: s). Propleura (Fig. 5A: pl) reduced in size, hardly abutting medially. Prosternum with anterior margin completely exposed only in E. reticulata (Fig. 5A); medially incised (A. vulgaris) or with acute median process (E. reticulata, Fig. 5A). Profurcal arms narrow, not distally broadened, but with distinct distal process (Fig. 6D) in A. vulgaris. Prepectus short (A. vulgaris, Fig. 6D: ppa) or absent (E. reticulata).

Mesonotum with reduced reticulation, transscutal articulation deep and complete, notaulus externally and internally complete. Scutoscutellar sulcus (Fig. 8A: sss) with characteristic submedian interruption, medially deeply impressed. Axillar sulcus (Fig. 8A: axs) externally weakly impressed but corresponding to distinct internal ridge (A. vulgaris) or completely absent (E. reticulata, Fig. 10G). Mesoscutellar-axillar complex with a characteristic pit posterior to axilla in both species (Figs 8A, 10G). Axilla (Fig. 8A: ax) with long setae at least posteriorly. Mesoscutellum in A. vulgaris with about posterior quarter differentiated as frenum (Fig. 8A: fr) by foveolate frenal line (frl), the frenal line with corresponding internal ridge, but mesoscutellum of E. reticulata with row of foveae near posterior margin (Fig. 15B: fov) (see discussion of frenal line).

Prepectus: In E. reticulata broad, ventrally (Fig. 10H: pre) with pattern of deep, median and submedian impressions, posterolaterally with rounded extension overlapping mesopleuron (Fig. 10G); externally completely separated from mesopleuron by deep furrow (Fig. 10H) but internally fused with anteromedian portion of lower mesepisternum and not subdivided by carinae (Fig. 12F). In A. vulgaris prepectus narrower, completely separated from mesepisternum internally and externally, and internally subdivided by complete carinae.
Mesopleuron: In *E. reticulata* most external mesopleural features (mesopleural sulcus, transepimeral sulcus, acropleural sulcus, sculpture, setation) are reduced. Acropleural ridge (Fig. 12F: *acr*) developed only dorsally, not reaching anterior margin of mesopectus. Mesopleuron with two vertical parallel depressions laterally (Fig. 10H) corresponding to internal apodemes. Mesepisternum separated by distinct transepisternal sulcus (Fig. 10H: *tess*) into lower and upper mesepisternum; lower mesepisternum anteriorly with procoxal depression (Fig. 10H: *pcd*) and corresponding internal swelling. Mesodiscrimenal line (Fig. 10H: *dc2*) externally weakly impressed, with two mesofurcal pits (*f2p*); posterior pit anterior to carina of mesotrochantinal plate corresponding to (posterior) mesofurcal base (Figs 10H, 12F); anterior

pit at anterior end of mesodiscrimenal line, the line not extending to anterior margin of mesepisternum (Fig. 10H), with pit internally corresponding to low swelling within mesodiscrimenal lamella, the lamella extending to anterior mesepisternal margin (Fig. 12F). Mesotrochantinal plate with median carina (Fig. 10H: mc), mesocoxal foramen surrounded by sclerotised cuticle interrupted dorsolaterally. Mesofurca with tenuous bridge, and mesodiscrimenal lamella straight and narrow (Fig. 12F). In *A. vulgaris*, mesopleuron with mesofemoral depression, mesopleural sulcus

and transepisternal sulcus developed; transepiemer al sulcus short with deep pit corresponding to internal apodeme. Acropleural ridge arch-shaped, reaching anterior margin of mesoscutum. Mesocoxal foramen completely surrounded by cuticle. Mesodiscrimenal lamella broader, slightly diverging, extending to anterior mesoplastic margin.

Metanotum similar to Pteromalinae (Fig. 15B). Metepisternum with sharp transverse carina and two metatruar pits. Metapleura with medtrual arms widely separated, distally clavate (Figs 17E, F: f3a), metadiscrimenal lamella (dcl3) well developed and extending to anterior margin of metepisternum, metapleural plate (mp) reduced in size, completely fused with metapleural arm. Metapleural arms in E. reticulata shifted posteriorly (Fig. 17E).

Propodeum with distinct nucha and spiracle rounded with distinct outer margin (Fig. 15B). Propodeal surface with irregular reticulation and single row of foveolae along anterior margin (A. vulgaris), or smooth with median carina, plicae, and two rows of foveolae along anterior and posterior margin (E. reticulata, Fig. 15B).

Petiole (Figs 15B, 20F, G: pet) elongate in both species, reticulate, anterior margin with distinct carina, overlapping nucha of propodeum.

**PTEROMALIDAE, CLEONYMINAE**

*Thaumasura* sp. and *Notanisus* sp.

Pronotum anteriorly slightly elongate, bell-shaped in dorsal view; in *Thaumasura* sp. with indication of median sulcus. Propsectus resembles that of Pteromalinae. Propfrural arm (Fig. 6E: f3a) with distal process, only in *Thaumasura* sp. with rounded opening near propfrural base.

Mesonotum dorsally flattened (Fig. 11A); notaulus externally and internally complete (*Notanisus* sp.) or incomplete (*Notanisus* sp.). Axillula widely separated (*Thaumasura* sp.) or medially abutting (*Notanisus* sp.). Dorsal limit of axillula traceable only in *Thaumasura* sp., as axillular carina (Fig. 11A: axlc). Posterior margin of mesoscutellum forming scutellar lip (Fig. 11A: sell) and marked by foveolae (fov) (*Thaumasura* sp.) or indistinct and smooth (*Notanisus* sp.). Prepectus broad, medially fused with mesepisternum in external view, lateral edge overlapping mesopleuron (Fig. 11A). Internally, prepectus completely separated from mesepisternum in *Thaumasura* sp. (Fig. 12G), but medially fused with mesepisternum in *Notanisus* sp., and both species characterised by two broad, medially fused carinae that separate prepecti internally (Fig. 12G), the carinae in *Notanisus* sp. exceeding posterior limit of prepectus and abutting anterior end of mesodiscrimenal lamella. Mesopleuron with external mesopleural sulcus, transepimeral sulcus, and mesomeric depression distinctly developed (Fig. 11A), but transepimeral sulcus weakly indicated. Acropleuron and upper mesepimeron smooth, the upper mesepimeron in *Thaumasura* sp. with characteristic setation dorsally, just below subalar pit (Fig. 11A: sap); mesepisternum and lower mesepimeron reticulate (Fig. 11A). Internally, mesopleuron with weak indication of transepimeral sulcus; ridge corresponding to mesopleural sulcus present and distinct (Fig. 12G: mpr) (*Thaumasura* sp.) or absent (*Notanisus* sp.); acropleural ridge (Fig. 12G: acr) curved, connecting dorsal and anterior margin of mesoscutum. Mesodiscrimenal externally present as weakly indicated line extending to anterior margin of mesepisternum (*Thaumasura* sp.) or as deep sulcus not extending to anterior mesepisternal margin (*Notanisus* sp.). Mesodiscrimenal lamella anteriorly straight (*Notanisus* sp.) or only slightly diverging (*Thaumasura* sp.), posteriorly distinctly diverging (Fig. 12G: dcl3).

Metanotum very similar to Pteromalinae (Figs 15C, E). Lateral surface of metaleuron in *Thaumasura* sp. reticulate and extensively pilose (Fig. 11A: pl3); in *Notanisus* sp. bare, with anterior half smooth and posterior half reticulate (Fig. 15E: pl3). In *Thaumasura* sp. metepisternum smooth (Fig. 15D: eps3), separated from reticulate lateral metaleuron by carina, but with complete transverse and incomplete median longitudinal carina; mesocoxal depression distinct; transverse propodeal foramen enlarged and connected with circular metacoxal foramen by surrounding carinae; single metalebral pit (Fig. 15D: f3p) close to anterior metepisternal margin, which is slightly extended medially and abuts mesotrochantinal plate (mp); metalebral arms (Fig. 17H: f3a) medially fused anterior to metadiscrimenal lamella (dcl3), metapleural plate (mp) separate from metafurca. In *Notanisus* sp. metepisternum externally without transverse carina; metadiscrimenal line present as sulcus; mesocoxal depression distinct; metacoxal and propodeal foramina more or less circular and connected by surrounding carinae; metalebral pit situated medially close to anterior metepisternal margin, laterally with two separate openings (Fig. 15F); internally metalebral arms (Fig. 17G: f3a) clearly separated and distinctly clavate distally, metapleural plate (mp) not fused with metafurca, metadiscrimenal lamella (dcl3) extending to anterior metepisternal margin.

Propodeum of *Thaumasura* sp. (Fig. 15C) short, without distinct nucha, anterior margin with row of foveolae; median area narrow, flanked by plicae (pli) and with median and two submedian carinae, posterior margin of median area carinate; lateral propodeal surface extensively pilose, spiracle kidney-shaped with distinct outer margin. Propodeum of *Notanisus* sp. with distinct nucha, dorsal surface smooth, but with one transverse row of foveolae at anterior margin, one pair of longitudinal rows of foveolae flanking median carina and another lateral pair connecting anterior and posterior propodeal margin; propodeal spiracle (Fig. 15E: psp) at anterior end of lateral row of foveolae.

Petiole anelliform and strongly transverse (*Thaumasura* sp.) or cylindrical (*Notanisus* sp.).
PTEROMALIDAE, SPALANGINAE

Spalangia nigripes Curtis, 1839

Pronotum bell-shaped in dorsal view, internally with broad ridge (Fig. 5C) anterior of posterior margin; collar elongate, with fine sculpture, anterior margin smooth, the margin posteriorly delimited by sulcus (Fig. 5B: s), and separated from collar by transverse, foveolate sulcus; collar with sparse pilose punctures, but posterior margin smooth; lateral panel bare, with fine sculpture, dorsally limited by deep triangular cuticular impression (Fig. 5B). Propleura (Fig. 5D: pl₁) medially abutting along entire length, lateral margins cari-

Fig. 6. Prothorax of Chalcidoidea. A, Clytina giraudi (Signiphoridae): mesosoma, dorsal view (anterior to the left); B, Gonatocerus morrilli (Mymaridae): pronotum, dorsolateral view (anterior to the top). C–H, profurca (anterior to the top) of: C, Trichilogaster sp. (Pteromalidae, Ormocerinae), dorsal view; D, Asaphes vulgaris (Pteromalidae, Asaphinae), dorsal view; E, Thaumasura sp. (Pteromalidae, Cleonyminae), posterior view; F, Spalangia nigripes (Pteromalidae, Spalangiinae), dorsal view; G, Torymus bedeguaris (Torymidae, Toryminae), dorsal view; H, Antrocephalus sp. (Chalcididae, Haltichellinae), dorsal view.
nate; surface of propleuron with fine reticulation laterally (Fig. 5B), but mainly smooth ventrally apart from reticulate area anteriorly, just posterior to head articulation (Fig. 5D).

Prosternum small (Fig. 5D: st.), triangular, anterior margin exposed, prodiscerninal line a broad sulcus, median process conspicuous (Fig. 5D). Profurcal arms completely fused with prosternum along its entire width, fusion lines of profurcal arms proximally indiscernible; profurcal pits minute, shifted posteriorly (Fig. 6F: f gr); position of articulation point between propleuron and profurcal arm at posterior end of propectus; propleural arm narrow, elongate, rod-like (Fig. 6F: ppa).

Mesonotum with notaulus foveolate (Fig. 5B: not), reaching transscutal articulation internally (Fig. 5B: notr) and externally; transcutal articulation straight, laterally interrupted. Axilla enlarged, triangular, anterolateral edge with rounded impression and corresponding internal apodeme (Fig. 8B: a), internal axillary phragma short (axph). Scutocutellar sulcus foveolate, medially with deep impression. Axillula indistinct. Frenal line foveolate (Fig. 15G: f rl), with corresponding internal ridge (Fig. 8B: f rr). Prepectus large and strongly reticulate, lateral triangular area delimited by sharp carina (Fig. 11C), prepecti ventrally with large rounded fovea, and medially fused with mesepisternum, the inner surface with subdividing carinae (Fig. 12H: c) only indicated anteriorly and prospinasternal apodeme (Fig. 12H: psa) minute, situated on anterior prepectal margin. Mesopleuron predominantly smooth, mesopleural sulcus only indicated anteriorly, transepisternal sulcus (Fig. 11C: tems) with deep, rounded depression and corresponding internal ridge (Fig. 11B: temr), and posterior margin of mesopleuron lateral to mesoscoxal foramen with second depression (Fig. 11C). Acropleural sulcus indiscernible; internally, acropleural ridge only posteriorly developed, forming bridge-like, vertical ridge (Fig. 11B: acr). Transepisternal sulcus (Fig. 11D: tess) with deep foveolae discernible as swellings on inner surface (Fig. 11B).

Mesodiscerninal line a deep sulcus; mesofurcal pit (Fig. 11D: f g) conspicuous, close to centre of mesepisternum. Mesotrochantinal plate (Fig. 11D: mtp) with median carina, and mesoscoxal foramen completely surrounded by sclerotised cuticle. Mesopespect internally with mesodiscerninal lamella (Fig. 12H: dcl 3 ) straight, not extending to anterior margin of mesepisternum; mesofurcal base situated in middle of mesodiscerninal lamella (Fig. 13A: dcl 3 ) where lamella reaches maximum height.

Metanotum (Fig. 15G) predominantly smooth, but anterior margin with continuous row of foveolae; metascutellum (mts) laterally marked by incurred sulci and sparsely pilose. Metapleuron (Fig. 11C) dorsally not clearly separated from propodeum, strongly reticulate and pilose. Metepisternum (Figs 11D, 15H: eps 3 ) anteriorly slightly prolonged to abut mesotrochantinal plate, short, with sharp transverse carina medially interrupted by pair of submedian carinae, the transverse carina laterally extended and continuous with carina that extends to propodeal foramen (Fig. 15H). Metapleural pits (Fig. 15H: f p) minute, widely separate and close to anterior metepisternal margin, the margin usually partly overlapped by mesopleuron (Fig. 11D). Metacoxal and propodeal foramina small and rounded (Fig. 15H). Metafurca u-shaped, with metapetalur arms (Fig. 18A: f f) basally fused, metapectal plate (mp) reduced in size, completely fused with metafurcal arm. Metadiscerninal lamella indistinct, not extending to anterior metepisternal margin but posteriorly almost reaching propodeal foramen.

Propodeum (Fig. 15G) with coarse punctuation apart from smooth pair of submedian rectangular areas, including foveolate row along anterior margin, on either side of median carina (mc), and laterally between anterior and posterior margins; propodeal spiracle (psp) at anterior margin anterior of lateral row of foveolae; posterior margin of propodeum prolonged into distinct nucha (Fig. 15G).

Petiole elongate (Figs 15G, H: pet), cylindrical with coarse sculpture, anterior margin with lateral extensions that exceed nucha.

**ORMYRIDAE**

*Ormyrus* sp.

Pronotum mainly pilose and covered with transverse striae, lateral panel smooth. Propleura with posterior margins incurved, prosternum posteromedially extended but without distinct process. Profurca with arms slender and distally extended, propleural arm reduced in size.

Mesoscutum externally lacking notaulus, internal ridge developed but incomplete. Scutocutellar and axillar sulci weakly impressed, internal corresponding ridges separate from each other. Prepectus reduced in size, laterally rounded, medially compressed with anteromedian margin slightly extended and overlapping mesepisternum. Prepectus medially not separated from mesepistemum in external view, prepecti internally separated by complete carinae. Mesopleuron ventrally with striate reticulation, laterally smooth. Acroneural sulcus with complete internal ridge, mesopleural sulcus with weakly developed internal ridge, transepisternal sulcus absent. Mesocoxal foramen completely surrounded by sclerotised cuticle.

Lateral panel of metanotum similar to Pteromalinae, but metacocoxal (Fig. 16A: mts) completely smooth and extending from anterior to posterior margin of metanotum. Metapleuron bare and triangular in lateral view. Metepisternum (Fig. 16B: eps 3 ) with median metafurcal pit and laterally with additional pair of submedian pits close to anterior metepisternal margin. Metafurcal foramen conspicuously enlarged with surrounding carina, propodeal foramen small and rounded. Metafurca (Fig. 18B) appearing u-shaped in anterior view with metafurcal arms (f f) medially fused,
transverse carina. Metafurca (Fig. 18 plate, and bearing median metafurcal pit. Mesocoxal depression dorsally. Internally, acropleuron bordered by distinct carinae. Mesopleuron laterally with weak impressions of mesopleural sulcus and transepimeral sulcus; upper mesepimeron smooth and lower mesepimeron striate. Acropleuron smooth, ventrally with distinct acropleural sulcus, which delimits sculptured mesofemoral depression dorsally. Internally, scutoscutellar ridge laterally broadened at position of axillulae. Mesoscutellum subdivided by punctuate sulcus; upper mesoscutellum smooth posteriorly. Frenal line present in Monodontomerus sp. (Fig. 8D: frr) and bearing internal ridge (Fig. 8C: frr); frenum with finer sculpture than rest of mesoscutellum. Frenal line absent in Podagrion sp. and T. bedeguaris but mesoscutellum smooth posteriorly. Mesoscutellum with distinct foveolate posterior margin in all Toryminae (Fig. 8D: fov). Prepecti broadly fused in external view but internally separated by complete carinae (Fig. 13B: c); prepecti completely separated from mesepisternum (internally and externally). Acropleuron smooth, ventrally limited by distinct sulcus; internally with complete ridge (Fig. 13B: acr). Mesepimeron completely smooth, transepimeral sulcus developed. Mesepisternum slightly reticulate with mesoxodal foramen and mesofurcal pit as in Pteromalinae. Posterior margin of mesopleuron straight (Monodontomerus sp.), incurved (Podagrion sp.) or incised midway (T. bedeguaris) (Fig. 16C). Transepimeral sulcus with internal ridge developed in Monodontomerus sp. and Podagrion sp. Mesofurca with median ridge at posterior end only in Monodontomerus sp.

Metanotum of T. bedeguaris and Podagrion sp. similar to Pteromalinae but metascutellum extending to anterior margin (Fig. 16C); in Monodontomerus sp. metascutellum smooth (Fig. 16E: mts), extending from anterior to posterior margin, with median longitudinal carina. Metapleuron (Fig. 16C: pl3) separated from propodeum (pd) by complete sulcus. In Monodontomerus sp. metapleuron triangular, with reticulation and complete pilosity; in Podagrion sp. metapleuron large and subrectangular, cuticle smooth, pilose only along outer margins; in T. bedeguaris metapleuron subrectangular with anterior margin extended,
cuticle smooth, pilose only at posterior margin (Fig. 16C). Metepisternum (Fig. 16D) smooth with transverse carina and posterolateral carina extending between metacoxal and propodeal foramina. Median longitudinal carina present in Monodontomerus sp. and Podagrion sp. (Fig. 16D). Single metafurcal pit situated at anterior metepisternal margin (Fig. 16D: \( f_{gp} \)). Metafurca highly variable in Toryminae. In Podagrion sp. metafurca y-shaped but broadly fused with metepisternum (Fig. 18D), metafurcal arms \((f_{ga})\) broad from base to apex, metadiscrinemal lamella \((dcl_{3})\) present at anterior metepisternal margin between metafurcal arms, metapectal plate \((mp)\) rounded, clearly separate from meta-

![Figure 7](image-url)

Fig. 7. Profurca of Chalcidoidea. A–E, Profurca (anterior to the top) of: A, Leucospis sp. (Leucospidae), posterior view; B, Schizaspidea nasua (Eucharitidae, Eucharitinae), dorsal view; C, Aprostocetus sp. (Eulophidae, Tetrastichinae), dorsal view; D, Ericydnus sp. (Encyrtidae, Tetracnemiinae), dorsal view; E, Trichogramma evanescens (Trichogrammatidae), posterior view. F, Centrodora sp. (Aphelinidae, Aphelinae); pro- and mespectus, posterior view. G–H, Profurca of: G, Clytina giraudi (Signiphoridae), dorsal view; H, Gonatocerus morrilli (Mymaridae), dorsal view.
furca. Metafurca in Monodontomerus sp. y-shaped (Fig. 18E), broadly (but less extensively than in Podagrion sp.) fused with metepisternum, metafurcal arm proximally slender, distally clavate, metadiscriminal lamella extending to anterior margin of metepisternum, metapectal plate separate from metafurca. Metafurcal arms separate in T. bedeguaris but basally orientated towards each other (as in M. dorsalis) (Fig. 18F), metafurcal arms with distinct clava and dorsal extension at proximal end; metadiscriminal lamella present and distinct at anterior metepisternal margin, metapectal plate transverse and clearly separate from metafurcal arm.

**Fig. 8.** Mesonotum of Chalcidoidea. A–H, Mesonotum (anterior to the left) of: A, Asaphes vulgaris (Pteromalidae, Asaphinae), dorsal view; B, Spalangia nigripes (Pteromalidae, Spalangiinae), ventral view; Monodontomerus sp. (Torymidae, Toryminae); C, ventral view; D, dorsal view; E, Eurytoma sp. (Eurytomidae, Eurytominae), ventral view; F, Tetramesa sp. (Eurytomidae, Eurytominae), ventral view; G, Chalcis sp. (Chalcididae, Chalcidinae), ventral view; Antrocephalus sp. (Chalcididae, Haltichellinae); H, ventral view; I, dorsal view; Leucospis sp. (Leucospidae); J, dorsal view; K, ventral view; L, Schizaspidea nasua (Eucharitidae, Eucharitinae), ventral view.
Propodeum highly variable in Torymiae. In *Monodontomerus* sp. medially smooth (Fig. 16E), median carina present (mc), anterior margin with posteromedially extended row of foveolae; posterior margin with short nucha (Fig. 16E: *mu*) flanked by row of foveolae extending to propodeal spiracle (psp). Propodeum in *Podagrisn* sp. with fine reticulation and distinct pair of oblique carina meeting at anterior propodeal margin and leading to posterior margin; nucha slightly developed. Propodeum in *T. bedeguaris* almost completely smooth (Fig. 16C) with inconspicuous row of foveolae along anterior margin; nucha absent.

