Insect Systematics and Diversity, 8(3), 1; 2024, ixae007
https://doi.org/10.1093/isd/ixae007
Monograph

Taxonomy

The parasitic louse genus *Myrsidea* (Amblycera: Menoponidae): a comprehensive review and world checklist

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Subject Editor: Carol Von Dohlen

Received on 22 July 2023; revised on 29 February 2024; accepted on 19 March 2024

Myrsidea Waterston, 1915 (Phthiraptera: Menoponidae) is the most diverse genus of avian chewing lice. *Myrsidea* has a global distribution, is thought to be highly host-specific, and parasitizes mostly passerine birds. However, the rate of taxonomic studies describing new species is relatively low, and it is thought that much of the diversity of *Myrsidea* is yet to be discovered. This low rate of taxonomic description for this genus, and many others, may be related to the time-consuming nature of morphological species description and a lack of expertise in louse taxonomy. Furthermore, most of the taxonomic revisions and reviews have focused on specific host families, and no comprehensive review of the morphology and molecular work of *Myrsidea* has been completed in the last 20 years. Here, we review the taxonomy and systematics of *Myrsidea* to (i) describe this chewing louse genus and its biological importance; (ii) describe current problems with its taxonomy; (iii) simplify and summarize morphological descriptions; (iv) summarize molecular data; and (v) provide a comprehensive checklist of the *Myrsidea* species, with all publications and localities of occurrence included. Together, we hope that this information will provide researchers with a single source of information on the genus *Myrsidea*, making it easier for work to proceed on its taxonomy, systematics, ecology, and evolution. Importantly, our work highlights important gaps in our knowledge of *Myrsidea*, providing guideposts on where future work on *Myrsidea* is needed.

Key words: checklist, phylogeny, taxonomy, morphology, lice

Introduction

Parasitic lice (Insecta: Phthiraptera) are a diverse group of wingless ectoparasites of birds and mammals around the world. The genus *Myrsidea* Waterston, 1915 (Phthiraptera: Menoponidae) has a cosmopolitan distribution and is the most speciose genus of parasitic lice (Price et al. 2003, Sychra et al. 2021). Although there are many described species, few efforts have been made to synthesize this knowledge. The first major review on *Myrsidea* was published by Theresa Clay (1966), which was part of a series of manuscripts focusing on morphological data (e.g., Clay 1966, Tandan and Clay 1971, Tandan 1972). In a review of all chewing lice, Price et al. (2003) recognized 207 *Myrsidea* species, parasitizing 281 bird species. More than 95% of *Myrsidea* species parasitize birds of the order Passeriformes (Price et al. 2003), which is also the largest order of birds, containing approximately two-thirds of avian diversity. Over the last 20 years, the number of newly described *Myrsidea* species has

rapidly grown, mainly due to partial taxonomic revisions focusing on *Myrsidea* from specific host families (e.g., Price and Dalgleish 2006, 2007, Price et al. 2005, 2006, 2008a, 2008b, Kounek et al. 2011b, 2013, Kolencik et al. 2018). Given their high host specificity and the considerable lack of knowledge about the occurrence of this genus on passerines, Price et al. (2003) expected that the majority of the diversity of this genus is still unknown. Correspondingly, Valim and Weckstein (2013) estimated the potential diversity of *Myrsidea* in Brazil alone at ~960 undescribed species and likened the currently recognized diversity of *Myrsidea* as "*just a drop in the bucket*."

It is thought that there are likely thousands of undescribed *Myrsidea* species worldwide (Valim and Weckstein 2013). This unknown diversity poses a challenge for traditional taxonomic methods to describe new species as it requires well-trained specialists, multiple slide-mounted specimens for each species, and morphological data of other species for comparison. Integration of new molecular and technological methods, such as whole genome sequencing (Johnson 2022), scanning electron microscopy (Cicchino and Valim 2015), computed tomography (Faulwetter et al. 2013), computer vision (Valan et al. 2021), and machine learning (for extracting the trait data) can be helpful additions in describing new taxa and traits by providing robust genetic data, novel morphological characteristics, and easier access to already published data. The description of new taxa requires the comparison with already published data for the morphological delimitation of species or the description of new species, which can often be very time consuming. However, the first step to beginning any taxonomic revision or description is a comprehensive understanding of the current diversity of the group of interest to place newly described species into context. Here, we review the taxonomy and phylogeny of the genus *Myrsidea* with the aim of providing this background information. We believe that this review can serve as a manual for new descriptions or redescriptions of *Myrsidea* species with the aim to motivate and enable other authors to continue to work on this extremely diverse group of ectoparasites.

Materials and Methods

Morphology

Illustrations for this study were created in Adobe Illustrator 2020 and from slide-mounted specimens using high-quality images from a Luminera Infinity 1 camera and Olympus BX41 microscope. Most illustrations are based on specimens that we analyzed but are partially supplemented with drawings reillustrated from already published materials (Figs. 1–729; more detail is included in figure legends). The best practices used for slide mounting of the louse specimens are described in Palma (1978) and could be further modified as suggested by some authors (e.g., Kolencik et al. 2018). One important methodological note worth mentioning is to be careful not to push too hard on the coverslip or on the specimen, as this can deform or extrude morphologically important body structures (e.g., genital sac sclerites in males), making them difficult or impossible to study.

