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# ZOOTAXA



# The morphological diversity of Mymaridae (Hymenoptera): an atlas of scanning electron micrographs. Part 1. General overview and structure of the head

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#### Abstract

This is the first in a series of studies that aim to provide a comprehensive overview of the morphological diversity of Mymaridae (Hymenoptera), a monophyletic family of small parasitic wasps that are postulated as the sister group of other Chalcidoidea. The external cranial morphology of 65–75 genera and subgenera of Mymaridae (fairyflies) is described and illustrated with almost 430 scanning electron micrographs, including 73 micrographs of the anterior, 68 of the posterior, 75 of the dorsal, 75 of the lateral, and 67 of the ventral views of the head, plus 71 micrographs of the ventral view of the mouthparts. Twenty-one annotated figures illustrate the terms used for morphological structures. Two appendices list the 64 morphological terms and 5 measurements that are defined and illustrated, and the 116 currently recognized valid genera and subgenera of Mymaridae, including collection localities for those that are illustrated. Discussion of head morphology characteristic of Mymaridae is preceded by an overview that includes discussion of best practices for taxonomic descriptions and why these and accurate identifications require well preserved and imaged specimens. Aspects of intraspecific variation, colour, secondary sexual dimorphism, setation (chaetotaxy), surface sculpture and morphometrics are also treated as all of these are often important for describing and distinguishing species. Many of the features illustrated have not previously been used in Mymaridae systematics but may prove to be useful for helping to identify and describe genera and species.

Key words: morphology, terminology, fairyflies

#### Introduction

Morphology provides the greatest source of information useful for recognition and identification of taxa, including those of Mymaridae (Hymenoptera), commonly referred to as fairyflies. Most specimens are less than one millimeter in length, often have faint sculpture, and usually have a weakly sclerotized antennae and metasoma that shrivel on air drying, making Mymaridae difficult to study, describe and image. Careful examination of well-prepared specimens is therefore required to prepare sufficiently accurate and complete descriptions needed to identify correctly any particular taxon. Because of their size, specimens are usually slide mounted in a permanent mounting medium so that only a dorsal or lateral view is visible in a given specimen. If a series of specimens of the same species is available, they can be slide mounted to show different views, and some can be critical point dried, card- or point mounted, and stored in a pinned collection. Illustrations of the described features are used not only to supplement descriptions but also to illustrate identification keys, with which specimens are identified to genus or species. Among the large number of visible external or internal structures that could be studied most are not used or, if used, often are often not well described or have been described in different ways by different authors or differently by the same author over time. The result is that the features of different species often cannot be properly compared and contrasted. Many of those features are, of course, common to all members of a taxon, e.g., all species in a given genus, so describing them is repetitious and pointless. The features in common for any particular taxon level should be eliminated from the description and placed in a description of the next higher, more inclusive category. This results in shorter and more succinct descriptions at any particular level, and if the features are well illustrated all that is needed to define the taxon morphologically. Ideally, other types of biological information, such as behavior, phenology, ethology, hosts and distribution, as well as molecular data should be given to supplement morphological descriptions for the circumscription of taxa. However, for many species such supplemental information does not exist and will take considerable time to obtain (Fernandez-Triana 2022). Incidentally, soaking specimens for sufficient time to extract DNA not only provides molecular data but clears specimens better for slide mounting, as all the internal soft tissues are completely removed. Even when available, information other than morphological often cannot be used for comparison with the numerous previously described species known only from a type specimen or short series of specimens that lack such information.

Photographs and scanning electron micrographs (SEMs), hereafter referred to as micrographs, can complement line drawings, which are often used advantageously to illustrate some structures such as male genitalia, but any method that produces good illustrations to complement written descriptions greatly helps identifying a taxon correctly. A variety of optical microscopes, scanning electron microscopes, and digital photography enable publishing completely in-focus images of an entire specimen or selected parts of a specimen. This has made detailed illustrations of specimens much easier, though the main problem often was, and sometimes still is, poor preparation of specimens so details of body structure cannot be seen properly even with the best equipment. Pointel (1979), Bolte (1997), Platner et al. (1999) and Huber (2015) described methods that produce sufficiently well-preserved adult specimens for photography or micrography. Critical-point drying (Gordh & Hall 1979) or chemical drying (Heraty & Hawks 1998) maintains the shape and structural integrity of tiny and often weakly sclerotized specimens, which is essential to preserve specimens in suitable condition for habitus illustrations that show general appearance and, especially, body colour, for accurate interpretation of their morphological features. While light microscopy is one of the best ways to observe external structures of larger insects, SEM is better used to observe and obtain suitable images for insects measuring less than about 1 mm in length, such as most Mymaridae. Micrographs taken with an environmental scanning electron microscope (ESEM) have the added advantage of not requiring a specimen to be gold coated. Although the micrographs may not be as sharp (compare F46-SEM with F47-ESEM), non-coated specimens can be returned in an unharmed condition into a collection.

Debauche (1948) treated the Mymaridae of Belgium. Through careful observation, supplemented with line drawings and a comprehensive discussion of morphological characters, his work was a major milestone in elucidating the morphology and taxonomy of the family. Yet his species descriptions are full of features present in all species of a genus, or even all genera in the family. In addition, many are described in such vague and subjective terms that it is impossible to determine exactly what was meant. Debauche also stressed a few characters, such as setation of antennal segments and wing venation, to the exclusion of others that could perhaps have been used. Luckily, his identification keys usually include at least one of the essential features needed to identify a specimen correctly to species, and the holotype measurements provided help to characterize them. A major weakness in his monograph, common to most taxonomic publications, is insufficient treatment of infraspecific variation. Even today many descriptions are replete with vague terms, and intraspecific variation is often not addressed adequately, though often this is due the lack of sufficiently long series for study. Although it is poor taxonomic practice to describe a species based on one specimen and to describe features in vague or inadequate terms, the latter issue can partly be compensated for by providing suitable illustrations. Another problem that is still commonplace is to include features that apply to the next higher category and so are useless at the level treated, whether genus or familygroup. Conversely, many features that could be taxonomically useful or diagnostic at the species level may not be included in a description. The Debauche example is not to disparage his work relative to other taxonomists who study Mymaridae. His work was chosen simply as an example of the problems encountered in many publications. The other extreme is perhaps that of Ogloblin, one of the earliest and most prolific describers of Mymaridae for the Neotropical region, who tended to give the length to the nearest micrometer of, for example, each seta of the mesosoma or fore wing venation. This descriptive format is exact but is not really necessary and often distracts from other details more important for species recognition and the fact that individuals of species vary morphologically.

An exhaustive treatment of morphological terms and their synonyms used for adult Hymenoptera is the HAO— Hymenoptera anatomy and ontology portal (HAO 2021, Yoder *et al.* 2010). For particular family-group taxa within parasitic Hymenoptera, exemplary treatments of internal and external structure and terms are Ronquist & Nordlander (1989) for *Ibalia* Latreille (Ibaliidae) and Karlsson & Ronquist (2012) for *Opius* Wesmael and *Biosteres* Förster (Braconidae). Gibson (1997) treated the external morphology of Chalcidoidea. Debauche (1948) is the oldest and still perhaps the best general account of morphology of Mymaridae, though many included terms are no longer used. Greater detail can be obtained by studying particular structures at higher magnifications, for example Basibuyuk & Quicke (1995) for the antennal cleaner of Hymenoptera, and Burks & Heraty (2015) and Cruaud *et al.* (2020) for the postocciput and postgena in Chalcidoidea and Chalcididae, respectively. Kamp *et al.* (2022) used microtomography to study mandible articulations and associated musculature in Chalcidoidea. For Mymaridae, Chiappini *et al.* (2001) treated the female clava, and Ogloblin (1960) described the trabeculae. Huber (2015) illustrated some leg structures, Viggiani (1970, 1973, 1989, 1994, 2004) and Chiappini & Mazzoni (2000) described the male genitalia, and Jackson (1969) and King & Copland (1969) treated the female genitalia.

Study of the female antenna is essential for species and often also genus identification for Mymaridae. The female antenna is therefore usually well illustrated with line drawings or photographs in most taxonomic treatments. Not much can be usefully added with micrographs except perhaps at the level of studying sensilla and their distribution, especially on the female clava (Baaren *et al.* 1999, 2007).

The present paper details the external morphology of the head and mouthparts of Mymaridae, using micrographs to illustrate at least one species for about 65–75 of the ~115 currently recognized valid extant genera and subgenera. Those illustrated encompass 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, e.g., Noyes & Valentine (1989), Lin *et al.* (2007) and Huber (2015), are included. In a few cases, subgeneric names are used even though the subgenera were placed in synonymy. We do this because those previously recognized subgenera show some interesting morphological differences and in time they may again be recognized, at least as valid subgenera.

#### Materials and methods

Appendix 2 is an alphabetical list of the valid (as of 2022) genera and subgenera of Mymaridae, with author and year of publication for each. To avoid needless repetition the author names are therefore not provided for generic names cited in the text. Most specimens were imaged 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 Collections of Insects, Arachnids and Nematodes (CNC). Several specimens were needed for different views and method of imaging. When few specimens of a particular genus were available a single head may have been used for several views by affixing it as lightly as possible to the metal stub using double-sided carbon tape, imaging one side, then gently rotating the head and affixing it in another position to image another side. Unfortunately, this sometimes resulted in setae being broken off, e.g., Anneckia (Fig. C7), and/or a slight film of the adhesive remaining on the specimen, obscuring its surface sculpture, e.g., Cremnomymar (Fig. B20) and Eustochus (Fig. B29). In addition, it was not always possible to obtain enough specimens of a particular species of a genus from the same locality to image. Instead, specimens of what likely was the same species but almost certainly of the same genus, were used from several localities, sometimes even from different countries. More recently (2006–2016), uncoated specimens of some genera were micrographed by J. Read, using an environmental scanning electron microscope and the pinned specimens, mounted on triangular card points, were returned to the collections to which they belong (usually the CNC). The number of genera illustrated varies depending on structure and view. Usually only one species per genus is illustrated, usually using a female but sometimes both sexes if distinct sexual dimorphism occurs. A few genera are illustrated with two or three different species or, where the sexes differ greatly, a male and a female of either the same species (where the association is probably correct) or different species in the same genus or subgenus. If any subgenera other than the nominal subgenus are illustrated they are named e.g., Anaphes (Patasson), but not otherwise. The purpose of this study is to illustrate the external structural diversity among the genera and occasionally the subgenera of Mymaridae in order to provide information about what features might be useful to distinguish taxa, at least at the genus level. In almost all cases the species was not identified. Because almost always only a single species is illustrated, sometimes based on only a single micrographed specimen, variety among the species of a genus cannot be assessed. Up to five, rarely more, generic names and figure numbers are listed after description of a particular character to illustrate variation across the genera. The normal situation, i.e., that found in most of the genera illustrated here, is not referenced with generic names. This is to avoid mentioning every genus for every feature of every character treated, which would result in an extremely long publication with a great deal of mostly uninformative repetition.

We illustrate external morphology using micrographs. Internal morphology of sclerotized parts of the head such as the tentorium, ocular rim and ocular apodeme also vary and are sometimes useful to help define genera. Internal morphology is illustrated with photographs. Both photographs (Figs 1, 13–21) and micrographs (Figs 2–12) are labelled with acronyms of structures cited in the text and listed alphabetically in Appendix 1. The micrographs without acronyms (following the photographs) are grouped alphabetically by genus for each view in the following

order: anterior, posterior, dorsal, lateral, ventral, mouthparts. Figure letter/number combinations are used for the different view to distinguish them from the 21 introductory figures. For brevity in the text, the genera mentioned are followed by the relevant figure without stating each time "Fig." or "Figs", i.e., *Acmopolynema*-A1 instead of *Acmopolynema* (Fig. A1). Not every genus has every view. Occasionally several species are illustrated for a given genus and view. A separate number is given for every genus and subgenus but the same number with different letters is given for different species or different sexes within the same genus or subgenus.

We also discuss intraspecific variation, colour, sexual dimorphism, setation (chaetotaxy) and sculpture in general terms. Because measurements have not always been taken in the same way by different workers or even the same worker over time, suggestions are given at the appropriate places for standardizing these. Standardized measurements are essential so that those important in helping to define taxa are comparable, at least in the future if not at present. Surface sculpture and setation are also discussed as separate categories under the various structures. For anterior, dorsal, posterior and ventral views, structures are visible bilaterally, e.g., the two eyes, two toruli, or two mandibles, but only one side is discussed so these structures are referred to in the singular, e.g., "torulus abutting transverse trabecula, mandible with 4 teeth". For serially homologous structures, e.g., legs, the plural is used when referring to two or more of the structures (none occur on the head).

Depending on the structure and view, the morphological terms and their abbreviations we use are limited mainly to those used in taxonomic papers on Chalcidoidea. A given structure often has more than one name and various authors have sometimes been inconsistent in their use of terms, particularly for names of head structures. We usually do not include synonyms of the terms we use, but these can mostly be found in the morphological treatments listed above, particularly the HAO. No attempt is made to determine if a given term used for similar structures in different taxa is for homologous structures because this is beyond the scope of the present study. Many homologies are still not resolved across taxa, either among the genera of Mymaridae and certainly not across Chalcidoidea.

Several views of the head are needed to illustrate morphological variety across the family. Structures not usually treated in taxonomy of Mymaridae, such as the back of the head and the mouthparts, may well yield many new morphological features that could be used to advantage in generic or species descriptions. At the species level, quantitative differences in proportions of different structures, particularly of the female antenna, qualitative differences such as the number and distribution of multiporous plate sensilla (mps), sculpture and setal positions, and colour or colour pattern are important to distinguish species. Such features are best treated in revisionary studies of particular genera.

Cleared and slide-mounted specimens were photographed with a Jenoptik ProgRes C14<sup>plus</sup> CCD camera attached to a Nikon Eclipse E800 compound microscope using Image-Pro Plus<sup>™</sup> and a motorized stage. A combined image consisting of a complete stack of up to 80–90 source layers that includes dorsal and ventral surfaces as well as all internal structures is usually much too confusing to interpret surface features easily. Using Zerene Stacker<sup>™</sup> substacks were created from the source layers as the basis for retouching. The images produced were enhanced as needed with Adobe<sup>®</sup> Photoshop.

By combining layers into substack images, and using these images showing cascading focal planes to retouch the output image it is possible to show only the structures needed for the view desired for illustration (Figs 1, 13–20). For transparent structures it is difficult to show only the dorsal or ventral surface without this stacking and retouching method using present software technology. A longitudinal section of the transverse trabecula shows the inrolled cuticle (Fig. 21). The specimen from which this image was made, by I. Mikó, University of New Hampshire, was imaged between two #1.5 coverslips with a Nikon A1R-HD CLSM at the University of New Hampshire Instrumentation Center. Three excitation wavelengths were used, 409, 487, and 560 nm, and three emission ranges of 435–470, 500–540, and 570–645 nm. The resulting image sets was assigned pseudo-colours that reflected the fluorescence spectra. Volume-rendered micrographs and media files were created using FIJI (Schindelin *et al.* 2012).

#### Results

#### **OVERVIEW OF EXTERNAL MORPHOLOGY**

In this section we provide a general overview of infraspecific variation, morphometry, coloration, secondary sexual dimorphism, setation and sculpture in Mymaridae.

