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A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera)

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Abstract

Chalcidoidea (Hymenoptera) is extremely diverse with an estimated 500 000 species. We present the first phylogenetic analysis of the superfamily based on both morphological and molecular data. A web-based, systematics workbench mx was used to score 945 character states illustrated by 648 figures for 233 morphological characters for a total of 66 645 observations for 300 taxa. The matrix covers 22 chalcidoid families recognized herein and includes 268 genera within 78 of 83 subfamilies. Morphological data were analysed alone and in combination with molecular data from ribosomal 18S (2105 bp) and 28S D2–D5 expansion regions (1812 bp). Analyses were analysed alone and in combined datasets using implied-weights parsimony and likelihood. Proposed changes in higher classification resulting from the analyses include: (i) recognition of Eriaporidae, *revised status*; (ii) recognition of Cynipencyrtidae, *revised status*; (iii) recognition of Azotidae, *revised status*; (iv) inclusion of Sycophaginae in Agaonidae, *revised status*; (v) reclassification of Aphelinidae to include Aphelininae, Calesinae, Coccophaginae, Eretmocerinae and Eriaphytinae; (vi) inclusion of Cratominae and Panstenoninae within Pteromalinae (Pteromalidae), *new synonymy*; (vii) inclusion of Epichrysomallinae in Pteromalidae, *revised status*. At a higher level, Chalcidoidea was monophyletic, with Mymaridae the sister group of Rotoitidae plus the remaining Chalcidoidea. A eulophid lineage was recovered that included Aphelinidae, Azotidae, Eulophidae, Signiphoridae, Tetracampidae and Trichogrammatidae. Eucharitidae and Perilampidae were monophyletic if Eutrichosomatinae (Pteromalidae) was included, and Eupelmidae was monophyletic if *Oodera* (Pteromalidae: Cleonyminae) was included. Likelihood recovered a clade of Eupelmidae + (Tanaostigmatidae + (*Cynipencyrtus* + Encyrtidae). Support for other lineages and their impact on the classification of Chalcidoidea is discussed. Several life-history traits are mapped onto the new phylogeny.

Without question, Chalcidoidea is one of the most megadiverse groups of insects. Their morphological diversity is staggering (Fig. 1). They range in size from such veritable giants as females of *Leptofoenus* (Pteromalidae), which exceed 20 mm, to the minute and morphologically bizarre male of *Dicopomorpha echmepterygis* (Mymaridae), the smallest known specimen of which is 0.13 mm long. Males of *D. echmepterygis* have lost eyes, ocelli, mouthparts, antennal flagellum, wings, tarsi except for a highly modified arolium, and virtually any other feature that places them as parasitic wasps (Fig. 1a). Other bizarrities include male fig wasps, which can be reduced to turtle-like fighting machines that bear no resemblance to their corresponding females and are hardly recognizable as chalcidoids, or the grotesquely enlarged scutellum (Fig. 1h) of *Galearia latreillei* (Eucharitidae) and the dart-shaped ovipositor sheaths (Fig. 1j) of *Cameronella* (Pteromalidae). Convergent morphology is also rampant, and enlarged femora, enlarged acropleura, reductions in the number of antennal and tarsal segments, as well as reductions in wings and wing venation have all been proposed as being independently derived in very distantly related taxonomic groups. Matching their great morphological diversity is their numerical diversity, with estimates of more than 500 000 species, of which only about 22 506 have been described (Heraty, 2009; Noyes, 2011). The extreme numerical and morphological diversity has resulted in a large number of higher taxa being described relative to other superfamilies of parasitic Hymenoptera, with 19 families and 83 subfamilies prior to the present study (Noyes, 2011). As a result, no single individual has previously been able to conduct a comprehensive phylogenetic analysis based on morphology, and there have been only a few proposals for higher-level relationships of Chalcidoidea that either are not phylogenetic (Grissell, 1987; Gibson, 1990; Noyes, 1990) or are based on only limited character systems and relatively few taxa (Gibson, 1986a; Heraty et al., 1997; Heraty and Schauff, 1998; Krogmann and Vilhelmsen, 2006).

The morphological and numerical diversity of Chalcidoidea is closely matched by their biological diversity. Although mostly parasitoids, phytophagous species are known from six families: Agaonidae, Eulophidae, Eurytomidae, Pteromalidae, Tanaostigmatidae and Torymidae. Their animal host range includes 13 insect orders, spiders, ticks, mites, pseudoscorpions and even gall-forming Nematoda (Austin et al., 1998; Gibson et al., 1999). Single species such as *Dibrachys microgastri* (Pteromalidae) and *Eupelmus vesicularis* (Eupelmidae) can have an extremely wide host range that includes several orders and numerous families, whereas many other species appear to be narrowly oligophagous or monophagous, for example, some *Aphytis* or *Aphelinus* (Aphelinidae). Species attack all life stages from eggs to adults and, as internal parasitoids, often multiple life stages. Species can be primary, secondary, or even tertiary parasitoids, with some taxa required to parasitize their own species to complete development (heteronomous autoparasitism) (Hunter and Woolley, 2001). Because of its members' host associations and life-history traits, Chalcidoidea is one of the most important groups for biological control of other insects in both natural and agricultural ecosystems (Noyes and Hayat, 1994; Heraty, 2009). Some Chalcidoidea, especially *Trichogramma* (Trichogrammatidae) and *Nasonia* (Pteromalidae), are also model organisms for numerous studies of sex determination, the influence of bacterial endosymbionts and the genetics of speciation (2223 publications and 34 155 citations from Web of Science, 17 August 2012). However, there has not been a robust phylogenetic hypothesis to provide an evolutionary framework for these studies.

Members of the Chalcidoidea appear to have undergone their spectacular radiation in a relatively short time. Both Mymaridae and Mymarommatoidea occur in Cretaceous amber deposits, with the first mymarids recorded from upper Albian deposits, 97–110 Ma (Gibson et al., 2007; Poinar and Huber, 2011). "Eulophoid" fossils have been found in mid-Cretaceous (Yoshimoto, 1975; Schmidt et al., 2010) and lower-Cretaceous amber (Kaddumi, 2005; photo of *Minutoma yathribi* Kaddumi suggests Tetracampidae: Bouceklytinae; J.T.H.), but otherwise the greatest diversity of Chalcidoidea does not appear until the Eocene with the appearance of most family groups, including Eucharitidae, Eupelmidae and Torymidae (Gibson, 2008; Heraty and Darling, 2009). Their rapid post-Cretaceous diversification parallels similar radiations in the angiosperms and insects (Wiegmann et al., 2000; Hunt et al., 2007; Regier et al., 2009; Bell et al., 2010). Perhaps as a result of this rapid radiation, the classification of Chalcidoidea has been highly unstable, with the recognition of anywhere from nine to 24 families (Bouček, 1988b; Gibson et al., 1999). Nineteen families were recognized prior to this study, with between 78 and 89 subfamilies (depending on the source), and 2098 genera and 25 206 species described (Noyes, 2011). Previous analyses of relationships of Chalcidoidea within Hymenoptera based either on morphological or molecular data strongly support their monophyly within the Proctotrupomorpha sensu Sharkey et al. (2011). Königsmann (1978) proposed Chalcidoidea as the sister group of Cynipoidea following most earlier workers (e.g. Ashmead, 1896; Bradley, 1955), whereas Rasnitsyn (1988) proposed Platygastroidea as their sister group, primarily because of

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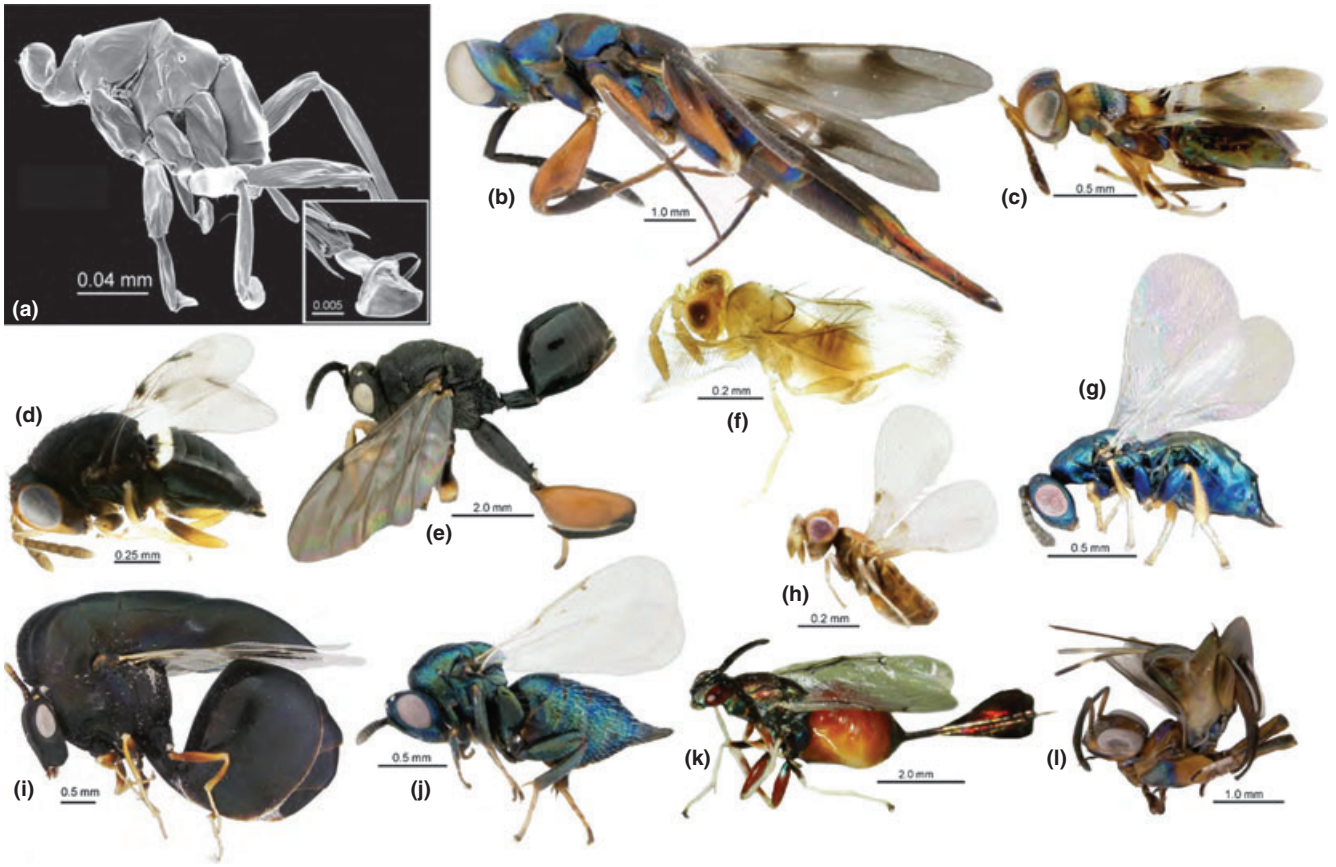


Fig. 1. Habitus images. Male: (a) *Dicopomorpha echmepterygis* (Mymaridae); inset is enlargement of metatarsus. Females: (b) *Lycisca* sp. (Pteromalidae: Cleonyminae). (c) *Cheiloneurus fulvescens* (Encyrtidae). (d) *Promuscidea* sp. (Eriaporidae). (e) *Chalcis sispes* (Chalcididae). (f) *Cales noacki* (Aphelinidae: Calesinae). (g) *Otitesella* (Pteromalidae: Otitesellinae). (h) *Aphelinoidea* sp. (Trichogrammatidae). (i) *Galearia latreillei* (*Eucharitidae*). (j) *Ormyrus* sp.1 (Ormyridae). (k) *Cameronella* sp. (Pteromalidae: Colotrechninae). (l) *Tineobius* sp. (Eupelmidae). Character state associations explained in text.

structural similarity between the larvae of Mymaridae and Scelionidae, two groups of egg parasitoids. However, more recent analyses placed the sister group of Chalcidoidea as either Mymarommatoidea (Gibson, 1986a; Sharkey et al., 2011) or Diaprioidea (Heraty et al., 2011; Munro et al., 2011; Sharkey et al., 2011). These same analyses all place Mymaridae as the sister group of the remaining Chalcidoidea, as originally proposed by Gibson (1986a). The morphological analyses of Vilhelmsen et al. (2010) placed Chalcidoidea most frequently as sister group of the clade Mymarommatoidea + Maamingidae. Using 666 chalcidoid taxa and 56 outgroup taxa, Munro et al. (2011) provided the first comprehensive molecular analysis for the superfamily using two gene regions (18S and 28S). The results provided support for most subfamily groups and monophyly of several families (Agaonidae, Encyrtidae, Eucharitidae, Leucospidae, Mymaridae, Ormyridae, Signiphoridae and Trichogrammatidae). Two families, Eulophidae and Tanaostigmatidae, were monophyletic if *Trisecodes* and *Cynipencyrtus*, respectively, were excluded—both of which are appropriate exclusions as discussed in the literature (Gibson, 1990; Burks et al., 2011) and below. Several other families were paraphyletic or polyphyletic (Aphelinidae, Chalcididae, Eupelmidae, Eurytomidae, Pteromalidae, Tetracampidae and Torymidae). Pteromalidae has long been considered as a polyphyletic group (Gibson et al., 1999) and dispersion across the tree was expected, but the absence of monophyly for Chalcididae was surprising because several proposed morphological synapomorphies support their monophyly (Wijesekara, 1997). The lack of any strong support for the backbone of the molecular tree beyond Mymaridae was problematic, and several alternative scenarios were possible depending on alignment or method of analysis, including the monophyly of Chalcididae in at least one case (Munro et al., 2011).

Compiling morphological data across Chalcidoidea necessarily requires a collaborative approach to tap the combined resources and knowledge of a large, global group of researchers to address a complex phylogenetic problem. We now have the "cybertaxonomic" tools necessary to be able to undertake such a study.

The web-based taxonomic workbench management system mx (http://purl.org/NET/mx-database; Yoder et al., 2006–present) was used to compile, score and illustrate 233 characters and 945 character states so that these could be interpreted unambiguously by 26 different chalcidologists in 10 different countries for 300 taxa across 78 subfamily taxa. The characters and character states used for the analysis resulted from a series of workshops involving the study participants, at which we initially evaluated 733 characters derived from the literature and used either for phylogenetic or morphological comparisons. Characters were evaluated for their applicability for inferring relationships, homology and ability to be scored across as many taxa as possible. Because of the morphological complexity of Chalcidoidea, many of these original characters were eliminated from this analysis although they may need to be reconsidered in future evaluations.

During the project, we developed cybertaxonomic approaches that can be applied to any group of organisms. The results of the analyses of our combined molecular and morphological data form a new framework for understanding relationships within Chalcidoidea and the evolution of one of the most speciose groups within the Hymenoptera. The further strengthening of phylogenetic hypotheses within Chalcidoidea should help to accelerate the recognition and interpretation of new chalcid taxa, and the recruitment of new researchers to study this fascinating and megadiverse group of insects.

Materials and methods

Taxonomic sampling

A total of 300 operational taxonomic units (OTUs) were included in this study (Appendix 1). These encompass the 19 families, 78 subfamilies, 268 genera and 283 species of Chalcidoidea recognized prior to this study. All figures and tables included in this work follow the prior classification, except for Table 2, in which we present our revised family classification. The only subfamilies not sampled were Austroterobiinae, Elatoidinae, Louriciinae, Neodiparinae, Nefoeninae, Parasaphodinae and Storeyinae (all Pteromalidae and monogeneric except for Austroterobiinae). One or more specimens, including dissections whenever possible, were used to score each OTU. Most internal features, such as musculature and internal cuticular features, were not included because it was not possible to score them across the breadth of taxa. For most taxa, we coded both male and female features for each OTU, but with a preference for coding females because of their tendency to have more morphological diversity than males. However, Eupelminae (Eupelmidae) exhibit even stronger sexual dimorphism, and males and females were treated as separated OTUs with all characters scored independently (Appendix 1). Most character scoring was done for each group by the taxonomic expert for that group, although J.M.H., J.L. and R.A.B. scored OTUs for almost all families. *Dirhinus giffardii* was purposefully coded twice by R.A.B. and G.D. as a check on investigator bias in coding taxa. Four outgroup taxa included exemplars of Mymarommatoidea (Mymarommatidae, two species), Platygastroidea (Scelionidae s.s., one species) and Diaprioidea (Diapriidae, one species).

Excluding the newly proposed families, we follow the family-group classification of Chalcidoidea of Noyes (2011), with additional resolution from the following: Agaonidae follows Cruaud et al. (2010); Aphelinidae follows Hayat (1998); Chalcididae follows Narendran (1989) and Delvare and Bouček (1992); Cleonyminae follows Gibson (2003); Eucharitidae follows Heraty (2002); Eulophidae follows Burks et al. (2011); Pteromalidae follows Delucchi (1962), Graham (1969), Hedqvist (1971) and Bouček (1988a); Toryminae follows Grissell (1995); and Trichogrammatidae follows Owen et al. (2007). Families, subfamilies and tribes recognized herein are summarized in Table 1 and Appendix 1, along with their abbreviations used in the text and figures.

Terminology

Morphological terms generally follow Gibson (1997), with additional terms for the head from Kim and Heraty (2012), and for the mesosoma from Krogmann and Vilhelmsen (2006). A list of abbreviations used for structure in the text and figures is given in Appendix 2. We have vetted our terms through the Hymenoptera Anatomy Ontology (HAO: http://portal.hymao.org) for consistency across Hymenoptera (Appendix 2). We use the term bristle for a stouter seta that is clearly differentiated from other shorter and thinner setae on the relevant structure, though the difference between a bristle and seta can sometimes be difficult to define because it is one of relative size. Where appropriate for clarity, we refer to the equivalent terms in HAO in the text (e.g. basal ring versus cupula). Each morphological term is defined explicitly either here or in the respective character and state descriptions in mx.

A few deviations from traditional terminology for Chalcidoidea require explanation. We agree with Onagbola and Fadamiro (2008b) that the antennal structure that has sometimes been called the terminal button in some Pteromalidae (generally the fourth claval segment) should be considered as a separate, 12th flagellomere that is homologous with the apical flagellomere of Rotoitidae; therefore, in most Chalcidoi-

Table 1
Monophyly of family-group taxa of Chalcidoidea

Code	Taxonomy (ML/PAR/BY)	Genera	Species	Individuals	Monophyly
AG	**Agaonidae (76/757)**	5	5	5	+/+/+
AGA	"Agaoninae"[a]	2	2	2	−/−/−
AGB	"Blastophaginae"	1	1	1	n/a
AGK	Kradibiinae	1	1	1	n/a
AGT	Tetrapusinae	1	1	1	n/a
AP	**Aphelinidae (33/1168)**	18	25	25	−/−/−
APA	Aphelininae	7	7	7	+/+/+
APAI	Aphelinini	2	2	2	−/−/−
APAY	Aphytini	3	3	3	−/−/−
APAE	Eutrichosomellini	2	2	2	−/+/−
APZ	Azotinae	1	3	3	+/+/+
APC	Coccophaginae	5	9	9	−/−/−
APCC	Coccophagini	1	1	1	n/a
APCE	Euxanthellini	1	1	1	n/a
APCY	Physcini	1	1	1	n/a
APCP	Pteroptricini	2	6	6	+/+/+
APR	Eretmocerinae	1	2	2	+/+/+
APY	Eriaphytinae	1	1	1	n/a
APO	Eriaporinae	1	1	1	n/a
APE	Euryischiinae	2	2	2	+/+/+
CH	**Chalcididae (87/1464)**	20	24	25	+/+/+
CHC	Chalcidinae	8	10	10	−/−/−
CHCB	Brachymeriini	1	1	1	n/a
CHCC	Chalcidini	3	5	5	+/+/+
CHCR	Cratocentrini	2	2	2	+/+/+
CHCP	Phasgonophorini	2	2	2	−/−/−
CHD	Dirhininae	1	2	3	+/−/+
CHE	Epitraninae	1	2	2	+/+/+
CHH	Haltichellinae	9	9	9	+/+/+
CHHA	Haltichellini	5	5	5	−/−/−
CHHY	Hybothoracini	3	3	3	−/−/−
CHTR	Tropimeridini	1	1	1	n/a
CHS	Smicromorphinae	1	1	1	n/a
EN	**Encyrtidae (460/3735)**	8	9	9	+/+/+
ENE	Encyrtinae	6	7	7	+/+/+
ENT	Tetracneminae	2	2	2	−/+/+
EU	**Eucharitidae (55/423)**	14	14	14	+/+/−
EUA	Akapalinae	1	1	1	n/a
EUE	Eucharitinae	8	8	8	+/+/+
EUE	Eucharitini	6	6	6	+/+/+
EUE	Psilocharitini	2	2	2	+/−/+
EUG	Gollumiellinae	2	2	2	−/+/−
EUO	Oraseminae	3	3	3	+/+/+
EL	**Eulophidae (297/4472)**	22	23	23	(+/+/+)*
ELI	Eulophidae i.s.	1	1	1	n/a
ELE	Entedoninae	5	5	5	+/+/+
ELN	Entiinae	3	3	3	+/+/+
ELU	Eulophinae	6	7	7	−/+/+
ELO	Opheliminae	2	2	2	+/+/+
ELT	Tetrastichinae	5	5	5	+/+/+
EP	**Eupelmidae (45/907)**	13	13	18	+[†]/−/−
EPC	Calosotinae	5	5	5	+/−/+
EPE	Eupelminae	5	5	10	+/+/+
EPN	Neanastatinae	3	3	3	+/−/+
EY	**Eurytomidae (88/1424)**	16	17	17	+/+/+
EYB	Buresiinae	2	2	2	+/+/+
EYE	Eurytominae	10	10	10	+/+/+
EYH	Heimbrinae	1	1	1	n/a
EYR	Rileyinae	3	4	4	−/−/−
LEU	**Leucospidae (4/134)**	2	2	2	+/+/+
MY	**Mymaridae (103/1424)**	13	14	14	+/+/+
MYI	Mymaridae i.s.	1	1	1	n/a

Table 1
(*Continued*)

Code	Taxonomy (ML/PAR/BY)	Genera	Species	Individuals	Monophyly
MYA	Alaptinae	3	3	3	−/−/−
MYE	Eubroncinae	1	1	1	n/a
MYM	Mymarinae	8	9	9	−/−/−
ORM	**Ormyridae (3/125)**	2	2	2	+/+/+
PE	**Perilampidae (15/277)**	12	15	15	−/−/−
PEI	Perilampidae i.s.	1	1	1	n/a
PEC	Chrysolampinae	4	5	5	+/−/+
PEP	Perilampinae	4	6	6	+/+/+
PEM	Philomidinae	3	3	3	+/+/+
PT	**Pteromalidae (588/3506)**	83	88	89	−/−/−
PTI	Pteromalidae i.s.	1	1	1	n/a
PT01	Asaphinae	2	2	2	+/+/+
PT26	Austrosystasinae	1	1	1	n/a
PT02	Ceinae	1	1	1	n/a
PT03	Cerocephalinae	2	2	2	+/+/+
PT04	Chromeurytominae	1	1	1	n/a
PT05	Cleonyminae	7	7	7	−/−/−
PT05D	Chalcedectini	1	1	1	n/a
PT05C	Cleonymini	2	2	2	+/+/+
PT05L	Lyciscini	3	3	3	+/+/+
PT05O	Ooderini	1	1	1	n/a
PT06	Coelocybinae	3	3	3	−/−/−
PT07	Colotrechninae	1	1	1	n/a
PT08	Cratominae	1	1	1	n/a
PT09	Diparinae	4	5	6	−/−
PT09D	Diparini	3	3	3	−/+/+
PT09N	Neapterolelapini	1	2	3	+/+/+
PT27	Ditropinotellinae	1	1	1	n/a
PT10	Epichrysomallinae	3	3	3	+/+/+
PT11	Eunotinae	6	7	7	+/−/−
PT11E	Eunotini	4	5	5	+/−/−
PT11M	Moranilini	1	1	1	n/a
PT11T	Tomocerodini	1	1	1	n/a
PT12	Eutrichosomatinae	3	3	3	−/−/−
PT13	Herbertiinae	1	1	1	n/a
PT28	Keiraninae	1	1	1	n/a
PT14	Leptofoeninae	2	3	3	+/+/+
PT15	Macromesinae	1	1	1	n/a
PT16	Miscogastrinae	8	8	8	−/−/−
PT16M	Miscogastrini	3	3	3	−/−/−
PT16S	Sphegigastrini	4	4	4	+/+/+
PT16T	Trigonoderini	1	1	1	n/a
PT17	Ormocerinae	6	6	6	−/−/−
PT17I	Ormocerinae i.s.	1	1	1	n/a
PT17M	Melanosomellini	3	3	3	−/−/−
PT17S	Systasini	2	2	2	+/+/+
PT18	Otitesellinae	2	2	2	−/−/−
PT19	Panstenoninae	1	2	2	+/+/+
PT20	Pireninae	2	2	2	+/+/+
PT21	Pteromalinae	13	13	13	−/−/−
PTI	Pteromalinae i.s.	1	1	1	n/a
PT21M	Micradelini	1	1	1	n/a
PT21P	Pteromalini	11	11	11	−/−/−
PT22	Spalangiinae	1	2	2	+/+/+
PT23	Sycoecinae	1	1	1	n/a
PT24	Sycophaginae	5	5	5	+/+/+
PT25	Sycoryctinae	2	2	2	+/−/−
ROT	**Rotoitidae (2/2)**	2	2	2	+/+/+
SI	**Signiphoridae (4/76)**	4	4	4	+/+/+
SIS	Signiphorinae	1	1	1	n/a
SIT	Thysaninae	3	3	3	−/−/−
TAN	**Tanaostigmatidae (9/92)**	3	3	3	(+/+/+)‡

Table 1
(*Continued*)

Code	Taxonomy (ML/PAR/BY)	Genera	Species	Individuals	Monophyly
TE	**Tetracampidae (15/50)**	8	8	8	−/−/−
TEM	Mongolocampinae	3	3	3	−/−/−
TEP	Platynocheilinae	1	1	1	n/a
TET	Tetracampinae	4	4	4	+/−/+
TO	**Torymidae (68/986)**	15	15	15	+/+/+
TOM	Megastigminae	4	4	4	+/+/+
TOT	Toryminae	11	11	11	+/+/+
TOTI	Toryminae i.s.	2	2	2	n/a
TOTC	Chalcimerini	1	1	1	n/a
TOTM	Microdonteromerini	3	3	3	+/+/+
TOTN	Monodontomerini	1	1	1	n/a
TOTP	Palachiini	1	1	1	n/a
TOTO	Podagrionini	1	1	1	n/a
TOTT	Torymini	1	1	1	n/a
TOTY	Torymoidini	1	1	1	n/a
TR	**Trichogrammatidae (83/839)**	4	4	4	+/+/+
TRO	Oligositinae	1	1	1	n/a
TROO	Oligositini	1	1	1	n/a
TRT	Trichogrammatinae	3	3	3	−/−/−
TRTI	Trichogrammatinae i.s.	2	2	2	n/a
TRTT	Trichogrammatini	1	1	1	n/a
CAL	**Calesinae incertae sedis (1/4)**	1	2	2	+/+/+

The estimated diversity (genera/species) after family names is derived from Noyes (2011). Our sampled diversity is indicated as: genera/species/individuals. Monophyly (+) is indicated for the likelihood (extended consensus)/implied weights parsimony / Bayesian results. Taxa represented by a single operational taxonomic unit or *incertae sedis* (*i.s.*) were considered not applicable (n/a) for clade monophyly. Codes are the classification abbreviations used on trees and in data matrices.

*Without *Trisecodes*.

†Including *Oodera* sp.

‡Without *Cynipencyrtus*.

dea, the maximum number of antennomeres is 14 not 13. For the antenna, the subsections of the flagellum, the flagellomeres, are referred to as "segments" when referring to the number of antennal segments. We discuss the number of flagellomeres with special reference to the basal flagellomere and the clava. Only the basal flagellomere is considered as an anellus in this analysis, unlike most works on Chalcidoidea, in which all reduced basal flagellomeres that lack multiporous plate sensilla (MPS) are considered as anelli. We interpret the clava as consisting of 1–6 differentiated apical flagellomeres or clavomeres that are either broadly connected or fused. The flagellomeres between the anellus and clava constitute the funicle, which is comprised of a series of narrowly connected articulating segments. The radicle in Hymenoptera is a differentiated subsection of the basal segment of the antenna, the scape, and as such we do not include this as segment within the antennal count (Goulet and Huber, 1993) as opposed to Isidoro et al. (1996) and Onagbola and Fadamiro (2008a).

Terms applied to the wing venation of Chalcidoidea have otherwise been used only for Platygastroidea (Narendran et al., 1977; Bouček, 1988a; Gibson, 1997). Attempts to homologize their reduced wing venation with that of other Hymenoptera were made by Burks (1938) and Bradley (1955), largely following Ross (1936). We have tried to summarize the homologous venation of Diapriidae and selected Chalcidoidea in Fig. 6. Notably, venation comparable to the diapriid genus *Belyta* (Fig. 6a) occurs in some Ormocerinae (e.g. *Espinosa*, Fig. 6d,e), and even more so in the ormocerine genus *Plastobelyta* (cf. fig. 4 of Yoshimoto, 1972). The most complete wing venation occurs in some Leucospidae (Fig. 6b) and Chalcididae (Burks, 1938; Narendran et al., 1977). A distinct basal vein (Rs + M) occurs in the fore wing of a very few Chalcidoidea (e.g. some Ormocerinae, Fig. 6d), whereas only a pigmented remnant of the same vein (e.g. some Ceinae, Fig. 6h) or a fold (e.g. Leucospidae, Fig. 6b) is found in most Chalcidoidea. The extent of wing venation in Chalcidoidea was found to be size-dependent by Danforth (1990). However, some chalcidoids, such as *Rotoita* (Rotoitidae) and some Ormocerinae and Ceinae, have more complete venation than most Chalcidoidea even though they are often quite small. The parastigma (= premarginal vein) is a unique component of the Sc + R (submarginal) vein. Distally, the parastigma is defined either by the hyaline break (hb, Fig. 6a,b,d,h,i) (= costal hinge of Bradley, 1955) or, if there is no hyaline break, then by the junction of the vein with the anterior margin of the wing. Proximally,

Sc + R is defined by the submarginal break (smb, Fig. 6b,c) or by the junction with the basal vein, Rs + M (Fig. 6b,c,i). Even if smoothly joined, the parastigma can usually be differentiated by being thicker than the submarginal vein, but also by the lack of any campaniform sensilla along the posterior margin of the vein (present on the submarginal vein of most taxa). The parastigma usually has one or more parastigmal sensilla (Fig. 6a–d,i). The fore wings of Mymaridae represent a special case. In Mymaridae, the apex of the parastigma is defined by the distal macrochaeta (dm) and the parastigma extends to the stigmal vein (Fig. 6l–m). Consequently, a marginal vein is considered to be absent from most mymarids, though both *Australomymar* and *Borneomymar* have a distinct marginal vein based on position of the dm. Using the dm as a point of reference, the parastigma may or may not bear a campaniform sensillum, which can occur distal or proximal to the dm in Mymaridae. The stigmal vein, as defined for Chalcidoidea, is typically composed of a narrower stigmal vein (= 2r) that apically has a usually wider or enlarged stigma, which is formed by the junction of Rs + 2r + r−m (Fig. 6b,c). In Mymaridae, the stigmal vein/stigma is often so short that the two parts cannot be distinguished (Fig. 6k,m). Either the stigma or the distal extension of Rs from the stigma always includes a series or group of campaniform sensilla (uncal sensilla). These sensilla and a distal remnant of the Rs vein form the uncus (Fig. 6g) when they extend from the stigma. Other features of the wings are described in the character list.

Morphological data

A total of 233 characters were selected from an initial list of 733 characters compiled from a survey of a wide variety of phylogenetic studies, reviews and taxonomic treatments (Copland and King, 1971; Darling, 1983, 1988, 1991; Schauff, 1984, 1991; Gibson, 1986a, 1989, 1995, 2003, 2009b; Graham, 1987; LaSalle, 1987; Woolley, 1988; Delvare, 1992; van Noort, 1992; Polaszek and Hayat, 1992; Heraty, 1994, 2002; LaSalle and Schauff, 1994; Noyes and Hayat, 1994; LaSalle et al., 1997; Wijesekara, 1997; Rasplus et al., 1998; Gibson et al., 1999; Krogmann and Vilhelmsen, 2006; Desjardins et al., 2007; Lotfalizadeh et al., 2007; Gates, 2008; Burks et al., 2011; Kim and Heraty, 2012). The final 233 characters were deemed potentially phylogenetically informative and scorable across all Chalcidoidea. All characters, OTUs and images were entered into mx (Yoder et al., 2006–present), with each referenced to a unique mx identification code. A complete list of the characters evaluated is available at the Dryad Data Repository (doi: 10.5061/dryad.gm201).

Data compilation

Our objective was to create a "living" matrix that can be scored by registered users for taxa included in this paper, and for future additions of taxa, or correction of any errors of observation or interpretation of structure. All character data were scored in mx either using a "one-click" coding method that sequentially presented cells (by row or column) to the user, or by a traditional table-like view in which individual cells were clicked then coded. When making a character state choice for a taxon, the user was presented with the OTU and character names, the associated states, images illustrating character states and a detailed textual description. For each choice, the user selected a level of confidence indicating whether the coding was based on observed structure, was a suspect observation, or was from the literature or inferred based on known congeners. The objective of the confidence levels was to allow cross-checking of the matrix after scoring had taken place and to aid future analyses by documenting inferred or otherwise tentatively coded states. Taxa were scored in a series of submatrices that could be optimized for a particular taxon (i.e. family group), with each submatrix contributing data to the overall "working" matrix. Matrices are exportable as TNT, Nexus, or NeXML formats for analysis. Images used in the matrix were deposited as a collection in MorphBank (http://www.morphbank.net/805664). The morphology matrix (Nexus format, with trees), combined matrix (TNT format) and supplementary figures mentioned in the text are available via Dryad (doi: 10.5061/dryad.gm201). Fully illustrated character descriptions are available at http://purl.org/NET/chalcidoidea. A dynamic public interface to the dataset, also to appear at this URL, is presently being described in a companion publication.

Characters

Within the following character list, numbers in brackets are the mx character identification code and reference the online mx file, which contains associated text and figures. Citations following each character refer to state descriptions that may be the same as, or similar to, those presented here, providing both a historical context and a link to further discussion.

Antenna characters (1–19).

1 [877] 12th flagellomere (female): **0**, not present (not defined by suture); **1**, present (defined by suture).

The antenna of most Chalcidoidea has previously been interpreted as maximally being composed of 13 segments, including 11 flagellomeres with at most a three-segmented clava. However, as discussed above, we agree with Onagbola and Fadamiro (2008b) that

what has sometimes been called the "terminal button" or "terminal nipple" in Pteromalidae (Graham, 1969) should be considered a separate, 12th flagellomere that is homologous with the apical flagellomere of Rotoitidae. Rotoitidae has a 12-segmented flagellum, including a six-segmented clava. Other than Rotoitidae, a clearly evident 12th flagellomere was reported in Chalcidoidea previously only in *Diglochis* (Pteromalidae: Pteromalinae) and some Eucharitidae (Dzhanokmen, 1979; Gibson, 1986a; Bouček and Noyes, 1987; Heraty, 2002). When present, there is a similar distinct border around the terminal button as found between other, larger claval segments, and such a segment is common for several chalcidoid groups that have previously been considered to have an 11-segmented flagellum. Unlike the preceding claval segments, the reduced terminal segment usually does not have MPS, though a distinct MPS is found on the terminal button of *Chromeurytoma* (Pteromalidae: Chromeurytominae) (Fig. 2g).

2 [873] Flagellomere one MPS (female): –, inapplicable (F1 considered as absent or fused with following segment); **0**, without MPS; **1**, with MPS.

Multiporous plate sensilla (MPS) in Chalcidoidea were described by Barlin et al. (1981) and Barlin and Vinson (1980), and elaborated upon by Basibuyuk and Quicke (1999). Although the number of basal flagellomeres lacking MPS varies within Chalcidoidea, at least the basal flagellomere (F1) lacks MPS in all females (and all males with the exception of Mymaridae, see character 19). Some Chalcidoidea have been shown to lack a homologous F1 based on other structural evidence. Where F1 could be interpreted confidently as absent, we scored this as inapplicable (treated as missing data). For example, within Eucharitidae, F1 was shown to be fused with F2 in *Gollumiella* (Fig. 2a,b) and proposed to be lost (likely fused with F2) in all Eucharitini (Heraty, 2002; Heraty et al., 2004). An anellus (= F1) was also proposed to be absent in all Aphelininae with the exception of *Mashimaro* (Kim and Heraty, 2012). In *Marietta* (Aphelininae), the presence of a coeloconic sensillum on F2 on the minute basal flagellomere (character 11; cf. fig. 203 of Kim and Heraty, 2012) would support their homology with F2 of other taxa; thus F1 would be absent and inapplicable. In both Eucharitini and Aphelinidae, the basal flagellomere (homologous F2) usually has distinct MPS, again suggesting homology to the F2 of other taxa. Outgroups may or may not have MPS on the true basal flagellomere. Citation: Lotfalizadeh et al. (2007, char. 63).

3 [874] Flagellomere one setae: –, inapplicable (F1 considered as absent or fused with following segment); **0**, present; **1**, absent.

Absence of setae from the first flagellomere is mainly associated with taxa that have a much reduced F1, but similarly reduced anelliform basal funiculars may also be bare. This character can sometimes be polymorphic within strongly dimorphic species. For example, females of *Arachnophaga eucnemia* (Eupelminae) have a distinct F1 and setae, whereas males have a much more reduced F1 and lack setae; however, only females were scored.

4 [875] Flagellomere one shape: –, inapplicable (F1 considered as absent or fused with following segment); **0**, as long as or longer than broad (subquadrate to obviously longer than broad); **1**, broader than long to strongly transverse (ring-like or anelliform); **2**, asymmetrically elongate, with an acute dorsal process (which may be subdivided into up to three parts).

The size and shape of the first flagellomere is one of the most widely used characters in Chalcidoidea, proving useful for species-level description to family-group classification. A cylindrical F1 that is as long as broad or longer is considered plesiomorphic (Fig. 2b,c). A ring-like F1 (state 1) can vary in shape, being discoidal (much wider than long) or wedge-shaped (some Aphelinidae and Trichogrammatidae). An F1 with an acute dorsal process (state 2) can be difficult to assess, but is known only for Agaonidae (Grandi, 1929). Species having the projection transversely subdivided we consider as having only a single anellus. Citations: Schauff (1984, char. 7; 1991, char. 5); Graham (1987, char. 19); Gibson (1995, char. 3); Grissell (1995, char. 2); Gibson (2003, char. 11); Lotfalizadeh et al. (2007, chars 61, 62); Gates (2008, char. 1); Kim and Heraty (2012, char. 3).

5 [880] Length of radicle: **0**, not more than two times as long as broad; **1**, four times or more as long as broad (= very long); **2**, between two and four times as long as broad (= long).

The radicle is the basal, petiolate part of the scape by which it is attached to the head. This is long or very long in a few Chalcidoidea, including species of *Cales* (Aphelinidae: Calesinae), *Callimomoides* (Pteromalidae: Louriciinae) and *Storeya* (Pteromalidae: Storeyinae).

6 [878] Articulation of pedicel and scape (female): **0**, scape without apicoventral depression, antenna appearing straight; **1**, scape with apicoventral depression, antenna appearing geniculate.

A geniculate antenna is typical of most Chalcidoidea and refers to the pedicel and flagellum normally being held at an angle to the scape (Fig. 2a–c). A non-geniculate antenna is characteristic of some outgroups, but is also observed in some Eucharitidae (i.e. *Stilbula*) and *Chiloe* (Rotoitidae), presumably because of secondary loss of the apicoventral depression on the scape. Citations: Gibson (1986a, char. 3); Bouček and Noyes (1987).

7 [882] Number of flagellomeres (female): **0–9**, **A–F** (10–15) flagellomeres (actual count).

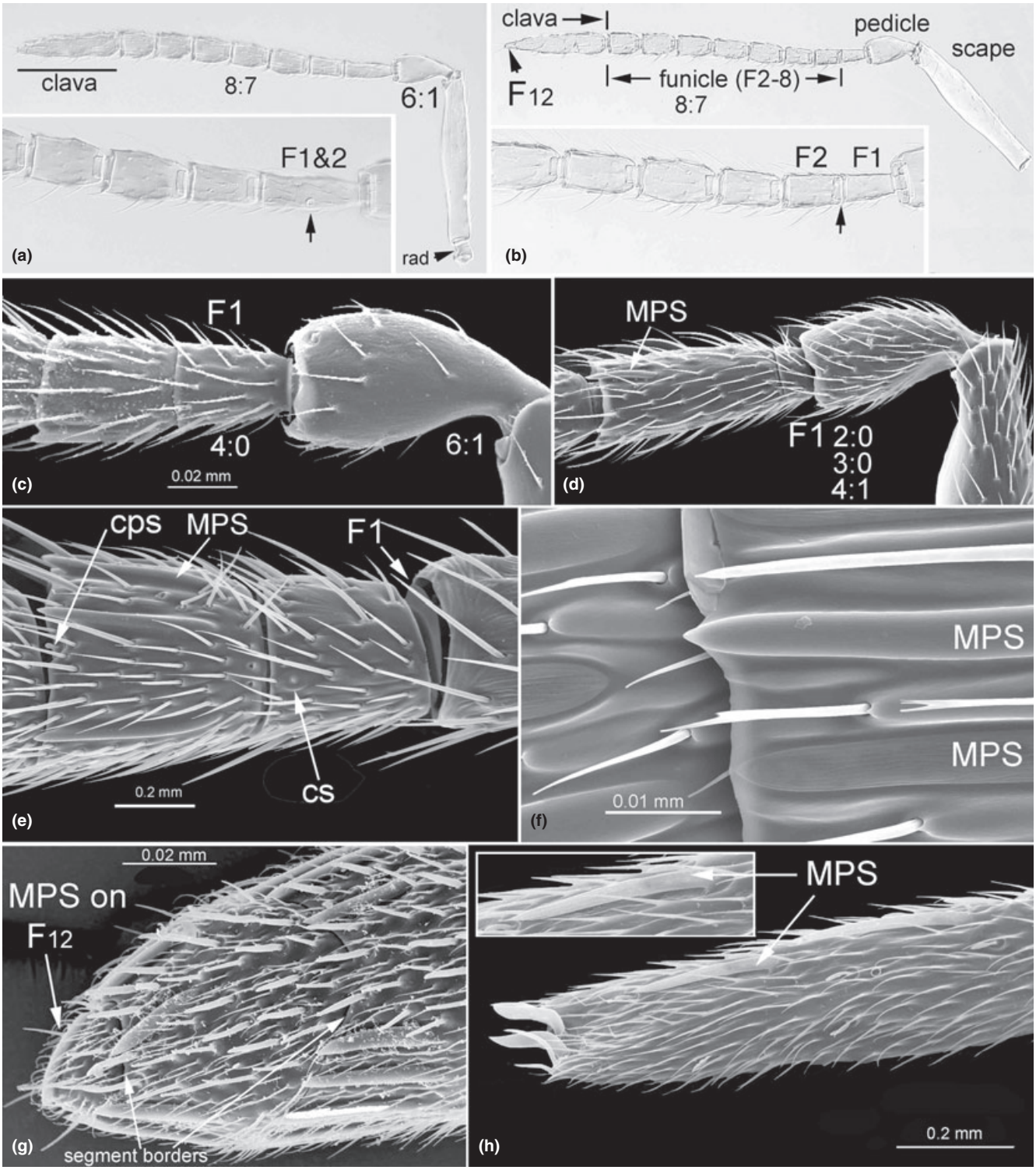


Fig. 2. Antennae. (a–c) *Gollumiella buffingtoni* (Eucharitidae); (a) female, (b,c) male. (d) *Psilocharis afra* (Eucharitidae), female. (e) *Moranila* sp. (Pteromalidae: Moranilinae), female. (f) *Dirhinus giffardi* (Chalcididae), female. (g) *Chromeurytoma* sp. (Pteromalidae: Chromeurytominae), female clava. (h) *Cales noacki* (Aphelinidae: Calesinae), female. Character state associations explained in text.