Detailed information regarding the museum specimens examined for this study is included in Supplementary Appendix 1.

Molecular Data and Phylogenetic Analyses

For molecular data analyses, we used all the available *Myrsidea* DNA sequence data from the GenBank (NCBI) nucleotide database (Supplementary Table S1). A total of 498 *Myrsidea* samples had sequences of a 379-bp fragment of the mitochondrial cytochrome oxidase subunit I gene (COI, Hafner et al. 1994). We also included 3 new *Myrsidea* sequences from hummingbirds collected in Peru (GenBank accession numbers: OR924469, OR924470, OR965459) and sequences of 5 outgroup specimens—3 *Apomyrsidea Kolencik, Sychra and Allen, 2021*, 1 *Dennyus* Neumann, 1906, and 1 *Menacanthus* Neumann, 1912 to reconstruct the phylogeny of *Myrsidea* (Fig. 730A–D; Supplementary Table S1). Outgroup selection was based on the following criteria. (i) Genus *Dennyus* is the most commonly used outgroup in past phylogenetic studies of *Myrsidea* as it was considered to be the closest relative of *Myrsidea* (Cruickshank et al. 2001, Marshall 2003). (ii) However, a recent study by Kolencik et al. (2021) separated *Myrsidea* parasitizing formicariid bird hosts into a new genus, *Apomyrsidea*, which would now be considered the closest relative of *Myrsidea* (Kolencik et al. 2021). (iii) Lastly, *Menacanthus* was included as a more distantly related genus of Amblyceran lice (Martinů et al. 2015, Kolencik et al. 2021). We rooted the tree with a clade including *Dennyus* and *Menacanthus* (Fig. 730D).

All sequences were aligned in MAFFT v.7 using the progressive method FFT-NS-2 (Katoh et al. 2019). We removed any duplicate sequences that were identical in both the sequence and host data, resulting in a phylogenetic tree with 335 unique specimens (including outgroups). We used the "ModelFinder" function (Kalyaanamoorthy et al. 2017) in IQTree v2.1.1 (Minh et al. 2020) to estimate the best model fit for the Bayesian information criterion, and then to reconstruct the maximum likelihood phylogenetic tree we performed both the fast branch SH-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010) and Ultrafast Bootstrap approximation (UFBoot; Hoang et al. 2018) to assess clade support. Sh-aLRT and UFBoot reliability values differ slightly, with satisfactory values for SH-aLRT ≥ 80% and for UFboot ≥ 95% (Minh et al. 2020) (Supplementary Dataset S2).

FigTree v.1.4.4 was used to edit the phylogenetic tree, color the nodes according to UFboot values and tip names according to the host groups, and we further edit the tree in Adobe Illustrator. Bird silhouettes were added to illustrate host associations for all *Myrsidea* parasitizing nonpasserine hosts (Fig. 730A–D; Supplementary Fig. 1).

Lastly, we used MEGA11 (Tamura et al. 2021) to calculate the mean variability between sequences of the same locus (*p*-distance), with substitution type set as nucleotide, method as *p*-distance, substitutions including Transitions + Transversions, rates as uniform, gaps/missing data treated as pairwise deletion, for all codon positions.

The Checklist

The data for this review and checklist were collected from 301 publications (see *References*), mostly focusing on or including *Myrsidea* chewing lice (Supplementary Dataset S1; https://github.com/StanleeKol/MyrsideaReview or DOI: 10.5281/zenodo.10356167). Moreover, we also included information from additional slide-mounted specimens examined by the authors (Supplementary Appendix 1). This helped us to either verify and/or illustrate the specific morphological characteristics denoted in published studies, for example, the morphology of the genital sac sclerite in males (Figs. 139–729).