Intraspecific variation. Determining the limits of intraspecific variation within species that result from various factors, particularly geographic distribution, host, and/or phenology in species with several generations per year, is a persistent problem in taxonomy. In Mymaridae, most species have been defined and distinguished on the basis of females only, usually because interspecific features have been found mainly on this sex. Males often cannot be correctly associated with conspecific females so are generally ignored. In a few genera (Dicopomorpha, Litus, Platystethynium) males of some or all of the species are very rarely collected. For some genera males are still unknown or, perhaps, have not yet been correctly associated, even generically, with their corresponding females. Examination of numerous, well prepared, card- or slide-mounted specimens of a species often reveal considerable individual variation. The obvious differences are between conspecific males and females (see below). Differences may also occur in body length, and measurements and ratios of various body parts, and in colour, though less so in colour pattern. Other differences are most evident in laboratory colonies where numerous individuals are available for study but where inbreeding is unavoidable; deformed antennae are often found, including partial to complete fusion of flagellar segments, reduction or partial fusion or, more rarely, increase in the number of mps, and distortions such as shortened, enlarged, or crooked mps. In the field, gynandromorphs are occasionally found, where one antenna is female and the other male, such as for one specimen of *Erythmelus* and one of *Polynema* in the CNC. Elsewhere on the body, displacement, duplication or loss of one of the campaniform sensilla on the scutellum, or loss or duplication of setae on any part of the body can occur. Exceptionally, a specimen is collected in which an entire tarsal segment is lost (Huber & Thuróczy 2018, fig. 102). Intraspecific variation may occur within the same sex due to rearing from different hosts (see Huber & Rajakulendran 1988). Describing new species on the basis of one or very few individuals or basing a new species on only a slight difference in a single morphological feature is therefore discouraged unless non-morphological evidence supports their recognition as likely a "good" species.

**Morphometrics**. Mymaridae include the smallest known insects. Some males of *Dicopomorpha echmepterygis* measure as little as 130 µm in length but are aberrant in that they are wingless, eyeless, and have reduced segmentation in the tarsi and antenna (Huber & Noyes 2015; Huber *et al.* 2020, figs 356–369). Because most Mymaridae are 1 mm or less in length the most appropriate unit of measurement in descriptions is a micrometer (µm), with the only exception perhaps being for body length. General but useful descriptive terms for body length may thus conveniently be defined as follows: minute, less than 0.2 mm or 200 µm (some *Alaptus, Kikiki, Dicopomorpha* males); small, 0.2–0.5 mm or 200–500 µm (females of *Dicopomorpha*, many other genera); medium, 0.5–1.0 mm or 500–1000 µm (most genera); large, 1.0–2.5 mm or 1000–2500 µm (some genera); very large, greater than 2.5 mm or 2500 µm (some *Australomymar, Erdosiella, Megamymar, Neotriadomerus, Paranaphoidea*). Specimens of most species are 300–1200 µm in length. Within a given genus there may be a considerable range among the included species, covering several of the above categories.

Fully winged specimens of any species are best for comparison because the smallest of them are normal in appearance, with all appendages and sensory organs fully developed. Their body length, excluding the antenna and the portion of the ovipositor that projects posterior to the apex of the gaster, ranges from 160  $\mu$ m (0.16 mm), for some specimens of Kikiki to 5000 µm (5.0 mm) for Neotriadomerus longissimus Huber, and an undescribed Australomymar sp. from New Zealand (Huber 2017) with an ovipositor over twice that length when extended. In the Nearctic and Neotropical regions, the longest species belong to Acmopolynema varium Girault at 2500 μm (Huber et al. 2020) and Megamymar waorani Huber at 4800 μm (Huber & Read 2022), respectively. The largest Oriental species (in an undescribed genus) is about 2800 µm in length. Measurement of body length is often somewhat inaccurate because of shriveling of the head and metasoma in air-dried specimens and, possibly, slight enlargement of the metasoma in critical-point-dried specimens. Cleared and slide mounted specimens can be measured more accurately but up to 25% increase in length, mainly of the metasoma, may occur due to maceration in KOH (Triapitsyn 2019; Huber 2021; Huber & Read 2022), and it is often difficult to prepare a specimen with the head oriented vertically for accurate measurement. Intact bodies, i.e., with head still attached to mesosoma, that are slide mounted in lateral view are best for measurement of body length (excluding exserted part of ovipositor). Air-dried, chemically dried or critical-point dried specimens, especially those with a petiolate gaster, may also have the metasoma not exactly in line with the rest of the body so they cannot be accurately measured in either dorsal or lateral views. Debauche (1948, fig. 1) measured body parts of specimens mounted in lateral view and then added the measurements together to obtain total body length but this can be slightly misleading (see under Head, below). Body length gives a useful overall size of specimens and rounding to the nearest five micrometers is probably sufficient, except for the smallest species. In any case, considerable intraspecific size variation often occurs, making extremely accurate (to the nearest micrometer) body length measurements unnecessary and pointless.

Measurements and ratios of various structures are needed to define species so unambiguous definition of the end points of the structure being measured is essential for accuracy, repeatability and comparison. Absolute measurements and ratios of the antennal segments and wings of females are the most needed and used for species identification and description. Specimens cleared in KOH and permanently mounted in lateral view on slides are best used to measure many body parts such as the ovipositor length (ovipositor sheath length is usually preferable because the end points are easier to determine), and proportions of the various appendages. However, in practice, it is often difficult to get all the parts completely flat for accurate measurement. Because measurements of cleared specimens may be greater than for critical point dried specimens both should be measured, if possible. If the specimen is flattened almost to the point of being crushed the parts can be accurately measured but the specimen may then be unsuitable for photography because the head, mesosoma and/or gaster are more or less squashed, and thus are distorted or broken. Detached wings mounted flat in Canada balsam under a separate coverslip are best (and easiest to prepare) for accurate measurement.

**Colour**. Colour, if pigment (chemical) based, may fade with time in dry, pinned or card-mounted specimens, especially if exposed to light, whereas structural (physical) colorations will not fade (a very few Mymaridae have the latter). Specimens kept in ethanol or other preservative for more than a year or two at room temperature, even when kept in the dark, will fade even more quickly than dry specimens. Black will fade to brown, and yellow will fade to almost white. Therefore, for colour to be described correctly, it is important to describe it from fresh specimens, when possible. For best colour retention dry specimens should be kept in the dark and liquid-preserved specimens in a freezer (-20°C) until they can be critical-point dried or chemically dried and then card or point mounted. They may also be kept in small gelatin capsules pinned in a dry collection; these may later be used for SEM or perhaps for extraction of DNA. Colour may change slightly as the cuticle of freshly emerged (callow or teneral) specimens sometimes have a red gaster, e.g., some *Gonatocerus* and *Lymaenon*, perhaps resulting from assimilation of products from the host egg, but the colour soon disappears as the adult hardens and full sclerotization is attained. The specimen is then typically yellow or brown. Teneral adults of species that are dark coloured may also have light markings on the head, especially the vertex, and H-like markings on the mesothorax that disappear when the adult is fully sclerotized (Huber 2015, fig. 5).

Most Mymaridae are black or various shades of brown or yellow, either uniformly so or with various patterns of light and dark markings. It may be difficult to distinguish between a final adult pattern of light lines and a similar pattern if the specimen happens to be teneral; the sclerotization of the head may indicate which is which. Regardless of whether the body is mainly light or dark coloured, those parts that undergo high stress or unusual wear and tear or provide structural support are strongly sclerotized and dark, e.g., apical tarsomere of each leg, mandibular teeth, oral cavity rim, postocciput, and ovipositor sheaths. Internally, the tentorium (Figs 19, 20) and perhaps the hypostoma, are also dark. The trabeculae (Figs 1, 13) are dark because they consist of several layers of inrolled cuticle, though each layer is comparatively relatively thin (Figs 21a,b). In Figs 21a,b, the colours are pseudo-colours that reflect the fluorescence spectra used. The two, fused, layers of cuticle are distinguished by a reddish layer that is more sclerotized and the greenish layer that is less sclerotized. The inrolled trabecula is not enriched with resilin, but the bluish regions of other head tissue shown in the figures are resilin rich. Members of some species of *Dicopomorpha* may have a distinct mother-of-pearl (opalescent) sheen, and some of *Anaphes* and *Himopolynema* have a distinct blue sheen.

Body colour pattern in males and females of a species is usually similar. When differences occur, as in most species that are light in colour, i.e., not uniformly black or dark brown, the male almost always has more extensive dark areas. In these species, females may be predominantly yellow whereas the corresponding males are light to dark brown or at least have larger areas of brown, on the gaster in particular. Exceptionally (*Parastethynium*), the male is distinctly lighter than the female, and species whose males are highly modified (*Platystethynium*) and probably do not leave the host egg, are also lighter in colour. Colour differences between males and females is perhaps mainly due to different physical requirements. The generally darker males (in light-coloured species) probably reflect their need to fly more in search of females. A darker body probably allows faster absorption and retention of heat, needed to rapidly warm (and perhaps keep warm) their flight muscles. Females presumably spend relatively less time flying except to disperse, and more time searching for host eggs by walking around in microhabitats and on substrates in/on which their host eggs are laid. Body colour can sometimes be correlated with adult habitat preferences. Both sexes of species partly or entirely associated with water, e.g., *Eustochus (Caraphractus)* and *Ptilomymar*, or soil and

mosses, e.g., *Eubroncus, Eustochus (Eustochus)* and *Litus*, are heavily melanized, and therefore usually uniformly dark brown or black. Heavy sclerotization better protects against abrasion and accidental crushing as the individual moves around. Both sexes of species that parasitize eggs of hosts laid on or in plant tissue and/or species that are weakly sclerotized and therefore relatively soft bodied, e.g., *Anagrus, Erythmelus, Gonatocerus, Omyomymar*, are often light coloured. Species living in forests, perhaps other than in the sunlit canopies, and cold places (arctic or alpine) are usually dark brown or black, probably to absorb more heat. Thus, tropical species of many genera are yellow or patterned with brown, whereas those occurring at high altitude or latitude are dark brown or black. Regional patterns may occur, e.g., in the tropics, species from several, unrelated genera have a white clava in females. There are, of course, many exceptions to the above generalizations, e.g., most species of *Polynema* and *Stephanodes* are dark brown, regardless of habitat or provenance.

Wings typically are more or less hyaline in most species, except for a very narrow brown margin, e.g., most *Anaphes*, except basally behind the venation where the brown suffusion is usually more extensive. Some species of many genera, e.g., *Acmopolynema, Camptopteroides, Richteria*, may have patterned wings, usually as brown spots or bands on the fore wing.

**Secondary sexual dimorphism.** Apart from the obvious differences in the external and internal genitalia, other differences between males and females may occur in the head and gaster. Sexually dimorphic differences may be correlated, e.g., mandible length is often correlated with gena length, the mandible being longer or stouter the more developed the gena. Presumably a more developed gena is necessary for the more massive muscles that are needed to operate the correspondingly larger mandibles, e.g., males of *Krokella*, *Omyomymar* and *Tanyxiphium* have a longer gena and wider head than corresponding females. If sexual dimorphism occurs in the mesosoma it is associated with extreme wing reduction in one of the sexes, e.g., *Chrysoctonoides, Chrysoctonus, Platystethynium*.

Secondary structural dimorphism may include differences in:

- 1. Spiracle on  $mt_8$  (=  $gt_6$ ). Present in female, always (?) absent in male.
- 2. Wings. Shortened or absent in female and present in male, though sometimes vice versa.
- 3. Mandible. Sometimes relatively larger in one sex, usually the male (Krokella-A40a,b; Omyomymar-A51a,b).
- 4. Gena. Sometimes longer in male (Erdosiella-D26a,b; Omyomymar-D52, D53).
- 5. Ocelli. Sometimes larger in male.
- 6. Eye. Smaller or larger in one sex.
- 7. Scape (or radicle only). Shorter in male.
- 8. Flagellum. Length, shape, and number (except in *Neotriadomerus*) of flagellomeres and their sensilla, particularly the multiporous plate sensilla.

Setation (mechanosensory sensilla). Mymaridae have relatively few mechanosensory sensilla on the head and mesosoma. They include setae (tactile mechanoreceptors), which are usually very noticeable, and campaniform sensilla (proprioceptors), which are usually only seen in cleared specimens. Both types occur in nearly the same locations on each sclerite, regardless of the genus. Ghiradella (2010) classified setae into two types, microchaetae and macrochaetae, but for the purpose of this paper we refer to all simply as setae. Setae are more numerous on the metasoma, and most numerous on the antenna, mouthparts and legs. Sensilla, in general, are most diverse in structure and function on the antenna and the mouthparts. The most numerous are setae but several other types occur, such as gustatory and olfactory receptors (Chiappini 2001). The setae on the legs and the metasoma are fairly uniform, with the most obvious difference being the four elongate setae arising from the cerci. The number and position of setae and their length, thickness and shape of apex (blunt, acute) may be helpful to define or distinguish between taxa. Setation is treated at the end of the discussion of each body part.

**Sculpture**. Sculpture may be entirely absent so the cuticle surface is completely smooth, but when present may be conveniently divided into microsculpture and macrosculpture. Microsculpture is a superficial pattern on the cuticle that mirrors epidermal cell borders and is thus unicellular in origin. When microsculpture is present, the "mesh" is the margin, outline or imprint of the cell and has a wide variety of shapes, from isodiametric to stretched in various directions. The part within the outline or mesh is a cell imprint or sculpticell (Allen & Ball 1980; Schiff *et al.* 2012) and it never has a sensory structure within it. A sculpticell outline is either impressed below the level of the sculpticell or is raised above the level of the sculpticell. Hereafter, sculpture defined by impressed lines is termed "engraved" whereas that defined by ridges is termed "raised". The microsculpture of most mymarid

genera is engraved, with the sculpticells flat (*Camptopteroides*-A14, C14) or, rarely, convex (*Erdosiella*-E25b), or sometimes appearing concave like a golf ball (*Camptopteroides* (*Alalinda*)-C14) or, rarely, shingle-like, in which one side of a sculpticell is higher than the other so the sculpticells look like fish scales and appear to overlap (scape of *Stephanodes*), or wrinkled, in which the sculpticells are not distinct but the cuticle is slightly wavy (*Krateriske*-C40). When taxonomic publications are illustrated with good-quality images of the body sculpture there is usually no need to use any of the numerous terms described in Eady (1968) or Harris (1979); description of the shape of the sculpticells suffice, e.g., the sculpticells longitudinally reticulate, or isodiametric, etc. The microsculpture of specimens of Mymaridae is fairly uniform, and reference to an appropriate image usually eliminates the need for detailed descriptions and terms with highly specific meanings.

Macrosculpture is multicellular and does not correspond to the borders among epithelial cells. It includes pointlike structures (punctures or punctations), line-like structures (sulci or grooves) that are below the cuticle surface, i.e., invaginations, and carinae that are above the cuticle surface, i.e., evaginations [see diagrams in Ronquist & Nordlander (1989)]. Deep invaginations of the epithelium are pits, e.g., the anterior and posterior tentorial pits of all genera, the pits between the toruli of a few genera that are deeper than wide (*Platyfrons*-A57, *Palaeoneura* (*Doriclytus*)-A58), or that are on the vertex and are shallow, much wider than deep (*Palaeoneura*-C54, *Stephanodes*-C69a–c, *Tetrapolynema*-C72). Multicellular structures also include setae and other sensory structures, and always appear between or at the junction of the sculpticells. The setae and campaniform sensilla on the wings occur almost entirely on the venation and as fringe setae around the wing edge. The various sclerites of the head are discussed separately below and, where relevant, sculpture and setation are treated after each.

