The morphological diversity of Mymaridae (Hymenoptera): an atlas of scanning electron micrographs. Part 2. Structure of the mesosoma

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Abstract

This is the second in a series of studies that aim to provide a comprehensive overview of the morphological diversity of Mymaridae (Hymenoptera) or fairyflies, a monophyletic family of small parasitic wasps postulated to be the sister group of all other Chalcidoidea. The external morphology of the mesosoma of about 65–75 taxa, representing 55–65% of the 115 currently valid described genera and subgenera, is described and illustrated with almost 269 scanning electron micrographs, including 77 micrographs of the dorsal, 71 micrographs of the lateral, 59 micrographs of the ventral, 53 micrographs of the anterior, and 9 micrographs of the posterior views of the mesosoma. Twenty annotated figures of the external and major internal structures are given. Two appendices list the morphological terms used, and names of the 75 genera and subgenera of Mymaridae illustrated. The variety of characters and their features that could be used to help define morphologically the genera, and possibly also the species, of Mymaridae is discussed.

Keywords: morphology, terminology, fairyflies

Introduction

Huber et al. (2023) treated the head and mouthparts as the first paper on external morphology of Mymaridae (Hymenoptera) illustrated with scanning electron micrographs. The present paper is on the external morphology of the mesosoma, again using micrographs to illustrate at least one species for ~65–75 of the ~115 currently recognized valid extant genera and subgenera of Mymaridae. Those illustrated cover most of the morphological diversity in the family because at least one genus of all the tribes or clusters of similar genera so far proposed is included. Structures not usually treated in taxonomy of Mymaridae, e.g., the ventral, anterior and posterior surfaces of the mesosoma, may well yield new morphological features that could be useful to include in generic or perhaps even species descriptions, thus helping to distinguish the taxa. Terms used in the text are illustrated (Figs 1–14), mostly following Burks et al. (unpublished) for Chalcidoidea in general. Krogmann and Vilhelmsen (2006) treated the mesosomal skeleton of Chalcidoidea and Vilhelmsen et al. (2010) provided an overview of the structural diversity and phylogenetic significance of the mesosoma in Apocrita. Both of these papers give context to the present paper, which is restricted mostly to external features of the mesosoma for Mymaridae, the most ancestral family of Chalcidoidea, sister group to all the remaining families (Heraty et al. 2013).

Material and methods

The methods described in Huber et al. (2023) apply to this paper as well. They tabulated all the valid fairyfly genera and subgenera and, for the taxa illustrated, their provenance. We refer the reader to that paper to avoid repetition but include an abbreviated version of their generic list here; it lists only the genera and subgenera illustrated in the present paper (Appendix 2). Most specimens were micrographed by K. Bolte between 1998 and 2004, using
the preparation method he described (Bolte 1997). The gold coated specimens are preserved on metal stubs in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Ottawa, Canada. Uncoated specimens of some genera were micrographed by J. Read from 2006–2016, using an environmental scanning electron microscope and the pinned specimens on triangular card points were returned to the collections in which they belong (usually the CNC). The number of genera illustrated varies, depending on structure and view. As much as possible only one species per genus was illustrated, usually from female specimens.

Depending on the structure and view the morphological terms and their abbreviations used here are limited mainly to those used in taxonomic papers on Mymaridae but updated where necessary to follow those used in the morphology chapter of a forthcoming treatment of Chalcidoidea (unpublished). Morphology of internal sclerotized parts of the mesosoma—the pro-, meso- and metfurca, and the pro- and mesophragma—to may vary though no study was undertaken by us to determine if useful taxonomic features occur there. However, three photographs (Figs 15b, 16b, 17b) are included to show these internal structures; another three (Figs 15a, 16a, 17a) show surface structures for comparison with the micrographs.

The micrographs are grouped alphabetically by genus for each view in the following order: dorsal, lateral, ventral, anterior, posterior. To see all the mesosoma views completely, the head must be removed for its anterior view (D1–D54) and the metasoma must be removed for its posterior view (E1–E9). Because these two views are rarely examined and used by taxonomists they are shown at the end of the micrographs. Because the head often partly conceals the pronotum, its removal allows mesosoma length to be measured accurately. Sometimes it may be best to measure mesosoma length from the anterior apex of the mesoscutum instead because it is rigid whereas the pronotum is flexible (depending on genus) and loosely attached to the mesonotum. Mesoscutal length is measured medially from the anterior margin of the mesoscutum to the transscutal articulation. Width of either the mesosoma or the mesoscutum is measured across the mesoscutum at its widest point between the lateroposterior angles of the lateral areas just anterior to the tegulae. Mesosoma height in lateral view is more difficult to measure accurately, but it is best made from the level of about the midpoint of the mesoscutellum to the level of about the posterior apex of the mesopleuron (these end points are rarely directly above each other). For accurate measurement of the pronotum in species with a distinct neck, the head may have to be removed to expose the anterior pronotal margin. Because this is destructive, an absolute measurement is rarely used; instead, the pronotal median length relative to the mesonotal median length is used.

Figure letter/number combinations, e.g. A1, B2, are used for the different views to distinguish them from the introductory figures with the structures named (Figs 1–17). For brevity in the text, the genera mentioned are followed by the relevant figure without stating each time “Fig. or Figs”, e.g., (Acmopolynema-A1) instead of (Acmopolynema, Fig. A1), except for the 17 figures with acronyms of structures mentioned in the text and listed in Appendix 1. Not every genus has all views; a separate number is given for every genus and subgenus but the same number with different letters, e.g., B25a,b, is given for different species or different sexes within the same genus or subgenus.

The description of a given structure is not necessarily the same for all species in a given genus or subgenus. Only a few specimens of one or, occasionally, two or three species of a genus were micrographed. Intraspecific variation may occur but as far as we know no exceptional or aberrant specimens were micrographed so the structures shown should be fairly representative for a given genus. Among the genera of Mymaridae the mesosoma shows considerable variation, perhaps more so than in other families of Chalcidoidea that have appeared more recently in the geological record.

Appendages of the mesosoma are not treated in this paper, even though useful diagnostic features occur on them. For the most part, wings and legs are best illustrated with photographs (light microscopy). Length measurements and proportions of the different leg segments, particularly of the tarsi are the simplest to obtain and may be useful to help define genera, and sometimes the species within a genus, e.g., Anaphes (Huber & Thuróczy 2018). Length, number and distribution of leg setae may also sometimes be useful to identify genera, e.g., species of Narayanella Subba Rao have long setae along the length of the metatibia. Huber (2015) published photographs and micrographs of legs of two species of Cosmocomoidea Howard, which may reveal the kinds of characters that could be studied. Other useful taxonomic features on legs are the number and distribution of the peg-like setae on the protibia and differences, among some genera at least, in the calcar and strigil. Details of wing venation, such as distribution of setae and campaniform sensilla on the veins are best illustrated with line drawings, perhaps supplemented with photographs or micrographs, as was done for Trichogramma Westwood (Pinto 1998).
Results

MESOSOMA (general)

The mesosoma is a sclerotized box (Goulet & Huber 1993, fig. 1) with rounded corners and eight openings—one anteriorly and posteriorly for attachment of the head and metasoma, respectively, and six ventrally for attachment of the three pairs of legs. Soft tissues (nerves, muscles, haemolymph) pass through these openings. The mesosoma dimensions range from long, slender, with length ~5.0× width and ~4.7× height (Erdosiella-A25a, B25b) to short and high, with length ~1.0× width and ~0.9× height (Dicopomorpha-A21a,b, Dicopomorpha (Dicopus)-A22).

The mesosoma (Figs 1–17) consists of four parts: prothorax, mesothorax, metathorax, and propodeum. The prothorax consists of the pronotum, visible dorsally (A1–A77) and laterally (B1–B72), the propleura, visible ventrolaterally (C1–C59), and the prosternum, visible ventromedially (D1–D53); the pronotum and propleura, and often the prosternum are also visible anteriorly (D1–D53). The mesothorax consists of the mesoscutum, mesoscutellum, and axillae, all visible dorsally (A1–A77) and dorsolaterally (B1–B72), and the prepectus and mesopectus, visible laterally (B1–B71) and ventrally (C1–C60). The metathorax consists of the metanotum, visible dorsally (A1–A77) and dorsolaterally (B1–B72), and the metapleuron, visible laterally (B1–B72), and the lower metepisternum, visible ventrally (C1–C59); these lateral + ventral parts together form the metapectus. The propodeum, visible dorsally A1–A77), laterally (B1–B72), and posteriorly (E1–E8) is undivided.