The number of flagellomeres includes the number of claval segments inferred from putatively partly fused segments (see character 10). If fusion lines were visible, the segments that appeared to form part of the clava were considered as separate flagellomeres (Fig. 2b; clava 4-segmented). A clava without any discernible

remnant of fusion lines was counted as one segment even though likely a composite of more than one segment. The fragmented first flagellomere of some species of Agaonidae was also counted as a single segment. *Eucharissa* (Eucharitidae) can have as many as 22 flagellomeres, but the maximum number scored is 15. Citations: Gibson (1986a, char. 1); Gates (2008, char. 4); Burks et al. (2011, char. 1).

8 [883] Number of flagellomeres between F1 and clava (female funicle): **0–9** flagellomeres (actual count).

The funicle in Chalcidoidea is typically defined as the flagellomeres between the anellus or anelli and the clava (Fig. 2b), though here we consider only F1 as an anellus (character 2). In Eucharitini, Mymaridae and Aphelininae, F1 is considered absent, and the segments between the pedicel and clava were counted as the funicle (Fig. 2a). The funicle is usually 3- or 4-segmented in taxa with a reduced number of antennal segment counts, and 7- or 8-segmented in those with a more complete complement. Species of some taxa (*Aditrochus*, *Espinosa*, *Orasema*) do not have a fused clava and can have as many as nine segments between the anellus and terminal segment (F13). Only *Eucharissa* (Eucharitidae) can have more segments (coded herein as the maximum of 9). Anelliform flagellomeres beyond F1 are considered as funicular segments, and therefore *Nasonia vitripennis* has seven funicular segments in females under our interpretation (not the traditional count of 6). A larger number of funicular segments (7) is presumed to be plesiomorphic (Bouček and Heydon, 1997). Citations: Schauff (1984, char. 4); Noyes and Hayat (1994, char. 19); Woolley (1988, char. 6); Heraty (1994, char. 5; 2002, char. 25); Gibson (2003, char. 14); Lotfalizadeh et al. (2007, char. 59); Kim and Heraty (2012, char. 2).

9 [885] Number of separate claval segments in female: **1–6** segments (actual count).

The concept of a clava in chalcid literature has varied, and sometimes the apical three flagellomeres have been considered as constituting the clava regardless whether they were differentiated from the other flagellomeres (Fig. 2a,b). Here we consider the number of claval segments as defined by rigid connections between segments, different from the more narrow and flexible connections of the funicular segments. The clava may or may not be enlarged or clavate, but whether differentiated by size or other features a flagellum is always considered to have a clava, and therefore any specimen with a flagellum has at least one claval segment. A clava is considered as one-segmented if there is no evidence of fusion between segments, even if it is presumed to be a fusion product of more than one segment. The spicule extending from the clava in *Cleonymus* (Pteromalidae) is not interpreted as homologous with the terminal button, following Gibson (2003), and thus the clava is interpreted as being one-segmented. This character may be redundant for presence of a 12th flagellomere (character 1 : 1). Citations: Schauff (1984, char. 5); Woolley (1988, char. 7); Gibson (1989, char. 2; 2003, char. 12); Noyes and Hayat (1994, char. 21); Lotfalizadeh et al. (2007, char. 68); Burks et al. (2011, char. 2); Kim and Heraty (2012, char. 1).

10 [884] Coeloconic sensillum on flagellomere 2 (female): –, inapplicable (F2 absent); **0**, without coeloconic sensillum; **1**, coeloconic sensilla present.

A circular coeloconic sensillum can be found laterally on F2 (cs, Fig. 2e), but are usually not visible without an SEM image or slide-mounted specimen. There are coeloconic sensilla on F2 and F4 in Trichogrammatidae (Pinto, 2006), but we coded for sensilla only on F2.

11 [892] Basiconic peg sensilla of antenna (female): **0**, absent; **1**, present.

Basiconic peg sensilla have been called sensilla ampullacea (Voegelé et al., 1975), multiporous peg sensilla (Barlin et al., 1981), grooved peg sensilla (Bin et al., 1989), basiconic capitate peg sensilla (Amornsak et al., 1998; Onagbola et al., 2009; Mottern et al., 2011), type s4 sensilla (Gibson et al., 2007), and thermo-hygroreceptive sensilla (van Baaren et al., 2007). Their shape is highly variable, ranging from long and thin to short and mushroom-like (cps, Fig. 2e). These sensilla often denote the apical boundary of a segment, even if segments are fused. We treat all these terms as synonymous, but this character needs to be explored more thoroughly across all taxa, with our coding representing only a cursory analysis.

12 [1994] Socketed MPS: **0**, MPS socketed; **1**, MPS not socketed (Fig. 2e).

Multiporous plate sensilla that are socketed at the base occur in most other Proctotrupomorpha, including Diapriidae (Basibuyuk and Quicke, 1999), but not Mymarommatidae. We coded for presence of socketed MPS in *Rotoita* (cf. fig. 76, Gibson et al., 2007), although these authors state this as being a "fine groove…reminiscent of a socket". If socketed, this would be the only occurrence reported for Chalcidoidea. Citation: Basibuyuk and Quicke (1999, char. 3).

13 [888] Separation of MPS from antennal surface in female: **0**, free along most of length of MPS; **1**, fused to antennal surface along most of length, but with distal end free (Fig. 2d–g).

Outgroups commonly have the MPS free along most of their length, or they have the MPS recessed (Evaniidae) or flush (Pelecinidae) with the antennal wall (Basibuyuk and Quicke, 1999). Chalcidoidea usually have state 1, but females of *Cales* (Fig. 2h) and some Trichogrammatidae have MPS parallel to the flagellomere surface and attached only basally (Mottern et al., 2011). *Acanthochalcis* (Chalcididae) and other taxa with sunken MPS (characters 14, 15) were coded as

state 1 even though the distal end is not free but recessed into the surface, as for the rest of the sensillum (cf. lower MPS, Fig. 2f). Citations: Gibson (1986a, char. 4); Basibuyuk and Quicke (1999, chars 6, 13).

14 [886] MPS elevation relative to antennal surface in female: **0**, at least some MPS recessed into surface of flagellum along entire length; **1**, all MPS raised on outer surface of flagellum.

The MPS are often sunk below or flush with the surface of the antenna in outgroups that have MPS (Basibuyuk and Quicke, 1999). Most chalcidoids have state 1, but a few have been found with some sunken MPS, especially within Chalcididae (Fig. 2f). Citation: Heraty (2002, char. 30).

15 [1987] Polymorphic MPS elevation relative to antennal surface (female): **0**, either all raised or all sunken below surface of flagellomere; **1**, alternating between raised and sunken on same transverse row; **2**, some sunken, but not in a pattern; **3**, alternating rows of raised and sunken on same flagellomere.

This character reflects polymorphism observed in MPS distribution on the flagellum of some chalcidids (*Dirhinus* and *Epitranus*, Fig. 2f).

16 [893] Scape glands (male): **0**, without a set of pores; **1**, with a set of pores; **2**, with a set of pores contained in deep funnel-like depressions; **3**, organized structures.

Pores are found on the ventral surface of the male scape in many taxa, but may be visible only with SEM or slide mounts, and range from simple pores to prominent structures (i.e. *Aphelinus*, Aphelinidae). State 2 is known only for Chrysolampinae (Perilampidae) (cf. Darling, 1986). In Entedoninae (Eulophidae), the pores appear to be localized in raised structures along the male scape. For simplicity, the organized structures of *Aphelinus* (Aphelinidae) and some Eulophidae were coded the same as state 3. Citations: Schauff (1991, char. 2); LaSalle and Schauff (1994, char. 2); Heraty (1994, char. 3; 2002, char. 22).

17 [894] Number of flagellomeres (male): **0–9**, **A–F** (10–15) flagellomeres (actual count).

Coded as discussed under character 7. Citation: Graham (1987, char. 18).

18 [1984] Number of flagellomeres between F1 and clava (male): –, inapplicable (F1 considered as absent or fused with following segment); **0–9**, **A–C** (0–12) flagellomeres.

If apical flagellomeres are not fused, the terminal segment is considered to be the clava, as discussed for character 9. Eucharitidae and most Aphelininae (Aphelinidae) lack a true F1 (see discussion for character 2), and in these families the funicle includes all flagellomeres between the pedicel and clava. Citations: Woolley (1988, char. 5); Heraty (1994, char. 4; 2002, char. 31).

19 [1988] MPS on first flagellomere in males: –, inapplicable (F1 considered as absent or fused with following segment); **0**, absent; **1**, present.

Coded as discussed under character 2. Based on the number of flagellomeres in most male mymarids, the latter can be confidently coded as uniquely having MPS on the first flagellomere, whereas although Aphelininae (Aphelinidae) and some Eucharitidae have MPS on the superficial first flagellomere, this can be shown as the result of the fusion of the first and second flagellomeres.

Head characters (20–50).

20 [895] Anterior and posterior surfaces of the head joined by an arc of pleated membrane: **0**, absent; **1**, present.

Possessed by all extant Mymarommatoidea and extending along the occiput from the base of each mandible (Gibson et al., 2007). Citation: Gibson (1986a, char. 6).

21 [896] Rasp-like sculpture on frons: **0**, absent; **1**, present.

A longitudinal row of strongly raised transverse ridges near each eye occurs in many parasitoids of wood-boring beetles (Vilhelmsen and Turrisi, 2011) and may be a functionally convergent trait.

22 [903] Form of antennal scrobe: **0**, shallow but present even as a minor impression; **1**, deep with margins abruptly defined; **2**, deep with margins not abruptly defined; **3**, deep with margins carinate; **4**, absent.

An antennal scrobe is a depression above each torulus for reception of the scape (Fig. 3a,b,e). Abruptly defined refers to a scrobe with a steep lateral wall that has distinct edges. Absent means that no trace of a depression is visible. Citations: Darling (1983, char. 1); LaSalle (1987, char. 2); Delvare (1992, chars 17, 18); Heraty (1994, char. 9; 2002, char. 3); Noyes and Hayat (1994, char. 14); Gibson (2003, char. 3); Lotfalizadeh et al. (2007, chars 16, 26); Gates (2008, char. 13).

23 [897] Inner orbits of eyes: **0**, ventrally divergent; **1**, ventrally subparallel.

This character was developed for Cleonymini (Pteromalidae) and taxa with a similar head shape (Gibson, 2003). The increase in the angle of divergence begins near the centre of the face, being abruptly and more strongly divergent than dorsal to this point. A continuous angle of divergence along the entire height of the eye is not the same state. In typical cleonymines, the eye has a concave margin between two convex margins along the length of the "divergence". In Aphelinidae (i.e. Eutrichosomellini) the eyes are ventrally divergent but evenly convex. Citation: Gibson (2003, char. 5).

24 [899] Position of ventral margin of toruli relative to oral cavity: **0**, ventral margin of torulus near middle

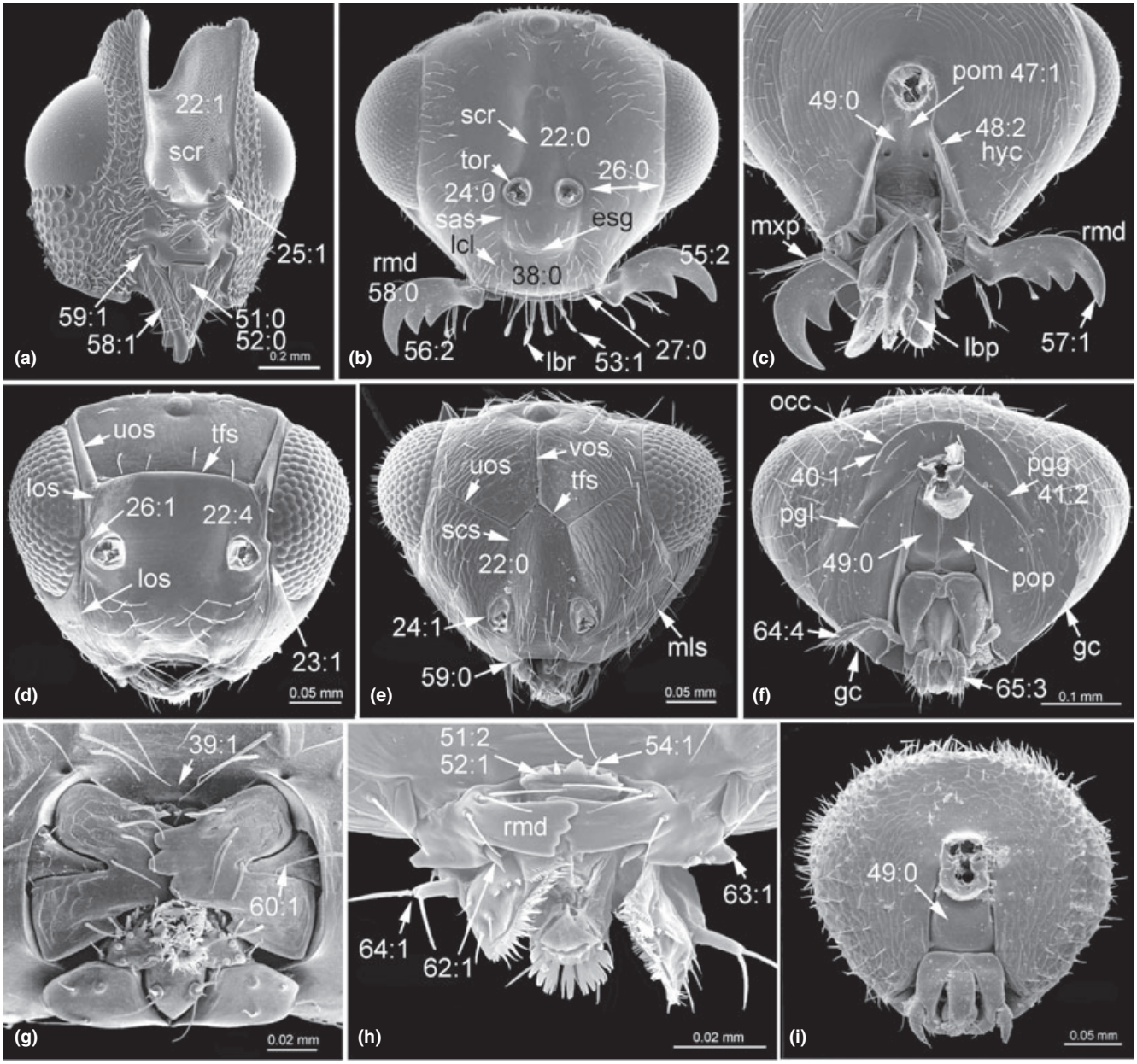


Fig. 3. Heads. (a) *Dirhinus giffardi* (Chalcididae), female. (b,c) *Psilocharis afra* (Eucharitidae), female; (b) anterior, (c) posterior. (d) *Acmopolynema varium* (Mymaridae), female. (e) *Eriaphytis chackoi* (Aphelinidae: Eriaphytinae), female. (f) *Asaphes* sp. (Pteromalidae: Asaphinae), female, posterior head. (g) *A. varium*, female mouthparts, ventral view. (h) *Cales noacki* (Aphelinidae: Calesinae), female mouthparts, frontoventral view. (i) *Chiloe micropteron* (Rotoitidae), female, posterior. Character state associations explained in text.

of head or higher; **1**, ventral margin of torulus in lower third of face or adjacent to clypeus; **2**, toruli located on lobes below main body of face.

The toruli vary greatly in their position throughout Chalcidoidea, from near the vertex (some Pteromalinae) to lobes near the mouth (Pteromalidae: Spalangiinae). Citation: Delvare (1992, char. 16).

25 [900] Expansion of lateral and ventral margins of toruli: **0**, lateral and ventral margins of torulus not raised; **1**, lateral and ventral margins of torulus raised.

State 1 refers to when the lateral and ventral margins of the toruli are distinctly produced forward and oriented in such a way that they almost face each other (Fig. 3a). Citations: Wijesekara (1997, char. 3); Lotfalizadeh et al. (2007, char. 19); Gates (2008, char. 8).

26 [901] Distance of torulus from eye: **0**, more than one torular diameter away from eye; **1**, less than one torular diameter from eye.

This distance measured as the longest diameter of a torulus (from rim to rim). This character primarily contrasts most Mymaridae from other Chalcidoidea.

27 [905] Shape of apical margin of clypeus: **0**, straight, slightly concave or slightly convex; **1**, bilobed; **2**, with three denticles arranged asymmetrically; **3**, with three denticles arranged symmetrically; **4**, a single broad projection separated from rest of face by incisions; **5**, triangularly pointed medially; 6, with tooth-like projection medially; **7**, strongly convex medially; **8**, strongly concave medially; **9**, with an asymmetrical single projection.

The relative shape of the clypeus has been used with some success to assess phylogenetic relationships in Eulophidae (Gumovsky, 2011), Pteromalidae (Heydon, 1989), Tetracampidae (Gumovsky, 2011) and Torymidae (Grissell, 1995). However, it is variable across Chalcidoidea. State 0 approximates what can be termed a simple clypeal margin. For states 7 and 8, the convexity or concavity is at least as deep as the clypeal width. Citations: Graham (1987, char. 1); Heraty (1994, char. 12); Grissell (1995, char. 6); Lotfalizadeh et al. (2007, chars. 4, 5); Gates (2008, char. 9).

28 [908] Trabeculae (internal ingrowths) on head anteriorly: **0**, absent; **1**, present.

Trabeculae are defined by the presence of an internal "bar" derived from a cuticular infolding visible in slide mounts of Mymaridae (Schauff, 1984). Externally, the transverse trabecula of mymarids is similar to the transfacial line found in other taxa (character 30), including *Adryas* (Trichogrammatidae), but only mymarids and rarely Encyrtidae (Noyes, 2010) (e.g. *Oobius*) and a eulophid species near *Ceranisus* (Eulophidae) (Noyes, pers. commun.) have the cuticular infolding. Citation: Gibson (1986a, char. 6).

29 [909] Upper ocular sulcus (uos) of head anteriorly: **0**, absent; **1**, present.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow. The upper ocular sulcus (uos, Fig. 3d,e) connects the ocular (eye) margin with the transfacial line. In some cases it parallels the eye margin; in others it extends laterally from the eye margin to the scrobe. In *Coccophagus* (Aphelinidae), this sulcus forms a transverse line across the head. This is usually found in small, weakly sclerotized taxa, but is also found in a few large-bodied taxa such as *Phenaceupelmus* (Eupelmidae) and some Tetracampinae (Tetracampidae). Citations: Gibson (1986a: 6); Schauff (1991, char. 7); LaSalle and Schauff (1994, char. 5); Burks et al. (2011, char. 8).

30 [910] Transfacial sulcus (tfs) of head anteriorly: **0**, absent; **1**, present.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow. The tfs extends transversely across, or forms the dorsal border of, the antennal scrobe (Fig. 3d,e). No other sulcus crosses this area, even though the tfs and uos may form a completely continuous sulcus. This feature is external to, and may be homologous with, the horizontal trabecula of mymarids, but lacks cuticular infolding (character 28). State 1 is also found in *Phenaceupelmus* (Eupelmidae). Citations: Gibson (1986a, char. 6); Schauff (1991, char. 7); LaSalle and Schauff (1994, char. 5); Burks et al. (2011, char. 8); Kim and Heraty (2012, char. 7).

31 [911] Scrobal sulcus (scs) of head anteriorly: **0**, absent; **1**, present.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow (Fig. 3e). A scrobal sulcus was coded as absent in *Phenaceupelmus* (Eupelmidae) because even though there are two quite a distinct vertical sulci on the frons, both of which ventrally are connected to the lateral limit of the transfacial sulcus, they do not extend ventral to the transfacial sulcus on either side of the scrobal depression.

32 [912] Lower ocular sulcus (los) of head, below toruli: **0**, absent; **1**, present; **2**, present as short sulcus at ventral margin of eye.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow. This sulcus extends from the lower margin of the eye to the clypeal margin, sometimes accompanied by an inverted U-shaped carina across the lower face (Fig. 3d). This sulcus is not homologous to the malar sulcus that connects the eye and mouth margin. Citation: Schauff (1991, char. 31).

33 [913] Vertical ocellar sulcus (vos) [vertical below median ocellus]: **0**, absent; **1**, present.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow (vos, Fig. 3e). Citations: Graham (1987, char. 6); Gibson (1995, char. 10, 47).

34 [914] Subantennal sulcus (sas) [vertical grooves below toruli]: **0**, absent; **1**, present; **2**, not impressed exteriorly, but visible through cuticle.

Subantennal grooves delineate the lateral limits of the supraclypeal area (Fig. 3b). State 2 is found in some Philomidinae (Perilampidae) in which there is no surface sulcus, but where a vertical bar is visible through the cuticle. Citations: LaSalle (1987, char. 4); Heraty (2002, char. 8); Burks et al. (2011, char. 9).

35 [1969] Interantennal projection from lateral view: **0**, absent or not visible from lateral view; **1**, projection visible in lateral view, but simple, not discoid; **2**, projection visible in lateral view, discoid; **3**, projection visible in lateral view, with a bilobed projection.

The interantennal area is the area of the face between the toruli that is delineated by the inner margins of the scrobes. This area is convex or otherwise projects in some chalcidoids and is therefore visible in lateral view. An expanded, discoid interantennal projection occurs in some Chalcididae (Delvare, 1992; Wijesekara, 1997). State 3 is known from some Cerocephalinae (Pteromalidae). Citations: LaSalle (1987,

char. 3); Delvare (1992, char. 15); Wijesekara (1997, char. 4); Heraty (2002, char. 6).

36 [915] Epistomal groove (dorsal clypeal groove): **0**, absent; **1**, present

The epistomal groove delineates the dorsal limit of the clypeus between the tentorial pits. It is coded as present if visible either as a sulcus, impressed groove, channel, or ridge. Citation: Kim and Heraty (2012, char. 8).

37 [916] Lateral clypeal line (lcl): **0**, absent; **1**, present.

The lateral clypeal line delineates the lateral limit of the clypeus. It is coded as present if visible either as a sulcus, impressed groove (Fig. 3b), channel, or ridge. Citation: Burks et al. (2011, char. 10).

38 [1967] Dimensions of clypeus: **0**, less than 3 times as broad as long; **1**, more than three times as broad as long.

The anterior tentorial pits are used as landmarks for the dorsolateral margins of the clypeus when the epistomal groove is absent. Citation: Burks et al. (2011, char. 11).

39 [1986] Inflection of clypeus: **0**, not inflected, on same plane as face; **1**, inflected into oral cavity, not on same plane as face.

The clypeus is part of a strongly inflected slope in Mymaridae and Rotoitidae, hidden in part by the projecting labrum and often not visible anteriorly. The point of inflection seems to be at the anterior tentorial pits, when these are visible.

40 [917] Occipital carina: **0**, complete curved carina present; **1**, only vertical lateral portion of carina present on either side of occipital foramen; **2**, only present dorsally; **3**, absent.

The occipital carina (occ) is distinct from the postgenal lamina of Asaphinae (pgl, Fig. 3f) and Moranilini (both Pteromalidae) and some Eurytomidae, which extends laterally from the dorsal margin of the occipital foramen. Citations: Delvare (1992, char. 23); Gibson (2003, char. 9).

41 [920] Postgenal groove: **0**, absent; **1**, present, not accompanied by postgenal lamina; **2**, present, accompanied by distinct postgenal lamina.

The postgenal groove (pgg, Fig. 3f) extends laterally from the occipital foramen and may or may not be associated with a distinct postgenal lamina (pgl). Citations: Lotfalizadeh et al. (2007, char. 39); Gates (2008, char. 11).

42 [922] Genal carina: **0**, absent; **1**, present; **2**, angular but not carinate.

The genal carina is a raised carina or sharp edge between the gena and the postgena, especially along the ventral part towards the mouth corner (gc, Fig. 3f). State 2 is known for Eunotinae (Pteromalidae) and Encyrtidae. Citations: LaSalle et al. (1997); Wijesekara (1997, char. 9); Gibson (2003, char. 10); Lotfalizadeh et al. (2007, char. 12).

43 [1981] Subapical genal tooth: **0**, absent; **1**, present as a blunt corner; **2**, present as a projecting tooth.

In some hard-bodied chalcidoids, the genal carina ends in a corner-like process or a projecting tooth-like process, the subapical genal tooth. An extra carina usually extends from this projection to the mouth corner, and some other carinae are generally associated with the area. This character is independent from the presence of an actual genal carina, therefore absence of a carina does not make this character inapplicable. Citation: Gates (2008, char. 12).

44 [918] Transoccipital sulcus: **0**, absent; **1**, present; **2**, entire vertex area membranous.

This character refers only to a sharply incised transverse sulcus with sharp margins, not to an impressed groove. Citations: Schauff (1984, char. 16); LaSalle (1987, char. 1); Burks et al. (2011, char. 7); Kim and Heraty (2012, char. 15).

45 [919] Vertical occipital sulcus: **0**, absent; **1**, present.

This character refers only to a sharply incised sulcus, not to an impressed groove or furrow. The vertical occipital sulcus is medial on the occiput and usually connects to the transoccipital sulcus (character 44). Citation: Schauff (1984, char. 17).

46 [1972] Sulci extending ventrally from posterior tentorial pits: **0**, absent or vestigial; **1**, present.

These sulci are ventral extensions of the posterior tentorial pits and extend alongside the postocciput (Lotfalizadeh et al., 2007). Internally, extensions of the posterior tentorial arm contact the head along the sulcus. Citation: van Noort (1992); Lotfalizadeh et al. (2007, char. 48).

47 [924] Postoral microtrichia strip (pom): **0**, absent; **1**, present as a set of cuticular ridges.

The postoral microtrichia (pom) occur as a distinct strip of raised cuticular ridges between the foramen magnum and the oral cavity, and are present in most taxa (Fig. 3c). They are found on either the hypostomal bridge or the postgenal bridge, if present, or sometimes both. No suture or ornamentation is present in *Chiloe* (Rotoitidae) (Fig. 3i). In *Asaphes* (Pteromalidae) there is a pair of postoccipital plates (pop) that mostly cover the strip, but it is visible between them (Fig. 3f). The postoral microtrichia are the same as the microtrichia of Vilhelmsen (1996) and the median stripe of ornamentation on the postgenal bridge of Lotfalizadeh et al. (2007). Citations: van Noort (1992, char. 5); Lotfalizadeh et al. (2007, chars 56, 57); Gates (2008, char. 16).

48 [1973] Hypostomal carina (hyc): **0**, complete across cranial bridge; **1**, curved mesally but incomplete; **2**, present as extensions from hypostomal carinae

extending dorsally between postgena and postocciput, not curved mesally (Fig. 3c); **3**, entirely absent.

The hypostomal carina occurs between the oral cavity and the posterior surface of the head, indicating a hypothetical separation between hypostomal and genal structures. In some Chalcidoidea, this carina has a dorsal extension that proceeds dorsally to the foramen magnum. If this extension is part of the true hypostomal carina, it would indicate that medial areas comprise a true hypostomal bridge. However, the ultimate derivation of these structures in different Chalcidoidea is unknown. Citation: Gates (2008, char. 17).

49 [927] Postoral bridge: **0**, absent; **1**, present and distinct from hypostomal bridge; **2**, present and fused with hypostomal bridge, but slightly elevated above it; **3**, uncertain, ventral part of cranial bridge not elevated above dorsal part, accompanied by hypostomal sulci; **4**, uncertain, all landmarks absent except pits; **5**, uncertain, all landmarks absent except postgenae separated by a suture; **6**, uncertain, no landmarks visible.

The classic postgenal bridge is a mesal extension and fusion of the postgenae over a hypostomal bridge. Therefore the two structures are separate and there are no hypostomal elements in the postgenal bridge. Cases where the postgenae meet but do not fuse medially (i.e. *Acmopolynema*, Mymaridae) are not considered as a postgenal bridge. *Cleonymus* (Pteromalidae) has a nearly classic postgenal bridge (state 1), which is separate from and raised above hypostomal tissues. In some Toryminae (Torymidae), however, the hypostomal and postgenal bridges are fused (state 2). In such cases, the derivation of the bridge can be difficult to discern, especially when either bridge is very short compared with the other. In Chalcididae, dissected specimens indicate that only in Cratocentrini is a definitive postgenal bridge present, with derivation of the postoral bridge less certain in other members of the family. In *Megastigmus transvaalensis* and *Neomegastigmus* (Torymidae), there is a potential postgenal bridge where apparent hypostomal sulci are superficially indicated along the bridge, but where the hypostomal carinae converge and meet medially (state 3). This also differs from other states in that the postgenal bridge is not elevated above the hypostomal bridge. States similar to this are known from outgroups, but are rare in Chalcidoidea. In some small-bodied taxa, such as Aphelinidae and Trichogrammatidae, it sometimes is not clear what kind of cranial bridge is present due to a lack of landmarks (scored as state 4). Cases where a definite suture is present medially, but all other landmarks are absent, were scored as state 5. Note that "suture" does not refer to the postoral microtrichia (character 47). Citations: Wijesekara (1997, char. 10); Rasplus et al. (1998, char. 2).

50 [928] Postoccipital extension: **0**, absent; **1**, present.

This structure occurs in Agaoninae (van Noort, 1992; as median keel; Rasplus et al., 1998, as postoccipital bridge). These plate-like extensions of the postocciput can be partially or completely fused.

Mouthpart characters (51–65).

51 [929] Relation between labrum and clypeus: **0**, labrum with consistently exposed ventral plate, abutting clypeal margin; **1**, labrum without exposed ventral plate; **2**, labrum projecting forward as a horizontal shelf.

Darling (1988) hypothesized that a broad labrum contiguous with the apical margin of the clypeus (state 0) is the ground-plan state for Chalcidoidea. This character was used by Wijesekara (1997) as a synapomorphy supporting the monophyly of Chalcididae. Citations: Wijesekara (1997, char. 7); Gates (2008, char. 14).

52 [930] Structure of labrum: **0**, strongly sclerotized, often with surface sculpture; **1**, lightly sclerotized, without surface sculpture.

In Chalcididae and Philomidinae (Perilampidae), the labrum is generally a plate-like sclerite that is similar in appearance and properties to other exposed cuticle of the head (Fig. 3a). In other Chalcidoidea, the labrum is composed of thinner and more flexible cuticle different from that of the face and body. Citation: Darling (1988).

53 [931] Labral digits: **0**, absent; **1**, present.

Labral digits are comparatively rare, but characteristic of Eutrichosomatinae (Pteromalidae), Perilampidae and Eucharitidae (Fig. 3b) (Darling, 1988). If a median pair of setae were partially digitate, but the lateral setae were absent or sessile, this was coded as state 0 (absent). Citations: Darling (1983, char. 11; 1988); Heraty (1994, char. 14; 2002, char. 16).

54 [932] Marginal labral setae: **0**, setae not restricted to apical margin, projecting upwards from labral surface, not in same plane as their sockets; **1**, setae restricted to apical margin and projecting directly forward in same plane as their sockets.

In Perilampidae, Eucharitidae (Fig. 3b) and a few other chalcidoids (Fig. 3h), the sockets of the labral setae occur at the extreme margin of the labrum, such that the setae project straight forward from the actual margin of the labrum (Darling, 1988). In other chalcidoids, the marginal setae arise from sockets that are located on the dorsal surface of the labrum. Citations: Darling (1988); Heraty (1994, char. 14).

55 [933] Left mandible dentition: –, inapplicable (no mandible); **0**, not forming any recognizable tooth; **1–6**, code for actual number of teeth; **7**, many tiny denticles.

Some taxa have a small accessory tooth at various positions on the mandible, but this is not considered as a true tooth if there is no associated internal rod

(cf. fig. 15, Ronquist, 1989). Mandibles are only rarely completely missing (e.g. *Indosema*, Eucharitidae). Citations: Schauff (1984, char. 14); Woolley (1988, char. 1); Heraty (2002, char. 15); Kim and Heraty (2012, char. 11).

56 [934] Dentition of right mandible relative to left: –, inapplicable (no mandible); **0**, one less tooth; **1**, equal number of teeth; **2**, one more tooth.

Asymmetry in mandibular tooth count occurs in several chalcidoid groups, including many genera of Pteromalinae (Pteromalidae). If both mandibles have several tiny denticles, they are considered equal (state 1). Citation: Gibson (1995, char. 1).

57 [1965] Length of mandibular teeth: –, inapplicable (no mandible); **0**, ventral tooth about the same length as dorsal one; **1**, ventral tooth much longer than dorsal one; **2**, ventral tooth much shorter than dorsal one.

For mandibles with more than two teeth, the dorsalmost and ventralmost tooth were compared.

58 [1966] Mandibular tooth orientation: –, inapplicable (no mandible); **0**, endodont; **1**, exodont.

Exodont mandibles have the teeth recurved outwards and not meeting medially when closed (Fig. 3a), whereas endodont mandibles have the teeth directed in the same plane as the tooth and meeting or overlapping when closed (Fig. 2b,d,e,g,h). Endodont mandibles are the normal condition. Exodont mandibles are known from Mymarommatoidea, Dirhininae (Chalcididae) and some other chalcidoid species. Citations: Schauff (1984, char. 15); Gibson (1986a, char. 5).

59 [939] Mandibular base: –, inapplicable (no mandible); **0**, at least dorsally concealed by genal margin; **1**, exposed, mouth margin thickened and incised for reception of dorsal corner of mandible; **2**, exposed, condyles elongate and visible externally, mouth margin not incised for reception of mandible lateral to clypeus; **3**, exposed, mouth margin not incised, condyles not visible.

An exposed mandibular base of the mandible that articulates with the genal margin is found in Chalcididae (Fig. 3a). The mandible has a distinct condyle in *Epitranus* (state 1), but when slightly opened the margin is flush with the genal margin rather than underneath. The condition in Mymaridae and Rotoitidae is distinct because there is a prominent external muscle or ligament attachment externally (character 60) (Fig. 3g). State 1 was used by Wijesekara (1997) as a synapomorphy supporting the monophyly of Chalcididae. No other chalcidoids possess an exposed mandibular base. Citations: Wijesekara (1997, char. 8); Gates (2008, char. 15).

60 [1964] Exposed muscle of mandible: –, inapplicable (no mandible); **0**, not exposed, or only exposed near extreme base of mandible; **1**, exposed and visible, extending into elongate angular incision along mandible.

The posterior craniomandibular muscle attaches far from the mandibular base in some chalcidoids such as Mymaridae (Fig. 3g), where it is visible and tapers to a narrow apex. In most other chalcidoids, this attachment is more rounded and is usually hidden.

61 [935] Mandibular appendage: **0**, absent; **1**, present.

This is a rasp-like posteriorly directed appendage on the mandible of Agaoninae (Agaonidae) and a few Sycoecinae (Pteromalidae). Citation: Ramirez (1991, char. 39).

62 [936] Socketed spine (peg) on ventral margin of mandible: –, inapplicable (no mandible); **0**, absent; **1**, present.

The form and distribution of a mandibular peg in Chalcidoidea (Fig. 3h) is discussed in Heraty and Schauff (1998).

63 [940] Posteroventral corner of mandible: –, inapplicable (no mandible); **0**, not overlapping genal margin, with or without sharp projection; **1**, overlapping genal margin as a sharp projection.

State 1 is best observed in Calesinae (unplaced subfamily) (Fig. 3h) (Mottern et al., 2011) but has also been found in other chalcidoids, including Eulophidae.

64 [941] Maxillary palp segments: **0–6** segments.

The last palpal segment may be present only as a peg-like or dome-like articulated process. Citations: Noyes and Hayat (1994, char. 27); Heraty (2002, char. 18); Kim and Heraty (2012, char. 12).

65 [942] Labial palp segments: **0–5** segments.

Citations: Noyes and Hayat (1994, char. 28); Heraty (2002, char. 19); Kim and Heraty (2012, char. 13).

Mesosoma characters (66–138).

66 [946] Visibility of pronotum from dorsal view: **0**, mesoscutum anteriorly not abruptly convex, pronotum visible medially in dorsal view, even if only a margin; **1**, mesoscutum anteriorly abruptly convex above pronotum and concealing it in dorsal view medially.

This character refers to whether or not the dorsal aspect of the pronotum is visible medially in dorsal view (Fig. 4d–h); visibility of the neck region is not included. State 1 is characteristic for Eucharitidae (Fig. 4i), but is also found in Philomidinae (Perilampidae), some Rotoitidae and some Eulophidae. Citations: Heraty (1994, char. 21; 2002, char. 37); Kim and Heraty (2012, char. 17).

67 [1995] Indication of pronotal collar: **0**, collar not indicated mesally, not distinct from collum/neck region (therefore absent); **1**, collar indicated by dorsal curvature, but not delimited by any particular feature; **2**, collar delimited by a carina, edge, groove, or elevation in sculpture.

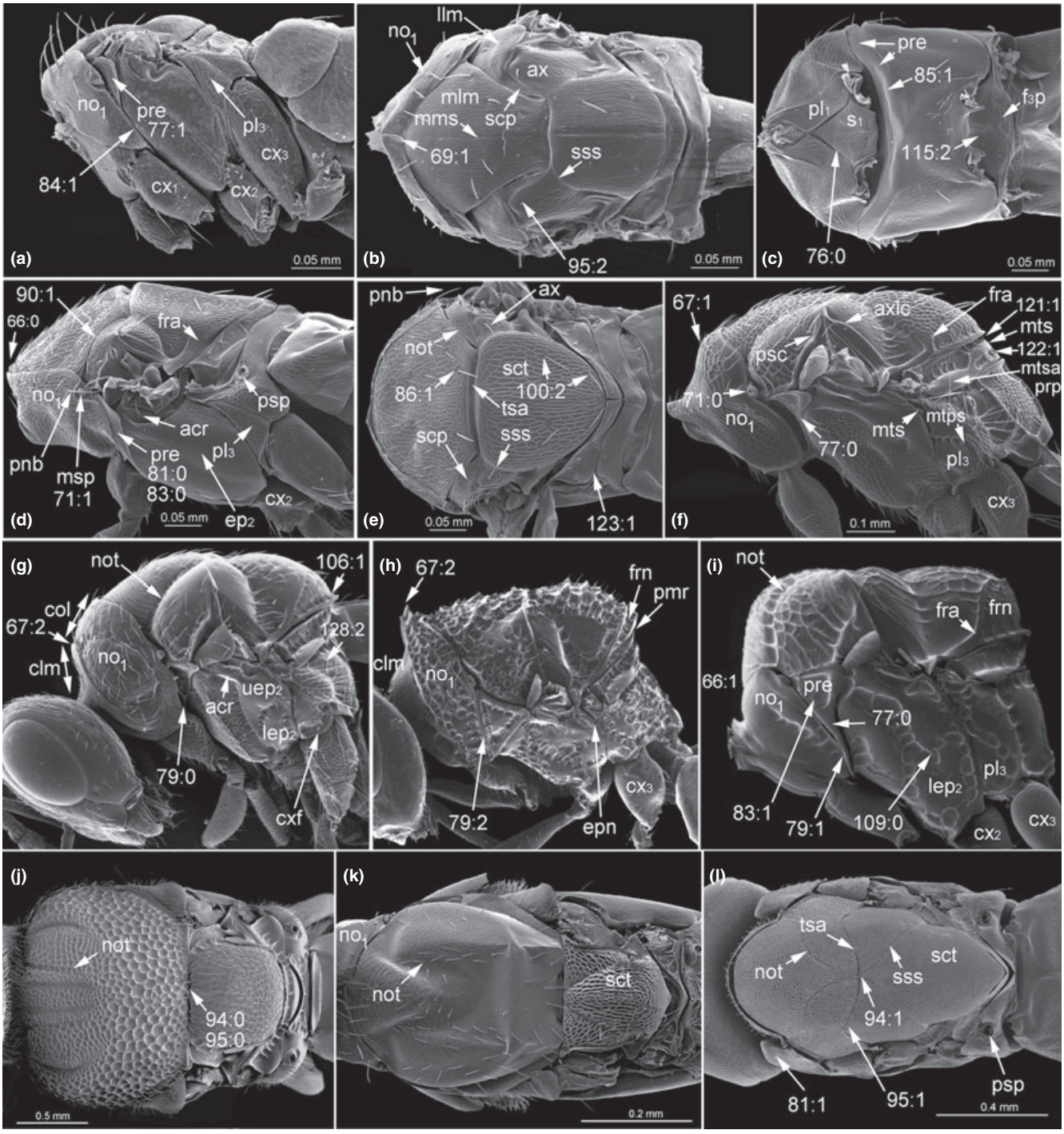


Fig. 4. Mesosoma. (a) *Pachamama speciosa* (Trichogrammatidae). female, lateral. *Mirufens* sp. (Trichogrammatidae), male, dorsal. (c–e) *Coccobius fulvus* (Aphelinidae), female; (c) ventral, (d) lateral, (e) dorsal. (f) *Polstonia pelagocorypha* (Pteromalidae: Pteromalinae), female, lateral. (g) *Chrysolampus schwarzii* (Perilampidae: Chrysolampinae), female, lateral. (h) *Steffanolampus salicetum* (Perilampidae: Perilampinae), female, lateral. (i) *Neolosbanus palgravei* (Eucharitidae), female, lateral. (j) *Balcha indica* (Eupelmidae: Calosotinae), female, dorsal. (k) *Zaischnopsis bouceki* (Eupelmidae: Eupelminae), female, dorsal. (l) *Tanaostigma howardi* (Tanaostigmatidae), female, dorsal. Character state associations explained in text.