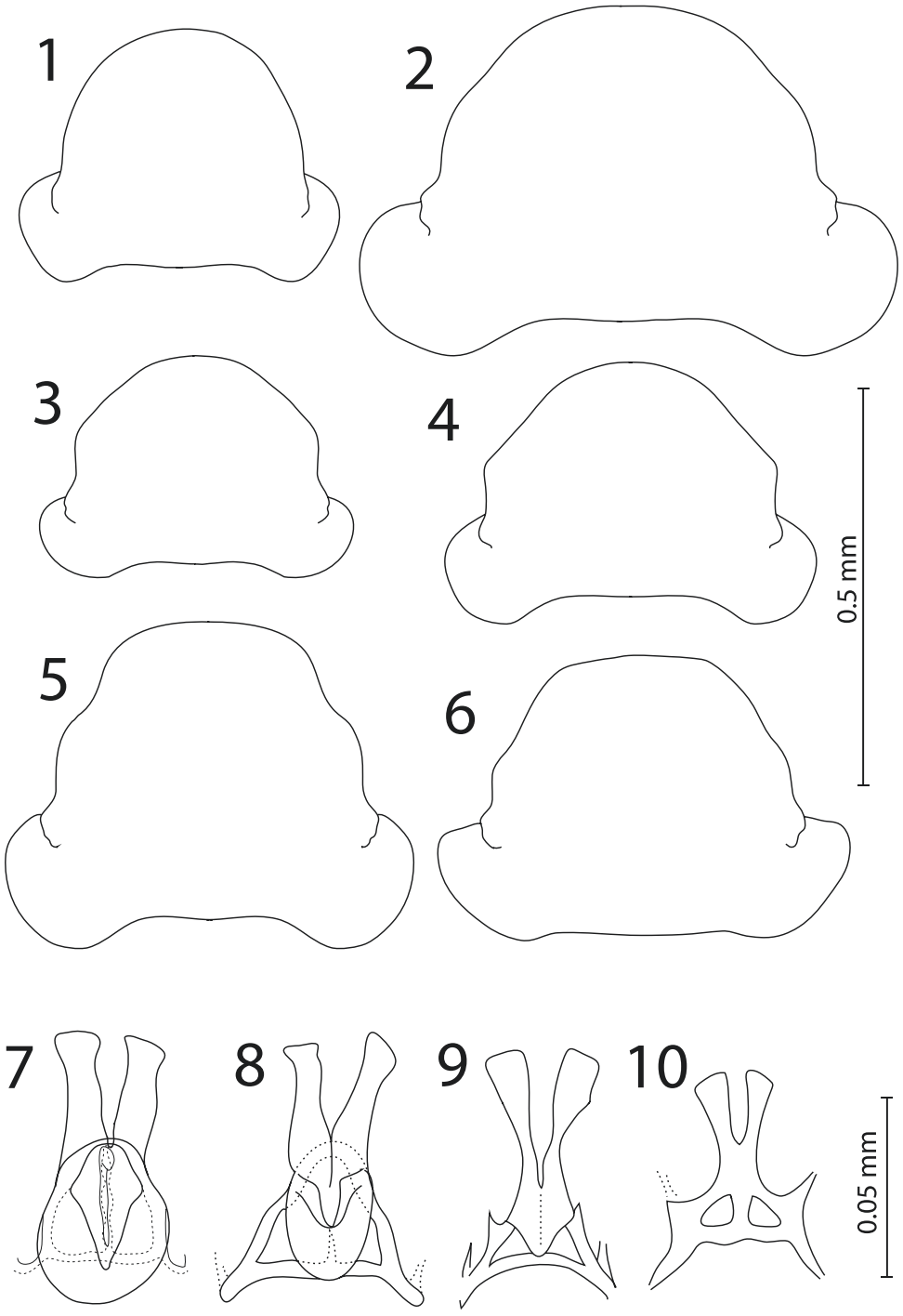
Bird taxonomy.

Avian distribution and breeding range follow the IOC v12.2 World Bird List (Gill et al. 2022). More detailed information and explanation of general regions can be found at https://www.worldbirdnames.org. The authorships of all *Myrsidea* chewing lice and their bird hosts are included in The Checklist of *Myrsidea* (Supplementary Dataset S1), and thus, we do not include them in the text of this review.