PROTHORAX

Pronotum. Structure. The pronotum (Figs 1–4: no.) consists of a median panel that merges more or less distinctly into each lateral panel; the border between median and lateral panels is indistinct anteriorly but posteriorly is considered to be at the level of the spiracle. In addition to being separated from the lateral panels by a more or less abrupt change in curvature, a line of setae (Acmopolynema-D1, Palaeoneura-D38, Palaeoneura (Chaetonymar)-D39, Stephanodes-D50a,b), and/or change in sculpture (Narayanella-D32) may occur. The pronotum is almost always shorter than the mesoscutum. In dorsal view (A1–A78) the posterior margin of the pronotum is more or less concave, closely following the contour of the convex anterior margin of the mesoscutum, with the lateral panels (best seen in lateral view) extending to just posterior of the spiracle. The pronotum is appressed tightly (Agalmopolynema-A2, Ischiodasys-A36, Pitomymar-A66) or loosely (Anaphes-A6, Arescon-A8) against the mesoscutum. If tightly appressed, its posterior margin often slightly overlaps the anterior margin of the mesoscutum (Boudiennyia-A10, Ceratanaphes-A14, Yoshimotoana-A76); if loosely appressed, it sometimes appears slightly separated from it (Anaphes-A6, Neostethynium-A47, B46); the slight separation of pronotum from mesoscutum may, however, be an artefact of critical point drying the specimens. Medially, the median panel of the pronotum is short, vertical and scarcely visible (Alaptus-A3a,b, Anagroidea-A4, Anaphes-A6, Arescon-A8, Tanyxiphium-A73a) or long and clearly visible (Acmopolynema-A1, Cneocomymar-A17). The median panel in dorsal or anterior views (D1–D53), is undivided, i.e., entire (Anagrus-D5, Anaphes-D6, Boudiennyia-D9, Camptopteroides-D12, Chysoctonus-D14, Ooctonus-D37, Stephanocampta-D49, Yoshimotoana-D53) or divided medially. When the median panel is divided, it is by a longitudinal sulcus (Anagroidea-D4, Ceratanaphes-A14, D13, Cleruchus-A16, Gastrogonatocerus-A33, Parastethynium-A58, Schizophragma-D47), or by a carina that is complete (Acmopolynema-D1, Palaeoneura (Chaetonymar)-A56, D39, Polyneura-D43, Tetrapolynema-A74) or incomplete (Mymar-A44, D31), or by two submedian longitudinal sulci or carinae that delimit a median membranous or sclerotized area. The two lobes of the median panel usually abut medially for more (Acmopolynema-D1, Kalopolynema-D27) or less (Anneckia-D7, Erythmelus-D21, Erythmelus (Parallelaptera)-D22) than their greatest length but sometimes the lobes are clearly separated by a membranous area (Lymaneura-D29, Tanyxiphium-D52) or, rarely, a sclerotized plate (Ptilomymar-D45, Stephanodes-D50a,b). Sometimes the submedian area of the median panel is noticeable only by a slight change in elevation or sculpture and very weakly indicated by submedian and converging sulci (Omyomymar (Chaetonymar)-D39). Rarely, the median panel is divided transversely by a distinct carina into a longer anterior neck and shorter posterior collar (Figs 1, 2, Boudiennyia-B10). Whether or not the median panel is mediolongitudinally divided, it is almost always shorter medially than laterally (where the median panel merges more or less abruptly into the lateral panels). If divided, the shape of each lobe is distinctly triangular because their
junction is short (Camptoptera-D11, Eustochus-D24, Macrocamptoptera-D30) or more rectangular because the junction is long (Acmopolyneuma-D1, Anagroidea-D4, Narayanella-D32, Stethynium-D52).

In lateral view (B1–B71), the median panel is almost horizontal (Erdsiella (Tanaomymar)-B25a, Narayanella-B44, Tetrapolynema-B70, Yoshimotoana-B71) to vertical (Anaphes-B6, Lymaenon-B41, Pitomymar-B62) but sometimes it is vertical in one sex (Tanyxiphium female-B69a) and more horizontal in the other (Tanyxiphium male-B69b). The pronotum slopes ventrally to its anterior margin where it is sometimes more or less reflexed dorsally (Anaphes-B6, Boudiennyia-B10, Eustochus (Caraphractus)-B31). It is strongly convex (Australomymar-B9) to flat (Anagrus-B5). The median panel merges laterally, more or less smoothly, into a vertical lateral panel, which is usually more or less triangular (Camptoptera-B12, Platyrans-B57, Stephanocampta-B66) to fusiform (Callodicopus, B11) and about 3× as long as high at about the level of the spiracle (Anaphes-B6, Kalopolyneuma-B37, Stephanocampta-B66) to almost as high as long (Eustochus (Caraphractus)-B31). Exceptionally, the lateral panel of the pronotum is higher than long, trapezoidal and apparently rigidly connected to the mesopleuron (Ptilomymar-B62). The lateral panel almost always has a depression of variable width for reception of the foreleg when the foreleg is appressed against the mesosoma. In anterior or lateral views, the depression is shallow and indistinct (Anagrus-B5, D5, Camptoptera-B12, Chrysocotonus-D14, Cleruchus-B16, Eustochus-B30, Macrocamptoptera-D30) to deep and distinct (Agalopolyneuma-B2, D2, Anaphes-B6, Boudiennyia-B10, Ceratanaphes-B14, Pseudanaphes-D44). It is usually oblique (Anaphes-B6, Ischiodyasys-B36), sometimes horizontal (Agalopolyneuma-A2, Cneomymar-A17, Kalopolyneuma-B37) or almost vertical (Alaptus-B3, Eustochus (Caraphractus)-B31). When the depression is vertical or apparently absent, the femur may instead be appressed in the depression between the posterior margin of the pronotum and the prepectus (Dicopomorpha-B22a,b, Omyomymar-B50). Rarely, the depression is narrow and along the ventral margin of the lateral panel (Ptilomymar-B62, Stephanocampta-B66).

In anterior view, in genera with the pronotum not medially divided, the posterior (dorsal) margin is almost straight (Camptopteroides-D12, Litus-D28, Ooctonus-D37), somewhat concave between the notaui (Stephanocampta-D49), slightly sinuate (Acmopolyneuma-D1, Anaphes-D6) or slightly convex (Yoshimotoana-D53). In genera with a divided pronotum, the posterior margin in anterior view is narrowly or widely concave (Oticomicromeris-D35) to more or less deeply notched, V-like (Anneckia-D7). The median length is thus almost as long as (Anagrus-D5, Anaphes-D6, Yoshimotoana-D53) to much shorter than (Anneckia-D7, Stephanocampta-D49) the sublateral length. The anterior (ventral) margin is more or less Π-shaped with a narrow or wide dorsal apex and the ventral apices of the lateral arms more (Eustochus-D24, Stethynium-D52) or less (Ptilomymar-D45, Stephanocampta-D49) widely separated. The gap ventral and medial to the Π is occupied by the propleura.

**Sculpture.** Rarely, the pronotum is completely smooth (Cneomymar-B17, D15, Kraterisbe-B39) but even if the rest of the pronotum appears smooth there is at least some sculpture dorsally on the lateral panel, often as a longitudinal strip anterior or ventral to the spiracle (Acmopolyneuma-B1, D1, Agalopolyneuma-B2, D2, Neomymar-B45, Palaeoneura (Chaetomymar)-D39, Polynema-D43, Polynema (Doriclytus)-B58). Otherwise, the pronotum is fairly uniformly covered with often faint sculpture, rarely engraved (Gonatocerus-D25) but usually slightly (Camptoptera-D11, Stephanocampta-D49) to distinctly (Anagroidea-D4, Litus-D28, Richteria-D46, Stethynium-D52) raised. The scutellars are isometric (Anagroidea-D4, Ooctonus-D37, Yoshimotoana-D53) to elongate, either more or less vertically (Alaptus-D3, Callodicopus-D10, Omyomymar-D36, Tanyxiphium-D52) or more or less horizontally (Anaphes-D6, Boudiennyia-D9, Erythmelus-D21, Ptilomymar-D45).

**Setation.** Usually at least four pairs of setae occur, apparently always on the median panel. If only 4 setae are present, the posterior pair is usually longer, more widely spaced and more lateral, and the anterior pair is shorter, closer together and more median (Tanyxiphium-D52). Rarely, only the posterior pair appears to be present (Litus-D28, Stephanocampta-D49). Often, additional pairs occur, arranged in various ways (Acmopolyneuma-D1, Ceratanaphes-D13, Neomymar-D33, Palaeoneura-D38, Platyrans-D42). The setae are short, fine, and inconspicuous (Cosmocomoidea-D16, Litus-D28) and apically pointed to long, thick and conspicuous (Entricopteris-D20, Neomymar-D33, Palaeoneura (Chaetomymar)-D39) and often apically truncate.

**Mesothoracic spiracle.** The mesothoracic spiracle (Figs 2–4: msp) appears to be part of the pronotum as it is surrounded anteriorly, ventrally, posteriorly and sometimes narrowly dorsally by pronotal cuticle. In lateral view (B1–B61) the spiracle is clearly visible on the lateral panel of the pronotum, dorsal or anterodorsal to the dorsal apex of the prepectus, usually fairly close to it (Acmopolyneuma-B1, Neomymar-B45, Palaeoneura (Chaetomymar)-B54), far from it (Ptilomymar-B62) and, rarely, almost as far as the anterior apex of the notaui (Eustochus (Caraphractus)-B31, Stephanodes-B67a,b). The spiracle is usually oval, with the opening slightly below, slightly above, or more or
less flush with the surface of the surrounding cuticle (*Lymaenon*-B41) but sometimes it is at the apex of a short tube above the surface (*Cneomymyar*-B17, *Neomymar*-B45). The spiracle opening is small but the surrounding cuticular rim or area may be large (*Eustochus* (*Caraphractus*)-B31, *Ptilomymar*-B62).