This is difficult to code for male and some female Eupelminae (Eupelmidae) where medially the pronotum is a continuous surface in a single plane and moveable relative to the mesonotum. Depending on the orientation of the pronotum in any single specimen, the collar can be vertical and not distinctly visi-

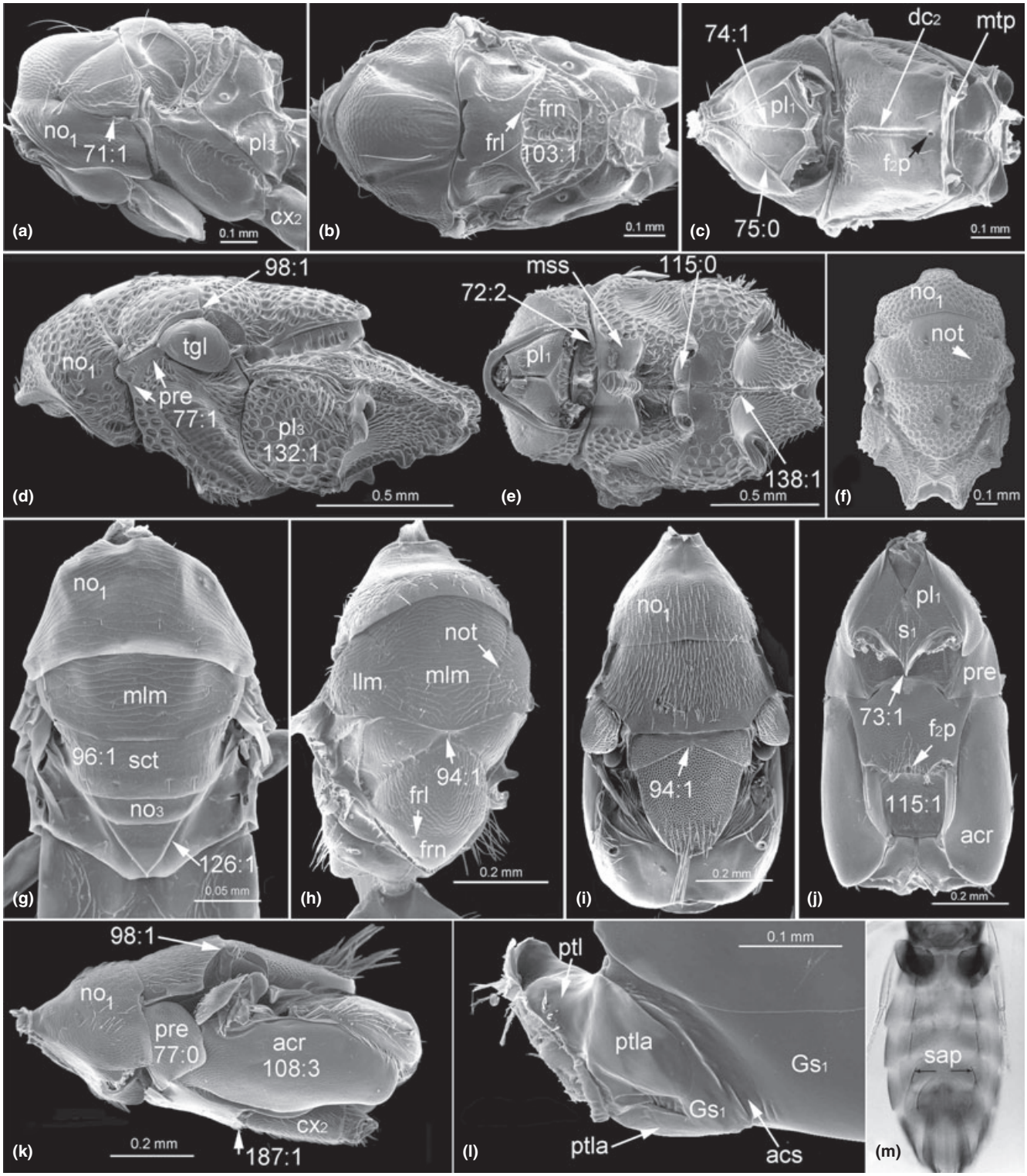


Fig. 5. (a–k) Mesosoma. (a–c) *Australomymar* sp. (Mymaridae); (a) lateral; (b) dorsal; (c) ventral. (d–f) *Dirhinus giffardii* (Chalcididae: Dirhininae); (d) lateral; (e) ventral; (f) dorsal. (g) *Thysanus* sp. (Signiphoridae), female, dorsal. (h) *Austrotoxeuma* sp. (Perilampidae: Chrysolampinae), female, dorsal. (i–k) *Cheiloneurus fulvescens* (Encyrtidae), female; (i) dorsal; (j) lateral; (k) ventral. (l) Petiole, *Chrysomalla hesperis* (Perilampidae: Chrysolampinae), female, sublateral. (m) Gaster, *Clytina* sp. (Signiphoridae), female. Character state associations explained in text.

ble in dorsal view, or more horizontal and then visible. However, some male and most female eupelmines have a more distinctly differentiated collar laterally where a definite change in curvature to the neck can be observed (state 1). Male eupelmines with the pronotum almost vertical medially were coded as state 0 because mesally the collar is not distinct from the collum. Citations: Delvare (1992, chars. 26, 27); Gibson (1995, char. 15); Krogmann and Vilhelmsen (2006, char. 2); Lotfalizadeh et al. (2007, chars. 75, 76); Burks et al. (2011, char. 12).

68 [945] Length of pronotal collar in dorsal view: –, inapplicable (lack of collar); **0**, short, less than half length of mesoscutal lateral lobe; **1**, long, at least half as long as mesoscutal lateral lobe.

This character is applicable only to taxa with a clearly defined collar. Citation: Krogmann and Vilhelmsen (2006, char. 5).

69 [948] Median division of pronotum: **0**, not divided; **1**, divided by median suture, line of weakness, or full separation (Fig. 4b); **2**, with a longitudinal carina, ridge or set of longitudinal rugae mesally.

A medially divided pronotum has been found in some Mymaridae and other taxa that are typically small-bodied. A more superficially divided pronotum has been found in some larger-bodied taxa, such as some Eupelmidae. Citations: Polaszek and Hayat (1992, char. 8); Noyes and Hayat (1994, char. 29); Gibson (1995, char. 14, 2003, char. 18); Kim and Heraty (2012, char. 16).

70 [958] Isolated large bristle on posterolateral corner of pronotum: **0**, absent; **1**, present.

A strong bristle is located consistently in the same position on the posterolateral corner of the pronotum in many taxa (pnb, Fig. 4d,e) and is distinct from the dorsal transverse row of setae sometimes found on the pronotum.

71 [1946] Mesothoracic spiracle enclosed by pronotal cuticle: **0**, not enclosed; **1**, enclosed; **2**, partially enclosed.

In a few chalcidoids, such as *Coccobius fulvus* (Aphelinidae) and *Gonatocerus ashmeadi* (Mymaridae), the mesothoracic (= anterior) spiracle is entirely enclosed by pronotal cuticle (Figs 4d and 5a). This is easy to assess because the area is exposed and flat. If the spiracle is hidden or otherwise difficult to see, it is not enclosed. The spiracles are enclosed in some Eucharitidae (i.e. *Pseudochalcura*) (Heraty, 2002). Citations: Heraty (1994, char. 26; 2002, char. 70).

72 [1974] Posteroventral mesal projections of pronotum: **0**, no projection extending across prepectus ventrally; **1**, with a ventromesal projection that articulates with the mesepisternum posterior to the prepectus; **2**, with a ventromesal projection that crosses the prepectus, but does not articulate with the mesepisternum (Fig. 4a).

States 1 and 2 occur in taxa with a pronotum that is closely associated with the propleural/prosternal area such as in *Heimbra* (Eurytomidae) or *Coccobius* (Aphelinidae) and do not occur in taxa that have a less extensive pronotum not closely associated with the ventral structures. Citation: Lotfalizadeh et al. (2007, char. 78).

73 [960] Posterior margin of prosternum: **0**, median spine-like process absent (Fig. 4c); **1**, median spine-like process present (Fig. 5j); **2**, forked process present.

The form and shape of a median spine-like process is variable, and it may articulate posteriorly with the mesepisternum. Different forms of a spine-like process are lumped into state 1, but a more thorough assessment is required to better refine the homology with function.

74 [961] Prodiscriminal line: **0**, absent; **1**, externally indicated as a channel or ridge (Fig. 5c).

The prodiscriminal line is a longitudinal division on the ventral surface of the fused mesepisterna mesally, corresponding internally to a discriminal lamella. Richards (1956) referred to the prodiscriminal line as the median sternal groove. Externally, the line can be indicated as a uniform groove or sculptured channel, but we chose not to separate the different structures into different states. A channel-like groove may be very faint, but still present. In Neanastatinae (Eupelmidae), what likely is the discriminal lamella sometimes is evident through the cuticle, but is not present externally and therefore was coded as state 0. Citations: Schauff (1984, char. 24); Krogmann and Vilhelmsen (2006, char. 13).

75 [963] Propleura posterior angle: **0**, posterior margins diverging angularly along prosternum; **1**, posterior margins transverse, propleura meeting along almost their entire length.

This character refers to the posterior half of the propleura, which may either remain parallel or diverge to form an inverted V-like angle (Fig. 5c). In Philomidinae (Perilampidae), the propleura do not diverge, but rather the entire prosternum is posterior to the propleura, which was scored as state 1. Citation: Gauthier et al. (2000); Burks et al. (2011, char. 20).

76 [966] Shape of posterior margin of propleuron: **0**, convex or straight; **1**, concave; **2**, reflexed.

The posterior margin of the propleuron is between the procoxal attachment and the point of juncture between the propleura. The propleuron at the procoxal attachment and at the anterior "neck" region is arguably about the same in all taxa, whereas there is a clear difference in shape of the posterior margins of the propleura along the prosternum itself between these two points. In cases where the propleura are in contact for a long distance until reaching a very short prosternum, as in Eulophinae (Eulophidae), Spalangiinae (Pteromalidae) and others, we ignore the surface

along the procoxal attachment and refer only to the margin bordering the prosternum. Citation: Krogmann and Vilhelmsen (2006, char. 15).

77 [1979] Size and shape of exposed lateral panel of prepectus: –, inapplicable (fused to pronotum or absent); **0**, as high as or higher than long and more than half length of tegula; **1**, longer than high and more than half length of tegula; **2**, small, less than half tegula length.

This character originated as a means of coding prepectal variation within Chalcididae, and has been expanded to code other variation observed in other families. In Trichogrammatidae, the prepectus is vertical but short, less than half the length of the tegula, and therefore was scored as state 1 (Fig. 4a). Except for male Eupelminae (Eupelmidae), most eupelmids have a prepectus that is longer than high, but the measurement sometimes is not clear-cut for those taxa in which the prepectus does not extend to the tegula, or in eupelmids with the pronotum much narrower than the mesoscutum so that anteriorly the prepectus is substantially curved. Citations: Schauff (1984, char. 60); Wijesekara (1997, char. 13); Gibson (2003, char. 28); Krogmann and Vilhelmsen (2006, char. 69); Lotfalizadeh et al. (2007, char. 89); Gates (2008, char. 19).

78 [970] Prepectus: **0**, absent; **1**, present, exposed between pronotum and mesepisternum, at least dorsally; **2**, present, entirely concealed under posterolateral margin of mesoscutum.

The presence or absence of a prepectus was discussed by Gibson (1999, character 11). The fused prepectus of most Eucharitidae and Perilampidae was coded as state 1 (cf. Heraty, 1989). State 2 occurs in Rotoitidae (Gibson, 1999). Citations: Gibson (1986a, char. 9); Wijesekara (1997, char. 12); Krogmann and Vilhelmsen (2006, chars. 67, 68).

79 [973] Association between prepectus and pronotum: –, inapplicable (no external aspect of prepectus apparent); **0**, loosely associated; **1**, rigidly associated but not fused; **2**, fused.

In state 0, the prepectus is associated primarily with the mesepisternum, in a different plane from the pronotum (Fig. 4g). In state 1, it is closely associated with, and more or less in the same plane as, both the pronotum and the mesepisternum (Fig. 4i). In state 2, it is completely fused with the pronotum (Fig. 4h). Citations: Heraty (1994, char. 19; 2002, char. 63); Krogmann and Vilhelmsen (2006, char. 72).

80 [1980] Prepectus relationship to tegula: –, inapplicable (no external aspect of prepectus apparent); **0**, prepectus extending to tegula; **1**, prepectus not extending to tegula.

In state 1, the lateral lobe of the mesoscutum contacts the acropleuron between the apex of the prepectus and base of the tegula. Citations: Gibson (1986a, char. 10; 1989, char. 3; 1995, char. 20); Heraty (2002, char. 65, 66).

81 [971] Structure of prepectus: –, inapplicable (no external aspect of prepectus apparent); **0**, lateral surface of prepectus relatively flat anteriorly, not extending far over or under pronotum (Fig. 4a,d,f–i); **1**, prepectus extending as bulbous lobe anteriorly, exterior to pronotum (Fig. 4i); **2**, prepectus extending as bulbous lobe anteriorly, but interior to pronotum, possibly with membranous anterior portion (cf. figs 44, 48 of Gibson, 1989); **3**, prepectus extending interior to pronotum and divided into exterior lateral panel and interior prepectal strut (cf. figs 87, 89, 115 and 116 of Gibson, 1989); **4**, prepectus expanded anteriorly but without internal apodemes (cf. fig. on page 589 of Goulet and Huber, 1993).

This character is presented and discussed in detail by Gibson (1989). State 0 occurs in most chalcidoids, where the prepectus is often foveate or otherwise sculptured. State 1 occurs in Tanaostigmatidae (Fig. 4i), state 2 in *Cynipencyrtus*, and states 2 and 3 in various Eupelmidae, Encyrtidae and Aphelinidae with an enlarged acropleuron. States 1–3 are correlated with a secondarily lengthened internal mesoscutal apodeme to which a greatly enlarged acropleural muscle is attached, along with expansion of the prepectus around the anteriorly projecting part of this apodeme so that the prepectus retains its connection to the pronotum. The condition in Philomidinae (Perilampidae) (state 4) is unique within Chalcidoidea. Citation: Gibson (1989, char. 10).

82 [982] Setation of lateral panel of prepectus: –, inapplicable (no external aspect of prepectus apparent); **0**, bare; **1**, setose.

The prepectus is usually bare in Chalcidoidea, but its exposed lateral panel can be setose in some taxa, such as certain Cleonyminae and other Pteromalidae (Gibson, 2003).

83 [983] Structure of lateral panel of prepectus: –, inapplicable (no external aspect of prepectus apparent); **0**, without either fovea or raised rim, though possibly heavily sculptured; **1**, foveate and with posterior and/or dorsal rim; **2**, heavily sculptured but without raised rim.

State 1 refers to any fovea on the surface of the lateral panel of the prepectus, defined by a dorsal, posterior and/or anterior carina (Fig. 4i). A heavily sculptured lateral panel may potentially obscure any presence of a rim, but typically state 2 refers to features of the small prepectus found in Eurytomidae and Chalcididae.

84 [974] Pronotum posteroventrally: **0**, not overlapping prepectus; **1**, overlapping prepectus, reaching mesepisternum and completely covering ventrolateral aspect of prepectus.

In some smaller-bodied species, the pronotum can extend ventrally across the prepectus to contact the mesepisternum. This state was not found to be dependent on body flexure. Citation: Kim and Heraty (2012, char. 20).

85 [980] Posterior margin of prepectus ventrally: **0**, separated from mesepisternum by complete suture; **1**, partially or completely fused ventromedially (between coxae) with mesepisternum; **2**, lateral panels abutting mesepisternum at their termini, prepectus not continuous ventrally.

Eupelmidae were coded as state 1, but it is sometimes difficult to determine whether there is a complete suture between the prepectus and mesepisternum, or just a line of weakness that acts as an articulation. When the mesoscutum arches during jumping, the lateral surface of the prepectus rotates downward to a greater or lesser degree, and the anterior surface of the prepectus is rotated upward into the body along a line of articulation formed between the juncture of the prepectus and mesepisternum (cf. Gibson, 1986a; figs 37, 38). Citations: Krogmann and Vilhelmsen (2006, char. 73); Kim and Heraty (2012, char. 19).

86 [1000] Stout setae (bristles) on mesoscutal mid lobe: **0**, no differentiated bristles; **1**, one pair of bristles; **2**, two or more pairs of bristles.

Citations: Schauff (1991, char. 4); Polaszek and Hayat (1992, char. 10); LaSalle and Schauff (1994, char. 4); Burks et al. (2011, char. 15); Kim and Heraty (2012, char. 21).

87 [989] Number of stout bristles on lateral lobe of mesoscutum: **0–2**, or **3** when 3 or more bristles present.

Coded using the same concept of bristles as used in character 86. Citation: Kim and Heraty (2012, char. 22).

88 [986] Shape of lateral lobe of mesoscutum in dorsal view: **0**, broadly triangular or quadrate; **1**, with strongly narrowed posteromedial portion (scapular flange).

This character refers to the overall shape of each mesoscutal lateral lobe. State 1 is found in aphelinids and similar taxa with a clearly defined scapular flange (scp, Fig. 4b). If the lateral lobes are fused with the midlobe with no discernible suture or furrow, the structure was coded as state 0.

89 [992] Development of notauli: **0**, present and extending length of mesoscutum; **1**, present, but not extending posteriorly to transscutal articulation; **2**, absent, no indication of notauli.

The notauli are external representations of the internal notaular ridges that are found in all taxa whether or not the notauli are present. Traces of notauli are evident anteriorly on the mesoscutum in different genera of Neanastatinae (Eupelmidae) depending on position of the pronotum over the mesoscutum; otherwise, the dorsal surface of the mesoscutum is flat and they were therefore coded as having state 2 (cf. Gibson, 2009a). Female Eupelminae were scored as having notauli based on the furrows that separate the anteroadmedian triangular part of the mesoscutum from the lateral lobes extending to the spiracles (Fig. 4k), which indicates they are homologous with notauli. Citations: Darling (1983, char. 18); LaSalle (1987, char. 11); Woolley (1988, char. 8); Gibson (1989, char. 7; 2003, char. 19); Schauff (1991, char. 14); Delvare (1992, char. 31); Heraty (1994, char. 23; 2002, char. 42); Noyes and Hayat (1994, char. 34); Wijesekara (1997, char. 11); Krogmann and Vilhelmsen (2006, char. 33); Lotfalizadeh et al. (2007, char. 80); Gates (2008, char. 26); Burks et al. (2011, char. 14).

90 [933] Appearance of notauli: –, inapplicable (no indication); **0**, foveate, groove-like, or present as a superficial line or slight change in depth of surface sculpture; **1**, sulcate (deeply and sharply incised).

A foveate sulcus or shallow groove is typical of large-bodied species, whereas small-bodied species often have a deep sulcate groove (Fig. 4d,e). Foveate notauli are often crossed by numerous transverse ridges (Fig. 4i). Citation: Schauff (1984, char. 31).

91 [997] Median mesoscutal sulcus: **0**, absent; **1**, at least some trace of a median longitudinal line present.

A median mesoscutal sulcus sometimes occurs in small-bodied chalcidoids (mms, Fig. 4b), as opposed to a carina found in the same location in some larger-bodied Hymenoptera.

92 [998] Transscutal articulation: **0**, present and complete; **1**, obliterated medially but present at lateral edges; **2**, obliterated between axilla and lateral lobe of mesoscutum.

The transscutal articulation is the transverse line of weakness formed by the juncture of the mesoscutum and scutellar–axillar complex, which enables the mesoscutum and mesoscutellum to flex during flight as a result of contraction of the dorsolongitudinal and dorsoventral flight muscles. Obliterated means complete fusion with no external indication. Citations: Polaszek and Hayat (1992, char. 12); Heraty (1994, char. 24; 2002, char. 44); Krogmann and Vilhelmsen (2006, char. 38).

93 [1001] Mesoscutum and scutellar–axillar complex: –, inapplicable (articulation absent); **0**, articulation hinge-like (normal); **1**, articulation capable of separating when flexed, connected by membrane medially; posterior margin of mesoscutum always overlapping scutellar margin.

The mesoscutum flexes relative to the scutellar–axillar complex along the transscutal articulation when present. Normally the line of flexion acts as a hinge because the two sclerites rotate along a line of weakness; however, in Encyrtidae, Tanaostigmatidae and some Eupelmidae, the margins of the two sclerites separate from each other during flexion (state 1). Citation: Gibson (1989, char. 8).

94 [1018] Separation of axillae: **0**, broadly separated mesally such that scutellum truncate anteriorly; **1**, meeting or nearly meeting mesally such that scutellum acute anteriorly; **2**, axillae fused and forming a united transverse band such that scutellum separated from transscutal articulation.

If the scutellum was at all truncate anteriorly, it was scored as state 0; but it was scored as state 1 if the anterior angle of the scutellum was acute (Fig. 5h,i). State 2 occurs in Philomidinae (Perilampidae), Signiphoridae and some Eucharitini (Eucharitidae). Although coded the same, we doubt that the condition in Signiphoridae (axillae marked by internal carinae only) is homologous with the perilampid lineage (Philomidinae and Eucharitidae). In slide mounts of Signiphoridae, the mesoscutum does extend to the transscutal articulation and thus the structure is more likely a special derivation of state 0; however, based on external morphology we coded this as a transverse band (state 2). There were difficulties in coding states 1 and 2 because the extent to which the axillae are separated medially is complicated by the breadth and angle of the scutoscutellar sulcus, which separates the scutellum from the axillae. Citations: Woolley (1988, char. 10); Krogmann and Vilhelmsen (2006, char. 40); Lotfalizadeh et al. (2007, char. 85).

95 [1022] Position of axilla: **0**, not advanced; **1**, slightly, but distinctly advanced; **2**, anterior margin advanced by more than one-third length of lateral lobe of mesoscutum.

Coding this character is problematic because there are no clear positional landmarks that can be used across families. The size and position of the axillae impact on features of the surrounding structures that correlate with several other characters in this matrix. This character has been used to help define Aphelinidae, Eulophidae and Trichogrammatidae and to help define several pteromalid groups (Graham, 1969; Bouček, 1988a). The original concept was applied only to "strongly" advanced axillae, but intermediate structures led to our attempt to indicate axillar position more precisely. State 0 is distinguished from state 1 by having a very straight transscutal articulation with no anterior curvature laterally. Citations: Schauff (1984, char. 28); Polaszek and Hayat (1992, char. 13); Krogmann and Vilhelmsen (2006, char. 39); Burks et al. (2011, char. 16); Kim and Heraty (2012, char. 32).

96 [1004] Scutoscutellar sulcus between axilla and scutellum: **0**, present along entire junction between axilla and scutellum; **1**, obliterated along entire junction between axilla and scutellum; **2**, obliterated along middle portion of junction between axilla and scutellum; **3**, obliterated posteriorly; 4, obliterated anteriorly; 5, obliterated laterally.

Obliterated means complete fusion with no external indication (Fig. 5g). In *Encarsia* (Aphelinidae) there is a distinct internal line visible in slide mounts, but externally there is only a very faint indication from the surface sculpture and it was therefore coded as obliterated. Citations: Heraty (1994, char. 22; 2002, char. 45); Krogmann and Vilhelmsen (2006, chars 48, 49); Lotfalizadeh et al. (2007, char. 86).

97 [1023] Number of bristles on axilla: **0**, absent (fine setation or similarly stout setae may be present); **1**, one; **2**, two; **3**, more than two.

In *Jambiya* (Perilampidae) the axillar setae are all bristle-like, but because they are not differentiated from one another they were coded as state 0. There is some taxonomic discrepancy as to how this character is coded relative to the definition of bristle that was given, because Aphelinidae was scored as having bristles even when there were no "normal" (weak, hair-like) setae for comparison. Citations: Polaszek and Hayat (1992, char. 14).

98 [1007] Parascutal and axillular carinae: **0**, not meeting at transscutal articulation, or forming a Λ-shaped connection (Fig. 4f); **1**, meeting at transscutal articulation, forming a ∩-shaped connection (Fig. 5d).

The parascutal carina is formed by the posterolateral margin of the mesoscutum, whereas the axillar carina is the carina that separates the dorsal and lateral surfaces of the axilla. State 1 was proposed as a character of Chalcididae (Wijesekara, 1997), but it also occurs in other taxa such as Encyrtidae, *Coccobius* (Aphelinidae), *Heimbra* (Eurytomidae) and female Eupelmidae. In the latter taxa the meeting of the carinae in a ∩-shape may be associated with a dorsal compression of the mesosoma and therefore not homologous with the condition in Chalcididae. Citations: Wijesekara (1997, char. 18); Gates (2008, char. 30).

99 [1011] Submedian lines of scutellum: **0**, absent; **1**, present as parallel grooves that do not meet posteriorly; **2**, present as grooves that converge or meet along posterior margin of scutellum.

The submedian lines are on the scutellum medial to the junction with the axillula. This is not the same as an often similar groove, the axillular groove, which separates the scutellum from the axillula (character 101). Citations: Graham (1987, char. 31); Schauff (1991, char. 15); Burks et al. (2011, char. 18).

100 [1012] Bristles on scutellar disc: **0**, absent (possibly with fine setae or similarly stout setae); **1**, one pair; **2**, two pairs; **3**, more than two pairs.

Citations: Graham (1987, char. 33); Schauff (1991, char. 1); Polaszek and Hayat (1992, char. 14); LaSalle and Shauff (1994, char. 1); Burks et al. (2011, char. 17); Kim and Heraty (2012, char. 24).

101 [1025] Form of axillula relative to scutellum: –, inapplicable (no external indication of axillula); **0**, axillula not enlarged, its dorsal margin straight or not visible in dorsal view; **1**, axillula expanded and enlarged, its dorsal margin arched mesally.

The axillula in most chalcidoids is a more or less triangular region that forms the lateral surface of the scutellum posterior to each axilla. Because of its position, most chalcidoids lack a distinct axillula as seen in dorsal view, though in lateral view it is visible as a more or less vertical region that is often differentiated from the scutellum by a line below the level of the dorsal curvature of the scutellum. State 1 is characteristic of typical Colotrechninae (Pteromalidae) and Sycophaginae (Agaonidae), in which the line that differentiates the axillula from the scutellum appears on the dorsal surface because the axillula is enlarged and visible as a dorsal region lateral to the median scutellar region. The axillular grooves are different from and can cooccur with, the submedian grooves that occur in some Eulophidae (Burks et al., 2011).

102 [1956] Scutellar apex projection: **0**, no projection; **1**, frenum projecting posteriorly; **2**, area anterior to frenum projecting.

State 1 occurs in Heimbrinae (Eurytomidae) and some Eucharitidae, and refers to a strong posterior projection consisting of only the frenum. State 2 refers to a scutellar projection that includes areas anterior to the frenum, in which case the frenum is on the ventral surface of the projection. Citations: Heraty (2002, char. 49–51); Krogmann and Vilhelmsen (2006, char. 57).

103 [1008] Size of frenum: –, inapplicable (frenum absent with no external indication laterally); **0**, frenum comprising less than half dorsal surface of scutellum; **1**, frenum comprising half or more dorsal surface of scutellum.

Based on position of the scutellar sensilla and the internal cuticular invagination associated with the frenal line (character 104), we interpret the "posterior scutellum" of Mymaridae (frn, Fig. 5b) as likely homologous with what is termed the frenum in other chalcidoids. State 1 is defined for those mymarids in which the "posterior scutellum" is large, and occupies more than half of the scutellar disc. Citation: Schauff (1984, char. 32).

104 [1027] Frenum as defined mesally: **0**, not indicated; **1**, defined across the scutellum dorsally; **2**, defined ventral to apical margin of scutellum.

This character refers to how the frenum is defined mesal to the frenal arm (character 105). State 1 reflects a frenum that is dorsally differentiated from the scutellum by some sort of frenal "line" (sulcus, carina or change in surface sculpture) (Figs 4h,i and 5h). State 2 is associated with a specialized structure in which the scutellum extends posteriorly (character 103). Except for male Eupelmidae, which definitely lack a dorsally defined frenum, "jumping" eupelmids typically have a scutellum with a vertically convex apical surface that is somewhat smoother than the dorsal surface, over which the metascutellum rotates when the mesonotum arches during jumping. This region was coded as state 2 because it is an apically differentiated region of the scutellum, even though the region is not defined across the scutellum "dorsally" as it is in other chalcidoids coded as state 2. Citations: Delvare (1992, char. 34); Heraty (1994, char. 27; 2002, char. 48); Grissell (1995, char. 15); Wijesekara (1997, char. 20); Gibson (2003, char. 22); Krogmann and Vilhelmsen (2006, char. 59).

105 [1028] Frenal indication as defined by the position of the frenal arm: **0**, frenum differentiated laterally by frenal arm; **1**, frenum not differentiated laterally.

The frenal arm (fra) is a modification of a raised rim that originates from the posterior notal wing process that extends along the posterior margin of the scutellum before typically bifurcating and diverging dorsally from the posterior margin (Fig. 4d,f,i). The frenal arm is the anteriorly directed portion of the bifurcation and is continuous with the frenal line in those chalcids with the frenum defined dorsally (character 104). However, those chalcidoids that lack a mesally defined frenum usually still have the frenal arm visible as a short lateral bifurcation, and this defines the frenum laterally (state 0; Fig. 4f). If the scutellum has a clearly visible rim that does not have a distinct anterior branch separated from the posterior edge of the scutellum (i.e. some Aphelinidae), this was coded as state 1. Citation: Gibson (2003, char. 23); Krogmann and Vilhelmsen (2006, char. 61).

106 [1010] Marginal rim of scutellum: **0**, absent; **1**, present.

The posterior margin of the scutellum sometimes has a strongly transverse "rim" differentiated by crenulae or a sulcus (Fig. 4g,h). Some chalcidoids have both a frenum and marginal rim (e.g. Gibson, 2003; figs 11, 14), but it can be difficult to determine whether a strongly transverse, posteriorly differentiated region of the scutellum is a marginal rim or a reduced frenum when only one of these region is present (e.g. Gibson, 2003; fig. 12). Various Neanastatinae (Eupelmidae) were scored as having a marginal rim, even though it is just a very thin flange apically or apicolaterally on the scutellum (cf. Gibson, 2009a). Citations: Darling (1983, char. 9); Gibson (2003, char. 23); Krogmann and Vilhelmsen (2006, char. 56).

107 [1036] Position of mesothoracic spiracle relative to mesoscutum: **0**, situated below and separated from exposed lateral edge of mesoscutum by part of pronotum; **1**, situated at or above exposed lateral edge of mesoscutum.

State 1 has been postulated as a synapomorphy for Chalcidoidea (Gibson, 1986a). Some chalcidoids have the mesothoracic spiracle secondarily surrounded by cuticle (character 71), but the spiracle is at the level of the lateral edge of the mesoscutum (Fig. 4d). Citations: Gibson (1986a, char. 11; 1999, char. 9).

108 [1030] Expansion of acropleuron: **0**, a small differentiated area ventral to tegula, and mesopleuron usually impressed medially (Fig. 4g); **1**, expanded over halfway across mesopleuron, but leaving mesopleural sulcus and entire mesepimeron exposed; **2**, expanded almost entirely across mesopleuron, with only lower mesepimeron exposed; **3**, expanded across entire mesopleuron, hiding mesepimeron (Fig. 5k).

In most chalcidoids, the acropleuron is a small region dorsally on the mesopleuron below the base of the fore wing. Internally, the region is the site of attachment for a muscle that in "jumpers" (most Eupelmidae as well as Encyrtidae, Tanaostigmatidae and some Aphelinidae) is variably enlarged. Externally, this is evident as a variably enlarged acropleuron (Gibson, 1989). The different states defined represent the different extents to which the acropleuron is expanded in different chalcidoids. Citation: Gibson (1989, char. 3); Krogmann and Vilhelmsen (2006, char. 77); Kim and Heraty (2012, char. 30).

109 [1034] Transepimeral division: **0**, present; **1**, absent.

The mesepimeron may (state 0, Fig. 4i) or may not (state 1) be divided into an upper and lower mesepimeron by a sulcus or discrete change in sculpture. Citations: Heraty (2002, char. 60); Krogmann and Vilhelmsen (2006, char. 83).

110 [1033] Posterior margin of upper mesepimeron: **0**, margin even; **1**, margin with distinct notch (= spiracle?).

A notched upper mesepimeron (epn, Fig. 4h) likely represents an opening for the metathoracic spiracle or a remnant of where the metathoracic spiracle once was (Gibson and Huber, 2000), though this has yet to be proven through dissections. Its phylogenetic significance may be problematic because it can be variable even within species [e.g. *Halticoptera dimidiata* (Pteromalidae) has a distinct notch only in some specimens]. The notch is usually dorsal on the horizontal margin of the acropleuron in eupelmids with a fully expanded acropleuron.

111 [1983] Mesepimeron relative to metapleural/propodeal complex: **0**, posterior margin of mesepimeron not overlapping metapleural/propodeal complex; **1**, posterior margin of mesepimeron overlapping metapleural/propodeal complex.

The mesepimeron may be expanded posteriorly, overlapping the anterior edge of the metapleuron. This occurs in a variety of taxa, including Spalangiinae and Ceinae (Pteromalidae) and some Eulophidae (Darling, 1991; Gibson, 2009b). Citation: Burks et al. (2011, char. 22).

112 [1041] Mesepisternal shelf: **0**, absent; **1**, present, defined by ridge or carina.

The mesepisternal shelf is an anterior region of the mesepisternum just posterior to the procoxae that generally appears as a flattened plate on the anterior, ventral surface of the mesopectus (mss, Fig. 5e). It has been termed as the mesepisternal shelf of *Perilampidea* and some other Pteromalinae (Pteromalidae) (Bouček and Heydon, 1997), and is the same as the division of the mesepisternum in *Horismenus* and similar eulophids (Hansson, 2009). Citations: Krogmann and Vilhelmsen (2006, char. 91); Lotfalizadeh et al. (2007, char. 105).

113 [1042] Mesothoracic discrimen: **0**, sulcate or foveate (dc_2, Fig. 5c); **1**, raised carina, at least anteriorly; **2**, absent, or present only as a smooth unsculpted area.

The mesothoracic discrimen is a median, ventral feature of the mesopectus anterior to the mesofurcal pit that represents the external indication of the invaginated mesofurca. The discriminal lamella of the mesofurca is sometimes visible through the cuticle even when an external indication is absent, but a discrimen was coded as present only if visible as an external feature. Citations: Graham (1987, char. 44); Krogmann and Vilhelmsen (2006, char. 92).

114 [1043] Membranous region anterior to each mesocoxa: **0**, absent; **1**, present.

Some chalcidoids are able to rotate their mesocoxae anteriorly out of the mesocoxal fossae (character 115) so that the middle legs can be directed straight forward. In such instances, there is a membranous region anterior to each mesocoxa that enables the coxa to rotate. Citations: Gibson (1989, char. 6); Krogmann and Vilhelmsen (2006, char. 97).

115 [1126] Relationship of mesotrochantinal plate and metasternum: **0**, mesotrochantinal plate inflected internally and extending to or almost to the anterior edge of the metasternum (Fig. 5e); **1**, mesotrochantinal plate inflected internally, but with conspicuous membranous region separating it from the anterior edge of the metasternum (Fig. 5j); **2**, mesotrochantinal plate inflected internally and metasternum extending anteriorly between mesocoxal fossae so as to abut posterior edge of plate (Fig. 4c); **3**, mesotrochantinal plate extending posteriorly in same plane as mesosternum.

This character was defined by Gibson (1989) to describe the different types of mesocoxal articulation found in chalcidoids. In some Pteromalidae, the basic structure is like state 1, but the membranous area is sclerotized. State 3 is a specialized structure found in *Oodera* (Pteromalidae), female Eupelminae, and both sexes of Calosotinae (Eupelmidae), in which the mesotrochantinal plate extends posteriorly so that the trochantinal lobes are visible externally and articulate with the base of the mesocoxae. Citation: Gibson (1989, char. 6; 1995, char. 22).

116 [1045] Position of mesofurcal pit (f_2p): **0**, on mesopectus adjacent to mesocoxal cavity (Fig. 5j); **1**, on mesopectus but clearly removed from mesocoxal cavity (Fig. 5c); **2**, on mesotrochantinal plate.

This character was problematic due to difficulty in defining what constitutes "adjacent" relative to "clearly removed" from the mesocoxal cavity. We considered "adjacent" as being within less than one diameter of the pit from the mesocoxal cavity. State 1 includes structures in which the pit is placed in a secondary depression, as in *Cirrospilus coachellae* (Eulophidae). An external pit is absent from some taxa, such as *Thysanus* (Signiphoridae). Citation: Krogmann and Vilhelmsen (2006, char. 94).

117 [1037] Position of tegula relative to humeral plate: **0**, tegula not covering humeral plate; **1**, tegula covering humeral plate.

Assessment of states was difficult in Dirhininae and Epitraninae (Chalcididae), where the tegula reaches to about the apex of the humeral plate but did not always seem to completely cover it, possibly due to differing flexion of the wing base. Citations: Wijesekara (1997, char. 16); Gates (2008, char. 23).

118 [1038] Number of setae on tegula: **0–3** setae (actual count); 4 or more setae.

A count of tegula setae was made to determine their phylogenetic value. This proved difficult, even on slide mounts and SEMs, due to curvature of the tegula and specimen breakage.

119 [1046] Longitudinal division of metascutellum (= dorsellum): **0**, undivided or at most by a shallow sculptural groove; **1**, divided medially by a longitudinal sulcus.

State 1 does not include structures in which the metascutellum is "divided" by only a shallow sculptural groove (e.g. some Pteromalidae: Miscogastrinae and Eulophidae: Tetrastichinae), but does occur in *Coccobius* (Aphelinidae).

120 [1047] Metanotal shape: **0**, not protruding as horizontal triangular plate posterior to scutellum; **1**, protruding as a horizontal triangular plate (often also translucent or light-coloured) posterior to scutellum.

State 1 occurs only in *Elasmus* (Eulophidae) and *Euryischia* (Eriaporidae) (LaSalle et al., 1997). The metanotum of *Metapelma* (Eupelmidae) also protrudes as a horizontal triangular flange, but under rather than posterior to a protuberant scutellum, and because of this structural difference *Metapelma* was coded as having state 0. In both cases, the metascutellum is not differentiated from the metanotum.

121 [1998] Metascutellum anterior extent: **0**, extending to anterior edge of exposed surface of metanotum; **1**, not extending to anterior edge of exposed surface of metanotum (Fig. 4f).

This and character 122 assess the relative size of the metascutellum (Krogmann and Vilhelmsen, 2006). The metascutellum is a differentiated dorsomedian region of the metanotum, which may or may not extend to the anterior margin of the metanotum. The anterior margin of the metanotum has an edge, which is generally indicated by a rim. This character could not be assessed externally in *Metapelma* (Eupelmidae) because the metascutellum protrudes as a flange under the apex of the protuberant scutellum. The posterior, convex part does not reach the anterior margin of the metanotum under the scutellum, and was scored as state 1. Citation: Krogmann and Vilhelmsen (2006, char. 108).

122 [1999] Metascutellum posterior extent: **0**, extending to posterior edge of exposed surface of metanotum; **1**, not extending to posterior edge of exposed surface of metanotum (Fig. 4f).

This character is similar to character 121 except in that it codes whether or not the posterior edge of the metascutellum extends to the posterior edge of metanotum. Citation: Krogmann and Vilhelmsen (2006, char. 109).

123 [1048] Metanotal scutellar arm (mtsa): **0**, overlapping anterior edge of propodeum (Fig. 4f); **1**, abutting anterior edge of propodeum or separated from it by a gap (Fig. 4e); **2**, overlapped by anterior edge of propodeum; **3**, absent.

The metanotum has a region (metascutellar arm after Krogmann and Vilhelmsen, 2006) lateral to the metascutellum that we call the lateral panel (see character 124) (Fig. 4f). The lateral panel usually is composed of a convex, flange-like posterolateral surface that articulates with the propodeum and typically also a more anterior concave area that usually has some incomplete longitudinal carinae. The more posterior, flange-like part of the lateral panel we call the metanotal scutellar arm and the anterior, concave part we call the metanotal trough. In most chalcidoids, the metanotal scutellar arm extends over a depression in the anterolateral part of the propodeum, near the spiracle (state 0). Small-bodied chalcidoids sometimes have the metanotal scutellar arm greatly reduced. In *Idioporus* (Pteromalidae), the metanotal scutellar arm appears to extend beneath the propodeal margin (state 2), whereas the strongly reduced metanotum of *Chiloe* (Rotoitidae) does not have a flange (state 3). Citations: Heraty (2002, char. 52).

124 [2000] Length of metascutellar arm: **0**, more than half length of lateral panel (Fig. 4f–i); **1**, less than half length of lateral panel but forming a convex flange and not reduced to a carina; **2**, reduced to a thin carina (Fig. 4d,e).

This character refers to the relative structure and size of the swollen metanotal arm. The lateral panel includes both the metanotal scutellar arm and metanotal trough.

125 [1049] Metascutellar setae: **0**, absent; **1**, present.

This character codes whether or not setae are present on the metascutellum. Citation: Gibson (2003, chars 26, 27).

126 [1067] Lateral sulci delimiting triangular median region of propodeum: **0**, absent; **1**, present (Fig. 5g).

State 1 occurs in Signiphoridae and *Marietta* (Aphelinidae). Citation: Woolley (1988, char. 9).

127 [1068] Setal pattern of propodeal disc: **0**, bare; **1**, setose, with setae on each side directed toward midline; **2**, evenly setose or pilose; **3**, with a few setae directed laterally.

The propodeum is divided into a median propodeal disc, sometimes called the propodeal plical region if delineated by plical carinae, and a region lateral to the spiracles, the "propodeal callus" (Graham, 1969). Although the propodeal callus often has setae, this is much less common for the disc. *Lambdobregma schwarzii* (Eupelmidae) has setae on the propodeal disc that did not match exactly any of the states, but probably is closest to state 1 because most setae are more or less directed to the midline and the disc is not evenly setose. This is a species-specific rather than generic feature for *Lambdobregma*. Citations: Noyes and Hayat (1994, chars 56, 57); Gibson (2003, chars 33, 34, 35); Krogmann and Vilhelmsen (2006, char. 146); Lotfalizadeh et al. (2007, char. 117); Burks et al. (2011, char. 24).

128 [1069] Shape of propodeal spiracle: **0**, elliptical; **1**, circular; **2**, reniform (= kidney shaped) (Fig. 4g).

There is a marginal incision of the spiracle in some Eucharitidae, but the spiracle was coded as circular. Citations: Delvare (1992, char. 36); Wijesekara (1997, char. 22); Heraty (2002, char. 55); Krogmann and Vilhelmsen (2006, char. 137); Gates (2008, char. 35).

129 [1070] Position of propodeal spiracle: **0**, separated from hind margin of metanotum by at most its own maximum diameter; **1**, separated from metanotum by at least 1.5 times its own maximum diameter.

The longest axis of the spiracle was used to measure its diameter. State 1 is a character that in the past was used to differentiate Ceinae (Pteromalidae), but it also occurs in some other taxa. In some instances, the length of the propodeum relative to the size of the spiracle complicates interpretation of this character. For example, only state 0 is possible in Signiphoridae because the total length of propodeum is only about three times the diameter of spiracle, although the spiracle is at midlength of the propodeum. This is the same for most Neanastatinae and female *Phenaceupelmus* (Eupelminae), in which the propodeum is more or less transverse and the spiracle is at about midlength. Because of the length of the propodeum and the size of the spiracle, only state 0 is possible for these taxa (Gibson, 2009a). However, male *Phenaceupelmus* have state 0 because the propodeum is longer and the spiracle is obviously closer to the anterior than posterior margin. Citations: Graham (1987, char. 37); Krogmann and Vilhelmsen (2006, char. 134).

130 [1071] Enclosure of propodeal spiracle (psp): **0**, spiracle entirely surrounded by propodeal cuticle (Fig. 4d); **1**, spiracle only partially surrounded by propodeal cuticle, narrowly open anteriorly.

State 1 occurs in some genera of Tetrastichinae (Eulophidae), Trichogrammatidae and some other small-bodied species.

131 [2004] Peritrema of propodeal spiracle: **0**, absent; **1**, present.

The peritreme is the marginal rim of the spiracle. An enlarged, recessed peritreme that is covered by a dense hydrophobic pubescence in Agaonidae *sensu stricto* is the peritrema (Compton and McLaren, 1989).

132 [1050] Shape of metapleuron (pl_3): –, inapplicable (metapleuron not differentiated); **0**, subtriangular; **1**, broadly rectangular or nearly square (Fig. 5d).