Petiole reduced in size (T. bedeguaris and *Monodontomerus* sp.) or ventrally extended (*Podagrisn* sp.).

**EURYTMIDAE, EURYTMINAE**

*Eurytoma* sp. and *Tetramesa* sp.

Pronotum with collar large, rectangular in dorsal view, with punctuate sculpture and dense pilosity. Collum short, separated from collar by incomplete carina. Collum and lateral panel of pronotum bare and with very fine sculpture. Propectus internally with reduced propleural arms. Prosternum (Fig. 5E: s1) with straight posterior margin.

Mesonotum deeply punctuate and pilose. Mesoscutum with notaual externally complete and foveolate; corresponding internal ridge (notr) reaching transscutal articulation in *Eurytoma* sp. (Fig. 8E) but not in *Tetramesa* sp. (Fig. 8F). Axilla narrow, axillar phragma (axph) elongate (*Eurytoma* sp., Fig. 8E) or short (*Tetramesa* sp., Fig. 8F). Axillula present but indistinct, axillar sulcus weakly impressed; internally scutoscutellar ridge (ssr) laterally broadened only in *Tetramesa* sp. (Fig. 8F). Lateral panel of axilla smooth (*Tetramesa* sp.) or with irregular sculpture (*Eurytoma* sp.). Frenal arm smooth extending into sculptured mesoscutellum, frenal line absent. Prepectus broad and mediadly fused with mesepisternum. Prepectus in *Eurytoma* sp. ventrally smooth with median carina (Fig. 5E: mc); in *Tetramesa* sp. with irregular reticulation. Prepecti internally separated by mediadly fused carinae (Fig. 13C: c). Mesopleuron with mesopleural sulcus and transpleural sulcus developed; transepisternal sulcus present and foveolate (*Eurytoma* sp.) or absent (Eurytoma sp.). In *Eurytoma* sp. anteromedian portion of mesepisternum formed into epicenium, marked by enlarged smooth procoxal depression, laterally and posteriorly flanked by epicenimarin carinae (Fig. 5E: epc). Mesodiscrimerial line with mesofurcal pit (Fig. 16F: *f2p*) anterior to carina of mesotrochantinal plate and additional pit close to anterior mesepisternal margin (Fig. 5E). Mesotrochantinal plate (Fig. 16F: *mtp*) smooth with round median depression, mesocoxal foramen completely encircled by sclerotised cuticle. Mesepisternum in *Tetramesa* sp. without epicenium; mesodiscrimerial line posteriorly with mesofurcal pit, anteriorly slightly extended but not leading into additional pit; mesocoxal foramen completely surrounded by sclerotised cuticle. Mesopleuron internally smooth in both species, apart from arch-shaped acropleural ridge in *Tetramesa* sp. (Fig. 13C: acr). Mesodiscrimerial lamella (Fig. 13C: dcl) straight, not extending to anterior margin of mesepisternum.

Lateral panel of metanotum similar to Pteromalinae but covered with scattered setae. In *Tetramesa* sp. metascutellum reticulate, extending from anterior to posterior margin of metanotum. In *Eurytoma* sp. metascutellum with curved carina, extending only to anterior margin of metanotum. Metapleural dorsally not separate from propodeum and with similar punctuate sculpture. Metepisternum (Fig. 16F) ventromedially smooth and posterolaterally marked by carinae; transverse carina present but medially incomplete, submedian carina connecting transverse carina and propodeal foramen. Pair of submedian metafurcal pits developed (Fig. 16F: *f3p*), conspicuously enlarged, close to anterior metepisternal margin. Metafurcal arms (Fig. 18G, H: *f3a, f2p*) clearly separated from each other, distally clavate and slightly extended dorsally; metadiscrimerial lamella (dcl) large and present at anterior metepisternal margin; metapectal plate (mp) separate (*Tetramesa* sp., Fig. 18G) or fused with metafurcal arm (*Eurytoma* sp., Fig. 18H).

Propodeum with coarse reticulation and two irregular submedian vertical carinae, nucha absent.

Petiole reticulate, slightly (Tetramesa sp.) or distinctly elongate (*Eurytoma* sp.).

**CHALCIDIDAE, CHALCIDINAE**

*Chalcis* sp.

Pronotum densely pilose; complete transverse carina separating coarsely punctuate collar from finer sculptured collum. Propleura large, laterally pilose; prosternum with conspicuous prodiscrimerial line externally, median process absent. Profurca with large profurcal arms ventrally fused with prosternum.

Mesonotum punctuate with extensive pilosity. Notaual externally foveolate and complete, corresponding internal ridge reaching transscutal articulation (Fig. 8G: notr). Mesoscutellar–axillar complex with axilla narrow and widely separated, scutoscutellar sulcus indistinct, axillula traceable. Internally, axillar phragma very short (Fig. 8G: axph), hardly overlapping mesoscutum; scutoscutellar ridge (ssr) straight, posteromedially abutting short median ridge (Fig. 8G). Posterior margin of mesoscutellum broad and flattened, medially with slight incuration. Mesophragma with acute posterior lobes, pseudophragma large. Prepectus reduced to narrow strip, hardly visible in lateral view, not overlapping mesopleuron; internally without subdividing ridges. Mesopleuron sparsely punctuate and pilose. Acropleuron smooth with curved striae, ventrally delimited...
by distinct sulcus. Mesofemoral depression conspicuous, with highly transverse foveolae; mesopleural sulcus not clearly recognisable, transepimeral sulcus foveolate. Internally, mesopleuron with complete acropleural ridge and transepimeral sulcus slightly impressed; mesodiscriminal lamella distinctly diverging anteriorly and posteriorly.

Metascutellum with coarse reticulation and short setation; lateral panel of metanotum with large, sparsely pilose foveolae. Metapleuron enlarged in lateral view, punctuate and densely pilose, not clearly separated from propodeum; with tiny, curved process laterally to metacoxal articulation. Metepisternum medially smooth, with sharp, complete

Fig. 9. Mesonotum of Chalcidoidea. A–H, Mesonotum of: Perilampus sp. (Perilampidae, Perilampinae), A, lateral view (anterior to the left); B, ventral view (anterior to the top); C, Aprostocetus sp. (Eulophidae, Tetrastichinae); ventral view (anterior to the top); D, Blastophaga psenes (Agaonidae, Agaoninae), dorsolateral view (anterior to the left); E, Eupelmus atropurpureus  (Eupelmidae, Eupelminae), lateral view (anterior to the left); F, Ericydnus sp. (Encyrtidae, Tetracneminae), ventral view (anterior to the left); Centrodora sp. (Aphelinidae, Aphelininae); G, dorsal view (anterior to the left), H, ventral view (anterior to the top).
transverse carina; metadiscaliminal line distinct, leading from propodeal foramen to anterior metepisternal margin; metafurcal pits not observed. Internally, metafurcal arms slender (Fig. 19A: \( f_{3a} \)), mediately not connected but with \( u \)-shaped orientation, metadiscaliminal lamella \( (dcl_{3}) \) enlarged, tapering distally, reaching level of articulation point between metafurcal arm and metapleural apodeme, metapleural plate \( (mp) \) transverse, fused with metafurcal arm.

Propodeum coarsely reticulate, without nucha; propodeal spiracle enlarged, kidney-shaped, outer margin indistinct.

Petiole (Fig. 20H) cylindrical, dorsally with sparse setation, anteriorly with sharp carina and constricted to enable articulation with propodeum.

**CHALCIDIDAE, HALTICHELLINAE**

*Antrocephalus* sp.

Pronotal cuticle completely covered by regular piliferous punctures (Fig. 5F), transverse carina \( (c) \) sharp but mediately incomplete. Prosternum without median process, prodiscaliminal line indistinct. Internally, profurca with broad arms that partly fuse with prosternum, propleural arm distinct, disc-like (Fig. 6H: \( ppa \)).

Mesoscutum with notaulus foveolate and complete externally (Fig. 8I: \( not \)) and internally (Fig. 8H: \( notr \)); transscutal articulation straight and complete (Fig. 8I: \( tsa \)). Axilla narrow and widely separated (Fig. 8I: \( ax \)), lateral panel of axilla with complex cuticular folding and conspicuous setation; internally axillar phragma short (Fig. 8H: \( axph \)). Scutoscutellar sulcus indistinct, corresponding ridge curved (Fig. 8H: \( ssr \)). Axillula absent. Posterior margin of mesoscutellum between frenal arms broad and carinate, with smooth reticulation, conspicuously upcurved, mediately deeply incised, separating acute submedian processes (Fig. 8H). Prepectus narrow, laterally rounded and slightly overlapping mesopleuron, medially fused with mesepisternum. Internally, prepecti separated from mesepternum by complete furrow, without subdividing carinae (Fig. 13D). Mesopleuron mainly covered with piliferous punctures, mesofemoral depression broad and striate, transepimeral sulcus absent. Anteromedian portion of mesepternum delimited by sharp epicnemial carina into smooth epicnemium, with median longitudinal carina and procoxal depression enlarged. Mesofurcal pit slit-like, extending for entire length of mesotrochantinal plate and anteriorly interrupting carina; mesocoxal foramen completely surrounded by sclerotised cuticle. Internally, mesopleuron smooth apart from posterior part of acropleural ridge; mesodiscaliminal line extending to anterior mesepternal margin, slightly diverging anteriorly, mesofurca with horizontal plate narrow and straight (Fig. 13D: \( hp \)).

Metanotum with metascutellar arm carinate, metascutellum narrow with wave-like carina extending to posterior margin of metanotum. Metapleuron large with piliferous punctures, metapleural sulcus not clearly developed. Metepisternum ventromedially smooth and surrounded by carinae. Complete transverse carinae present, metadiscaliminal line carinate, connecting propodeal foramen with anterior metepisternal margin; mesocoxal depression circular and surrounded by carina. Metafurcal pits not observed. Metafurcal arms (Fig. 19B: \( f_{3a} \)) basally slender, apically slightly clavate, clearly separated from each other, metadiscaliminal lamella \( (dcl_{3}) \) present at anterior metepisternal margin and greatly enlarged, mediately broadened and tapering distally, reaching level of articulation point between metafurcal arm and metapleural apodeme, metapleural plate \( (mp) \) transverse, fused with metafurcal arm.

Propodeum coarsely and irregularly reticulate, distinguishable from punctate metapleuron; spiracle large, kidney-shaped with indistinct outer margin; submedian vertical carina present; nucha absent.

Petiole short, slightly reticulate, with pair of acute lateral processes.

**LEUCOSPIDAE**

*Leucospis* sp.

Pronotum enlarged, rectangular in dorsal view, densely covered with piliferous punctures. Conspicuous transverse carina present, close to posterior margin of pronotum. Pronotum laterally with distinct incurvation anterior to large mesothoracic spiracle.

Propleuron large with sharp lateral carina, lateral surface smooth with curved pattern of finer sculpture, distinguishable from reticulate ventral surface. Prosternum triangular with straight posterior margin, profurcal base externally marked by pair of submedian processes (Fig. 7A). Profurca with profurcal arms greatly enlarged and completely fused with entire breadth of prosternum; propleural arm (Fig. 7A: \( ppa \)) enlarged, flattened and rounded apically.

Mesonotum densely covered with piliferous punctures, notaulus externally absent (Fig. 8J) but internal ridge anteriorly developed (Fig. 8K: \( not \)). Transscutal articulation laterally interrupted, median part \( u \)-shaped (Fig. 8J: \( tsa \)). Preaxilla and tegula anteriorly elongate, nearly reaching posterior pronotal margin; preaxillar surface smooth with single row of short setae present at posterior margin. Axilla reduced in size, only visible under high magnification as tiny ellipsoid area at lateral mesonotal margin, lateral panel of axilla smooth with shallow impressions and dense pilosity. Axillar phragma large (Fig. 8K: \( axph \)). Scutoscutellar sulcus only laterally traceable as posterior limit of axilla. Axillula smooth and triangular in shape. Prepectus ventrally reduced, lateral panel with piliferous punctures but anteriorly smooth and flattened for accommodation of mesothoracic spiracle. Prepecti (Fig. 13E: \( pre \)) internally not completely separated from mese-
pisternum, subdivided by distinct carinae. Mesopleuron laterally with piliferous punctures, ventrally with coarse punctuation and reduced pilosity. Acropleuron externally with same sculpture as mesopleuron and separated from latter by a complete sulcus, corresponding to complete internal ridge. Mesofemoral depression short, reaching only half of the mesopleural height, conspicuously broadened and characterised by smooth cuticle. Mesopleural sulcus externally only traceable, but internally with broad corresponding ridge (Fig. 13E: mpr). Mesepisternum ventrolaterally with smooth pro-

![Fig. 10. Mesonotum and mesopectus of Chalcidoidea. A, B, Encarsia formosa (Aphelinidae, Coccophaginae): A, mesosoma, dorsal view (anterior to the top); B, mesonotum ventral view (anterior to the left). C, D, Mesonotum of: C, Clytina giraudi (Signiphoridae), ventral view (anterior to the top); D, Gonatocerus morrilli (Mymaridae), ventral view (anterior to the left). E, Cyrtogaster vulgaris (Pteromalidae, Miscogasterinae): mesopectus, ventral view (anterior to the top). F, Trichilogaster sp. (Pteromalidae, Ormocerinae): mesothorax, ventral view (anterior to the left). G–H, Enoggera reticulata (Pteromalidae, Asaphinae): G, mesosoma, lateral view (anterior to the left); H, meso- and metathorax, ventral view (anterior to the top).]
coxal depression, corresponding to conspicuous internal swelling (Fig. 13E). Mesofurcal pit tiny, situated at wave-like carina of mesothrocochinal plate; mesocranial foramen small, completely encircled by sclerotised cuticule. Mesofurca enlarged, with thickened mesofurcal bridge, mesodiscrimenal lamella anteriorly strongly diverging (Fig. 13E).

Metanotum with lateral panel resembling that of Pteromalinae, metascutellum with v-shaped carina extending to posterior margin of metanotum. Metapleuron large, triangular in lateral view, with piliferous punctures, separated from propodeum by weak indication of foveolate sulcus. Ventrally metepisternum smooth without transverse furrow from propodeum by deep furrow (Fig. 11E). Rod-like prosopinasternal apodeme internally developed (Fig. 7B: psa) with corresponding external pit anterior to fused prepectus.

Mesopleuron laterally reduced, acropleural sulcus externally weakly indicated, with complete internal ridge; mesopleural sulcus externally indistinguishable. Mesoscutellar–axillar complex subtriangular in lateral view, with smooth, broad incurvations, closely abutting prepectus (not overlapping) mesoscutum, laterally completely fused to posterior margin of metanotum. Prepectus closely abutting mesopleuron laterally, ventral portion reduced to narrow carina, completely separated from mesepisternum by deep furrow (Fig. 11E). Rod-like prosopinasternal apodeme internally developed (Fig. 7B: psa) with corresponding external pit anterior to fused prepectus.

Mesopleuron laterally reduced, acropleural sulcus externally weakly indicated, with complete internal ridge; mesopleural sulcus externally indistinguishable. Large mesofurcal pit (Fig. 11E: f3p) present between mesoaxillar foramina, mesodiscrimenal line externally only visible between mesofurcal pit and carina of mesothrocochinal plate. Mesocoxal foramen (Fig. 11E: fCX) completely enclosed by sclerotised cuticule. Mesodiscrimenal lamella anteriorly diverging, posteriorly with stem-like base; mesofurcal bridge completely fused with metapleuron and horizontal plate (Fig. 13F).

Metanotum with metascutellum and metascutellar arm narrow and carinate. Mesopleuron laterally reduced, subtriangular and coarsely reticulate. Metapleuron shallow with distinct pit within anterior end. Metepisternum with single mesofurcal pit situated closer to propodeal margin than to anterior metepisternal margin (Fig. 11E: f3p). Metafurca (Fig. 19D) differentiated into slender base and slightly broadened, dorsally curved arms (f3a), metafurca shifted posteriorly, mesodiscrimenal lamella (dcl) extends anteriorly and posteriorly of metapleuron; metapleural plate (mp) broad, widely separated from metafurca.

Propodeum with irregular, partly reduced reticulation, anterior margin with transverse row of foveolate apodeme; propodeal spiracle reduced in size.

Petiole smooth, conspicuously elongate and cylindrical in shape.

**EUCHARITIDAE, EUCHARITINAE**

*Schizaspidia nasua* (Walker, 1846)

Mesosoma anteriorly and posteriorly strongly compressed. Pronotum reduced with straight posterior margin, closely abutting (not overlapping) mesoscutum, laterally completely fused with narrow prepectus. Prosternum small with anterior margin not covered by propleura. Profurca with arms fused as profurcal bridge (Fig. 7B), bridge dorsomedially with raised septum (see discussion); propleural arm (Fig. 7B: ppa) large, rod-like, posteriorly orientated and closely abutting prepectal arms.

Mesonotum with smooth anterolateral incisure posterior to mesothrocochinal spiracle. Mesoscutellum broad, with notaulus complete and foveolate externally, corresponding internal ridge (Fig. 8L: notr) reaching transscutal articulation (tsa). Prophragma absent. Mesoscutal margin anterolaterally with smooth, broad incurvations, closely abutting prepectus and mesothrocochinal spiracles. Transscutal articulation straight and complete. Mesocoxal–axillar complex subtriangular in dorsal view, narrower than mesoscutum, dorsal surface of axillae narrow, medially abutting; axillar phragma short (Fig. 8L: asph). Foveolate scutoscutellar sulcus deeply impressed, curved, medially abutting transscutal articulation; corresponding internal ridge (Fig. 8L: ssr) straight and separated from transscutal articulation. Axillula absent. Mesoscutum posterodorsally with bifurcate process (Fig. 8L); posterior margin reflexed, anteriorly flanked by row of foveolae.

Prepectus (Fig. 13F: pre) completely fused with pronotum (not), fusion lines indiscernible externally and internally. Postspiracular apodeme fused along its entire length with pronotum. Prepectus closely abutting mesopleuron laterally, ventral portion reduced to narrow carina, completely separated from mesepisternum by deep furrow (Fig. 11E). Rod-like prosopinasternal apodeme internally developed (Fig. 7B: psa) with corresponding external pit anterior to fused prepectus.

Mesopleuron laterally reduced, acropleural sulcus externally weakly indicated, with complete internal ridge; mesopleural sulcus externally indistinguishable. Large mesofurcal pit (Fig. 11E: f3p) present between mesoaxillar foramina, mesodiscrimenal line externally only visible between mesofurcal pit and carina of mesothrocochinal plate. Mesocoxal foramen (Fig. 11E: fCX) completely enclosed by sclerotised cuticule. Mesodiscrimenal lamella anteriorly diverging, posteriorly with stem-like base; mesofurcal bridge completely fused with mesofurca and horizontal plate (Fig. 13F).

Metanotum with metascutellum and metascutellar arm narrow and carinate. Mesopleuron laterally reduced, subtriangular and coarsely reticulate. Metapleuron shallow with distinct pit within anterior end. Metepisternum with single mesofurcal pit situated closer to propodeal margin than to anterior metepisternal margin (Fig. 11E: f3p). Metafurca (Fig. 19D) differentiated into slender base and slightly broadened, dorsally curved arms (f3a), metafurca shifted posteriorly, mesodiscrimenal lamella (dcl) extends anteriorly and posteriorly of metapleuron; metapleural plate (mp) broad, widely separated from metafurca.

Propodeum with irregular, partly reduced reticulation, anterior margin with transverse row of foveolate apodeme; propodeal spiracle reduced in size.

Petiole smooth, conspicuously elongate and cylindrical in shape.

**PERILAMPIDAE, PERILAMPINAE**

*Perilampus* sp.

Pronotum disc-like, flattened, dorsally and laterally with piliferous punctures, anteriorly smooth with semicircular row of foveolae. Prosternum with acute median process. Profurca arms fused as profurcal bridge as in *S. nasua*, bridge medially with raised septum, propleural arm rod-like, longer than in *S. nasua*, closely abutting prepectus.