**Propleura. Structure.** The *propleura* are visible in ventral view (C1–C60) or, if the head is removed, in anterior view (D1–D54). In ventral view a *propleuron* (Figs 5–8; pl.) is somewhat triangular or lozenge-shaped and distinctly wider posteriorly than anteriorly (*Alaptus*-C3, *Anagroidea*-C4, *Eustochus*-C27, *Eustochus* (*Caraphractus*)-C28, *Yoshimotoana*-C59) to oval or fusiform and as wide or not much wider or sometimes slightly narrower posteriorly than anteriorly at the anterior apex of the prosternum (*Agalmopolynema*-C2, *Ceratanaphes*-C14, *Anagrus*-C5, *Gastrogonatocerus*-C29, *Lymaenon*-C34, *Stethynium*-C57). The medial margin is usually straight or almost so for its entire length along the prosternum (*Cneomymyar*-C17, *Kalopolynema*-C32, *Stephanodes*-C56a,b) or concave anteriorly (*Octonus*-C42, *Polynema* (*Doriclytus*)-C49, *Polynema* (*Restisoma*)-C50, *Ptilomymar*-C51, *Richteria*-C52) or slightly convex (*Erdosiella* (*Tanaomymar*)-C23, *Gonatocerus*-C30). The medial margins together are either parallel for most of their length except posteriorly (*Alaptus*-C3, *Boudiennyia*-C10, *Camptopteroideis*-C13, *Eustochus* (*Caraphractus*)-C28) or, most often, convergent anteriorly, forming a more or less acute angle (*Acnopolyrena*-A1, *Anaphes*-C6, *Steganogaster*-C54) where they meet just anterior to the anterior apex of the prosternum. The circular gap that allows passage of soft internal structures (muscles, nerves, etc.) from head to mesosoma is surrounded by the anterior parts of the propleura that converge ventral to the gap, then again dorsal to the gap (Fig. 7). The propleura usually have a slightly thickened rim where they border the gap. Anteriorly, the propleura are sometimes completely separated by a gap occupied by the anterior apex of the prosternum (*Alaptus*-C3, *Dicopomorpha* (*Dicopulus*)-C20, *Dicopus*-C21, *Kalopolynema*-C32, *Macrocamptoptera*-C35, *Parastethynium*-C46). More often, the propleura meet anterior to the prosternum where their junction is short (*Acnopolyrena*-C1, *Anagrus*-C5, *Camptoptera*-C12, *Erythmelus*-C24, *Palaeoneura*-C43, *Schizophragma*-C53), longer (*Arescon*-C8, *Ptilomymar*-C51) or very long (*Boudiennyia*-C10, *Eubroncus*-C26, *Eustochus*-C27, *Octonus*-C42, *Yoshimotoana*-C59). The latter two states correspond with those taxa having parallel medial margins for much of their length except posteriorly where the margins diverge abruptly (*Eustochus* (*Caraphractus*)-C28), sometimes at a right angle (*Eubroncus*-C26, *Ptilomymar*-C51).

**Sculpture.** The propleura are sometimes completely smooth or apparently so (*Cremnomymar*-C19, *Entrichopteris*-C22, *Palaeoneura*-C43, *Polynema*-C43, *Stephanodes*-C56a,b). If sculpture is present, it almost always is similar to that on the pronotum. It is engraved, with the sculpticells transverse (*Alaptus*-C3) or, more often, longitudinal (*Gonatocerus*-C30, *Lymaenon*-C34) or raised, with the sculpticells isodiametric or almost so (*Anaphes*-C6, *Eustochus* (*Caraphractus*)-C28, *Macrocamptoptera*-C35, *Omyomymar*-C40, *Octonus*-C42), transversely striate (*Camptoptera*-C12, *Camptopteroideis*-C13) or longitudinally striate (*Schizophragma*-C53, *Stethynium*-C57). If the propleura and prosternum are removed the dorsolongitudinal flight muscles are visible, attached anteriorly to the double-arched prophragma (*Litus*-C33).

**Setation.** Usually, each propleuron has one seta, usually closer to the medial than the lateral margin (*Lymaenon*-C34, *Omyomymar*-C40). Rarely, there are two (*Octonus*-C42, *Polynema*-C44) or more (*Richteria*-C52) setae.

is sometimes thickened (Callodicopus-C11, Dicopomorpha (Dicopus)-C20, Kalopolynema-C32) and/or the lateral margins are thickened, at least in part (Eustochus (Caraphractus)-C28, Kalopolynema-C32, Ptilomymar-C51). Rarely, the posterior margin is thickened (Ptilomymar-C51, Richteria-C52). Profurcal pits (Fig. 6: fp) are sometimes visible between the procoxae, either as a single large median pit (Eustochus-C27, Stephanodes-C56a) or two smaller submedian pits (Neomymar-C37, Platytrois-C47, Polyomna-C43, Polynema (Doriclytus)-C49) sometimes connected by a transverse sulcus (Palaeoneura (Chaetomymar)-C44); rarely, the pits are minute (Yoshimotoana-C59).

Sculpture. If sculpture is present, it usually matches that on the propleura, but is frequently absent or apparently so (Agalpolynema-C2, Alaptus-C3, Anagrostis-C5, Cneomymar-C17, Neomymar-C37, Tetrapolynema-C58). When present it is more or less faintly engraved (Anneckia-C7, Australomymar-C10, Lymaenon-C34) or more or less raised (Anagroidea-C4, Anaphes-C6, Camptoptera-C12, Ceratanaphes-C14, Omyomymar-C40, Ooctonus-C42), with the sculpticells isodiametric (Ooctonus-C42) or longitudinal (Omyomymar (Caenomymar)-C41a, Ptilomymar-C51) or transverse (Ceratanaphes-C14).

Setation. Rarely, the prosternum is apparently asetose (Erythmelus-C24, Erythemus (Parallelaptera)-C25, Gonatocerus-C30) but usually there is at least one pair of setae (Alaptus-C3, Omyomymar-C40, Schizophragma-C53) and often two or more pairs (Acimopolyemna-C1, Boudienfya-C10, Cneomymar-C17, Polynema (Doriclytus)-C49, Stephanodes-C56a,b); rarely, almost the entire prosternum is setose (Steganogaster-C54).

MESOTHORAX

Mesoscutum. Structure. The mesoscutum (Figs 1, 2: msc) is almost always divided by notaui into a median mesoscutal midlobe (Figs 1, 3, 4, 8: mlm) and, on each side, a lateral mesoscutal lateral lobe (Figs 1, 3, 4, 8: ltm). The mesoscutum is separated posteriorly from the mesocutellum by the transverse transscutal articulation (Figs 1–3: ts). In dorsal view, the three lobes together are wider than long (Acimopolyemna-A1, Anaphes-A6, Cremnomyemna-A20, Dicopomorpha-A21a,b) or, rarely, longer than wide (Arescon-A8). The posterior margin of the mesoscutal midlobe is distinctly wider than the posterior margin of the mesoscutal lateral lobe (Alaptus-A3a,b, Callodicopus-A11, Camptoptera-A12, Dicopomorpha-A21a,b, Dicopomorpha (Dicopus)-A22, Stethynium-A72) to distinctly narrower than a lateral lobe (Cneomymar-A17, Mymar-A44, Erdosella-A25a).

Each notaual (Figs 1–3: not) is a longitudinal sulcus that extends from or almost from the anterior margin of the mesoscutum to the transscutal articulation. The anterior apex of a notaual is distinctly anterior to the position of the mesothoracic spiracle. The two notaui usually converge slightly posteriorly to the transscutal articulation though rarely they are almost parallel (Dicopomorpha-A21a,b). They are usually narrow and distinct (Acimopolyemna-A11, Anaphes-A6, Neotriadomerus-A48, Sthethynium-A72); rarely wide (Neomymar-A46, Palaeoneura-A56) to very wide and distinct (Tetrapolynema-A74) or wide but indistinct (Australomymar-A9). Sometimes, the notaui are barely visible externally (Cosmocomopsis-A19, Gahanopsis-A32, Gastroganotocerous-A33, Gonatocerus-A34, Steganogaster-A69) or are shallow depressions indicated only by a slight change in sculpture (Eustochus-A30, Eustochus (Caraphractus)-A31) or not even that (Tanyxiphium-A73a,b). Sometimes a notaual ends as a distinct, usually circular pit a short distance from the anterior margin of the mesonotum (Acimopolyemna-A11, Agalpolynema-A2, Kalopolynema-A37, Palaeoneura-A55, Palaeoneura (Chaetomymar)-A56, Platytrois-A59); occasionally, the pit is lengthened and curved, comma-like (Entrichopteris-A24, Mymar-A44) or continues to the anterior margin as a short, fine sulcus (Neomymar-A46). Usually, the notaui posteriorly are straight and anteriorly either curve outward (Ooctonus-A54, Yoshimotoana-A76) or are straight (Palaeoneura-A55, Palaeoneura (Chaetomymar)-A56, Polyemna (Restisoma)-A62, Schizophragma-A68). Exceptionally, the notaui are slightly sinuate (Alaptus-A3a,b, Camptoptera-A12, Litus-A41) with both the anterior and posterior apices curved, outward and inward, respectively, or are entirely absent (Dicopomorpha-A21c) or apparently absent (Ptilomymar-A66). In lateral view, the mesoscutum posteriorly is usually almost flat (Eustochomorpha-B28) to slightly convex and anteriorly more strongly convex (Ooctonus-B52, Paracmotemnus-B55) but sometimes it is almost entirely flat (Chrysoctonus-B16, Entrichopteris-B24, Erdosella (Tanaomymar)-B25a, Erdosella-25b, Mymar-B43, Narayanaless-B44) to strongly and evenly convex (Australomymar-B9, Eustochus-B30, Eustochus (Caraphractus)-B31). In anterior view, the median and lateral lobes together usually form a low and evenly convex arch (Acimopolyemna-D1, Camptopteroides-D12, Ischiodasys-D26, Tanyxiphium-D52); sometimes the median and lateral lobes appear as three slightly convex arches (Anagrostis-D5, Anaphes-D6, Richteria-D46).
Sculpture. Microsculpture is rarely completely absent (Stephanodes, A71a,b). When present, it is engraved and often indistinct (Lymaenon-A42, Mymar-A44, Polyneuma (Doriclytus)-A61) to raised and distinct (Anagroidea-A4, Eustocho-A30, Eustocho (Caraphractus)-A31, Litus-A41, Polyneuma (Restiosoma)-A62). The sculpticells are more or less isodiametric (Anagroidea-A4, Macrocamptoptera-A43), or partly or entirely stretched longitudinally (Anagrus-A5, Arescon-A8, Erythmelus-A26, Schizophragma-A68) or transversely (Camptoptera-A12) or both (Callicolopus-A11).