In state 0, the metapleuron tapers strongly towards the hind wing base, whereas in state 1 there are two dorsal corners (i.e. truncate dorsal margin), thus forming a rectangular metapleuron. In Torymini (Torymidae), metapleural shape is affected by the anterior margin being produced anteriorly, but the dorsal angle is the same for a subtriangular metapleuron. In *Rotoita* (Rotoitidae), the metapleuron is linear and extends to the base of the hind wing, but was coded as state 0 because of its narrow linear aspect. Citation: Krogmann and Vilhelmsen (2006, char. 115).

133 [1842] Setation of metapleuron: –, inapplicable (metapleuron not differentiated); **0**, setose; **1**, entirely bare; **2**, bare in anterior part; **3**, bare posteriorly, but with at least a few setae anteriorly.

The metapleuron is bare throughout many chalcidoid families, but can be setose in taxa containing large-bodied species (Fig. 5d). Citations: Gibson (1995, chars 23, 52; 2003, char. 31); Krogmann and Vilhelmsen (2006, char. 118).

134 [1051] Metapleural–propodeal supracoxal flange (cxf): **0**, absent; **1**, present.

The propodeum of larger-bodied chalcidoids usually has its posterolateral margin developed into a distinct flange, the supracoxal flange, which extends over the base of the metacoxa, the supracoxal flange (Fig. 4g). Sometimes the anterior and posterior endpoints of the supracoxal flange are indicated by shallow pits. Presence of a supracoxal flange was scored only in those taxa where it overlapped the base of the metacoxa, not just the coxal articulation. The flange is absent in most small-bodied Chalcidoidea.

135 [1062] Metapleural sulcus (mtps): **0**, present as a furrow, row of foveae, or carina; **1**, absent.

The metapleuron may be separated from the propodeum, at least superficially, by an impression (Fig. 4f), which is absent in some taxa, especially Eurytominae (Eurytomidae). Citations: Krogmann and Vilhelmsen (2006, char. 116); Lotfalizadeh et al. (2007, char. 119).

136 [1054] Number of metafurcal pits: –, inapplicable (absent); **0**, single median pit; **1**, lateral (paired) pits (Fig. 4c).

A median metafurcal pit can be difficult to observe in some taxa (e.g. *Cleonymus*, Pteromalidae) and metafurcal pits can sometimes be entirely absent (e.g. Mymarommatidae). Citations: Krogmann and Vilhelmsen (2006, char. 120); Lotfalizadeh et al. (2007, char. 120).

137 [1053] Position of metafurcal pits: –, inapplicable (absent); **0**, at anterior margin of metasternum; **1**, near midlength of metasternum (Fig. 4c).

Coding this character was problematic when the metasternum is greatly reduced and because position of the metafurcal pits varies between the two described states. Rarely, the metafurcal pits are absent or they may be hidden by an expanded mesopectus.

138 [1976] Paired lobes at posteroventral edge of metapleural shelf, directly posterior to metacoxae: **0**, absent; **1**, present.

These are short, approximated lobes that project posteriorly between the metacoxae, over the base of the metacoxal cavity. They are found in Dirhininae and Epitraninae (Chalcididae) (Fig. 5e).

Wing characters (139–175).

139 [1072] Wingedness (female): **0**, macropterous (fully winged) (Fig. 1b–k); **1**, brachypterous (wings present but conspicuously reduced); **2**, apterous (wings completely absent) (Fig. 1a).

Brachypterous and apterous species are known from most families of Chalcidoidea. This affects very few taxa in our analysis, and because we preferentially score females, this is not a problem for some of the fig-associated taxa with dimorphic wingless males. Citations: Noyes and Hayat (1994, char. 42); Gibson (1995, char. 29).

140 [1073] Number of setae on humeral plate of fore wing: **0–4** setae (actual count); **5** or more setae.

We arbitrarily set a limit for counting setae at 4, with five or more setae being considered pilose (state 5). Citation: Gibson (2003, char. 36).

141 [1851] Basal posterior lobe (bpl) of fore wing: **0**, absent; **1**, present.

The posterior margin of the fore wing of some chalcidoids has a small, convex, lobe-like projection defined by the distal narrowing of the posterior wing margin behind the sclerotized anal vein (state 1) (Fig. 6b). This lobe had not previously been observed in Chalcidoidea, but appears to be posterior and more distal to the vanal area described by Gibson (2004).

142 [1074] Basal vein of fore wing: **0**, present as a sclerotized tubular vein; **1**, present as a pigmented fold; **2**, absent or present only as a non-pigmented fold; **3**, present as a setal line.

The Rs + M in the basal area of the wing is the basal vein. Some Miscogastrinae (Pteromalidae) have a sclerotized tubular vein, but most chalcidoids lack a tubular basal vein and have the "vein" indicated only by a pigmented fold (Fig. 6a,d,h) or a convex fold and/or a line of setae. Although scored, setal lines do not seem to have phylogenetic importance and are variable within most higher-level groups.

143 [1997] Basal cell setation: **0**, completely setose; **1**, not completely setose.

The basal cell (bc) is delineated anteriorly by the submarginal vein (Sc + R), distally by the basal vein (Rs + M) (character 142) and posteriorly by the mediocubital fold (M + Cu) (Fig. 1c). The amount of setation and setal pattern within the basal cell varies widely across different taxa, complicating coding of the character. Therefore we scored only complete, even setation (state 0) versus setation being variably reduced to entirely absent. Anything less than complete setation was coded as state 1, even if the apical third of the cell is setose. Setation of the basal cell does not include the vanal region, which is posterior to the mediocubital fold and often bare. Citations: Noyes and Hayat (1994, char. 48); Gibson (1995, chars 32, 55).

144 [1076] Cubital vein of fore wing: **0**, present as a sclerotized tubular vein; **1**, present as a pigmented fold (Fig. 6b,d); **2**, absent or present only as a non-pigmented fold; **3**, present as a setal line.

The cubital vein (Cu) runs parallel to the hind margin of the fore wing. It is tubular and pigmented in some Ormocerinae (Pteromalidae), Leucospidae (Fig. 6b) and Chalcididae (Bradley, 1955; Danforth, 1990).

145 [1079] Length of costal cell of fore wing: **0**, more than one-third fore wing length (Fig. 6b,d); **1**, less than one-third fore wing length (Fig. 6c,h,k).

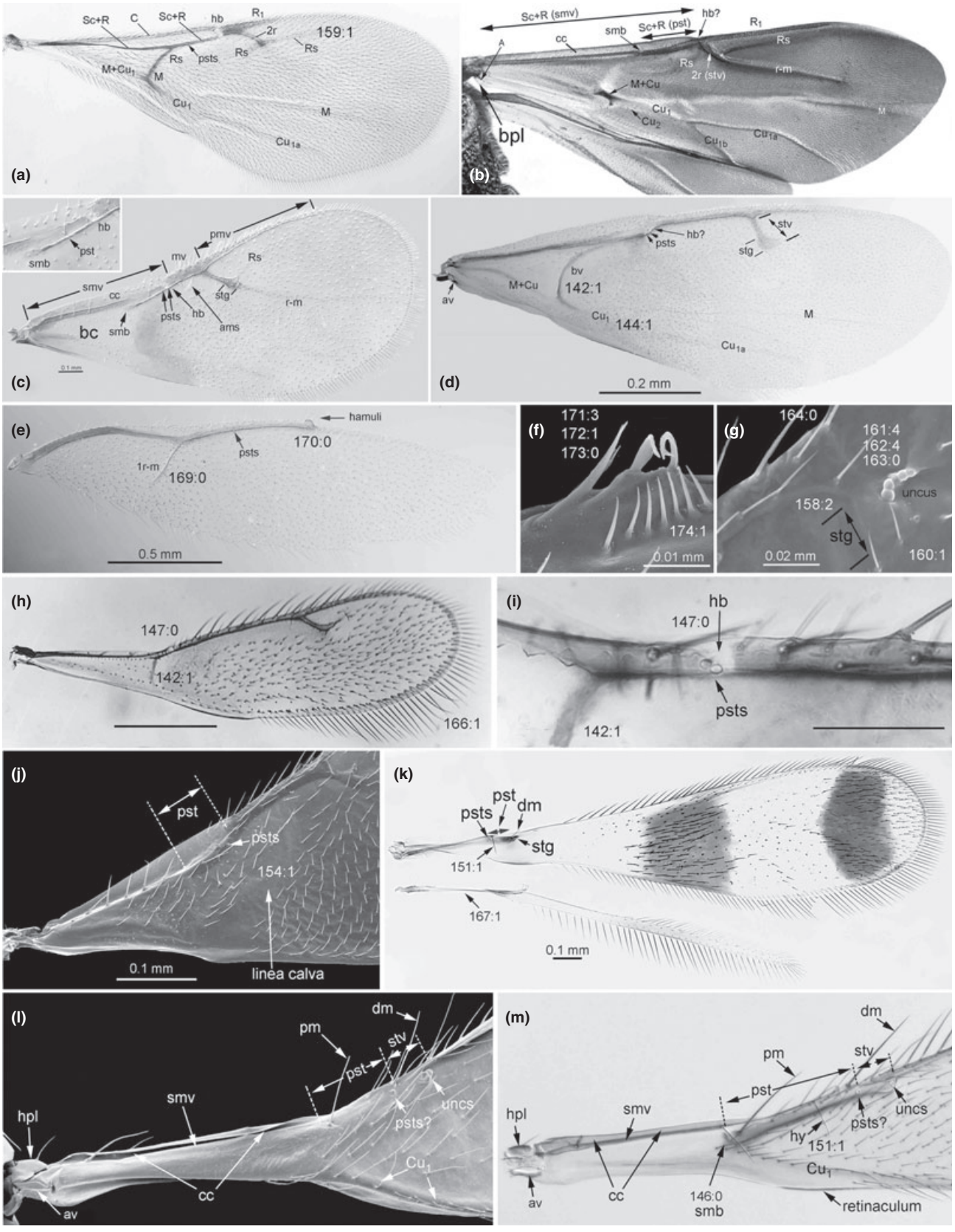
The costal cell is the wing membrane anterior to the submarginal vein, between the humeral plate and the junction of the submarginal vein with the wing margin. In some taxa (e.g. Hybothoracini, Chalcididae), the marginal vein extends horizontally before the actual wing margin, and the apex of the costal cell is considered to end at the base of the marginal vein. *Neanastatus* (Eupelmidae) has a costal cell that is less than one-third the wing length, but this unusual structure is because the "marginal" vein is unusually long and likely is a composite of both the marginal vein and the parastigma of the submarginal vein because the parastigmal sensilla are on the apparent marginal vein. Citations: Schauff (1984, char. 41); Wijesekara (1997, char. 30).

146 [1078] Joining of submarginal vein with parastigma of fore wing: **0**, smooth; **1**, abrupt (Fig. 6c).

An abrupt joining of the parastigma with the more basal part of the submarginal vein was used by Gauthier et al. (2000) to define Cirrospilini (Eulophidae), but this structure is more widespread across Chalcidoidea, including Mymaridae. Citation: Schauff (1991, char. 9).

147 [1077] Hyaline break (unpigmented area) of parastigma of fore wing: **0**, present; **1**, absent.

As discussed in "Terminology", the basal limit of the parastigma is readily apparent in some chalcidoids because a hyaline region separates it from the rest of


(a)
Sc+R
C
Sc+R
hb
R1
2r
159:1
Rs
psts
Rs
Rs
M+Cu1
M
Cu1
M
Cu1a
(b)
Sc+R (smv)
hb?
smb
Sc+R (pst)
R1
A
cc
Rs
Rs
2r (stv)
r-m
M+Cu
Cu1
Cu2
M
bpl
Cu1b
Cu1a
(c)
hb
pmv
smb
pst
mv
Rs
smv
cc
stg
r-m
psts
hb
bc
smb
ams
0.1 mm
(d)
hb?
psts
stv
stg
bv
av
M+Cu
142:1
Cu1
144:1
M
Cu1a
0.2 mm
(e)
hamuli
170:0
psts
1r-m
169:0
0.5 mm
(f)
171:3
172:1
173:0
174:1
0.01 mm
(g)
164:0
161:4
162:4
163:0
uncus
158:2
stg
0.02 mm
160:1
(h)
147:0
142:1
166:1
(i)
hb
147:0
psts
142:1
(j)
pst
psts
154:1
0.1 mm
linea calva
(k)
pst
psts
dm
stg
151:1
167:1
0.1 mm
(l)
dm
pm
stv
pst
smv
uncs
hpl
psts?
Cu1
cc
av
(m)
dm
pm
stv
pst
uncs
hpl
smv
psts?
hy
151:1
Cu1
av
cc
146:0
smb
retinaculum

the submarginal vein (Fig. 6c,h,i). The parastigma of *Chrysomalla* (Perilampidae) has a distinct light area medially but the vein is not constricted (cf. Darling, 1986). Citation: Darling (1991, char. 1).

148 [2130] Parastigmal constriction of fore wing: **0**, parastigma not constricted medially; **1**, parastigma constricted at hyaline break.

This character differs from character 147 in that it refers to the shape of the parastigma. The parastigma can be distinctly pinched at the hyaline break or pinched at the expected location of the hyaline break even if this is absent.

149 [1087] Stout bristles on sclerotized posterior extension of parastigma of fore wing: **0**, bristles absent; 1–3 bristles (actual count).

In a very few chalcidoids (e.g. Aphelinidae, Eriaporidae), the base of the parastigma is extended as a "spur" onto the wing membrane and this can have 1–3 stout bristles. Citation: Hayat (1998).

150 [1088] Tuft of erect, thickened setae on parastigma of fore wing: **0**, absent; **1**, present.

This feature occurs in some Pteromalidae (Cerocephalinae, Storeyinae) and Eulophidae.

151 [1095] Hypochaeta of fore wing: **0**, absent; **1**, one or rarely two present at parastigma.

In Mymaridae, the hypochaeta is a posteriorly directed seta on the ventral surface of the fore wing that originates from the membrane anterior to the parastigma between two macrochaeta (hy, Fig. 6m). Mymarids usually have a single hypochaeta. Citations: Schauff (1984, char. 47); Gibson (1986a, char. 613).

152 [1086] Campaniform sensilla on parastigma of fore wing: **0**, no sensilla; **1–4** sensilla (psts, Fig. 6i) (actual count).

Observation with a compound microscope is often required to observe these correctly.

153 [1099] Specular area (speculum): –, inapplicable (wing or wing setation entirely absent); **0**, bare dorsally and ventrally; **1**, setose dorsally and ventrally (speculum absent); **2**, bare dorsally, setose ventrally; **3**, setose dorsally, bare ventrally.

The speculum is a bare region between Rs + M (usually visible only as a fold or remnant of the vein) and more distal setae on the disc of the wing (state 0). Presence of a speculum can be subjective when it is relatively small or when it has a few setae within it. Citation: Heraty (1994, char. 37).

154 [1097] Linea calva of fore wing: **0**, absent; **1**, present, incomplete or complete.

A linea calva is interpreted here in its traditional sense, as a narrow, oblique bare band on the fore wing (Fig. 6j). It is characteristic of Encyrtidae and some Aphelininae, but also occurs in some Eupelmidae. The linea calva may represent a reduced speculum in some taxa, but co-occurs with a speculum in some Aphelininae and *Eretmocerus*. Citations: Polaszek and Hayat (1992, char. 23); Noyes and Hayat (1994, char. 47); Gibson (1995, char. 30).

155 [1098] Filum spinosum of fore wing: **0**, absent; **1**, present.

The filum spinosum is a row of differentiated, thickened or peg-like setae along the posterior margin of the linea calva, which occurs only in Encyrtidae. Citation: Noyes and Hayat (1994, char. 52).

156 [1080] Length of marginal vein of fore wing: **0**, shorter than length of stigmal vein including stigma; **1**, between 1 and 3 times length of stigmal vein including stigma; **2**, more than three times length of stigmal vein including stigma.

Length of the marginal vein is measured from its base (where the costal cell ends) to its apex (juncture of the stigmal and postmarginal veins) (Graham, 1969). Relative lengths of one and three times were chosen because these appeared to be the most phylogenetically informative ratios when surveying across chalcidoid families. Citations: Schauff (1991, char. 7); Noyes and Hayat (1994, char. 46).

157 [1096] Ventral surface of admarginal area of fore wing: **0**, with numerous undifferentiated setae; **1**, with 1–3 rows of setae; **2**, with elongate setae present only near stigma (adstigmal setae); **3**, without setae (i.e. bare).

Admarginal setae are one or more rows of setae on the ventral surface of the fore wing near the marginal vein that are differentiated from the other ventral setae by being longer and/or segregated (ams, Fig. 6c). Here we code the ventral area of the fore wing along the marginal vein as the admarginal area so that absence of admarginal setae, either because the region is uniformly setose or entirely bare, can be contrasted with presence of admarginal setae behind the marginal vein or elongate setae only near the stigma, the adstigmal setae. Admarginal setae can be obscured if overlain by setae on the dorsal surface of the wing. Citation: Darling (1991, char. 9).

158 [1081] Length of stigmal vein (including stigma) of fore wing: **0**, more than five times the narrowest width of the stigmal vein; **1**, between 2–5 times the

Fig. 6. (a–m) Wings. (a) *Belyta* sp. (Diapriidae). (b) *Leucospis slossonae* (Leucospidae). (c) *Perthiola mazaneci* (Eulophidae: Opheliminae), fore wing; inset is enlargement of parastigma. (d,e) *Espinosa nothofagi* (Pteromalidae: Ormocerinae), (d) fore wing; (e) hind wing. (f) *Cirrospilus coachellae* (Eulophidae: Eulophinae), hamuli. (g) *Haeckeliania* sp. (Trichogrammatidae), stigmal vein. (h,i) *Spalangiopelta canadensis* (Pteromalidae: Ceinae), (h) fore wing; (i) parastigma. (j) *Eriaphytis chackoi* (Eriaporidae), fore wing. (k) *Acmopolynema varium* (Mymaridae), wings. (l) *Ooctonus* sp. (Mymaridae), fore wing SEM image. (m) *Gonatocerus* sp. (Mymaridae), fore wing, light microscope image. Character state associations explained in text.

narrowest width of the stigmal vein; **2**, less than 2 times the narrowest width of the stigmal vein.

The ratios chosen are arbitrary, but they parse out a very long, intermediate length and short or sessile stigmal vein. Citation: Schauff (1991, char. 27).

159 [1075] Rs vein of fore wing: **0**, present as a sclerotized tubular vein; **1**, present as a pigmented fold; **2**, absent, or present only as a non-pigmented fold; **3**, present as a setal line.

As discussed in "Terminology", the Rs vein is the continuation of the uncus toward the apical margin of the wing. This character codes for only that part of the venation beyond the uncus (Fig. 6b,c) which is defined by the uncal sensilla (characters 161, 163).

160 [1089] Stigma of fore wing: **0**, absent (not differentiated from stigmal vein) (Fig. 6b); **1**, less than twice length of stigmal vein basal to stigma (Fig. 6c,d); **2**, enlarged, greater than or equal to twice length of stigmal vein basal to stigma.

As discussed in "Terminology", the stigma is a variably enlarged differentiated apical region of the stigmal vein (2r). Citations: Darling (1983, chars. 6, 7); LaSalle (1987, char. 15); Polaszek and Hayat (1992, char. 21); Gates (2008, char. 28).

161 [1090] Arrangement of uncal sensilla of fore wing: **0**, grouped in a single cluster; **1**, arranged in a straight line; **2**, forming an L-shaped pattern with the basal sensillum posterior to the others; **3**, forming an L-shaped pattern with the basal sensillum anterior to the others; **4**, forming an offset line of sensilla (Fig. 6g).

Campaniform sensilla on the uncus, or on the stigmal vein when the uncus is not developed (see character 163), are arranged in different patterns coded as the different states. Citation: Kim and Heraty (2012, char. 44).

162 [1091] Number of uncal sensilla of fore wing: **0–5** sensilla (actual count); **6** or more sensilla.

Citation: Kim and Heraty (2012, char. 45).

163 [1092] Uncus of fore wing: **0**, present and projecting as a linear process; **1**, absent (not differentiated from stigma or stigmal vein).

The uncus of the fore wing is a short, tubular or pigmented remnant of the Rs vein that projects from the distal margin of the stigma or stigmal vein (Fig. 6g,h).

164 [1082] Length of postmarginal vein of fore wing: **0**, absent, or shorter than stigmal vein including stigma (Fig. 6j,k); **1**, longer than stigmal vein including stigma, but shorter than costal cell (Fig. 6b–d,h); **2**, longer than costal cell.

The length of the postmarginal vein (pmv) includes the tubular portion of the vein only, not any distal pigmented remnant (see also character 165). The base of the postmarginal vein (pmv) is measured at the juncture of the postmarginal vein with the stigmal vein (Graham, 1969). For state 2, the costal cell is assumed to be longer than the stigmal vein (stv) including the stigma. In *Anorasema* (Eucharitidae), the pmv is extremely long and extends to the apex of the wing but is still shorter than the costal cell and therefore coded as state 1. The pmv is also somewhat longer than the costal cell in *Neanastatus* (Eupelmidae), but regardless of length was coded as state 1 because the costal cell is hypothesized to be secondarily shortened because the parastigma is integrated with the marginal vein (see character 145). In some Eupelminae, the pmv is exactly the same length as the stv (e.g. *Eupelmus urozonus*) and was scored as state 1, but without confidence. Citations: Polaszek and Hayat (1992, char. 20); Heraty (1994, char. 36; 2002, char. 78); Burks et al. (2011, char. 29).

165 [1100] Enlarged seta marking apex of postmarginal vein of fore wing: **0**, absent; **1**, present.

Observed in some Encyrtidae, and used as a means of determining the end of the postmarginal vein.

166 [1849] Marginal fringe setae of fore wing: **0**, absent, or short and not longer than tegula (Fig. 6a,b,d); **1**, moderate, longer than tegula, but shorter than width of fore wing (Fig. 6c,h,k); **2**, elongate, longer than width of fore wing.

The length of the marginal fringe of setae as interpreted for this character is based on the longest setae that project from the distal or posterior margin of the fore wing. Citations: Noyes and Hayat (1994, char. 45).

167 [1101] Hind wing structure: **0**, wing membrane extending to base of wing; **1**, wing base stalk-like, with membrane originating distally (Fig. 6k); **2**, with only stalk-like vein, without membrane and apically bifurcate (haltere-like).

State 1 was first proposed as a specialized structure characteristic of most Mymaridae, but a few mymarids have state 0, and some other very small chalcidoids (e.g. some Trichogrammatidae) have state 1. State 2 is a highly specialized structure that occurs only in Mymarommatoidea. Citations: Schauff (1984, char. 45); Gibson (1986a, char. 15).

168 [1109] Marginal vein of hind wing (male): **0**, at most only slightly thicker than submarginal vein; **1**, expanded and thickened, much thicker than submarginal vein.

An enlarged, swollen marginal vein occurs mainly in Platynocheilinae and Mongolocampinae (Tetracampidae) and some Pteromalidae, in addition to a few species of other families.

169 [1106] Spur vein (1r-m) of hind wing: **0**, present as a sclerotized process (Fig. 6e); **1**, absent; **2**, present only as a setal track; **3**, pigmented but not a sclerotized process.

Neanastatus and *Phenaceupelmus* (Eupelmidae) were coded as state 0 because at least some specimens have a very short (angular) sclerotized projection. Some eupelmids have a differentiated hyaline spur or streak

that definitely is not pigmented and therefore was coded as state 1. Citations: Wijesekara (1997, char. 32); Heraty (2002, char. 81).

170 [1108] Position of hamuli: **0**, not beyond midlength of wing; **1**, beyond midlength of wing (Fig. 6e).

Hamuli are hook-like setae on the anterior margin of the hind wing that interlock with the recurved posterior edge of the fore wing during flight (Basibuyuk and Quicke, 1997).

171 [1102] Number of hamuli of hind wing: **0–4** hamuli (actual count); **5** or more hamuli (Fig. 6f).

The hamuli rarely exceed 4 in number, but if so the number is variable, thus state 5 was chosen as a maximum. Up to seven hamuli occur in Philomidinae (Perilampidae).

172 [1957] Shape of 1st hamulus: **0**, curved toward wing surface, like the other hamuli; **1**, straight or only slightly curved, with other hamuli strongly curved towards wing surface or apparently curved towards wing base (Fig. 6f).

A straight first hamulus was found in some Chalcidoidea. This state was confirmed as accurate by examination of point-mounted and slide-mounted specimens. Citation: Wijesekara (1997, char. 30).

173 [1105] Location of basalmost hamulus: **0**, near the others (Fig. 6f); **1**, distant from the others.

State 1 occurs in Brachymeriinae (Chalcididae). Citation: Wijesekara (1997, char. 30).

174 [1104] Additional erect setae opposite to hamuli: **0**, absent; **1**, present (Fig. 6f).

This character refers to a group of minute setae opposite the hamuli. They were proposed as a synapomorphy for Chalcidoidea (Basibuyuk and Quicke, 1997), but several unrelated chalcidoid taxa lack the setae.

175 [1853] Erect setae on hind wing parastigma: **0**–4 setae (actual count).

The parastigma of the hind wing of most Chalcidoidea has one or more setae. As the numbers of setae increase, the number appears to be more variable both within a species and even between different wings of the same specimen, which resulted in some polymorphic coding.

Leg characters (176–202).

176 [1110] Number of tarsomeres of fore leg: **3–5** tarsomeres (actual count).

A five-segmented tarsus is plesiomorphic. A reduced tarsomere count has been used to define higher chalcidoid taxa, such as Eulophidae, Trichogrammatidae and some subfamilies of Aphelinidae. Recently, some species have been found that form exceptions to these rules. Only males of *Dicopomorpha echmepterygis* (Mymaridae; Fig. 1a) and males of some of the specialized male fig associates have fewer than three tarsomeres. Citations: Schauff (1984, char. 51); LaSalle et al. (1997); Burks et al. (2011, char. 26).

177 [1111] Number of tarsomeres of midleg compared with fore leg: **0**, same; **1**, one fewer.

Macromesinae (Pteromalidae) has been characterized by having four tarsomeres on the midleg as opposed to five on other legs. This condition also occurs in males of Tetracampinae (Tetracampidae). Citation: Graham (1969); Burks et al. (2011, char. 27).

178 [1113] Posterior preapical bristle of profemur: **0**, absent; **1**, present.

There is usually only a single strong bristle in smaller-bodied species, but in some larger-bodied species there may be several long bristles with one distinctive bristle in a homologous position.

179 [1118] Protibial carina: **0**, protibia not carinate ventrally; **1**, protibia with sinuate, ventral carinate margin over about basal half to three-quarters; **2**, protibia with carinate margin along entire ventral length.

A protibial carina is present in some Lyciscini and Heydeniini (Pteromalidae). Citation: Gibson (2003, char. 42).

180 [1116] Apical margin of protibia: **0**, without horizontally directed stout spur or elongation; **1**, with horizontally directed socketed spur; **2**, with two or more socketed spurs; **3**, without socketed spur but apical margin distinctly expanded giving the appearance of a spur.

The apical margin of the protibia of some chalcidoids, particularly those associated with galls or parasitoids of wood-boring beetles, often have one (state 1) or more (state 2) stout, socketed spines or spurs, or the margin projects into a denticle but is not socketed (state 3). Citations: Gibson (1989, char. 18); Wijesekara (1997, char. 23).

181 [1114] Shape of protibial spur (calcar): **0**, curved; **1**, straight.

Most Chalcidoidea have a curved protibial spur termed the calcar (Fig. 7g). Eulophidae, Tetracampidae, Trichogrammatidae and some species of Aphelinidae and Pteromalidae have a relatively straight spur. The variation in this character was discussed by LaSalle et al. (1997). Citations: Woolley (1988, char. 28); Basibuyuk and Quicke (1995, char. E); Heraty (2002, char. 72); Burks et al. (2011, char. 25).

182 [1115] Apex of protibial spur: **0**, cleft tip; **1**, single tip (Fig. 7g).

A cleft apex occurs in both types of protibial spur scored in character 181. Citations: Woolley (1988, char. 28); Basibuyuk and Quicke (1995, char. D).

183 [1121] Comb of fore basitarsus: **0**, basitarsus without any comb of seta; **1**, basitarsus with comb of closely set, stout setae.

The basitarsal comb is a series of specialized, typically spatulate setae on the ventral margin of the basal

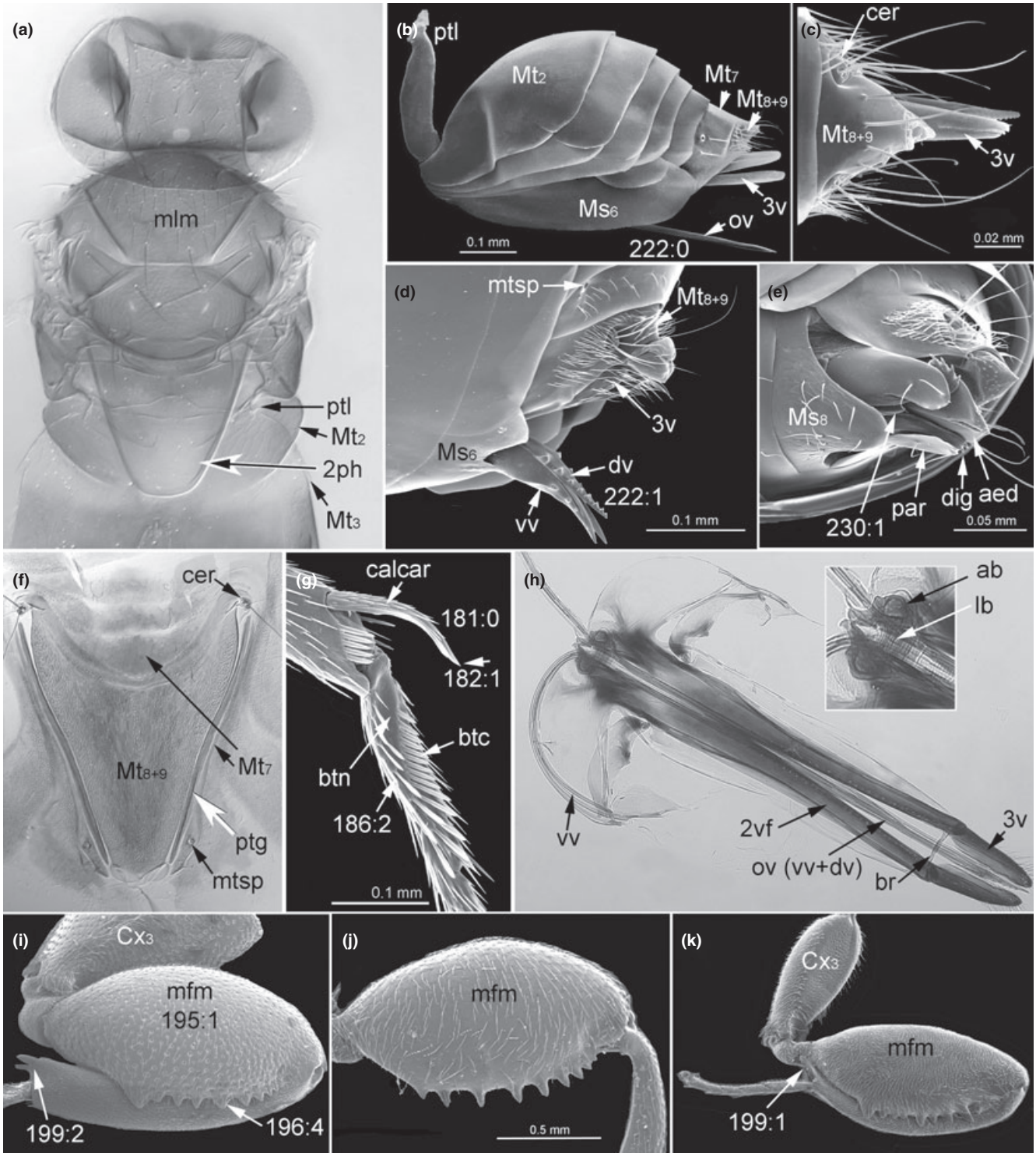


Fig. 7. (a) *Aphelinus* sp. (Aphelinidae), head and mesosoma, dorsal view. (b,c) *Acmopolynema varium* (Mymaridae): (b) metasoma, lateral view; (c) apex of gaster, dorsal view. (d) *Orasema* sp. (Eucharitidae), apex of female gaster, lateral view. (e) *Psilocharis afra* (Eucharitidae), apex of male gaster, subventral view. (f) *Anagyrus pseudococci* (Encyrtidae), gaster in dorsal view, with paratergites. (g) *Orasema* sp., calcar and basitarsus, inner side. (h) *Nasonia vitripennis* (Pteromalidae: Pteromalinae), ovipositor; inset is enlargement of laminated bridge. (i–k) hind legs: (i) *Leucospis affinis* (Leucospidae); (j) *Brachymeria* sp. (Chalcididae); (k) *Podagrion* sp. (Torymidae). Character state associations explained in text.

tarsomere of the fore leg (Fig. 7g). The setae along with the protibial spur function as an antennal cleaning organ. Citation: Basibuyuk and Quicke (1995, char. J).

184 [1123] Orientation of comb of fore basitarsus: **0**, longitudinal or nearly so; **1**, strongly oblique.

In state 0, the setae of the comb are aligned longitudinally in the direction of the basitarsal notch (character 185) (Fig. 7g), whereas in state 1 the setae are aligned almost transversely across the ventral side of the basitarsus. State 1 seems to be correlated with the absence of a basitarsal notch. Citation: Basibuyuk and Quicke (1995).

185 [1120] Basitarsal notch of fore leg: **0**, absent; **1**, present.

The basitarsal notch (btn) is a longitudinal, concave, bare trough on the ventral surface of the basitarsus along the basitarsal comb of the fore leg. Citation: Basibuyuk and Quicke (1995, char. I).

186 [1122] Setation of basitarsus of fore leg: **0**, with one row of paddle-shaped setae; **1**, with more than one row of paddle-shaped setae; **2**, with ordinary setae; **3**, without setae.

Ceratogramma and possibly other Trichogrammatidae have three paddle-shaped setae in two rows. Citation: Basibuyuk and Quicke (1995, char. K).

187 [1125] Insertion of mesocoxa: **0**, anteroventral margin of mesocoxa distinctly posterior to midline, widely separated from procoxa; **1**, anteroventral margin of mesocoxa at or anterior to midline of mesopleuron, more equidistant from insertion of pro- and metacoxa (Fig. 5k).

This character has long been used as a feature to distinguish Eupelmidae (state 0) from Encyrtidae (state 1). Both of these taxa have an elongate, almost horizontal mesopleuron; the difference is always obvious, but it can be very difficult to assess accurately in some pteromalid lineage taxa and some Tanaostigmatidae, in which the mesopleuron is orientated obliquely.

188 [1129] Preapical bristle on anterior surface of mesofemur: **0**, absent; **1**, present, directed ventrally.

The preapical bristle is distinct from any surrounding setae. This character may be partly correlated with small body size, but a bristle is found in some large-bodied species of certain taxa (especially Eulophidae).

189 [1130] Preapical bristle on posterior surface of mesofemur: **0**, absent; **1**, present.

This character varies in similar patterns as character 188, but rarely co-occurs with it.

190 [1128] Mesotibial apical pegs: **0**, mesotibia with at most robust spines along anteroapical edge; **1**, mesotibia with row or patch of thickened pegs along anteroapical edge.

Most "jumping" chalcidoids with a greatly enlarged acropleuron have a row or patch of usually dark, comparatively short and thick pegs along the anteroapical margin of the mesotibia. The pegs are nothing more than modified setae and sometimes there is little structural difference between pegs and comparatively strong, spine-like setae of some other taxa. Citation: Gibson (1989, char. 13; 1995, char. 35).

191 [1132] Mesotibial spur: **0**, slender; **1**, robust.

State 0 (slender) is clearly less than half the width of the basitarsus. State 1 (robust) is at least half the width of the basitarsus. Citations: Gibson (1989, char. 4); Delvare (1992, char. 42); Noyes and Hayat (1994, char. 40).

192 [1133] Mesotarsal peg pattern: **0**, mesotarsus without pegs, with rows of setae along both antero- and posteroventral edges; **1**, mesotarsus with row of pegs along posteroventral edge and row of setae along anteroventral edge; **2**, mesotarsus with row of pegs along anteroventral edge and row of setae along posteroventral edge; **3**, mesotarsus with row of pegs along anteroventral edge and mixed row of setae and pegs along posteroventral edge; 4, mesotarsus with row of pegs along both antero- and posteroventral edges; **5**, mesotarsus with irregular pattern of pegs.

This character was first proposed by Gibson (1989) in an attempt to describe the different mesotarsal peg patterns of various "jumping" chalcidoids (states 1–5) relative to most chalcidoids (state 0) that do not have a modified mesotarsus. State 5 was constructed to apply to those Encyrtidae having the pegs in complex patterns but not aligned as a row along either edge of the basitarsus. Citation: Gibson (1989, char. 5; 1995, char. 37).

193 [1134] Metacoxal structure: **0**, not enlarged; **1**, enlarged and compressed, plate-like; **2**, enlarged with flat inner surface; **3**, enlarged with convex inner surface.

State 1 occurs in *Elasmus* (Eulophidae) and *Euryishia* (Aphelinidae, Euryischiinae). An enlarged coxa with a convex outer surface was further separated into two states depending on whether the surface is flat (state 1) or convex (state 2) (Gates, 2008). Citations: Wijesekara (1997, char. 24); Gates (2008, char. 32).

194 [1135] Dorsal metacoxal surface: **0**, rounded or acutely angled, but not carinately margined; **1**, carinately margined, often as an externally crenulate ridge along at least half of dorsal length.

This character was introduced by Gibson (2003) to describe variation within Cleonyminae (Pteromalidae). It is not the same as the subapical ridge found in some taxa, which is instead likely a modification for reception of the femur. Citations: Gibson (2003, char. 44); Gates (2008, char. 25).

195 [1138] Metafemur size: **0**, not enlarged (more than three times as long as broad); **1**, enlarged (less than or equal to three times as long as broad).

Historically, an enlarged metafemur (Figs 1e and 7i–j) has been considered to be a feature of Chalcididae and Leucospidae, but occurs also in some Pteromalidae, Torymidae and Eulophidae. An enlarged metafemur does not always co-occur with specific states of any other characters of the hind leg, but some derived

states of other characters may depend on its presence. Citation: Gates (2008, char. 27).

196 [1139] Structure of metafemur: **0**, without denticles or teeth ventrally; **1**, with single, rounded preapical lobe; **2**, with acutely angled lobes or spine-like teeth of irregular size, shape and spacing, mostly or entirely within apical half; **3**, with small, uniform teeth similar to blade of saw over most of length; **4**, with large, regular, lobelike teeth (Fig. 7i, j); **5**, with irregular tiny denticles.

The coding for this character follows Gibson's (2003) coding of Cleonyminae (Pteromalidae). Citations: Gibson (2003, char. 46); Gates (2008, char. 27).

197 [1142] Rows of specialized metatibial setae: **0**, absent; **1**, present dorsally, arranged in parallel or diamond-shaped patterns; **2**, present ventrally, in a single row; **3**, with vague rows of spines similar in size to the tibial fringe spines.

State 1 occurs in *Elasmus* (Eulophidae) and *Euryischia* (Aphelinidae). State 2 is the "pecten" of *Macroglenes* (Pteromalidae: Pireninae). Citations: Graham (1969); LaSalle et al. (1997).

198 [1977] Ventral carinae of metatibia: **0**, absent; **1**, two ventral carinae present, one lateral and one mesal.

State 1 of this character occurs in some taxa that have an enlarged metafemur, but does not always co-occur with that character.

199 [1140] Apex of metatibia: **0**, right-angle truncate without sharply pointed projection or spine; **1**, diagonally truncate, ventroposterior corner acute; **2**, diagonally truncate, ventroposterior corner elongated into spine; **3**, diagonally truncate, outer tibial spur incorporated into a spine.

A right-angle truncation (state 0) is common in Chalcidoidea, whereas a diagonal truncation has been hypothesized as an apomorphy derived independently in Chalcididae and Leucospidae (Wijesekara, 1997). State 1 refers to a short extension of the metatibial apex, as opposed to state 2 as found in *Acanthochalcis* (Chalcididae). State 2 includes those structures in which the two metatibial spurs are placed mesally on the elongation, whereas in state 3 the outer metatibial spur is at the apex of the acute elongation of the metatibia. Citations: Grissell (1995, char. 11); Wijesekara (1997, char. 26); Gibson (2003, char. 47); Gates (2008, char. 34).

200 [1141] Number of metatibial spurs: **0–2** spurs (actual count).

Two metatibial spurs is hypothesized as plesiomorphic within Hymenoptera (Bouček, 1988a,b; Bouček and Heydon, 1997). Citations: Heraty (1994, char. 47; 2002, char. 73); Wijesekara (1997, char. 27); Gates (2008, char. 33).

201 [1112] Tarsal claws: **0**, simple (tapered to apex); **1**, with one extra projection; **2**, with two or more extra projections.

The tarsal claws of Philomidinae and Leucospidae are pectinate with at least two subapical spines, whereas they are simple or at most with a single subapical tooth in other taxa. Citations: Delvare (1992, char. 50); Wijesekara (1997, char. 28).

202 [1144] Lamina on metatarsal claws: **0**, absent; **1**, present.

The metatarsal claw of some Ormyridae and Torymidae is bifid with a subapical tooth that is broad and flat. Tarsal claws of the other legs are similar in shape, but with a slightly less-defined lamina, possibly because of size-related variation. State 0 includes structures where one or more subapical teeth are present but not broadly truncate.

Metasoma characters (203–221).

203 [1145] Relation between mesophragma and metasoma: **0**, not extending into metasoma (extending to apex of propodeum); **1**, extending into distinct petiole, but not through it into gaster; **2**, extending through petiole into gaster (Fig. 7a).

States 1 and 2 occur in Aphelinidae, a few Eulophidae, Mymaridae and Trichogrammatidae, which have an associated broad propodeal foramen and a petiole that is not constricted. However, this character is not entirely correlated with petiole dimensions because some taxa have a broad, short petiole and do not have the mesophragma extending into the gaster (i.e. Eupelminae).

204 [2002] Dimensions of Mt_1 (petiole): **0**, Mt_1 narrow, less than twice as broad as long (gaster petiolate); **1**, Mt_1 very broad, at least three times as broad as long (gaster sessile).

State 0 refers to Mt_1 forming a distinct petiole compared to the rest of the gaster and is characteristic of most Chalcidoidea (Fig. 1d,e,g–i). State 1 refers to the very short and broad Mt_1 that occurs in Aphelinidae, most Encyrtidae and Trichogrammatidae (Figs 1f,k and 7a). *Neanastatus* (Eupelmidae) is somewhat intermediate between the two states, but for a eupelmid it is quite narrow and was scored as state 0. Citations: Schauff (1984, char. 61; 1991, char. 21); Darling (1991, char. 4); Delvare (1992, char. 52); Krogmann and Vilhelmsen (2006, char. 148); Lotfalizadeh et al. (2007, char. 138); Gates (2008, char. 47).

205 [1148] Setation of elongate Mt_1 (petiole): –, inapplicable (petiole short); **0**, not setose along entire length; **1**, one row of erect setae on each side along entire length; **2**, with irregularly distributed setae or with more than one row of setae along entire length.