# ATLAS OF HEAD MORPHOLOGY

Major head regions and morphometrics. The head capsule or cranium is a sclerotized box/capsule with rounded corners and four openings-two anteriorly for the antennae, one ventrally (the oral cavity) for the mouthparts, and one posteriorly (the occipital foramen) to allow passage of internal structures, e.g., the alimentary canal, blood vessels, and nerves into the rest of the body. All Mymaridae have an orthognathous head, with the oral cavity located ventrally. In anterior or dorsal views, the greatest width is usually greater than the height or length, respectively. In lateral view, the height is almost always greater than the greatest length. Thus, almost always, head width > head height > head length (Goulet & Huber 1993, fig. 1). In dorsal view, the posterior margin is more or less strongly concave so head length differs depending on whether measured medially or sublaterally. The head posterior margin is slightly concave (Anaphes-C6, Cosmocomoidea-C19, Litus-C42, Stephanocampta-C68) to strongly concave (Alaptus-C3, Camptoptera-C12, Dicopomorpha (Dicopulus)-C23), often straight (Arescon-C8, Callodicopus-C11, Boudiennyia-C10, Ischiodasys-C37) or, exceptionally, convex (Eubroncus-C29). In lateral view, the anterior margin is often more curved than the posterior margin and sometimes is strongly angular (Anagroidea-D4, Ceratanaphes-D15, Eubroncus-D29) or almost straight (Erythmelus-D27, Eubroncus-D29, Zeyanus-D75). Because the anterior margin of the head in dorsal view is usually somewhat convex, its midpoint logically should be taken as the anterior limit when measuring head (or body) length, but in practice taking these measurements in dorsal view from the anterior margin of the transverse trabecula is more accurate and gives a more consistent measurement. To obtain its greatest length, the head in lateral view is measured at its widest point. When adding head length from a separated head to the mesosoma + metasoma length to obtain total body length the head in dorsal view must be measured at its midpoint because it tends to "wrap around" the anterior margin of the pronotum, overlapping it slightly. If both are measured in lateral view, adding a separately measured head length to mesosoma + metasoma length would give a total body length that is slightly greater than it actually is. Heads that are strongly triangular in lateral view (Eubroncus-D29, Platystethynium, Huber & Read (2021, fig. 8)) have the head length greater than its height; most heads are rectangular, however. Thin heads (some Erythmelus-D27, Zeyanus-D75) have a width up to 2.0× its length, whereas thick heads (*Cnecomymar*-C18, *Stephanodes*-C69c) have a head width about  $1.3-1.4\times$ its length. Exceptionally (*Eubroncus*-C29) width is about  $0.9 \times$  length. Head shape is best described using the three different views, anterior, dorsal and lateral. In addition, the degree of curvature of the various sclerites and the angles of junction between them, in particular the angle between the face and vertex, or vertex and occiput, should be described. In anterior view the head narrows more or less distinctly to the oral cavity.

Trabeculae, sulci and head regions. Trabeculae are bars of inrolled cuticle (Figs 21a,b; Ogloblin 1960, fig. 4)

whose presence on the head defines unequivocally, and apparently without exception, all members of Mymaridae and distinguishes this family from other Chalcidoidea. Polilov (2017, fig. 7c) illustrated the head of Megaphragma mymaripenne Timberlake (Chalcidoidea: Trichogrammatidae), which shows cross sections of cuticular folds that appear to be trabeculae but these are not the same as the trabeculae of Mymaridae. Ogloblin (1935) coined the term "trabecula" and named them the transverso-frontal, interno-orbital, and frontal trabecula, whereas Debauche (1948) used different terms (transversal, frontal, susorbital). This was because he was unaware of Ogloblin's paper, as explained by Ogloblin (1960), who confused one of Debauche's terms when identifying them with his own. Partly different terms are used here, as shown in, for example, Huber et al. (2015), Huber & Thuróczy (2018) and Huber et al. (2020). The transverse trabecula (Fig. 1: trt) extends horizontally between the eyes and separates the dorsal margin of the face from the anterior margin of the vertex; it is entire and straight. The preorbital trabecula (Fig. 1: **pot**) extends almost always from the lateral apex of the transverse trabecula and is directed usually lateroventrally to the inner eye margin and then continues ventrally for a short distance to the lateral edge of the torulus, ending at about its mid-height; it is the shortest trabecula, though it continues ventrally as the preorbital sulcus (see below). The supraorbital trabecula (Fig. 1: sot) extends longitudinally along each side of the vertex parallel for at least part of its length to the dorsal margin of the eye and closest to the eye at the trabecula midpoint. It begins anteriorly, usually at the junction of the transverse and preorbital trabeculae, and ends posteriorly at about the level of lateral ocelli. Rarely, the supraorbital trabecula is separated, even at its midpoint, by a distinct gap from the eye (Ceratanaphes-C15). The supraorbital trabecula is either entire or, more often, divided into two or more (seven in some Camptoptera) parts separated by unsclerotized (light in colour) cuticle and is usually straight but sometimes evenly bowed outwards or slightly angled at about its midpoint. Anteriorly, the supraorbital trabecula usually meets the transverse trabecula but sometimes (Anaphes-A6) it continues unbroken ventrally along the inner eye margin to about the mid-height level of the torulus before extending ventrally as the preorbital sulcus; a separate preorbital trabecula is, however, still present.

Because the trabeculae consist of at least two layers of inrolled cuticle (Figs 21a, b; Ogloblin 1960, fig. 21), they appear to be heavily sclerotized and dark in colour under light microscopy. However, each layer is sometimes and, in part, no more sclerotized or darker than the surrounding cuticle, e.g., Callodicopus [Huber et al. (2021), fig. 351]. When this is the case the trabeculae (most often the supraorbital trabecula) appear to be broken into short sections, as in Alaptus, Camptoptera, and Dicopus (see Huber et al. 2020). Because under light microscopy the trabeculae appear as thickened bars darker than the surrounding cuticle, Debauche (1948) referred to them as carinae, but they are clearly not carinae in structure. In micrographs, all that is visible are sutures associated with the trabeculae (cf. Figs 1, 2), i.e., a transverse suture dorsal to the toruli that extends between the eyes that separates the face from the vertex, a suture laterally along the vertex that separates it from the dorsal rim of each eye, and a short, oblique suture extending from the end of the transverse suture to the inner rim of the eye and ending at the torulus at mid height. These sutures/sulci are the demarcation lines between what appears to be four separate sclerites comprising the top, front and sides of the head. These apparent sclerites are the vertex (region dorsal or posterior to the transverse suture), the face (region ventral to the transverse suture and between the eyes, see further below), and the two eyes, each surrounded by a narrow cuticular rim. It is emphasized here that the head "sclerites" represent secondary subdivisions of the head, not the morphologically separate sclerites that originally fused to form the head capsule in primitive insects. In colour photographs, the trabeculae are clearly seen as well as the parascrobal area, which is the area dorsolateral to each torulus between the eye and the junction of the trabeculae (Fig. 1). Both micrographs and photographs are needed to determine exactly how the trabeculae meet at their common junction. Posteriorly, the supraorbital trabecula may extend for a short distance, at a right angle towards the lateral ocellus (Huber 2020, fig. 5). The supraorbital trabecula and sulcus may extend ventrally onto the occiput, rarely as a sclerotized bar broken into short segments (Huber 2020, figs 165, 186), more often as a sulcus (see below). In micrographs, it is visible only as the sulcus (Callodicopus-B11). The trabeculae are often separated from each other by unsclerotized cuticle (conjunctiva) at their junction dorsolateral to each torulus. A transverse structure posterior to the lateral ocelli that is dark like a trabecula (it also consists of inrolled cuticle) occurs only in *Callodicopus* and *Dicopus* (Huber et al., 2020, figs 165, 372–374) but in micrographs it appears to be a modified vertexal sulcus (Callodicopus-B11, Dicopus-B23) (see below).

Lateral to the supraorbital and preorbital trabeculae are the sulci that separate the trabeculae from the dorsal and inner rim of the eye. The eye rims are usually so narrow they are not visible, at least in micrographs. A **parascrobal area** (Fig. 1: **psa**) next to each inner eye rim and bordered medially by the junction of the three trabeculae, is usually

present; its widest point is at the level of or just ventral to the apex of the transverse trabecula. The parascrobal area is sometimes large (*Ceratanaphes*-A15, *Cleruchus*-A17), sometimes narrow and linear (*Camptopteroides* (*Alalinda*)-A14), and sometimes apparently absent (*Ptilomymar*-A62). In photographs, a large parascrobal area may occur medial to the anterior apex of the supraorbital trabecula in addition to a small one lateral to the supraorbital trabecula (Huber *et al.*, 2020, fig. 87 *Anagrus*). The **vertexal sulcus** (Figs 4, 6: **vts**) is posterior to the lateral ocelli and is usually present. It extends transversely between the eyes from the posterior apex of the supraorbital trabecula extension onto the occiput so sometimes is at the dorsal margin of the occipital foramen. It is usually divided medially into two parts (*Callodicopus*-B11, *Dicopus*-B23) but sometimes appears continuous (*Arescon*-B8, *Omyomymar* (*Caenomymar*)-B47). The **supraorbital trabecula extension** (Figs 3, 5: **sse**), when present, is most often a sulcus only (*Anaphes*-B6, *Callodicopus*-B11). It extends ventrally onto the occiput and is either aligned with the supraorbital trabecula or it is angled medially towards or to the dorsolateral apex of the occipital foramen, or sometimes both in the same genus, e.g., *Anaphes* (Huber & Thuróczy 2018, figs 4, 33).

In Mymaridae the face appears as a distinct sclerite separated by the transverse trabecula from another apparent sclerite, the vertex; therefore, the term frontovertex, which is often used in older literature for the combined frontal surface of the head above the toruli and dorsal surface of the head, is confusing and should not be used. The posterior region of the head is conveniently treated as a sclerite as well but is not often clearly demarcated ventrolaterally (ventral to each eye) or posterodorsally (posterior to the vertex). A fifth, ring-like area, the postocciput, encircles the occipital foramen. In addition to the above, measurements help define head shape. The measurements are relative and best given as ratios, and include face height/width (best measured at the level of lower margin of torulus from one inner eye margin to the other), vertex length/width (from posterior margin of lateral ocelli to transverse trabecula), gena width at dorsal and/or ventral edges of eye, gena length relative to eye length, and malar space relative to eye height. Measurements may be complemented with degree of curvature, e.g., face ventral to eyes strongly or weakly curved medially towards oral cavity, and angles, e.g., vertex meeting occiput at right angle or obtuse angle, and either sharply margined or blunt and rounded.

Face. Structure. The front of the head (Figs A1–A73) consists mostly of the face, the area between the eyes that extends from the ventral margin of the transverse trabecula to the anterior margin of the oral cavity. At about the midheight of a torulus the preorbital trabecula, which is taken to be the lateral edge of the face, becomes the **preorbital** sulcus (Figs 1, 2, 8–10: pos), which continues ventrally along the inner rim of the eye for a short distance before diverging from the inner orbit at about its midpoint and continuing ventrally towards the anterolateral angle of the oral margin. The face width is the horizontal distance between the preorbital sulci. Because the face often narrows ventrally due to a slight convergence of the preorbital sulci, the level at which the face width is best measured is at the ventral margin of the antennal foramina, which is its widest point. The face limits described above are the best for height and width measurements because the dorsal, lateral and ventral face edges are all unambiguous and clearly visible in both photographs and micrographs. In anterior view, the face is usually slightly higher than wide, though sometimes wider than high (Paracmotemnus-A55) and rarely up to 4× as wide as high (males of Platystethynium, Huber & Read, 2021, fig. 13a). The area dorsal to the ventral margin of the torulus is the upper face (Figs 1, 2: upf). Its height is the distance from the ventral margin of the torulus to the ventral margin of the transverse trabecula. The area ventral to the torulus is the lower face (Figs 1, 2: lof). Its height is the distance from the ventral margin of the torulus to the anterior margin of the oral cavity. The upper face is much wider than high whereas the lower face is about as high as or clearly higher than wide. For practical reasons, face measurements, if useful, e.g., perhaps for species of *Eubroncus* and of the *Cleruchus* group of genera, should be of the lower face only. For other genera, two width measurements of the face might sometimes be useful, one just ventral to the toruli and one at the widest point of the face because the lower part of the preorbital sulcus slightly bulges laterally (Camptopteroides-A13, A-14, Krateriske-A39). The upper face and about half or more of the lower is sometimes more or less depressed medially and submedially, so the dorsal halves of the lateral margins appear distinctly raised (Nepolyema-A49, Stephanodes-A67, D69b). Exceptionally, a prominent rectangular elevation is present (Eubroncus-A29, C29, D29). A more or less well demarcated depression may occur dorsal to each torulus, the antennal scrobe (Fig. 2: scr) (Anagrus-A5, Cosmocomoidea-A19, Krateriske-A39, Omyomymar-51a, Ooctonus-A52, Stethynium-A68). A vertical facial sulcus (Fig. 2: vfs) sometimes occurs medially between the toruli and extends from the transverse trabecula (Agalmopolynema-A2, Cnecomymar-A18, Neomymar-A46, Omyomymar-A51a). Occasionally, a small pit occurs next to the medial margin of each torulus (Polynema (Doriclytus)-A58, Stephanodes-A67). The clypeus (Fig. 2: cly) is the lower area of the face between the anterior tentorial pits. Its dorsal and lateral margins are rarely defined

in Mymaridae but if so then only faintly (Alaptus-A3, Anagrus-A5, Arescon-A8, Cremnomymar-A21, Erdosiella-A26b). A tentorial pit, when visible, indicates the ventral point of the lateral margin of the clypeus. In most genera the clypeus cannot be distinguished, but if it is evident its limits (as the clypeal area) could be taken arbitrarily and conveniently (though not strictly accurately) as a wider area margined laterally by the preorbital sulci and dorsally by the transverse sulcus between them (Erythmelus-E26, Erythmelus (Parallelaptera)-E27). The ventral margin of the clypeus is often slightly inflected into the oral cavity (Acmopolynema-F1) but sometimes projects slightly as a distinct rim between the anterior tentorial pits (Arescon-F8). A straight or curved subantennal sulcus (Figs 1, 2: sas) is sometimes present and extends ventrally from the medioventral margin of the antennal foramen towards the oral cavity. It is thin and sharp (Gastrogonatocerus-A33, Gonatocerus-A34, Stethynium-A68) or wider and more diffuse (Ceratanaphes-E15, Cremnomymar-A21, Kalopolynema-A37, Palaeoneura-A53, Schizophragma-A64). When the subantennal sulcus extends almost to oral cavity it sometimes curves sharply towards the lateral margin to join the preorbital sulcus, forming a weakly defined, narrow, horizontal epistomal area dorsal to the oral margin (Anneckia-E7, Gahanopsis-E31, Gastrogonatocerus-E32, Gonatocerus-E33). In lateral view, the face bulges anteriorly ventral to the toruli, either just ventral to or at some distance ventral to the toruli and almost always recedes slightly to the oral cavity. If the face recedes strongly then there is a sharp angle at or just ventral to the ventral margin of the antennal foramen. There has been a concomitant change in the adductor muscle origin from the gena to the frons with a great anterior prolongation of the face and vertex. Consequently, in lateral view the face (and therefore the entire head) is triangular (Anagroidea-D4, Ceratanaphes-D15, Cleruchus-D17, Eubroncus-D29). In ventral view, the ventral part of the lower face bulges anteriorly, sometimes extremely so (Eubroncus-D29) and the dorsal part of the lower face appears relatively depressed, especially submedially and sometimes also medially though the median area is also sometimes raised. The level at which the change occurs is more or less ventral to the ventral edge of the toruli.