Setation. Usually one, more or less prominent adnotaular seta (Fig. 3: ans) occurs on the mesoscutal midlobe near each notalus, near the posterior margin (Gahanopsis-A32, Litus-A41, Stethynium-A72), about midway between anterior and posterior margins (Dicopomorpha-A21a,b) or closer to the anterior margin (Arescon-A8, Lymaenon-A42); adnotaular setae are sometimes absent (Acmopolynema-A1, Cneecomymar-A17, Mymar-A44, Platyriones-A59, Polyneuma (Doriclytus)-A61). Exceptionally, two or more adnotaular setae occur (Steganogaster-A69). A lateral mesoscutal seta, sometimes truncate apically (Cneecomymar-A17), is always present at the posterolateral corner of the lateral lobe.

Mesoscutellar-axillar complex. Structure. The mesoscutellum + axillae together form the mesoscutellar-axillar complex (Figs 1, 2: sac), which consists of the mesoscutellar disc (Figs 1–4: setd) [anterior scutellum, of authors] medially, the axilla (Figs 1–4: ax) anterolaterally and the axillula (Figs 1–4: axi) laterally, and the frenum (Figs 1–4: fre) [posterior scutellum, of authors] posteriorly. The mesoscutellar disc is separated from the axillula by a sharp angle, the axillular carina (Figs, 1, 2: axcl). It is separated from the frenum by the frontal line (Fig. 1: frl), which is sometimes a distinct transverse sulcus (Alaptus-A3a,b, Anagus-A5, Dicopomorpha-A21a,b, Dicopus-A23, Parastethynium-A58, Schizophragma-A68, Stethynium-A72, Tinkerella-A75) or a straight or curved row of punctures (Acmopolynema-A1, Camptopteroides-A13, Erdosiesta-A25a, Eustocho-A30, Kalopneuma-A37) or a fine sulcus (Heptonagonocerus-A35), or a slight change in elevation (Neotriamorsus-A48) and/or a change in sculpture (Anagroidea-A4, Australomymar-A9, Dicopomorpha (Dicopus))-A22, Litus-A41, Macrocamptoptera-A43, Ooctonus-A54, Yoshimotawa-A76) or only by a slight change in sculpture (Cosmocomoidea-A18, Cosmocomopsis-A19, Eustocho (Caraphractus)-A31, Mymar-A44, Zeyanus-A77) or the frontal line is apparently absent (Boudienyllia-A10). The mesoscutellar disc is shorter than (Krateriske-A39, Lymaenon-A42, Proagonocerus-A64, Schizophragma-A68, Stethynium-A72), about as long as (Alaptus-A3a,b, Anagroidea-A4, Australomymar-A9, Chrysoconus-A15, Dicopus-A23, Kiki-A38, Krokella-A40) or, rarely, much longer than the frenum (Eustochochomera-A28, Palaeoneura-A55, Palaeoneura (Chaeotonymar)-A56, Richteria-A67, Stephanodes-A71a,b). Occasionally, the frenum is longitudinally divided by a median sulcus (Anagrus-A5, Kiki-A38, Krokella-A40, Oomyommar-A52, Schizophragma-A68, Stethynium-A72). Internally, so only exceptionally visible in micrographs, the position of the campaniform sensilla (Alaptus-A3a,b, Dicopomorpha (Dicopus))-A22, Krokella-A40, Lymaenon-A42, Parastethynium-A58, Tanyxiphium-A73a,b) relative to each other and the edges of the mesoscutellar disk, and the size and shape of the fenestra (Fig. 14) provide useful features to help characterize the genera. The axilla is lateral to the mesoscutum and separated from it by the scutocutellar suture (Fig. 1: sss). The axilla consists of a more or less horizontal triangular panel dorsally (the axilla proper), separated laterally by a change in angle and often by a sinuate axillar carina (Figs, 1, 2: axcl) from the almost vertical lateral panel of the axilla (Figs 1–4: lpa); the axillar carina continues posteriorly along the ventral edge of the axillula to the mesoscutal arm (Figs, 1, 2) posterior to the axillula. The carina is distinct (Anaphes-A6, B6, Nepolyommar-A49, Palaeoneura-A55, Steganostrum-A69) to indistinct or apparently absent (Alaptus-A3a,b, B3, Dicopomorpha-A21a,b, B21a,b). The axilla is small (Acmopolynema (Alaptyrus), Mymar-A44, Narayannella-A45, Nepolyommar-A49) to large (Alaptus-A3a,b, Anagroidea-A4, Boudiennyia-A10, Erythmelus-A26, Stephanocampta-A70, Zeyanus-A77). The axilla usually does not project anteriorly or, if it does, projects only slightly so its anterior margin (which forms the posterior margin of the lateral lobe of the mesoscutum) is in line with the transscutal articulation (Acmopolynema-A1, Anagroidea-A4, Eustocho-A30, Notoymmar-A50, Proaescon-A63, Tinkerella-A75, Yoshimotawa-A76). Sometimes the axilla strongly projects anteriorly so its anterior margin forms a sharp angle with the transscutal articulation (Alaptus-A3a,b, Anagrus-A5, Arescon-A8, Litus-A41, Stephanocampta-A70), before curving laterally to the mesoscutal margin anterior to the tegula (Figs 1, 2, tl). Occasionally, the anterior margin of the axilla is slightly posterior to the transscutal articulation and ends just posterior to the tegula (Stephanodes-A71a,b). The anterior margin of the axilla is straight or almost so (Acmopolynema-A1, Cleruchus-A16, Kalopolynema-A37, Notomymmar-A50, Yoshimotawa-A76) or more or less curved (Oomyommar-A52, Ooctonus-A54, Stethynium-A72, Zeyanus-A77). The axillula sometimes had a deep pit anterodorsally (Polyneuma (Doriclytus)-B58, Pseudanaphes-
B61), medioventrally (Paracotonemus-A57, Platysfer-A59) or posteroventrally (Ooctonus, Fig. 2). Sculpture. If the mesoscutellum is not obviously divided transversely (and sometimes even if it is divided) the sculpture, if any, on the posterior part (frenum) is the same as or similar to that on the anterior part (mesoscutellar disc and axillula) (Acromyomymar-A1, Agalmapolynema-A2, Anaphes-A6, Cleruchus-A16, Dicopus-A23, Gahanopsis-A32, Gonatocerus-A34, Platysfer-A59, Zeyanus-A77); otherwise it may often be very different (Alaptus-A3a,b, Anagroidea-A4, Dicopomorphora-A21a,b, Litmus-A41, Schizophragma-A68, Yoshimotona-A76). The frenal sculpture almost always is apparently absent or, if present, engraved or raised as on the mesoscutellum but it is sometimes more well defined and prominent (Alaptus-A3a,b, Dicopomorpha-A21a, Ooctonus-A54, Pitilomyomar-A66, Stephanocampta-A70, Tetrapolynema-A74, Yoshimotona-A76). The frenal sculpture is sometimes more stretched longitudinally compared to that on the mesoscutellum (Litmus-A41, Oomyomymar-A52, Parastethynium-A58, Stethynium-A72). Some sculpture is present on one or both (Anagroidea-A4) axillary panels and may be faint or distinct, if on one it may be either the lateral panel (Australomymar-B9) or the axilla (Polynema (Doriclytus)-B58). Rarely, the axilla is smooth (Mymar-A44, Neomyomar-A46, Stephanodes-A71a,b). Even if there is no apparent sculpture on the mesoscutellum at least one panel of the axilla will have some sculpticells.

Setation. A mesoscutellar seta occasionally occurs laterally on the mesoscutellar disc; this is not to be confused with the seta on the axilla, which is almost always present. The frenum is asetose. A minute, inconspicuous seta is on the lateral panel of the axilla. The axilla has a longer seta, sometimes extremely long (Neomyomar-A46, B45, Palaeomyomar (Chaetomyomar)-A57, B54).