The presence of a single lateral row of petiolar setae was used by Gibson (2003) as a feature of Leptofoeninae and Nefoeninae relative to other Cleonyminae (Pteromalidae). The petiole of possibly every chalcidoid has at least one lateral seta, which would constitute being setose along its entire length when the petiole is

very short. Therefore this character refers only to species with an elongate petiole. Derived states of this character also occur in the presumably unrelated Pteromalidae *Polstonia* (Sphegigastrini) and *Neapterolelaps* (Diparinae). Citations: Gibson (2003, char. 52); Krogmann and Vilhelmsen (2006, char. 151).

206 [1146] Mt_1 (petiole), ventral surface: **0**, membranous with tergal margins separated along length or at most fused by a narrow bar across apical margin; **1**, fused ventrally with median suture present; **2**, completely fused ventrally with no suture present.

In *Polstonia* there is a superficial line ventrally along the petiole, but this is not a suture and therefore was coded as state 2. Citations: Heraty (2002, char. 83); Krogmann and Vilhelmsen (2006, char. 149); Gates (2008, char. 38).

207 [1961] Fusion of Mt_1 (petiole) with metasomal sternite 2 (= Gs_1): **0**, not fused; **1**, fused.

Species with a ventrally membranous petiole were coded as state 0. Citations: Lotfalizadeh (2007, char. 198); Gates (2008, char. 48).

208 [1147] Ventral lamina of Mt_1 (petiole): –, inapplicable (petiole absent or membranous ventrally); **0**, absent; **1**, present.

In Chrysolampinae, Philomidinae and Perilampinae (Perilampidae), the posterior margin of the petiole gives rise to a pair of thin transverse laminae (ptla) that slide over the surface of the anterior region of Gs_1 (anterior to the antecostal sulcus) (Fig. 5l). For taxa with a ventrally membranous petiole, the laminae were coded either as inapplicable (Eupelmidae) or present because the laminae may occur in taxa that have a largely membranous petiole, such as *Chrysomalla* (Chrysolampinae) and *Torymus* (Torymidae).

209 [1156] Antecostal sulcus of female metasomal sternite 2 (= Gs_1): **0**, present; **1**, absent.

The antecostal sulcus (acs, Fig. 5l) is a transverse sulcus medially on metasomal sternite 2 (third abdominal sternite or first gastral sternite) that internally is associated with attachment of the antecostal muscles, which attach to the middle of the sternite even when the sulcus is absent. The antecostal sulcus can be present in taxa lacking a ventrally fused petiole (e.g. *Nasonia* and others). Citations: Heraty (1994, char. 40; 2002, char. 92).

210 [1149] Anterior projections on Ms_3–Ms_6 in females: **0**, apodemes absent; **1**, apodemes present.

Anteriorly projecting apodemes from metasomal sternites 3 through 6 (gastral sternites 2–5) occur in Azotidae and Signiphoridae (Fig. 5m). Similar projections, although blunt and not rod-like, are found in Euryischiinae (Eriaporidae) and *Mongolocampe bouckei* (Tetracampidae). Citation: Woolley (1988, char. 12).

211 [1155] Relationship between Mt_8 and Mt_9 (females): **0**, Mt_8 and Mt_9 separate and articulating (Fig. 7f); **1**, Mt_8 and Mt_9 fused as syntergum, at most with dorsal suture between cerci indicating line of fusion (Fig. 7b–d); **2**, Mt_8 and Mt_9 part of an internal ovipositor system (scelionid-type ovipositor).

Most female chalcidoids have only eight apparent metasomal (seven gastral) tergites because the terminal two tergites are fused into a syntergum (state 0). The epipygium of Torymidae and a few other Pteromalidae is considered as a separate ninth metasomal tergite, following Grissell (1995), but not the anal plate of some Eupelmidae, following Gibson (1995). Citations: Gibson (1989, char. 15); Wijesekara (1997, char. 34); Burks et al. (2011, char. 30).

212 [1153] Separation of Mt_8 and Mt_9 (females): –, inapplicable (Mt_8 and Mt_9 fused into syntergum); **0**, Mt_8 and Mt_9 separate, but without interceding membranous region; **1**, Mt_8 and Mt_9 separated by a membranous region.

Most chalcidoids with a separate Mt_9 have it articulating broadly with the posterior margin of Mt_8. State 1, in which the two are separated by a membranous region, is part of a complex of states defining Torymidae, but similar structures are present in a few other taxa. In Rileyinae, Buresiinae and *Heimbrella* (all Eurytomidae) and Chalcididae, a remnant of the separation between Mt_8 and Mt_9 is visible as a transverse carina followed by deep depressions in which the cercal plates are found (Lotfalizadeh et al., 2007); this special state was not coded here. Citations: Grissell (1995, char. 24); Lotfalizadeh et al. (2007, char. 150).

213 [1170] Apex of hypopygium (females): **0**, not upturned; **1**, sharply upturned.

The hypopygium is the apical metasomal sternite. For state 1, the apex of the hypopygium must reach or extend beyond the apex of the metasoma. State 1 occurs in Parasaphodinae and Storeyinae (Pteromalidae), both of which were not coded in this analysis, and some Aphelinidae. Citation: Bouček (1988a); Kim and Heraty (2012, char. 48).

214 [1157] Structure and mode of extension of ovipositor (female): **0**, ovipositor with first and second valvulae (= stylets) rotating ventrally during oviposition; **1**, ovipositor protruding posteriorly from metasomal apex during oviposition.

State 0 is the plesiomorphic apocritan structure in which the gastral sternites are displaced anterior to the ovipositor base and the ovipositor sheaths (= third valvulae) are visible ventrally along the midline of the gaster or immediately dorsal to the hypopygium if this extends to the apex of the gaster. During oviposition, the ovipositor valvulae rotate downward and the associated sternites are also displaced downward, away from the tergites. This structure is characteristic of Chalcidoidea. State 1 is a derived condition in some outgroup taxa such as Platygastroidea and Diapriidae, in which the ovipositor is concealed within the metaso-

ma and the ovipositor is exerted posteriorly instead of rotating ventrally during oviposition. In these taxa, the apical exposed tergites and sternites are rigidly connected and are not displaced during oviposition. Citation: Gibson (1986a, char. 19).

215 [1158] Paratergites between Mt_8 + Mt_9 and outer plates of ovipositor: **0**, paratergites absent, with Mt_8 and Mt_9 or fused syntergum forming broad connection with outer plates of ovipositor; **1**, paratergites absent, but with syntergum separated from outer plates of ovipositor by membranous region; **2**, paratergite present between syntergum and outer plate of ovipositor (Fig. 7f).

Paratergites are elongate, sclerotized, or at least differentiated membranous filaments that occur in the membranous region between the syntergum (Mt_8 + Mt_9) and the outer plate of the ovipositor posterior to each cercus in some Encyrtidae (ptr, Fig. 7f). Paratergites are correlated with advanced cerci and may represent lateral portions of the syntergum that were isolated from the median part of the syntergum when the cerci were displaced anteriorly on the syntergum (Noyes and Hayat, 1994). They are usually sclerotized, but are membranous in some species of Tetracnemini (Encyrtidae).

216 [1167] Group of short setae anterior to cercus (cercal brush): **0**, absent; **1**, present.

The cercal brush is a row of rigid, straight setae on Mt_7 immediately anterior to the rim surrounding the cercus. Citation: Desjardins et al. (2007, char. 28).

217 [1161] Insertion of cercus on metasoma (female): –, inapplicable (cerci absent); **0**, cercus arising from sclerotized portion of Mt_9 or apparent metasomal tergum 8 (Mt_8 + Mt_9) (Fig. 7c–e); **1**, cercus arising from membranous area lateral to Mt_9; **2**, cercus arising from membranous area surrounded by isolated part of syntergum.

State 1 is characteristic of Torymidae (Grissell, 1995). State 2 is a specialized structure of some Encyrtidae in which the cerci arise from membrane with a crescent-shaped lateral sclerite that we interpret as an isolated part of Mt_8 + Mt_9. Cerci are absent from some species of *Philomides* (Perilampidae). Citation: Grissell (1995, char. 23).

218 [1162] Shape of cercus: –, inapplicable (cerci absent); **0**, digitiform (peg-like and cylindrical) with setae apical; **1**, projecting, but not forming a cylindrical peg and with setae scattered; **2**, flattened (button-like).

In state 0, the cercus is cylindrical with all setae essentially apical. In state 1, the cercus projects irregularly with setae scattered along its length, and only a few at the extreme apex. In state 2, the cercus is flattened, button-like rather than projecting (Fig. 7c–e). It was difficult to code some taxa because state 1 and state 2 are variants of similar structure.

219 [1163] Position of cercus: –, inapplicable (cerci absent); **0**, not conspicuously advanced, tergites transverse (Fig. 7b); **1**, slightly advanced, Mt_7 forming a flap-like structure between cercal bases; **2**, conspicuously advanced anteriorly, with some tergites V-like between, or M-like between and around, the cerci (Fig. 7f).

Relative position of the cerci affects the shape of the preceding tergites. Female Eupelminae were coded as slightly advanced because the penultimate tergum (Mt_7) has a distinct curvature on its posterior margin that partly surrounds the cercus (cf. figs 298, 300 in Gibson, 1989). State 2 is a condition of Encyrtidae and some Aphelinidae (state 2).

220 [1164] Cercal setae: –, inapplicable (cerci absent); **0**, no setae kinked; **1**, at least one seta kinked.

Most chalcidoids have the setae arising from the cercus all similar except perhaps in length (Fig. 7c,d). Tanaostigmatidae are characterized by at least one cercal setae strongly kinked and unusually long (Bouček, 1988a), though a few pteromalids and eulophids have a similar setal structure. Citation: LaSalle (1987).

221 [1166] Number of cercal setae (female): **0–9** setae (actual count).

Citation: Schauff (1984, char. 63).

Genitalia characters (222–232).

222 [1172] Ovipositor valvulae (= stylet) shape (female): **0**, needle-like; **1**, expanded.

Expanded valvulae (Fig. 7d) can have various shapes from scimitar-like, e.g. *Jambiya* (Perilampidae) to subapically expanded, e.g. *Orasema* (Eucharitidae). Citations: Heraty (1994, char. 42; 2002, char. 95).

223 [1173] Connection between bases of 2nd valvulae (female): **0**, laminated bridge present (Fig. 7h); **1**, single transverse sclerotized bar present; **2**, absent, no sclerotized connection between second valvulae at base; **3**, laminated bridge present and elongate, extending far beyond bulbous articulation.

The laminated bridge (state 0; lb, Fig. 7h) is apparently a set of sclerotized "sheets" connecting the second valvulae near the bulbous articulation (Copland and King, 1971; cf. fig. 9). This structure is expected to occur in all chalcidoids except mymarids, which have a spur replacing the bulbous articulation (King and Copland, 1969). State 2 occurs in various taxa, including some Eucharitidae and *Eulophus* (Eulophidae). In these taxa there is a single sclerotized connection between the valvulae. State 3 occurs in various fig wasps with an elongate ovipositor.

224 [1175] Sclerotized bridge between ovipositor sheaths (second valvifers) (female): **0**, sclerotized bridge between valvifers absent; **1**, sclerotized bridge present, connecting valvifers at their junction with third valvulae (br, Fig. 7h); **2**, sclerotized bridge present laterally, but incomplete medially.

The ovipositor sheath is comprised of the second valvifers distally and third valvulae proximally. The sclerotized bridge is an internal connection across the second valvifers at their apices just distal to the third valvulae (Heraty and Darling, 2007).

225 [1179] Tergites of metasoma (male): **0**, separate; **1**, fused into a carapace beyond the third metasomal tergite.

Within Chalcidoidea, state 1 occurs in Leucospidae and some Ormyridae.

226 [1180] Terminal metasomal sternite (male): **0**, present as a whole sclerite (Ms_8, Fig. 7e); **1**, divided posterior to penultimate sternite (base of genital capsule exposed).

State 1 occurs in some Mymaridae and Trichogrammatidae.

227 [1182] Annular basal ring of male genital capsule: **0**, present; **1**, absent.

The basal ring (= cupula) is assumed to be lost from the male genital capsule of most Chalcidoidea, but an apparent basal ring occurs in some Eucharitidae. The basal ring is not the same as the membranous connective tissue that forms a sheath around the base of the genitalia in Chalcidoidea. Citation: Gibson (1986a, char. 20).

228 [1187] Aedeagal apodemes (male): **0**, present; **1**, absent.

Aedeagal apodemes (= valvura) are rod-like anterior extensions of the aedeagus; they are not the same as similar internal structures of the aedeagus found in *Cales* (unplaced subfamily).

229 [1183] Volsellar digitus (male): **0**, present; **1**, absent.

The digitus is the apical articulating portion of the volsellus (dig, Fig. 7e) of the male genitalia. Citations: Gibson (1986a, char. 21); Noyes and Hayat (1994, char. 64).

230 [1184] Intervolsellar process (male): **0**, absent; **1**, present (Fig. 7e).

The intervolsellar process is a ventromedian extension of the male genital capsule that extends between the volsellae.

231 [1188] Parameres (male): **0**, present (Fig. 7e); **1**, absent.

Parameres are lateroventral appendages of the male genital capsule lateral to the volsellae. If only one ventrolateral appendage is present, it may not be possible to determine if it is the paramere or the volsella, and in such instances this character was scored as inapplicable. Citations: Darling (1983, char. 8); Noyes and Hayat (1994, char. 64).

232 [1189] Apical bristle(s) of paramere (male): **0**, present (Fig. 7e); **1**, absent.

The paramere may have a bristle that is subapical in position, but both bristle positions were scored as state 0. Citation: Delvare (1992, char. 63).

233 [870] Metallic body colour: **0**, absent (Fig. 1d–f,h,k); **1**, present, weak (Fig. 1l); **2**, present, distinct (Fig. 1b,c,g,i,j).

This character was not used to construct the final phylogeny, but was mapped on the final phylogeny. For distinguishing between weak (state 1) and strong (state 2) metallic colour, state 1 was coded when the mesosoma was mostly non-metallic and state 2 when at least the mesosoma was distinctly metallic. Metallic colour is unusual within other Proctotrupomorpha. Citations: Darling (1983, char. 19; 1991, char. 6); Gibson (1986a, char. 22); Delvare (1992, char. 2); Noyes and Hayat (1994, char. 1); Krogmann and Vilhelmsen (2006, char. 1).

Molecular data

Data were included for two gene regions, 18S and 28S D2–D5, based on the analysis of Munro et al. (2011). We used the SSME dataset from this study, which incorporated a secondary structure model for the conserved regions following Gillespie et al. (2005), with a MAFFT E-INS-i alignment of the regions of ambiguous alignment (Katoh et al., 2002). Two sequences from that study required correction. In Munro et al. (2011), the 28S sequence for *Doddifoenus* (Pteromalidae) was mistakenly paired with partial 28S of *Dirhinus giffardi* (Chalcididae); correction of this error subsequent to publication resulted in monophyly of the Leptofoeninae (*Leptofoenus* + *Doddifoenus*). For *Idioporus* (Pteromalidae), the sequence was difficult to align with other taxa, and the result was a spurious placement in Eucharitidae (Munro et al., 2011). We resequenced this region for this analysis and found no error, but a large insert was found to cause the problematic alignment and it was deleted for this analysis. Thirty-two new sequences were also generated for this study, following the extraction, PCR amplification and sequencing protocols of Munro et al. (2011), with all new sequences deposited on GenBank (Appendix 1). Where possible, morphological OTUs were paired with their molecular counterparts (Appendix 1). When molecular data were not available for a given morphological OTU species, sequences from a congeneric relative were chosen instead. Our final dataset contained about one third of these interspecific chimeras ("ch" on trees). Taxa having only molecular data were then deleted from the matrix. Removing these taxa generated 56 alignment columns containing only gaps within several regions of ambiguous alignment (RAAs) of 28S and these columns were deleted. The reduced gene partitions were 18Sa: 1–506; 18Sb: 507–1412; 18Sc: 1413–2105; 28S D2: 2106–3090; 28S D3: 3091–3536; 28S D4–D5: 3537–3861. Seventeen taxa were included in the analysis that had morphology data but

no molecular data (* on trees) (Appendix 1). The final dataset included 300 OTUs and 4093 characters.

Phylogenetic analyses

The morphological and combined datasets were analysed separately using parsimony and probabilistic methods. All trees were rooted with *Archaeoteleia* (Platygastroidea) and *Belyta* (Diaprioidea). Multistate morphological characters were treated as unordered. Characters coded as inapplicable were treated as missing data. Gaps were also treated as missing data.

Parsimony methods

Two parsimony approaches were taken. Equally weighted (EW) heuristic searches were performed in TNT ver. 1.1 (Goloboff et al., 2003, 2008b) under New Technology methods using a sectorial search, ratchet weighting probability of 5% with 50 iterations, tree-drifting of 50 cycles, tree-fusing of five rounds, and a best score hit of 10 times. Implied weights (IW) analyses using a concavity function (k) that weights against homoplastic data (Goloboff, 1993) were also conducted. Choosing a k value is arbitrary, with lower values weighting more strongly against homoplastic characters. In combined analyses, concavity values can disproportionately affect the molecular partition, which in some cases contains a greater amount of homoplasious data (Goloboff et al., 2008a). Goloboff et al. (2008a) suggested that the concavity value k should be calculated as a function of N, which is the ratio of a single extra step to the cost of the most homoplastic character. Following Forero et al. (accepted), we calculated k for a series of N values (5, 10, 15, 25, 50, 100, 500, 1000) using a TNT script written by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucumán, Argentina). The resulting k values ranged inversely from 163.12 to 4.1. MP trees were calculated for each k value using a Traditional Search in TNT. An N value of 25 (k = 50.195) was the largest value that provided consistent monophyly of certain groups (i.e. Rotoitidae). Smaller values of k did not provide increased resolution, and also did not converge on a single solution. We chose this k (50.195) for a subsequent IW New Technology search as outlined for the EW analysis. Nodal supports were calculated using 1000 standard bootstrap replicates on the EW data.

Probabilistic methods

Maximum likelihood (ML) analyses and associated rapid bootstrapping (1000 replicates) were performed using the MPI-parallelized RAxML 7.2.8-ALPHA (Stamatakis, 2006b). For the molecular dataset, we used the same partition scheme and evolutionary models as Munro et al. (2011). This includes six partitions: 18Sa, 18Sb, 18Sc, 28SD2, 28SD3, 28SD4 + D5, each under a GTR nucleotide substitution model with among-site rate variation modelled by a discrete gamma approximation with four discrete categories. A GTRCAT approximation of models was used for ML rapid bootstrapping (Stamatakis, 2006a). For the morphological dataset, we used the Mk (Markov k) model of Lewis (2001) with equal state frequencies and characters treated as unordered. Given that RAxML does not support polymorphic characters, any such character states were recoded as missing (?) prior to analysis (affecting 31 characters). To accommodate parameter variation in separate runs (Regier et al., 2009), we conducted 20 RAxML analyses with different seed numbers for computing starting trees and rapid bootstrap analyses. An extended majority-rule consensus tree was computed from the 20 resulting best known RAxML trees using the software Consense from the PHYLIP package (Felsenstein, 2005). The relative Robinson–Foulds (RF, Robinson and Foulds, 1981) distances between all 20 trees and the consensus tree were computed with Treedist, also from the PHYLIP package. ML analyses were conducted on a 150-core Linux cluster at Centre de Biologie et de Gestion des Populations (CBGP, Montferrier-sur-Lez, France).

Bayesian analyses were conducted using a parallel version of MrBayes ver. 3.2.1 (Ronquist et al., 2012). We used the same partition scheme and evolutionary models as for the ML analyses. While MrBayes does support polymorphic characters, it does not support characters with more than 10 states. Thus characters (#7, 17, 18) were recoded as "additive characters" by including an extra character for coding. The first character was coded as 0–9, and OTUs with states A–E coded as 9. The second character was coded as 0–5, and OTUs with states 0–9 were coded as 0, while species with states A–E were coded as 1–5. We assumed across-partition heterogeneity in model parameters by considering the rate multiplier parameter m. Parameter values for the model were initiated with default uniform priors and branch lengths were estimated using default exponential priors. To improve mixing of the cold chain and prevent it from becoming trapped in local optima, we used Metropolis-coupled Markov chain Monte Carlo (MCMC) with each run including a cold chain and seven incrementally heated chains. The heating parameter was set to 0.02 in order to allow swap frequencies from 20 to 70%. We performed two independent runs of 100 million generations. All values were sampled every 10 000 generations. For determination of burn-in, we examined the plot of overall model likelihood against generation number to find the point where the likelihood started to fluctuate around a constant value. Conver-

gence was also evaluated using Tracer ver. 1.5 (Rambout and Drummond, 2009). Bayesian analyses were conducted on the Texas A&M Brazos cluster.

Character mapping

For the combined results, morphological characters were mapped onto the IW tree and the extended consensus RAxML tree using Mesquite ver. 2.75 (Maddison and Maddison, 2012), and for the extended consensus RAxML tree using Winclada ver. 1.00.08 (Nixon, 2002). Only unambiguous character state changes were optimized.

Results

Morphology only

We were interested in comparing the morphology results using parsimony (EW TNT; 11 trees, length 5296, R.I. 0.61; Fig. 8) and likelihood methods in RAxML (one tree, when mapped using parsimony with length 5331, R.I. 0.60) because we use the same likelihood parameters for the morphology partition in the combined RAxML analyses. Although longer, the RAxML tree was only 0.66% longer than the EW TNT tree, and both tree-building methods showed general congruence for higher-level groups (Fig. S1). Chalcidoidea was not monophyletic in either analysis due to the placement of Mymarommatoidea, which was nested within a Rotoitidae–Mymaridae clade in the likelihood (RAxML) results, and within Eucharitidae in the TNT results (Fig. 8). Both results tend to support an apical grouping of the smaller, soft-bodied taxa (including Mymaridae), probably because these are characterized by a large number of reduction features that were treated as derived. Families that were monophyletic in both results include Agaonidae, Chalcididae, Encyrtidae, Eucharitidae, Eurytomidae, Leucospidae, Mymaridae, Ormyridae, Eurytomidae, Signiphoridae, Tanaostigmatidae (excluding *Cynipencyrtus*, which was sister-group of Encyrtidae), Torymidae and Trichogrammatidae. Eulophidae was not monophyletic in either analysis, being rendered as paraphyletic or polyphyletic by Ceinae (Pteromalidae), Tetracampidae and Trichogrammatidae. Aphelinidae, Eupelmidae, Perilampidae, Pteromalidae and Tetracampidae were never monophyletic, and males and females of Eupelminae, which exhibit strong sexual dimorphism, grouped in separate clades. Both results supported a monophyletic group that included *Cynipencyrtus* and *Oodera* with Eupelmidae + Tanaostigmatidae + Encyrtidae.

Overall, these results were expected given the strong convergence of traits for some taxa and the strong character support for some groups such as Chalcididae. Importantly, our character coding appears to have been consistent, with taxa historically considered as closely related always grouping together, if not in a monophyletic assemblage then in a paraphyletic group. We recognize that, even using numerous images and detailed character state descriptions, the diverse structure encompassed by the 78 sampled subfamilies and 22 families of Chalcidoidea that we recognize (Tables 1 and 2) made it difficult for each of the specialists to interpret all coding the same way. A few differences were found between the coding of *Dirhinus giffardi* (Chalcididae) by R.A.B. and G.D. in our single test case, but despite the differences, the two OTUs formed a monophyletic group in both analyses. Further, taxa grouped as expected, even if coded by multiple investigators.

Combined analyses

The equal weights (EW) parsimony analysis resulted in eight trees of length 20 572 (R.I. 0.48) (Fig. S2). The implied weights (IW) analysis resulted in a single tree, which unweighted was 20 637 steps (R.I. 0.47) (Fig. 9). The IW results were similar to likelihood results based on molecular data only (Munro et al., 2011) or the combined likelihood results reported herein, with Rotoitidae monophyletic and the sister group of the remaining Chalcidoidea. Overall, the EW and IW results were similar, but in the EW analysis *Idioporus* (Pteromalidae) were basal to Rotoitidae and the clade of Encyrtidae + Tanaostigmatidae + Eupelmidae was not recovered. The EW results were less resolved and are not discussed further. The extended consensus RAxML tree (Fig. 10) was highly resolved, with most nodes found in all 20 best known likelihood (BKL) trees. Both RAxML and Bayesian analyses produced essentially the same topology, but the Bayesian analyses did not reach convergence (average deviation of split frequencies of 0.96). For the Bayesian results, we report only the posterior probability support for selected clades.

The parsimony (IW), likelihood (RAxML) and Bayesian analyses of the combined data support Mymaridae as the sister group of the remaining Chalcidoidea, with Rotoitidae as the next successive group (Figs 9 and 10). The basal position of both taxa is driven by the molecular data (Munro et al., 2011). Family level support for some groups occurs only in the combined results, for example the monophyly of Eulophidae (excluding *Trisecodes*). As well, a monophyletic Eupelmidae, including *Oodera* (Pteromalidae: Cleonyminae), is the sister group of Tanaostigmatidae + (*Cynipencyrtus* + Encyrtidae) in the likelihood topology (monophyletic but poorly resolved in EW or IW). This is the first time that this group and the rela-

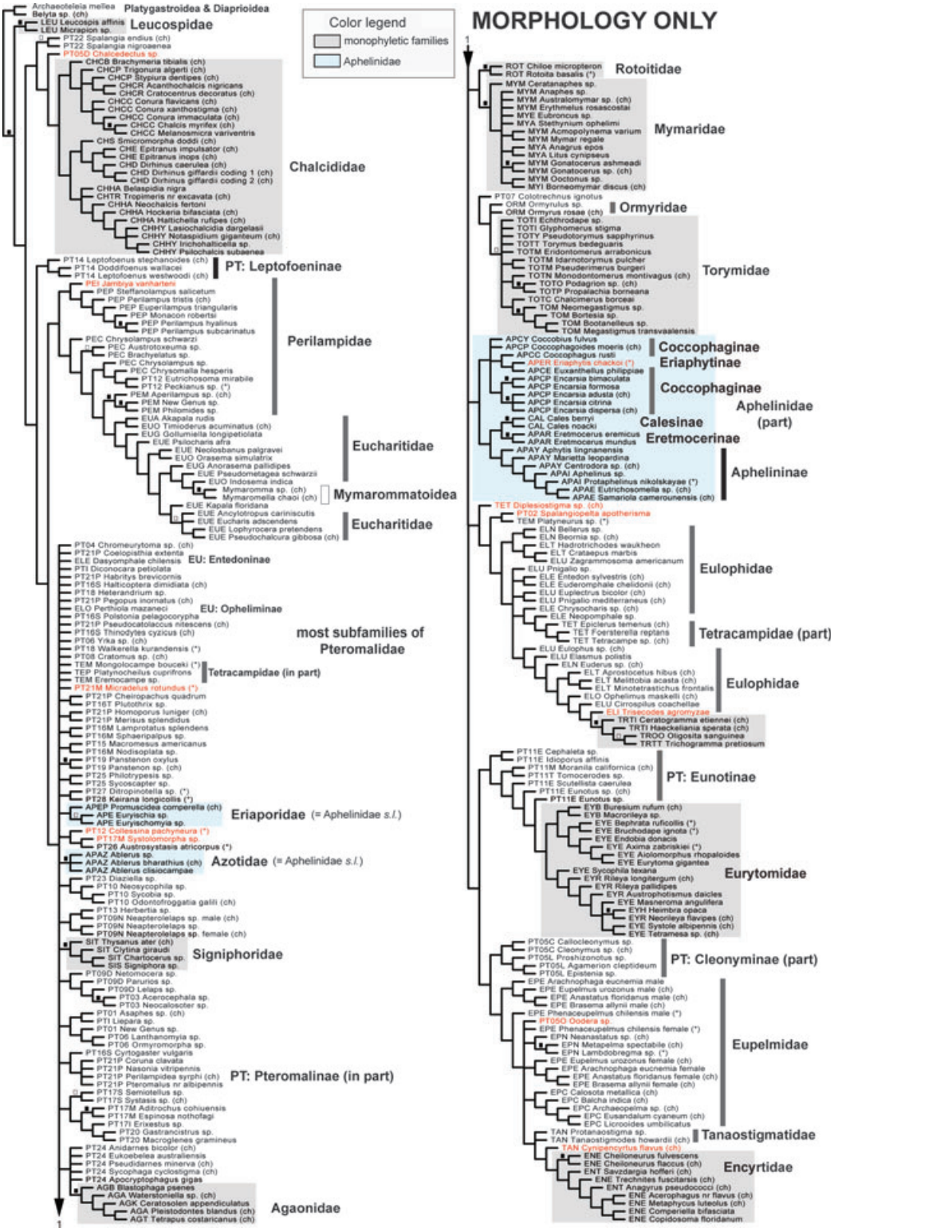


Fig. 8. Morphology data. Equal weights results: 11 trees, tree length = 5296 steps, R.I. 0.61, 232 morphological characters. Black squares indicate unweighted bootstrap support > 70%; open squares indicate bootstrap support of 60–70%. Black vertical lines indicate monophyletic groups, grey bars are paraphyletic or polyphyletic groups. Operational taxonomic unit names with prefix indicating classification (Table 1) and suffix indicating whether taxa are interspecific chimeras (ch) or if molecular data are lacking (*). Red highlighted taxa are discussed in text.

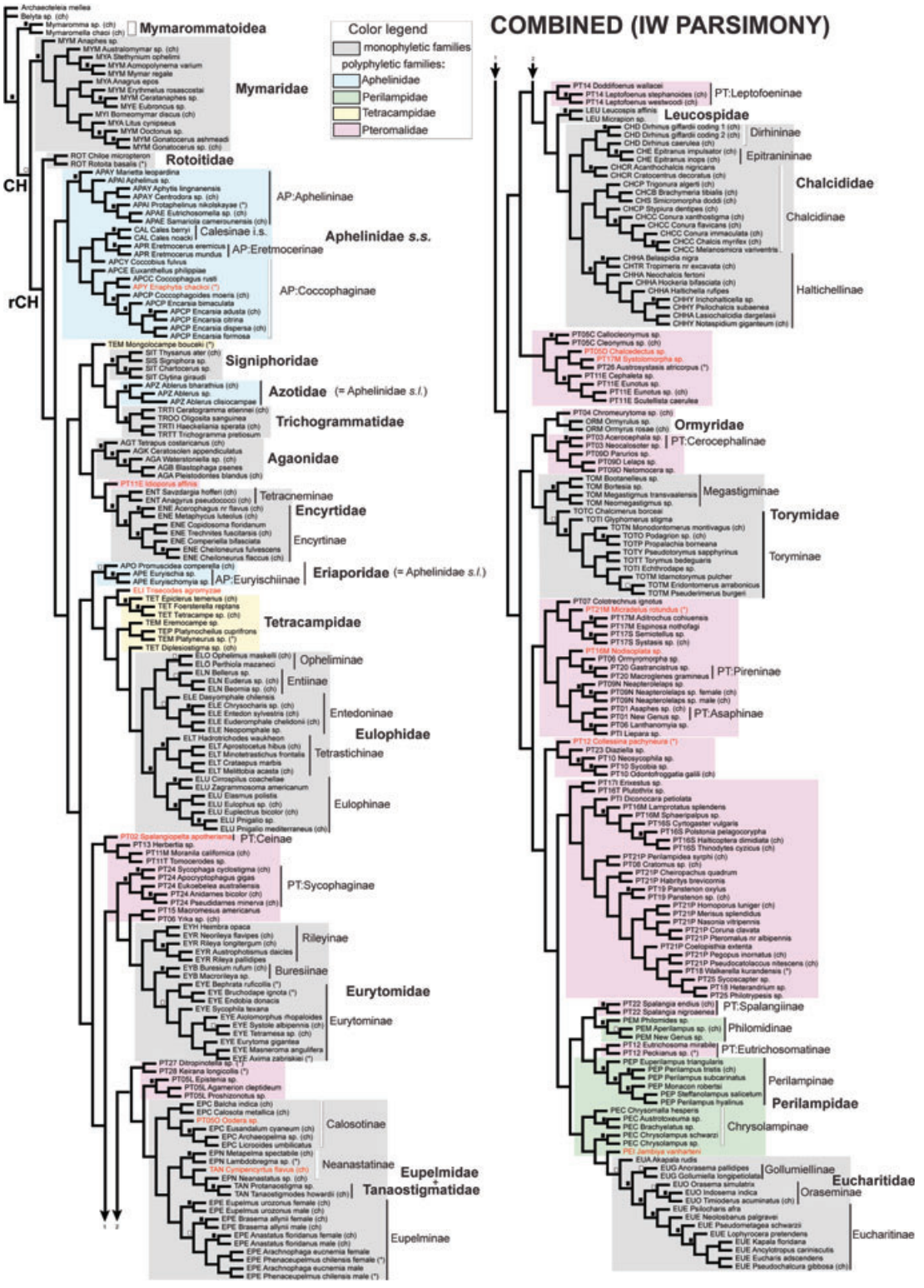


Fig. 9. Combined data. Implied weights results: one tree, $N = 25$, $K = 50.195$, tree length = 216.06 weighted steps, 20 637 unweighted steps; 232 morphological characters; 18S, 28S D2–D5. Black squares indicate unweighted bootstrap support > 70%; open squares indicate bootstrap support of 60–70%. Operational taxonomic unit names with prefix indicating classification (Table 1) and suffix indicating whether taxa are interspecific chimeras (ch) or if molecular data are lacking (*). Red highlighted taxa are discussed in text.

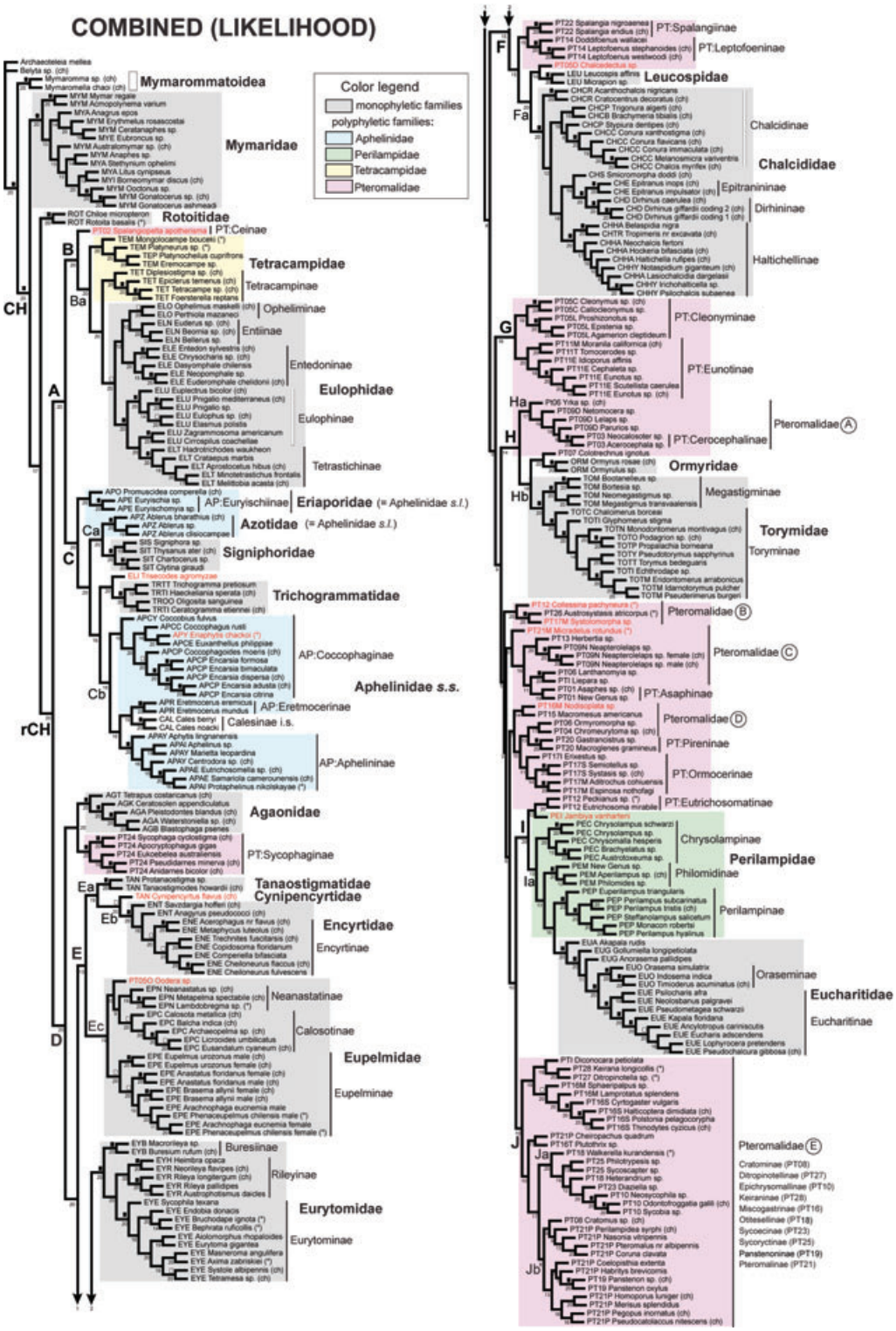


Fig. 10. Combined data. RAxML results. Extended majority rule consensus for 20 best known likelihood (BKL) trees, with each analysis started using a different seed number. Combined data: 232 morphological characters; 18S, 28S D2–D5. Numbers below nodes correspond to number of times the clade occurs among the 20 trees. Black squares indicate bootstrap support > 70%; open squares indicate bootstrap support of 60–70% in all 20 trees. Operational taxonomic unit names with prefix indicating classification (Table 1) and suffix indicating whether taxa are interspecific chimeras (ch) or if molecular data are lacking (*). Red highlighted taxa are discussed in text.

tionship of *Oodera* with Eupelmidae have been recovered in a phylogenetic analysis. Perilampidae and Eucharitidae form a monophyletic group that includes the Spalangiinae and Eutrichosomatinae in the parsimony results (Fig. 9) and only the Eutrichosomatinae in the likelihood results. Aphelinidae were never recovered as monophyletic without the inclusion of Signiphoridae and Trichogrammatidae in the likelihood results, and they are even more dispersed in the parsimony results. In general, more traditional subfamilies and tribe groups are supported in the likelihood results, and we use these as our foundation for character mapping and group discussion.

Discussion

The following discussion of relationships is based on the likelihood (RAxML) results (Fig. 10), but where necessary with reference to the IW parsimony (Fig. 9) and morphology results (Fig. 8 and Fig. S1). Unambiguous character state changes were mapped onto the parsimony tree (Fig. S3) and the likelihood extended consensus tree (Fig. S4), and summarized in Tables 2 and 3, along with support across the various analyses. When discussing character support for the various groups below, we focus only on certain characters that might be considered as important for defining the relationships in question. Within the character discussions, a brief discussion of the character distribution is provided within parentheses after the character number and state assignment to provide some context for the distribution of the character. We would like to stress that there is extensive homoplasy across the trees, and that some characters have complex models of state change. This may complicate the interpretation and recognition of synapomorphies in terminal taxa. For example, a one-segmented maxillary palpus (64 : 1) is mapped as supporting the monophyly of Mymarommatoidea and Chalcidoidea, but most chalcidoids have more segments. Also, since only unambiguous state changes are plotted, it may not be possible to find all of the state changes relevant to a particular character on the trees. More detailed information on character distribution is available as supplementary data (Data S1, Fig. S2).

Mymarommatoidea + Chalcidoidea

Diaprioidea has been suggested as the sister group of Chalcidoidea in recent molecular analyses (Castro and Dowton, 2006; Heraty et al., 2011; Munro et al., 2011), but Mymarommatoidea is strongly supported as its sister group when morphological data are included (Sharkey et al., 2011) or considered (Gibson, 1986a, 1999). A sister-group relationship between Mymarommatoidea and Chalcidoidea was supported in our combined analyses (Figs 9 and 10). Our outgroup sampling is extremely limited for assessing support for this clade, but monophyly of Mymarommatoidea + Chalcidoidea is supported by several features (Table 3), including loss of socketed MPS (12 : 1), absence of an occipital carina (40 : 3), maxillary palp one-segmented (64 : 1), metascutellar setae absent (125 : 0), metapleuron bare (133 : 3), costal cell more than one-third fore wing length (145 : 1), antecostal sulcus absent (209 : 1) and ovipositor rotating ventrally during oviposition (214 : 0). Sharkey et al. (2011) proposed absence of an occipital carina as a supporting character, although various Chalcidoidea have a distinct carina. They also proposed absence of labial palp segments as a synapomorphy, but while Mymarommatoidea lack palpi, Mymaridae and Rotoitidae have either one or two palpal segments, thus the character is equivocal at this level. Some of the synapomorphies supporting Mymarommatoidea + Chalcidoidea are optimizations based on a limited outgroup sampling. For example, ovipositor rotation (214) is plesiomorphic for both Proctotrupomorpha and Hymenoptera, but the alternate state (214 : 1) is characteristic of one of our outgroups (Platygastroidea) and was treated as the outgroup state in the analysis. Further, some features that were optimized as synapomorphies may be parallel reductions associated with small size. An example is the putative synapomorphy based on a one-segmented maxillary palp, which occurs in multiple segments (up to 5) in many Chalcidoidea.