Mesoscutum with median lobe punctuate and shortly pilose, lateral lobe partly smooth and bare (Fig. 9A). Notaulus foveolate, reaching transscutal articulation externally (Fig. 9A: not) and internally (Fig. 9B: notr). Transscutal articulation laterally interrupted. Dorsal surface of axillae widely separated, medially punctuate, laterally smooth (Fig. 9A: ax). Scutoscutellar sulcus (Fig. 9A: sss) shifted posteriorly, reaching lateral margin of mesonotum far behind posterior wing process (wp), lateral panel of axilla (lax) scaly reticulate, limited by broad carina extending to posterior wing process, posteriorly with additional carina
delimiting small triangular area. Axillula (Fig. 9A: axl) large and triangular, smooth and bare, dorsally bordered by sharp carina, rest of mesoscutellum punctuate with short setae. Internally, scutoscutellar ridge (Fig. 9B: ssv) semicircular, shifted posteriorly relative to posterior wing process, laterally not broad; axilllar ridge absent. Axillary phragma (Fig. 9B: axph) short with irregular anterior margin. Frenal arms smooth, connected by carinate frenal line (Figs 9A, B: frl), forming posterior margin of mesoscutellum in dorsal view. Two rows of foveolae situated posteriorly to carinate frenal line, inflected under mesoscutellum (Fig. 9B). Prepectus triangular in lateral view, smooth with inner row of foveolae running parallel to outer margin, median portion of fused prepecti narrow, completely separated from mesepisternum. Prepectus (Fig. 5G: pre) fused with pronotum (no1) but not as extensively as in S. nasua: fusion lines clearly visible externally and internally, postspiracular apodeme (pspa) apically not fused with pronotum. Prepectus internally incompletely separated from mesepisternum, laterally inflected under latter. Prospinasternal apodeme distinct (Fig. 13G: psa), situated anterior to mesofurca, flanked by two minute pits. Mesopleuron sparsely punctuate, with acropleural sulcus, mesopleural sulcus and transplemerial sulcus foveolate, internally with corresponding swellings or ridges (Fig. 13G). Mesofurcal pit situated between mesocoxal foramina but closer to anterior carina than in S. nasua; mesocoxal foramen dorsally not encircled by sclerotised cuticle. Mesofurca (Fig. 13G) with discrimal lamella (dcl2) anteriorly extensively broadened and diverging, posterior base of mesofurca stem-like, laterally flanked by diverging discrimal lamella, horizontal plate (hp) wide.

Metanotum similar to Pteromalinae. Metapleuron small and triangular in lateral view, dorsally limited by foveolate sulcus. Metepisternum without transverse carina, antero-laterally with depression accommodating mesocoxa and posterolateral corner of mesopleuron. Single metafurcal pit present at anteromedian metepisternal margin. Metafurca (Fig. 19E) relatively short, u-shaped, arms (f3a) medially fused, distally slightly thickened; medadiscrimal lamella (dcl3) nearly extending to anterior margin of metepisternum; metapleural plate (mp) dorsally rounded, clearly separate from metafurca.

Propodeum with foveolate anterior margin, medially with vertical carina laterally flanked by smooth, subrectangular areas; nucha absent.

Petoile moderately enlarged with pair of lateral processes.

**EULOPHIDAE, EULOPHINAE**

*Cirrospilus coachellae* Gates, 2000

Pronotum enlarged without differentiation into collum and collar, coarsely reticulate, with scattered setae; deep sulcus extending from posterolateral margin of pronotum, just above mesothoracic spiracle, to anterior margin. Prosternum without median process. Profurcal arm slender, ventrally projecting, not fused with prosternum; propleural arm reduced in size.

Mesonotum with notalus deep and complete with long adnotalar setae, transscutal articulation deeply sinuate, axilla extended anteriorly, sublateral groove developed, two pairs of elongate setae present on mesoscutellum. Axillula small, dorsally limited by carina; axilllar ridge internally developed and separate from scutoscutellar ridge. Prophragma large with distinct lateral margin. Prepecti (Figs 11F, 13H: pre) completely separated from each other externally and internally, medially with well developed prospinasternum; prospinasternal apodeme (Fig. 13H: psa) distinct, externally corresponding to shallow pit (Fig. 11F: pps). Prepectus laterally abutting, but not overlapping mesopleuron (Fig. 11F). Mesopleuron with acropleural sulcus, mesopleural sulcus and transepimeral sulcus distinctly developed externally (Fig. 11F) and internally (Fig. 13H). Mesepisternum sparsely pilose; mesofurcal pit (Fig. 11F: f3p) anterior to indistinct, sinuate carina (c) of mesotrochantinal plate. Mesofurca (Fig. 13H) with bridge extremely narrow medially, horizontal plate conspicuously broadened all over, medadiscrimal lamella anteriorly straight, terminating far behind anterior mesepisternal margin, posterior end strongly diverging.

Metascutellum large, projecting anteriorly, with weak reticulate sculpture, extending from anterior to posterior margin of metanotum; lateral panel with scattered setae, smooth metascutellar arms and slightly indicated anterior row of foveolae. Metapleuron subtriangular in lateral view, separated from propodeum by complete sulcus. Metacoxal and propodeal foramina enclosed by soft cuticle. Metafurca with arms clearly separate, extremely narrow throughout; metapleural plate reduced, traceable only lateral to metafurcal arms and completely fused with the latter; medadiscrimal lamella not observed.

Propodeum slightly reticulate, medially with smooth stripe, only a few setae present laterally; propodeal spiracle circular, propodeal foramen anteriorly extended.

Petoile anelliform, smooth with pair of tiny lateral tubercles.

**EULOPHIDAE, ENTEDONINAE**

*Entedon ergias* Walker, 1839

Pronotum with fine reticulation. Collar reduced to narrow rim, posteriorly flanked by elongate setae, anteriorly separated from collum by carina, anterolateral corner of collar extended, forming sharp edge. Propleuron with sharp lateral carina, mediadventral part and posterolateral corner with conspicuous sculpture, prosternum with short median process. Profurcal arm with short stem, propleural arm inconspicuous.
Mesonotum with reticulate sculpture, nota
talus externally weakly impressed but reach
ing transscutal articulation; corre-
sponding internal ridge only anteriorly developed. Midlobe of mesoscutum with two pairs of elongate setae. Transscutal articulation slightly sinuate, axillae widely sepa-
rated from each other, scutocutellar sulcus medially deeply incised. Axillar sulcus deep and conspicuous with corre-
sponding internal ridge, axillula smooth. Mesoscutellum with pair of elongate setae. Prepecti large, with reticulate sculpture, posterolateral edges acute and extended. Prepecti

Fig. 11. Mesonotum and mesopectus of Chalcidoidea. A, *Thaumasura* sp. (Pteromalidae, Cleonyminae): mesothorax, lateral view (anterior to the left). B–D, *Spalangia nigripes* (Pteromalidae, Spalangiinae): B, mesopectus, anterior view; C, mesothorax, lateral view (anterior to the left); D, meso-
externally and internally delimited by carinae (Fig. 14A; c). Prepecti situated lateral to prospinasternum that is externally formed as broad fovea. Internally, prospinasternal apodeme (Fig. 14A; psa) well developed between prepecti, posteriorly orientated and close to mesofurca. Lateral mesopleuron smooth apart from reticulate mesofemoral depression and slightly sculptured lower mesepimeron; acropleural sulcus, mesopleural sulcus and transepimeral sulcus developed with corresponding internal ridges (Fig. 14A). Separation line between mesopleuron and metapleuron medially incomplete. Mesepisternum ventrally with inconspicuous reticulation, procoxal depression slightly indicated. Mesofurcal pit

Fig. 12. Mesopterus of Chalcidoidea. A, B, Ericynius sp. (Encyrtidae, Tetracneminae): A, mesopterus, dorsolateral view (anterior to the left); B, meso- and metathorax, ventral view (anterior to the left). C, Trichogramma evanescens (Trichogrammatidae), meso- and metathorax, ventral view (anterior to the top). D–H, Mesopterus of: D, Centrodora sp. (Aphelinidae, Aphelininae), dorsolateral view (anterior to the left); E, Trichilogaster sp. (Pteromalidae, Ormocerinae), anterolateral view; F, Enoggera reticulata (Pteromalidae, Asaphinae), dorsal view (anterior to the top); G, Thaumasura sp. (Pteromalidae, Cleonyminae), dorsal view (anterior to the top); H, Spalangia nigripes (Pteromalidae, Spalangiinae), dorsal view (anterior to the top).
anterior to carina of mesotrochanterinal plate, mesocoxal foramen completely encircled by sclerotised cuticle. Mesofurca (Fig. 14A) with distinct bridge, discrimenal lamella anteriorly and posteriorly distinctly broadened, not diverging laterally.

Metascutellum (Fig. 16G: mts) with wavelike carina, lateral panel of metanotum (hno₃) with broad anterior margin. Metapleuron subrectangular in lateral view. Metepisternum surrounded by conspicuous carinae, sharp transverse carina developed, connected with propodeal foramen by submedian carina. Metafurcal pits widely separated from each other, close to anterior metepisternal margin; metafurcal pits and anterolateral portion of metepisternum normally overlapped by mesopleuron. Metafurcal pits clearly separated (Fig. 19F: f₃a), laterally fused to metapetal plates (mp), metadiscrimenal lamella (dcl₃) distinct, extending to anterior metepisternal margin.

Propodeum (Fig. 16G) smooth with median carina (mc), posterior margin prolonged to nucha and anteriorly flanked by foveolate sulcus, propodeal spiralire (psp) with distinct outer margin, anterolaterally bordered by sinuate sulcus, cuticular process present posterior to spiracle.

Petiole reduced, anelliform.

**EULOPHIDAE, TETRASTICHINAE**

*Aprostocetus* sp.

Pronotum slightly reticulate and sparsely pilose. Prosternum with anterior margin exposed, without median process. Internally, profulcal arms slender, ventrally extended, not fused with prosternum (Fig. 7C), propleural arm (ppa) reduced in size.

Several mesonotal structures developed as in *C. coachellae* (Eulophinae). Mesoscutum large with deep notaular, reaching transscutal articulation externally and internally (Fig. 9C notr); notaular flanked by row of long adnotualar setae. Median mesocoscutal sulcus present, lacking internal ridge. Transscutal articulation deeply sinuate resulting in anteriorly extended, widely separated axillae. Scutocutellar sulcus externally weakly developed, internally with distinct ridge (Fig. 9C: ssr). Conspicuous cuticular folding present at axilla/axillula boundary (Fig. 16H). Longitudinal axillalar sulcus weakly impressed (Fig. 16H: axis), running parallel to deep submedian sulcus (s) (= submedian groove); axillalar suclus with corresponding internal ridge (Fig. 9C: axlr) separated from scutocutellar ridge. Mesoscutellum with two pairs of elongate setae, lateral to submedian sulci (Fig. 16H). Internally, mesoscutellum anterolaterally covered by septum (Fig. 9C), septum medially interrupted by large, anteriorly narrowing triangular opening.

Prepecti slightly reticulate, externally not clearly separate from smooth prospinasternum. Prepecti laterally without mobility but rigidly associated with mesopleuron; internally subdivided by complete carinae (Fig. 14B: c), which exceed anterior margin of mesepisternum posteriorly. Acropleuron externally not differentiated but internally marked by complete ridge (Fig. 14B: acr). Mesopetal sulcus distinct, transsepimeral sulcus posteriorly situated and originating from near mesocoxa; internally mesopetal sulcus and transsepimeral sulcus with corresponding ridges (Fig. 14B: mpr, temr). Mesofurcal pit present anterior to carina of mesotrochanterinal plate, mesocoaxal foramen dorsally not encircled by sclerotised cuticle. Mesofurca without bridge (Fig. 14B), anterolaterally projecting apodemes present, horizontal plate (hp) with same shape as in *C. coachellae*; discrimenal lamella posteriorly broad and strongly diverging, anteriorly narrow, only slightly diverging.

Metanotum with reduced foveolae on lateral panel anterior to metascutellum arms (Fig. 16H: mts), metascutellum (mts) smooth, extending from anterior to posterior margin of metanotum. Metapleuron subtriangular in lateral view, separated from propodeum by complete, postero dorsally arched sulcus. Metepisternum externally without conspicuous structure. Soft cuticle encloses enlarged metacoaxal and propodeal foramina as in *C. coachellae*, sclerotised cuticle restricted to narrow intermediate ridges (Fig. 19G). Single metafurcal pit close to anterior metepisternal margin. Metafurca (Fig. 19G) v-shaped with arms (f₃a) straight, distally only slightly thickened and medially fused at level of metepisternum, metadiscrimenal lamella (dcl₃) reduced in size, not extending to anterior metepisternal margin and posteriorly terminating far beyond propodeal foramen, metapetal plate (mp) short, inconspicuous, widely separated form metafurca.

Propodeum (Fig. 16H: pd) smooth, with median carina and large circular spiralire, propodeal foramen anteriorly extended.

Petiole broad, reduced in size.

**AGAONIDAE, AGAONINAE**

*Blastophaga pseuens* (Linnaeus, 1758)

Mesosoma characterised by smooth cuticle. Pronotum large (Fig. 9D: no.), widely overlapping mesoscutum; without transverse carina. Propleura medially separated, pro sternum large without median process. Profurca with broad arms lacking stem, propleural arm reduced.

Mesoscutum (Fig. 9D: sc) with irregular posterior margin, overlapping anterior margin of mesoscutellum (scl). Notoal (Fig. 9D: not) externally incomplete but internal ridge reaches transscutal articulation. Axilla (Fig. 9D: ax) small, widely separated, shifted to lateral mesonotal margin, scutocutellar sulcus (ss) indistinct. Internal axilllar phragma extremely short. Axillula indistinct on mesoscutellar surface, axillular sulcus only anteriorly indicated. Mesoscumellum internally with septum; septum continuous
with scutoscutellar ridge, medially with subtriangular, anteriorly pointed opening. Opening smaller than in *Aprostocetus* sp. (Eulophidae: Tetrastichinae), anteriorly not reaching scutoscutellar ridge. Posterior margin of mesoscutellum slightly incised, overlapping anterior margin of metanotum (Fig. 9D). Prepecti without conspicuous sculpture, laterally distinctly overlapping mesopleuron, medially fused with mesepistemum. Mesopleuron externally without any differentiation apart from conspicuous lateral pit (pollen pocket). Mesofurcal pit situated at level of anterior margin of mesocostral foramen, mesotrochantinal plate not distinguishable from rest of mesopleuron, without anterior carina;

![Fig. 13. Mesospectus of Chalcidoidea.](image-url)
mesocoaxal foramen not surrounded by sclerotised cuticle. Mesospectus internally with mesodiscriminal lamella reduced anterior and posterior to mesofurca.

Metanotum (Fig. 9D: no3) without differentiated metasternum; anterior margin slightly reticulate, posterior margin overlapping propodeum. Metapleural triangular in lateral view, separated from propodeum by complete sulcus. Metepisternum ventrally inconspicuous, metafurcal pits widely separated, situated just posterior to mesocoaxal foramina.

Propodeum enlarged, smooth and bare apart from lateral setae. Propodeal spiracle situated close to posterior margin within broad sulcus; sulcus covered by rows of short cuticular thorns.

Petiole broad, without sculpture.

**AGAONIDAE, OITISELLINAE**

Eujacobsonia mirabilis Grandi, 1923

Pronotum enlarged, dorsally flattened and rectangular in dorsal view; cuticle smooth, dorsomedially covered with field of fine comb-like setation, laterally flanked by few setae. Propodeum (Fig. 5H: pl1) enlarged, its medioventral margins closely abutting along most of their length, only posteriorly diverging; propleural surface mainly covered with stout setae, mixed with long, tufted setae along medioventral margin and underneath head articulation. Prosternum (Fig. 5H: s1) smooth, posteriorly rounded, almost completely covered by propleura. Profurcal arm lacking stem, propleural arm reduced.

Mesoscutum with deeply incised notaulus, reaching transsternal articulation externally and internally. Median mesoscutal sulcus only anteriorly developed, without corresponding internal ridge. Axilla small, triangular in shape, widely separated and shifted to lateral mesonotal margin, scutoscutellar sulcus present as weak cuticular impression; axillula absent. Prepecti medially narrowed, laterally rounded, overlapping mesopleuron; medially completely separated from meseptisternum in external view. Internally, prepecti not delimited by carinae, medially fused with meseptisternum. Mesopleuron with distinct acropleural sulcus, and corresponding internal ridge; mesopleural sulcus and transepimeral sulcus externally well developed with low internal swellings. Mesepimeron bare and smooth, meseptisternum ventrolaterally with stout setae (Fig. 11G). Mesofurcal pit (Fig. 11G: fp) slit-like, situated anterior to acarinate mesostrochantinal plate (mp); mesocoaxal foramen (fcx2) not completely encircled by sclerotised cuticle. Mesofurcal bridge present with distinctly elongate median process, horizontal plate wide, not tapering ventrally, mesodiscriminal straight, not extending to anterior meseptisternal margin.

Metanotum medially overlapped by extended mesosternum; lateral panel with slightly reticulate sculpture.

Metapleura subrectangular with weak sculpture. Anterior portion of metepisternum with pair of tiny metafurcal pits, normally covered by mesopleuron. Metafurcal arms widely separated from each other, straight throughout with short apical clava; metadiscriminal lamella present as short inconspicuous septum, not extending to anterior metepisternal margin; metapectal plate rounded, not fused with metafurcal arm.

Propodeum with two submedian sulci, leading from propodeal foramen to anterior margin; spiracle situated close to posterior margin within broad sulcus leading from propodeal foramen to lateral metapleura, spiracle internally with numerous sensilla.

Petiole inconspicuous, anelliform, dorsal surface with slight reticulation.

**AGAONIDAE, SYCORYCTINAE**

Philotrypesis caricae (Linnaeus, 1762)

Pronotum large, with weak reticulate sculpture, carina absent. Propleura medially rounded, with smooth cuticle and few scattered setae; proepisternum smooth, without median process, an irregular row of elongate setae present along posterior margin. Prodiscernal line situated posterior to this row, developed as deep sulcus that diverges posterolaterally and leads to distinct profurcal pits. Profurca with slightly anteriorly extended arms not fused with proepisternum; propleural arm short but not as strongly reduced as in Agaoninae and Otitesellinae.

Mesonotum with reduced sculpture (weakly reticulate) and pilosity (only few very short setae). Notaulus developed as fine sulcus, reaching transsternal articulation externally, corresponding internal ridge complete. Transsternal articulation laterally with tiny interruption. Scutoscutellar sulcus and axillular sulcus externally not clearly developed; internal scutoscutellar ridge not broadened laterally. Prepectus externally and internally completely separated from meseptisternum, medially slightly narrowed, subtriangular in lateral view. Internally, prepecti separated by complete carinae; prospinasternal apodeme large, widely separated from anterior mesepisternal margin. Mesopleuron externally with mesopleural sulcus and transepimeral sulcus well developed, upper mesepimeron smooth in contrast to reticulate lower mesepimeron. Mesopleural sulcus with distinct internal ridge, transepimeral sulcus corresponds to low swelling. Acropleural sulcus externally indistinct but internally with complete ridge. Mesodiscriminal line externally inconspicuous, mesofurcal pit situated anterior to carina of mesostrochantinal plate; mesocoaxal foramen not surrounded by sclerotised cuticle.

Metapleura subrectangular in lateral view, dorsally separated from propodeum by complete sulcus. Metepisternum laterally bordered by carina, anteriorly by membranous strip,
two tiny metafurcal pits situated close to anterior metepisternal margin. Metafurca u-shaped, arms medially fused at level of metepisternum, arms proximally slender, distally with distinct clava; metadiscrimen not extending to anterior metepisternal margin; metapectal plate large, situated anterior to metafurca and clearly separated from the latter.

Propodeum with inconspicuous reticulation, spiracle circular with distinct outer margin, situated in middle of longitudinal axis of propodeum.
Petiole reduced, broad with smooth cuticle.

Fig. 14. Mesopectus of Chalcidoidea. A–H, Mesopectus of: A, *Entedon ergias* (Eulophidae, Entedoninae), dorsolateral view (anterior to the left); B, *Aprostocetus* sp. (Eulophidae, Tetrastichinae), anterior view; C, *Eupelmus atropurpureus* ♂ (Eupelmidae, Eupelminae), dorsal view (anterior to the top); D, *Ericydnus* sp. (Encyrtidae, Tetracneminae), anterior view; E, *Trichogramma evanescens* (Trichogrammatidae), anterior view; F, *Centrodora* sp. (Aphelinidae, Aphelininae), dorsal view (anterior to the top); G, *Encarsia formosa* (Aphelinidae, Coccophaginae), anterior view; H, *Clytina giraudi* (Signiphoridae), dorsal view (anterior to the top).
**EUPELMIDAE, EUPELMINAE**

*Eupelmus atropurpureus* Dalman, 1820

Conspicuous sexual dimorphism exhibited in mesosomal morphology.

**Female**

Pronotum bell-shaped in dorsal view, posterior margin medially incised; surface weakly sculptured with a few scattered setae along dorsal and dorsolateral surfaces; median sulcus indicated posteriorly. Propodea and prosternum with scattered setae; propleural arm short, rod-like; prosternum completely divided by narrow prodiscrinal line, median process absent. Profurcal arm with broad, short stem and expanded distal part that is not fused with prosternum.

Mesonotum dorsally flattened, mesoscutum without distinct notaurs externally or internally; parapsidal line indicated on lateral lobe of mesoscutum as straight, longitudinal line of smaller meshed sculpture, extending from transscutal articulation. Transscutal articulation straight and complete, scutocutellar sulcus weakly developed; axilla large, triangular, but externally indistinct due to weak posterior border (scutocutellar sulcus); axillar phragma not observed. Axillula developed as conspicuous sublateral depression anterior to curved frenal arm, the frenal arm posteriorly delimited by irregular rows of scale-like cuticular swellings leading semicircularly to posterior apex of mesoscutellum. Internally, mesonotum with lateral margin extensively expanded, heavily modified. Scutocutellar ridge with straight sides, medially fused at angle of \( \approx 90^\circ \), proximally meeting distinct axillular ridge. Mesophragma anteriorly orientated, median axis with outer ridge, leading into posterior process that extends into propodeum. Prepectus differentiated into lateral and frontal surfaces; lateral prepectal surface reticulate, elliptical, surrounded by deep furrow and slightly overlapping mesepisternum ventrally; frontal prepectal surface continuous with median part of prepectus, the median part medially incised, v-shaped, and extending into mesepisternum; frontal prepectal surface and median portion of prepectus smooth, and completely fused with reticulate mesepisternum; internally, prepectus subdivided by various carinae. Mesopleuron with enlarged acropleuron (Fig. 11H: *acr*) comprising entire lateral portion of mesopectus; acropleuron ventrally bordered by distinct acropleural sulcus with corresponding internal ridge (Fig. 11H: *acr*). Mesofurcal pit anterior to mesotrochantinal plate; mesotrochantinal plate directed posteriorly between mesocoxae in same plane as mesopectus; mesocoaxal foramen posteriorly not completely surrounded by sclerotised cuticle, but with strip of intercoaxal membrane. Mesopesopoc with invaginated internal septum (Fig. 11H) extending from posterior end to about one third of the mesospectral length. Mesofurca (Fig. 11H: *f2*) close to posterior margin of mesopectus, apodemes tapering anteriorly but still touching medially to form slender mesofurcal bridge.