Mesophragma. This phragma is visible only in cleared slide-mounds (Figs 15, 16: 2ph), unless the metasoma has been broken off in specimens in which the phragma projects into the metasoma (Litmus-A41). It does not extend into the metasoma in species with a narrow petiole (Cleruchus, Erythmelus, Gonatocerus, Ooctonus, Mymar) but it often extends more or less into the metasoma in species with a short and wide petiole (Alaptus, Anagrus, Callidicus, Litus, Neostethynium). Its apex is narrowly (Platypatasson, Stethynium) or widely rounded (Litmus-A41), truncate (Dicopus, Oomyomar) or more or less indented medially (Oomyomar, Schizophragma).

Prepectus. Structure. The prepectus (Figs 2, 4–6: pre) in lateral view is almost always visible (at least in cleared slide mounts) between the posterior margin of the lateral panel of the pronotum and the anterior margin of the mesoposterior, and in ventral view (procoxae must be removed to see this) it abuts the anterior margin of the mesepisternum. Exceptionally, an external prepectus is absent and the pronotum is rigidly associated with the mesopleuron (Ptilomyomar-B62), which led Gibson (1986) to hypothesize that its apparent absence is most likely the result of secondary fusion of the prepectus to the pronotum. In the other genera, the lateral panel of the prepectus is triangular (Acromyomymar-B1, Cneomymar-B17, Eurombros-B29, Eustochus-B30, Eustochus (Caraphractus)-B31, Narayanella-B44, Palaeoneura (Chaetomyomar)-B54), somewhat fusiform to narrowly rectangular (Anagrus-B5, Anaphes-B6, Enrichicoterresis-B24, Heptagonatocerus-B35, Kalopanemima-B37, Litmus-B40, Richteria-B63, Stephanodes-B67a,b), or linear (Chrysotoxotus-B15a,b, Gonatocerus-B34, Ischiodaysis-B36, Ooctonus-B52, Steganogaster-B65) and, in micrographs, barely or not visible externally (Alaptus-B3, Anagroidea-B4, Callicodorus-B11, Camiptoptera-B12, Dicopomorpha-B21a,b, Litmus-B40). In ventral view, the ventral panel of the prepectus is as long as the lateral panel, about half the length of the mesepisternum (Agalmapolynema-C2, Cremomyomar-C19, Platysfer-C47), to short and linear (Anagroidea-C4, Chrysotoxotus-C15, Macrocamptoptera-C35) and either continuous between the lateral panels or discontinuous, divided ventromedially by a more or less wide gap (Eustochus-C27, Ooctonus-C42, Richteria-C52, Stethynium-C57), which apparently may be membranous and is clearly differently sculptured (Oomyomar-C40, Oomyomar (Caenomyomar)-C41b, Stethynium-C57). A prospinasternal pit (pps) is sometimes present and is small and circular (Acromyomymar-C1, Cneomymar-C17, Cosmocomoidea-C18, Palaeoneura (Chaetomyomar)-C44). In some genera (Kalopanemima-C32, Neomyomar-C37, Polynema-C48) there is a median transverse depression at the anterior margin of the mesepisternum; a prospinasternal pit, if present, may be hidden inside the depression. Another pit occurs just posterior to the prepectus in some genera (Stephanocampta-C55, Yoshimotona-C59) but it is difficult to assess without examination of internal anatomy; it may or may not be a prospinasternal pit. Sometimes the prepectus is not visible (Alaptus-B3, Callicodorus-B11, Dicopomorpha-B21a,b, Pitilomyomar-B62) or barely visible (Octicromeris-B49).

Sculpture. Little or no sculpture is evident except rarely some engraved reticulate or elongate sculpticells occur (Cleruchus-B16); sometimes the sculpticells are conspicuous, raised and either longitudinal or transverse (Eustochus-B30, Eustochus (Caraphractus)-B31, Kalopanemima-B37, Litmus-B40, Narayanella-B44, Polynema (Restisoma)-B50, Richteria-B63).
Setation. The prepectus is asetose.

Mesoscutum. Structure. The mesoscutum consists of the more or less vertical mesopleuron laterally, the horizontal mesepisternum ventrally, and the vertical, transverse mesosternal plate posteriorly between the mesocoxal foramina. In lateral view, the mesopleuron (Figs 2, 4–7: pl.) is 1.8× as high as long (Ptilomymar-B62) to 4.4× as high as long (Alaptus-B3) and more or less narrowly (Oomyomar (Caenomymar)-B51b) to widely (Ischiodyas-C36) fusiform but sometimes more rectangular (Notomymar-B48) at least posteriorly (Cnecomymar-B17, Mymar-B43, Platynurs-B57, Stephanodes-B67a,b, Tetrapolynema-B70). The mesopleuron is almost horizontal (Agalmopynema-B2, Tetrapolynema-B70) to almost vertical (Dicopomorpha-B22a,b). A shallow mesofemoral depression (Figs 2, 5, 6: mfd) is usually present and extends obliquely from the tegula to the mesocoxal foramen. The depression is shallow and almost not visible, especially anteriorly (Acmopolynema-B1, Chrysotoconus-B15a,b, Coscomomopsis-B19, Cremnomymar-B20, Eubroncus-B29, Steganogaster-B65) to more or less distinctly visible (Alaptus-B3, Australomyark-B9, Ischiodyas-C36, Macrocamptoptera-B42, Platynurs-B57, Stephanocampa-B66) when it is sometimes margined or at least indicated by a line of sculpture (Camptopteroides-B13, Cosmomoidea-B18a, Ooctonus-B52, Stephanocampa-B66, Yoshimotoana-B71). The ventral surface of the mesoscutum (the mesepisternum) is distinguished from the mesopleuron by a change in angle that is more or less abrupt (Acmopolynema-C1, Anagroidea-C4, Eustochus (Caraphractus)-C28, Lymancon-C34, Macrocamptoptera-C35, Stethynium-C57) but sometimes so smoothly and gradually rounded the junction is barely discernible (Cnecomymar-C17, Kalopolyrna-C32). A more or less distinct longitudinal but sometimes incomplete sulcus (Arescon-C8, Ceratanaphes-C14, Cosmomoidea-C18, Gastrogontocerus-C29, Oomyomar (Caenomymar)-C41b, Schizophragma-C53, Stethynium-C57), carina (Boudiennyia-C10, Ptilomymar-B62) or change in sculpture (Camptopteroides-C13) may separate the mesepimeron from the mesepisternum. In ventral view, the mesepisternum is usually distinctly wider than long, rarely almost quadrate (C41b, C51) but sometimes so smoothly and gradually rounded the junction is barely discernible (Boudiennyia-C10, Ceratanaphes-C14) or, exceptionally, triangular (Oomyomar (Caenomymar)-C41b). The mesosdiscrimen (Figs 5, 6: dc.), when present as a longitudinal median sulcus, is faint (Acmopolynema-C1, Stethynium-C57) or distinct (Australomyark-C10, Macrocamptoptera-C35) but often is absent (Alaptus-C3, Cnecomymar-C17, Eustochus-C27, Kalopolyrna-C32, Lymancon-C34, Platynurs-C47). When present, the mesosdiscrimen extends most of the mesepisternum length but not to its anterior and posterior margins (Eustochus (Caraphractus)-C28, Gastrogontocerus-C30, Ooctonus-C42, Yoshimotoana-C59), but often it is shorter (Cleruchus-C16, Cosmomoidea-C18, Ooctonus-C42, Stephanodes-C56a,b). The mesofemoral pit (Figs, 5–7, 8: fu,p) is always present and usually distinct (Acmopolynema-C1, Australomyark-C9, Litus-C33, Neomyark-C37) but sometimes small and difficult to see (Eustochus-C27) or apparently absent (Ptilomymar-C51). It is usually circular or occasionally oval, and large (Steganogaster-C54) or small (Cnecomymar-C17) but sometimes it is elongate (Anagrus-C5, Cleruchus-C16, Gastrogontocerus-C30, Schizophragma-C53). Exceptionally, two pits occur, small and close together (Yoshimotoana-C59). The mesofemoral pit is usually in the posterior half of the mesepisternum (Oomyomar-C40, Stethynium-C57) or at or near the posterior apex of the mesosdiscrimen when that is visible (Australomyark-C9), but it is about midway between the anterior and posterior margins (Acmopolynema-C1, Cremomymar-C19, Neomyark-C37, Stephanodes-C56a,b) or, rarely, distinctly in the anterior half of the mesepisternum (Polynema-C48). A large, posterolateral depression margined anteriorly by a short carina is rarely present next to each mesocoxa (Gastrogonatocerus-C29).

Sculpture. The mesoscutum sometimes is apparently smoothly (Cnecomymar-B17, Cleruchus-B16, Cosmomoidea-B18b, Polynema (Doriclytus)-B58, Polynema (Restisoma)-B59, Stephanodes-B67a,b) but usually has engraved reticulate sculpture that is faint and indistinct (Anagrus-B5, Anaphus-B6, Ceratanaphes-B14, Heptagonatocerus-B35, Palaeoneura-B53, Stethynium-B68) or sometimes raised sculpture that is more or less distinct (Alaptus-B3, Anagroidea-B4, Callodicopus-B11, Camptopteroides-B13, Chrysotoconus-B15a,b, Eustochus-B30, Litus-B40, Ptilomymar-B62, Yoshimotoana-B71).