*Sculpture*. Within a given genus, the face of different species can have different microsculpture (*Dicopomorpha*-A22a-c) and/or setation (*Stephanodes*-A67a-c). The face is often entirely smooth (*Acmopolynema*-A1, *Boudiennyia*-A10, *Ischiodasys*-A36, *Neomymar*-A46), but if microsculpture is present it is restricted to some parts of the face (*Omyomymar*-A51a,b) or covers almost the entire face (*Anagroidea*-A4, *Anagrus*-A5). If the microsculpture is engraved it is usually indistinct, and either transverse (*Dicopomorpha*-A22b) or vertical (*Lymaenon*-A42) or both (*Stethynium*-A68) or more or less isodiametric (*Callodicopus*-A11, *Eustochus*-A30). If the microsculpture is raised it is usually distinct (*Anagroidea*-A4, *Litus*-A41, *Macrocamptoptera*-A43, *Richteria*-A63).

Setation. The upper face dorsal to the dorsal margin of the toruli is almost always asetose but rarely (*Eubroncus*-A29, *Gahanopsis*-A32, *Pseudanaphes*-A61) a few setae occur. Between and sometimes just ventral to the toruli, no setae (*Acmopolynema*-A1, *Erdosiella*-A26, *Kalopolynema*-A37, *Platyfrons*-A57), 1 seta (*Anagrus*-A5, *Anaphes*-A6, *Cleruchus*-A17, *Gonatocerus*-A34) or several setae (*Australomymar*-A9, *Krateriske*-A39, *Lymaenon*-A42) occur. The parascrobal area has 0 (*Ptilomymar*-A62), 1 (*Boudiennyia*-A10, *Camptoptera*-A12), 2 (*Camptopteroides*-A13) or 3+ (*Anaphes*-A6, *Australomymar*-A9) setae. The lower face usually has setae, usually sublaterally and laterally, from 2 (*Chrysoctonus*-A16, *Dicopomorpha*-A22) to many (*Erdosiella*-A26a, *Mymar*-A44, *Neotriadomerus*-A48). The median area of the lower face is usually asetose (*Cremnomymar*-A21, *Heptagonatocerus*-A35) but sometimes setose (*Erdosiella*-A26a, *Neotriadomerus*-A48, *Tetrapolynema*-A70). The setae are usually uniform in thickness and length but rarely with variable lengths and thickness (*Proarescon*-A60).

Antennal foramen. The antennal foramina are almost always closer to the inner rims of the eyes than to each other. Each foramen is surrounded by a sclerotized ring, the torulus (Fig. 1: tor), onto which the base of the antenna connects to the head and through which the haemolymph, muscles, nerves and tracheae of the antenna pass. The actual point of articulation is a small triangular sclerotized projection, the **antennifer** (Fig. 1: **afe**), that extends into the antennal foramen from the ventrolateral margin of the torulus. The foramen and torulus are circular (*Cnecomymar*-A18, *Polynema*-A58, A59, *Ptilomymar*-A62, *Stephanocampta*-A66) to triangular and higher than wide (*Alaptus*-A3, *Anagrus*-A5, *Cleruchus*-A17, *Omyomymar*-A51a,b, *Schizophragma*-A64), which may be accentuated by a shallow antennal scrobe (*Stethynium*-A68). The foramen is high on the face, with its dorsal margin touching the frontal trabecula (*Mymar*-A44, *Ptilomymar*-A62) to low on the face, with its ventral margin almost touching the mouth margin (*Platystethynium* males). Usually it is from 0.5–1.5× its vertical diameter from the transverse trabecula (*Acmopolynema*-A1, *Anaphes*-A6, *Boudiennyia*-A10) or even 2× (*Stephanodes*-A67).

**Tentoriun and tentorial pits**. The tentorium (Figs 19, 20: **ten**) is a rod-like invagination of the cranial wall and hence it is not visible in SEM micrographs. It can only be studied in cleared and slide-mounted specimens. The only

tentorial structure visible on some micrographs is the tentorial bridge (Figs 14, 19b, 20: **tbr**) (*Cosmocomoidea*-B19a, *Gahanopsis*-B31). The tentorium is usually H-shaped with the tentorial bridge much closer to the posterior than the anterior apices. The two long arms are usually straight and diverge to the anterior tentorial pits but occasionally (*Erythmelus*, Fig. 19b) the arms are concave, with the shortest distance between them medially, or convex (*Cleruchus*, Fig. 20), with the longest distance between them medially. The longitudinal arms are about equally wide apart at the anterior and posterior tentorial pits. The **anterior tentorial pits** (Fig.11: **atp**) are at the ventral margin of the face just outside the rim of the oral cavity but are often not visible externally. Each pit is large (*Boudiennyia*-F10, *Erdosiella*-F25, *Eustochus*-F29, *Narayanella*-F42) or small (*Neomymar*-F43, *Schizophragma*-F62, *Stephanocampta*-F64) and usually circular but sometimes transverse and slit-like (*Arescon*-F8, *Camptopteroides*-F13). Each pit is usually at the anterior margin of the oral cavity but sometimes is located more submedially, just above the anterior margin of the oral cavity on the postocciput but are only occasionally visible (*Chrysoctonus*-B16, *Gonatocerus*-B33, *Parastethynium*-B52).

**Oral cavity**. Anteriorly the oral margin includes the **clypeal margin** (Fig. 11: **clm**) medially, between the anterior tentorial pits, and the **paraclypeal margin** (Fig. 11: **pcm**) laterally, which extends to the preoral sulcus or, if present, the malar sulcus where these meet the oral margin. The oral cavity is slightly (*Stephanodes*-E62) to considerably (*Camptoptera*-E12, *Stephanocampta*-E61) wider than long. It is rimmed by unevenly thickened cuticle. In anterior view, the rim is usually thickest dorsolaterally and in ventral view the rim is thickest anterolaterally. The median section of the anterior rim is less or not at all thickened. In posterior view the rim is apparently not thickened when visible (it is usually hidden by the maxillae). In anterior or ventral views, the anterior and lateral margins of the rim are straight or slightly convex, in posterior view the dorsal margin (if visible) is straight (*Camptoptera*-B12, *Cleruchus*-B17) to strongly convex (*Anaphes*-B6) to weakly M-shaped (*Erythmelus*-B26). In posterior view, the oral cavity is either closed dorsally and separated from the occipital foramen (*Acmopolynema*-B1, *Anagroidea*-B4, *Arescon*-B8, *Zeyanus*-B68) or apparently open dorsally and confluent with it (*Alaptus*-B3, *Camptoptera*-B12, *Camptoptera*-B13, B14, *Litus*-B38). If open, the oral cavity is apparently much higher than wide (*Dicopomorpha*-B21, *Macrocamptoptera*-B40), although the maxillae would have to be completely removed to check this.

Eye. Except for males of *Dicopomorpha echmeptervgis*, all the species have compound eyes (Fig. 1: eye) that are almost always clearly visible in anterior, dorsal and lateral views (also in posterior and ventral views but little can be usefully discussed about those views). In anterior view, the following five measurements may be useful. 1. Eye greatest width (when normal eyes are present) relative to face width measured at the ventral margin of the toruli and from inner edge of each eye—from 0.17× (*Eustochus*-A30) to 0.77× (*Krateriske*-A39). 2. Eye curvature along lateral margin-from strongly convex (Cosmocomopsis-A20, Krateriske-A39, Neostethynium-A47, Paracmotemnus-A55) to weakly convex (Cleruchus-A17, Mymar-A44, Polynema (Doriclytus)-A58). 3. Gena visible or not visible lateral to eye-from not visible (most genera) to aligned with outer margin or slightly visible lateral to eye (Alaptus-A3, Chrysoctonus-A16, Cleruchus-A17, Kalopolyema-A37) to clearly visible at least ventrally (Omyomymar male-A51b, Ptilomymar-A62, Stephanodes-A67). 4. Eye height/malar space length (this is perhaps best determined in lateral view)-from 8.0× (Anneckia-A7) to 1.3× (Chrysoctonus-A16). 5. Eyes with inner margins slightly convergent (Stephanodes-A67a) or divergent (Parastethynium-A56, Zeyanus-A73); this is sometimes best determined by comparison with the preorbital sulcus, which ventrally may or may not strongly diverge from the eye inner margin. In dorsal view, the eye extends to varying extents towards or to the back of the head so the temple is absent (Callodicopus-C11, Dicopomorpha-C22, Gahanopsis-C33, Zeyanus-C75), short (Anneckia-C7, Australomymar-C9), long (Acmopolynema-C1, Agalmopolynema-C2) extremely long (Ptilomymar-C64) or, when the eye is reduced, even longer than the eye length (Chrysoctonus-C16a,b). If temple length is used at all, it is measured in dorsal view from the posterior apex of the eye to the back of the head (Fig. 7: TML). In lateral view, the eye occupies most of the side of the head (Figs D7–D75) and, in ventral view, usually about half of the head (Figs E1-E67). An eye often has several hundred small ommatidia (Fig. 2: omm) (Erdosiella-D26a, Krateriske-D40). Rarely, the eye is more or less reduced, with fewer, larger ommatidia (females of Chrysoctonus-D16, Kikiki-D39). When the ommatidia are appressed against one another, as is usually the case, their outline is hexagonal, but when separated by a gap their outline is circular (Camptoptera-D12, Litus-D42, Ptilomymar-D64). Ocular setae (Fig. 2: ocs) occur among at least some of the ommatidia but may appear to be completely absent (Eustochus (Caraphractus)-D32, Ptilomymar-D64). Setae are usually shorter in length than the diameter of an ommatidium and usually inconspicuous but sometimes fairly numerous, longer and conspicuous (Anneckia-C7,

D7, Eubroncus-C29, D29). Eye shape is best described by its shape in lateral view; it is usually more or less oval, with the anterior edge more rounded than the posterior edge, which is straight, at least in its ventral portion, or sometimes slightly concave medially. The posterior edge is usually more or less strongly oblique so that the ventral edge is narrower and more strongly curved than the dorsal edge, which is wider and less strongly curved to almost straight medially. The longest part of the eye is usually near the dorsal edge. Greatest eye height in anterior or lateral view and greatest eye length in lateral view define eye size. Height/length varies from 1.4× (Erythmelus (Parallelaptera)-D28) to 0.8× (Tetrapolynema-D72). In dorsal or lateral views, the eye occupies the entire side of the head, from the level of the transverse trabecula to the posterior-most point (Dicopomorpha-Figs C22, C23, D22, D23; Gahanopsis-C33, D33; Krateriske-C40, D40; Parastethynium-C57, D58) or, more often, the eye is shorter so a short to fairly long gena is visible. Rarely, the eye is shorter than the temple (*Chrysoctonus*-C16a,b, D16). In posterior view, the eye is barely or not visible (Alaptus-B3, Anagrus-B5, Cleruchus-B17, Kalopolynema-B36), or is more or less visible (most genera) to strongly bulging (Neomymar-B43). In ventral view, the eye contour aligns more (Acmopolynema-E1, Callodicopus-E11) or less (Camptoptera-E12) smoothly with the contour of the gena. In lateral view, the eye, measured from the junction of the eye with the face, occupies less than  $0.3 \times (Chrysoctonus$ -D16) to  $0.8 \times$  the head length (Anneckia-D7). In lateral view, the anterior edge of the eye at torulus level is flush with the anterior edge of the face (most genera) to more posterior than the face anterior margin (Anagroidea-D4 Camptoptera-D12, Camptopteroides-D13, Eubroncus-D29).

**Ocular rim and ocular apodeme**. Although they are not visible in micrographs, these two internal structures are mentioned here because they vary among genera. In cleared slide-mounts, an internal eye rim is visible, almost always with a thicker, somewhat triangular area at the base of the ocular apodeme (Figs 15b, 16). The ocular apodeme is usually long, thin, and apically pointed (Fig. 15b) but occasionally short, thick, and apically blunt (Fig. 16). Rarely, the apodeme is absent because the anterior wall of the rim is so thick it appears to occupy half the eye width.

Gena. Structure. In lateral view the gena (Figs 1-12: gen) is the area on the side of the head posterior to and ventral to the eye. The gena is sometimes defined more narrowly as the area posterior to the ventral half of the eye while the temple is the area posterior to the dorsal half of the eye but in lateral view the junction between temple and gena is arbitrary. Therefore in Mymaridae, for convenience, the temple is only referred to when the head is seen in dorsal view, e.g., when it is necessary to compare eye length with temple length. In posterior view the area ventral to the dorsal margin of the occipital foramen is the gena whereas the area dorsal to this is the occiput (see further below). If no sulci are present on the back of the head, the line of demarcation between gena and occiput is somewhat arbitrary, at least lateral to the occipital foramen (Fig. 3). But if a more or less transverse sulcus is present (Figs 4–6) then the gena and occiput may conveniently be defined, respectively, as the areas ventral to and dorsal to the sulcus, regardless of its length and shape. Males sometimes have a relatively smaller eye and relatively wider gena than corresponding females (Omyomymar-D52, O. (Caenomymar)-D53). The malar space, measured along the malar sulcus (Fig. 9: mls) when this is visible externally, is the shortest distance between the ventral-most point of the eye and the oral cavity (usually its anterolateral angle). It is shorter than the eye height except when the eye is greatly reduced (female *Chrysoctonus*-D16). The malar sulcus is present and distinct (*Cosmocomopsis*-D20, Gonatocerus-D35, Lymaenon-D43, Tinkerbella-D73) or indistinct (Alaptus-D3, Arescon-D8, Gahanopsis-D33). Sometimes, the malar sulcus continues dorsally along the posterior edge of the eye (Anagrus-D5, Ceratanaphes-D15, Cleruchus-D17, Lymaenon-D43, Progonatocerus-D62). If the sulcus ends clearly at the lowest point of the eye (Fig. 9) only that should be treated as the "true" malar sulcus, but if it continues dorsally far from the posterior edge of the eye to meet above the occipital foramen the corresponding sulcus from the other side it is the **postorbital** sulcus (Fig. 10: poc) [alternately named the postgenal sulcus (Gibson 1997)]. In lateral view, the anterior margin of the gena extends to the malar sulcus if present (Anagrus-D5, Gonatocerus-D35, Octomicromeris-D51) or to the preorbital sulcus (Fig. 1: pos). The preorbital sulcus ventral to the lowermost level of the eye is sometimes directed posteriorly (Anagroidea-D4, Camptoptera-D12, Litus-D42). It cannot be confused with the malar sulcus because the preorbital sulcus extends dorsally anterior to the eye to the lateral margin of the torulus. The malar area is an arbitrarily defined area (no demarcation line posteriorly) ventral to the eye and dorsal to the mouth margin. The malar area is well defined only when a malar sulcus is present, in which case it could be treated as the somewhat triangular area between the preorbital sulcus and malar sulcus.

*Sculpture*. The sculpture laterally on the gena is essentially the same as posteriorly on the back of the head. *Setation*. At least one, and occasionally a few, setae usually occur posterior to the preorbital sulcus and ventral

to the eye (*Cremnomymar*-D21, *Erdosiella*-D26a,b, *Neomymar*-D47). If a malar sulcus is present one or two setae may occur in the malar area (*Heptagonatocerus*-D36).