Metanotum comparatively long, anteromedially deeply incised by acute posterior mesoscutellar margin, and laterally overlapping by enlarged acropleuron; metasculletum smooth, extending from anterior to posterior metanotal margin, metasculellar arms well defined, smooth anteriorly and bordered by large, slightly reticulate lateral panel. Metapleura partly overlapped by acropleuron, the overlapped portion smooth but exposed part narrow and subrectangular, slightly reticulate, and dorsally and ventrally limited by complete sulcus. Ventral metepisternum smooth without conspicuous features, median metafurcal pit close to medi ally prolonged posterior margin of metepisternum. Metfurca u-shaped, arms straight, distally slightly clavate and medially fused at level of metepisternum; metadiscalmeral lamella not extending to anterior metepisternal margin; metapleural plate separate from metafurca. Propodeum medially short and deeply incised by enlarged, transverse propodeal foramen; dorsal surface smooth, lateral surface with slight reticulation and sparse setation; spiracle enlarged, circular with distinct outer margin. Petiole reduced, anteriorly modified with hook-like structure.

**Male**

Pronotum completely reticulate; dorsally with dense pilosity, laterally bare. Propectus as in female. Mesonotum with notaurs externally weakly developed but complete, corresponding internal ridge distinct, reaching transscutal articulation. Transscutal articulation laterally discontinuous. Axilla large and triangular; axillae externally separated, but internally scutocutellar ridge triangularly pointed; axillar phragma developed as in Pteromalinae. Axillula indistinct, sulcus only developed anteriorly; internally with distinct axillular ridge. Frenal arm (Fig. 9E: *fra*) smooth, posteroventrally flanked by small area with scaly cuticle, the area less conspicuous than in female. Prepectus without frontal surface, medially completely separated from mesepisternum externally and internally (Fig. 14C); lateral panel triangular; prepecti separated internally by complete carinae (Fig. 14C: *c*), the carinae not medially abutting, flank ing transverse prospinasternum (*psn*); prospinasternal apodeme absent. Acropleuron transverse, slightly enlarged compared to Pteromalinae, but not comprising complete lateral surface as in female; ventrally limited by distinct acropleural sulcus corresponding to complete internal ridge. Mesopleuron with mesopleural sulcus only indicated posteriorly, without internal ridge; transepineural sulcus only developed dorsally but corresponding to complete internal ridge, the ridge originating close to mesocoxa; upper mesepimeron smooth, lower mesepimeron reticulate. Mesocoaxal foramen medially separated by mesotrochantinal plate (without membrane anterior to coxa as in female), but internally with large
membranous strip between mesotrochantinal plate and metabisternum. Mesodiscriminal lamella (Fig. 14C: dcl) anteriorly straight, nearly extending to anterior mesepisternal margin; posteriorly diverging. Mesofurcal bridge broad (Fig. 14C), not as slender as in female.

Metanotum slightly different from female: metascutellum large but anterior and posterior row of foveolae weakly developed, metascutellar arm less defined. Lateral metapleuron larger than in female, triangular and slightly reticulate. Posterior portion of ventral metepisternum reduced. Metacoxal foramen enlarged, separated from propodeal foramen by narrow cuticular strips, all foramina surrounded by membrane (Fig. 19H) as in Aprostocetus sp. (Eulophidae: Tetrastichinae). Anterior metepisternum short, with reticula-

---

**Fig. 15.** Metathorax–propodeum complex of Chalcidoidea. A–H, Metathorax–propodeum complex of: A, Trichilogaster sp. (Pteromalidae, Ormocerinae), dorsal view; B, Enoggera reticulata (Pteromalidae, Asaphinae), dorsal view; Thaumasura sp. (Pteromalidae, Cleonyminae), C, dorsal view; D, ventral view; Notanisus sp. (Pteromalidae, Cleonyminae), E, lateral view; F, ventral view (anteromedian part, anterior to the top); Spalangia nigripes (Pteromalidae, Spalanginae), G, dorsal view; H, ventral view (antero to the top).
tion, median metapleural furcal pit situated approximately in the middle of median axis of metepisternum. Metafurca (Fig. 19H) similar to female with arms (f, a) slender, metadiscrimineral lamella (dcl,) short, not extending to anterior metepisternal margin, metapleural plate (mp) inconspicuous and separate from metafurcal arm.

Propodeum medially not constricted as in female, propodeal foramen smaller and rounded; median carina present on propodeal surface, plicae posteriorly indicated.

Petiole transverse, smooth, with lateral tubercle.

**ENCYRTIDAE, TETRACNEMINAE**

*Erycydnus* sp.

Pronotum with fine sculpture and dorsal pilosity; lateral panel bare, posteriorly curved. Prosternum completely divided by fine median prodiscriminal line, posterior margin with median process. Profurcal arm slender, not fused with prosternum, apical part not extensively broadened, with acute anteromedially pointed process (Fig. 7D); propleural arm (ppa) rod-like.

Mesoscutum broadened anterolaterally, attaining maximum width at articulation point with tegula, tapering posteriorly to transscutal articulation; mesoscutal surface with slight reticulation and dense pilosity. Notaulus and corresponding internal ridge (Fig. 9F: notr) only developed anteriorly. Ventral mesoscutal margin laterally with distinct, anteriorly projecting mesoscutal process (Fig. 9F: sctp). Transscutal articulation straight, laterally discontinuous. Axillae triangular, mediadly abutting; axillar phragma (Fig. 9F: apxh) enlarged, slightly curving ventrally, away from the mesoscutum. Scutocutellar sulcus and corresponding ridge (Fig. 9F: ssv) with straight sides fused at an angle of ~90°. Mesoscutellar-axillar complex slightly reticulate and densely pilose, with longer setae on mesoscutellum, of ~90°. Mesoscutellar–axillar complex slightly reticulate with slight reticulation and dense pilosity. Notaulus and cor-

**TRICHOCOGRAMMATIDAE**

*Trichogramma evanescentia* Westwood, 1833

Pronotum reduced, hardly visible in dorsal view, slightly reticulate with few setae at posteralateral margin. Propleura and prosternum bare, slightly reticulate. Prosternum with indication of complete discrimaline line. Profurcal arms fused medially above short stem, arms slender with subrectangular apical portion; propleural arm short (Fig. 7E).

Mesonotum with weak sculpture, pairs of elongate setae present on: midlobe of mesoscutum (two), lateral lobe of mesoscutum (one), dorsal surfaces of axillae (one), mesoscutellum (two). Notaulus deep, reaching transscutal articu-
Transcutal articulation (Fig. 17B: *tsa*) medially deep and sinuate, forming continuous w-shaped furrow with notaüli (*not*). Axilla (Fig. 17B: *ax*) extended anteriorly, differentiating narrow scapular flange from lateral lobe of mesoscum (situated between axilla and notaülus). Internally, axillar phragma elongate, laterally extended, inner margin with distinct ridge, lying adjacent to notaülar ridge. Axillula distinct with smooth cuticle, anteriorly marked by deep pit, dorsally not delimited by sulcus, internally delimited by distinct ridge. Mesosphragma greatly

---

enlarged, posteriorly extending into metasoma. Prepectus (Fig. 12C; pre) with distinct, rounded lateral lobe; rest of prepectus indiscernible from mesepisternum. External features of mesopleuron reduced apart from deep mesopleural sulcus (Fig. 12C; mps), corresponding to distinct internal ridge (Fig. 14E; mpr). Mesofurcal pit (Fig. 12C; fgp) enlarged, situated between mesocoxal foramina (fcx3). Mesofurca (Fig. 14E) with apodemes and bridge absent, mesodiscriminal lamella (dcl) anteriorly diverging, extending to anterior mesepisternal margin.

Metascutellum slightly reticulate, extending from anterior to posterior margin of metanotum, lateral panel with two pairs of short setae (Fig. 17B). Metapleuron triangular and narrow in lateral view, bearing row of tiny thorns at boundary with mesepimeron. Metepisternum (Fig. 12C; eps, j) well developed ventrally between enlarged metacoxal foramina (fcx3) but medially constricted; metadiscriminal line and metafurcal pits not observed. Metafurcal arms (Fig. 20B; f2a) hook-like, widely separated from each other and situated at lateral margin of metapleuron; metadiscriminal lamella and metapexial plate absent.

Propodeum (Fig. 17B; pd) broadly transverse, bare apart from two pairs of lateral setae, spiracle (psp) situated at anterior margin in lateral end of antecostal sulcus.

Petiole (Fig. 17B; pet) nearly as broad as propodeum and second metasomal tergite; developed as narrow strip, dorsally with medially interrupted row of thorns; petiole not visible in ventral view but hidden under metepisternum (Fig. 12C).

**APHELINIDAE, APHELININAE**

Centrodora sp.

Pronotum (Fig. 9G; no1) well developed in dorsal view, slightly reticulate and dorsally pilose, median sulcus (s) present. Pronotum laterally deeply incised for accommodating mesothoracic spiracles. Prosternum completely divided by prodiscriminal line, without median process. Profurcal arms basally fused along broad stem, apical part subrectangular; propleural arm short (Fig. 7F).

Mesonotum with slight reticulation, covered by few scattered setae. Mesoscutum with notafulus deep, reaching transscutal articulation externally (Fig. 9G; not) and internally (Fig. 9H; notr). Notauli medially connected by deep transscutal articulation; lateral mesoscutal lobe partly fused with axilla (Fig. 9G; ax), only dorsolaterally separated by incomplete transscutal articulation. Median mesoscutal sulcus (Fig. 9G; mms) present, posteriorly continuous with median sulcus on mesoscutellum; both sulci correspond to internal ridges (Fig. 9H). Axilla slightly extended anteriorly, not clearly defined: anterior extent incompletely marked by transscutal articulation, posterior extent not defined due to absence of scutocutellar sulcus (Fig. 9G); lateral panel of axilla smooth; internally, axillary phragma (Fig. 9H; axph) enlarged, extending anterotlaterally, not adjacent to mesoscutum. Axillula smooth dorsally without sulcus; internally, posterior border marked by distinct ridge (Fig. 9H; axr) clearly separated from arched scutocutellar ridge (ssr). Mesophragma with straight anterior margin, posteriorly extended into metasoma; pseudophragma reduced. Lateral panel of prepectus well developed, rounded, median portion of prepectus indiscernible from mesepisternum and probably completely fused with latter. Inner prepectal surface posterolaterally with large vertical prepectal ridge (Fig. 7F; prr). External mesopleural features reduced apart from mesopleural sulcus developed in posterior half of mesoscepal surface and corresponding to distinct internal ridge (Figs 12D, 14F; mpr). Internally, enlarged acropleuron with septum, anterior to mesopleural ridge (Fig. 12D). Mesofurca (Fig. 14F) with apodemes projecting anteriorly, mesofurcal bridge absent, mesodiscriminal lamella (dcl) strongly diverging anteriorly and posteriorly.

Metanotum with enlarged, slightly reticulate metascutellum (Fig. 9G: mts), separated from lateral panel by oblique sulci; lateral panel smooth with metasternal arm indiscernible. Metapleuron reduced in lateral view, triangular in shape. Anterior portion of metepisternum short, bearing single median metapleural pit. Metafurca v-shaped, with arms slender, medially fused; metafurcal base only anteriorly and posteriorly connected with metepisternum (Fig. 20C); metadiscriminal lamella reduced, metapexial plate absent.

Propodeum (Fig. 9G: pd) enlarged without pilosity, dorsally smooth, laterally slightly reticulate. Spiracle circular, close to anterior propodeal margin (Fig. 9G).

Petiole narrower than propodeum but nearly as broad as second metasomal tergite, dorsolaterally covered by tiny thorns.

**APHELINIDAE, COCCOPHAGINAE**

Encarsia formosa Gahan, 1924

Pronotum dorsally reduced, similarly shaped as in Trichogramma evanescentis. Propectal structures very close to Centrodora sp.

Mesonotum with deep reticulate sculpture apart from weaker sculptured lateral lobes of mesoscutum (Fig. 10A). Mid lobe of mesoscutum with four irregular rows of long setae, lateral lobe with three setae (Fig. 10A). Notaulus and transscutal articulation developed as in T. evanescentis (Trichogrammatidae) (Figs 10A, B). Axilla (Fig. 10A: ax) extended anteriorly, differentiating scapular flange (scf) from lateral lobe of mesoscutum; internally, axillar phragma (Fig. 10B: axph) adjacent to mesoscutum, anterior margin notched. Scutocutellar sulcus (Fig. 10A: sss) externally marked by line of finely striate cuticle; internally, with corresponding, arched ridge (Fig. 10B: ssr). Axillula externally
and internally not defined. Mesophragma (Fig. 10B: \( ph_3 \)) enlarged, extending far into metasoma, anterior margin straight, pseudophragma absent. Prepectus laterally rounded, clearly separated from lateral mesopleuron but medially with complete fusion to mesepisternum, making its posterior border indiscernible in external view; lateral separation line internally marked by carina (Fig. 14G: c). Mesopleuron lacking conspicuous external features. Mesofurcal pit close to anterior, carinate margin of mesotrochantinal plate. Mesopleural sulcus externally absent, but its position internally indicated by ridge (Fig. 14G: mpr). Acropleuron externally indiscernible, internally well defined by acropleural ridge (Fig. 14G: acr) and enlarged as in Centrodora sp. but septum only posteriorly indicated. Mesofurca (Fig. 14G).

Fig. 17. Metathorax-propodeum complex of Chalcidoidea. A–B, Posterior mesosoma, dorsal view (anterior to the top) of: A, Ericydnus sp. (Encyrtidae, Tetracneminae); B, Trichogramma evanescens (Trichogrammatidae). C–H, metafurca, anterior view of: C, Panstenon oxylus (Pteromalidae, Panstenoninae); D, Trichilogaster sp. (Pteromalidae, Ormocerinae); E, Enoggera reticulata (Pteromalidae, Asaphinae); F, Asaphes vulgaris (Pteromalidae, Asaphinae); G, Notanisus sp. (Pteromalidae, Cleonyminae); H, Thaumasura sp. (Pteromalidae, Cleonyminae).
with apodemes and horizontal plate absent, arms \( f_{2a} \) posteromedially curved, mesosdiscrimenal lamella \( dcl_{2} \) strongly diverging anteriorly, nearly reaching prepectal carina laterally.

Metanotum (Fig. 10A: \( no_{3} \)) fused with propodeum \( (pd) \); two pairs of reduced setae present on lateral panel. Metapleuron narrow and triangular in lateral view, separated from propodeum by complete sulcus. Metafurcal arms (Fig. 14G: \( f_{3a} \)) slender as in \textit{Centrodora} sp., medially just separated, metadiscrimenal lamella and metapectal plate absent.

Propodeum (Fig. 10A: \( pd \)) reduced to short strip, medially constricted; cuticle smooth apart from weakly sculptured lateral area, latter bearing two pairs of setae.

Petiole (Fig. 10A) broadly transverse, only slightly constricted relative to propodeum and metasoma, dorsally with inconspicuous median sulcus.

---

**Fig. 18.** Metafurca of Chalcidoidea. \( A-H \), Metafurca, anterior view of: \( A \), \textit{Spalangia nigripes} (Pteromalidae, Spalangiinae); \( B \), \textit{Ormyrus} sp. (Ormyridae); \( C \), \textit{Megastigmus dorsalis} (Torymidae, Megastigminae); \( D \), \textit{Podagrion} sp. (Torymidae, Toryminae); \( E \), \textit{Monodontomerus} sp. (Torymidae, Toryminae); \( F \), \textit{Torymus bedeguaris} (Torymidae, Toryminae); \( G \), \textit{Tetramesa} sp. (Eurytomidae, Eurytominae); \( H \), \textit{Eurytoma} sp. (Eurytomidae, Eurytominae).
SIGNIPHORIDAE

*Clytina giraudi* Erdös, 1957

Pronotum (Fig. 6A: *no*.) dorsoventrally flattened and greatly enlarged, its median length surpassing combined length of meso- and metathorax. Pronotal surface weakly sculptured, dorsally with scattered setae (Fig. 6A). Pronotum dorso-laterally incised for accommodating mesothoracic spiracle. Propleura and prosternum smooth, latter with acute median extension (Fig. 7G). Articulation point between profurca and propleuron situated close to posterior corner of propleuron, profurca short with arms thickened throughout, propleural arm short (Fig. 7G).

Mesonotum reduced in size, transscutal articulation (Fig. 6A: *tsa*) continuous and slightly curved posteriorly. Mesoscutum (Fig. 6A: *sc*) with weak sculpture, notaulus

![Fig. 19. Metafurca of Chalcidoidea. A–H, Metafurca, anterior view of: A, *Chalcis* sp. (Chalcididae, Chalcidinae); B, *Antrocepalus* sp. (Chalcididae, Haltichellinae); C, *Leucospis* sp. (Leucospidae); D, *Schizaspis nasua* (Eucharitidae, Eucharitinae); E, *Perilampus* sp. (Perilampidae, Perilampinae); F, *Entedon ergias* (Eulophidae, Entedoninae); G, *Aprostoeetus* sp. (Eulophidae, Tetrastichinae); H, *Eupelmus atropurpureus* δ (Eupelmidae, Eupelminae).](image-url)
absent; internal notaular ridge (Fig. 10C: *notr*) developed only anteriorly, lateral to prothoragmal articulation, hardly exceeding mesoscutal margin. Dorsal surface of axilla and scutoscutellar sulcus externally absent (Fig. 6A), lateral panel of axilla smooth with short seta. Axillar phragma (Fig. 10C: *axph*) slightly elongate, and (as in *Centrodora* sp.) extended anterolaterally, not adjacent to mesoscutum, inner margin with distinct carina. Position of axillula might be indicated by smooth pit, posterior to lateral panel of axilla. Mesoscutellar–axillar complex internally covered by septum with narrow incision medially; septum anterolaterally continuous with inner margin of axillar phragma (Fig. 10C).

---

Fig. 20. Metafurca and petiole of Chalcidoidea. *A–D*, Metafurca of: *A*, *Ercydus* sp. (Encyrtidae, Tetracneminae), anterior view; *B*, *Trichogramma* evanescens (Trichogrammatidae), lateral part, anterior view; *C*, *Centrodora* sp. (Aphelinidae, Aphelininae), median part, posterior view; *D*, *Gonatocerus* morrilli (Mymaridae), anterior view. *E–H*, Petiole of: *E*, *Panstenon* oxylus (Pteromalidae, Panstennoninae), ventrolateral view; *F*, *Asaphes* vulgaris (Pteromalidae, Asaphinae), lateral view; *G*, *Enoggera* reticulata (Pteromalidae, Asaphinae), ventral view; *H*, *Chalcis* sp. (Chalcididae, Chalcidinae), lateral view.
Mesophagma greatly extended (its median length surpassing median length of whole mesosoma), extending far into metasoma. Prepectus laterally well developed, rounded, overlapping mesopleuron, ventromedially fused with mesopleuron; lateral separation line internally marked by carina (Fig. 14H: c). Mesopleuron externally without conspicuous structures. Mesofurca (Fig. 14H) without apodemes or bridge, arms (f3a) projecting laterally, mesodiscriminal lamella (dcl) distinctly diverging anteriorly nearly reaching lateral prepectal carina, and also diverging posteriorly. Metanotum similar to Centrodora sp., with large, weakly sculptured metasclerite (Fig. 6A: mts) separated by oblique sulci from lateral panel of metanotum, latter smooth with two short setae. Metapleuron triangular in lateral view with reticulate sculpture, tiny metapleural pit present at posterior metapleural margin, close to metacoxal foramen. Separation line between metapleuron and propodeum indistinct, probably indicated by shallow sulcus leading from metapleural pit to anterior metapleural margin. Metepisternum without conspicuous structures, pair of tiny metafurcal pits situated far from anterior metepisternal margin, close to middle of its longitudinal axis, pits widely separated from each other. Pits lead internally to slender, laterally curved metafurcal arms; mesodiscriminal lamella and metapleural plate absent.

Oblique metanotal sulci posteriorly continuous with pair of propodeal sulci; these join close to posterior margin of propodeum, separating median triangular, weakly sculptured area from rest of propodeum (Fig. 6A). Posterior margin of propodeum extended, reaching semicircularly above metasoma; propodeal spiracle (Fig. 6A: psp) distinct, circular, situated close to anterolateral propodeal margin. Propodeum laterally and posteriorly bordered by second metasomal tergite (Fig. 6A: mt2), posterolaterally flanked by petiole.

Petiole (Fig. 6A: pet) dorsally reduced to pair of rounded, medially clearly separate lobes, ventral portion of petiole indiscernible.

**MYMARIDAE**

*Gonatocerus morrilli* (Howard, 1908)

Pronotum (Fig. 6B) with weak, indistinct reticulation, dorsal surface with two pairs of short setae anteriorly and two pairs of elongate setae posteriorly, complete median longitudinal sulcus present. Mesothoracic spiracles apparently completely surrounded by pronotal cuticle in external view. Propectal surface smooth and bare, proepisternum with trace of complete longitudinal discremmal line bearing distinct round pit centrally. Profurcal arms separated, with short broad bases, gradually thickened apically (Fig. 7H); propleural arm (Fig. 7H: ppa) short, upcurved.