Gibson (1986a) proposed three additional internal features as synapomorphies for Mymarommatoidea + Chalcidoidea: the mesotrochanteral-depressor muscle without an fu_2-tr_2 or mesoscutal portion of t_2-tr_2, axillar phragma as the site of origin for at least part of t_2-tr_2, and the absence of a basal ring in the male genitalia. Of these, we scored only for presence of a basal ring, which is present in some derived Chalcidoidea (i.e. Eucharitidae), but not in any of the more basally situated members. Presence of only t_2-tr_2 as a mesotrochanteral depressor is a reductional feature, though presence of axillar phragmata, cuticular extensions of the axillae that project anteriorly below the mesoscutum, is uniquely shared by Mymarommatoidea and Chalcidoidea. In Mymarommatoidea, they are cylindrical, rod-like structures that are the sole sites of attachment of the t_2-tr_2 muscles, whereas in Chalcidoidea they are flat, plate-like structures, and the t_2-tr_2 muscles originate from both these and the axillae (Gibson, 1986a, 1999; Krogmann and Vilhelmsen, 2006). Gibson (1986a, 1999) hypothesized that mymarommatids secondarily lost the posterior portion of t_2-tr_2 from the axilla, but Vilhelmsen and Krogmann (2006) suggested that the axillar phragmata are serial homo-

Table 2
Monophyly and character support for families of Chalcidoidea

Taxonomy	Support RAxML/TNT/Bayes	Synapomorphies
Agaonidae	100/100/1.00	**4(2)**, 7(9), *38(0)*, 55(1), **61(1)**, 65(0), 85(1), 89(2), 96(3), 113(2), 115(1) *123(0)*, **131(1),** 183(0), 185(0), 203(2), 204(1), *211(0)*, *212(1)*, *217(1)*, *223(3)*
Aphelinidae	–/–/–	N/A
Azotidae	100/100/1.00	*7(7)*, *23(0)*, 27(4), *54(1)*, 81(3), 83(1), 84(1), 92(2), 97(1), *105(0)*, *115(2)*, 130(1), 146(0), *170(1)*, 175(1), 189(0), 212(1), 216(1), 220(1), 229(1), 231(1)
Chalcididae	94–99/< 50/0.67	41(1), 42(1), 49(1), 51(0), 52(0), *59(1)*, 72(2), 77(2), *98(1)*, 112(1), 113(1), *124(2)*, *134(0)*, *144(2)*, 161(0), **199(2)**, *206(2)*, 230(1)
Cynipencyrtidae	Not applicable	3(1), *8(6)*, 9(1), 11(0), *23(1)*, *37(0)*, 100(1), *104(1)*, 113(2), *115(0)*, 116(1), *140(3)*, *141(0)*, *147(0)*, *153(0)*, 165(1), 166(1), 192(3), 200(1), 221(2)
Encyrtidae	94–100/84/0.91	5(1), 38(1), *64(4)*, *65(3)*, *93(1)*, *94(1)*, *108(3)*, 128(1), 133(0), *153(1)*, 154(1), 187(1), 190(1), *191(1)*, *192(5)*, **219(2)**
Eriaporidae	48–55/63/0.92	38(0), *54(1)*, 64(3), *70(1)*, 145(0), *188(1)*, 218(1)
Eucharitidae	76–81/63/–	**94(2)**, 109(1), 124(1), 128(1), 134(0), *163(1)*, 182(1), *183(0)*, *206(2)*, *218(2)*, 222(1)
Eulophidae	(69–74/< 50/0.99)*	17(8), 95(2), *115(1)*, 144(3), 176(4)
Eupelmidae	12–18†/–/–	37(1), 46(1), 49(2)
Eurytomidae	81–88/< 50/1.00	24(0), 41(1), 46(1), 49(1), 85(1), *133(0)*, 135(1), 147(0), 148(1), *186(0)*, 207(1)
Leucospidae	100/100/1.00	1(1), 2(1), 9(4), 24(0), 74(0), 104(0), 127(2), *142(1)*, *156(0)*, 159(1), *225(1)*
Mymaridae	100/99/1.00	19(1), 26(1), **28(1)** 29(1), 32(1), 49(5), 51(0), 55(3), 60(1), *70(1)*, *86(1)*, 87(1), 96(4), 97(1), *101(1)*, ***103(1)***, *144(3)*, 146(0), *151(1)*, 152(0), 158(1–2), **167(1)**, 178(1), 188(1), 189(1), *226(1)*
Ormyridae	69–75/57/0.98	*40(0)*, *89(1)*, *104(0)*, 109(1), *158(1)*, 193(2), *194(1)*, *221(4)*
Perilampidae	–/–/–	N/A
Pteromalidae	–/–/–	N/A
Rotoitidae	76–83/< 50/1.00	***9(6)*,** 78(2)
Signiphoridae	100/99/1.00	*5(1)*, 7(5), *8(3)*, 17(4), 47(0), 70(0), 89(2) 95(0), 100(0), 126(1), 132(1), 135(1), *156(2)*, *158(2)*, 160(0), 161(0), 163(1) 170(0), 217(1), 218(1), 221(3)
Tanaostigmatidae	(99–100/98/1.00)‡	27(1), *46(0)*, *48(2)*, *49(0)*, *81(1)*, 82(1), *95(1)*, *98(0)*, 114(1), *123(2)*, 164(0), 169(0), 192(1), 220(1)
Tetracampidae	–/–/–	N/A
Torymidae	78–84/59/0.99	*46(1)*, 110(1), *141(1)*, 159(3), 186(2), 211(0), 217(1), *224(0)*
Trichogrammatidae	99–100/93/1.00	*8(1)*, *10(1)*, **18(1)**, 23(1), *29(1)*, *30(1)*, *34(1)*, **44(2)**, 55(3), 84(1), *88(1)*, 116(2), *144(0–3)*, 158(1), *162(4)*, 175(1), *176(3)*, *178(1)*, *181(1)*, 182(1), *183(0)*, *210(0)*

Support is reported as the range of bootstrap support in the 20 RAxML trees/bootstrap support in the unweighted Traditional Search in TNT/posterior probability for Bayesian consensus tree. Unambiguous synapomorphies [character (state)] are listed as follows: non-homoplasious synapomorphies in bold font; synapomorphies inferred in both likelihood extended consensus tree and implied weights (IW) parsimony are underlined; synapomorphies recovered in IW only are italicized.

–, Not monophyletic.

*Without *Trisecodes*.

†*Oodera* sp. included.

‡Without *Cynipencyrtus*.

logues of the prophragmal rods and the phragmata may have been derived independently in Mymarommatoidea and Chalcidoidea.

Whether or not the axillar phragmata are homologous in the two superfamilies, they are important for inferring relationships. Most "Symphyta" have t_2-tr_2 originating only from the mesoscutum, whereas parasitic Hymenoptera either have an anterior portion originating from the mesoscutum (t_2-tr_{2a}) and a posterior portion from the axilla (t_2-tr_{2b}) (Megalyridae and Ceraphronidae), or only t_2-tr_{2b} is present (Stephanidae and non-ismarine Diapriidae), or they entirely lack a tergal portion of the mesotrochanteral depressor (other groups) (Gibson, 1999; fig. 1). Gibson (1986a) hypothesized that presence of axillar phragmata indicated that Chalcidoidea evolved from some parasitic Hymenoptera lineage that had lost t_2-tr_{2a}, and that axillar phragmata evolved secondarily in the common ancestor of Chalcidoidea, functionally to enable secondarily enlargement of t_2-tr_{2b} axillar muscles for increasing jumping ability. If the groundplan state for Diaprioidea is presence of both t_2-tr_{2a} and t_2-tr_{2b}, as indicated by the musculature of Ismarinae, then among extant parasitic Hymenoptera only Stephanidae have t_2-tr_{2b} and lack t_2-tr_{2a}. This feature, and the unique structure of the prepectus of Chalcidoidea (see below), led Gibson (1986a) to hypothesize that Chalcidoidea represent one of the more basal lineages of parasitic Hymenoptera. Future expansion of our analysis to include internal cuticular features and musculature, which may be

Table 3
Character support for selected clades

Clade name	Support RAxML trees/TNT/Bayes	Synapomorphies
Mymarommatoidea + Chalcidoidea	97–99/88/1.00	**12(1),** 40(3), *47(0)*, 64(1), 109(1), 112(0)**, 125(0),** 133(1), 143(1), 144(2), 145(1), 147(1), 159(2), 209(1), **214(0)**
Chalcidoidea (CH)	80–86/64/1.00	**13(1), 78(1), 107(1)**, 136(1), 137(0)
Rotoidea + remaining CH	30–38/< 50/0.96	24(1), 64(2), *100(2)*, 104(0), *105(1)*, 156(1), 206(0)
Remaining CH	59–68/< 50/0.85	4(1), 22(0), 71(0), 152(2), 172(1), 174(1), *184(1)*
Clade A	7–12/–/0.39	184(1), 185(0), 189(1), 200(1)
Clade B	2–5/–/0.19	48(2), 109(0), 111(1)
Clade Ba	4–9/–/–	17(0), 18(5), 146(0), 181(1), 218(1)
Clade C	17–22/–/0.54	7(7), 18(3), 23(0), 70(1), 115(2), 137(1), 204(1)
Clade Ca	37–46/–/–	9(1), 152(1), 162(3), 180(1), 210(1), 211(0)
Clade Cb	25–34/< 50/–	97(1), 153(1), 221(3)
Clade D	8–15/–/0.35	38(0), 48(1), 55(3), 65(3), 140(5), 145(0)
Clade E	24–32/–/–	143(0)
Clade Ea	26–34/–/–	48(2), 93(1), 94(1)
Clade Eb	61–70/–/0.65	8(6), 67(1), 95(0), 98(1), 140(3)
Clade Ec	12–18/–/–	37(1), 46(1), 49(2)
Clade F	1–7/–/0.30	22(1), 133(0), 158(1), 206(2)
Clade Fa	27–33/–/0.16	68(0), 195(1), **196(3–4)**, 198(1)
Clade G	0–1/–/0.19	7(9), 17(9), 23(0), 82(1)
Clade G: Cleonyminae	13–20/–/0.67	55(2)
Clade G: Eunotinae	2–5/–/0.66	48(2), 68(0), 140(1), 164(0)
Clade H	0/–/–	49(2), 212(1)
Clade Ha	2–4/–/–	140(2), 157(1), 166(1)
Clade Hb	13–20/–/–	46(1), 124(0), 144(3)
Clade I	52–58/–/0.79	11(0), 16(1), 95(0), 158(1), 169(1)
Clade Ia	8–11/–/0.35	128(2), 141(1), 152(1), 186(2), 227(0)
Clade J	0–1/–/–	n/a
Clade Ja	14–19/–/0.39	17(8), 18(6), 46(1), 67(0), 74(0), 104(0), 118(1), 140(2), 147(0), 221(4), 223(3)
Clade Jb	2–3/–/–	73(1), 200(1)

Support is reported as the range of bootstrap support in the 20 RAxML trees/bootstrap support in the unweighted Traditional Search in TNT/posterior probability for Bayesian consensus tree. Unambiguous synapomorphies [character (state)] are listed as follows: non-homoplasious synapomorphies in bold font; synapomorphies inferred in both likelihood extended consensus tree and implied weights (IW) parsimony are underlined; synapomorphies recovered in IW only are italicized.

more conservative than many external features, could help clarify sister-group relationships of Chalcidoidea.

Chalcidoidea

Chalcidoid monophyly has been supported consistently in both morphological and molecular analyses (Gibson, 1986a; Dowton and Austin, 2001; Castro and Dowton, 2006; Gladun and Gumovsky, 2006; Vilhelmsen et al., 2010; Heraty et al., 2011; Sharkey et al., 2011). Chalcidoidea was monophyletic in all our combined results (Figs 9 and 10). This is not unexpected given our limited outgroup sampling, although Mymarommatoidea was mistakenly included within Chalcidoidea when only morphological data were considered (Fig. S1). This artificial placement of Mymarommatoidea within Chalcidoidea was also found in previous morphological analyses (Krogmann and Vilhelmsen, 2006). Support for monophyly of Chalcidoidea comes from structure of the multiporous plate sensilla (13 : 1), presence of an exposed prepectus (78 : 1) and position of the mesothoracic spiracle (107 : 1). These three autapomorphies were originally proposed by Gibson (1986a). Bouček and Noyes (1987) originally described Rotoitidae as lacking a prepectus, but both rotoitid genera were shown to have a slender prepectus that normally is concealed under the posterolateral margin of the pronotum (78 : 2) (Gibson and Huber, 2000). The latter structure was hypothesized as the groundplan structure for parasitic Hymenoptera by Gibson (Gibson, 1986a; fig. 2; Gibson, 1999) and, consequently might be the groundplan state for Chalcidoidea. Additional support for monophyly of Chalcidoidea based on the number and position of the metafurcal pits (136 : 1; 137 : 0; Table 3) is likely a mapping anomaly.

Mymaridae

The combined results all strongly support Mymaridae as monophyletic and as the sister group of the remaining Chalcidoidea. These results are concordant with

recent molecular (Campbell et al., 2000; Heraty et al., 2011; Munro et al., 2011) and combined results (Sharkey et al., 2011). The sister-group relationship between Mymaridae and the remaining Chalcidoidea is consistently supported in all analyses, but with bootstrap support only in the likelihood results. Support for monophyly of the remaining Chalcidoidea without Mymaridae includes: torulus with ventral margin in lower third of face (24 : 1), maxillary palpi two-segmented (64 : 2), scutellar disc with two pairs of bristles (100 : 2), frenum not indicated mesally or laterally (104 : 0, 105 : 1), marginal vein 1–3 times length of stigmal vein (156 : 1), and petiole with ventral surface membranous (206 : 0). None of these states offers meaningful support, because of either their likely polarity or variability within Chalcidoidea. Although not indicated as support, absence of MPS from the first flagellomere of males (19 : 0) could be the strongest evidence of a monophyletic Chalcidoidea excluding Mymaridae. Male mymarids are the only Chalcidoidea with 11 flagellomeres that also have MPS on the first flagellomere. Other chalcidoids with MPS on the first flagellomere have fewer than 11 flagellomeres, and other structural evidence indicates that presence of MPS on the apparent first flagellomere results from fusion of flagellomeres 1 and 2 (see characters 2 and 19). If the presence of MPS on all flagellomeres was a groundplan state of Chalcidoidea, and a uniquely retained symplesiomorphy of male Mymaridae, then absence in other Chalcidoidea (19 : 0) is evidence for monophyly of Chalcidoidea excluding Mymaridae. Quicke et al. (1992) also proposed that Chalcidoidea excluding Mymaridae was monophyletic, based on the presence of an apomorphic structure of the ovipositor (asymmetrical with overlapping dorsal valve in cross-section). This remains valid, though Gibson and Huber (2000) showed that *Chiloe* (Rotoitidae) has an intermediate structure, and suggested this could support Rotoitidae as the second-most basal clade of Chalcidoidea. The lack of other meaningful morphological support is probably based on this node being supported only in molecular or combined results (Figs 9 and 10), never in results based only on morphology (Fig. S1).

Mymaridae was supported by numerous apomorphies: toruli less than one diameter from eye (26 : 1), trabeculae present (29 : 1), various head sulci present (28 : 1, 29 : 1, 32 : 1, though widespread also in the eulophid clade), mandibular muscle exposed (60 : 1), frenum (= posterior scutellum in mymarid literature) more than half scutellar length (103 : 1) (polymorphic within family), submarginal break present (146 : 1, variable within remaining Chalcidoidea), fore wing hypochaeta present (151 : 1), campaniform sensilla on parastigma absent (152 : 0), stigmal vein relatively short (158 : 1–2), hind wing base stalk-like (167 : 1), profemur with preapical bristle (178 : 1) (absent in outgroups and rotoitids, but widespread in eulophid clade), mesofemur with preapical bristles (188 : 1, 189 : 1) and terminal metasomal sternite of male divided (226 : 1). Of these, at least the presence of MPS on the first flagellomere of males (19 : 1) may represent an error of polarity, as discussed above. Many of the other character state changes (characters 28, 29, 32, 146, 158, 178, 188, 189) occur independently within the aphelinid–eulophid lineage and some states, such as a stalk-like hind wing base (167 : 1), although characteristic of most mymarids, may not be groundplan features of the family but secondarily derived within the family. However, presence of trabeculae and a hypochaeta do appear to be autapomorphies of Mymaridae. Our relationships for genera within Mymaridae differ from those in Munro et al. (2011) in that the clade of mymarids with five tarsomeres (*Borneomymar*, *Gonatocerus*, *Litus*, *Ooctonus*) is again monophyletic, but nested within a group of taxa that are characterized by four tarsomeres. Our combined Bayesian analyses support separate clades, each with 4 or 5 tarsomeres, as found by Munro et al. (2011).

Superfamily relationships

Our results strongly support a sister-group relationship between Mymarommatoidea and Chalcidoidea, and between Mymaridae and the remaining Chalcidoidea. This raises the question of whether all should be classified within an inclusive superfamily, or whether Mymaridae should be recognized as its own superfamily separate from Chalcidoidea. We feel that the current superfamily-level classification is stable. As stated by Gibson (1986a), Mymarommatoidea and Chalcidoidea, including Mymaridae, are both supported as monophyletic and recognizable by external apomorphies. However, there are no reliable apomorphies that support the monophyly of Chalcidoidea without Mymaridae, and the principal features that support mymarommatoids and chalcidoids as a monophyletic group are internal and not included in our study. Further, the placement of Diaprioidea or Mymarommatoidea as the sister group of Chalcidoidea remains equivocal whether based only on molecular evidence or in a combined approach. Even in our combined analysis, the external morphological evidence for monophyly of Mymarommatoidea and Chalcidoidea is fairly weak, based on synapomorphies that are highly homoplastic within Chalcidoidea.

Rotoitidae. Rotoitidae is a well defined group with two genera, *Rotoita* in New Zealand and *Chiloe* in Chile (Bouček and Noyes, 1987; Gibson and Huber, 2000), which may represent a relict Gondwanan distribution. Rotoitidae were monophyletic in all our analyses, despite *Rotoita* being coded only for morphology. Monophyly was supported by two unambiguous character states: females with six claval segments (9 : 6)

and prepectus present but concealed under the mesoscutum (78 : 2), though this later feature may represent an error of polarity and a uniquely retained symplesiomorphy of Rotoitidae (see above, and Gibson and Huber, 2000). Recognition of a 12th flagellomere (1 : 1) in many chalcidoids means that a 12-segmented flagellum is not unique for Rotoitidae.

A sister-group relationship between Rotoitidae and the remaining Chalcidoidea (= rCH) was supported without bootstrap support in the combined parsimony analysis (Fig. 9) and in 17 of the 20 likelihood combined analyses (Fig. 10). Character state support included: flagellomere one anelliform (4 : 1, variable within rCH), antennal scrobe shallow (22 : 0, either shallow or strongly developed in most rCH), mesothoracic spiracle not enclosed (71 : 0, partially or completely enclosed in Mymaridae and rCH) and parastigma with one campaniform sensilla (152 : 1, these are likely present in Mymaridae, see Materials and methods), proximal hamulus straight (172 : 1, variable in Mymaridae and rCH) and erect setae opposite the hamuli (174 : 1; variable in Mymaridae and rCH). As noted above, Gibson and Huber (2000) further suggested that the structure of the second valvulae of the ovipositor in *Chiloe* supported Rotoitidae as the sister group of Chalcidoidea (cf. Quicke et al., 1992).

Clade A: Eulophidae—Aphelinidae

This group of taxa was recovered only in the combined likelihood trees (Fig. 10) and largely represents a clade of "soft-bodied" Chalcidoidea prone to shrivelling when air-dried (without critical-point drying or chemical treatment). The families included are Tetracampidae (paraphyletic), Eulophidae, Signiphoridae, Trichogrammatidae and a polyphyletic Aphelinidae. *Spalangiopelta* (Pteromalidae: Ceinae) was the only member included that would not be traditionally placed within this group of taxa. The four supporting characters are basitarsal comb oriented longitudinally (184 : 1), the absence of a basitarsal notch on the fore leg (185 : 0), anterior surface of mesofemur with preapical bristle (189 : 1) and presence of a single metatibial spur (200 : 1). None of these features provides convincing support; in particular, a single metatibial spur is possessed by many Pteromalidae. There is also a trend among these taxa to have one or more head sulci (characters 29–33, 44–45), which may be associated with being soft-bodied, as well as reductions in the number of flagellar segments and tarsi.

Clade B: Ceinae, Tetracampidae and Eulophidae

This group of taxa was recovered only in the combined likelihood trees (Fig. 10). Support for the entire clade was based on the hypostoma extending dorsally around the postocciput (48 : 2), absence of a transepimeral division (109 : 0) and posterior margin of the metepimeron overlapping the metapleural/propodea complex (111 : 1). All these features are highly variable within rCH. *Clade Ba* (Tetracampidae + Eulophidae) is based on having fewer than 10 antennal flagellomeres (17 : 10 or fewer), fewer than five funicular segments (18 : 5 or fewer), submarginal break absent (146 : 0, commonly present within clade), protibial spur straight (181 : 1) and cercus projecting but not peg-like (218 : 1).

Tetracampidae. Tetracampidae is likely a polyphyletic assemblage that includes three extant subfamilies: Mongolocampinae, Platynocheilinae and Tetracampinae (Gumovsky and Perkovsky, 2005). The different subfamilies have been classified in Aphelinidae, Eulophidae, or Pteromalidae (Bouček, 1988a; LaSalle et al., 1997; Gibson et al., 1999). In molecular-only analyses (Munro et al., 2011), Tetracampinae were scattered across the tree, with *Diplesiostigma* not grouping with other Tetracampinae. In our combined likelihood analyses (Fig. 10), Tetracampidae was paraphyletic with one clade composed of Platynocheilinae and Mongolocampinae, and the other clade composed of Tetracampinae (including *Diplesiostigma*) as the sister group of Eulophidae. There was less resolution of this grade in the parsimony results (Fig. 9), with *Trisecodes* as the sister group of part of the Tetracampinae and Tetracampidae paraphyletic relative to Eulophidae. Monophyly of Mongolocampinae and Platynocheilinae was based only on the scutellar disc lacking bristles (100 : 0), hamuli proximal to midlength of hind wing (170 : 0), protibial spur with a simple tip (182 : 1) and mesotibia with preapical bristle absent (189 : 0). Males of this group are also unusual in possessing a characteristic swollen marginal vein in the hind wing (168 : 1), but this could not be scored for the basal member of the group, *Mongolocampe bouckei*. Monophyly of Tetracampinae in the combined results is based on several putative synapomorphies (18 : 6, 29 : 1, 30 : 1, 39 : 1, 70 : 1, 153 : 1). The Tetracampinae–Eulophidae relationship was based only on having the lateral clypeal line present (37 : 1) and lateral panel of the prepectus foveate (83 : 1).

Eulophidae. Eulophidae is a well established family that in the past has been defined by 12 or fewer antennal segments, small and straight fore tibial spur and four or fewer tarsomeres (Gauthier et al., 2000; Burks et al., 2011). Eulophidae was monophyletic in all our analyses, with the exclusion of *Trisecodes*, which is the only proposed member having three tarsal segments, although males of *Melittobia* (Eulophidae: Tetrastichinae) have a three-segmented fore tarsus

(Gumovsky, 2011). The family and subfamily relationships match those obtained in the combined analyses of Burks et al. (2011), with the exception that Eulophinae were not monophyletic in the combined likelihood analyses, although they were in the IW analysis. Bayesian results also supported a monophyletic Eulophinae. Morphological support for the family includes male antenna with at most eight flagellomeres (17 : 8), axillae advanced (95 : 2), mesotrochantinal plate inflected and separated from the metasternum by membrane (115 : 1), cubital vein of fore wing marked by a setal line (144 : 3) and four tarsomeres (176 : 4). An acute (not cleft) calcar (182 : 1) has been proposed by various authors as characteristic of Eulophidae (Gibson et al., 1999), but this was shown to occur only in Eulophinae and Tetrastichinae (although cleft also within *Aprostocetus*) (Gumovsky, 2011).

Clade C: Eriaporidae, Azotidae, Signiphoridae, Trichogrammatidae and Aphelinidae

This group was monophyletic only in the likelihood analyses, with morphological support from the number of flagellomeres (7 : 7) and funicular segments (18 : 3), ventrally divergent eyes (23 : 0), posterolateral pronotal bristle present (70 : 1), mesotrochantinal plate inflected and metasternum extending anteriorly (115 : 2), metafurcal pits near midlength of metasternum (137 : 1) and sessile gaster (204 : 1). A sister-group relationship between the Eriaporinae + Euryischiinae (Eriaporinae s.l.) and the other *Clade C* taxa was based on the scutoscutellar sulcus lost (fused) between the axilla and scutellum (96 : 1), mesothoracic discrimen absent (113 : 2) and the mesophragma extending into the metasoma (203 : 2; reversed in *Trisecodes*, Eulophidae). The extension of the mesophragma through the petiole (Fig. 7a) is a major feature uniting this lineage. In Euryischiinae, the phragma extends into the petiole but not into the gaster (203 : 1). An extended phragma also occurs in Mymaridae that have a sessile gaster (*Anagrus*, *Anaphes*, *Stethynium* and *Litus* in our analysis) and Agaonidae.

Eriaporidae, revised status. Eriaporinae was first recognized by Ghesquière (1955). The varied taxonomic treatment of the included genera was summarized by Hayat and Verma (1980), which included the synonymy of Euryischiidae Shafee 1974 as a tribe of Eriaporinae. However, Hayat (1998) proposed that both subfamilies were unrelated within Aphelinidae, and further suggested that either subfamily might be better placed in Pteromalidae. Both Eriaporinae and Euryischiinae were monophyletic in our combined analyses, based on several features (Table 2). *Promuscidea* (Eriaporinae) was not included in the Munro et al. (2011) analysis using only molecular data. A likelihood analysis of our molecular matrix herein supports a similar grouping of Euryischiinae with Miscogastrinae (*Macroglenes* and *Gastrancistrus*, Pteromalidae) that also includes Eriaporinae, but Eriaporinae and Euryischiinae are not monophyletic. Neither subfamily ever grouped with Aphelinidae s.l. Eriaporinae and Euryischiinae were monophyletic, and sister group to Tetracampidae + Eulophidae in the parsimony results (Fig. 9) or to the eulophid–aphelinid lineage in the likelihood results (Fig. 10). The only synapomorphy shared in all of the results was maxillary palp with three segments (64 : 3). Other potential synapomorphies include a transverse clypeus (38 : 0), labral setae restricted to apical margin (54 : 1), corner of pronotum with bristle (70 : 1), elongate costal cell (145 : 0), mesofemoral bristle present (188 : 1) and a slightly advanced cercus (218 : 1).

Azotidae, revised status. This group, containing *Ablerus*, was proposed as a subfamily of Aphelinidae by Nikol'skaya and Yasnosh (1966). Azotidae is also a distinctive group, supported by 26 putative apomorphies (Table 2). We considered an alternate classification in which Azotinae and Signiphorinae would be treated as subfamilies in Signiphoridae. However, the sister-group relationship between the two taxa was not found in all analyses (e.g. Azotidae is sister to Trichogrammatidae in the IW analysis, Fig. 9). A family containing the two taxa (*Clade Ca*, Fig. 10) would be difficult to delineate morphologically, supported by a one-segmented clava (9 : 1), parastigma with one campaniform sensilla (152 : 1), three uncal sensilla (162 : 3), apex of protibia with horizontal socketed spur (180 : 1), anterior projections on $Ms_{3–6}$ (210 : 1), and Mt_8 and Mt_9 separate and articulating (211 : 0). Except for the narrow apodemes (210 : 1), the other features are homoplastic and found in several other groups of Chalcidoidea.

Signiphoridae. This family was monophyletic, and in our likelihood results formed a sister-group relationship with Azotidae. The results do not support the subfamily classification for Signiphorinae and Thysaninae discussed by Woolley (1988, 1997). The relationship between Signiphoridae and Azotidae (as Azotinae) was proposed by Woolley (1988) based on presence of a series of internal apodemes on metasomal sternites 3–6 (210 : 1). Although long, narrow projections on metasomal sternites 3–6 that appear to be apodemes are found only in Azotidae and Signiphorinae, the metasomal sterna of Eriaporidae (Euryischiinae) and *Mongolocampe boucekei* (Tetracampidae) also have wide, anterolateral projections that may represent a modification of this

condition. Signiphoridae s.s. is a distinctive group, and strongly supported based on 21 putative apomorphies (Table 2).

Trichogrammatidae. Trichogrammatidae is clearly a monophyletic group, with two subfamilies currently recognized, a paraphyletic Trichogrammatinae and a monophyletic Oligositinae (Owen et al., 2007). Monophyly of the family was strongly supported in all our analyses (Figs 8–10), with branch support from 22 character states, including two non-homoplastic synapomorphies, a 1-segmented funicle (18 : 1, may be 0 or 2 in other Trichogrammatidae not scored) and an entirely membranous vertex (44 : 2) (Table 2). A novel sister-group relationship with *Trisecodes* (Eulophidae) was supported by the presence of three-segmented tarsi (176 : 3) and states of nine other characters (24 : 0, 34 : 0, 54 : 0, 83 : 1, 130 : 1, 144 : 3, 146 : 0, 159 : 3, 181 : 1). Three-segmented tarsi outside of this group are found only within the genus *Pteroptrix* (Aphelinidae: Coccophaginae), *Kikiki* and *Enneagmus* (Mymaridae), on the fore legs of male *Melittobia* (Eulophidae), and in the morphologically simplified males of some fig-associated Pteromalidae (e.g. Otitisellinae). In *Trisecodes*, a petiolate gaster (203 : 0) and funicle with three flagellomeres (8 : 3; versus maximum of two in Trichogrammatidae) were used to exclude this genus from Trichogrammatidae (Delvare and LaSalle, 2000); however, features of the antenna, including the shape of the multiporous plate sensilla, are very similar to those of Trichogrammatidae. A sister-group relationship between Trichogrammatidae and Azotidae was recovered in the molecular-only results of Munro et al. (2011). We recovered a similar relationship in the parsimony analysis.

Aphelinidae. Aphelinidae is a paraphyletic or polyphyletic assemblage that currently includes eight subfamilies (Heraty et al., 1997; Hayat, 1998; Gibson et al., 1999; Campbell et al., 2000; Munro et al., 2011). The different subfamilies have been included in Eulophidae (Ashmead, 1904; Muesebeck et al., 1951), Encyrtidae (Girault, 1915; Gordh, 1979), or Pteromalidae (Hayat, 1985), or as distinct families (Compere and Annecke, 1961; Hayat, 1998). Based on molecular data, the subfamilies (including Eretmocerinae and Calesinae) were monophyletic but unrelated to each other (Campbell et al., 2000; Munro et al., 2011). At the family level, the group has been associated with Encyrtidae, Eulophidae, Signiphoridae and Trichogrammatidae (Compere and Annecke, 1961; Viggiani and Bataglia, 1984; Noyes, 1990; Rosen and DeBach, 1990).

Aphelinidae including eight subfamilies was not monophyletic in any of our analyses. In the combined likelihood and Bayesian analyses, Aphelinidae included Signiphoridae and Trichogrammatidae (Fig. 10), but for the first time this group did include all of the core subfamilies of Aphelinidae, including Calesinae, which currently is unplaced within Chalcidoidea (Mottern et al., 2011). The parsimony results support a polyphyletic grade of aphelinid taxa that includes Encyrtidae and, less likely, an association with Agaonidae (Fig. 9). Eriaporinae and Euryischiinae (Eriaporinae s.l.) always form a monophyletic group. Azotinae (previously part of Aphelininae) was the sister group of Signiphoridae. Coccophaginae is monophyletic, but only with the inclusion of *Eriaphytis* (Eriaphytinae), which was based on sharing a socketed peg on the mandible (62 : 0, also found in habrolepidine Encyrtidae) and the basal cell of the fore wing being setose (143 : 0, bare in *Encarsia*, Aphelinidae). *Eriaphytis* (Eriaphytinae) was included only with morphological data, and we regard this as an incorrect placement; more likely it is the sister group of Coccophaginae as suggested by Hayat (1998). *Euxanthellus* (Euxanthellini sensu Hayat, 1998) is included for the first time, nested within Coccophaginae. Eretmocerinae, Calesinae and Aphelininae form very distinct lineages, each supported by several distinct apomorphies that would support their subfamily status (Fig. S3). We propose that Aphelinidae should be restricted to include only Aphelininae, Calesinae, Coccophaginae, Eretmocerinae and tentatively Eriaphytinae, which together form a monophyletic group in all our analyses that included morphology (*Clade Cb*, Fig. 10). However, support for this family group is relatively weak, and includes axilla with one bristle (97 : 1, 0–2 bristles within the group), fore wing with specular area pilose (153 : 1, can be bare ventrally) and cercus with three setae (221 : 3, with reversal to four in some taxa).

Clade D: Agaonidae—Pteromalidae

This larger group constitutes the "hard-bodied" chalcidoids. The support indicated includes clypeus more or less quadrate (38 : 0), hypostomal carina curved mesally but incomplete (48 : 1), left mandible with three teeth (55 : 3), labial palp three-segmented (65 : 3), humeral plate with more than four setae (140 : 5) and submarginal break present (145 : 0), but all these features are highly variable within the clade.

Agaonidae. The six subfamilies of Agaonidae have been variously placed in Agaonidae, Eurytomidae, Pteromalidae, or Torymidae (Bouček, 1988a). Agaoninae, Epichrysomallinae, Otitesellinae, Sycoecinae, Sycophaginae and Sycoryctinae were all included in Agaonidae by Bouček (1988a). However, Rasplus et al. (1998) revised Agaonidae, and limited the family to include only Agaoninae (Agaonidae s.s.), but left Sycophaginae and Epichrysomallinae

unclassified to family. Cruaud et al. (2010) analysed Agaonidae s.s. and suggested that three or four subfamilies should be recognized (cf. Table 1). Agaonidae s.s. was strongly supported as monophyletic in all our analyses, with nine supporting character states from both analyses (Table 2), including basal flagellomere of females asymmetric (4 : 2), left mandible with a single tooth (55 : 1), mandibular appendage present (61 : 1), labial palpi absent (65 : 0), scutoscutellar sulcus obliterated posteriorly (96 : 3/4), mesotrochantinal plate inflected with membranous region (115 : 1), peritremata present (131 : 1), basitarsal comb of fore leg absent (183 : 0) and mesophragma extending into gaster (203 : 2). Overall, 21 potential synapomorphies were recognized (Table 3), but with some characters dependent on whether Sycophaginae were (likelihood) or were not (IW) sister to Agaonidae. We recovered a sister-group relationship with Sycophaginae, as originally proposed by Bouček (1988a), in the morphology-only and combined likelihood results (Fig. 10). Consequently, we propose inclusion of Sycophaginae in Agaonidae, *revised status*. Morphological support included upper mesepimeron with a distinct notch (110 : 1), antecostal sulcus of first gastral sternite present (209 : 0), $Mt_{8\&9}$ articulating without a membranous separation (211 : 0; 212 : 0), cercus arising from membranous area (217 : 1), digitiform cercus (218 : 0) and an elongated laminated bridge connecting the ovipositor valves (223 : 3). The elongate cercus and laminated bridge features are shared with some or all, respectively, of the fig associates placed in the Pteromalidae E group.

Clade E: Eupelmidae, Tanaostigmatidae, Cynipencyrtidae and Encyrtidae

Only one character state, a completely setose basal cell (143 : 0, Table 3), is mapped as a synapomorphy in the combined analysis for *Clade E*, but it is reversed in several taxa. Except for some Aphelinidae (e.g. Eutrichosomellini), *Clade E* constitutes the chalcid "jumpers" and includes taxa with an enlarged acropleuron (108 : 2) (Gibson, 1986b, 1989; Noyes, 1990). Eupelminae (Eupelmidae) is the exception within the group. Although females have a greatly enlarged acropleuron, males have a small acropleuron similar to other Chalcidoidea. The monophyly of Tanaostigmatidae and Encyrtidae was proposed by LaSalle and Noyes (1985) using features of both the adult and egg stages. Eupelmidae, Tanaostigmatidae and Encyrtidae were monophyletic in our combined likelihood (Fig. 10) and Bayesian analyses. Their monophyly was not supported using parsimony (Fig. 9), but neither was a relationship between Tanaostigmatidae and Encyrtidae and *Cynipencyrtus* was nested within Neanastatinae (Eupelmidae) as the sister group of *Neanastatus*. *Cynipencyrtus* was never placed in a monophyletic Tanaostigmatidae. Its correct familial classification remains questionable (LaSalle and Noyes, 1985; Gibson, 1989, 2008, 2009a; Noyes, 1990) because it is indicated as the sister group of Encyrtidae in our morphology-only (Fig. S1) and combined likelihood analyses (Fig. 10), but it lacks the autapomorphies of Encyrtidae (see below).

Eupelmidae. The monophyly of Eupelmidae has not been justified and it is potentially a grade-level taxon that could be paraphyletic to the encyrtid–tanaostigmatid clade (Gibson, 1989, 1993; Gibson et al., 1999). Based in part on extinct Baltic amber taxa, Gibson (2009a) suggested that Neanastatinae could be more closely related to the latter clade.

Oodera (Pteromalidae: Cleonyminae: Ooderini) is included in Eupelmidae in all our results. Like male eupelmines and other pteromalids, *Oodera* species lack an enlarged acropleuron, but they have posteriorly projecting mesotrochantinal lobes (115 : 3) and a membranous region anterior to each mesocoxa (114 : 1) such that the mesocoxae can rotate out of their fossae. This mesocoxal articulation structure is shared with Calosotinae and female Eupelminae, though Tanaostigmatidae and some Encyrtidae have similar structures (Gibson, 1989). The acropleuron is variably enlarged in both sexes of Calosotinae (108 : 1–3) and is only partly enlarged and not convex (108 : 1) in *Archaeopelma* (Gibson, 1989; fig. 27), forming a transformation series within the subfamily from only a partly enlarged to a greatly enlarged acropleuron. *Oodera* is the sister group of Calosotinae in our morphology-only RAxML analysis (Fig. S1), is nested within Calosotinae in our combined parsimony analysis (Fig. 9) and is the sister group of Neanastatinae + Calosotinae in our combined likelihood analysis (Fig. 10). Nesting of *Oodera* within Calosotinae is unlikely, but a sister-group relationship with Calosotinae is reasonable. A sister-group relationship with Calosotinae + Neanastatinae is also reasonable if the modifications enabling the mesocoxae to rotate anteriorly (114 : 1, 115 : 3) were secondarily lost from Neanastatinae. Consequently, there is support for classifying *Oodera* in Eupelmidae, as has sometimes been done (Ashmead, 1904; Nikol'skaya, 1952; Graham, 1969). However, for the purpose of stability, we prefer to retain the existing classification of *Oodera* as a tribe within Cleonyminae (Pteromalidae) until additional evidence is found to clarify its relationships and the monophyly and correct classification of Eupelmidae and its three subfamilies relative to Pteromalidae. Even without inclusion of *Oodera*, no single morphological feature is unique to Eupelmidae, and all the features used in combination to define the family are shared

with members of some other families (Gibson, 1989). This is illustrated by the strongly dimorphic males and females of Eupelminae, which form separate clades in our morphology-only analyses, as was found in previous morphological analyses (Krogmann and Vilhelmsen, 2006).

Eupelmidae, with the inclusion of *Oodera* and each of its three subfamilies, Calosotinae, Eupelminae and Neanastatinae, was monophyletic only in our combined likelihood analysis (Fig. 10). Character state support for Eupelmidae + *Oodera* (*Clade Ec*) included lateral clypeal sulcus present (37 : 1, reversed in Eupelminae), sulcate tentorial pits present (46 : 1, variable within *Clade E*), and postgenal bridge present and elevated (49 : 2, reversed within Eupelminae) (Table 3). Support for *Oodera* + Neanastatinae + Calosotinae included prepectus longer than high (77 : 1, variable in Eupelminae), lateral panel of prepectus setose (82 : 1, reversed in Neanastatinae), metapleuron setose (133 : 0, bare in *Neanastatus*) and mesotarsus with pegs along antero- and posteroventral edges (192 : 4, variable within clade). Eupelminae was monophyletic only when molecular data were included (identical sequences for males and females), and only two morphological features supported monophyly of this subfamily: complete hypostomal carina (48 : 0) and upper mesepimeron with a spiracular notch (110 : 1). Both character states are reversed within the subfamily. Gibson (1989) postulated two other synapomorphies for Eupelminae: sexual dimorphism (his character 1 : 2), and in females the mesotergal-trochanteral muscle (t_2-tr_2) being reduced to a small tendon-like muscle originating from the anteroventral angle of the axilla (his character 17 : 6). However, dissections have since shown that females of *Phenaceupelmus*, which was hypothesized as the most basal lineage of Eupelminae by Gibson (1995), have the plesiomorphic structure of t_2-tr_2 (17 : 1) (G.A.P. Gibson, unpublished). Therefore *Phenaceupelmus* is supported as the sister group of the remaining Eupelminae, which are supported as monophyletic by state 17 : 6. Our results never retrieved *Phenaceupelmus* as the basal lineage of Eupelminae (Figs 8–10 and S1).

Tanaostigmatidae. Tanaostigmatidae *sensu* LaSalle (1987) was monophyletic in all our analyses, and supported by states of 14 characters including the characteristic external extension of the prepectus (81 : 1, Fig. 4l) (Table 2). *Cynipencyrtus* was never included within the family or as its sister group. Rather, Tanaostigmatidae was supported as the sister group of *Cynipencyrtus* + Encyrtidae (*Clade Ea*) based on structures of the hypostomal carina (48 : 2), transscutal articulation (93 : 1) and axillae (94 : 1) (Table 3).

Cynipencyrtidae, revised status. *Cynipencyrtus* was originally described in Encyrtidae by Ishii (1928), treated as the tribe Cynipencyrtini in the subfamily Encyrtinae by Triapitzin (1973), and transferred to Tanaostigmatidae by LaSalle and Noyes (1985). As noted above, *Cynipencyrtus* was never included in Tanaostigmatidae or as its sister group in any of our analyses or of those of Munro et al. (2011) and its current classification in Tanaostigmatidae is therefore not supported. Parsimony (Fig. 9) nested *Cynipencyrtus* in Neanastatinae (Eupelmidae) as the sister group of *Neanastatus*. This sister-group relationship is based on a single shared state, a specialized structure of the transscutal articulation (93 : 1) that is shared also with Encyrtidae and Tanaostigmatidae. The only unambiguous character state supporting inclusion of *Cynipencyrtus* in Neanastatinae is prepectal structure (81 : 2), but Gibson (1989) hypothesized the structure in *Cynipencyrtus* represents an intermediate stage in the evolution of the prepectal structure of Encyrtidae (81 : 3) and is convergent to the structure possessed by *Neanastatus*. Both likelihood (Fig. 10) and Bayesian combined analyses and morphology-only (Fig. S1) analyses placed *Cynipencyrtus* as the sister group of Encyrtidae (*Clade Eb*), based on having a 6-segmented funicle (8 : 6, variable in Encyrtidae), pronotal collar indicated (67 : 1, variable in Encyrtidae), axilla not advanced (95 : 0, probable symplesiomorphy), parascutal carina meeting at the transscutal articulation (98 : 1, reversed in *Acerophagus* and *Metaphycus*) and fore wing humeral plate with three setae (140 : 3, highly variable) (Table 3). Prepectal structure (Gibson, 1989; fig. 48) also supports a sister-group relationship with Encyrtidae (Gibson, 1989; figs 115, 116) if 81 : 2 and 81 : 3 form a single transformation series as hypothesized by Gibson (1989). A *Cynipencyrtus* + Encyrtidae sister-group relationship suggests that similar, medially contiguous, transverse-triangular axillae (Gibson, 1989; character 11 : 2b, figs 65, 66) represent an additional synapomorphy, though Gibson (2008) described an extinct genus in Tanaostigmatidae from Baltic amber that has the same axillar structure in combination with the characteristic tanaostigmatid prepectal structure. Shared possession of mesotibial apical pegs (190 : 1) (Gibson, 1989; character 13 : 2, fig. 144) and similar pronotal structures (Gibson, 1989, figs 65, 66) could represent additional synapomorphies or also retained symplesiomorphies relative to Tanaostigmatidae.

Gibson (1989) stated that if *Cynipencyrtus* was demonstrated as the sister group of Encyrtidae, it probably was better to recognize three subfamilies: Tanaostigmatinae, Cynipencyrtinae and Encyrtinae in Encyrtidae. However, both Tanaostigmatidae and Encyrtidae are strongly supported as monophyletic and they are two of the most recognizable families within Chalcidoidea. Inclusion of the three as subfamilies in a single family would make delineation of Encyrtidae exceed-

ingly difficult, and possible only using a combination of features that are also possessed by some or most Eupelmidae and Aphelinidae. Inclusion of just *Cynipencyrtus* in Encyrtidae as a subfamily would result in the same problem of a delineating a readily definable Encyrtidae. *Cynipencyrtus* lacks advanced mesocoxae (187 : 0) and the fore wing has a speculum (154 : 0) rather than a linea calva and non-advanced cerci (219 : 0). Because of this, we prefer to recognize three families with the following proposed relationships: Tanaostigmatidae + (Cynipencyrtidae + Encyrtidae).

Encyrtidae. Encyrtidae was monophyletic in all analyses, with strong support by 15 putative synapomorphies (Table 2).