Vertex. Structure. The vertex (Figs 1, 7: vtx) is on the top of the head, bordered anteriorly and laterally by the frontal and supraorbital trabeculae, outside of which are corresponding sutures that distinguish the vertex as an independent sclerite, separate from the face and dorsal rim of the eye (Figs C1-C75). Posteriorly, the vertex is not separated from the occiput but its margin is more or less well defined. The demarcation between the two areas is best taken to be a transverse line or sharp angle in contact with the posterior margins of the lateral ocelli. The line is usually a sulcus, the vertexal sulcus (Fig. 4: vts) that is complete (Arescon-C8, Ceratanaphes-C15, Lymaenon-C43, Proarescon-B56) or incomplete, i.e., absent medially between the lateral ocelli (Eustochomorpha-C30) or absent (Ooctonus-B48, C53), but sometimes is only a sharp angle (Camptopteroides-B13, C14, Stephanocampta-B62, C68) or a blunt, more rounded angle (Agalmopolynema-C2, Anaphes-C6, Ischiodasys-C37) or apparently no angle at all (Anaphes-C6, Australomymar-C9, Ooctonus-B48, C53, Steganogaster-C67). It is sometimes difficult to determine if a partial or complete sulcus is the vertexal sulcus or the occipital sulcus (see Back of Head, below). When both a vertexal sulcus and an occipital sulcus are present (Arescon-B8) each can be named unequivocally. Exceptionally (Acmopolynema-C1), the change in angle between the vertex and occiput occurs between the lateral ocelli and median ocellus, giving the appearance that the posterior portion of the vertex bearing the lateral ocelli are part of the occiput. A short, incomplete extension of the supraorbital trabecula directed medially and in contact with the anterior margins of the lateral ocelli amplifies this effect. Also exceptionally, a medially divided vertexal (postfrontal) trabecula may extend across the vertex well posteroventral to the lateral ocelli (Dicopus-B23). Using the vertexal line as the demarcation between vertex and occiput, the vertex is almost always wider than long, often with the width posteriorly greater than the width anteriorly. Rarely, the vertex is almost as long as its posterior width (Eubroncus). Various lines or sulci occur on the vertex, either as a triangle or rectangle around the ocellar triangle or from the median ocellus towards or to the frontal or supraorbital trabeculae. The most complete set of these lines or sulci occur in poorly sclerotized heads; well sclerotized heads do not have them. The sulci around the ocellar triangle (Fig. 7: oct) sometimes appears slightly raised above the rest of the vertex, and if surrounded by a circumocellar sulcus (Fig. 7: cms) is named a stemmaticum (Fig. 7: stm) (Anagrus-C5, Arescon-C8, Kikiki-C39, Stethynium-C70, Tinkerbella-C73). The surface of the vertex is usually flat but sometimes a shallow, small (Palaeoneura-C54) to large (Stephanodes-C69a-c) pit occurs anterior or lateral to the median ocellus and lateral to or posterior to the lateral ocelli.

*Sculpture*. The cuticle is often apparently completely smooth (*Australomymar*-C9, *Mymar*-C45, *Neomymar*-C47, *Platyfrons*-C58). When microsculpture is present it is slightly and faintly engraved (*Acmopolynema*-C1, *Agalmopolynema*-C2, *Ischiodasys*-C37, *Narayanella*-C46) to more or less distinctly engraved (*Arescon*-C8, *Lymaenon*-C43) or raised (*Anagroidea*-C4, *Chrysoctonus*-C16a, *Eubroncus*-C29, *Eustochus*-C31, *Richteria*-C65) or apparently a mixture of both or, rarely, slightly wrinkled in places (*Krateriske*-C40), or dimpled, i.e. sculpticells concave (*Camptopteroides (Alalinda*)-C14). The mesh may be very fine (*Anaphes*-C6, *Boudiennyia*-C10, *Erythmelus*-C27) or coarser (*Dicopomorpha*-C23, *Litus*-C42, *Lymaenon*-C43). The sculpticells are isodiametric (*Camptopteroides*-C13, C14, *Chrysoctonus*-C16a, *Macrocamptoptera*-C44) to stretched more (*Erythmelus*-C27) or less (*Eubroncus*-C29, *Eustochomorpha*-C30) transversely or longitudinally or both (*Anagrus*-C5, *Schizophragma*-C66) or somewhat curved (*Camptoptera*-C12, *Ceratanaphes*-C15).

Setation. The ocellar triangle usually has 2 setae, often between the lateral ocelli, but sometimes there is another pair (*Anagrus*-C5, *Callodicopus*-C11). On the vertex outside the ocellar triangle there is almost always (except *Ischiodasys*-C37) at least one pair of seta lateral to or anterolateral to the median ocellus (*Camptopteroides*-C14), though sometimes there are several or numerous pairs of setae (*Acmopolynema*-C1, *Chrysoctonus*-C16a,b, *Cnecomymar*-C18, *Entrichopteris*-C25, *Polynema*-C59, C60, *Steganogaster*-C67). Along the dorsal rim of the eye, just lateral to the supraorbital trabecula/sulcus, most genera have one more or less median seta, one or more anterior setae (the same ones as seen in anterior view but sometimes more visible in dorsal view, so they are mentioned again here), and often one posterior seta that sometimes is a little posterior to the posterior edge of the vertex. A few have no setae (*Boudiennyia*-C10) or they are inconspicuous (*Camptopteroides*-C14). The setae are usually fairly short (*Agalmopolynema*-C2, *Cleruchus*-C17, *Dicopomorpha*-C22, *Eustochus*-C31) but sometimes intermediate in length (*Alaptus*-C3, *Cnecomymar*-C18, *Eubroncus*-C29, *Heptagonatocerus*-C36, *Mymar*-C45) to long (*Ischiodasys*-C37, *Neomymar*-C47). Usually, they narrow gradually to a point (*Kikiki*-C39, *Lymaenon*-C43, *Neotriadomerus*-C49, *Parastethynium*-C57) but quite often they are apically truncate (*Palaeomymar* (*Chaetomymar*)-C55, *Stephanodes*-

C69a,b, Tetrapolynema-C72) or are even slightly bifurcate (Neomymar-C47). Ocelli. An ocellus is usually slightly oval. The ocellar diameter is sometimes greater in males than in females. There are almost always three but, exceptionally, the median ocellus is absent (males of *Platystethynium*) or all three are absent (females of Chrysoctonus-C16a,b, males and females of some Cleruchus) and a slight change in sculpture may indicate where the ocelli used to be. In males of Dicopomorpha echmepterygis not even a change in sculpture indicates where the ocelli might have been. The ocelli are often on a slightly raised area of the vertex, often distinguished by a slight change in sculpture in the ocellar triangle so almost always each ocellus is tilted, with the **median ocellus** (Figs 1, 7: mo) directed more or less anteriorly and each lateral ocellus (Figs 1, 7: lo) directed more or less posterolaterally. An ocellus may also have its outer margin slightly below the adjacent surface of the vertex. The ocelli are arranged in a more obtuse triangle (Camptoptera-C12, Cleruchus-C17, Stephanocampta-C68) or less obtuse triangle (most genera), or rarely an equilateral triangle (Arescon-C8, Proarescon-C61). The ocellar triangle dimensions are given, respectively, by the postocellar length (POL), the shortest line between the medial margins of the lateral ocelli, and the lateral ocellar length (LOL), the shortest line between a lateral ocellus and the median ocellus. The position of the ocellar triangle on the vertex is defined by the ocellocular length (OOL), the shortest line between the lateral margin of a lateral ocellus and the eye, and the median ocellus-transverse trabecula length (MOTT), the distance from the anterior margin of the median ocellus to the transverse trabecula (Fig. 13). Jin & Li (2014) proposed OCL as the shortest distance from a lateral ocellus to the occipital margin, where the vertex meets the occiput, if that line is separated by a gap from a lateral ocellus (it is not separated if the vertexal line is taken to be the transverse sulcus touching the lateral ocelli). The greatest diameter of the median ocellus is useful as a unit of comparison with other measurements on the head or elsewhere. As described above, the ocellar triangle is sometimes surrounded by the circumocellar sulci (Fig. 7: cms), to form a stemmaticum (Anagrus-C5, Arescon-C8). Sometimes the stemmaticum is incomplete, without lines laterally (Kikiki-C39, Tinkerbella-C73).

Back of head (gena, occiput, postgena, and postocciput). Structure. The major landmarks on the back of the head (Figs B1–B68) are the occipital foramen (Fig. 3: ocf), the oral cavity ventrally, which in posterior view is usually hidden by the maxillae and labium except in a few genera (Anaphes-B6, Gahanopsis-B31), and the eyes laterally. The occipital foramen may appear T-shaped with short dorsal arms (Cosmocomoidea-B19b, Lymaenon-B39, Zeyanus-B68) or almost circular (Stephanodes-B63) or oval with a strong transverse constriction medially that subdivides the foramen almost into two circular areas (Camptoptera-B12) with the lower area smaller than the upper area. The foramen is usually midway between the oral cavity and dorsal margin of the vertex but sometimes it is much nearer the vertex than the oral cavity so the head in lateral view appears distinctly pendulous (a few Anagrus and Lymaenon—the relevant species are not illustrated). Using the occipital foramen as the principal marker, the back of the head is conveniently divided into two vaguely defined areas, the gena and the occiput. In Mymaridae at least, the gena (discussed separately in more detail, above) is conveniently defined as the area lateral to and ventral to the occipital foramen. The occipital (Figs 3-6: oc) is the area dorsal to the dorsal margin of the occipital foramen and ventral (or posterior) to the vertexal sulcus. In the apparent absence of any oblique or transverse sulci (Anaphes-B6, Australomymar-B9) or in the presence of at most only one definite sulcus (most Polynema group genera), the occiput and gena are each subdivided into smaller areas, also mostly with arbitrary limits. But if sulci or sutures are present, they may be used to define the areas non-arbitrarily. The **postocciput** (Figs 3–6: **pso**) is a ring of heavily sclerotized cuticle surrounding the occipital foramen, with its outer margin clearly distinguishable from the thinner surrounding cuticle of the occiput and gena. The postocciput thus has distinct, sharply defined inner and outer edges. The postgena is conveniently defined as the narrow area ventral to the foramen and dorsal to the hypostomal bridge (or posterior margin of the oral cavity), though for practical purposes the term is best not used in Mymaridae. The lateral margins of the postgena are in line with the lateral margins of the postocciput —there is no definite demarcation line between postgena (medially) and gena (laterally). In addition to the main markers on the back of the head, lines or sulci or sutures often are present, some of which appear to be unique to Mymaridae. Debauche (1948, figs 2–9) first illustrated and named them (in French), but modified terms are used here. Burks & Heraty (2015) clarified and named some features not treated by Debauche. Using these lines/sulci/sutures, the limits of the various areas on the back of the head can be defined more precisely. Because these markers, when present, vary among the genera. the areas they delimit are either not the same in relative size and/or are not necessarily homologous among the taxa. The occipital foramen is usually clearly separated from the oral cavity by the subforaminal bridge (Figs 3, 6: sfb), a closure of the head ventral to the postocciput, sometimes replaced by a lower tentorial bridge (Fig. 5: ltb), which may be entire, without a median sulcus (Anagrus-B5, Arescon-B8, Erythmelus-B26, B27, IschiodasysB35, *Steganogaster*-B61) but is more usually divided, with a median sulcus (*Acmopolynema*-B1, *Chrysoctonus*-B16, *Erdosiella*-B25, *Gonatocerus*-B33, *Narayanella*-B42). Often, a median strip of **postoral setae** (Fig. 6: **pom**) occurs (*Australomymar*-B9, *Boudiennyia*-B10, *Entrichopteris*-B24, *Mymar*-B41, *Stephanodes*-B63a–c), sometimes with most (or most visible) setae nearest the postocciput (*Polynema* (*Doriclytus*)-B54). Compared with the height of the occipital foramen or postocciput the distance between ventral edge of the postocciput or occipital foramen and the dorsal edge of the maxilla can be about 1.5–2.0× (*Acmopolynema*-B1, *Anaphes*-B6, *Eubroncus*-B28) to about 0.3–0.4× (*Australomymar*-B9, *Cosmocomoidea*-B19a,b, *Parastethynium*-B52, *Zeyanus*-B68) or there is no gap at all and the maxillae abut against the postocciput (*Alaptus*-B3, *Camptoptera*-B12, *Camptopteroides*-B13, *Dicopomorpha*-B21c, *Eustochus* (*Caraphractus*)-B30). If the subforaminal bridge is replaced by a lower tentorial bridge this separate median sclerite is narrow (*Callodicopus*-B11, *Dicopomorpha*-B21b) or wide (*Omyomymar*-B46a,b, *Stephanocampta*-B62). The **hypostomal carina** (**hyc**) borders the ventral margin of the gena; it is just dorsal to the oral cavity and almost always hidden behind the dorsal margins of the maxillae (*Acmopolynema*-B1, *Parastethynium*-B52, *Schizophragma*-B60, *Zeyanus*-B68) but sometimes is visible (*Ooctonus*-B48, *Polynema*(*Doriclytus*)-B54) and/or the posterior margin of oral cavity is also sometimes visible (*Anaphes*-B6, *Cosmocomoidea*-B19b, *Erythmelus*-B26, *Gahanopsis*-B31).

A transverse sulcus is usually present ventral to the vertexal line, sulcus or angle that indicates the posterior margin of the vertex (see under Vertex) and dorsal to the occipital foramen/postocciput. If the lateral arms of the transverse sulcus are directed dorsolaterally it is named the transoccipital sulcus (Figs 4, 5: tos) and if the arms are directed ventrolaterally it is named the **postorbital sulcus** (Fig. 8: poc). This somewhat arbitrary distinction does not necessarily imply homologies among similarly located sulci in different genera. Medially, the transoccipital sulcus is in contact with the dorsal margin of the postocciput (Anagroidea-B4, Anagrus-B5, Arescon-B8, Stethynium-B64) or clearly separated from it (Alaptus-B3, Erythmelus-B26, Neostethynium-B44, Stephanodes-B63a,b). Laterally, it extends dorsolaterally towards or to the posterior apex of a supraorbital suture or occasionally ventrolaterally to or towards the supraorbital suture extension, if present, or towards/past the posterior margin of the eye (Callodicopus-B11, Camptoptera-B12, Camptopteroides (Alalinda)-B14, Dicopus-B23, Gastrogonatocerus-B32, Zeyanus-B68). Conversely, it could be argued that the transoccipital sulcus extends from the posterior apex of a supraorbital trabecula/ sulcus or from near the eye (Anagrus-B5, Arescon-B8, Neostethynium-B44, Proarescon-B56, Schizophragma-B60, Stethynium-B64) or from the vertexal sulcus between the lateral ocellus and the eye margin (Heptagonatocerus-B34, Omyomymar-B46a) ventromedial to or just dorsal to the postocciput. In support of the latter argument are the cases where the transoccipital sulcus is absent medially and only present laterally (Acmopolynema-B1, Agalmopolynema-B2, Boudiennyia-B10, Cnecomymar-B18, Erdosiella-B25, Polynema (Doriclytus)-B54). The supraorbital suture extension is usually in line with the supraorbital suture (Anaphes (Patasson)-B6) but in a few species it is directed medially and extends towards or to the dorsal margin of the postocciput. Sometimes the transoccipital sulcus is absent laterally (Alaptus-B3, Camptopteroides-B13, Dicopomorpha-B21a,b, Stephanocampta-B62, Stephanodes-B63a-c). Occasionally, the transoccipital sulcus joins the supraorbital suture extension sublateral to the postocciput (Anagroidea-B4). In one genus (Callodicopus-B11) the transoccipital sulcus meets about half way along its length a long, sinuate supraorbital sulcus extension. Whether complete or incomplete, the vertexal sulcus and the transoccipital sulcus/supraorbital sulcus extension delimit a triangular (Heptagonatocerus-B34, Parastethynium-B52), semicircular (Anagrus-B5, Gonatocerus-B33, Neostethynium-B44), angular (Erythmelus-B26), W-shaped (Anagroidea-B4) or rectangular (Schizophragma-B60) occipital arch (Debauche 1948, fig. 5) that is often slightly depressed and less sculptured relative to the surrounding area. Even when the vertexal line is absent (Richteria-B59) or both vertexal and transoccipital sulci are faint or absent (Eustochus-B29, Eustochus (Caraphractus)-B30, Gahanopsis-B31) the occipital arch is still sometimes identifiable by a slight depression or change in sculpture. Sometimes, if an occipital arch is distinguishable, it is open ventromedially (Acmopolynema-B1, Agalmopolynema-B2, Boudiennyia-B10, some Cosmocomoidea-B19b, Entrichopteris-B24, Palaeoneura-B49, Richteria-B59). A median vertical occipital sulcus (Fig. 4: vcs) is sometimes present and extends ventrally from the vertexal line toward or to the transoccipital line (Callodicopus-B11, Camptoptera-B12, Camptopteroides (Alalinda)-B14, Dicopus-B23, Schizophragma-B60).