Mesonotum as weakly reticulate as pronotum. Notaulus complete externally, developed as lines anteriorly weaker impressed into cuticle than posteriorly; internal correspond-

ing ridge complete. One pair of large adnotaular setae developed. Mesoscotellar–axillar complex enlarged, longer than mesoscutum. Axilla externally not defined due to absence of scutocotellar sulcus. Internally, axillar phagma adjacent to mesoscutum. Scutocotellar ridge arched posteriorly, anteromedially with short septum penetrated by oval fenestrum (Fig. 10D). Axillula indistinct, indicated by smooth area posterior to smooth lateral panel of axilla and posteriorly delimited by carina; distinct axillular pit present at lateral mesoscotellar margin, just posterior to carina of lateral panel of axilla. Frenal arm indiscernible, frenal line absent. Mesophagma (Fig. 20D: ph2) posteriorly greatly extended, pseudophagma (pph) developed. Prepecti medially fused, forming broad strip that is posteromedially fused with mesepisternum, median rounded fovea present. Lateral part of prepectus not extended posteriorly, without mobility relative to mesopleuron and not overlapping the latter. Lateral mesopleuron lacking distinct external features apart from smooth femoral depression ventrally and anteriorly marked by faint sulci, and slightly indicated transepimeral sulcus. Mesofurcal pit situated closer to centre of mesepisternum than to posterior margin; carina of mesotrochantinal plate medially interrupted at mesofurcal pit by broad mesosclerotic line. Mesocoal foramen not surrounded by sclerotic cuticle. Mesofurca with apodemes absent, mesodiscriminal lamella anteriorly straight, not extending to anterior margin of mesepisternum, laterally diverging posterior to stem-like mesofurcal base.

Metanotum smooth with large ellipsoid metasclerite; pair of triangular, posteriorly projecting areas situated lateral to metasclerite. Metapleuron large and rounded in lateral view, dorsally delimited by foveolate sulcus. Ventral metepisternum subdivided by incomplete transverse carina. Anterior metepisternum laterally flanked by carina, with pair of tiny metafurcal pits close to anterior metepisternal margin; posterior part with median carina between metacoxal foramina. Metafurcal arms (Fig. 20D: f3a) erect, slender, only slightly thickened apically, laterally fused with metapleural plate (mp), medially connected by raised septum; mesodiscriminal lamella not present at anterior metepisternal margin. Propodeum elongate, with submedian carina; spiracle small, slightly ellipsoid, in distinct oval groove with smooth cuticle and position close to anterior propodeal margin. Small seta present at lateral margin close to median length of propodeum.

Petiole elongate, cylindrical, smooth, laterally with irregular striae and ventrally with distinct median longitudinal sulcus.

**Results of cladistic analyses**

*Equal weighting*

The analysis yielded nine minimal length trees with 952 steps, $CI = 0.221$, $RI = 0.501$. The strict consensus tree (Fig. 21) retrieved Mymarommatidae + Chalcidoidea as
monophyletic but with *Palaeomymar* (Mymarommatidae) nested deeply within Chalcidoidea. First to branch off within Chalcidoidea was *Spalangia* (Pteromalidae: Spalangiinae), followed by Eurytomidae (Eurytominae) and Chalcididae (Chalcidinae, Halithellinae), each forming a monophylum. Eucharitidae and Perilampididae came out as sister-groups. Of the families that were represented by more than one species, only Chalcididae, Eurytomidae, Eulophidae and Agaonidae were retrieved as monophyletic. Toryminae was also retrieved as a monophyletic group but with Megastigminae (Torymidae) basal to it and several other chalcidoid taxa. Pteromalidae was demonstrably not monophyletic with the representatives of Spalangiinae and Cleonyminae isolated from a clade comprising Ormocerinae, Asaphinae, Misco-gasterinae, Pteromalinae, and Panstenoninae. Within this clade, Asaphinae was monophyletic whereas Pteromalinae was paraphyletic with respect to Misco-gasterina and Panstenoninae. *Trichogramma* (Trichogrammatidae) formed

![Phylogenetic relationships of Chalcidoidea (equal weighting analysis).](image-url)

**Fig. 21.** Phylogenetic relationships of Chalcidoidea (equal weighting analysis). Strict consensus of nine equally parsimonious trees with a length of 952 steps, produced by unordered analysis in PAUP. Trees were rooted on *Megischus*. Only Bremer support values >1 are shown.
the sister-group of *Centrodora* (Aphelinidae: Aphelininae),
both clustered in an unresolved trichotomy with *Encarsia*
(Aphelinidae: Coccophaginiae), and a clade formed by
Signiphoridae, Mymaridae, and Mymarommatidae. Female
*Eupelmus* (Eupelmidae) and *Ericydus* (Encyrtidae) were
retrieved as sister-groups.

The same analysis with male *Eupelmus* (Eupelmidae)
resulted in 37 equally parsimonious trees of length 954 steps
and a largely unresolved strict consensus tree (not figured).

**Implied weighting**

The analysis under implied weights with \( k = 4 \) resulted in one
tree (Goloboff fit \(-86,787\)). The topology of this tree was
similar to the equal weights analysis (Fig. 22). The basalmost
clades were again *Spalangia*, Eurytomidae, Chalcididae, and
Leucospidae, but the latter three families now formed a
monophylum. Cleonyminae were not confirmed but turned
out paraphyletic with respect to the remaining Chalcidoidea
plus *Palaeomyrmex*. Torymidae as a whole were retrieved
with Toryminae being paraphyletic to *Megastigmus* (*Mega-
stigmata*). Within Pteromalidae only the representatives of
Panstenoninae, Pteromalinae and Miscogasterinae formed a
monophyletic group, in which Pteromalinae was paraphyletic with respect to Miscogasterinae. Aphelinidae was
retrieved as paraphyletic with respect to *Trichogramma*
(Trichogrammatidae).

The implied weight analysis (\( k = 4 \)) with male *Eupelmus*
(Eupelmidae) yielded one tree (Goloboff fit \(-83,778\))
\( (k = 4) \). The male of *Eupelmus* came out as sister-group
of Eulophidae and was isolated from *Ericydus* (Encyrtidae)
(Fig. 23).

**Discussion**

Below we will discuss the morphological findings of this
study with reference to the cladograms in Figs 21–23 and to
recent concepts of chalcidoid relationships as reviewed in
Gibson et al. (1999).

**Morphology**

**Pronotum**

The pronotum in Chalcidoidea is highly variable. A well
developed transnotal sulcus, lying close to the anterior pro-
notal margin, is probably plesiomorphic for the Hymeno-
ptera (Vilhelmsen 2000a). We found an anterior sulcus only
in those Chalcidoidea that were placed basally (i.e. *Spalangia nigripes*, *Schizaspida nasua*). However, it can be
problematic to decide whether a pronotum has a distinct
transnotal sulcus or just an upcurved and slightly constricted
anterior pronotal margin.

In many Chalcidoidea there is a separation of the pro-
notum into a posterior collar and an anterior collum (= neck).
This character has diagnostic relevance for several chalci-
doid families (e.g. Pteromalidae; Graham 1969). The separa-
tion line between collum and collar is often indicated by a
slightly or distinctly developed carina (e.g. Pteromalinae,
Miscogasterinae) or a sulcus (e.g. Asaphinae, Spalanginae).

The slanted lateral sulcus on the pronotum of *Spalangia*
(Fig. 5A: \( s \)) is unique within Chalcidoidea and constitutes
a putative synapomorphy of the subfamily. In Chalcididae
there is considerable variation in the development of the sepa-
ration line between collum and collar. Delvare and Bouček
(1992) defined seven different character states for the pro-
notal carina and postulated that a collar that is only laterally
delimited by a distinct carina is plesiomorphic for Chalcididae.
Bouček (1988a) regarded the formation of carinae as secondarily derived within Eurytomidae. For the
Chalcidoidea, the acquisition of a pronotal carina was prob-
ably not irreversible and several groups might have under-
gone secondary loss correlated with miniaturisation (e.g.
Trichogrammatidae, Aphelinidae).

*Spalangia nigripes* is the only chalcidoid species exam-
ined with a distinct internal transverse ridge close to the pos-
terior margin of the pronotum (Fig. 5C). Presumably this
ridge is the internal indication of the foveolate sulcus
(= punctuate cross line) that is characteristic of many
*Spalangia* spp. (Bouček 1963). This sulcus is situated in
exactly the same position as the internal ridge, but is absent
in other *Spalangia* spp., including *S. nigripes* (Fig. 5B). The
occurrence of the internal ridge in the latter species suggests
that this structure is present in all *Spalangia* spp., and a puta-
tive autapomorphy of the genus.

**Propectus**

The external morphology of the propectus is relatively
uniform within Chalcidoidea. In most species the medio-
ventral margins of the propleura abut posterior to the head
articulation and diverge posterolaterally, exposing a
diamond-shaped prosternum (Fig. 2B: \( s \)). In most other
Hymenoptera (apart from Xyeloidea and Tenthredinoidea;
Vilhelmsen 2000a), the medioventral margins abut for
almost their entire length and cover the anteroventral part of
the prosternum, if developed. This condition is probably
plesiomorphic for Apocrita whereas the condition described
for most Chalcidoidea is a putative autapomorphy. Only very
few non-chalcoid Apocrita have an exposed, diamond-
shaped prosternum (e.g. *Ycaploca evansi* Nagy, 1975
[Scolebythidae]; Vilhelmsen unpublished data) and must
have evolved it independently from Chalcidoidea. In
*Palaeomyrmex anomalum* (Mymarommatidae) the propleura
and prosternum are extensively fused, obscuring the bound-
aries between them (Vilhelmsen and Krogmann 2006). In
*Spalangia* the propleura (Fig. 5D: \( pl \)) strongly resemble the
condition hypothesised as plesiomorphic for Apocrita, and
the prosternum is reduced in size, resembling that of
*Monomachus* (Proctotrupoidae) (Vilhelmsen unpublished
data). Although *Spalangia* comes out basal in our analyses
many internal propectal characters (prosternum, profurca,
propleural arms) are conspicuously modified emphasising the highly apomorphic state of Spalangini (Krogmann 2005). It is therefore possible that the external configuration of the propectus is due to secondary modification. There are other Chalcidoidea (e.g. Agaonidae: Otitessellinae) which have the propodeum enlarged, covering most of the prosternum (Fig. 5H), but in these cases the propectum is well developed and the medioventral margins of the propodeum are not as closely abutting as in the outgroup taxa.

The propodeal arms are attachment sites for pronotal muscles and their presence is probably plesiomorphic for the Chalcidoidea because they are also present in most other Hymenoptera (Vilhelmsen 2000a), including Mymarommatidae. In Palaeomymar anomalous, they are fused with the profurcal arms, a possible autapomorphy for mymarommatids (Vilhelmsen and Krogmann 2006). The propodeal arms are highly variable within Chalcidoidea and their reduction is independent of body size. The arms can be well developed in small individuals (e.g. Mymaridae) but reduced in large ones (e.g. Eurytomidae). In Chalcididae and Leucospidae the propodeal arms (Figs 6H, 7A: ppa) are stout and rounded apically; this might be synapomorphic. In Pteromalinae the propodeal arms (Fig. 2D: ppa) are always conspicuously elongate and often broadened. This is probably derived within Chalcidoidea (Figs 21, 22).

The profurcal arms are clearly separate in nearly all Chalcidoidea and arise from two separate profurcal pits (Fig. 2C: f1p), whereas in ‘Symphyta’, the profurcal arms arise from a single propodeal pit (Vilhelmsen 2000a). In Chalcidoidea the profurcal arm is often differentiated into a narrow basal stem and an expanded apical part. The arm can be slightly broadened (most chalcidoid groups, Fig. 7D) or abruptly broadened so as to resemble a rectangular shovel (Trichogrammatidae, Aphelinidae, Figs 7E, F). In a few groups the entire arm is broadened, the stem being nearly absent (Fig. 7H). Only in Aphelelinidae and Trichogrammatidae are the propodeal arms fused above the level of the propectum so as to have a common stem (Figs 7E, F: f1), which possibly represents a synapomorphy. The propurca of Palaeomymar anomalous (Mymarommatidae) is also y-shaped with a single base (Vilhelmsen and Krogmann 2006), but in contrast to Trichogrammatidae and Aphelinidae it bears a distinct slit-like propurcal pit and its arms are slender. It is therefore possible that the observed similarities with Trichogrammatidae and Aphelinidae are homoplasious.

The apical portions of the profurcal arms are completely free in some chalcidoids (Fig. 6G) or even bear ventral processes (Figs 6D, E) whereas they are often at least partly fused to the propectum along their anteroventral margins (Fig. 2E). In Chalcididae the profurca is basally broad and the arms are extensively fused to the propectum (Fig. 6H). In Leucospidae the arms are completely fused to the propectum along the whole width of the propectum (Fig. 7A). A complete fusion between the profurca and propectum, major differences in the articulation between the profurca and propodeum, the size and position of the profurcal pits, and the extent of the dorsal surface of the propectum (Fig. 6F) are all putative autapomorphies of Spalangini. The posteriorly placed articulation point between the profurca and propodeum was otherwise found only in Clytina (Signiphoridae, Fig. 7G) and this state could be correlated with the presence of a prognathous head, which is also characteristic of Spalangini.

The profurcal bridge is present in various families of ‘Symphyta’ (Xiphydriidae, Orussidae) and Apocrita (Ibalidae, Megalyridae, Trigonidae, Apidae, Formicidae) (Snodgrass 1942; Markl 1966; Ronquist and Nordlander 1989; Vilhelmsen 2000a). Ronquist and Nordlander (1989) suggested that the profurcal bridge evolved multiple times within Hymenoptera, whereas the analyses of Vilhelmsen (2000a) revealed independent instances of secondary loss within Apocrita as more parsimonious. We observed the profurcal bridge only in Perilampidae and Eucharitidae. Here, the profurcal arms are extensively fused and have an anterior projection along the line of fusion (Fig. 7B: a). This projection is probably formed by a secondary fusion of the profurcal apodemes and adjacent tendons, which are present on the profurcal arms in most Chalcidoidea (Fig. 7D: a) and many ‘Symphyta’ (Vilhelmsen 2000a) and Apocrita (Vilhelmsen unpublished data). They serve as attachment sites for the profurco-laterocervical muscles (apodeme a6, tendon t6 in Vilhelmsen 2000a). Consequently, the profurcal bridge is most likely an apomorphic character state and not a ground plan feature of Chalcidoidea. The sister-group relationship between Eucharitidae and Perilampidae is already well supported (Heraty and Darling 1984; Darling 1988; Gibson et al. 1999) and retrieved by our analyses (Figs 21, 22); the profurcal bridge is an additional putative synapomorphy.

**Mesonotum**

Complete notaular are generally regarded as being plesiomorphic within Chalcidoidea. This assessment only partly reflects the actual development of the notaular in Chalcidoidea. We found at least partially developed internal notaular ridges in all macropterus Chalcidoidea, even in those species lacking any external indications of notaular (Clytina giraudi, Fig. 10C; Leucospis sp., Fig. 8K). Externally complete notaular can occur together with incomplete internal ridges and vice versa. The external indications of notaular are variable and can either be punctate (Fig. 1C: not), foveolate (Fig. 5B) or marked by deep sulci (Fig. 10A). It seems likely that complete internal notaular ridges are a ground plan feature of Chalcidoidea because they are present in those taxa that appear basal in our analyses and also in Mymaridae, which is indicated as sister-group to all other Chalcidoidea (Gibson et al. 1999). However, it is obvious that partial or total reduction of the notaular ridges occurred numerous times within the superfamily. We found the
highest degree of reduction in Leucospidae, Encyrtidae and Signiphoridae, where the ridges do not extend beyond the anterior half on the inside of the mesoscutum. A complete reduction of notaular ridges is characteristic of *Palaeomymar anomalum* (Mymarommatidae) (Vilhelmsen and Krogmann 2006).

A longitudinal median mesoscutal sulcus with a corresponding internal ridge was inferred to be the ground plan state of Hymenoptera (Gibson 1985) and is also known from fossils (Rasnitsyn 1980). In Apocrita this feature was previously only reported from Stephanidae, Megalyridae, and Ceraphronoidea; other apocritan groups (Cynipoidea, Chalcidoidea, Proctotrupoidea, Aculeata) were reported as having the median mesoscutal sulcus developed only externally (Gibson 1985). However, a percurrent (= with corresponding internal ridge) mesoscutal sulcus is also present in *Centrodora* sp. (Figs 9G, H: mms, msr), but this condition is probably secondary.

The transscutal articulation is present in Xiphydriidae, Orussidae and in most Apocrita (Gibson 1985). In Chalcidoidea, Outgroups

---

**Fig. 22.** Phylogenetic relationships of Chalcidoidea (implied weighting analysis). Single tree produced by unordered analysis in PAUP with $\kappa = 4$. Goloboff fit = -86,787. The tree was rooted on *Megischus*. 
In Chalcidoidea there is variation concerning its depth and completeness; Heraty (2002) mentions three eucharitid genera which lost the transscutal articulation entirely. In most Chalcidoidea the transscutal articulation is slightly interrupted at the level of the axillae (Fig. 2A) whereas representatives of Aphelinidae and Trichogrammatidae have the transscutal articulation developed only medially (Figs 9G, 10A: tsa). A continuous transscutal articulation that is deepened throughout was only observed in Pteromalidae (Asaphinae) (Fig. 8A: tsa), Chalcididae (Fig. 8I), Eucharitidae, and Signiphoridae (Fig. 6A). The transscutal articulation is interrupted laterally in the basalmost taxa displaying this feature: Xiphydriidae, Orussidae, and Stephanidae (Gibson 1985, Vilhelmsen unpublished data). A continuous transscutal articulation might have evolved independently multiple times within Chalcidoidea and Hymenoptera. It can be found in many apocritan taxa, including Mymarommatidae (Vilhelmsen and Krogmann 2006).

Fig. 23. Topological changes resulting from sexual dimorphism in Eupelminidae (Eupelminae). Single tree produced by unordered analysis in PAUP after implied weighting with \( k = 4 \) (same analysis as in Fig. 22 but with male characters of Eupelmus). Goloboff fit –83,778. The tree was rooted on Megischus.
The dorsal surface of the axillae can be distinguished from the mesoscutellar surface only in those taxa that possess a distinct scutoscutellar suture. Gibson (1985) suggested that large, medially abutting axillae are a ground plan feature of Apocrita and that size reduction of the axillae occurred several times. The same is apparently true for Chalcidoidea: axillae that resemble the proposed plesiomorphic condition were found within Pteromalidae (e.g. Asaphinae, Cleonyminae, Spalangiinae), Torymidae, Eupelmidae, Encyrtidae whereas a tendency for a separation between the axillae was observed in other Pteromalidae (Pteromalinae, Panstenoninae, Mischogasterinae), in Eurytomidae, and more significantly in Chalcidoidea and Leucospidae. In the latter group the axillae are extremely reduced and displaced to the uttermost lateral margin of the mesonotum. Another putatively secondary development is the condition observed in Eulophidae (Eulophinae, Tetrastichinae), Aphelinidae (Fig. 10A) and Trichogrammatidae (Fig. 17B) where the axillae are separated and clearly extended anteriorly. In Clytina giraudi (Signiphoridae) and Palaeoomymar anomalum (Mymarommatidae) the axillae are reduced externally.

The presence of axillary phragmata accommodating the origins of the mesotergal–trochanteral muscles is a putative synapomorphy of Mymarommatidae and Chalcidoidea (Gibson 1986a). In Chalcidoidea, these phragmata are flat, broad structures that are medially clearly separated and usually adjacent to the inside of the mesoscutum (Fig. 2F: axph). This condition is inferred to be the ground plan state for the Chalcidoidea in our analyses and was apparently modified in those Encyrtidae, Aphelinidae, and Signiphoridae that have the axillary phragmata displaced laterally and at least partly projecting away from the mesoscutum (Figs 9F, H, 10C: axph). Interestingly, this condition is also present in Rotoitidae (Fig. 21 in Gibson and Huber 2000), which are generally regarded as being basal within Chalcidoidea. In female Eupelmminae the axillary phragmata seem to be secondarily lost and the mesotergal–trochanteral muscles now arise from the anterocentral angle of the lateral axillar surfaces (Gibson 1986b). In Palaeoomymar anomalum (Mymarommatidae) the axillary phragmata are slender, cylindrical rods that are connected medially and project away from the mesoscutum into the lumen of the mesosoma (Vilhelmsen and Krogmann 2006); similar structures, absent from the Chalcidoidea and all other Hymenoptera, are present on the prothorax of P. anomalum and might be serial homologues of the axillary phragmata (Vilhelmsen and Krogmann 2006). This might indicate that the axillary phragmata have evolved independently in Mymarommatoidea and Chalcidoidea. On the other hand, position and function of the axillary phragmata strongly indicate homology (Gibson 1999) and support a sister-group relationship between the two superfamilies. Although it is uncertain which configuration of the axillary phragmata is the most plesiomorphic, the unusual shape of the axillary phragmata in Palaeoomymar and their median fusion probably represent a highly derived condition and may be correlated with the reduction of the axilla.