Setation. With few exceptions (Arescon-C8, Boudiennyia-C10, Ischiodyas-C31, Parasteathynium-C46, Steganogaster-C54) the mesoscutum is asetose but, when setae are present, there are only one or a few pairs, exceptionally many pairs (Steganogaster-C54).

The mesosternal plate (Figs 5, 7, 9, 10: mtp), visible only in posterior view (Figs 9, 10, E1-E9) when the metasoma and metacoxae are removed (E1-E9), is vertical and usually at or almost at a right angle to the mesoscutum. Rarely, it is almost horizontal so the mesocoxal foramina face ventrally (Polynema-C48, Ptilomymar-C51) instead of posteriorly (Acmopolynema-C1, Cnecomymar-C17, Litus-C33, Yoshimotoana-C59) or slightly posterovertrally (Eubroncus-C26, Palaeoneura (Chaetomymar)-C44). In ventral view, the junction between mesoscutum and

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mesotrochantinal plate is straight (Camptopteroides-C13, Ceratanaphes-C14, Lymaenon-C34), slightly sinuate (Neomymar-C37, Palaeoneura-C43) or slightly concave (Eustochus-C27). In posterior view, the plate is usually rectangular with straight anterior (dorsal) and posterior (ventral) margins (Ceratanaphes-E3, Kalopolynema-E5, Richteria-E8) but sometimes with both margins concave (Boudiennyia-E2) or one margin indented medially (Cosmocomoidea-E4) or one margin, the posterior one, concave (Anaphes-C6, Pilomymar-C51). Laterally, a more or less prominent and triangular, toothlike mesotrochantinal lobe (Figs 5, 7: mtl) extends posteriorly ventral to each mesocoxal foramen (Agalmopolyema-C2, Anaphes-C6, Anneckia-C7, Eustochus-C27, Stethynium-C57). The mesotrochantinal plate is almost always smooth and asetose. Exceptionally, there is some sculpture (Yoshimotoana-E9).

METATHORAX

Metanotum. Structure. The metanotum (Fig. 2: no.) consists of the dorsellum (Figs 1–4: dor) medially and the lateral panel of the metanotum (Figs 1–4: lpm) laterally. In dorsal view, the metanotum is concealed medially but not laterally by the frenum (Agalmopolyema-A2, B2, Camptoptera-A12, B12, Cneocomyr-A17, B17, Litus-A41, B40, Mymar-A44, B43, Nepolyema-A49, B39) or, rarely, hidden laterally but barely visible medially (Stephanocampta-A70). When the entire metanotum is visible, the lateral panel is sometimes longer than the dorsellum (Acemopolyema-A1, Kalopolynema-A37, Polyrena (Doricytus-A61, Polyrena (Restisoma)-A62, Richteria-A67, Stephanocampta-A71a,b) but usually is distinctly shorter (Anagrus-A5, Enrichopteris-A24, Zeyanus-A77). Occasionally the dorsellum and lateral panel are the same length (Camptopteroides-A13, Macrocamptoptera-A43). If the dorsellum is distinct (usually much less visibly distinct in micrographs than in photographs), its width is about equal to a lateral panel width (most genera) but sometimes is wider (Alaptus-A3a,b, Dicopus-A23, Ischiodyas-A36, Neomyrm-A46) or narrower (Erythmelus-A26, Erythmelus (Parallellaperta)-A27). The lateral panel is straight and, except at its lateral apex, uniformly wide (Anaphes-A6, Dicopomorpha-A21a, Lymaenon-A42, Schizophragna-A68, Tanyxiphius-A73a,b), wider medially than apically (Acemopolyema-A1, Agalmopolyema-A2, Neomyrm-A46), slightly wider laterally than medially (Creemonym-A20, Nepolyema-A49, Palaeoneura-A55) or slightly wider medially than laterally (Octonus-A54). The dorsellum follows, usually closely, the contour of the frenum so its anterior margin is straight (Arescon-A8, Cosmocomoidea-A18, Cosmocomopsis-A19, Eustochus-A30, Gonatocerus-A34, Macrocamptoptera-A43), rarely slightly sinuate (Alaptus-A3a,b, Omyomyrm-A52) but usually more or less concave (Ischiodyas-A36, Krateriske-A39, Neomyrm-A46, Stephanocampta-A71a,b). The posterior margin of the dorsellum is sometimes parallel to its anterior margin so the dorsellum is uniformly long, and either straight and strap-like (Lymaenon-A42) or more often curved (Anagroidea-A4, Neomyrm-A46, Stephanocampta-A71a,b). Usually, the posterior margin diverges from the anterior margin so the dorsellum is triangular (Anaphes-A6, Arescon-A8, Gonatocerus-A34, Krokella-A40, Progonatocerus-A64), with the posterior apex widely rounded (Anaphes-A6) to more pointed (Gonatocerus-A34). Exceptionally, the dorsellum has a median depression (Gahanopsis-A32) or a slightly concave median projection with raised margin that extends over the propodeum (Erythmelus-A26, B26, Erythmelus (Parallellaperta)-A27, B27). The dorsellum is almost always shorter than the frenum, rarely up to 0.8–0.9× its median length (Arescon-A8, Krokella-A40) but exceptionally longer, 1.2× its median length (Dicopus-A23).

Sculpture. The metanotum is usually smooth or apparently so. If sculpture is present, it is raised and reticulate (Anagroidea-A4, Eustochus-A30, Eustochus (Caraphractus)-A31, Octonus-A54) or coarsely striate, at least laterally (Australomyrm-A9, Boudiennyia-A10). The sculpture is sometimes mainly on the lateral panel (Eubroncus-A28).

Setation. Apart from two short, inconspicuous setae laterally near the anterior margin of the lateral panel, the metanotum is asetose. The setae are usually widely separated, with one seta near the lateral apex of the lateral panel and one near the lateral margin of the dorsellum (Acemopolyema-A1, Anagrus-A5, Anaphes-A6, Cosmocomoidea-B17a,b).

Metapectus. Structure. In lateral view, the only visible part of the metapectus is the metapleuron (Figs 1, 2, 9, 10, 13: pl.), a triangular area lateral to the propodeum but externally sometimes not distinguishably from it (Camptoptera-B12, Cleruchus-B16, Cneocomyr-B17, Lymaenon-B41, Notomyrm-B48, Richteria-B63). If distinguishable, the junction is indistinct, sometime due to a change in plane (Alaptus-B3, Eustochus (Caraphractus)-B30, Litus-B40, Macrocamptoptera-B42) or change in sculpture (Camptoptera-B12, Camptopteroides-B13).

In ventral view, the metapleco is a transverse plate, the lower metepisternum (*Micranaphes*-B22a,b, *B22b, *B1) but sometimes is more anterior (*the propodeum, usually at about the level of the posterior margin of the frenum or metanotum (*areas (*B71) but is sometimes flat (*Anagroidea*-B4, *Krateriske*-B39, *Steganogaster*-B65). The sulcus is narrow, deep and well defined (*Anaphe*-B6, *Cremonymyr*-B20, *Mymar*-B43, *Oocto*-B52) or wider, shallow and poorly defined (*Acmopolyne*-B1, *Callodicopus*-B11, *Dicopomorpha*-B21c, *Lymaenon*-B41, *Platyfrons*-B57). Rarely, the sulcus is indicated by a row of shallow punctures (*Yoshimotoana*-B71).

Sculpture. This matches the sculpture, if any, on the propodeum. Genera without engraved or raised sculpture on the propodeum do not have it on the metapleuron either. Those that have propodeal sculpture usually have matching sculpture on the metapleuron (*Alaptus*-B3, *Anagroidea*-B4, *Anagr*-B5, *Anaphes*-B6, *Camptopteroides*-B13, *Eustochus* (*Caraphractus*)-B31, *Oocto*-B52, *Yoshimotoana*-B71).

Setation. The metapleco is asetose.

## PROPODEUM

propodeum but occasionally abuts its anterior margin *(Cnecomymar-B17, Cremnomymar-B20, Dicopomorpha-B22a,b, Dicopomorpha (Dicopulus)-B23, Neomymar-B45, Tetrapolynema-B70). Often it is in *(Australomymar-B9, Cosmocomoidea-B18a,b, Cosmocomopsis-B19, Eubroncus-B29, Gonatocerus-B34) or just posterior to *(Acropolynema-B1, Octonus-B52) a more *(Octomicromeris-A51, Cosmocomoidea-A18) or less *(Zeyanus-A77) well defined depression along the anterolateral margin of the propodeum; this depression sometimes continues medially as a narrow groove *(Australomymar-B9, Pseudanaphes-B61). The spiracle is usually small and circular with a slightly raised rim *(Acropolynema-B1, Anagroidea-B4, Stephanodes-B67a,b), rarely it is large *(Gastrogonatocerus-B33) and sometimes it is elongate *(Ceratanaphes-B14, Stephanocampta-B66, Zeyanus-B72).