Results and Discussion

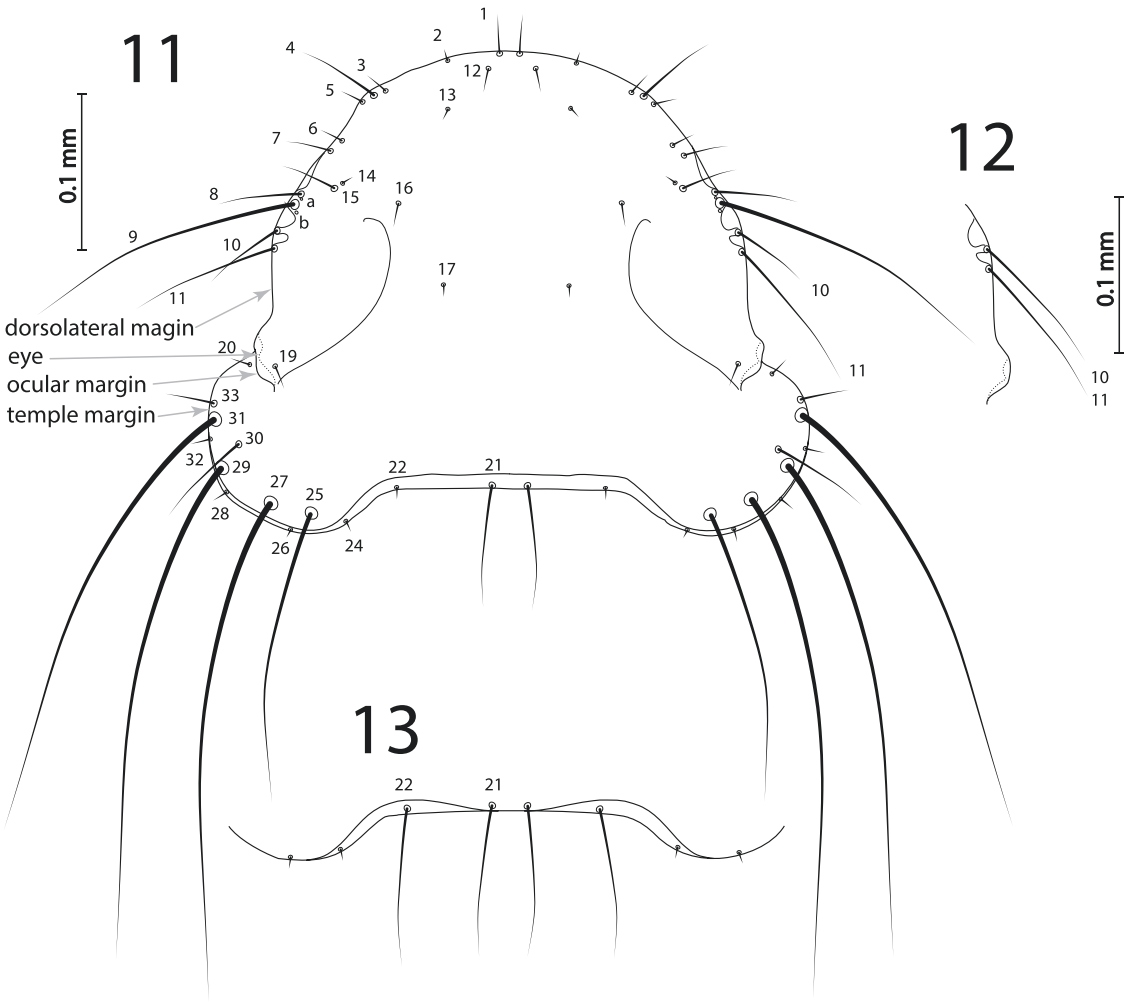
Systematics

Kingdom: Animalia Linnaeus, 1758
Phylum: Arthropoda Gravenhorst, 1843



Figs. 1–10. Head shape. 1, *M. pycnonoti*. 2, *M. ivanliteraki*. 3, *M. quadrifasciata*. 4, *M. novaeseelandiae*. 5, *M. mcleannani*. 6, *M. dissimilis*. 7–10, Hypopharynx: 7, fully developed (*M. sylviae*); 8, moderately reduced (*M. ivanliteraki*); 9, moderately reduced (*M. fasciata*); 10. completely reduced (*M. aynazae*).

Class: Insecta Linnaeus, 1758
Order: Psocodea Hennig, 1966
Suborder: Troctomorpha Roesler, 1944
Infraorder: Phthiraptera Haeckel, 1896
Parvorder: Amblycera Kellogg, 1896
Family: Menoponidae Mjöberg, 1910
Genus: *Myrsidea* Waterston, 1915
Synonyms: *Acolpocephalum* Ewing, 1927; *Alcediniphilus* Ansari, 1951; *Allomyrsidea* Conci, 1942; *Australmenopon* Conci, 1942; *Corvomenopon* Conci, 1942; *Densidea* Złotorzycka, 1964; *Eichlerinopon* Złotorzycka, 1964; *Lanimenopon* Złotorzycka, 1964; *Liquidea* Złotorzycka, 1964; *Myrsidella* Eichler, 1951; *Neomyrsidella* Złotorzycka, 1964; *Ramphasticola* Carriker, 1949; *Vulgidea* Złotorzycka, 1964; *Wolfdietrichia* Złotorzycka, 1973
Type species: *Myrsidea victrix* Waterston, 1915 by original designation.
Type host: "Yellow and black-billed toucan" = *Ramphastos ambiguus swainsonii* Gould, 1833.