The scutoscutellar suture is reduced in a few chalcidoid taxa but always indicated internally by a distinct ridge. This ridge is also present in all outgroup taxa and is probably a ground plan feature of the Apocrita. In Mymaridae, Eulophidae (Tetrastichinae), Agaonidae (Agaoninae), and Signiphoridae we observed the presence of a septum originating from the scutoscutellar ridge and spanning the mesoscutellum internally (Figs 9C, 10C, D). A similar condition is present in Mymarommatidae (Vilhelmsen and Krogmann 2006) and Maamingiidae (Vilhelmsen unpublished data).

The median portion of the scutoscutellar suture is deeply impressed in Asaphinae (Fig. 8A: sss) and (though less conspicuous) in other chalcidoid groups (Spalangiinae, Eurytominae, Entedoninae). According to Gibson and Huber (2000), this feature is also present in other apocritan taxa and was termed the anterior scutellar pit (Masner 1991), scutellar sulcus (Wharton et al. 1997) or scutellar furrow (Ronquist and Nordlander 1989). Gibson and Huber (2000) found this condition in Mymaridae (Australomymar) and Rotoitidae (Chiloec). The depth of the scutoscutellar suture is difficult to define and the median portion may appear to be more distinct if the lateral portion is absent or incomplete. We therefore scored the external appearance of the scutoscutellar suture as two separate characters (median and lateral portion of scutoscutellar suture).

In Perilampus sp. the scutoscutellar suture (Fig. 9A: sss) is shifted posterolaterally and reaches the lateral mesonotal margin far behind the posterior wing process. The lateral panel of the axilla (Fig. 9A: lax) is therefore narrower than the dorsal surface (ax). Furthermore, it is posteriorly adjacent to an additional, transverse carina that delimits a small triangular area (Fig. 9A). These features could be phylogenetically informative within the problematic genus Perilampus Latreille, which also has species with a ‘normal’ configuration of the scutoscutellar suture (Darling 1996).

In many chalcidoid species the axillula is not clearly defined externally due to the absence or weakness of the axillular sulcus or carina. There are also groups where the scutoscutellar suture is laterally broadened and appears triangular (Fig. 11C: sss) so that this region cannot clearly be termed as the axillula. Internal structures that clearly indicate an axillula are often missing as well. The scutoscutellar ridge is broad laterally in many groups (Fig. 8H: ssr) so that it is impossible to decide whether it is fused to a ridge that corresponds to a percurrent external axillular sulcus or whether such a ridge is absent. Although the smooth axillula is very conspicuous externally on the mesonotum in the Perilampus examined (Fig. 9A: axl), their posterior margin is not defined by internal structures (Fig. 9B) and their position relative to
the posterior wing process is also unusual because of the aberrant configuration of the scutoscutellar suture (see above). For the Chalcidoidea as a whole the axillula is weakly defined anatomically and consequently of limited value in phylogenetic analyses.

The frenum is an important diagnostic feature for Torymidae (Graham and Gijswijk 1998) and various subfamilies classified in Pteromalidae (Graham 1969). Gibson et al. (1999) speculate about the homology between the posterior scutellum in Mymarommatidae and Mymaridae and the frenum of the remaining Chalcidoidea. The homology was confirmed by Krogmann (2005) and Vilhelmsen and Krogmann (2006) based on external and internal features of the skeletal anatomy. Although the frenum is absent in the mymarid (Gonatocerus morrilli) we examined, it is present in a large number of mymarid genera (Huber 1997). We found it in some Pteromalidae (Asaphinae, Panstenoninae, Pteromalinae, Spalanginae), Torymidae (Mega-stigmatinae and Torymyna) and Perilampidae (Perilampinae). The frenal line varies from distinct (Fig. 8A: frl) to indistinct (Fig. 1C), and can even be carinate (Fig. 9B). In some Chalcidoidea a foveolate line is situated so close to the posterior margin of the mesoscutellum (e.g. Enoggera reticulata, Fig. 15B: fov) that it is difficult to decide whether it is homologous to the frenal line (Fig. 8D: frl) or the foveolate posterior mesoscutellar margin (Fig. 8D: fov) of other Chalcidoidea. The considerable variability makes the external frenal line difficult to score for the whole superfamly and we therefore only included the presence or absence of a distinct internal ridge as a character for our analysis. Apparently this feature is plesiomorphic for Chalcidoidea and secondarily lost in most of the species. We found an internal frenal ridge only in Asaphinae (Asaphes vulgaris), Spalanginae (Spalangia nigripes, Fig. 8B: frr) and Torymyna (Monodontomeres sp., Fig. 8C). Structures resembling external and internal frenal lines are observed in members of the Mymarommatidae (Vilhelmsen & Krogmann 2006) and Maamingidae (Vilhelmsen unpublished data). They need to be surveyed more thoroughly in other Apocrita to decide their possible phylogenetic significance.

In Chalcidoidea the prothorax is typically very short and its ventral margin medially incised (Figs 2F, G: php). This is characteristic of nearly all taxa examined and probably the ground plan feature of Chalcidoidea. The median incision is absent only in Trichilogaster (Ormocerinae; Fig. 10F), probably due to further size reduction of the prothorax, but the prothorax is completely reduced in Schizaspidea nasua (Eucharitinae) (Fig. 8L). The absence of the prothorax in representatives of Eucharitinae is correlated with the highly raised anterior mesoscutal margin, which accommodates the dorsolongitudinal flight muscles (Heraty 1989) and makes the prothorax obsolete.

The mesepisternum is distinctly elongate in Chalcidoidea. Its posterior margin is usually bilobed (Fig. 2H). The posterior mesepisternal margin is highly variable in Apocrita: Palaeomymar anomalum (Mymarommatidae) has a straight margin (Vilhelmsen and Krogmann 2006), whereas a bilobed margin is characteristic of various apocritan superfamilies (Vilhelmsen unpublished data). The pseudoepisternal lobes are distinct in many Chalcidoidea, but are absent from others, including those (Trichogrammatidae, Aphelinidae and Signiphoridae) that have the mesepisternum extending far into the metasoma. This is facilitated by a broadly transverse petiole in these taxa. The mesepisternum of the latter groups closely resembles the condition found in P. anomalum (elongate, straight ventral margin, pseudoepisternum absent) (Vilhelmsen and Krogmann 2006). However, these similarities are not necessarily evidence for a closer relationship between these groups and may be correlated with small body size. An elongate mesepisternum with a straight posterior margin is also found in Mymaridae, but here the pseudoprotuberance is clearly developed (Fig. 20D: ppb).

**Mespectus**

Presence of an exposed prepectus was suggested as an autapomorphy for Chalcidoidea by Gibson (1985). The prepectus is highly variable within the superfamly, and in few groups it is virtually absent (some Mymaridae; Gibson 1985) or slender and partially concealed (Rototoidae, Gibson and Huber 2000). In external view the prepectus is medially continuous with its opposite number, often forming an unpaired sclerite including the mesepisternum (Fig. 10E: pre, pss). In most chalcidooids the prepecti internally are separated by carinae (Figs 13B, H: c), whereas in others these carinae are incomplete or reduced due to partial or complete fusion between the prepecti and mesepisternum (Figs 12F, H). Complete (lateral and median) separation between the prepectus and mesepisternum by a furrow (i.e. the prepecti form a single sclerite) could have evolved secondarily within Chalcidoidea as this condition is not found in all outgroup taxa and also not in those Chalcidoidea that came out basal in our analyses (Spalangia) and in Mymaridae (Gonatocerus). Fusion between the prepectus and pronotum occurs frequently in Apocrita and has obviously evolved numerous times; it was recently observed in Palaeomymar anomalum (Mymarommatidae) (Vilhelmsen and Krogmann 2006). The incomplete fusion between the prepectus and pronotum observed in Perilampus indicates that the condition is secondary within Chalcidoidea. Another prepectal character with phylogenetic value could be the presence of upright cuticular ridges present in some Aphelinidae (Fig. 7F: prr), but also in Encyrtidae (Figs 9F, 12A).

The acropleuron is the attachment site for the retractor of the mesoscutum (pl2–t2c) (Gibson 1986b). The formation of an internal septum, forming a pocket for the enlarged pl2–t2c muscle was described for female Eupelminae (Gibson
It can also be found in Encyrtidae (Fig. 12A) that share an enlarged acropleuron with female Eupelminae. The internal septum in Eupelminae is the attachment site for p1<sub>2</sub>–fu<sub>2</sub> (normally originating from the upper mesepimeron) and for p1<sub>2</sub>–3ax<sub>2</sub>a (normally originating from the lower mesepimeron) (Gibson 1986b). The moderately enlarged acropleuron in Aphelinidae can also be correlated with the formation of an internal septum (Fig. 12D). However, the position of the acropleuron anterior to the mesofurca makes it more plausible that p1<sub>2</sub>–fu<sub>2</sub> and p1<sub>2</sub>–3ax<sub>2</sub>a still arise from the mesepimeron whereas these muscles cannot arise from an obviously reduced mesepimeron in Encyrtidae. This might indicate non-homology between the septum in Aphelinidae and Eupelmidae/Encyrtidae but remains speculative until the mesopleural musculature is investigated. In all other Chalcidoidea examined the acropleuron is internally delimited by an incomplete (only posterior, vertical portion present, Fig. 11B: acr) or complete, curved acropleural ridge (anterior, horizontal and posterior, vertical portion present, Fig. 3C). These differences might be due to the size of the p1<sub>2</sub>–t<sub>2</sub>c muscle.

In Chalcidoidea, the mesopleural sulcus and corresponding internal ridge is often well developed, extending from the ventral border of the acropleuron to the lateral articulation point of the mesocoxae (Figs 1A, 11F: mps), and the mesepimeron is large. This resembles the condition in basal Hymenoptera (Snodgrass 1910), except that the sulcus extends anterior to the pleural wing process in these taxa. In most Apocrita, the pleural sulcus and ridge are weakly developed or absent; the mesepimeral ridge observed along the posterodorsal margin of the mesopleuron in many Apocrita (e.g. Ibalia rufipes Cresson, 1879; Ronquist and Nordlander 1989) is apparently not homologous with the mesopleural ridge (Shcherbakov 1981). The presence of a well developed mesopleural sulcus and ridge anteriorly terminating in the acropleuron is unique within Apocrita and a putative autapomorphy of the Chalcidoidea.

The mesofurca in Chalcidoidea was examined by Heraty et al. (1997); they proposed the presence of a mesofurcal bridge to be a ground plan feature for the Chalcidoidea. This scenario is supported by the widespread occurrence of the mesofurcal bridge within Apocrita. However, because the mesofurcal bridge is absent in Mymarommatidae, Rotoitidae, and Mymaridae (Heraty et al. 1997) it remains possible that the mesofurcal bridge was absent in the ancestor and (re-)evolved within Chalcidoidea.

The position of the mesofurcal pit is variable within Chalcidoidea. In most groups the pit is directly anterior to the mesotrochantinal plate (Fig. 1B: f.p, mtp), whereas in a few groups it is situated more anteriorly (Fig. 11D), closer to the centre of the mesepisternum, or more posteriorly between the mesocoxal foramina (Fig. 11E). The posterior position of the mesofurcal pit (between the mesocoxal foramina) is widespread within non-chalcidoïd Hymenoptera, including Palaecomymar anomalous (Mymarommatidae) (Vilhelmsen and Krogmann 2006; Vilhelmsen unpublished data). There are a few taxa that possess an additional pit opposite to the anterior extent of the mesodiscriminal lamella (Fig. 10F). This pit is not continuous with the base of the mesofurca. It is therefore not homologous with the (posterior) mesofurcal pit and has to be regarded as secondarily developed within Chalcidoidea.

Another mesothoracic character with potential phylogenetic value concerns the mesocoxal foramina. According to Johnson (1988), a membranous connection between mesocoxae and metathorax (i.e. metepisternum) is a ground plan feature of the Hymenoptera. We found the mesocoxal foramina to be completely surrounded by sclerotised cuticle in Eurytomidae, Chalcididae, Leucospidae, Eucharitidae, Pteromalidae (only Asaphinae and Spalanginae) and Eulophidae (only Entedoninae). This feature also occurs in some Apocrita, and is present in Palaecomymar anomalous (Mymarommatidae) (Vilhelmsen and Krogmann 2006).

**Metathorax–propodeum complex**

The metanotum of Chalcidoidea is reduced in size and exhibits a limited number of characters that mostly refer to the configuration of the metascutellum and the metascutellar arms. The majority of Chalcidoidea have a reduced metascutellum (= dorsellum) separate from the anterior and posterior metanotal margin, which could be derived from a large, well defined metascutellum that was observed in representatives of Mymaridae, Eulophidae, Aphelelinidae, Signiphoridae and Trichogrammatidae.

According to Bucher (1948), the metepimeron in Chalcidoidea is reduced and the metapleural sulcus (if present) separates the metapleuron and propodeum. To avoid confusion with existing terminology we retain the more general term metapleuron for the lateral (visible) part, although it only consists of the lateral portion of the metepisternum. The ventral metepisternum (often erroneously termed metasternum) exhibits a large number of morphological characters, including the metapleural pits. The number of metapleural pits varies between one and three and the position of the metapleural arms does not always correspond to the position or number of metapleural pits. We included all these characters because they might be phylogenetically informative, but scored them as separate characters to avoid incorrect homologisation (lateral pits v. median pit). The metapleura of Chalcidoidea has never been studied in detail for more than a few taxa (e.g. Bucher 1948). It is morphologically more variable than the pro- and mesofurca (Figs 17C–H, 18, 19, 20A–D). Metapleural characters are useful for phylogenetic analyses of Chalcidoidea because they are quite constant at the subfamily level though often variable between higher taxa. Three different main metapleural types were identified, which might have evolved in the following transformation series leading from I to III (Fig. 24).
I metafurcal arms fused above the level of the metepisternum, with a shared base, resulting in a y-shaped metafurca, mostly situated anterior to the metadiscrimenal lamella, with a single median pit (Figs 24A, B).

II metafurcal arms fused at the level of the metepisternum resulting in an v- or u-shaped metafurca, mostly anterior to the metadiscrimenal lamella, with 1–3 pits (Fig. 24C).

III metafurcal arms separated from each other at the level of the anterior metepisternal margin but may be fused below this level (only observed in Megastigmus, Fig. 24E), mostly situated lateral to the metadiscrimenal lamella, with 1–2 pit(s) (Figs 24D–H).

A y-shaped metafurca with a single, median pit is probably a ground plan feature of the Chalcidoidea, because this condition is plesiomorphic for the Hymenoptera (Vilhelmsen 2000b). State II can be derived by reduction of the metafurcal base or by ventral shifting of the latter. State III could have evolved by further shifting via state II (present in Megastigmus) and/or (further) lateral separation of the metafurcal arms. An additional state could be included for species that have the arms separate but (still) orientated towards each other and with one single median pit (Torymus Fig. 24D), or two pits lying adjacent to each other in one median depression (Notanisus Figs 15F, 24F).

The metafurcal arms and the metapleural apodemes in Chalcidoidea may be connected by partial fusion between the posterior surface of the apodeme and the anterior surface of the arm. Because the fusion is normally concealed in anterior view by the metapleural apodeme, this condition is often difficult to observe. However, complete fusion between the metafurcal arms and metapleural apodemes, with indiscernible fusion lines, is a derived character state that is uncommon in Chalcidoidea, though present in Doddifoenus (Pteromalidae, Leptofoeninae) (Krogmann unpublished

---

Fig. 24. Possible transformation series between different configurations of the three (I–III) main metafurcal types in Chalcidoidea. Circles indicate number and position of metafurcal pits. Metafurca, anterior view of A, Podagrion sp. (Torymidae, Toryminae); B, Monodontomerus sp. (Torymidae, Toryminae); C, Thaumasura sp. (Pteromalidae, Cleonyminae); D, Torymus bedeguaris (Torymidae, Toryminae); E, Megastigmus dorsalis (Torymidae, Megastigmatae); F, Notanisus sp. (Pteromalidae: Cleonyminae); G, Asaphes vulgaris (Pteromalidae, Asaphinae); H, Lariophagus distinguendus (Pteromalidae, Pteromalinae).
data) and in many Apocrita (Weber 1926; Vilhelmsen unpublished data).

Paired metapectal plates (Fig. 4D: mp) lateral to the metapetiole are not present in any other Apocrita, making them a putative autapomorphy of Chalcidoidea. Bucher (1948) included these plates in his general term ‘inflection of the metapetiole’ which also included additional structures on the metapetiole. We use the term metapetial plate, as these structures are not inflected (i.e. refer to external pits or sulci). The metapetial plates may function as muscle attachment sites. They are absent in small chalcidoids, which often have a reduced metapetial with the metadiscriminal lamella absent. The metapetial arms are sometimes fused with the metapetial plates (Fig. 18H); this is probably a secondary development.

The propodeum of Chalcidoidea exhibits the highest morphological variation of all mesosomal components and is particularly prone to homoplasy. It even varies between closely related species and is therefore most informative on a lower taxonomic level.

Petiole

The most striking difference in the petiolar configuration is the presence of a sessile metasoma, that is broadly joined to the mesosoma (e.g. Trichogrammatidae, Aphelinidae, Signiphoridae) versus a metasoma that is anteriorly constricted, bearing a shortly transverse or distinctly elongate petiole (most Chalcidoidea). The sessile metasoma is always correlated with a distinct elongation of the mesosaphragma (see above) and might be phylogenetically relevant for Chalcidoidea. The external morphology of the petiole is apparently highly variable and therefore most informative within families (Chalcidididae, Wijesekara 1997) or genera (Cyrtogaster, Heydon 1989).

Chalcidoidea relationships

The readers are referred to Figs 21, 22 throughout this section, and additionally to Fig. 23 for the discussion of Eupelminae.

There are two major differences between chalcidoid relationships resulting from our analyses and other recently published hypotheses. 1. Palaeomymarinae is placed within Chalcidoidea, not outside (Gibson 1986a; Rasnitsyn et al. 2004); 2. Gonatocerus (Mymaridae) is not the sister-group of the remaining Chalcidoidea (e.g. Gibson et al. 1999; Campbell et al. 2001) but to Palaeomymarinae. The position of these taxa may be caused by reductional characters in the external anatomy and the furcae that could be correlated with miniaturisation. All families of small Chalcidoidea and Palaeomymarinae group together in our analyses. In general, our results reflect a more traditional view of chalcidoid phylogeny as expressed, for example, in Bouček (1988a).

According to this, the ancestor of Chalcidoidea was a rather large ectoparasitoid on hosts that decreased in body size, forcing the early chalcidoids to do the same. The large chalcidoids (Spalangiinae, Eurytomidae, Chalcididae, Leucospidae, Cleonyminae) come out basal in our analyses whereas the small ones are placed distally. However, this has to be weighed against evidence not included in our analyses that support mymarids as being basal chalcidoids (e.g. antennal features, Gibson 1986a; ovipositor features, Quicke et al. 1994; molecular data, Campbell et al. 2001, Krogmann 2005). Additional morphological evidence for the monophyly of Chalcidoidea (Gibson 1986a) from our study includes at least three putative autapomorphies: (1) presence of a largely exposed, triangular or diamond-shaped prosternum; (2) presence of a percurrent mesopleural sulcus, anteriorly terminating in the acropleuron; and (3) presence of paired metapectal plates lateral to the metafurca.

The Pteromalidae were not retrieved as monophyletic, which is in accordance with previous hypotheses (Gibson et al. 1999). The monophyly of Pteromalinae, Misco-gasterinae, and Panstenoninae, and the phylogenetic separation of Spalangiinae and Asaphinae from the ‘core group’ of Pteromalidae, were independently inferred from cladistic analyses based on molecular (Krogmann and Abraham 2004; Krogmann 2005) and morphological data (Török and Abraham 2002). The former three subfamilies may be grouped as Pteromalinae sensu stricto. Pteromalinae is not monophyletic because Pachycrepoidea and Cyrtogaster (Misco-gasterinae) come out as sister-groups. The systematic placement of Pachycrepoidea victinde miae within Pteromalinae was doubted by Van den Assem (1974). A closer relationship between Panstenoninae and Cleonyminae, suggested by Kerrich and Graham (1957), could not be confirmed. The distinctiveness of Spalanga led previous authors to place it in own family (Walker 1833) or unite it with Cerocephalinae as this subfamily is currently understood (Förster 1856). The isolated position and derived nature of Spalanga is underlined by molecular and morphological data (Krogmann 2005). Its basal position in our analyses is not supported by molecular data (Campbell et al. 2001) and its phylogenetic position within Chalcidoidea remains uncertain until additional critical taxa (e.g. Cerocephalinae, Diparinae) are included in analyses. The monophyly of Cleonyminae is uncertain (Gibson 2003), which is reflected by our results. Cleonyminae possess a large number of plesiomorphic features, but the hypothesis that all Pteromalidae are derived from either Cleonyminae or Ormocerinae (Bouček and Heydon 1997) was not confirmed here. The position of Ormocerinae is not stable; it may be placed inside or outside the ‘core’ of Pteromalidae. Asaphinae is a very distinct taxon and its mesosoma exhibits at least two putative autapomorphies: (1) pronotal sulcus medially discontinuous and with characteristic lateral curvature; and (2) scutocutellar suture laterally discontinuous. Asaphinae does not group with Pteromalinae, Misco-gasterinae, and Panstenoninae in the implied weights.
analysis (Fig. 22), which probably better reflects the phylogenetic relationships than the equal weights analysis (Fig. 21). Asaphinae are isolated from the major clades of Pteromalidae in all previous cladistic analyses (Campbell et al. 2001; Török and Abraham 2002; Krogmann and Abraham 2004).