Sculpture. Apart from obvious macrosculpture, the propodeum is smooth *(Acropolynema- A1, Cleruchus-A16, Cosmocomopsis-A19, Palaeoneura-(Chaetomymar)-A56, Stephanodes-A71a,b), engraved with fairly inconspicuous, mainly isodiametric sculpticells *(Ceratanaphes-A14, Lymaenon-A42, Neostethynium-A47, Notomymar-A50), more or less distinctly raised, distinct and conspicuous sculpticells that are elongate or irregular either medially *(Anagroidea-A4, Australomymar-A9, Richteria-A67) or laterally *(Cosmocomoidea-A18, Dicopomorpha-A21a,b, Dicopomorpha (Dicopulus)-A22), or fairly uniformly isodiametric sculpticells *(Eustochus-A30, Eustoctus (Caraphractus)-A31, Litus-A41, Macrocamptoptera-A43). Exceptionally, the propodeum is densely pitted *(Ioshimotoana-A76). Macrosculpture consists of median (Figs 3, 10: mc) or submedian, partial or complete, longitudinal carinae or sulci *(Acropolynema-A1, Anagroidea-A4, Anaphes-A6, Krateriske-A39, Lymaenon-A42, Platyrorns-A59, Polynema (Doricytus)-A61) in various configurations, rarely with additional carinae—the plica (Fig. 1: plc) and/or costula *(cos, Fig. 1) *(Boudiennyia-A10, Octonus-A54), or bizarre structures such as raised ‘fins’ with transluscent reticulations *(Ptilomymar-A66, Stephanocampta-B66). The metapleural pit *(Fig. 10, mtpp), which indicates the dorsal apex of the metapleural apodeme, is sometimes visible *(Entrichopteris-B24, Ischiodasys-B36, Kalopolynerma-B37, Neomymar-B45, Platyrorns-B57, Polynema (Restisoma)-B59, Polynema (Doricytus)-B58) at or near the metapleural sulcus. Sometimes the pit is longitudinally stretched *(Agalmopolynerma-B2, Anaphes-B6, Palaeoneura-B53) or occasionally the pit is joined by a fine sulcus to the metapleuron *(Richteria-B62, Stephanodes-B67a,b).

Setation. Almost always, one propodeal seta is present, usually posterior to the spiracle and close to it *(Alapatus-A3b, Krateriske-A39), but sometimes it is midway between the spiracle and dorsal margin of the metacoxal foramen *(Camptoptera-A12, Erodosiella-A24b, Tanyxiphium-A73a) or far from it *(Agalmopolynerma-B2, Entrichopteris-A24, Neomymar-A46, Schizophragma-A68, Tetrapolynema-A74). Occasionally the seta is medial to the spiracle *(Acropolynema-B1). Rarely, the seta is on a distinct tubercle *(Cremnomymar-A20) or there are 2 or more setae *(Tetrapolynema-A74, Ischiodasys-A36) or the seta is anterolateral to the spiracle and branched *(Ptilomymar-A66, B62).

Conclusions

The mesosoma of Mymaridae is no different from other Chalcidoidea in that it has an independent prepectus. However, in lateral view, it is very narrow and almost completely or completely hidden externally in some genera. Even when it is not visible externally, it is visible internally (except in *Ptilomymar-B62) in cleared slide mounts. More importantly, in all genera, the mesonotal spiracle is between the lateral panel of the pronotum and lateral lobe of the mesoscutum (Fig. 2), as for other Chalcidoidea. These features of the mesosoma distinguish all Chalcidoidea from other superfamilies of Hymenoptera (another fairly easily seen diagnostic feature is presence of multiporous plate sensilla on the antennal flagellum) (Gibson 1986). The variety of features illustrated here among the fairyfly genera supports the fact that they are an ancient lineage, at least 100 million years old (Poinar & Huber 2011). Even though all but two of the species are strictly egg parasitoids, some of the differences in overall proportions of the mesosoma reflect the shape of the host egg they emerged from, and some differences may reflect the habitat their hosts occur in (soil, water, on or in plant tissue). The mesosoma offers numerous features that may be used in taxonomy but many of them have not been used mainly because of the difficulty of seeing them, even on well-prepared slide mounts. Scanning electron microscopy is another tool useful for studying fairyfly external morphology and it is hoped that this survey of mesosoma structure across the genera of Mymaridae will provide further insights into their relationships and help those describing the genera to explore new characters useful in defining them.
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Over many years, Ann Fook Yang (AAFC, retired) quietly and efficiently maintained the scanning electron microscope in top working condition, which allowed us to obtain excellent results without worrying about whether it would break down or otherwise create problems. He also taught us how to use it and was always there to troubleshoot. We are very grateful for his considerable help.

References


APPENDIX 1.

List of acronyms used on figures 1–17 and in text.

2ph—mesophragma (Fig. 15a)
aac—acropleuron (Figs 2, 4)
ans—adnotaular seta (Figs 3, 15a)
aps—adpetiolar strip (Fig. 7)
ax—axilla (Figs 1–4, 11, 12, 15a) [= ax + lpa]
axc—axillar carina (Figs 1, 2)
axl—axillula (Figs 1–4, 14)
axlc—axillular carina (Figs 1, 2) [a sharp angle or ridge in Mymaridae, never a carina]
axs—axillar seta (Fig. 15a)
cos—costula (Figs 1, 13)
cvpr—cervical prominence (Figs 5–8)
cx₁—procoxa (Figs 2, 4, 5, 16a, 17a)
cx₂—mesocoxa (Figs 2, 16a, 17a)
cx₃—metacoxa (Figs 2–3, 13, 16a, 17b)
cx₁, f—procoxal foramen (Figs 6, 7)
cx₂, f—mesocoxal foramen (Figs 6, 7, 9, 10)
cx₃, f—metacoxal foramen (Figs 5, 6, 9, 10)
dc₁—prodiscrmen (Figs 5, 8, 17a,b)
dc₂—mesodiscrimen (Figs 5, 6, 7, 10, 17a,b)
dc₃—metadiscrimen (Figs 7, 17b)
dor—dorsellum (Figs 1–4m 15a) [= no₃m]
ep₂—meseipimeron (Figs 2, 4–7, 16a)
es₂—meseipisternum (Figs 2, 4–7)
f₁,p—profurcal pit (Figs 6, 7)
f₂, p—mesofurcal pit (Figs 5–7, 9)
f₃, p—metafurcal pit (Figs 5, 9, 10)
fre—frenum (Figs 1–4, 11, 12, 15a, 16a)
frl—frenal line (Fig. 1)
les₂—lower metepisternum (Figs 5–7, 9, 10, 17b)
llm—mesoscutal lateral lobe (Figs 1–4, 8, 15a, 16a)
lpa—lateral panel of axilla (Figs 1–4, 11, 12)
llp—pronotal lateral panel (Figs 2, 4, 7, 16a)
mc—median carina (sulcus) of propodeum (Figs 3, 10, 15a)
mdf—mesofemoral depression (Figs 2, 5, 6, 7)
mlm—mesoscutal midlobe (Figs 1–4, 8, 11, 12, 15a)
msa—mesoscutellar arm (Figs 1–3, 14, 15a)
msc—mesoscutum (Figs 1, 2) [= llm + mlm]
msp—mesothoracic spiracle (Figs 2–4, 7, 15a, 16a)
mss—mesoscutellum (Fig. 3) [= sctd + fre]
mtl—mesotrochantinal lobe (Figs 5–7, 17a)
mtp—mesotrochantinal plate (Figs 5–7, 9, 10, 17b)
impp—metapleural pit (Fig. 10)
mtps—metapleural sulcus (Figs 2–4, 9)
n₀₁—pronotum (Figs 1–6, 8, 15a)
n₀₂—mesothorax (Figs 1, 2, 9, 10)
n₀₃—metathorax (Figs 2, 9, 10) [= no₃m + no₃l]
n₀₃l—lateral panel of metanotum (Figs 1–4, 13, 15a, 16a)
n₀₃m—median panel of metanotum (Figs 1, 3, 4, 13, 15a, 16a) [= dor]
not—notaulus (Figs 1–3, 15a)
pap—postalar process (Figs 1–3)
pca—pronotal carina (Figs 1, 2)
pco—pronotal collar (Figs 1, 2)
pcs—propodeal collar seta (Figs 1, 3, 4, 10, 13, 15a)
pet—petiole (Figs 1, 2, 13, 17a, 17b)
pfd—profemoral depression (Figs 2, 4)
pl₁—propleuron (Figs 2, 4–8, 16a, 17a)
pl₂—mesopleuron (Figs 2–7, 10, 17a,b) [= ep₂ + es₂]
pl₃—metapleuron (Figs 1, 2, 4, 9, 10, 13, 16a)
plc—plica (Fig. 1)
plp—lateral panel of prepectus (Figs 2, 4)
plsl—mesopleural sulcus (Fig. 2)
pnk—pronotal neck (Figs 1, 2)
ppd—propodeum (Figs 1–4, 9, 10, 15a, 16a)
ppf—propodeal foramen (Figs 6, 9, 10)
pps—prospinasternal pit (Fig. 7)
pre—prepectus (Figs 2, 4–7, 17a) [= plp + pvp]
prede—prepectal discrimin (Fig. 7)
prs—propodeal spur (Figs 1, 2)
psp—propodeal spiracle (Figs 1–4, 10, 13, 15a, 16a)
pvp—ventral panel of prepectus (Figs 6, 7)
sac—scutellar-axillar complex (Figs 1, 2) [= sctd + fre + ax + lpa + axl]
sctd—mesoscutellar disc (Figs 1–4, 12, 15a, 16a)
sss—scutoscutellar suture (Fig. 1) (visible only as an internal ridge)

APPENDIX 2.
Genera and subgenera of Mymaridae illustrated, followed by figure numbers. When particular species were identified their names appear after the appropriate figure(s). Collecting localities for specimens micrographed are given in Huber et al. (2023).