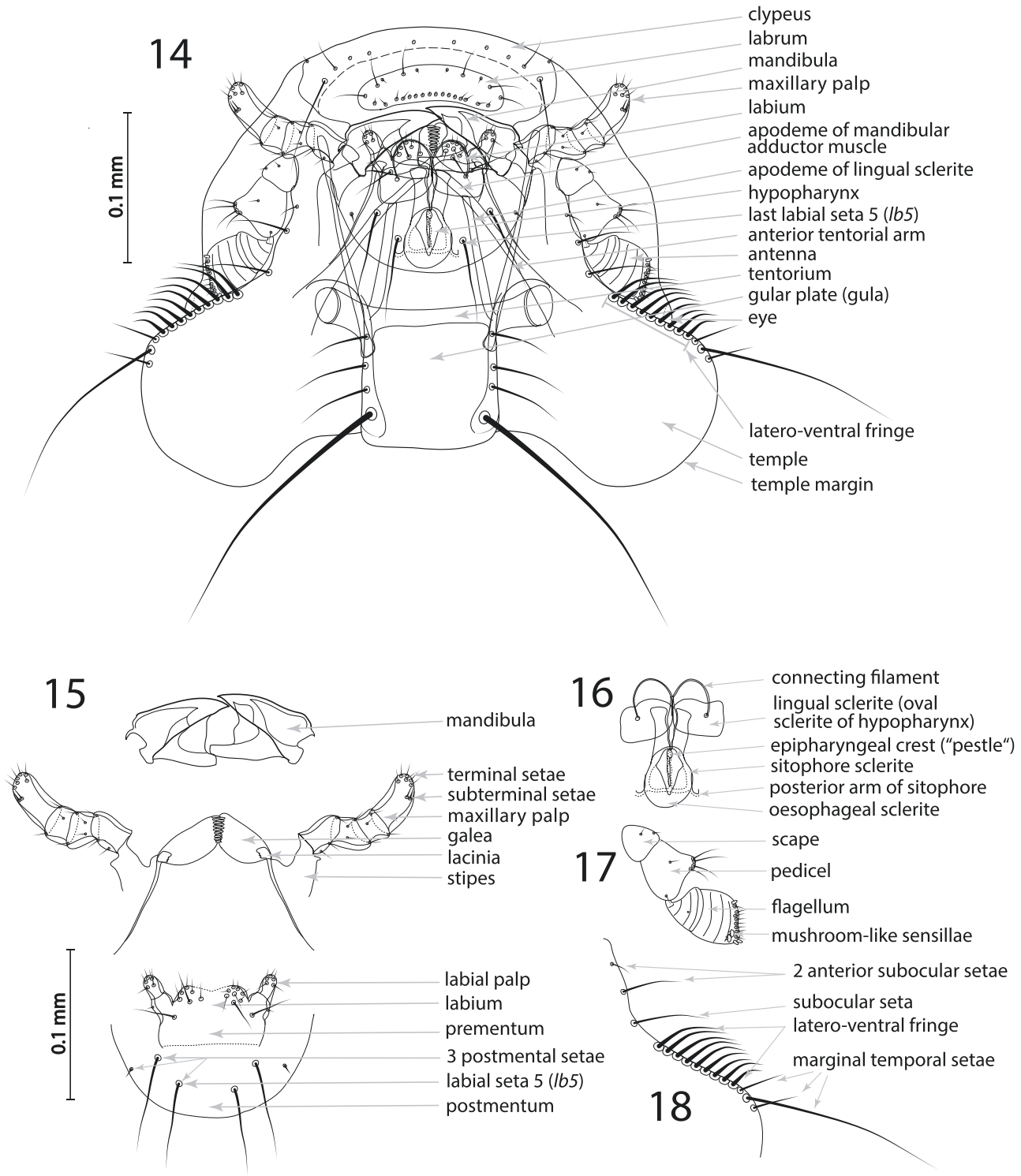
Figs. 11–13. 11, Characters of the dorsal head, the dorsal head setae (*dhs 1–33*), and sensilla (*a–b*) of *M. sylviae*. 12, Details of dorsolateral margin of the head of *M. quadrifasciata*. 13, Details of occipital margin of the head of *M. moylei*. Numbering of *dhs* is according to Clay (1969) as follows: anterior marginal setae (*dhs 1–7*), preocular setae (*dhs 8–11*), anterior dorsal setae (*dhs 12–13*), dorsal setae (*dhs 14–16*), mid-dorsal setae (*dhs 17*), ocular setae (*dhs 19–20*), occipital seate (*dhs 21–22*), temple setae (*dhs 24–33*).

Difficulties With Morphological Descriptions

The taxonomy and systematics of the chewing louse genus *Myrsidea* are based mainly on morphology. Although morphological description is the standard method for designating a new species, many descriptions of the morphology and morphometrics of *Myrsidea* are inconsistent. Currently, there are 2 main frameworks that differ in the counting of the marginal setae on the metanotum and tergites I–VIII, based on the work by Theresa Clay (Clay 1966) and Roger D. Price (e.g., Price et al. 2005), respectively. These authors differed in whether all characters should be described or only those that vary from one species to another. More specifically, Price included all marginal setae on the metanotum and all tergites in his descriptions. In contrast, Clay excluded (i) the most posterolateral setae on metanotum; (ii) the postspiracular setae on tergite I; (iii) the postspiracular setae and their lateral associated setae (Fig. 55; Figs. 3–5 in Clay 1970a) on tergites II–VIII from setal counts, due to their occurrence in all *Myrsidea* species (Valim and Weckstein 2013). Except for these differences, both authors excluded the 2 pairs of anterolateral setae on sternite II from setal counts (Figs. 71 and 72; Fig. 26 in Clay 1966).

Although these are only a few differences in the style of *Myrsidea* species descriptions, these differences result in general confusion in *Myrsidea* species determination, and the reader is forced to find out whether these setae were counted or not. Here, we agree with Valim and Weckstein (2013) that Clay's concept of not counting constant setae eliminates the problem of anomalous duplication or absence of these setae. This allows a more accurate comparison of character differences between *Myrsidea* species. To standardize the counting method, we recommend that all authors follow Clay's concept in all future descriptions. For more detailed information, see Clay (1966) and Valim and Weckstein (2013).