The close relationship between Leucospidae, Eurytomidae and Chalcididae is in accordance with recent hypotheses (Noyes 1990; Wijesekara 1997; Gibson et al. 1999). Though the monophyly of Leucospidae has never been seriously questioned, Eurytomidae are not retrieved as monophyletic in molecular analyses (Campbell et al. 2001; Chen et al. 2004). The autapomorphies proposed for Chalcididae (Wijesekara 1997) are not convincing according to Gibson et al. (1999), and Chalcididae might turn out as paraphyletic with respect to Leucospidae (Gibson 1993b).

Eucharitidae and Perilampidae were retrieved as sister groups; this is in accordance with Heraty and Darling (1984), Darling (1988), Gibson et al. (1999). The profurcal bridge constitutes a putative synapomorphy for both families (see above).

The monophyly of Torymidae is not confirmed by molecular data (Campbell et al. 2001; Krogmann and Abraham 2004) and morphological evidence from the eighth metastomal tergum (Grissell 1995) is also uncertain. Our results are contradictory: the equal weights analysis retrieves Torymidae as paraphyletic but confirms Torymidae, whereas the implied weights analysis confirms Torymidae but has Toryminae paraphyletic with respect to Megastigminae.

Monophyly of Ormyridae is supported by two autapomorphies (Gibson et al. 1999). Ormyridae have been classified within Pteromalidae (Riek 1970) or Torymidae (Bouček et al. 1981). Our analyses revealed no close relationship to Torymidae. A closer relationship between Ormyridae and representatives of Pteromalidae (Asaphinae) is supported by molecular data (Krogmann and Abraham 2004) and the implied weights analysis (Fig. 22).

The monophyly of Eupholidae is supported in all analyses, which is in accordance with molecular data (Gauthier et al. 2000; Campbell et al. 2001). However there seems to be no convincing autapomorphies for Eupholidae (LaSalle et al. 1997).

Agaonidae were not retrieved as monophyletic based on molecular data (Rasplus et al. 1998). This was not confirmed in our analyses. We also found no indication of a closer relationship between Oritsetellinae, Sycoryctinae and Pteromalidae as found by Rasplus et al. (1998). However, only representatives of three subfamilies were included in our analyses and they are mainly held together by reductional characters (e.g. surface sculpture, pilosity) which could be independently derived.

The sister-group relationship between *Eupelminus* and *Ericydus* is solely based on derived female characters (e.g. enlarged acropleuron with internal septum). If males are included in the analyses they cluster with Eulophidae (Fig. 23) based on putatively plesiomorphic features (e.g. acropleuron not enlarged, presence of percurrent transepimeral and axillular sulci). However all these character systems are prone to homoplasy and therefore it remains undecided if male or female characters are ‘more reliable’ from a phylogenetic perspective. Gibson (1989) states that apomorphic character states shared among female Eupelminae and other Eupelmidae, Encyrtidae, and Tanaostigmatidae form a functional complex and could therefore be the result of convergent evolution. Male Eupelminae have been described as pteromalid-like in structure (Gibson 1986b, 1989) but cluster with Eulophidae in our analysis. Internal morphological features of male *Eupelminus* like the metafurca (Fig. 19H) and the ridges mentioned above, are indeed different from Pteromalidae and closer to Eulophidae (Fig. 23).

The representatives of Aphelinidae and Trichogrammatidae form a monophyletic group in the implied weight analysis (Fig. 22). A close relationship between these families was proposed by Viggiani and Battaglia (1984). According to Woolley (1988), Aphelinidae could be paraphyletic with respect to Trichogrammatidae or Signiphoridae. A closer relationship between Signiphoridae/ Aphelinidae to Encyrtidae (Gordh 1979) was not confirmed in our analyses, which supports the view of Bouček (1988b), who regards morphological similarities between both groups as convergences resulting from adaptations to the same hosts (Coccoidea).

Conclusions

Our results confirm that the family classification of Chalcidoidea is insufficient and violates the principles of phylogenetic systematics. The analyses indicate that the subfamily classification is more stable but our taxon sampling, comprising less than a third of the subfamilies, is inadequate for providing a robust phylogenetic hypothesis for the superfamly. Our aim was rather to provide a nucleus dataset that covers the morphological variation of a major body region for the whole superfamily that can serve as a starting point for future phylogenetic studies. Unravelling the phylogeny of a group as diverse as the Chalcidoidea requires a collaborative effort involving multiple sources of information. The present study demonstrates that comparative morphology still has much to offer chalcidoid systematics, but only in combination with molecular, ecological and behavioural data will it be possible to create a system that reflects and not obscures the evolutionary history of Chalcidoidea.

Acknowledgments

This study arose from the first author’s PhD thesis, which was conducted in the Zoological Museum Hamburg and supported by a fellowship from the University of Hamburg. The first author is greatly indebted to his supervisor Rudolf
Abraham for advice and encouragement throughout the project and for numerous discussions on pteromalid and chalcidoind phylogeny. Renate Walter (ZMH) kindly assisted with preparing many of the SEM pictures. The staff from the Entomological Department of the Zoological Museum, Copenhagen is acknowledged for extensive help and for maintaining a great working atmosphere during two visits made by the first author. These visits were financed by the German Academic Exchange Service (April–July 2004) and the SYNTHESYS project of the European Union (May–August 2005). The second author acknowledges the Danish Natural Science Council for general support. Gary Gibson (CNC, Ottawa) thoroughly revised an earlier version of this manuscript and made substantial comments that greatly improved the paper. Special thanks are also due to John Heraty and Johan Liljeblad (University of California, Riverside) for organising the ‘Chalcid workshop’ (September 2005) on morphological character systems which provided essential information on character scoring and coding in Chalcidoidea. The following individuals donated specimens for our study or helped with the identification: Kathleen Campbell (University of California, Riverside, USA), Gérard Delvare (CIRAD, Montpellier, France), John Huber (CNC, Ottawa, Canada), Fiona Impson (ARC-Plant Protection Research Institute, South Australia), Michael Ohl (Museum für Naturkunde, Humboldt University Berlin, Germany), Ralph Peters (University of Hamburg, Germany), Matthias Schöller (Biological Consultancy, Berlin, Germany), Kai Schütte (University of Hamburg, Germany), Johannes Steidle (Institute for Zoology, University of Hohenheim, Germany), and Marc Török (Hamburg, Germany).

References


de Dalla Torre, C. G. (1898). ‘Catalogus Hymenopterorum hucusque descripturn systematicus et synonymicus. 5. Chalcididae et Proctotrupidae.’ (Engelmann: Leipzig, Germany.)


Manuscript received 14 April 2006, revised and accepted 14 September 2006.
Appendix 1. Taxa examined

ZMH = Zoological Museum Hamburg; ZMUC = Zoological Museum, University of Copenhagen

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of specimens</th>
<th>Voucher depository</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chalcidoidea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaonidae: Agaoninae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blastophaga pseues (Linnaeus, 1758)</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Otitesellinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eujacobsonia mirabilis Grandi, 1923</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Sycoryctinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philotrypes caricae (Linnaeus, 1762)</td>
<td>5 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Aphelinidae: Aphelininae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centrodrora sp.</td>
<td>6 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Coccophagidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Encarsia formosa Gahan, 1924</td>
<td>10+ (females and males)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Chalcididae: Chalcidinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalcis sp.</td>
<td>5 (females and males)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Haltichellinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antrocephalus sp.</td>
<td>1 (female)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Encyrtidae: Tetracneminae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ericydnus sp.</td>
<td>5 (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Eucharitidae: Eucharitinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schizaspidea nasua (Walker, 1846)</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Eulophidae: Entedoninae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Entedon ergias Walker, 1839</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Eulophinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cirrospilus coachellae Gates, 2000</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Tetrastichinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aprostocetus sp.</td>
<td>6 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Eupelmidae: Eupelminae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eupelmus atropurpureus Dalman, 1820</td>
<td>4 (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Eurytomidae: Eurytominae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eurytoma sp.</td>
<td>5 (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Tetramesa sp.</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Leucospidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leucospis sp.</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Mymaridae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gonatocerus morrilli (Howard, 1908)</td>
<td>10+ (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Ormyridae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ormyrus sp.</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Perilampidae: Perilampinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perilampus sp.</td>
<td>3 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Pteromalidae: Asaphinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asaphes vulgaris Walker, 1834</td>
<td>3 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Enoggera reticulata Naumann, 1991</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Cleonyminae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Notanisus sp.</td>
<td>1 (female)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Thaumasura sp.</td>
<td>4 (females)</td>
<td>ZMUC</td>
</tr>
<tr>
<td>Miscogasterinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyrtogaster vulgaris Walker, 1833</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Ormoceriniae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trichilogaster sp.</td>
<td>4 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Panstenoninae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panstenon oxylus (Walker, 1839)</td>
<td>1 (female)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Pteromalinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antisoperteromalus calandrae (Howard, 1881)</td>
<td>4 (females and males)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Cecidostiba semifascia (Walker, 1835)</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Dibrachys cavus (Walker, 1835)</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Lariopagus distinguendus (Förster, 1841)</td>
<td>5 (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Nasonia vitripennis (Walker, 1836)</td>
<td>10+ (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Pachycrepoides vindemmiae (Rondani, 1875)</td>
<td>4 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Spalangiinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spalangia nigripes Curtis, 1839</td>
<td>10+ (females and males)</td>
<td>ZMH, ZMUC</td>
</tr>
</tbody>
</table>

(continued next page)
### Appendix 1. (continued)

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of specimens</th>
<th>Voucher depository</th>
</tr>
</thead>
<tbody>
<tr>
<td>Signiphoridae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Clytina giraudi</em> Erdös, 1957</td>
<td>8 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td>Torymidae: Megastigmidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Megastigmus dorsalis</em> (Fabricius, 1798)</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Torymidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Torymus bedeguaris</em> (Linnaeus, 1758)</td>
<td>4 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td><em>Podagrion</em> sp.</td>
<td>3 (females)</td>
<td>ZMH, ZMUC</td>
</tr>
<tr>
<td><em>Monodontomerus</em> sp.</td>
<td>3 (females)</td>
<td>ZMH</td>
</tr>
<tr>
<td>Trichogrammatidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trichogramma evanescens</em> Westwood, 1833</td>
<td>10+ (females and males)</td>
<td>ZMH</td>
</tr>
</tbody>
</table>

Ceraphronoidea
Megaspilidae
*Megaspilus fuscipennis* (Ashmead, 1888) | 6 (females and males) | ZMUC |

Cynipoidea
*Ibaliidae* Ibiidae 1879 | 2 (females) | ZMUC |

Mymarommatidae
*Mymarommatidae*  
*Palaeomymar anomalum* (Blood & Kryger, 1922) | 10 (females) | ZMH, ZMUC |

Platygastridea
Scleroniidae
*Archeoteleia mellea* Masner, 1968 | 4 (females) | ZMUC |

Proctotrupoidea
Monomachidae
*Monomachus antipodalis* Westwood, 1874 | 6 (females and males) | ZMUC |

Vanhorniidae
*Vanhornia eucnemidarum* Crawford, 1909 | 6 (females and males) | ZMUC |

Stephanoida
Stephanidea
*Megischus* spp. | 4 (females) | ZMUC |
Appendix 2.  Character list

Mesosomal surface
(1) Metallic luster: 0, completely absent; 1, at least present on some body parts

Pronotum
(2) Pronotal transverse carina or sulcus: 0, absent; 1, developed only laterally (Fig. 5F); 2, extending across entire pronotum (Fig. 2A)
(3) Transverse sulcus at anterior margin of pronotum: 0, absent; 1, present (Fig. 5B)
(4) Median longitudinal sulcus: 0, absent; 1, partly developed; 2, present and complete (Fig. 6B)
(5) Shape of collar: 0, reduced, inconspicuous and not elongate (Fig. 6B); 1, present and forming small neck (Fig. 1A)
(6) Pilosity of collar: 0, pilose at least dorsally (Fig. 5F); 1, bare or only few setae mainly or exclusively present at anterior margin (Fig. 1A)
(7) Sculpture of collar (major part): 0, deep and/or conspicuous sculpture (Fig. 1A); 1, with weak sculpture or completely smooth (Fig. 6A)
(8) Pilosity of collar: 0, pilose (Fig. 1A); 1, covered by scattered setae (Fig. 6B); 2, bare
(9) Sculpture of pronotum relative to lateral panel: 0, pronotum sculptured throughout (Fig. 1A); 1, pronotum smooth or less sculptured laterally; 2, pronotum entirely smooth
(10) Pilosity of lateral panel of pronotum: 0, at least partly pilose, thus indistinct from rest of at least partly pilose pronotum; 1, without pilosity, thus distinct from rest of pronotum that bears at least several setae (Fig. 2A)
(11) Posterolateral margin of pronotum: 0, straight or with inconspicuous invagination for mesothoracic spiracle (Fig. 1A); 1, with distinct concavity accommodating mesothoracic spiracle (Fig. 2A); 2, surrounding mesothoracic spiracle

Propectus
(12) External surface of prosternum: 0, completely smooth (Fig. 5H); 1, with slight reticulation (Fig. 1B)
(13) Prodiscrimen line: 0, absent or indistinct (Fig. 5A); 1, present as distinct line or furrow (Fig. 2B)
(14) Transverse ventral carina at posterior margin of propectus: 0, absent or incomplete; 1, complete and conspicuous (Fig. 2C)
(15) Posterior margin of propectus: 0, almost or completely straight or slightly emarginate (Fig. 5E); 1, with broad convexity (Fig. 5H); 2, formed into a distinct spine (Fig. 5D)
(16) Ventral process of propectus close to articulation with procoxa: 0, inconspicuous; 1, present and visible in ventral view (Fig. 2B)
(17) Median margins of propleura: 0, propleura abutting medially along entire length or at least major part of length (Fig. 5D); 1, propleura meeting only apically, at most along half of their length, sometimes entirely separated (Fig. 1B)
(18) Dorsal margin of propectus: 0, completely or at least partly covered by propleura (Fig. 1B); 1, not covered by propleura, completely free (Fig. 5A)
(19) Pilosity of propleuron: 0, pilose (at least laterally) (Fig. 5B, D); 1, with a few setae (sometimes only two setae present) (Fig. 5A); 2, bare
(20) Lateral propleural surface: 0, anterior margin acarinate (Fig. 5F); 1, anterior margin carinate (Fig. 2B)
(21) Sculpture of lateral surface of propleura: 0, smooth or sculpture indistinct from rest of propleuron (Fig. 1A); 1, present and distinct from rest of propleuron (Fig. 5B)
(22) Base of profurcal arms: 0, separated from each other or fused at level of propectus (Fig. 7C); 1, fused above level of propectus, thus appearing y-shaped (Fig. 7E, F)
(23) Apical portion of profurcal arm: 0, not broadly fused with propectus (Fig. 6E); 1, broadly fused with propectus, shaft of profurcal arm completely recognisable (Fig. 6H); 2, broadly fused with propectus, basal part of profurcal shaft not recognisable (Fig. 6F)
(24) Anterior apodeme of profurcal arm: 0, absent or indistinct; 1, present and distinct (Fig. 7D)
(25) Ventral process of profurcal arm: 0, absent or indistinct (Fig. 6C); 1, present and distinct (Fig. 6D)
(26) Profurcal bridge: 0, absent (Fig. 7C); 1, present (Fig. 7B)
(27) Propleural arm: 0, at least somewhat elongated and conspicuous (Fig. 7B); 1, inconspicuous or absent (Fig. 7F)

Mesonotum
Prothorax
(28) Anterior margin: 0, invaginated (Fig. 2F); 1, straight (Fig. 10F)
(29) Length of prothorax: 0, tongue-like elongated, extending far beyond anterior mesocutellar margin; 1, not elongated (Fig. 2F)

Mesoscutum
(30) Surface of preaxilla: 0, smooth (Fig. 2A); 1, weakly reticulate (Fig. 9A)
(31) Pilosity of preaxilla: 0, bare (or only with scattered setae) (Fig. 2A); 1, pilose
(32) Parascutal carina: 0, adjacent to pronotum; 1, separate from pronotum (Fig. 2A)
(33) Notaulus externally: 0, complete and distinct (Fig. 8D); 1, distinct but incomplete posteriorly (not reaching transscutal articulation) (Fig. 1C); 2, absent
(34) Internal notaular ridge: 0, complete (reaching transscutal articulation) (Fig. 8B); 1, incomplete posteriorly (not reaching transscutal articulation) (Fig. 8K); 2, absent
(35) Median mesoscutal sulcus: 0, absent (Fig. 8A); 1, only developed anteriorly; 2, present and complete
(36) Internal ridge corresponding to median mesoscutal sulcus: 0, absent (Fig. 9F); 1, only developed anteriorly; 2, present and complete
(37) Boundary between mesoscutum and mesocutellum: 0, mesocutellum not overlapped by mesoscutum (Fig. 9G); 1, mesocutellum overlapped by mesoscutum anteromedially; 2, anterior margin of mesocutellum completely overlapped by mesoscutum (Fig. 9D)
(38) Transscutal articulation: 0, completely and deep in dorsal view (Fig. 6A); 1, interrupted at level of axilla (Fig. 2A)

Mesocutellar–axillar complex
(39) Dorsal surface of axilla: 0, at most slightly extended anteriorly (Fig. 8A); 1, extending anteriorly of median part of transscutal articulation for at least half of its length (Fig. 10A)

(continued next page)
Appendix 2. (continued)

(40) Distance between axillae: 0, smallest distance between axillae longer than width of axilla (Fig. 9D); 1, smallest distance between axillae equal to or less than width of axilla (Fig. 1C); 2, axillae abutting medially

(41) Pilosity of dorsal surface of axilla: 0, bare; 1, bearing scattered setae or setae restricted to outer margin; 2, pilose

(42) Length of axillary setae: 0, not elongate (Fig. 8D); 1, conspicuously elongate (Fig. 8A)

(43) Surface of lateral panel of axilla: 0, smooth or only weakly sculptured (Fig. 16C); 1, striate (Fig. 1A); 2, reticulate (Fig. 9A)

(44) Pilosity of lateral panel of axilla: 0, bare or only with scattered setae (Fig. 1A); 1, pilose

(45) Axillar phragma: 0, absent; 1, present (Fig. 2F)

(46) Shape of axillar phragma: 0, shorter than wide (Fig. 8B); 1, between one and two times as long as wide (Fig. 8E); 2, more than twice as long as wide (Fig. 9F)

(47) Orientation of axillar phragma: 0, adjacent to mesoscutum (Fig. 2F); 1, partly curving ventrally, away from mesoscutum (Fig. 9F); 2, completely free and separated from mesoscutum

(48) Scutoscutellar sulcus: 0, medially distinct and separate from transscutal articulation (Figs 1C, 8A); 1, medially absent or indistinct from transscutal articulation (Figs 8J, 9G)

(49) Scutoscutellar sulcus: 0, laterally complete and distinct (Fig. 1C); 1, laterally absent or interrupted (Fig. 8A)

(50) Ridge, corresponding to scutoscutellar sulcus: 0, adjacent to transscutal articulation medially (Fig. 8B); 1, separate from transscutal articulation (Fig. 8L)

(51) Mesoscutellum surface: 0, smooth or weakly sculptured (Fig. 9D); 1, reticulate (Fig. 9E); 2, coarsely punctuate (Fig. 9A)

(52) Mesoscutellum pilosity: 0, bare (Fig. 9D); 1, with one pair of setae; 2, with two pairs of setae (Figs 10A, 17B); 3, with four pairs of setae; 4, pilose or at least with more than four pairs of setae (Fig. 9E)

(53) Dorsal boundary of axillula: 0, indiscernible (Fig. 9E); 1, with distinct axillular sulcus or at least weakly delimited by slight impressions (Fig. 8A); 2, delimited by axillular carina dorsally (Fig. 11A)

(54) Axillar surface: 0, at least partly sculptured (Fig. 1A); 1, smooth (Fig. 9A)

(55) Internal ridge corresponding to axillar sulcus/carina: 0, absent or indistinct from scutoscutellar ridge (Fig. 8H); 1, present and distinct (Fig. 9H)

(56) Posterior margin of mesoscutellum in dorsal view: 0, without broad rim (Fig. 9G); 1, with broad carinate rim marked by foveolae (Fig. 15C); 2, with narrow rim indicated by sulcus (Fig. 16H)

(57) Mesoscutellar process: 0, absent (Fig. 8J); 1, present but short and not reaching metasoma in dorsal view (Fig. 8H); 2, elongate, overlapping anterior metasoma (Fig. 8L)

(58) Scale-like structures at posterolateral mesoscutellar margin (opposite frenal arm): 0, absent (Fig. 3H); 1, present (Fig. 9E)

(59) Frenum: 0, absent or inconspicuous in dorsal view (Fig. 9G); 1, present and distinct from rest of the mesoscutellum as differently sculptured area (Fig. 8D)

(60) Internal ridge corresponding to frenal line: 0, absent (or indistinct) (Fig. 8E); 1, present and distinct (Fig. 8B)

(61) Frenal arm: 0, not clearly extending dorsally into mesoscutellum (Fig. 9D); 1, clearly extending into mesoscutellum (Fig. 3H)

(62) Length ratio between mesoscutum and mesoscutellum (not including mesoscutellar processes, if any): 0, size ratio >1 or = 1 (Fig. 1C); 1, size ratio <1 (Fig. 10D)

(63) Median mesoscutellar sulcus: 0, absent; 1, present (Fig. 9G)

(64) Internal septum of mesoscutellum: 0, absent; 1, present (Fig. 9C)

Mesophragma

(65) Length of mesophragma: 0, mesophragma more than twice as long as wide (Fig. 10B); 1, mesophragma less than twice as long as wide (Fig. 2H)

(66) Pseudophragma: 0, absent or inconspicuous (Fig. 10B), 1, present and conspicuous, bilobed (Fig. 2H)