The transoccipital sulcus and postorbital sulcus do not occur together in the same genus, except perhaps in two (a few *Gastrogonatocerus*-D34, *Heptagonatocerus*-D36). The postorbital sulcus, when complete (a few *Cosmocomoidea*-B19b, *Gastrogonatocerus*-B34, *Neotriadomerus* [not illustrated], *Zeyanus*-B68), extends across the dorsal margin of the postocciput (exactly as does the transoccipital sulcus) either in contact with it or just dorsal

to it and continues lateroventrally as a more or less strongly curved sulcus to near the malar sulcus ventral to the eye. If the postorbital sulcus is incomplete, it is just dorsal to the dorsal margin of the postocciput and extends lateroventrally only a short distance (*Alaptus*-B3, *Dicopomorpha*-B21a, *Stephanodes*-B63a–c). If a postorbital sulcus is present instead of an transoccipital sulcus, the occiput is dorsal to it and the gena ventral and lateral to it (a few *Cosmocomoidea*-B19b). Sometimes, the postorbital sulcus is angled dorsal to the postocciput and extends as a straight sulcus to join with a greatly extended and outwardly curved supraorbital sulcus extension (*Callodicopus*-B11) or to the posterior edge of the eye ((*Stephanocampta*-B62) but does not extend to the malar sulcus. The postorbital sulcus is indistinct in a few genera (*Gonatocerus*-B33, *Litus*-B38).

*Sculpture*. Microsculpture is sometimes absent from the back of the head (*Agalmopolynema*-B2, *Cnecomymar*-B18, *Entrichopteris*-B24, *Neomymar*-B43, *Palaeoneura* (*Chaetomymar*)-B50, *Platyfrons*-B53, *Stephanodes*-B63a–c) or, if present, is sometimes only lateral, with the median area apparently smooth (*Anagrus*-B5, *Erythmelus*-B26, *Kalopolynema*-B36, *Lymaenon*-B39, *Parastethynium*-B52, *Stephanocampta*-B62). The microsculpture tends to follow the contour of the head but, if a transoccipital/postorbital sulcus is present, the sculpture dorsally is usually different (sculpticells finer or coarser, or more or less stretched or more or less prominent) than ventrally, sometimes extremely different (*Anagroidea*-B4). Usually, the dorsal microsculpture is more transverse and the ventral microsculpture is more vertical (*Alaptus*-B3, *Camptoptera*-B12, *Dicopomorpha*-B21a–c, *Erythmelus*-B26, *Eustochus* (*Caraphractus*)-B30, *Kalopolynema*-B36, *Litus*-B38, *Notomymar*-B45) but occasionally almost entirely vertical (*Cleruchus*-B17).

Setation. Setae are always present on the back of the head. There are very few (*Alaptus*-B3, *Callodicopus*-B11, *Camptopteroides*-B13, *Chysoctonus*-B16, *Stephanocampta*-B62) to many setae (*Ischiodasys*-B35, *Parastethynium*-B52, *Steganogaster*-B61), which in all cases are mostly submedial to lateral. Two or four, minute setae almost always occur lateral to and dorsal to the postocciput (*Acmopolynema*-B1, *Anagrus*-B5, *Cnecomymar*-B18, *Lymaenon*-B39, *Palaeoneura*-B49). The other setae are short (*Anaphes*-B6, *Schizophragma*-B60, *Stephanodes*-B63a–c) to longer (*Cnecomymar*-B18, *Cosmocomoidea*-B19a,b, *Ischiodasys*-B35, *Palaeoneura* (*Chaetomymar*)-B50, *Platyfrons*-B53, *Pseudanaphes*-B57). The setae are occasionally truncate apically (*Mymar*-B41, *Palaeoneura*-B49, B50, *Stephanodes*-B63a–c).

**Mouthparts**. The mouthparts (labrum, mandibles, labium, maxillae: Figs F1–F71) are suspended from the oral cavity, though the maxillae are partly external to the opening so in posterior view they almost always cover the oral cavity completely. In terms of useful taxonomic features, variety in the mouthparts of Mymaridae is mostly a matter of mandibles. The remaining mouthparts vary relatively little and, in any case, are often not easily seen except for the labium and maxillae (together forming the **labiomaxillary complex**) in posterior view. The **epipharynx** usually is not visible, though occasionally it is exposed (*Omyomymar*-F48a), and is covered with sensilla.

**Labrum**. *Structure*. The **labrum** (Figs 11, 12: **lbr**) is thin, flap-like and usually oval to rectangular with its apical edge straight or convex, rarely slightly sinuate (*Tanyxiphium*-F67a); rarely it is longer than wide (*Dicopus*-F23). In anterior or, better, ventral view the labrum is often only partly visible because it is usually reflexed internally into the oral cavity and its lateral and apical margins are often partly hidden by the closed mandibles (*Acmopolynema*-F1, *Alaptus*-F3). Sometimes the labrum projects anteriorly and is entirely exposed (*Anagroidea*-F4, *Callodicopus*-F11, *Dicopus*-F23).

Setation. The dorsal surface or apical margin usually has labral setae (Fig. 11: **lbs**). Rarely, the labrum has no setae (*Ptilomymar*-F60) but usually at least one median seta is present (*Alaptus*-F3, *Dicopomorpha* (*Dicopulus*)-F22, *Eustochus*-F29, *Macrocamptoptera*-F40), and sometimes two sublateral (*Cleruchus*-F17) to several subapical (*Eubroncus*-F28a) or apical (*Cosmocomoidea*-F19a,b, *Krateriske*-F36) setae in a transverse row. The ventral surface of the labrum is usually smooth and without setae, but sometimes setae are present on the ventral surface (*Anagroidea*-F4, *Camptopteroides*-F13, *Gonatocerus*-F33, *Litus*-F38).

**Mandible**. *Structure*. The **mandible** (Figs 2, 10–12: **man**) is almost always the largest and most conspicuous of the mouthparts, but sometimes it is small (*Tanyxiphium*-F67a), minute (*Erythmelus*-F26, *Krokella*-F37a, *Omyomymar*-F48a) or even absent, as in *Dicopomorpha echmepterygis* males (Huber *et al.* 2020). In ventral view the mandibles occupy most of the oral cavity. When closed, the apices cross so the teeth of one mandible are normally hidden by the other. The two mandibular condyles are hidden by the lateral margin of the foramen and articulate each mandible with the lateral margin of the oral cavity. The condyles are well separated and usually arranged obliquely, with the anterior condyle more medial than the posterior condyle (the anterior condyles are almost in line with the anterior tentorial pits). The condyles are more or less on the long axis of the head so that when mandibles open

and close they do so transversely in a lateromedial direction, i.e., inwards towards the median line of the head and outwards towards the lateral edge of the head. Rarely, the condyles are close together and rotated about 90° so the mandibles move longitudinally (Anagroidea-F4, Ceratanaphes-F15, Eubroncus-F28a,b), i.e., in an anterior/ posterior direction. The mandible adductor muscles (Fig. 10: mam) originate on the gena and their insertion is almost always visible in ventral view as a basally wide (Anaphes (Patasson)-F6, Gonatocerus-F33, Ooctonus-F50) to narrow (Entrichopteris-F24, Mymar-F41, Platyfrons-F55), triangular area on the lateral surface of the mandible between its two mandibular basal arms (Fig. 10: mba), which are correspondingly wide apart or close together at their base. The adductor muscle is sometimes almost hidden basally (Anneckia-F7, Arescon-F8, Camptoptera-F12, Litus-F38, Stephanocampta-F64, Tanyxiphium-F67a,b) or completely hidden basally (Erythmelus-F26, females of Krokella-F37a, females of Omyomymar-F48a). The basal arms of each mandible are not rimmed (Callodicopus-F11, Cleruchus-F17, Cosmocomoidea-F19a,b, Gahanopsis-F31, Gonatocerus-F33) or have a more or less distinct rim (Acmopolynema-F1, Cremnomymar-F20, Entrichopteris-F24, Kalopolynema-F35, Ptilomymar-F60, Stephanodes-F65a,b, *Tetrapolynema*-F68) along the adductor muscle and/or along the base. Each arm sometimes has a usually wide, shallow to deep, basal pit (Palaeoneura (Chaetomymar)-F52, Platyfrons-F55). The mandible base, at the widest visible point, is usually about 2× as wide as at the apex (across the teeth of a mandible), but sometimes 3× as wide (*Callodicopus*-F11). The basal 0.4-0.5 of the ventral (= posterior) margin of the mandible is distinctly wider than the apical 0.5-0.6 and almost always has a deep notch (Fig. 11: notch), and a blunt or sharp apex at the point where the mandible narrows abruptly. The notch is sometimes replaced by a distinct rounded swelling (males of Krokella-F37b) or a more gradual widening (Litus-F38, Neotriadomerus-F44, Paracmotemnus-F53, Stephanocampta-F64, Tetrapolynema-F68). No notch or abrupt widening occurs in some genera with normal mandibles (Tinkerbella-F69) or with greatly reduced mandibles in females (Omyomymar-F48a). The extreme base of the ventral margin of a mandible is more acute (Lymaenon-F39, Tanyxiphium-F67c, Yoshimotoana-F70, Zeyanus-F71) or less acute (Eustochus-F29, Kalopolynema-F35, Polynema-F56, Ptilomymar-F60). When visible, the base of the dorsal (= anterior) margin of the mandible is not or barely lobed (Acmopolynema-F1, Alaptus-F3, Cnecomymar-F18, Cremnomymar-F20, Entrichopteris-F24, Kalopolynema-F35, Mymar-F41, Neomymar-F43) to distinctly lobed with a rounded apex (Anaphes (Patasson)-F6, Boudiennyia-F10, Callodicopus-F11, Nepolynema-F45, Palaeoneura-F51, Polynema-F56), acute apex (Dicopomorpha (Dicopulus)-F22, Eustochus-F29, Gastrogonatocerus-F32), or sometimes a very narrow and acute apex (Schizophragma-F62). A socketed mandibular peg (Fig. 11: mdp) almost always occurs just distal to the dorsal basal arm of the mandible (Cnecomymar-F18, Lymaenon-F39, Palaeoneura-F51, F52, Platyfrons-F55, Proarescon-F58, Ptilomymar-F60, Steganogaster-F63, Stethynium-F66, Zeyanus-F71), which can be particularly large (Narayanella-F42) or it occasionally appears to be a long, thin seta (Krateriske-F36). If the mandibles are reduced to stubs without teeth, a wide gap occurs between them (Fig. 12) (females of Krokella-F37a, Omyomymar-F48a, Tanyxiphium-F67a); congeneric males have normal mandibles with distinct teeth that overlap when closed (Omyomymar-F48b, Tanyxiphium-F67c). Sometimes the mandibles are unusually large (Krokella-F37b). Mandibles that are not reduced (their apices almost always overlap when closed) vary considerably in the number, length and shape of their teeth. Most genera have three teeth (Acmopolynema-F1, Australomymar-F9, Boudiennyia-F10, Chrysoctonus-F16, Ooctonus-F50, Polynema-F56, Steganogaster-F63, Zeyanus-F71), whereas a few have five distinct teeth, with some smaller than others (Schizophragma-F62), some, including the putative most ancestral genera, have four more or less equal teeth (Arescon-F8, Neotriadomerus-F44, Proarescon-F58, Stethynium-F66, Tinkerbella-F69), others two teeth (Anneckia-F7, Ceratanaphes-F15, Dicopomorpha (Dicopulus)-F22, Eustochus-F29, Macrocamptoptera-F40) that are equal (Alaptus-F3, Callodicopus-F11, Camptopteroides-F13, Litus-F38) or distinctly unequal (Cleruchus-F17, Dicopus-F23). In addition, the mandibles of many genera have fine serrations, usually along the dorsal edge of at least one tooth (Anagrus-F5, Anaphes (Patasson)-F6, Arescon-F8, Notomymar-F46, Palaeoneura (Chaetomymar)-F52), and several have at least one distinct tooth and the second one wide and apically serrated (Anagroidea-F4, Eubroncus-F28a, Krokella-F37b, Notomymar-F46, Paracmotemnus-F53, Parastethynium-F54a). Occasionally, it appears that only one tooth is present (Camptoptera-F12, Stephanocampta-F64) probably because a small second tooth is hidden behind the first due to rotation of the mandible about its longitudinal axis. Minute mandibles have indistinct teeth (females of Omyomymar-F48a, some females of Tanyxiphium-F67b) or none at all (Erythmelus-F26, Erythmelus (Parallelaptera)-F27, some females of Tanyxiphium-F67a). The teeth have the apex fairly sharp (Anaphes (Patasson)-F6, Gahanopsis-F31, Ischiodasys-F34) to blunt (Acmopolynema-F1, Cnecomymar-F18, Erdosiella-F25a,b, Gonatocerus-F33) to a mixture of both (Eustochus (Caraphractus)-F30). Rarely, the ventral surface has numerous small denticles on its apical half (Eubroncus-F28b).

Sculpture. The mandible is almost always smooth. Occasionally, faint, usually reticulate sculpture occurs basally

(*Acmopolynema*-F1, *Anaphes*-F6, *Erdosiella*-F25a,b, *Eustochus*-F29). One or more short or long, narrow or wide, groove-like or pit-like **mandibular rods** (Fig. 11: **mdr**) may be visible (*Chrysoctonus*-F16, *Cremnomymar*-F20, *Gonatocerus*-F33, *Krokella*-F37b, *Notomymar*-F46, *Parastethynium*-F54a); they are sometimes particularly large (*Anneckia*-F7, *Eubroncus*-F28a).

Setation. At least two to several (frequently five) setae of the same or different lengths occur in a transverse row just distal to the apex of the adductor muscle insertion. Sometimes it is difficult to determine if the dorsal-most (anterior-most) seta replaces the mandibular peg or is the dorsal-most (anterior-most) seta of the transverse row of setae (*Neomymar*-F43, *Omyomymar* (*Caenomymar*)-F49); it is usually shorter than the others in the row.