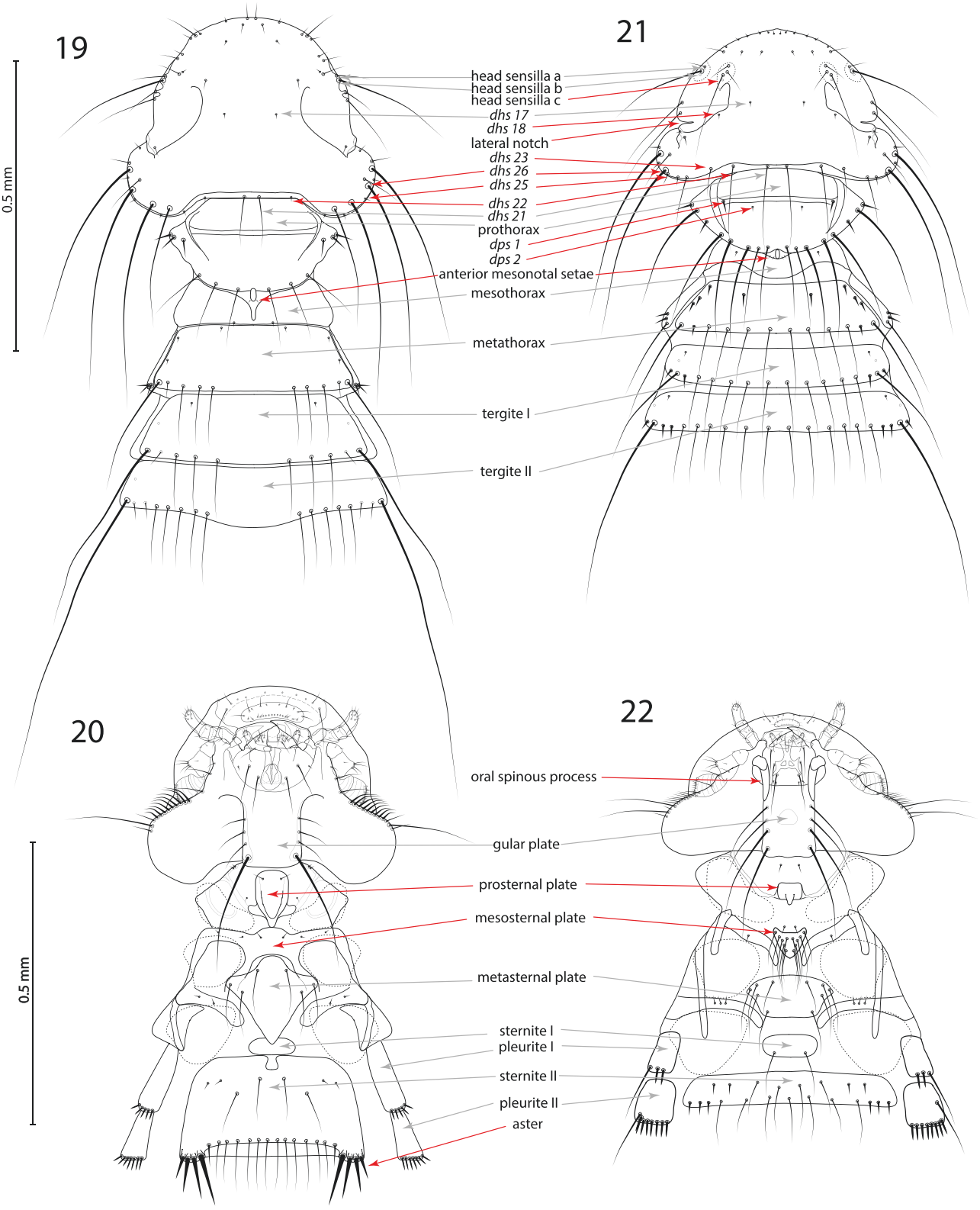
However, there is an exception for counting the sternal setae. Here, Clay (e.g., Clay 1966) often counted sternal setae separately as lateral, posterior, and anterior. Moreover, she often stated the numbers in ranges for each side (e.g., 2–4 left, 3–5 right), which can often cause deviation from the actual number as it can artificially extend the range of sternal setae for the species. Furthermore, many authors have counted all 3 sternal setal groups together (from both sides), except on sternite II, where setae are divided into those on the aster, anterior setae, and marginal setae (including posterior and lateral setae) (e.g., in Price and Dalgleish 2007, Valim and Weckstein 2013). However, because a simple presence of anterior setae on sternites III–VII can often help with the identification of species, we have adapted Clay's methodology to include a note about these setae in



Figs. 14–18. Characters of the ventral head and mouthparts of *M. sylviae*. 14, Ventral head. 15, the chewing mouthparts. 16, Hypopharyngeal sclerites. 17, Antenna. 18, Details of the ventrolateral margin.

recent papers (e.g., in Kolencik et al. 2017, 2018). Thus, we also recommend mentioning the presence or absence of anterior setae on sternite III–VII in all future publications on *Myrsidea* taxonomy.

Due to these different methods of specific setae descriptions, we found inconsistent numbers of setae described in the literature. To handle this, we read the methodology in each article to confirm which, if any, setae were excluded. Otherwise, in general, when using data from a paper by Price et al. that do not exclude setae in the counts, we suggest subtracting (i) 2 from the total counts of marginal metanotal setae; (ii) 2 from the total counts of marginal setae on tergite I; and (iii) 4 from total counts of marginal setae on tergites II–VIII.