Clade F: Chalcididae, Eurytomidae, Leucospidae and Pteromalidae (in part)

A clade of Eurytomidae + (Chalcididae + Leucospidae) has been discussed in the literature, but without character support (Gibson, 1990; Noyes, 1990; Wijesekara, 1997; Gates, 2008). We were not able to recover the monophyly of this group without inclusion of the pteromalid subfamilies Cleonyminae (Chalcedectini), Leptofoeninae and Spalangiinae (Fig. 10). Under parsimony, Chalcididae, Leptofoeninae and Leucospidae formed a clade, but Eurytomidae and Spalangiinae grouped elsewhere (Fig. 9). Parsimony also placed Leucospidae as the sister group of a monophyletic Chalcididae, whereas with likelihood, Leucospidae + Chalcedectini were the sister group. *Clade F* was based on a deep antennal scrobe with abrupt margins (22 : 1, variable within clade), metapleuron setose (133 : 0, reversed in a few taxa), stigmal vein length (158 : 1, variable) and petiole completely fused (206 : 2, membranous in Leucospidae and partially fused in Leptofoeninae). *Clade Fa*, Chalcedectini, Leucospidae and Chalcididae, was based on the pronotal collar short (68 : 0, variable in clade), metafemur enlarged (195 : 1), metafemur toothed (196 : 3–4) and metatibia with ventral carina (198 : 1).

Monophyly of Spalangiinae and Leptofoeninae (Pteromalidae) was based on the mesepimeron with posterior margin overlapping the metapleural complex (111 : 1), metascutellum separated from the metanotum (121 : 1) and metasomal sternite 2 (Gs1) without an antecostal sulcus (209 : 0). The inclusion of these taxa with the leucospid–chalcidid clade is based on having the basal flagellomere quadrate (4 : 0), mandible bidentate (55 : 2) and frenum defined across the scutellum (104 : 1). Except for the quadrate flagellomere, these other traits are more common in the other pteromalid subfamilies. Spalangiinae grouped with Perilampidae and Chalcedectini grouped with miscellaneous Pteromalidae in the parsimony analysis (Fig. 9), which also seems erroneous, whereas Leptofoeninae was still the sister group of Leucospidae and Chalcididae. A closer relationship between Leptofoeninae and Leucospidae may be only slightly more tenable. We never recovered a sister-group relationship between Eurytomidae and either one or both of Leucospidae and Chalcididae. In Leptofoeninae (*Leptofoenus*), Chalcedectini (*Chalcedectus*) and some Chalcididae (Cratocentrini, Phasgonophorini and *Brachymeria*), a deep postoccipital pit is present and associated with the insertion of the pronoto-postoccipital muscle (t_1-poc), which would provide additional support for this relationship (G. Delvare, pers. obs.).

Chalcididae. Monophyly of Chalcididae is based largely on four putative morphological synapomorphies (Wijesekara, 1997; Gibson et al., 1999). Five subfamilies and seven tribes are currently recognized: Chalcidinae (Chalcidini, Cratocentrini, Phasgonophorini and Brachymeriini), Dirhininae, Epitraninae, Haltichellinae (Haltichellini, Hybothoracini and Tropimerini) and Smicromorphinae (Bouček, 1988a; Delvare, 1992). An alternate classification by Wijesekara (1997) recognized Brachymeriinae (Phasgonophorini and Brachymeriini), Cratocentrinae and Dirhininae (Dirhinini and Epitranini), but not Smicromorphinae (tribe of Chalcidini) and Dirhininae were treated as a tribe of Chalcidinae. In molecular analyses, the family and some subfamilies were not monophyletic, with the groups scattered across the resulting trees (Campbell et al., 2000; Munro et al., 2011).

Chalcididae was monophyletic in all our results, with strong bootstrap support in the likelihood analysis (Figs 8–10 and S2). The subfamily Chalcidinae was never monophyletic, with Cratocentrini always forming a clade independent from the other tribes. The remaining Chalcidini (Brachymeriini, Chalcidini, Phasgonophorini) were monophyletic in most likelihood results (15/20). In the parsimony results, Chalcidinae included Smicromorphinae. Our results suggest a subfamily classification of Chalcidinae, Cratocentrinae, Dirhininae (with Epitranini), Haltichellinae and Smicromorphinae. The family Chalcididae was supported by 18 putative synapomorphies (Table 2), with the following characters states scored as present for all chalcidids: genal carina present (42 : 1), postoral bridge present (49 : 1) and labrum sclerotized with exposed ventral plate (51 : 0, 52 : 0), with additional support in the IW analyses from the parascutal and axillar carina ∩-shaped (98 : 1), metanotal scutellar arm reduced to thin carina (124 : 2), supracoxal flange absent (134 : 0), cubital vein present as non-pigmented fold (144 : 2), and petiole fused ventrally and without a suture (206 : 2).

Eurytomidae. Four subfamilies are currently recognized: Buresiinae, Eurytominae, Heimbrinae and

Rileyinae (Stage and Snelling, 1986; Lotfalizadeh et al., 2007; Gates, 2008). However, no morphological synapomorphies have been proposed to define the family (Gates, 2008). As well, independent molecular and morphological analyses have failed to recover their monophyly (Campbell et al., 2000; Chen et al., 2004; Lotfalizadeh et al., 2007; Munro et al., 2011). Based on molecular results, Chen et al. (2004) proposed elevating Rileyinae to family status, whereas based on morphology Lotfalizadeh et al. (2007) found Rileyinae to consist of two clades of unrelated taxa (*Rileya* and *Macrorileya* + *Buresium*) and placed the latter group in Eurytominae. All our combined results support a monophyletic Eurytomidae (Figs 8–10), with strong bootstrap support in the likelihood analyses. Rileyinae was included within Eurytomidae, but with Heimbrinae grouping internally with *Neorileya*. Buresiinae (*Macrorileya* + *Buresium*) and Eurytomidae were both monophyletic, and our results support recognition of Buresiinae as a subfamily. Morphological support for the family was based on 11 putative synapomorphies that include medial position of the toruli (24 : 0), postgenal groove present (41 : 1), posterior tentorial pits sulcate (46 : 1), postoral bridge present (49 : 1), prepectus fused with mesepisternum ventrally (85 : 1, reversed in *Bephrata*), metapleuron setose (133 : 0), metapleural suture absent (135 : 1), parastigma constricted at hyaline break (147 : 0, 148 : 1), basitarsus with one row of paddle-shaped setae (186 : 0) and petiole fused with metasomal sternite 2 (Gs1) (207 : 1, reversals in *Heimbra* and *Rileya longitergum*). Further support from characters not scored include the anterior thoracic spiracle covered by the pronotum and not visible externally and mesotrochantinal plate completely sclerotized with the mesocoxal cavities closed posteriorly.

Leucospidae. Leucospidae is a recognized mono-phyletic group of four genera considered to be closely related to Chalcididae (Bouček, 1974; Wijesekara, 1997; Gibson et al., 1999; Munro et al., 2011). The two genera included in our analysis were monophyletic in all our results with strong bootstrap support (Figs 8–10; Table 2).

Clade G: Pteromalidae: Cleonyminae and Eunotinae

Four character states define *Clade G* (Table 3), including number of antennal flagellomeres (7 : 9; 17 : 9), eyes with inner orbits ventrally divergent (23 : 0) and prepectus with lateral panel setose (82 : 1, reversed in clade). These character states are variable across Chalcidoidea.

Cleonyminae (Pteromalidae) is composed of six tribes, Boucekiini, Chalcedectini, Cleonymini, Heydeniini, Lyciscini and Ooderini (Gibson, 2003). The relationships between tribes are not clear. In his morphological phylogenetic analysis, Gibson (2003) was not able to recover monophyly of Cleonyminae, which also included Louriciinae and Hetreulophini (Pteromalidae: Colotrechninae). Using molecular data, Cleonyminae were not monophyletic, and the four tribes analysed, Chalcedectini (one genus), Cleonymini (three genera), Lyciscini (five genera) and Ooderini (one genus), were scattered (Munro et al., 2011). In our likelihood results, *Oodera* (Ooderini) grouped with Calosotinae (see under Eupelmidae) and Chalcedectini with Leucospidae. Cleonymini and Lyciscini were monophyletic in *Clade G* (Cleonymini), but based only on a having a bidentate mandible (55 : 2). Boucekiini and Heydeniini were not included in our analysis.

LaSalle et al. (1997) proposed that Eunotinae (Pteromalidae) was monophyletic with inclusion of *Idioporus*. Based on molecular data alone, Eunotinae were monophyletic, exclusive of *Idioporus*, which grouped in an unusual position with Perilampidae (Munro et al., 2011). We resequenced all genes for *Idioporus affinis*, as discussed above and deleted the 28S–D2 region for our analyses. Our resulting parsimony analyses did not support Eunotinae (three different groups; Fig. 9); however they were paraphyletic, including *Idioporus*, in both morphology-only analyses (Fig. S1). Eunotinae were monophyletic, including *Idioporus*, in the combined likelihood analysis (Fig. 10) with support based on dorsal extensions of the hypostoma (48 : 2), short pronotal collar (68 : 0), humeral plate with a single seta (140 : 1, 1–3 in clade) and postmarginal vein short or absent (164 : 0, state 2 in *Eunotus* sp.2).

Clade H: Cerocephalinae–Torymidae

This larger group was supported by only two character states: postoral bridge present and continuing ventrally to hypostomal bridge (49 : 2, variable in clade) and metasomal tergites 8 and 9 separated by a membrane (212 : 1, reversed in *Ormyrus rosae*, and inapplicable for Diparinae, Cerocephalinae and Colotrechninae, which have a syntergum). This is probably an artificial group.

Clade Ha (Pteromalidae A) includes Coelocybinae (PT06), Diparinae (Diparini; PT09D) and Cerocephalinae (PT03). Support includes humeral plate with two setae (140 : 2, variable), fore wing admarginal area with row of setae (157 : 1, with adstigmal setae in Cerocephalinae) and fore wing with marginal fringe relatively long (166 : 1, fringe sometimes absent in clade). The Neapterolelapini (Diparinae) grouped with Herbertiinae in Pteromalidae *Clade C*. The Diparini grouped with Cerocephalinae in the IW analyses, with *Yrka* (Coelocybinae) distantly related.

Clade Hb includes Colotrechninae, Ormyridae and Torymidae (Fig. 10), and is based on sulci extending from the posterior tentorial pits (46 : 1, reversed in *Neomegastigmus*), metanotal scutellar arm broad (124 : 0) and cubital vein present as a setal line (144 : 3, reversed in *Ormyrulus* and *Echthrodape*). A clade of Ormyridae and Torymidae was recovered with parsimony, but with a sister-group relationship between Ormyridae and Cerocephalinae + Diparini (Fig. 9). With likelihood, Ormyridae is sister group of Colotrechninae (Fig. 10). The relationship between Colotrechninae and Ormyridae was based on pronotal collar short (68 : 0), notauli distinct but incomplete (89 : 1), marginal vein long (156 : 2), stigmal vein relatively long (158 : 1) and metacoxa dorsally carinate (194 : 1). The placement of Ormyridae within Torymidae is not supported by any of our analyses. A sister-group relationship between Ormyridae and Torymidae has been suggested previously (Grissell, 1987; Noyes, 1990).

Ormyridae. The monophyly of Ormyridae is not in doubt, but its placement with regard to other Chalcidoidea is uncertain (Hanson, 1992, 1997). Ormyridae has been included as a subfamily in Pteromalidae (Burks, 1979), Torymidae (Bouček et al., 1981), or as its own family (Bouček, 1988a). With molecular data, Ormyridae was monophyletic but distantly placed from Torymidae (Munro et al., 2011). The two genera included herein were monophyletic with high bootstrap support based on eight character states, including occipital carina present (40 : 0, partial or complete in Torymidae and Pteromalidae), frenum not indicated dorsally (104 : 0, variable in Torymidae and Pteromalidae), transepimeral division absent (109 : 1, variable in Torymidae) and metacoxa enlarged with flat inner surface (193 : 2, variable in Torymidae). Males of Ormyridae also have the metasomal tergites fused into a carapace (225 : 1, scored only for *Ormyrus*), and we did not code for the characteristic pits on the gastral tergites, which are unique for Ormyridae, nor for their unusually robust and curved metatibial spurs.

Torymidae. Torymidae currently includes only two subfamilies, the largely phytophagous Megastigminae and the mostly parasitic Toryminae, with the latter divided into seven tribes (Grissell, 1995). The family has included Agaoninae and Sycophaginae (= Idarninae), but these were removed by Bouček (1988a). Based on molecular data, Torymidae was not monophyletic, with Megastigminae and Toryminae not grouping together (Campbell et al., 2000; Munro et al., 2011). Torymidae, including Megastigminae, was monophyletic in all of our results. A sister-group relationship between the two subfamilies was supported only in the combined analyses (Figs 9 and 10). Monophyly of the family was supported by sulci extending from tentorial pits (46 : 1), mesepimeron with posterior margin notched (110 : 1), fore wing with basal lobe present (141 : 1), fore wing with Rs absent (159 : 3), basitarsus with ordinary setae (186 : 2, variable), metasomal tergites 8 and 9 articulating (211 : 0), cercus arising from membranous area (217 : 1) and valvifers without sclerotized bridge between them (224 : 0).

Pteromalidae B–D

This is a grade of various subfamilies or unassociated species of Pteromalidae. While some of the subfamilies included are monophyletic and strongly supported, the relationships between groups are generally suspect.

Pteromalidae B

This is a disassociated group of three pteromalid taxa including *Collessina* (Eutrichosomatinae; PT12, coded only for morphology), Austrosystasinae (PT26, coded only for morphology) and *Systolomorpha* (Pteromalidae: Ormocerinae, Melanosomellini; PT17M). *Systolomorpha* also did not group with the other Melanosomellini in the molecular analysis of Munro et al. (2011). All three genera are Australian. *Collesina* was placed with doubt in Eutrichosomatinae, with Ormocerinae suggested as a potential alternate placement (Bouček, 1988a).

Pteromalidae C

This group includes *Micradelus* (Pteromalinae: Micradelini; PT21M, morphology only), which did not group with the other Pteromalinae (*Clade J*). Other Pteromalidae included are Asaphinae (PT01), Herbertiinae (PT13), Neapterolelapini (Diparinae; PT09N) and *Lanthanomyia* (Coelocybinae; PT06). *Liepara* was unplaced to subfamily, but had strong bootstrap support for a grouping with *Lanthanomyia* based on eye orbits divergent (23 : 0), mesoscutal lateral lobe with a single bristle (87 : 1), scutellum with two pairs of bristles (100 : 2) and mesofemur with a preapical bristle on the posterior surface (189 : 1). The other two genera of Coelocybinae occur in *Clade Ha* (*Yrka*) and Pteromalidae D (*Ormyromorpha*).

Pteromalidae D

This group includes *Nodisoplata* (Miscogastrinae: Miscogastrini; PT16M), Macromesinae (PT15), *Ormyromorpha* (Coelocybinae; PT06), Chromeurytominae

(PT04), Pireninae (PT20) and Ormocerinae (Melanosomellini, Systasini and *incertae sedis*; PT17).

Clade I: Perilampidae, Eucharitidae and Eutrichosomatinae (Pteromalidae)

Eucharitidae and Perilampidae have been considered as a monophyletic group based on having planidiaform first-instar larvae and adults with a profurcal bridge (Krogmann and Vilhelmsen, 2006). Eutrichosomatinae have not previously been included as part of this complex, although they do have a structure of the labrum (Darling, 1988) and habitus similar to Perilampinae. The genus *Jambiya* was included in Perilampidae by Heraty and Darling (2007), but with an uncertain position. Perilampidae and Eucharitidae were monophyletic in some, but not all, molecular-only analyses of Munro et al. (2011). *Clade I* was supported in our likelihood (Fig. 10) and Bayesian analyses. The same clade was supported in the morphology-only analyses (Figs 8 and S1), but included Mymarommatoidea in the likelihood results. The combined parsimony analysis included the same *Clade I* taxa, together with Spalangiinae (Fig. 9). Morphological support for *Clade I* includes antenna without basiconic peg sensilla (11 : 0, found in some Perilampinae), male scape with glandular pores (16 : 1, includes pores in depressions, and loss of pores in *Euperilampus triangularis*), axillae not advanced (95 : 0, slightly advanced, state 1, in various members), stigmal vein relatively long (158 : 1, variable but also very small or lost in some Eucharitinae) and hind wing without spur vein (r-m) (169 : 1, present in *Chrysolampus schwarzii*). Support for *Jambiya* and Eutrichosomatinae is based on labral digits present (53 : 1, absent in all Chrysolampinae that were scored), mandibular dentition unequal (56 : 2) and fore wing without hyaline break (147 : 0). In the parsimony analyses, *Jambiya* was the sister group of Eucharitidae. *Clade Ia*, Eucharitidae and Perilampidae excluding *Jambiya*, was supported by the propodeal spiracle reniform (128 : 2, circular in Eucharitidae s.s.), fore wing with posterior lobe (141 : 1, absent in *Chrysomalla*), parastigma with one sensilla (152 : 1, variable), basitarsus with unmodified setae (186 : 2) and basal ring of male genitalia present (227 : 0, variable and scored for few taxa).

Perilampidae. Subfamilies included within the family are Chrysolampinae, Philomidinae and Perilampinae, though the different groups have in the past been treated as separate families or as subfamilies of Pteromalidae (Gibson, 1993; Darling, 1997; Gibson et al., 1999). *Akapala* (Akapalinae) was also first classified in Perilampidae, but was transferred to Eucharitidae by Bouček (1988a). *Jambiya* was included in Perilampidae by Heraty and Darling (2007). Based on molecular data, Perilampidae formed a grade composed of Akapalinae, Philomidinae, Chrysolampinae, Perilampinae and *Jambiya*, with *Jambiya* as the sister group of Eucharitidae s.s. (Munro et al., 2011). Our likelihood results also support Perilampidae as a grade, but with *Jambiya* as the sister group of Eutrichosomatinae and Akapalinae as the sister group of Eucharitidae (Fig. 10). Each of Chrysolampinae, Philomidinae and Perilampinae was monophyletic. In the morphology-only analyses and under combined parsimony, Perilampidae was also a grade, but Chrysolampinae was not monophyletic.

Eucharitidae. Monophyly of this family is strongly supported based on morphological features (Heraty, 2002). The three subfamilies, Gollumiellinae, Oraseminae and Eucharitinae have been defined using both morphological and molecular data (Heraty et al., 2004; Heraty and Darling, 2009). Akapalinae and Philomidinae were proposed by Bouček (1988b) as belonging to Eucharitidae, but neither group was included with Eucharitidae s.s. in the molecular analyses of Munro et al. (2011). Our results offer strong support for Eucharitidae s.s., the three subfamilies, and a sister-group relationship with Akapalinae (Figs 9 and 10). Gollumiellinae were not monophyletic in the likelihood results, but were in the parsimony analyses and in molecular studies with more extensive taxon sampling (Heraty et al., 2004; Munro et al., 2011). Morphological support for Eucharitidae including Akapalinae is based on 11 putative apomorphies, including the axillae meeting or being fused medially (94 : 2), metanotal scutellar arm reduced (124 : 1), propodeal spiracle circular (128 : 1), supracoxal flange absent (134 : 0), calcar simple and not cleft (182 : 1), basitarsal notch absent (185 : 0) and petiole fused ventrally without a sulcus (206 : 2, reversed in *Indosema* and *Timioderus*).

Clade J: Pteromalidae E

A pteromalid complex that included Cratominae, Miscogastrinae, Otitesellinae, Panstenoninae, Pteromalinae, Sycoecinae and Sycoryctinae was first proposed based on molecular data by Munro et al. (2011). We recovered the same grouping, with the addition of Ditropinotellinae and Keiraninae, which were coded only for morphology and Epichrysomallinae (PT10), which were monophyletic but distantly related to this complex in Munro et al. (2011). There were no unambiguous morphological features that supported this clade. A paraphyletic *Clade J* was recovered in the IW analysis, but without Ditropinotellinae and Keiraninae (Fig. 9). A grouping of Ditropinotellinae, Keiraninae and Miscogastrinae was

recognized in the likelihood analyses based on the prosternum with a spine-like process (73 : 1) and the axillae joined or nearly joined medially (94 : 1). The Miscogastrinae (Miscogastrini and Sphegigastrini) were defined by having a tridenticulate clypeus (27 : 2, variable within clade). The same taxa were dispersed in the IW analysis. *Nodisoplata* (Miscogastrini) was distantly placed in the Pteromalidae D group. Within *Clade J*, *Plutothrix* (Trigonoderini) did not group with the other Miscogastrinae. *Clade Ja*, which included Epichrysomallinae, Otitesellinae, Sycoryctinae and Sycoecinae, was based on 11 unambiguous characters, including the number of male flagellomeres (17 : 8, 18 : 6), pronotal collar absent (67 : 0), frenum absent (104 : 0), parastigma with hyaline break (147 : 0) and ovipositor valves with an elongated laminated bridge connecting them (223 : 3) (Table 3). This clade includes all the fig wasp parasites and associates that are not included in Agaonidae. Epichrysomallinae was described and included in Torymidae (Stouthamer et al., 1992), transferred to Pteromalidae (Bouček et al., 1981) then to Agaonidae (Bouček, 1988b) and left unclassified to family (Rasplus et al., 1998). We propose inclusion of Epichrysomallinae in Pteromalidae, *revised status*. The elongated laminated bridge is also shared with Agaonidae + Sycoecinae. The latter feature may be correlated with a long ovipositor, but it does not occur in Torymidae, which also have a long ovipositor. *Clade Jb*, which includes Cratominae, Panstenoninae and Pteromalinae, is based on prosternum with a spine-like process (73 : 1, shared with *Clade Ja* and with reversals within clade) and metatibia with a single spur (200 : 1, with reversals in *Habritys* and *Perilampidea*). *Micradelus* (Pteromalinae, coded for morphology only) was distantly placed in the Pteromalidae D group.

Conclusions

Chalcidoidea repeatedly has been shown to be a strongly supported monophyletic group (Gibson, 1986a; Heraty et al., 2011; Munro et al., 2011; Sharkey et al., 2011). The sister group of Chalcidoidea is Diaprioidea in molecular analyses (Castro and Dowton, 2006; Heraty et al., 2011; Munro et al., 2011) and Mymarommatoidea or Mymarommatoidea + Maamingidae in morphological or combined analyses (Gibson, 1986a, 1999; Sharkey et al., 2011), including the present study. Our addition of morphological data to the molecular data of Munro et al. (2011) for Chalcidoidea greatly improved the resolution of both families and family group taxa across the superfamily (Fig. 10). However, both types of data were critical for resolving the current pattern of relationships. Molecular data were essential for anchoring the base of the tree to Mymaridae and Rotoitidae, whereas morphological data provide essential evidence for the monophyly of several families such as Chalcididae, Eurytomidae and Torymidae. With the use of a novel online morphological character-coding system developed in mx, our research community was able to score 233 characters for 300 taxa in 78 subfamilies (Noyes, 2011 recognizes 83 family or subfamily groups), with representation of almost all tribes of Chalcidoidea. For such a morphologically complex group, our results show considerable resolution and closely mirror some of the earlier intuitive concepts proposed by Bouček (1988b), Gibson (1990) and Noyes (1990), and in some aspects the molecular results of Munro et al. (2011).

Mymaridae is demonstrably monophyletic and indicated as the sister group of the remaining Chalcidoidea, with Rotoitidae as the sister group of the rest. With some minor exclusions or inclusions, the families Agaonidae s.s., Chalcididae, Encyrtidae, Eucharitidae, Eulophidae, Eupelmidae, Eurytomidae, Leucospidae, Mymaridae, Ormyridae, Rotoitidae, Signiphoridae, Tanaostigmatidae, Torymidae and Trichogrammatidae were indicated as monophyletic. The families Aphelinidae, Perilampidae, Pteromalidae and Tetracampidae were never supported as monophyletic.

Based on our results, changes in classification that we institute at this time are: recognition of Azotidae Nikol'skaya and Yasnosh, 1966 (based on *Azotus*), *revised status*, Eriaporidae Ghesquière, 1955 (Euryischiinae and Eriaporinae) *revised status*, and Cynipencyrtidae Triapitzin, 1973 (monotypic based on *Cynipencyrtus*) *revised status* as families; Agaonidae to include Sycophaginae *revised status*; Aphelinidae to include Aphelininae, Calesinae, Coccophaginae, Eretmocerinae and Eriaphytinae; Cratominae and Panstenoninae to be treated as synonyms with Pteromalinae, *new synonymy*; Pteromalidae to include Epichrysomallinae *revised status*.

Our results suggest recognizing seven family-level taxa within a "soft-bodied clade": Aphelinidae (Aphelininae, Calesinae, Coccophaginae, Eretmocerinae, Eriaphytinae), Azotidae, Eriaporidae (Eriaporinae, Euryischiinae), Eulophidae, Signiphoridae (Signiphorinae, Thysaninae), Tetracampidae, Trichogrammatidae (Oligositinae, Trichogrammatinae). Ceinae (Pteromalidae) is included within this group in our analyses, but we feel that its placement herein is more uncertain. The subfamilies of Signiphoridae and Trichogrammatidae are based on more extensive analyses of those families (Woolley, 1988; Owen et al., 2007), but we find no support for monophyly of the subfamily Thysaninae and we propose not recognizing Thysaninae as independent of Signiphorinae.

The Agaonidae should be redefined to include Sycophaginae. The other fig-associated subfamilies, Epichrysomallinae, Otitesellinae, Sycoecinae and Syco-

ryctinae, were monophyletic and nested distantly within Pteromalidae (Pteromalidae E, Fig. 10). Our results suggest that *Cynipencyrtus* should be removed from Tanaostigmatidae. *Cynipencyrtus* is indicated as the most likely sister group of Encyrtidae. Because it lacks the distinctive morphological features by which Encyrtidae is defined, we recognize it as its own family rather than as a subfamily within Encyrtidae.

A "planidiaform-larva" clade composed of Eucharitidae and Perilampidae is indicated. Relationships between subfamilies within this clade are equivocal and no changes are warranted at this time within the clade. However, Eucharitidae may have to be redefined in the future to include Perilampidae and Eutrichosomatinae (Pteromalidae). At issue is the treatment of Pteromalidae, which, as expected, has various relationships with other family groups across the tree. While some of these newly proposed relationships are tenable, such as Ooderini (Cleonyminae) as the sister group of Calosotinae (Eupelmidae), any changes in the classification of these groups needs additional attention beyond the scope of this study.

Within our results, several hypotheses of trait evolution can be re-evaluated, of which we chose to examine metallic coloration, phytophagy, egg parasitism, heteronomy, planidiaform larvae and parasitism of Sternorrhyncha.

A metallic blue/green coloration of the body is a common feature within Chalcidoidea that has earned one of the model organisms, *Nasonia vitripennis*, the common name "jewel wasp". Almost all members of some lineages such as Toryminae and Pteromalinae have metallic coloration over the entire body, whereas in others (Aphelinidae, Chalcididae, Mymaridae) it is a rare attribute of only some members. Within the species *Cirrospilus vittatus* (Eulophidae), females can range from almost entirely metallic to mostly yellow with characteristic patches of metallic coloration. The adaptive significance of coloration is not well studied in Hymenoptera, but wing interference pattern colours (WIPs), which also have a strong blue, green, or red colour, have been shown to have both species-specific and sexually dimorphic characteristics that would suggest colour is under strong selective pressure (Shevtsova et al., 2011). Within Proctotrupomorpha, metallic coloration is otherwise exceedingly rare, occurring only in very few Platygastroidea (*Oxyscelio*, *Sceliomorpha*, *Chromateleia* and some *Telenomus*; N. Johnson, pers. commun.) and one species of *Pycnostigmus* (Cynipoidea) (Buffington and van Noort, 2007). As a character, weak or distinct patterns of metallic colour could be scored for all taxa, and we selected this as a trait of interest for analysis. Metallic coloration is absent in Rotoitidae and most Mymaridae (some species within *Anaphes* group, *Polynema* group, and *Himopolynema* have blue metallic colour on the head and mesosoma). Our mapping of metallic colour patterns shows a general dispersion across that tree that shows no correlation at least to the other life-history traits mapped in Fig. 11. It is unclear why such a distinctive colour would be developed independently or lost in so many lineages of Chalcidoidea, but nowhere else. So far, we have not observed any correlation with WIP colour patterns, which are more widespread across Proctotrupomorpha, and are found in both metallic and non-metallic species.

Five life-history traits that could be inferred for most taxa were mapped across the molecular phylogeny for Chalcidoidea of Munro et al. (2011), focusing on patterns of phytophagy, egg parasitism, planidial larvae, Sternorrhyncha parasitism and heteronomous parasitism. The consolidation of several lineages in our combined results reduced the number of independent events for some traits (Fig. 11).

Phytophagy is proposed to have developed at least 10 times in Chalcidoidea: Agaonidae (including Sycophaginae), Eulophidae (Opheliminae and some Tetrastichinae), Eurytomidae (cf. Lotfalizadeh et al., 2007), Tanaostigmatidae, Tetracampidae (Mongolocampinae), Torymidae (Megastigminae and some Toryminae), the fig-associated Pteromalidae (Epichrysomallinae, Otitesellinae, Sycoecinae and also some Sycoryctinae) that form a monophyletic group distantly related to the Agaonidae and gall-associated Pteromalidae (Ormocerinae: Melanosomellini) (Fig. 11). Phytophagy is not a plesiomorphic trait for the superfamily.

Outside the Chalcidoidea, egg parasitism is known to occur only within the Platygastroidea. Our combined results show no change in the number of potential shifts to egg parasitism within Chalcidoidea (at least nine times, Fig. 11) from the molecular-only results of Munro et al. (2011). Species of Mymaridae are almost all egg parasitoids of Hemiptera and Coleoptera (Huber, 1986), but the mode of parasitism is unknown for both Mymarommatoidea and Rotoitidae. If all three groups are egg parasitoids, then egg parasitism would likely be ancestral for the superfamily. Even if ancestral, our results would suggest that egg parasitism has been derived numerous times in Aphelinidae (*Centrodora*), Eupelmidae (*Lambdobregma* [Neanastatinae] and several genera of Eupelminae, e.g. *Anastatus*, some *Arachnophaga*, *Brasema*, *Eupelmus*), Encyrtidae (at least 20 genera), Eulophidae (common in Entedoninae and Tetrastichinae), some Eurytomidae (*Archirileya*, *Eurytoma*, *Macrorileya*), Pteromalidae (*Acroclisoides*, *Agiommatus*, *Enoggera*), Signiphoridae (some *Signiphora* and *Thysanus*), Tetracampidae (*Foersterella*), Torymidae (Monodontomerini: *Amoturoides*, *Chrysochalcissa*, *Oopristus*, *Rhynchoticida*; Palachiini and Podagrionini) and Trichogrammatidae (cf. more complete summaries for taxa not coded in our analysis

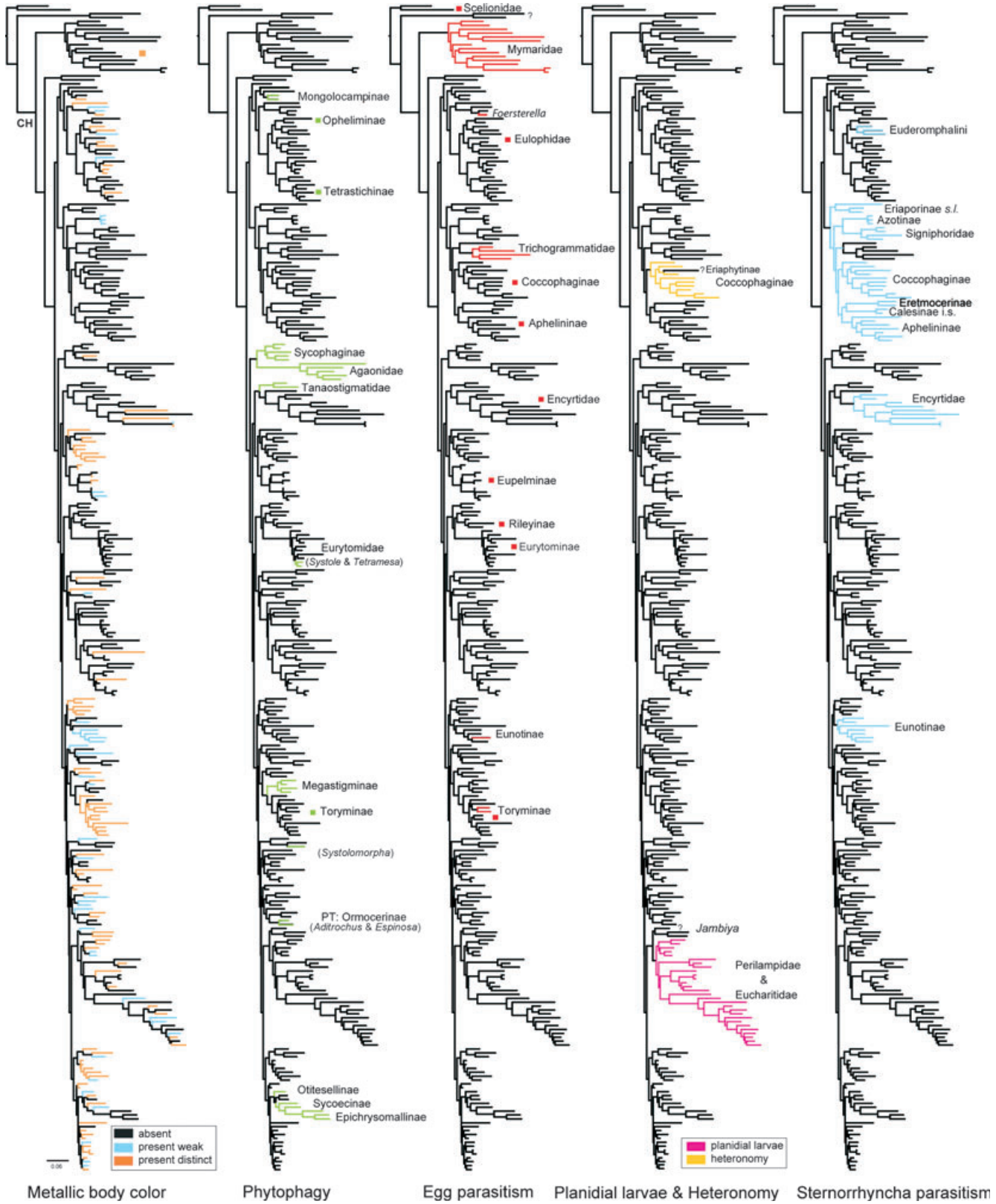


Fig. 11. Mapping of metallic body colour (character 233) and five life-history traits. The phylogram used for mapping is the RAxML tree with the lowest Robinson–Fould distance to the RAxML extended consensus tree. Coloured squares refer to presence of a trait in a clade, but not in a member sampled in this study. CH, Chalcidoidea.

in Bouček et al., 1981; Polaszek, 1991). Depending on the resolution of parasitism in Mymarommatidae and Rotoitidae, egg parasitism may be primitive for the superfamily, but there are numerous obvious shifts to egg parasitism in very divergent lineages across the Chalcidoidea.

For the molecular-only results, we also propose a unique origin for heteronomy (different host requirement for different sexes) in the Coccophaginae (Fig. 11). Our results include Eriaphytinae within this lineage, but this may be an artefact since its placement is based only on morphological data. However, based on characteristics such as presence of a mandibular tooth, they may be closely related or potentially a sister group to Coccophaginae. Heteronomy is an unlikely trait for Eriaphytinae, since *E. chackoi* is a gregarious parasitoid, with both sexes reared from a single host (Hayat, 1998).

The presence of mobile planidial larvae is associated with oviposition occurring somewhere other than on or in the host, with the larva responsible for gaining access to the host. Within Hymenoptera, planidial larvae are found only in the ichneumonid genus *Euceros* and within Chalcidoidea, only in the Eucharitidae and Perilampidae (Heraty and Darling, 1984; Darling, 1992). Our results continue to support a single origin of planidial larvae in Chalcidoidea, although the immature stages of both *Jambiya* (Perilampidae) and Eutrichosomatinae are unknown.

Four independent origins are proposed for the evolution of parasitism of Sternorrhyncha: in Encyrtidae (mostly endoparasitoids, some egg predators), Eunotinae (Pteromalidae) (egg predators), Eulophidae (Entedoninae: Euderomphalini) (endoparasitoids) and the Clade C aphelinid–trichogrammatid lineage (ecto- and endoparasitoids) (Fig. 11). There are enough records of Mymaridae (*Alaptus*) parasitizing scale insects that some may well be correct, even though species of *Alaptus* are considered to be reliably reared only from Psocoptera. If true, this would then represent a fifth evolution of parasitism on Sternorrhyncha, but perhaps a minor one. This is a dramatic decrease from the 10 events proposed in Munro et al. (2011), which was largely the result of a fragmentation of the aphelinid subfamilies. Because of these host associations, these three groups include some of the most spectacular successes for the biological control of scales, aphids and whiteflies (Noyes and Hayat, 1994; Heraty, 2009).

Referring primarily to the larger hard-bodied Cleonyminae (Pteromalidae), Bouček (1988a) proposed that parasitoids of wood-boring beetles possessed the greatest number of plesiomorphic characters, and by implication would be basal within Chalcidoidea. Among the "hard-bodied" chalcidoid lineages, wood-boring beetle parasitoids occur in the Chalcididae [Chalcidinae (Chalcidini, Cratocentrini, Phasgonophorini), Haltichellinae], Encyrtidae, Eupelmidae [Calosotinae, Neanastatinae (*Metapelma*) and a few Eupelminae], Eurytomidae, Perilampidae (*Monacon*, *Steffanolampus*; Perilampinae) and Pteromalidae (Cerocephalinae, Cleonyminae, Leptofoeninae, Macromesinae, Pteromalinae) and Torymidae (Toryminae). Numerous records also occur for Eulophidae (Entedoninae, Eulophinae, Tetrastichinae) attacking Scolytinae (Curculionidae), Buprestidae and Cerambycidae (Noyes, 2011). Also, as egg parasitoids, *Camptoptera* (Mymaridae) attack Scolytinae (Curculionidae) on conifers (Huber and Lin, 1999) and *Uscana* (Trichogrammatidae) attack eggs of Bruchinae (Chrysomelidae) (Noyes, 2011). However, Bouček was referring to morphology associated with larval parasitism only, and did not consider egg parasitoids. The morphological structure of the wood-boring beetle-larvae parasitoids as being ancestral within Chalcidoidea is not supported in our results. Instead, the base of our trees (Figs 9 and 10) represents a mix of diverse host associations: mostly Hemiptera and Coleoptera for Mymaridae, mostly Holometabola for the tetracampid–eulophid lineage, mostly Sternorrhyncha for the aphelinid–trichogrammatid lineage, and phytophagy in fruits of *Ficus* for Agaonidae. These host associations may simply reflect the explosive radiation of potential host groups.

The relationships from both of the combined analyses (Figs 9 and 10) are congruent with available paleontological records, with the main clades branching off in concordance with their representation (although limited) in fossil resins. The basal clades are represented by a grade of groups recorded from Cretaceous ambers (78–115 Ma) that include Mymarommatidae, Mymaridae (upper Albian age; Yoshimoto, 1975; Gibson et al., 2007; Poinar and Huber, 2011; McKellar and Engel, 2012) and Rotoitidae (Coniacian-Santonian age, Taymyr amber, A.G., unpublished data). The Ethiopian amber "eulophoid" inclusions from Late Cenomanian amber (93–95 Ma) (Schmidt et al., 2010) and Jordanian amber (ca. 125 Ma) (Kaddumi, 2005) represent another branch—the aphelinid–trichogrammatid lineage. The remaining groups are common in Eocene deposits (ca. 40 Ma), suggesting their origin in the late Cretaceous or soon after. The intensive post-Cretaceous diversification of chalcidoids may be the result of similar radiations in the diversifications of angiosperms, their potential host groups, and the Cretaceous biocenotic crisis (Wiegmann et al., 2000; Hunt et al., 2007; Regier et al., 2009; Bell et al., 2010).

This is the first time a comprehensive, web-based taxonomic workbench such as mx has been used by an international research community to study phylogenetic relationships in a megadiverse group such as

Chalcidoidea. The project would not have been possible without the online tools in mx and MorphBank used to evaluate and discuss alternate proposals for character state coding, together with the digital images supporting each character state. This new technology made it possible to comprehensively evaluate and reconcile conflicting hypotheses of homology and resulting terminology across virtually all Chalcidoidea, which was not possible previously. The mx platform provides novel methods for online character coding and facilitates the integration of multiple sources and types of data. However, this project is only the first step in the application of cybertaxonomic tools in Chalcidoidea. Many more characters, which we were not able to score meaningfully across all of Chalcidoidea, offer potential phylogenetic information. With more focused studies on smaller phylogenetic clusters, these data can be added to the existing dataset and reanalysed. Our coding in mx is also dynamic, and we hope to score more taxa to continually improve our taxon sampling. As we continue to accumulate more genetic and morphological evidence, we expect to obtain a better understanding of the factors affecting the radiation and success of this hyperdiverse and economically invaluable group of insects.

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Appendix 1

List of specimens used in this study with Genbank accession numbers. Classification abbreviations (Abb.) referred to in cladograms and following Noyes (2011). OTU id refers to reference number in mx.