Prepectus

(67) Free prepectus: 0, absent; 1, present

(68) Configuration of prepectus: 0, concealed laterally; 1, exposed laterally (Fig. 1A)

(69) Shape of prepectus in lateral view: 0, triangular or subtriangular (Fig. 1A); 1, rounded

(70) Prepectal overlap in lateral view: 0, overlapping mesopleuron anteriorly (Fig. 1A); 1, not overlapping mesopleuron (Fig. 11F)

(71) Median portion of prepectus: 0, forming a broad strip that is not or only slightly narrower than lateral panel of prepecti (Figs 10H, 12F); 1, prepecti medially reduced to a very narrow strip (Fig. 1B)

(72) Prepectus-pronotum configuration: 0, prepectus separate from pronotum (Fig. 1A); 1, prepecti completely fused with pronotum (Fig. 5G)

(73) Prepectus–mesepisternum configuration: 0, prepectus at least partly fused with mesepisternum ventromedially (Fig. 11F); 1, prepectus completely separate from mesepisternum by deep furrow (Fig. 3A)

(74) Pronotal depression on prepectal surface: 0, absent or inconspicuous; 1, present and distinct (Fig. 10E)

(75) Prepectus internally (1): 0, posterior boundary of prepectus with complete carina separating it from mesopleuron (Fig. 12G); 1, boundary of prepectus with carina incomplete or absent, prepectus partly fused with mesopleuron internally (Fig. 12H)

(76) Prepectus internally (2): 0, prepecti completely separated by carinate (Fig. 12G); 1, prepecti not or incompletely separated by carinate (Fig. 12H)

Mesophragma

(77) Acropleuron: 0, acropleuron not enlarged (Fig. 1A); 1, acropleuron greatly enlarged, comprising largest part of mesophragma in lateral view (Fig. 12B)

(78) Internal ridge corresponding to acropleural sulcus: 0, present (Fig. 12E); 1, absent

(continued next page)
Appendix 2. (continued)

(79) Development of internal ridge corresponding to acropleural sulcus: 0, complete; reaching anterior margin of mesopectus, without septum (Fig. 12E); 1, complete, reaching anterior margin of mesopectus, continuous with conspicuous septum and forming cavity (Fig. 12D); 2, incomplete, not reaching anterior margin of mesopectus, marking only posterior boundary of acropleuron (Fig. 11B)

(80) Mesofemoral depression: 0, only weakly indicated or absent; 1, present and distinct (Fig. 1B)

(81) Mesopleural sulcus: 0, at least partly indicated and originating anteroventrally to mesocoxa and leading to acropleuron (Fig. 1A); 1, absent between mesocoxa and acropleuron

(82) Internal ridge corresponding to mesopleural sulcus: 0, absent or not clearly defined; 1, present and distinct (Fig. 12E)

(83) Transepimeral sulcus: 0, only weakly indicated or absent (Fig. 1A); 1, present and distinct so that mesepimeron is separated into lower and upper mesepimeron (Fig. 3H)

(84) Internal ridge corresponding to transepimeral sulcus: 0, absent or not clearly defined; 1, present and distinct (Fig. 14B)

(85) Surface sculpture of upper mesepimeron: 0, completely reticulate (Fig. 1A); 1, dorsal margin and posterior half reticulate; 2, only dorsal margin reticulate (Fig. 3H); 3, completely smooth (Fig. 16C)

(86) Setal pattern of upper mesepimeron: 0, entirely bare (Fig. 3H); 1, partly to entirely setose, at least with some setae in subalar pit (Fig. 11A)

(87) Surface sculpture of lower mesepimeron: 0, completely reticulate (Fig. 3H); 1, completely smooth (Fig. 16C)

(88) Transepisternal sulcus: 0, mesepisternum not separated into lower and upper mesepisternum; 1, mesepisternum separated into lower and upper mesepisternum by distinct transepisternal sulcus (Fig. 10H)

(89) Anterior margin of mesepisternum: 0, without two submedian incisions; 1, with two submedian incisions or sharp edges for articulation with prepectus (Fig. 3A)

(90) Procoxal depressions: 0, only weakly indicated or absent; 1, present and distinct (Fig. 3A)

(91) Epicnemium: 0, missing or indistinct, at least without protruding margin; 1, present and distinct, its posterior margin with a sharp epicnemial carina (Fig. 5E)

(92) Mesodiscrimen externally: 0, absent or indistinct; 1, present as distinct line or sulcus (Fig. 10E)

(93) Mesofurcal pits: 0, one present (Fig. 1B); 1, two present (Fig. 10H)

(94) Position of (posterior) mesofurcal pit: 0, close to centre of mesepisternum (Fig. 11D); 1, close to posterior border of mesepisternum at level of anterior margin of mesotrochantinal plate (Fig. 10H); 2, between mesocoxal foramina (Fig. 12C)

(95) Carina at the anterior margin of mesotrochantinal plate: 0, absent (Fig. 11G); 1, present but interrupted medially (Fig. 11F); 2, present and complete (Fig. 10H)

(96) Median carina between mesocoxal foramina: 0, absent (Fig. 11G); 1, present but incomplete; 2, present and complete (Fig. 11D)

(97) Intercoxal membrane: 0, completely absent or inconspicuous and reduced to small strip posterior to mesocoxal foramina (Fig. 11G); 1, present and conspicuous, at least as long as median length of mesotrochantinal plate (Fig. 12B)

(98) Mesocoxal foramen: 0, completely enclosed by sclerotised cuticle (Fig. 11D); 1, incompletely enclosed by sclerotised cuticle (Fig. 3G)

(99) Internal mesopleuron: 0, posterior margin without septum; 1, posterior part of mesopleuron continuous with septum (Fig. 11H)

(100) Mesofurcal bridge (Heraty et al. 1997): 0, present and complete (Fig. 14A); 1, absent but anterior apodemes present (Fig. 14B); 2, absent and apodemes absent (Fig. 14E)

(101) Lobe or ridge at posterior base of mesofurca: 0, present (Fig. 3E); 1, absent

(102) Discrimenal lamella (1): 0, extending to anterior margin of mesepisternum (Fig. 3E); 1, not extending to anterior margin of mesepisternum (Fig. 13H)

(103) Discrimenal lamella (2): 0, undivided anteriorly (Fig. 14C); 1, divided anteriorly (Fig. 14F)

(104) Discrimenal lamella (3): 0, undivided posteriorly (Fig. 12H); 1, divided posteriorly (Fig. 13H)

(105) Horizontal plate of mesofurca: 0, not extended anteromedially (Fig. 14G); 1, anteromedially extended, forming narrow strip with parallel sides (Fig. 13D); 2, anteromedially extended and distinctly tapering ventrally (Fig. 3D); 3, anteromedially extended but only slightly tapering ventrally, conspicuously broadened all over (Fig. 14B)

Metanotum

(106) Metanotum relative to propodeum: 0, not fused with propodeum; 1, posteriorly fused with propodeum (Fig. 10A)

(107) Metanotum relative to mesoscutellum: 0, metanotum not overlapped by mesoscutellum; 1, mesoscutellum extends up to middle of metanotum (Fig. 15B); 2, mesoscutellum extends to posterior margin of metanotum so that only part of lateral panel is visible in dorsal view; 3, metanotum overlaps posterior margin of mesoscutellum (Fig. 3H)

(108) Metascutellum (1): 0, extends to anterior margin of metanotum (Fig. 16C); 1, does not extend to anterior margin of metanotum (Fig. 4A)

(109) Metascutellum (2): 0, extends to posterior margin of metanotum (Fig. 16H); 1, does not extend to posterior margin of metanotum (Fig. 4A)

(110) Pilosity metascutellum: 0, pilose or at least with some setae (Fig. 15G); 1, bare (Fig. 16H)

(111) Median carina at metascutellum: 0, absent (Fig. 16H); 1, present (Fig. 16E)

(112) Pilosity of lateral panel of metanotum: 0, pilose; 1, bare (Fig. 16H); 2, pair of setae (sometimes reduced to wart-like structures) present (Fig. 17B)

(113) Surface of lateral panel of metanotum: 0, foveolae not recognisable (Fig. 16H); 1, foveolae at least indicated by longitudinal ridges (Fig. 4B)

(114) Metascutellar arms: 0, reduced or at most forming narrow carina (Fig. 15A); 1, broad, but at most as broad as half of median length of lateral panel (Fig. 16H); 2, broader than median length of lateral panel (Fig. 16E)

Metapectus

(115) Shape of lateral metapleuron: 0, triangular or subtriangular (Fig. 3H); 1, not triangular (Fig. 16C)

(continued next page)
Appendix 2. (continued)

(116) Separation between metapleuron and propodeum: 0, not clearly visible (Fig. 11C); 1, separated by incomplete sulcus; 2, separated by complete sulcus (Fig. 3H)

(117) Sculpture of metapleuron: 0, reticulate (as propodeum) (Fig. 1A); 1, anterior half smooth, posterior half reticulate (Fig. 15E); 2, anterior half reticulate, posterior half smooth; 3, completely smooth (Fig. 16C)

(118) Pilosity of metapleuron: 0, completely pilose (Fig. 16F); 1, only lateral margins pilose; 2, only caudal half pilose (Fig. 11A); 3, bare (Fig. 3H)

(119) Relation between mesopleuron and metapleuron: 0, developed as separate sclerites; 1, partly fused ventrally; 2, completely fused ventrally and laterally

(120) Pair of submedian metafurcal pits: 0, two submedian pits present and clearly separate from each other (Fig. 16F); 1, submedian pits absent (Fig. 16D)

(121) Median metafurcal pit: 0, absent (Fig. 16F); 1, present, but consisting of two holes in one shared pit or depression (Fig. 15F); 2, present as single pit (Fig. 16D)

(122) Metadiscrimen externally: 0, inconspicuous or absent (Fig. 3G); 1, present as a line; 2, present as deep sulcus

(123) Metapleural depression for mesocoxa: 0, absent or inconspicuous; 1, present and distinct

(124) Carina on posterior part of metepisternum: 0, two submedian carinae present (Fig. 16F); 1, one median carina present (Fig. 16D); 2, completely absent

(125) Transverse metapleural carina: 0, complete and sharp (Fig. 16D); 1, incomplete (Fig. 16F); 2, absent

(126) Carina connecting metacoxal foramen with propodeal foramen: 0, absent; 1, present (Fig. 16D)

(127) Proximal part of metacoxa: 0, without sharp transverse carina; 1, with sharp transverse carina

(128) Area between metacoxal and propodeal foramina: 0, broadly sclerotised (Fig. 17E); 1, sclerotised parts restricted to narrow strips (Fig. 19G)

(129) Metapleural arms: 0, ventrally fused above level of metapleuron thus appearing y-shaped (Fig. 18D); 1, ventrally fused at or slightly above level of metapleuron thus appearing u-shaped (Fig. 18J) or v-shaped (Fig. 19G); 2, ventrally clearly separated from each other (Fig. 18G)

(130) Metapleural plate: 0, present (Fig. 18J); 1, absent (Fig. 14G)

(131) Configuration of metapleural plate with metafurca: 0, completely or partly fused with basal part of metafurcal arm (Fig. 18H); 1, clearly separate from metafurcal arm (Fig. 18G)

(132) Metadiscriminal lamella (1): 0, extending to anterior margin of metepisternum (Fig. 18G); 1, not extending to anterior margin of metepisternum (Fig. 18A)

(133) Metadiscriminal lamella (2): 0, not conspicuously elongate at anterior margin of metepisternum (Fig. 19F); conspicuously elongate at anterior margin of metepisternum, reaching level of articulation point between metafurcal arm and metapleural apodeme (Fig. 19J)

Propodeum

(134) Position of propodeal spiracle: 0, near anterior margin of propodeum (Fig. 16C); 1, at middle of propodeum or further posteriorly

(135) Sensilla inside propodeal spiracle: 0, absent; 1, present

(136) Spiracular rim: 0, inconspicuous or inside propodeum (Fig. 15G); 1, distinct and above propodeum (Fig. 15B)

(137) Spiracular shape: 0, oval; 1, kidney-shaped (Fig. 16C); 2, circular (Fig. 15B)

(138) Paraspiracular sulcus: 0, absent; 1, present (Fig. 16E)

(139) Median longitudinal carina: 0, absent or indistinct; 1, present and straight (Fig. 15G); 2, present but posteriorly diverging into two diagonal carinae

(140) Pair of submedian carinae: 0, absent or indistinct; 1, present, with median sulcus; 2, present, but without median sulcus (Fig. 16A)

(141) Costula (transverse carina): 0, absent or indistinct; 1, present (Fig. 4B)

(142) Plicae: 0, absent or indistinct; 1, present but not extending to anterior propodeal margin (Fig. 17A); 2, present and extending to anterior propodeal margin (Fig. 15B)

(143) Basal forvea: 0, absent or indistinct; 1, present and distinct (Fig. 4B)

(144) Nucha: 0, absent or indistinct (Fig. 17A); 1, present and distinct (Fig. 4A)

(145) Propodeal sculpture: 0, reticulate (Fig. 15G); 1, smooth or only weakly reticulate (Fig. 15B)

(146) Propodeal pilosity: 0, bare; 1, conspicuous pilosity exclusively on lateral surface (Figs 4, 15B); 2, pilose over entire surface, but with longer or more dense pilosity on lateral surface (Fig. 15C); 3, uniformly pilose over entire surface

Petiole

(147) Ventrall portion of petiole: 0, exposed (Fig. 15H); 1, concealed (Fig. 12C)

(148) Size of petiole: 0, elongate, in dorsal view at least slightly longer than wide (Fig. 4G); 1, not elongate, mostly transverse (Fig. 4H)

(149) Ventrall surface of petiole: 0, longitudinally not divided; 1, longitudinally divided by complete median sulcus (Fig. 20E); 2, only distally divided by incomplete median sulcus

(150) Surface sculpture: 0, strongly reticulate (Fig. 4G); 1, smooth or with only shallow impressions (Fig. 4H)

(151) Pilosity of petiole: 0, present (Fig. 20H); 1, absent (Fig. 4G)

(152) Lateral surface: 0, pair of lateral tubercles present (Fig. 20E); 1, pair of lateral tubercles absent (Fig. 20H)

(153) Median longitudinal carina: 0, absent; 1, present dorsally (Fig. 4G)

(154) Anterolateral edges of petiole: 0, not extended; 1, extended and protruding (Fig. 15G, H); 2, complete anterior margin of petiole carinate and slightly overlapping nucha of propodeum (Figs 15B, 20G)
### Appendix 3. Data matrix

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisopteromalus</td>
<td>000110001</td>
</tr>
<tr>
<td>Cecidostiba</td>
<td>120011001</td>
</tr>
<tr>
<td>Dibrachys</td>
<td>100011001</td>
</tr>
<tr>
<td>Larilogaster</td>
<td>000111100</td>
</tr>
<tr>
<td>Nasonia</td>
<td>000110011</td>
</tr>
<tr>
<td>Pachycrepoides</td>
<td>120011001</td>
</tr>
<tr>
<td>Cyrtogaster</td>
<td>120011011</td>
</tr>
<tr>
<td>Panstenon</td>
<td>100011011</td>
</tr>
<tr>
<td>Trichilogaster</td>
<td>000011101</td>
</tr>
<tr>
<td>Asaphes</td>
<td>110000101</td>
</tr>
<tr>
<td>Enoggera</td>
<td>110000101</td>
</tr>
<tr>
<td>Notanus</td>
<td>100101001</td>
</tr>
<tr>
<td>Thaumasura</td>
<td>100110011</td>
</tr>
<tr>
<td>Spalangia</td>
<td>021010001</td>
</tr>
<tr>
<td>Ormyrus</td>
<td>100000111</td>
</tr>
<tr>
<td>Megagnosticus</td>
<td>100000111</td>
</tr>
<tr>
<td>Monodontomorphae</td>
<td>100010001</td>
</tr>
<tr>
<td>Podagrion</td>
<td>100010001</td>
</tr>
<tr>
<td>Tormyus</td>
<td>010001001</td>
</tr>
<tr>
<td>Eurytoma</td>
<td>010000100</td>
</tr>
<tr>
<td>Tetramesa</td>
<td>010010011</td>
</tr>
<tr>
<td>Chalis</td>
<td>010010001</td>
</tr>
<tr>
<td>Anthrocephalus</td>
<td>010010001</td>
</tr>
<tr>
<td>Leucospis</td>
<td>010001001</td>
</tr>
<tr>
<td>Schizaspis</td>
<td>101000101</td>
</tr>
<tr>
<td>Perilampus</td>
<td>000011101</td>
</tr>
<tr>
<td>Cirrhopus</td>
<td>000070000</td>
</tr>
<tr>
<td>Aprostocerus</td>
<td>100007000</td>
</tr>
<tr>
<td>Entedon</td>
<td>120011001</td>
</tr>
<tr>
<td>Eujacobsonia</td>
<td>000171221</td>
</tr>
<tr>
<td>Blastophaga</td>
<td>000000111</td>
</tr>
<tr>
<td>Philotyriseps</td>
<td>000012122</td>
</tr>
<tr>
<td>Eupelmae</td>
<td>100000001</td>
</tr>
<tr>
<td>Eupelmae female</td>
<td>100010001</td>
</tr>
<tr>
<td>Ericadyus</td>
<td>111011001</td>
</tr>
<tr>
<td>Trichogramma</td>
<td>000070101</td>
</tr>
<tr>
<td>Centrodora</td>
<td>002070101</td>
</tr>
<tr>
<td>Encarscia</td>
<td>002070101</td>
</tr>
<tr>
<td>Clytina</td>
<td>000071101</td>
</tr>
<tr>
<td>Gonatocerus</td>
<td>000071101</td>
</tr>
<tr>
<td>Palaeoemyrma</td>
<td>000001107</td>
</tr>
<tr>
<td>Megaspilus</td>
<td>001000007</td>
</tr>
<tr>
<td>Monomachus</td>
<td>021010000</td>
</tr>
<tr>
<td>Vanhornia</td>
<td>001000100</td>
</tr>
<tr>
<td>Archaeoteleia</td>
<td>020010000</td>
</tr>
<tr>
<td>Italia</td>
<td>011010000</td>
</tr>
<tr>
<td>Megischus</td>
<td>020010120</td>
</tr>
</tbody>
</table>

(continued next page)
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisopteromalus male</td>
<td></td>
</tr>
<tr>
<td>Caccidosta male</td>
<td></td>
</tr>
<tr>
<td>Dibrachys male</td>
<td></td>
</tr>
<tr>
<td>Lariophagus male</td>
<td></td>
</tr>
<tr>
<td>Nasonia male</td>
<td></td>
</tr>
<tr>
<td>Pachyperipoides male</td>
<td></td>
</tr>
<tr>
<td>Cyrtogaster male</td>
<td></td>
</tr>
<tr>
<td>Panstemon male</td>
<td></td>
</tr>
<tr>
<td>Trichilogaster male</td>
<td></td>
</tr>
<tr>
<td>Asaphes male</td>
<td></td>
</tr>
<tr>
<td>Enisoggera male</td>
<td></td>
</tr>
<tr>
<td>Notanias male</td>
<td></td>
</tr>
<tr>
<td>Thaumastara male</td>
<td></td>
</tr>
<tr>
<td>Spalangia male</td>
<td></td>
</tr>
<tr>
<td>Ormyrus male</td>
<td></td>
</tr>
<tr>
<td>Megastigmus male</td>
<td></td>
</tr>
<tr>
<td>Monodontomerus male</td>
<td></td>
</tr>
<tr>
<td>Podagrin male</td>
<td></td>
</tr>
<tr>
<td>Tarymus male</td>
<td></td>
</tr>
<tr>
<td>Eurytoma male</td>
<td></td>
</tr>
<tr>
<td>Tetramesa male</td>
<td></td>
</tr>
<tr>
<td>Antrocephalus male</td>
<td></td>
</tr>
<tr>
<td>Leucospius male</td>
<td></td>
</tr>
<tr>
<td>Schizaspidia male</td>
<td></td>
</tr>
<tr>
<td>Perilampus male</td>
<td></td>
</tr>
<tr>
<td>Cirrospilus male</td>
<td></td>
</tr>
<tr>
<td>Aprostocetus male</td>
<td></td>
</tr>
<tr>
<td>Entedon male</td>
<td></td>
</tr>
<tr>
<td>Enacosophia male</td>
<td></td>
</tr>
<tr>
<td>Blastophaga male</td>
<td></td>
</tr>
<tr>
<td>Philotrypes male</td>
<td></td>
</tr>
<tr>
<td>Eupelmus male</td>
<td></td>
</tr>
<tr>
<td>Eupelmus female</td>
<td></td>
</tr>
<tr>
<td>Ericydus male</td>
<td></td>
</tr>
<tr>
<td>Trichogramma male</td>
<td></td>
</tr>
<tr>
<td>Centrodora male</td>
<td></td>
</tr>
<tr>
<td>Encarsia male</td>
<td></td>
</tr>
<tr>
<td>Clytina male</td>
<td></td>
</tr>
<tr>
<td>Gonatocerus male</td>
<td></td>
</tr>
<tr>
<td>Palacomyharz male</td>
<td></td>
</tr>
<tr>
<td>Megaspius male</td>
<td></td>
</tr>
<tr>
<td>Monomachus male</td>
<td></td>
</tr>
<tr>
<td>Vanhorna male</td>
<td></td>
</tr>
<tr>
<td>Archaeoleptia male</td>
<td></td>
</tr>
<tr>
<td>Italia male</td>
<td></td>
</tr>
<tr>
<td>Megischas male</td>
<td></td>
</tr>
</tbody>
</table>

http://www.publish.csiro.au/journals/is