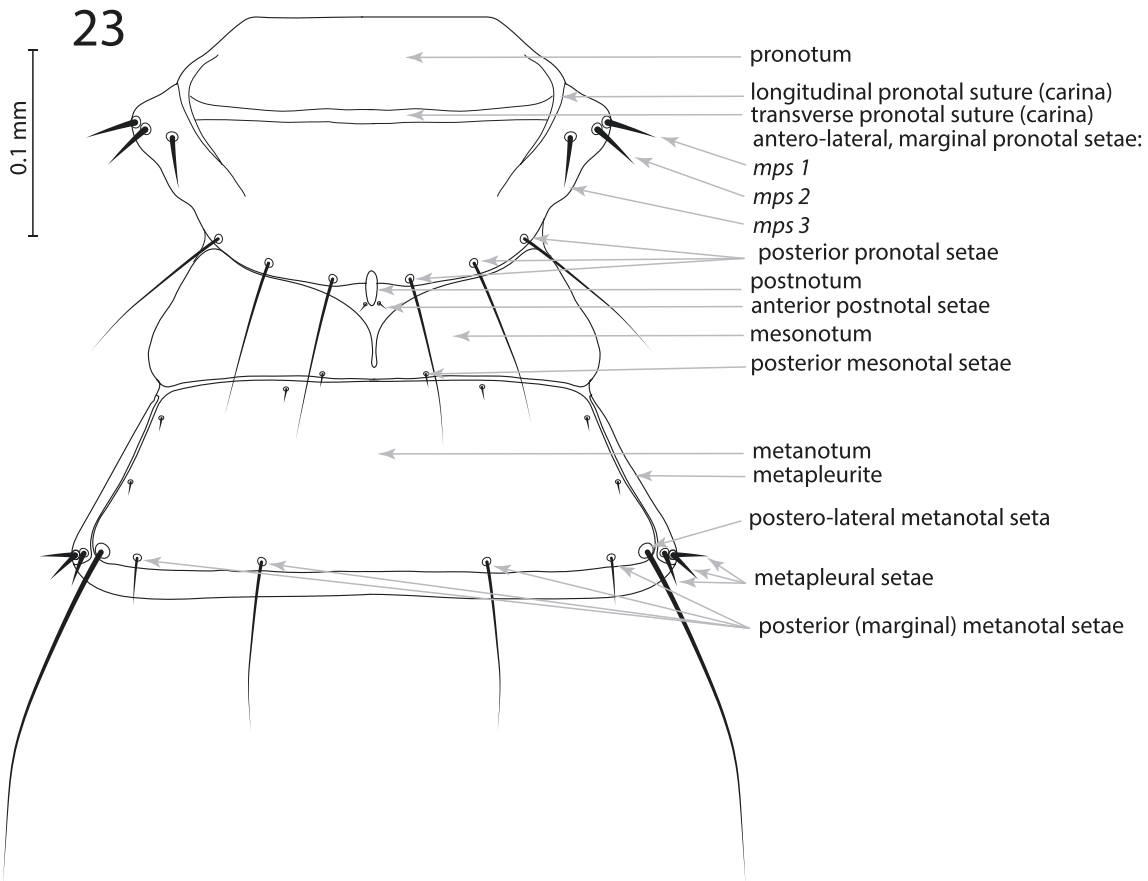


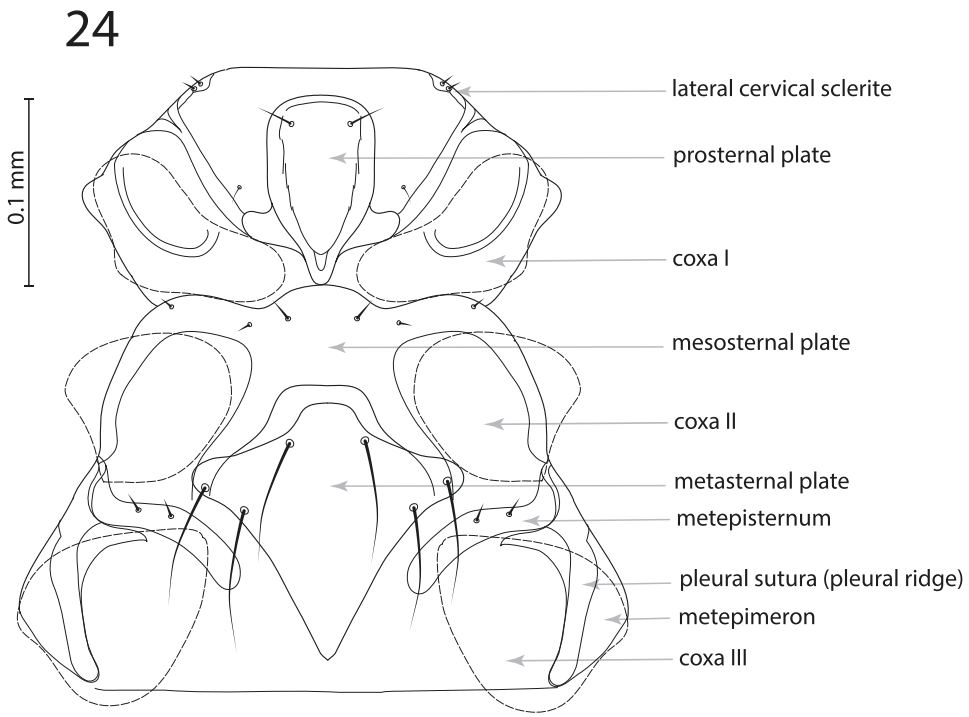
Figs. 19–22. Characters of the head, thorax, and first 2 abdominal segments of representatives of the 2 most common chewing louse genera occurring on passerine birds (comparison). 19–20, *Myrsidea sylviae*: 19, dorsal view; 20, ventral view. 21–22, *Menacanthus curuccae*: 21, dorsal view; 22, ventral view.