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
	Chalcidoidea							
AG	Agaonidae							
AGA	"Agaoninae"							
AGA		*Pleistodontes blandus*	10735	*Pleistodontes* nr *blandus*	ch	JN623045	JN623534	JN623865
AGA		*Waterstoniella* sp.	10923	*Waterstoniella* sp. nr *errata*	ch	GQ367635	GQ367737	GQ367830
AGB	"Blastophaginae"							
AGB		*Blastophaga psenes*	10829	*Blastophaga psenes*		GQ367602	GQ367703	GQ367799
AGK	Kradibiinae							
AGK		*Ceratosolen appendiculatus*	10830	*Ceratosolen appendiculatus*		GQ367597	GQ367698	GQ367794
AGT	Tetrapusinae							
AGT		*Tetrapus costaricanus*	10733	*Tetrapus ecuadoranus*	ch	GQ367663	GQ367761	GQ367857
AP	Aphelinidae							
APA	Aphelininae							
APAI	Aphelinini							
APAI		*Aphelinus* sp.	19955	*Aphelinus* sp.		JN623062	JN623550	JN623883
APAI		*Protaphelinus nikolskayae*	10717	n/a		n/a	n/a	n/a
APAY	Aphytini							
APAY		*Aphytis lingnanensis*	19958	*Aphytis lingnanensis*		JN623067	AY635333//AY640359	Missing
APAY		*Centrodora* sp.	19959	*Centrodora* sp. 6	ch	JN623072	JN623557	JN623888
APAY		*Marietta leopardina*	19956	*Marietta leopardina*		Missing	AY635299//AY640325	Missing
APAE	Eutrichosomellini							
APAE		*Eutrichosomella* sp.	10700	*Eutrichosomella* sp.	ch	JN623065	AY635293//AY640319	Missing
APAE		*Samariola camerounensis*	10714	*Samariola* sp.	ch	JN623066	JN623552	JN623892
APZ	Azotinae							
APZ		*Ablerus bharathius*	11220	*Ablerus* sp. 6	ch	JN623113	AY599328	JN623915
APZ		*Ablerus clisiocampae*	11210	*Ablerus clisiocampae*		JN623105	AY599322	Missing
APZ		*Ablerus* sp.	11221	*Ablerus* sp. 1		JN623108	AY599323	JN623912
APC	Coccophaginae							
APCC	Coccophagini							
APCC		*Coccophagus rusti*	6376	*Coccophagus rusti*		JN623081	AY599377	JN623898
APCE	Euxanthellini							
APCE		*Euxanthellus philippiae*	21458	*Euxanthellus philippiae*		Missing	JQ801691	JQ801691
APCY	Physcini							
APCY		*Coccobius fulvus*	6379	*Coccobius fulvus*		GQ410673	JN623558	JN623893
APCP	Pteroptricini							
APCP		*Coccophagoides moeris*	11529	*Coccophagoides fuscipennis*	ch	JN623080	AY599378	JN623897
APCP		*Encarsia adusta*	10711	*Encarsia cibcensis*	ch	Missing	AF254227//AY599404	Missing
APCP		*Encarsia bimaculata*	10710	*Encarsia bimaculata*		JN623087	AF254218//AY599395	Missing
APCP		*Encarsia citrina*	10719	*Encarsia citrina*		Missing	AF254236//AY599403	Missing
APCP		*Encarsia dispersa*	10729	*Encarsia guadeloupae*	ch	Missing	AF254193//AY599383	Missing
APCP		*Encarsia formosa*	10728	*Encarsia formosa*		Missing	AF223377//AY599387	Missing

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
APR	Eretmocerinae							
APR		*Eretmocerus eremicus*	20997	*Eretmocerus eremicus*		JN623063	AY599369	JN623889
APR		*Eretmocerus mundus*	20998	*Eretmocerus mundus*		Missing	AF273667//AF273665	Missing
APY	Eriaphytinae							
APY		*Eriaphytis chackoi*	8875	n/a		n/a	n/a	n/a
APO	Eriaporinae							
APO		*Promuscidea comperella*	10721	*Promuscidea unfasciativentris*	ch	JQ801684	JQ801697	JQ801698
APE	Euryischiinae							
APE		*Euryischia* sp.	20954	*Euryischia* sp.		JN623101	AY599368	Missing
APE		*Euryischomyia* sp.	20955	*Euryischomyia* sp.		JN623102	JN623567	JN623906
CH	Chalcididae							
CHC	Chalcidinae							
CHCB	Brachymeriini							
CHCB		*Brachymeria tibialis*	10605	*Brachymeria* sp. 4	ch	JN623126	JN623579	JN623925
CHCC	Chalcidini							
CHCC		*Chalcis myrifex*	10607	*Chalcis flebilis*	ch	JN623128	JN623582	JN623928
CHCC		*Conura flavicans*	10610	*Conura miniata*	ch	JQ801672	JQ801689	Missing
CHCC		*Conura immaculata*	10609	*Conura* sp. 1	ch	JN623133	JN623586	JN623933
CHCC		*Conura xanthostigma*	10614	*Conura* sp. 2	ch	JN623134	JN623587	JN623934
CHCC		*Melanosmicra variventris*	10608	*Melanosmicra variventris*		JQ801681	JQ801696	Missing
CHCR	Cratocentrini							
CHCR		*Acanthochalcis nigricans*	6384	*Acanthochalcis nigricans*		GQ410679	JN623592	JN623939
CHCR		*Cratocentrus decoratus*	10595	*Cratocentrus pruinosus*	ch	JN623139	JN623593	Missing
CHCP	Phasgonophorini							
CHCP		*Stypiura dentipes*	10600	*Stypiura* sp.	ch	JN623138	JN623591	JN623938
CHCP		*Trigonura algerti*	10611	*Trigonura californica*	ch	JN623140	JN623594	JN623940
CHD	Dirhininae							
CHD		*Dirhinus caerulea*	10616	*Dirhinus* sp. 2	ch	JN623142	JN623596	JN623941
CHD		*Dirhinus giffardii* coding 1	10615	*Dirhinus* sp. 5	ch	JN623145	JN623599	JN623944
CHD		*Dirhinus giffardii* coding 2		*Dirhinus* sp. 5	ch	JN623145	JN623599	JN623944
CHE	Epitraninae							
CHE		*Epitranus impulsator*	10617	*Epitranus* sp. 1	ch	JN623146	JN623600	JN623945
CHE		*Epitranus inops*	10618	*Epitranus* sp. 3	ch	JN623148	JN623602	JN623947
CHH	Haltichellinae							
CHHA	Haltichellini							
CHHA		*Belaspidia nigra*	10620	*Belaspidia nigra*		JQ801671	JQ801687	Missing
CHHA		*Haltichella rufipes*	10624	*Haltichella rufipes*		JQ801673	Missing	Missing
CHHA		*Hockeria bifasciata*	10623	*Hockeria* sp.	ch	JN623155	JN623610	JN623955
CHHA		*Lasiochalcidia dargelasii*	10625	*Lasiochalcidia dargelasii*		JQ801679	Missing	Missing
CHHA		*Neochalcis fertoni*	10622	*Neochalcis fertoni*		JQ801682	Missing	Missing
CHHY	Hybothoracini							
CHHY		*Irichohalticella* sp.	10636	*Irichohalticella* sp.		JN623157	JN623612	JN623957
CHHY		*Notaspidium giganteum*	10627	*Notaspidium* sp.	ch	JN623158	JN623613	JN623958
CHHY		*Psilochalcis subaenea*	10626	*Psilochalcis subaenea*		JQ801685	Missing	JQ801699
CHTR	Tropimeridini							
CHTR		*Tropimeris nr excavata*	10621	*Tropimeris* sp.	ch	JQ801686	JQ801701	JQ801701
CHS	Smicromorphinae							

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
CHS		*Smicromorpha doddi*	10606	*Smicromorpha* sp.	ch	JN623160	JN623615	JN623959
EN	Encyrtidae							
ENE	Encyrtinae							
ENE		*Acerophagus* nr *flavus*	18873	*Acerophagus* sp.	ch	JN623190	AY599309	JN623974
ENE		*Cheiloneurus flaccus*	6389	*Cheiloneurus fulvescens*	ch	JN623191	AY599308	Missing
ENE		*Cheiloneurus fulvescens*	10707	*Cheiloneurus fulvescens*		JN623191	AY599308	Missing
ENE		*Comperiella bifasciata*	18876	*Comperiella bifasciata*		JN623192	AY599317	Missing
ENE		*Copidosoma floridanum*	18875	*Copidosoma floridanum*		JN623193	AY599319	Missing
ENE		*Metaphycus luteolus*	18870	*Metaphycus* sp.	ch	JN623195	AY599310	JN623975
ENE		*Trechnites fuscitarsis*	10708	*Trechnites* sp.	ch	JN623198	AY599318	Missing
ENT	Tetracneminae							
ENT		*Anagyrus pseudococci*	10702	*Anagyrus nr. pseudococci*	ch	Missing	AY599315	Missing
ENT		*Savzdargia hofferi*	10699	*Savzdargia* sp.	ch	JN623203	JN623628	JN623979
EU	Eucharitidae							
EUA	Akapalinae							
EUA		*Akapala rudis*	10522	*Akapala rudis*		JN623320	AY672943	JN624066
EUE	Eucharitinae							
EUE	Eucharitini							
EUE		*Ancylotropus cariniscutis*	10535	*Ancylotropus cariniscutis*		JN623228	AY552239	JN624005
EUE		*Eucharis adscendens*	10541	*Eucharis adscendens*		Missing	AY672979	Missing
EUE		*Kapala floridana*	9177	*Kapala floridana*		JN623234	AY671849	Missing
EUE		*Lophyrocera pretendens*	21453	*Lophyrocera pretendens*		AY552304	AY552227	JN624009
EUE		*Pseudochalcura gibbosa*	10540	*Pseudochalcura prolata*	ch	Missing	GQ331918	GQ331918
EUE		*Pseudometagea schwarzii*	11222	*Pseudometagea schwarzii*		JN623242	AY552215	Missing
EUE	Psilocharitini							
EUE		*Neolosbanus palgravei*	10532	*Neolosbanus palgravei*		JN623236	AY552213	JN624010
EUE		*Psilocharis afra*	9005	*Psilocharis afra*		JN623243	AY552210	JN624014
EUG	Gollumiellinae							
EUG		*Anorasema pallidipes*	11223	*Anorasema pallidipes*		JN623250	AY552189	JN624019
EUG		*Gollumiella longipetiolata*	10524	*Gollumiella longipetiolata*		JN623252	AY552191	JN624020
EUO	Oraseminae							
EUO		*Indosema indica*	10525	*Indosema indica*		JN623253	JN623661	JN624021
EUO		*Orasema simulatrix*	10527	*Orasema simulatrix*		JN623259	AY552206	JN624027
EUO		*Timioderus acuminatus*	10596	*Timioderus peridentatus*	ch	JN623266	AY552195	JN624034
EL	Eulophidae							
ELE	Entedoninae							
ELE		*Chrysocharis* sp.	14217	*Chrysocharis* sp.	ch	JN623165	HM364911//HM364981	HM364981
ELE		*Dasyomphale chilensis*	14202	*Dasyomphale chilensis*		JN623167	HM364938//HM365008	HM365008
ELE		*Entedon sylvestris*	11240	*Entedon zanara*	ch	JN623168	JN623621	JN623964
ELE		*Euderomphale chelidonii*	11236	*Euderomphale* sp.	ch	JN623169	HM364961//HM365022	HM365022
ELE		*Neopomphale* sp.	14214	*Neopomphale* sp.		JN623170	HM364941//HM365011	HM365011
ELN	Entiinae							
ELN		*Bellerus* sp.	14201	*Bellerus* sp.		JN623176	HM364949//HM365014	HM365014
ELN		*Beornia* sp.	14204	*Beornia* sp.	ch	Missing	JQ801688	JQ801688
ELN		*Euderus* sp.	11239	*Euderus* sp.	ch	JN623177	AY599259//HM364969	Missing
ELU	Eulophinae							
ELU		*Cirrospilus coachellae*	6377	*Cirrospilus coachellae*		GQ410672	AY599268	JN623968

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
ELU		*Elasmus polistis*	11237	*Elasmus polistis*		JN623182	AY599264	JN623969
ELU		*Eulophus* sp.	11241	*Eulophus* sp.	ch	JN623183	JN623623	JN623970
ELU		*Euplectrus bicolor*	12153	*Euplectrus* sp.	ch	JN623184	HM364953//HM365017	HM365017
ELU		*Pnigalio mediterraneus*	11672	*Pnigalio* sp.	ch	JN623187	AY599279//HM364965	HM364965
ELU		*Pnigalio* sp.	14207	*Pnigalio* sp.		JN623187	AY599279//HM364965	HM364965
ELU		*Zagrammosoma americanum*	14206	*Zagrammosoma americanum*		JN623189	AY599263//HM364968	HM364968
ELI	*Incertae sedis*							
ELI		*Trisecodes agromyzae*	14205	*Trisecodes agromyzae*		JN623171	HM364964//HM365025	HM365025
ELO	Opheleminae							
ELO		*Ophelimus maskelli*	11242	*Ophelimus maskelli*	ch	JN623172	HM364944//HM365012	HM365012
ELO		*Perthiola mazaneci*	20953	*Pertioloa mazaneci*		JN623185	JN623624	JN623971
ELT	Tetrastichinae							
ELT		*Aprostocetus hibus*	11238	*Aprostocetus* sp.	ch	JN623179	AY599265//HM364966	HM364966
ELT		*Crataepus marbis*	14211	*Crataepus marbis*		Missing	AY599262//HM365021	JN623967
ELT		*Hadrotrichodes waukheon*	14203	*Hadrotrichodes waukheon*		JN623180	HM364959//HM365020	HM365020
ELT		*Melittobia acasta*	11235	*Melittobia digitata*	ch	Missing	U02951	U02951
ELT		*Minotetrastichus frontalis*	21226	*Minotetrastichus frontalis*		Missing	D2753	D2753
EP	Eupelmidae							
EPC	Calosotinae							
EPC		*Archaeopelma* sp.	10679	*Archaeopelma tropeotergum*	ch	Missing	JN623630	JN623980
EPC		*Balcha indica*	10666	*Balcha* sp.	ch	JN623204	JN623631	JN623981
EPC		*Calosota metallica*	10674	*Calosota* sp.	ch	JN623205	JN623632	JN623982
EPC		*Eusandalum cyaneum*	10667	*Eusandalum* sp. 1	ch	JN623206	JN623633	JN623983
EPC		*Licrooides umbilicatus*	10675	*Licrooides umbilicatus*		JN623209	JN623636	JN623986
EPE	Eupelminae							
EPE		*Anastatus floridanus* female	10689	*Anastatus* sp.	ch	JN623210	JN623637	JN623987
EPE		*Anastatus floridanus* male	10690	*Anastatus* sp.	ch	JN623210	JN623637	JN623987
EPE		*Arachnophaga eucnemia* female	10695	*Arachnophaga eucnemia*		JN623211	JN623638	JN623988
EPE		*Arachnophaga eucnemia* male	10696	*Arachnophaga eucnemia*		JN623211	JN623638	JN623988
EPE		*Brasema allynii* female	10693	*Brasema* sp.	ch	JN623212	AY599306	JN623989
EPE		*Brasema allynii* male	10694	*Brasema* sp.	ch	JN623212	AY599306	JN623989
EPE		*Eupelmus urozonus* female	10687	*Eupelmus* sp.	ch	JN623215	AY599307	JN623992
EPE		*Eupelmus urozonus* male	10688	*Eupelmus* sp.	ch	JN623215	AY599307	JN623992
EPE		*Phenaceupelmus chilensis* female	10691	n/a		n/a	n/a	n/a
EPE		*Phenaceupelmus chilensis* male	10692	n/a		n/a	n/a	n/a
EPN	Neanastatinae							
EPN		*Lambdobregma* sp.	10680	n/a		n/a	n/a	n/a
EPN		*Metapelma spectabile*	10681	*Metapelma* sp. 2	ch	JN623225	JN623650	JN624002
EPN		*Neanastatus* sp.	10682	*Neanastatus* sp. 2	ch	JN623227	JN623652	JN624004
EY	Eurytomidae							
EYB	Buresiinae							
EYB		*Buresium rufum*	10638	*Buresium naso*	ch	JN623270	JN623669	JN624036
EYB		*Macrorileya* sp.	10639	*Macrorileya* sp.		JQ801680	Missing	JQ801695
EYE	Eurytominae							
EYE		*Aiolomorphus rhopaloides*	14196	*Aiolomorphus rhopaloides*		JN623268	JN623667	JN624035
EYE		*Axima zabriskiei*	21339	n/a		n/a	n/a	n/a
EYE		*Bephrata ruficollis*	10646	n/a		n/a	n/a	n/a

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
EYE		*Bruchodape ignota*	10645	n/a		n/a	n/a	n/a
EYE		*Endobia donacis*	10644	*Endobia donacis*		JQ801674	JQ801690	JQ801690
EYE		*Eurytoma gigantea*	6378	*Eurytoma gigantea*		GQ410671	JN623670	JN624037
EYE		*Masneroma angulifera*	20864	*Masneroma angulifera*		JN623275	JN623673	Missing
EYE		*Sycophila texana*	14198	*Sycophila texana*		JN623277	JN623675	Missing
EYE		*Systole albipennis*	21250	*Systole coriandri*	ch	JN623278	JN623676	Missing
EYE		*Tetramesa* sp.	21251	*Tetramesa* sp. 1	ch	JN623279	AY599281	Missing
EYH	Heimbrinae							
EYH		*Heimbra opaca*	20860	*Heimbra opaca*		JN623281	JN623678	JN624038
EYR	Rileyinae							
EYR		*Austrophotismus daicles*	14197	*Austrophotismus daicles*		JN623282	JN623679	Missing
EYR		*Neorileya flavipes*	20861	*Neorileya* sp.	ch	JQ801675	JQ809471	JQ809471
EYR		*Rileya longitergum*	14199	*Rileya grisselli*	ch	JN623284	JN623681	JN624039
EYR		*Rileya pallidipes*	10631	*Rileya pallidipes*		JN623286	AY599298	JN624041
LEU	Leucospidae							
LEU		*Leucospis affinis*	10603	*Leucospis affinis* (a)		JN623290	AY599276	Missing
LEU		*Micrapion* sp.	11226	*Micrapion* sp.		JN623296	JN623689	JN624049
MY	Mymaridae							
MYA	Alaptinae							
MYA		*Anagrus epos*	9134	*Anagrus epos*		JN623299	JN623692	JN624051
MYA		*Litus cynipseus*	9133	*Litus cynipseus*		JN623300	JN623693	JN624052
MYA		*Stethynium ophelimi*	9129	*Stethynium ophelimi*		JN623301	JN623694	JN624053
MYE	Eubroncinae							
MYE		*Eubroncus* sp.	9137	*Eubroncus* sp. 2		JN623303	JN623696	Missing
MYI	*Incertae sedis*							
MYI		*Borneomymar discus*	21242	*Borneomymar madagascar*	ch	JN623304	AY599254	JN624054
MYM	Mymarinae							
MYM		*Acmopolynema varium*	6387	*Acmopolynema varium*		JN623305	AY599251	JN624055
MYM		*Anaphes* sp.	9127	*Anaphes victus*		JN623306	JN623697	JN624056
MYM		*Australomymar* sp.	6381	*Australomymar* sp.	ch	GQ410668	JN623698	JN624057
MYM		*Ceratanaphes* sp.	9128	*Ceratanaphes* sp.		JN623307	AY599252	JN624058
MYM		*Erythmelus rosascostai*	9126	*Erythmelus rosascostai*		JN623308	JN623699	JN624059
MYM		*Gonatocerus ashmeadi*	6380	*Gonatocerus ashmeadi*		JN623309	JN623700	JN624060
MYM		*Gonatocerus* sp.	10642	*Gonatocerus triguttatus*	ch	JN623310	AY599253	JN624061
MYM		*Mymar regale*	9135	*Mymar regale*		JN623311	JN623701	JN624062
MYM		*Ooctonus* sp.	9131	*Ooctonus* sp.		JN623312	JN623702	Missing
ORM	Ormyridae							
ORM		*Ormyrulus* sp.	10650	*Ormyrulus* sp.		JN623316	JN623706	JN624064
ORM		*Ormyrus rosae*	10649	*Ormyrus* sp. 1	ch	JN623317	JN623707	JN624065
PE	Perilampidae							
PEC	Chrysolampinae							
PEC		*Austrotoxeuma* sp.	9147	*Austrotoxeuma* sp.		JN623322	AY552187	JN624068
PEC		*Brachyelatus* sp.	9148	*Brachyelatus* sp.		JN623321	AY552184	JN624067
PEC		*Chrysolampus schwarzi*	9149	*Chrysolampus schwarzi* (a)		JN623325	AY672937	Missing
PEC		*Chrysolampus* sp.	9152	*Chrysolampus* sp. 3		JN623329	AY672939	Missing
PEC		*Chrysomalla hesperis*	9155	*Chrysomalla hesperis*		JN623330	AY672940	Missing
PEI	*Incertae sedis*							

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
PEI		*Jambiya vanharteni*	10543	*Jambiya vanharteni*		JN623331	JN623711	JN624071
PEP	Perilampinae							
PEP		*Euperilampus triangularis*	9158	*Euperilampus triangularis*		JN623338	AY552174	Missing
PEP		*Monacon robertsi*	11479	*Monacon roberstsi*		JN623340	JN623716	JN624078
PEP		*Perilampus hyalinus*	9160	*Perilampus hyalinus*		JN623344	AY552179	JN624081
PEP		*Perilampus subcarinatus*	9162	*Perilampus subcarinatus*		JN623353	AY552175	JN624087
PEP		*Perilampus tristis*	6395	*Perilampus subcarinatus*	ch	JN623353	AY552175	JN624087
PEP		*Steffanolampus salicetum*	9163	*Steffanolampus salicetum*		JN623354	AY552177	JN624088
PEM	Philomidinae							
PEM		*Aperilampus* sp.	10570	*Aperilampus* sp.	ch	JN623332	AY672941	JN624072
PEM		New Genus sp.	20927	Philomidinae new genus		JN623334	AY672942	JN624074
PEM		*Philomides* sp.	20949	*Philomides* sp.		JN623333	JN623712	JN624073
PT	Pteromalidae							
PT01	Asaphinae							
PT01		*Asaphes* sp.	6388	*Asaphes suspensus*	ch	JN623355	JN623727	JN624089
PT01		New Genus sp.	14018	Asaphinae new genus		JN623356	JN623728	JN624090
PT26	Austrosystasinae							
PT26		*Austrosystasis atricorpus*	14248	n/a		n/a	n/a	n/a
PT02	Ceinae							
PT02		*Spalangiopelta apotherisma*	11488	*Spalangiopelta apotherisma*		JN623358	JN623730	JN624092
PT03	Cerocephalinae							
PT03		*Acerocephala* sp.	14019	*Acerocephala* sp.		JN623360	JN623731	JN624094
PT03		*Neocalosoter* sp.	14020	*Neocalosoter* sp.		JN623362	JN623733	Missing
PT04	Chromeurytominae							
PT04		*Chromeurytoma* sp.	6391	*Chromeurytoma* sp.	ch	JN623363	JN623734	JN624096
PT05	Cleonyminae							
PT05D	Chalcedectini							
PT05D		*Chalcedectus* sp.	13975	*Chalcedectus* sp.		JN623365	JN623736	JN624098
PT05C	Cleonymini							
PT05C		*Callocleonymus* sp.	14165	*Callocleonymus* sp.		JN623364	JN623735	JN624097
PT05C		*Cleonymus* sp.	6366	*Cleonymus* sp.	ch	GQ410678	AY599278	JN624099
PT05L	Lyciscini							
PT05L		*Agamerion cleptideum*	14031	*Agamerion cleptideum*		JN623367	AY599287	JN624101
PT05L		*Epistenia* sp.	13974	*Epistenia* sp.		JN623368	AY599282	Missing
PT05L		*Proshizonotus* sp.	14030	*Proshizonotus* sp.		JN623371	JN623738	JN624104
PT05O	Ooderini							
PT05O		*Oodera* sp.	13972	*Oodera* sp.		JN623372	JN623739	JN624105
PT06	Coelocybinae							
PT06		*Lanthanomyia* sp.	13984	*Lanthanomyia* sp.		JN623374	JN623741	JN624107
PT06		*Ormyromorpha* sp.	13976	*Ormyromorpha* sp.		JN623375	JN623742	JN624108
PT06		*Yrka* sp.	10569	*Yrka* sp.	ch	JN623376	JN623743	JN624109
PT07	Colotrechninae							
PT07		*Colotrechnus ignotus*	10660	*Colotrechnus ignotus*		JN623377	JN623744	JN624110
PT08	Cratominae							
PT08		*Cratomus* sp.	20867	*Cratomus megacephalus*	ch	JN623379	JN623746	JN624112
PT09	Diparinae							
PT09D	Diparini							

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
PT09D		*Lelaps* sp.	13977	*Lelaps* sp.		JN623381	AY599280	Missing
PT09D		*Netomocera* sp.	14028	*Netomocera* sp.		JN623383	JN623749	JN624115
PT09D		*Parurios* sp.	13809	*Dipara* sp.		JN623380	JN623747	JN624113
PT09N	Neapterolelapini							
PT09N		*Neapterolelaps* sp.	14029	*Neapterolelaps* sp. 1		JN623385	JN623751	JN624117
PT09N		*Neapterolelaps* sp. female	10662	*Neapterolelaps* sp. 2	ch	JN623386	JN623752	JN624118
PT09N		*Neapterolelaps* sp. male	10663	*Neapterolelaps* sp. 2	ch	JN623386	JN623752	JN624118
PT27	Ditropinotellinae							
PT27		*Ditropinotella* sp.	14246	n/a		n/a	n/a	n/a
PT10	Epichrysomallinae							
PT10		*Neosycophila* sp.	11208	*Neosycophila* sp. 1		JN623406	JN623772	JN624138
PT10		*Odontofroggatia galili*	11207	*Odontofroggattia ishii*	ch	JQ801683	HM770696	HM770696
PT10		*Sycobia* sp.	11209	*Sycobia* sp.		JN623411	JN623777	JN624143
PT11	Eunotinae							
PT11E	Eunotini							
PT11E		*Cephaleta* sp.	14027	*Cephaleta sp.*		JN623414	JN623780	JN624146
PT11E		*Eunotus* sp.	6392	*Eunotus* sp. 1	ch	JN623415	AY599295	Missing
PT11E		*Eunotus* sp.	14026	*Eunotus* sp. 2		JN623416	JN623781	JN624147
PT11E		*Idioporus affinis*	6393	*Idioporus affinis*		JN623417	Missing	JN624148
PT11E		*Scutellista caerulea*	10549	*Scutellista caerulea*		JN623418	AY599294	Missing
PT11M	Moranilini							
PT11M		*Moranila californica*	6394	*Moranila* sp.	ch	JN623419	JN623783	JN624149
PT11T	Tomocerodini							
PT11T		*Tomocerodes* sp.	13982	*Tomocerodes* sp.		JN623420	JN623784	JN624150
PT12	Eutrichosomatinae							
PT12		*Collessina pachyneura*	14247	n/a		n/a	n/a	n/a
PT12		*Eutrichosoma mirabile*	10612	*Eutrichosoma mirabile*		JN623421	AY599286	JN624151
PT12		*Peckianus* sp.	14160	n/a		n/a	n/a	n/a
PT13	Herbertiinae							
PT13		*Herbertia* sp.	14021	*Herbertia* sp.		JN623422	JN623785	JN624152
PTI	*Incertae sedis*							
PTI	Lieparini							
PTI		*Liepara* sp.	14209	*Liepara* sp.		JN623382	JN623748	JN624114
PT28	Keiraninae							
PT28		*Keirana longicollis*	14164	n/a		n/a	n/a	n/a
PT14	Leptofoeninae							
PT14		*Doddifoenus wallacei*	8758	*Doddifoenus wallacei*		JN623423	JN623786	JN624153
PT14		*Leptofoenus stephanoides*	10656	*Leptofoenus* sp. 1	ch	JN623424	AY599283	JN624154
PT14		*Leptofoenus westwoodi*	10659	*Leptofoenus* sp. 2	ch	JN623425	AY599284	JN624155
PT15	Macromesinae							
PT15		*Macromesus americanus*	14158	*Macromesus americanus*		JN623426	JN623787	JN624156
PT16	Miscogastrinae							
PT16M	Miscogastrini							
PT16M		*Lamprotatus splendens*	11478	*Lamprotatus splendens*		JN623429	JN623790	JN624159
PT16M		*Nodisoplata* sp.	14159	*Nodisoplata* sp.		JN623438	JN623798	JN624169
PT16M		*Sphaeripalpus* sp.	14156	*Sphaeripalpus* sp.		JN623430	JN623791	JN624160
PT16S	Sphegigastrini							

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
PT16S		*Cyrtogaster vulgaris*	11487	*Cyrtogaster vulgaris*		JN623432	JN623792	JN624162
PT16S		*Halticoptera dimidiata*	11484	*Halticoptera laevigata*	ch	JN623427	JN623788	JN624157
PT16S		*Polstonia pelagocorypha*	10546	*Polstonia pelagocorypha*		JN623433	AY552173	JN624163
PT16S		*Thinodytes cyzicus*	11492	*Thinodytes* sp.	ch	JN623431	AY552172	JN624161
PT16T	Trigonoderini							
PT16T		*Plutothrix* sp.	13978	*Plutothrix* sp.		Missing	JN623794	JN624165
PT17	Ormocerinae							
PT17I	*Incertae sedis*							
PT17I		*Erixestus* sp.	13981	*Erixestus* sp.		JN623478	JN623832	JN624205
PT17M	Melanosomellini							
PT17M		*Aditrochus cohiuensis*	13971	*Aditrochus coihuensis*		JN623435	JN623795	JN624166
PT17M		*Espinosa nothofagi*	13970	*Espinosa nothofagi*		JN623436	JN623796	JN624167
PT17M		*Systolomorpha* sp.	10580	*Systolomorpha* sp.		JN623437	JN623797	JN624168
PT17S	Systasini							
PT17S		*Semiotellus* sp.	13983	*Semiotellus* sp.		JN623439	JN623799	JN624170
PT17S		*Systasis* sp.	13969	*Systasis* sp.	ch	Missing	JQ801700	Missing
PT18	Otitesellinae							
PT18		*Heterandrium* sp.	11217	*Heterandrium* sp.		JN623442	JN623802	JN624173
PT18		*Walkerella kurandensis*	11219	n/a		n/a	n/a	n/a
PT19	Panstenoninae							
PT19		*Panstenon oxylus*	11490	*Panstenon oxylus*		JN623444	JN623805	JN624176
PT19		*Panstenon* sp.	10665	*Panstenon* sp.	ch	JN623445	JN623804	JN624175
PT20	Pireninae							
PT20		*Gastrancistrus* sp.	13968	*Gastrancistrus* sp.		JN623446	AY599293	Missing
PT20		*Macroglenes gramineus*	13967	*Macroglenes* sp.		JN623447	JN623806	JN624177
PT21	Pteromalinae							
PTI	*Incertae sedis*							
PTI		*Diconocara petiolata*	13980	*Diconocara petiolata*		JN623455	JN623813	JN624184
PT21M	Micradelini							
PT21M		*Micradelus rotundus*	21032	n/a		n/a	n/a	n/a
PT21P	Pteromalini							
PT21P		*Cheiropachus quadrum*	11504	*Cheiropachus quadrum*		JN623451	JN624260	JN624260
PT21P		*Coelopisthia extenta*	11480	*Coelopisthia extenta*		JN623452	JN623810	JN624181
PT21P		*Coruna clavata*	11481	*Coruna clavata*		JN623453	JN623811	JN624182
PT21P		*Habritys brevicornis*	11483	*Habritys brevicornis*		JN623456	JN623814	JN624185
PT21P		*Homoporus luniger*	11485	*Homoporus* sp.	ch	JN623457	JN623815	JN624186
PT21P		*Merisus splendidus*	11493	*Merisus splendidus*		JN623459	JN623817	JN624188
PT21P		*Nasonia vitripennis*	6382	*Nasonia vitripennis*		GQ410677	JN623821	JN624192
PT21P		*Pegopus inornatus*	11491	*Pegopus* sp.	ch	JN623460	JN623818	JN624189
PT21P		*Perilampidea syrphi*	14157	*Perilampidea* sp.	ch	JN623461	JN623819	JN624190
PT21P		*Pseudocatolaccus nitescens*	11500	*Pseudocatolaccus guizoti*	ch	JN623462	AY552171	Missing
PT21P		*Pteromalus nr albipennis*	14162	*Pteromalus albipennis*		JN623465	AY552170	JN624193
PT22	Spalangiinae							
PT22		*Spalangia endius*	14161	*Spalangia erythromera*	ch	JN623466	JN623822	JN624194
PT22		*Spalangia nigroaenea*	10661	*Spalangia nigroaenea*		JN623467	JN623823	JN624195
PT23	Sycoecinae							
PT23		*Diaziella* sp.	11218	*Diaziella* sp.		JN623469	JN623825	JN624197

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
PT24	Sycophaginae							
PT24		*Anidarnes bicolor*	11203	*Anidarnes* sp.	ch	JN623470	JN623826	JN624198
PT24		*Apocryptophagus gigas*	11205	*Apocryptophagus gigas*		JQ801670	HM770698	HM770698
PT24		*Eukoebelea australiensis*	11206	*Eukobelea* sp.		JN623471	HM770667	HM770667
PT24		*Pseudidarnes minerva*	11202	*Pseudidarnes* sp.	ch	JN623474	JN623828	JN624201
PT24		*Sycophaga cyclostigma*	11204	*Sycophaga sycomori*	ch	JN623475	JN623829	JN624202
PT25	Sycoryctinae							
PT25		*Philotrypesis* sp.	11216	*Philotrypesis* sp.		JN623476	JN623830	JN624203
PT25		*Sycoscapter* sp.	11215	*Sycoscapter* sp.		JN623477	JN623831	JN624204
ROT	Rotoitidae							
ROT		*Chiloe micropteron*	6390	*Chiloe micropteron*		GQ410669	JN623834	JN624206
ROT		*Rotoita basalis*	20856	n/a		n/a	n/a	n/a
SI	Signiphoridae							
SIS	Signiphorinae							
SIS		*Signiphora* sp.	21257	*Signiphora* sp. 3		JN623481	AY599343	Missing
SIT	Thysaninae							
SIT		*Chartocerus* sp.	21256	*Chartocerus* sp. 1 (a)		JN623488	AY599336	JN624212
SIT		*Clytina giraudi*	21244	*Clytina giraudi*		JN623495	JN623835	JN624218
SIT		*Thysanus ater*	10676	*Thysanus* sp. 3	ch	JN623498	AY599354	JN624220
TAN	Tanaostigmatidae							
TAN		*Cynipencyrtus flavus*	10556	*Cynipencyrtus* sp.	ch	JN623500	JN623836	JN624222
TAN		*Protanaostigma* sp.	14219	*Protanaostigma* sp.		JN623501	JN623837	JN624223
TAN		*Tanaostigmodes howardii*	10703	*Tanaostigmodes albiclavus* (a)	ch	JN623503	AY599304	Missing
TE	Tetracampidae							
TEM	Mongolocampinae							
		Eremocampe sp.	21296	*Eremocampe* sp.		JN623506	AY599356	JN624225
		Mongolocampe bouceki	20857	n/a		n/a	n/a	n/a
		Platyneurus sp.	21335	n/a		n/a	n/a	n/a
TEP	Platynocheilinae							
TEP		*Platynocheilus cuprifrons*	20858	*Platynocheilus cuprifrons*		JN623507	JN623838	JN624226
TET	Tetracampinae							
TET		*Diplesiostigma* sp.	21334	*Diplesiostigma bisetosum*	ch	JN623508	JN623839	Missing
TET		*Epiclerus temenus*	21227	*Epiclerus* sp. 1	ch	JN623509	AY599357	Missing
TET		*Foersterella reptans*	6383	*Foersterella reptans*		JN623511	AY599360	JN624227
TET		*Tetracampe* sp.	21294	*Tetracampe* sp.	ch	JN623512	JN623840	JN624228
TO	Torymidae							
TOM	Megastigminae							
TOM		*Bootanelleus* sp.	10697	*Bootanelleus* sp.		TOOSHORT	JN623841	JN624229
TOM		*Bortesia* sp.	21249	*Bortesia* sp.		JQ801677	JQ801693	JQ801693
TOM		*Megastigmus transvaalensis*	6385	*Megastigmus transvaalensis*		GQ410676	JN623843	JN624232
TOM		*Neomegastigmus* sp.	21248	*Neomegastigmus* sp.		JQ801676	JQ801692	JQ801692
TOT	Toryminae							
TOTC	Chalcimerini							
TOTC		*Chalcimerus borceai*	21243	*Chalcimerus borceai*		JQ801678	JQ801694	JQ801694
TOTI	*Incertae sedis*							
TOTI		*Echthrodape* sp.	10732	*Echthrodape* sp.		JN623516	JN623845	JN624234
TOTI		*Glyphomerus stigma*	10677	*Glyphomerus stigma*		JN623518	JN623847	JN624236

Appendix 1 (*Continued*)

Abb.	Classification	Morphological OTU	OTU id in Mx	Molecular OTU	Chimeras	GenBank accession numbers		
						18S	28S-D2D3	28S-D4D5
TOTM	Microdontomerini							
TOTM		*Eridontomerus arrabonicus*	10706	*Eridontomerus arrabonicus*		Missing	JN623848	JN624237
TOTM		*Idarnotorymus pulcher*	10730	*Idarnotorymus pulcher*		JN623520	JN623851	JN624240
TOTM		*Pseuderimerus burgeri*	10715	*Pseuderimerus burgeri*		JN623521	JN623852	JN624241
TOTN		*Monodontomerus montivagus*	10716	*Monodontomerus* sp.	ch	JN623523	JN623855	JN624243
TOTP	Palachiini							
TOTP		*Propalachia borneana*	10713	*Propalachia borneana*		Missing	JN623856	JN624244
TOTO	Podagrionini							
TOTO		*Podagrion* sp.	10683	*Podagrion* sp.	ch	JN623524	AY599269	JN624251
TOTT	Torymini							
TOTT		*Torymus bedeguaris*	10722	*Torymus bedeguaris*		Missing	JN624256	JN624256
TOTY	Torymoidini							
TOTY		*Pseudotorymus sapphyrinus*	10726	*Pseudotorymus sapphyrinus*		Missing	JN624254	JN624254
TR	Trichogrammatidae							
TRO	Oligositinae							
TROO	Oligositini							
TROO		*Oligosita sanguinea*	14133	*Oligosita sanguinea*		JN623530	AY623551	Missing
TRT	Trichogrammatinae							
TRTT	Trichogrammatini							
TRTT		*Trichogramma pretiosum*	14132	*Trichogramma pretiosum*		AY940359	AY599408	Missing
TRTI		*Trichogrammatini incertae sedis*						
TRTI		*Ceratogramma etiennei*	11527	*Ceratogramma masneri*	ch	AY940340	AY623492	Missing
TRTI		*Haeckeliania sperata*	14131	*Haeckeliania* sp. 2	ch	AY940343	AY623497	Missing
CAL	Calesinae *incertae sedis*							
CAL		*Cales berryi*	20999	*Cales berryi*		JN623119	AY599257	JN623920
CAL		*Cales noacki*	6375	*Cales noacki*		JN623121	JN623574	JN623921
	Non Chalcidoidea							
	Proctotrupoidea							
	Diapriidae							
	Belytinae							
		Belyta sp.	6398	*Belyta* sp.	ch	JN623118	JN624258	JN624258
	Mymarommatoidea							
	Mymarommatidae							
		Mymaromella chaoi	20995	*Mymaromella mira*		GQ410666	GQ374773	GQ374773
		Mymaromma sp.	6386	*Mymaromma* sp.		JN623313	JN623703	Missing
	Platygastroidea							
	Scelionidae							
	Scelioninae							
		Archaeoteleia mellea	6397	*Archaeoteleia mellea*		GQ410639	GQ374746	GQ374746

Appendix 2

Abbreviations for morphology

ab	Articulating bulb	HAO_0001704
acr	Acropleuron	HAO_0001155
acs	Antecostal sulcus	HAO_0000099
aed	Aedeagus	HAO_0000091
ax	Axilla	HAO_0000155
btc	Basitarsal comb	HAO_0001180
btn	Basitarsal notch	HAO_0000177
br	Bridge of second valvifer	HAO_0001780
cer	Cercus	HAO_0000191
clm	Pronotal collum (neck)	HAO_0000837
col	Pronotal collar	HAO_0000832
cps	Coeloconic peg sensillum	HAO_0002001
cs	Coeloconic sensillum	HAO_0000213
cx1, 2, 3	Pro-, meso- metacoxa	HAO_0000228
cxf	Supracoxal flange	No url assigned
dc2	Mesodiscrimineal line	HAO_0000545
dig	Digitus	HAO_0000385
dv	Dorsal valve (second valvula)	HAO_0001658
ep2	Mesepimeron	HAO_0000299
epn	Epimeral notch	HAO_0002006
esg	Epistomal groove	HAO_0000306
F1–12	Flagellomeres 1–12	HAO_0000342
f2p	Mesofurcal pit	HAO_0000549
f3p	Metafurcal pit	HAO_0000594
fra	Frenal arm	HAO_0001903
frl	Frenal line	HAO_0000354
frn	Frenum	HAO_0000355
gc	Genal carina	HAO_0001755
hyc	Hypostomal carina	HAO_0000413
lb	Laminated bridge of ovipositor	HAO_0001548
lbp	Labial palp	HAO_0000450
lbr	Labrum	HAO_0000456
lcl	Lateral clypeal line	No url assigned
lep2	Lower mesepimeron	HAO_0000299
llm	Lateral lobe of mesoscutum	HAO_0000466
los	Lower ocular sulcus	HAO_0000299
mfm	Metafemur	HAO_0001140
mlm	Median lobe of mesoscutum	HAO_0000575
mls	Malar sulcus	HAO_0000504
mms	Median mesoscutal sulcus	HAO_0000523
MPS	Multiporous plate sensillum	HAO_0000640
Ms6	Female hypopygium	HAO_0000410
Ms8	Male hypopygium	HAO_0000410
msp	Mesothoracic spiracle	HAO_0000582
mss	Mesosternal shelf	HAO_0001647
Mt	Metasomal tergite	HAO_0002005
Mt8 + 9	Syntergum	HAO_0000987
mtp	Mesotrochantinal plate	HAO_0000543
mtps	Metaplerual sulcus	No url assigned
mts	Metascutellum	HAO_0000625
mtsp	Metathoracic spiracle	HAO_0000769
mtsa	Metanotal scutellar arm	No url assigned
mtsp	Metasomal spiracle	No url assigned
mxp	Maxillary palp	HAO_0000515
no1	Pronotum	HAO_0000853
no3	Metanotum	HAO_0000603
not	Notaulus	HAO_0000647
occ	Occipital carina	HAO_0000653
ov	Ovipositor	HAO_0000679
par	Paramere	HAO_0000395
pgg	Postgenal groove	HAO_0002019

pgl	Postgenal lamina	HAO_0002020
2ph	Mesophragma	HAO_0000558
pl1	Propleuron	HAO_0000862
pl3	Metapleruon	HAO_0001271
pmr	Posterior marginal rim of metascutellum	No url assigned
pnb	Pronotal bristle	No url assigned
pom	Postoral microtrichia	HAO_0000532
pop	Postoccipital plate	No url assigned
pre	Prepectus	HAO_0000811
prp	Propodeum	HAO_0000051
psc	Parascutal carina	HAO_0000697
psp	Propodeal spiracle	HAO_0000329
ptl	Petiole	HAO_0000020
ptla	Petiolar lamina	HAO_0002018
ptr	Paratergite	No url assigned
rad	Radicle	HAO_0000889
rmd	Right mandible	HAO_0000506
s1	Prosternum	HAO_0000873
sap	Sternal apodemes	HAO_0002007
sas	Subantennal sulcus	HAO_0000965
scp	Scapular flange	HAO_0001680
scr	Scrobe	HAO_0000912
scs	Scrobal sulcus	HAO_0001679
sct	Mesoscutellum	HAO_0000574
sss	Scutoscutellar sulcus	HAO_0000919
tfs	Transfacial sulcus	HAO_0002016
tgl	Tegula	HAO_0001508
tor	Torulus	HAO_0001022
tsa	Transscutal articulation	HAO_0001204
uep2	Upper mesepimeron	HAO_0000299
uos	Upper ocular sulcus	No url assigned
3v	Third valvula	HAO_0001012
2vf	Second valvifer	HAO_0000927
vos	Vertical ocellar sulcus	HAO_0002022
vv	Ventral valve (first valvula)	HAO_0000339
Wing abbreviations		
ams	Admarginal setae	No url assigned
bc	Basal cell	No url assigned
bpl	Basal posterior lobe	No url assigned
bv	Basal vein	HAO_0000736
C	Costal vein	HAO_0000225
cc	Costal cell	HAO_0000226
Cu	Cubital vein	HAO_0000237
dm	Dorsal macrochaeta	No url assigned
hb	Hyaline break	No url assigned
hpl	Humeral plate	HAO_0000403
hy	Hypochaeta	No url assigned
M	Medial vein	HAO_0000519
mv	Marginal vein	HAO_0000512
pmv	Postmarginal vein	HAO_0000783
pst	Parastigma (premarginal vein)	No url assigned
psts	Parastigmal sensilla	No url assigned
R	Radial vein	HAO_0000783
2r	Second radial crossvein	No url assigned
r-m	Radio-medial crossvein	No url assigned
Rs	Radial sector vein	No url assigned
Sc	Subcubital vein	No url assigned
smb	Submarginal break	No url assigned
smv	Submarginal vein	HAO_0000972
stg	Stigma	No url assigned
stv	Stigmal vein	No url assigned

HAO terms are detailed in Hymenoptera Anatomy Ontology (http://purl.obolibrary.org/obo/).