*Acnopolyneuma* Ogloblin, 1946. Figs A1, B1, C1, D1.
*Alaptus* Westwood, 1839. Figs A3, B3, C3, D3.
*Anagroidea* Girault, 1915. Figs A4, B4, C4, D4.
*Anagrus* (*Anagrus*) Haliday, 1833. Figs A5, B5, C5, D5.
*Anaphes* (*Patasson*) Haliday, 1833. Figs A6, B6, C6, D6.
*Arescon* Walker, 1846. Figs A8, B8, C8, D8. All *A. dimidiatus* (Curtis).
*Australomymar* Girault, 1929. Figs A9, B9, C9, D9.
*Boudiennyia* Girault, 1937. Figs A10, B10, C10, D9, E2.
*Camptoptera* Foerster, 1856. Figs A12, B12, C12, D11.
*Cleruchus* Enock, 1909. Figs A17, B16, C16.
*Cnecomymar* Ogloblin, 1963. Figs A18, B17, C17, D15.
*Cosmocomopsis* Huber, 2015. Figs A20, B19. All *C. sevae* (Risbec).
*Cremnomymar* Ogloblin, 1952. Figs A21, B20, C19, D17.
*Dorya* Noyes & Valentine, 1989. Fig. 14.
**Erdosiella** (*Tanaomymar*) Annecke & Doutt, 1961. Figs A26b, B25a, C23 [*Tanaomymar* is a synonym and still treated as one here but is included for illustration]


**Erythmelus** (*Parallelaptera*) Enock, 1909. Figs A28, B27, C25, D22. All *E. panis* (Enock).


**Eustocho** (*Caraphractus*) Walker, 1846. Figs A32, B31, C28. All *E. cinctus* (Walker).

**Eustocho** (*Eustocho*) Haliday, 1833. Figs A31, B30, C27, D23.

**Gahanopsis** Ogloblin, 1946. Figs A33, B32. All *G. deficiens* (Ogloblin).

**Gastrogonatocerus** Ogloblin, 1935. Figs A34, B33, C29.

**Gonatocerus** Nees, 1834. Figs A35, B34, C30, D25. All *G. rivalis* Girault.

**Heptagonatocerus** Huber, 2015. Figs A36, B35. Both *H. madagascarensis* Huber.


**Kalopolynema** Ogloblin, 1960. Figs A38, B37, C32, D27, E5. All *K. ema* (Schauff & Grissell).


**Litus** Haliday, 1833. Figs A42, B40, C33, D28. All probably *L. cynipseus* Haliday.

**Lymaenon** Walker, 1846. Figs A43, B41, C34, D29.

**Macrocamptoptera** Girault, 1910. Figs A44, B42, C35, D30. All *M. metotarsa* (Girault).

**Mymar** Curtis, 1829. Figs A45, B43, D31.

**Narayanella** Subba Rao, 1976. Figs A46, B44, C43, D32.

**Neomymar** Crawford, 1913. Figs A47, B45, C37, D33.

**Neostethynium** Ogloblin, 1964. Figs A48, B46, C38, D34.


**Notomymar** Doutt & Yoshimoto, 1970. Figs A51, B48. All *N. aptenosoma* Doutt & Yoshimoto.

**Octomicromeris** Huber, 2015. Figs A52, B49, D35.

**Omyomymar** (*Caenomymar*) Yoshimoto, 1990. Subgenus synonymized by Aquino et al. (2016) and still treated as a synonym here. Figs A53, B51a, B51b, C41a, C41b.


**Ooctonus** Haliday, 1833. Figs A55, B52, C42, D37 All *O. hemipterus* (Haliday).


**Parastethynium** Lin & Huber, 2011. Figs A59, B56, C46, D41 All *P. maxwelli* (Girault).

**Platyfrons** Yoshimoto, 1990. Figs A60, B57, C47, D42.

**Platystethynium** (*Platypatasson*) Ogloblin, 1946. A60.

**Polynema** (*Doriclytus*) Foerster, 1847. Figs A62, B58, C49.

**Polynema** (*Polynema*) Haliday, 1833. C48, D43.


**Proarescon** Huber, 2017. Fig. A64. *P. similis* (Huber).

**Progonatocerus** Huber 2015. Figs A65, B60. All *P. albiclava* Huber.

**Pseudanaphes** Noyes & Valentine, 1989. Figs A66, B61, D44.


**Richteria** Girault, 1920. Figs A68, B63, C52, D46, E8.

**Schizophragma** Ogloblin, 1949. Figs A69, B64, C53, D47. All *S. bicolor* (Dozier).

**Steganogaster** Noyes & Valentine, 1989. Figs A70, B65, C54, D48.

**Stephanocampta** Mathot, 1966. Figs A71, B66, C55, D49.
**Stephanodes** Enock, 1909. Figs A71a, B67a, C56a, D50—all *S. polynemoides* Yoshimoto. Figs A71b, B67b, C56b, D50b—all *S. septentrionalis* Huber.

**Stethynium** Enock, 1909. Figs A73, B68, C57, D52. All *S. triclavatum* Enock.


**Tetrapolynema** Ogloblin, 1946. Figs A75, B70, C58.

**Tinkerbella** Huber & Noyes, 2013. Fig. A75. *T. nana* Huber & Noyes.


**Zeyanus** Huber, 2015. Figs A78, B72.
FIGURES 1, 2. Mymaridae, mesosomes. 1, dorsal; 2, lateral. Acronyms explained in Appendix 1.
FIGURES 5, 6. Mymaridae, mesosomes. 5, ventral; 6, ventral. Acronyms explained in Appendix 1.
FIGURES 7, 8. Mymaridae, mesosomas. 7, ventral; 8, anterior. Acronyms explained in Appendix 1.
FIGURES 9, 10. Mymaridae, mesosomas. 9, posterior; 10, posterior. Acronyms explained in Appendix 1.
FIGURES 11–13. Mymaridae. 11, dorsum of mesonotum, internal; 12, scutellum, slightly below surface, photograph with transmitted light; 13, propodeum. Acronyms explained in Appendix 1.
FIGURE 14. Mymaridae mesonotum, detached from remainder of mesosoma, dorsal.
FIGURES 15a,b. Mymaridae, mesosomas, dorsal. 15a, surface; 15b, internal. Acronyms in Appendix 1.
FIGURES 16a, b. Mymaridae, mesosomas, lateral. 16a, surface; 16b, internal. Acronyms in Appendix 1.
FIGURES 17a,b. Mymaridae, mesosomes, ventral. 17a, surface; 17b, internal. Acronyms in Appendix 1.
FIGURES A8–A15. Mymaridae mesosomes, dorsal.
FIGURES A16–A21c. Mymaridae mesosomes, dorsal.
FIGURES A22–A29. Mymaridae mesosomes, dorsal.
FIGURES A30–A37. Mymaridae mesosomes, dorsal.
FIGURES A38–A45. Mymaridae mesosomes, dorsal.
FIGURES A46–A53. Mymaridae mesosomes, dorsal.
FIGURES A54–A61. Mymaridae mesosomes, dorsal.
FIGURES A62–A69. Mymaridae mesosomes, dorsal.
FIGURES A70–A75. Mymaridae mesosomes, dorsal.
FIGURES A76, A77. Mymaridae mesosomes, dorsal.
FIGURES B9–B15b. Mymaridae mesosomes, lateral.
FIGURES B16–B21b. Mymaridae mesosomas, lateral.
FIGURES B29–B36. Mymaridae mesosomas, lateral.
FIGURES B37–B44. Mymaridae mesosomes, lateral.
FIGURES B45–B51b. Mymaridae mesosomes, lateral.
FIGURES B52–B59. Mymaridae mesosomes, lateral.
FIGURES B60–B67a. Mymaridae mesosomas, lateral.
FIGURES B67b–B72. Mymaridae mesosomes, lateral.
FIGURES C1–C8. Mymaridae mesosomes, ventral.
FIGURES C17–C25. Mymaridae mesosomes, ventral.
FIGURES C26–C33. Mymaridae mesosomes, ventral.
FIGURES C34–C41a. Mymaridae mesosomes, ventral.
FIGURES C41b–C48. Mymaridae mesosomes, ventral.
FIGURES C49–C56a. Mymaridae mesosomes, ventral.
FIGURES C56b–C59. Mymaridae mesosomes, ventral.
FIGURES D37–D42. Mymaridae mesosomes, anterior.
FIGURES D49–D53. Mymaridae mesosomas, anterior.

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lobulata (Hemiptera: Lophopidae), and description of a new species of *Parastethynium* from Indonesia. *Zootaxa* 2733: 49–61.


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