Maxilla. The maxillae (Figs 3-6: max) together cover the posterior margin of the oral cavity and are best seen in posterior view (Figs B1–B68). Each maxilla consists of a basal, usually transverse cardo (Fig. 6: crd) and usually larger apical stipes (Fig. 6: sti). The cardo may actually be internal and may be mislabelled in Fig. 6 (see also Fig. 19a, which may show the actual cardo), in which the labelled region might just be the base of the stipes separated by a shallow transverse sulcus. Details of maxillary sensilla are best seen in ventral view (Figs F1-F71). In posterior view, the stipes together are slightly wider than long (Acmopolynema-B1), almost quadrate (Anagroidea-B4, Anaphes-B6, Australomymar-B9), slightly long than wide (Callodicopus-B11), to over 1.5× as long as wide (Camptopteroides (Alalinda)-B14, Dicopomorpha-B21a, Macrocamptoptera-B40). The medial margins of the stipites abut proximally (= dorsally) for part of their length and separate distally (= ventrally) for most of their length, exposing the labium between them, in part (Acmopolynema-B1, Boudiennyia-B10, Stephanodes-B63) to entirely (Anagroidea-B4, Dicopomorpha-B21, Lymaenon-B39). The lateral margin of a maxilla is evenly convex (Neomymar-B43, Ooctonus-B48), angular (Arescon-B8) or almost straight (Macrocamptoptera-B40). The 1-segmented maxillary palp (Fig. 11: mxp) connects to the stipes posterolaterally (Australomymar-F9, Boudiennyia-F10, Cosmocomoidea-F19). It has a single apical seta, rarely more (Proarescon-F58). At least one seta usually also occurs on the stipes near the base of the maxillary palp (Krateriske-F36, Notomymar-F46, and sometimes even on it (Gastrogonatocerus-F32, Gonatocerus-F33). The galea (Figs 11, 12: gal) has 1 or 2 (Dicopomorpha (Dicopulus)-F22) to 10 (Pseudanaphes-F59, Steganogaster-F63) peg-like setae in a cluster (Erdosiella-F25b) or in a row laterally (Gonatocerus-F33). The lacinia (Figs 11, 12: lac) is often visible (Krateriske-F36, Nepolynema-F45) as a fringe along the medial margin of the galea. The fringe is entirely visible along the inner margin of the galea if the mandibles are greatly reduced (females of Erythmelus-F26, Omyomymar-F48a).

*Sculpture and setation*. If sculpture is present on the cardo, and less often the stipes (*Camptopteroides*-B13, *Camptopteroides* (*Alalinda*)-B14, *Dicopomorpha*-B21a–c), it is transverse and may bear rows of short acantha apically (*Callodicopus*-B11, *Stephanocampta*-B62). One or two setae may occur on the cardo and stipes.

Labium. The labium (Figs 5, 6: lab) is best seen in ventral (Figs F1–F71) or posterior view (Figs B1–B68). In posterior view, it is about  $1.2 \times$  as long as its widest point (*Eustochus*-B29) to about  $3.0 \times$  as long as wide (Dicopomorpha-B21a-c). The labium consists of a basal prementum (Figs 3-6: prm), and an apical glossa (Figs 3-6: glo) with a dense apical fringe of setae. The prementum is generally narrow and triangular in shape, sometimes distinctly so (Alaptus-B3) with straight or slightly concave lateral margins (Anneckia-B7, Dicopomorpha-B21a-c), or less triangular with slightly convex margins (Arescon-B8, Polynema (Restisoma)-B55) at least in the apical half, or wider and more rectangular (Camptoptera-B12, Eustochus-B29, Notomymar-B45, Paracmotemnus-B51). The base (dorsal apex) of the prementum is sometimes partly hidden by the maxillae (Cnecomymar-B18, Narayanella-B42, Polynema (Doriclytus)-B54, Stephanodes-B63a). Each labial palp (Figs 11, 12: lbp) is on the posterior surface of the prementum, near its apex and usually near its lateral margin. In ventral view, the palp appears 1segmented and seta-like, with two (rarely perhaps only one) setae apparently arising from its base (Acmopolynema-F1, Richteria-F61) or from the labial surface posterior and dorsal (= posterior) to the palp and separated from it (Cremnomymar-F20, Palaeoneura-F51). The labial palp is almost always short but occasionally long (Zeyanus-F71). The labial palps are close together (Eustochus-F29, Narayanella-F42, Platyfrons-F55) or far apart (Gahanopsis-F31, Macrocamptoptera-F40). A palp is usually thin, almost seta-like (most genera) but occasionally is thicker (Anagrus-F5) or thick and peg-like (Australomymar-F9, Cosmocomoidea-F19a,b) and with 2 apical setae as well as the one or two setae arising from the labium.

Sculpture and setation. The labium is smooth and without surface setae except at or near the base of the palpi.

### Conclusions

Among the genera of Mymaridae the cranial morphology is remarkably varied. The head differs significantly from other Chalcidoidea only in the distinct separation of the face from the vertex by the transverse trabecula, which effectively divides the two areas into separate sclerites. Many of the features illustrated in the micrographs may not have been used in descriptions because of the difficulty in describing them from card mounted or perhaps even from slide mounted specimens, which are the normal preparation methods used for their taxonomy. Nevertheless, we considered it worthwhile to illustrate the structures with micrographs and to try and reconcile the names applied to them with those used for other Chalcidoidea. If nothing else, the micrographs provide a visual overview of much of the generic diversity and morphological complexity among a considerable proportion of genera of the smallest known Hymenoptera. If such a study were undertaken for the heads of the genera of other Chalcidoidea perhaps they would be shown to be as morphologically diverse as in Mymaridae.

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**APPENDIX 1**. List of acronyms used on figures 1–21 and in text.

afe-antennifer (Figs 1, 19b)

- ata—anterior tentorial arm (Figs 19b, 20)
- atp-anterior tentorial pit (Fig. 11)
- clm—clypeal margin (Fig. 11)
- cly—clypeus (Fig. 2)
- cms-circumocellar sulcus (Figs 7, 13)
- crd-cardo (Fig. 6, 19a)
- cvpr—cervical prominence (Figs 13, 20)
- eye-compound eye (Figs 1, 6, 13, 15a)
- gal—galea (Figs 11, 12, 15a, 17, 19a)
- gen-gena (Figs 1-3, 5, 6, 8-10, 12-15a, 18, 19a)
- glo-glossa (Figs 3, 4, 6, 9-12, 17, 18, 19a)
- hyc-hypostomal carina (Fig. B48)
- lab—labium (Figs 3, 4, 6, 15a)
- lac-lacinia (Figs 11, 12, 15a, 17)
- lbp—labial palp (Figs 11, 12, 17, 18)

lbr-labrum (Figs 11, 12) lbs-labral setae (Figs 10, 11) lo—lateral ocellus (Figs 1, 4, 7, 13, 15a, 19a) lof—lower face (Figs 1, 2, 10, 15a) LOL—lateral ocellar line [shortest distance between a lateral ocellus and median ocellus] (Fig. 13) ltb—lower tentorial bridge (Fig. 5) mam-mandible adductor muscle (Fig. 10) man-mandible (Figs 11, 12, 15a, 17) max-maxilla (Figs 3-6, 9) mba-mandibular basal arm (Figs 10, 17) mdp-mandibular peg (Fig. 11) mdr-mandibular rod (Figs 11, 17) mdt-mandibular tooth (Figs 11, 17) mls-malar sulcus (Figs 8-10, 15a) mo-median ocellus (Figs 1, 7, 13) MOTT-median ocellus to transverse trabecula distance (Fig. 13) mxp—maxillary palp (Figs 11, 12, 17, 18) oc—occiput (Figs 3–6, 14) ocf-occipital foramen (Figs 3, 14, 19a,b) ocs-ocular setae (Fig. 2) oct-ocellar triangle [when circumocellar sulcus absent] (Fig. 7). omm-ommatidium (Fig. 2) OOL-ocellar-ocular line [shortest distance between a lateral ocellus and eye margin] (Fig. 13) orm—oral margin (Figs 1, 3, 8–11, 17) [= clm medially + pcm laterally] pcm—paraclypeal margin (Fig. 11) POL—posterior ocellar line [shortest distance between lateral ocelli] (Fig. 13) poc-postorbital carina (Figs 8-10) [a sulcus in Mymaridae; a carina in other Chalcidoidea] pom-postoral microtrichia (Fig. 6) pos-preorbital sulcus (Figs 1, 2, 8-10, 14, 15a) [lower ocular sulcus (los) in other Chalcidoidea] pot-preorbital trabecula (Fig. 1) prm—prementum (Figs 3-6, 9, 17, 19a) psa-parascrobal area (Fig. 1) pso-postocciput (Figs 3, 6) pta-posterior tentorial arm (Figs 19b, 20) ptp-posterior tentorial pit (Fig. 19a) sas—subantennal sulcus (Figs 1, 2) scr-antennal scrobe (Fig. 2) sfb—subforaminal bridge (Figs 3, 4, 6) sot—supraorbital trabecula (Figs 1, 13, 15a) sse—supraorbital suture extension (Figs 3, 5, 13) sti—stipes (Figs 6, 11, 12) stm-stemmaticum (Fig. 7). tbr-tentorial bridge (Figs 19a, 20) ten-tentorium (Fig. 19) TML-temple length (Fig. 7) tor-torulus (Fig. 1) tos-transoccipital sulcus (Figs 4-6) trt-transverse trabecula (Fig. 1) upf—upper face (Figs 1, 2) vcs-vertical occipital sulcus (Figs 4, 14) vfs-vertical facial sulcus (Fig. 2) [vertical ocellar sulcus (vos) in other Chalcidoidea] vts-vertexal sulcus (Figs 4, 6, 7) vtx-vertex (Figs 1, 2, 7, 13)

**APPENDIX 2**. Valid world genera and subgenera of Mymaridae (as of December, 2022). The specimen collecting localities for taxa illustrated are followed by their figure numbers. When particular species were identified their names appear after the appropriate figure(s).

*Acmopolynema* Ogloblin, 1946. USA, Texas, Cameron Co., Southpoint Ranch. Figs A1, B1, C1, D1, E1, F1. *Acmotemnus* Noyes & Valentine, 1989. Not illustrated.

- *Agalmopolynema* Ogloblin, 1960. Chile, Valdivia, 30 km W. La Union; Arauco, Pata de Gallina. Figs A2, B2, C2, D2, E2, F2.
- *Alaptus* Westwood, 1839. USA, Florida, Highlands Co., Archbold Biological Research Station. Figs A3, B3, C3, D3, E3, F3.
- Allanagrus Noyes & Valentine, 1989. Not illustrated.
- Allarescon Noyes & Valentine, 1989. Not illustrated.
- Anagroidea Girault, 1915. Costa Rica, Guanacaste, Santa Rosa National Park. Figs A4, B4, C4, D4, E4, F4.
- Anagrus (Anagrus) Haliday, 1833. Canada, Ontario, Ottawa. Figs A5, B5, C5, D5, E5, F5.
- A. (Anagrella) Bakkendorf, 1962. Not illustrated.
- A. (Paranagrus) Perkins, 1905. Not illustrated.
- Anaphes (Anaphes) Haliday, 1833. Not illustrated.
- Anaphes (Patasson) Haliday, 1833. Canada, Quebec, Ste.-Clotilde-de-Châteauguay; USA, Illinois, Centralia, laboratory culture. Figs A6, B6, C6, D6, E6, F6.
- *Anneckia* Subba Rao, 1970. Papua New Guinea, East New Britain, Raunsepna. Figs A7, B7, C7, D7, E7, F7 (all *A. oophaga* Subba Rao).
- Apoxypteron Noyes & Valentine, 1989. Not illustrated.
- Arescon Walker, 1846. Czech Republic, Moravia, Ramspurk National Park. Figs A8, B8, C8, D8, E8, F8 (all *A. dimidiatus* (Curtis)).
- Australomymar Girault, 1929. Chile, Concepción, La Raqueta. Figs A9, B9, C9, D9, E9a, b, F9.
- Bocacciomymar (Boccacciomymar) Triapitsyn & Berezovskiy, 2007. Not illustrated.
- Bocacciomymar (Prosto) Triapitsyn & Berezovsky, 2007. Not illustrated.
- Borneomymar Huber, 2002. Not illustrated.
- *Boudiennyia* Girault, 1937. Australia, New South Wales, Dorigo National Park. Figs A10, B10, C10, D10, E10, F10. *Callodicopus* Ogloblin, 1955. Costa Rica, Guanacaste, Guanacaste National Park. Figs A11, B11, C11, D11, E11, F11.
- *Camptoptera* (*Camptoptera*) Foerster, 1856. USA, Florida, Monroe Co. Figs A12, B12, C12, D12, E12, F12.

Camptoptera (Eofoersteria) Mathot, 1966. Not illustrated.

- *Camptopteroides* (*Camptopteroides*) Viggiani, 1974. Australia, Mt. Lewis; Malaysia, Sabah. Figs A13, B13, C13, D13, E13, F13.
- Camptopteroides (Alalinda) Huber, 1999. Costa Rica, Alajuela and Limón. Figs A14, B14, C14, D14, E14, F14.
- *Ceratanaphes* Noyes & Valentine, 1989. Australia, Queensland, Muswellbrook Camp. Figs A15, B15, C15, D15, E15, F15.
- Chrysoctonoides Huber, 2015. Not illustrated.
- *Chrysoctonus* Mathot, 1966. USA, Florida, Gainesville; Central African Republic, Sangha-Mbaéré, Dzanga-Ndoki National Park. Figs A16, B16, C16a (*C. apterus* Mathot), C16b, D16, E16, F16.
- Cleruchoides Lin & Huber, 2007. Not illustrated.
- Cleruchus Enock, 1909. Canada, Alberta, Waterton Lakes National Park. Figs A17, B17, C17, D17, E17, F17.
- Cnecomymar Ogloblin, 1963. USA, Florida. Figs A18, B18, C18, D18, E18, F18.
- *Cosmocomoidea* Howard, 1908. USA, Texas, Cameron Co.; California, Contra Costa Co., Moraga; Florida, Long Pine Key; Canada, Quebec, Gatineau: Figs A19, B19a,b (*C. dolichocerus* (Girault)), C19, D19, E19 (*C. dolichocerus*), F19a, F19b (*C. dolichocerus*).
- Cosmocomopsis Huber, 2015. Madagascar, Fianarantsoa Province. Figs A20, C20, D20 (all C. sevae (Risbec)).

Cremnomymar Ogloblin, 1952. Chile, Juan Fernandez Is., Massatierra. Figs A21, B20, C21, D21, E20, F20.

Cybomymar Noyes & Valentine, 1989. Not illustrated.

- *Dicopomorpha (Dicopomorpha)* Ogloblin, 1955. Malaysia, Sabah. Figs A22a-c, B21a-c (*D. echmepterygis* Mockford), C22, D22a,b, E21a,b, F21a,b.
- *Dicopomorpha (Dicopulus)* Ogloblin, 1955; subgenus synonymized by Yoshimoto (1990) and still treated as a synonym here. Costa Rica, Guanacaste, Guanacaste National Park. Figs A23, B22, C23, D23, E22, F22.

Dicopus Enock, 1909. Country and locality not recorded. A24, B23, C24, D24, E23, F23.

Dorya Noyes & Valentine, 1989. Not illustrated.

- *Entrichopteris* Yoshimoto, 1990. Costa Rica, Guanacaste, Guanacaste National Park. Figs A25, B24, C25, D25, E24, F24.
- *Erdosiella* Soyka, 1956. Venezuela, Aragua, Henri Pittier National Park. Figs A26a, A26b, B25, C26, D26a, D26b, E25a, E25b, F25a,b.

Erythmelus (Erythmelus) Enock 1909. USA, Texas, Brazos Co., College Station. Figs A27, B26, C27, D27, E26, F26.

- *Erythmelus (Parallelaptera)* Enock, 1909. Iran, Alborz, Karaj. Figs A28, B27, C28, D28, E27, F27 (all *E. panis* (Enock)).
- *Eubroncus* Yoshimoto, Kozlov & Trjapitzin, 1972. Japan, Fukuoka Prefecture, Fukuoka. Figs A29, B28, C29, D29, E28, F28a,b.
- *Eustochomorpha* Girault, 1915. Australia, Western Australia, Stirling Range National Park. Figs C30, D30 (both *E. haeckeli* Girault).
- Eustochus (Eustochus) Haliday, 1833. Japan, Ibaraki Prefecture. Figs A30, B29, C31, D31, E29, F29.
- *Eustochus (Caraphractus)* Walker, 1846. Canada, Ontario, Ottawa area. Figs A31, B30, C32, D32, E30, F30 (all *C. cinctus* Walker).
- *Gahanopsis* Ogloblin, 1946. Costa Rica, San José, San José. Figs A32, B31, C33, D33, E31, F31 (all *G. deficiens* (Ogloblin)).
- *Gastrogonatocerus* Ogloblin, 1935. USA, Texas, Brewster Co.; Travis Co., Austin; Mexico, Michoacan. Figs A33, B32, C34, D34, E32, F32.
- *Gonatocerus* Nees, 1834. USA, Missouri, Williamsville; Canada, Gatineau Park. Figs A34, B33, C35, D35, E33, F33 (all *G. rivalis* Girault).
- *Heptagonatocerus* Huber, 2015. Madagascar, Fianarantsoa Province. Figs A35, B34, C36, D36 (all *H. madagascarensis* Huber).
- Himopolynema Taguchi, 1977. Not illustrated.
- Ischiodasys Noyes & Valentine, 1989. New Zealand, South Island, Punakaiki. Figs A36, B35, C37, D37, E34, F34.
- *Kalopolynema* Ogloblin, 1960. USA, Florida, Doval Co., Fort Caroline; Alachua Co., Gainesville; Maryland, Charles Co., Patuxent. Figs A37, B36, C38, D38, E35, F35 (all *K. ema* (Schauff & Grissell)).
- *Kikiki* Huber & Beardsley, 2000. Costa Rica, Heredia, La Selva Biological Station. Figs A38, C39, D39 (all *K. huna* Huber).
- Kompsomymar Lin & Huber, 2007. Not illustrated.
- Krateriske Huber, 2015. French Guiana. Figs A39, B37, C40, D40, E36, F36 (all K. guianensis Huber).
- Krokella Huber, 1993. Costa Rica. A40a, A40b, C41a,b, D41, E37a,b, F37a,b.
- Litus Haliday, 1833. Slovenia, Radovljica. Figs A41, B38, C42, D42, E38, F38 (all probably L. cynipseus Haliday).
- Lymaenon Walker, 1846. USA, Texas, Cameron Co. Figs A42, B39, C43, D43, E39, F39.
- *Macrocamptoptera* Girault, 1910. USA, South Carolina, Pendleton; Canada, Ontario, Carleton Place and Eganville. Figs A43, B40, C44, D44, E40, F40 (all *M. metotarsa* (Girault)).
- Megamymar Huber, 2022. Not illustrated.
- Mimalaptus Noyes & Valentine, 1989. Not illustrated.
- Mymar Curtis, 1829. USA, Florida. Figs A44, B41, C45, D45, E41, F41.
- Mymarilla Westwood, 1879. Not illustrated.
- *Narayanella* Subba Rao, 1976. Hong Kong, Kowloon; Vietnam, 20 km S. Dalat; Nepal, Pokhara. Figs A45, B42, C46, D46, E42, F42.
- *Neomymar* Crawford, 1913. Costa Rica, Guanacaste, Guanacaste National Park. Figs A46, B43, C47, D47, E43, F43. *Neopolynemoidea* Huber, 2022. Not illustrated.
- Neostethynium Ogloblin, 1964. USA, South Carolina, Clemson. Figs A47, B44, C48, D48.
- Neotriadomerus Huber, 2017. Australia, Queensland. Figs A48, F44 (N. gloriosus Huber), C49 (N. darlingi Huber).
- Nepolynema Triapitsyn, 2014. Japan, Aichi Prefecture. A49, D49, E44, F45 (all N. grande (Taguchi)).
- Neserythmelus Noyes & Valentine, 1989. Not illustrated.
- Nesomymar Valentine, 1971. Not illustrated.
- Nesopatasson Valentine, 1971. Not illustrated.
- Notomymar Doutt & Yoshimoto, 1970. South Georgia Island. Figs B45, D50, E45, F46 (all N. aptenosoma Doutt & Yoshimoto).

Octomicromeris Huber, 2015. Madagascar, Toliara Province. Figs A50, C50, D51, F47.

- *Omyomymar* (*Omyomymar*) Schauff, 1983. USA, Florida, Gainesville; South Carolina, Pendleton. Figs A51a,b, B46a,b, C51, D52, E46a,b, F48a,b.
- *Omyomymar* (*Caenomymar*) Yoshimoto, 1990; subgenus synonymized by Aquino *et al.* (2016) and still treated as a synonym here. Costa Rica, Guanacaste, Guanacaste National Park. Figs B47, C52, D53, E47, F49.
- *Ooctonus* Haliday, 1833. Canada, Ontario, St. Lawrence Islands National Park and Ottawa. Figs A52, B48, C53, D54, E48, F50 (all *O. hemipterus* (Haliday)).
- *Palaeoneura (Palaeoneura)* Waterhouse, 1915. USA, New Hampshire, Strafford Co., Durham. Figs A53, B49, C54, D55, E49, F51 (all *P. mymaripennis* Dozier).
- *Palaeoneura* (*Chaetomymar*) Ogloblin 1946; subgenus synonymized by Triapitsyn & Berezovskiy (2007) and still treated as a synonym here. Hawaiian Islands, Oahu I., Maunawili trail. Figs A54, B50, C55, D56, E50, F52 (all *P. sophoniae* (Huber)).
- *Paracmotemnus* Noyes & Valentine, 1989. Australia, Queensland, Mt. Glorious National Park. Figs A55, B51, C56, D57, E51, F53.
- Paranaphoidea Girault, 1913. Not illustrated.
- Parapolynema Fidalgo, 1982. Not illustrated.
- *Parastethynium* Lin & Huber, 2011. Papua New Guinea, West New Britain, Dami Oil Palm Research Station. Figs A56, B52, C57, D58, E52, F54a,b (all *P. maxwelli* (Girault)).
- Platyfrons Yoshimoto, 1990. Costa Rica, San José, San José. Figs A57, B53, C58, D59, E53, F55.
- Platypolynema Ogloblin, 1960. Not illustrated.
- Platystethynium (Platystethynium) Ogloblin, 1946. Not illustrated.
- Platystethynium (Platypatasson) Ogloblin, 1946. Not illustrated.
- Polynema (Polynema) Haliday, 1833. Canada. Figs E54, F56.
- Polynema (Doriclytus) Foerster, 1847. Canada, Ontario, Richmond. Figs A58, B54, C59, D60.
- *Polynema* (*Restisoma*) Yoshimoto, 1990; subgenus synonymized by Triapitsyn & Fidalgo (2006) and still treated as a synonym here. Costa Rica, San José, San José. Figs A59, B55, C60, D61, E55a,b, F57a,b.
- Polynemoidea Girault, 1913. Not illustrated.
- Polynemula Ogloblin, 1967. Not illustrated.
- Porcepicus Huber, 2022. Not illustrated.
- Prionaphes Hincks, 1961. Not illustrated.
- Proarescon Huber, 2017. Thailand, Nakhon Si Thammarat. Figs A60, B56, C61, F58.
- Progonatocerus Huber 2015. Malaysia, Sabah, Danum Valley. Figs C62, D62 (all P. albiclava Huber).
- *Pseudanaphes* Noyes & Valentine, 1989. Nepal, Lalitpur; Australia, Brown Mountain. Figs A61, B57, C63, D63, E56, F59.
- Ptilomymar Annecke & Doutt, 1961. Canada, Ontario; USA, Florida. Figs A62, B58, C64, D64, E57, F60.
- *Richteria* Girault, 1920. Australia, Australian Capital Territory, Canberra; South Australia, Brookfield Conservation Area. Figs A63, B59, C65, D65, E58, F61.
- Schizophragma Ogloblin, 1949. USA, Georgia, Sapelo Island. Figs A64, B60, C66, D66, E59, F62 (all S. bicolor (Dozier)).
- Scleromymar Noyes & Valentine, 1989. Not illustrated.
- Steganogaster Noyes & Valentine, 1989. New Zealand, South Island, Punakaiki. Figs A65, B61, C67, D67, E60, F63.
- Stephanocampta Mathot, 1966. Gabon, Forêt de la Mondah; Ecuador, Napo, Hacienda, Aragon. Figs A66, B62, C68, D68, E61, F64.
- Stephanodes Enock, 1909. Venezuela, Mérida, Mérida. Figs A67a, B63a, C69a, D69a, E62a, F65a (all S. polynemoides Yoshimoto); Canada, British Colombia, Sorrento. Figs B63b, C69b, D69b, E62b, F65b (all S. septentrionalis Huber); Switzerland, Zurich, Dielsdorf. Fig. A67b, E62c (all S. similis Foester); Australia, New South Wales, Monga State Forest. Figs A67c, B63c, C69c, D69c (all Stephanodes sp.).
- *Stethynium* Enock, 1909. USA, Washington, Goldendale. Figs A68, B64, C70, D70, E63, F66 (all *S. triclavatum* Enock).
- Tanyostethium Yoshimoto, 1990. Not illustrated.
- *Tanyxiphium* Huber, 2015. Colombia, Vichada, PNN El Tuparro; Seychelles, Cousin Island. Figs A69, F67a (*T. ?perforator* (Ogloblin)), B65a,b (*T. seychellense* Huber), C71a,b (*T. breviovipositor* Huber), D71, E64a,b (*T. seychellense* Huber), F67b,c.

Tetrapolynema Ogloblin, 1946. Costa Rica, Heredia. Figs A70, B66, C72, D72, E65, F68.

*Tinkerbella* Huber & Noyes, 2013. Costa Rica, Heredia, La Selva Biological Station. Figs A71, C73, D73, F69 (all *T. nana* Huber & Noyes).

Vladimir Triapitsyn, 2013. Not illustrated.

Xenopolynema Ogloblin, 1960. Not illustrated.

*Yoshimotoana* Huber, 2020. Dominican Republic, Pedernales. Figs A72, B67, C74, D74, E66, F70 (all *Y. masneri* (Yoshimoto)).

Zelanaphes Noyes & Valentine, 1989. Not illustrated.

Zeyanus Huber, 2015 Malaysia, Sarawak, Gunung Buda near Limbang. Figs A73, B68, C75, D75, E67, F71.

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FIGURES 1–6. Mymaridae heads. Anterior (1, 2) and posterior (3–6). Acronyms explained in Appendix 1.



FIGURES 7–12. Mymaridae heads (7–10) and mouthparts (11, 12). Acronyms explained in Appendix 1.



FIGURES 13–18. Mymaridae heads (13–16) and mouthparts (17, 18). Acronyms explained in Appendix 1.



FIGURES 19–21. Mymaridae head structures. 19a, head, posterior; 19b, tentorium; 20, tentorium; 21a, section through transverse trabecula; 21b, enlargement of 21a. Acronyms explained in Appendix 1.



FIGURES A1-A6. Mymaridae heads, anterior.



FIGURES A7-A12. Mymaridae heads, anterior.



FIGURES A13-A18. Mymaridae heads, anterior.


FIGURES A19-A22. Mymaridae heads, anterior.



FIGURES A23-A27. Mymaridae heads, anterior.



FIGURES A28-A33. Mymaridae heads, anterior. A29 inset shows entire mandibles.



FIGURES A34-A39. Mymaridae heads, anterior.



FIGURES A40-A44. Mymaridae heads, anterior.



FIGURES A45–A50. Mymaridae heads, anterior.



FIGURES A51-A55. Mymaridae heads, anterior.



FIGURES A56–A61. Mymaridae heads, anterior.



FIGURES A62-A67a. Mymaridae heads, anterior.



FIGURES A67b-A71. Mymaridae heads, anterior.



FIGURES A72, A73. Mymaridae heads, anterior.



FIGURES B1–B6. Mymaridae heads, posterior.



FIGURES B7-B12. Mymaridae heads, posterior.



FIGURES B13-B18. Mymaridae heads, posterior.



FIGURES B19-B21. Mymaridae heads, posterior.



FIGURES B22–B27. Mymaridae heads, posterior.



FIGURES B28–B33. Mymaridae heads, posterior.



FIGURES B34–B39. Mymaridae heads, posterior.



FIGURES B40-B45. Mymaridae heads, posterior.



FIGURES B46–B50. Mymaridae heads, posterior. hyc = hypostomal carina.



FIGURES B51–B56. Mymaridae heads, posterior.



FIGURES B57–B62. Mymaridae heads, posterior.



FIGURES B63–B65. Mymaridae heads, posterior.



FIGURES B66–B68. Mymaridae heads, posterior.



FIGURES C1–C8. Mymaridae heads, dorsal.



FIGURES C9–C16a. Mymaridae heads, dorsal.



FIGURES C16b–C23. Mymaridae heads, dorsal.



FIGURES C24–C31. Mymaridae heads, dorsal.



FIGURES C32–C39. Mymaridae heads, dorsal.



FIGURES C40–C46. Mymaridae heads, dorsal.



FIGURES C47–C54. Mymaridae heads, dorsal.



FIGURES C55–C62. Mymaridae heads, dorsal.



FIGURES C63–C69b. Mymaridae heads, dorsal.



FIGURES C69c-C75. Mymaridae heads, dorsal.



FIGURES D1–D9. Mymaridae heads, lateral.



FIGURES D10–D18. Mymaridae heads, lateral.


FIGURES D19–D26a. Mymaridae heads, lateral.



FIGURES D26b–D34. Mymaridae heads, lateral.



FIGURES D35–D43. Mymaridae heads, lateral.



FIGURES D44–D52. Mymaridae heads, lateral.



FIGURES D53–D61. Mymaridae heads, lateral.



FIGURES D62–D69b. Mymaridae heads, lateral.



FIGURES D69c–D75. Mymaridae heads, lateral.



FIGURES E1–E8. Mymaridae heads, ventral.



FIGURES E9–E15. Mymaridae heads, ventral.



FIGURES E16-E22. Mymaridae heads, ventral.



FIGURES E23–E29. Mymaridae heads, ventral.



FIGURES E30–E37. Mymaridae heads, ventral.



FIGURES E38–E45. Mymaridae heads, ventral.



FIGURES E46–E52. Mymaridae heads, ventral.



FIGURES E53–E59. Mymaridae heads, ventral.



FIGURES E60-E64. Mymaridae heads, ventral.



FIGURES E65–E67. Mymaridae heads, ventral.



FIGURES F1-F8. Mymaridae mouthparts, ventral.



FIGURES F9-F16. Mymaridae mouthparts, ventral.



FIGURES F17–F22. Mymaridae mouthparts, ventral.



FIGURES F23–F27. Mymaridae mouthparts, ventral.



FIGURES F28–F31. Mymaridae mouthparts, ventral.



FIGURES F32–F37. Mymaridae mouthparts, ventral.



FIGURES F38–F45. Mymaridae mouthparts, ventral.



FIGURES F46–F52. Mymaridae mouthparts, ventral.



FIGURES F53–F58. Mymaridae mouthparts, ventral.



FIGURES F59–F65. Mymaridae mouthparts, ventral.



FIGURES F66–F71. Mymaridae mouthparts, ventral.