Morphology of *Myrsidea*

How Does *Myrsidea* Differ From Other Genera?

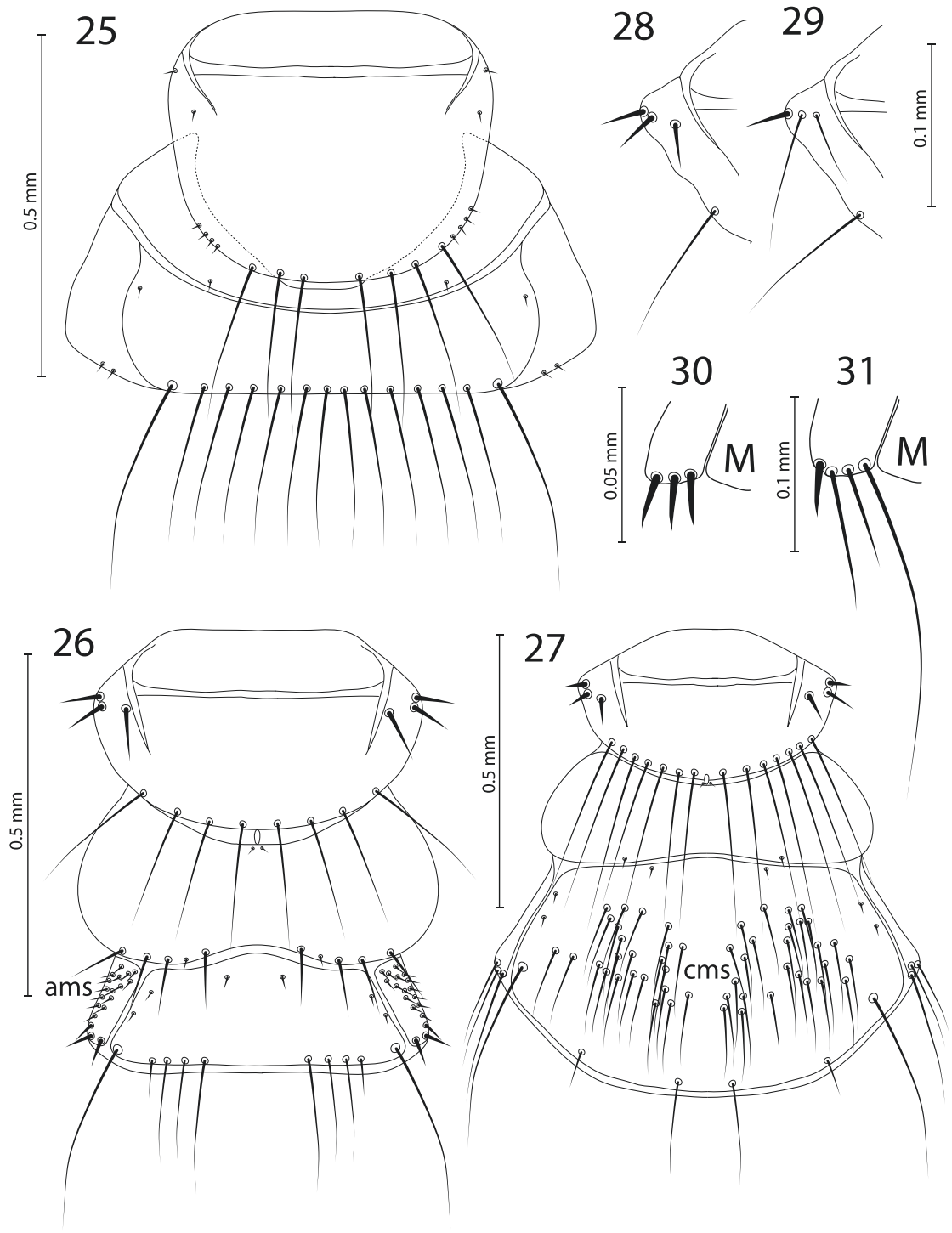
The genus *Dennyus*, which occurs on swifts (Apodidae), has been considered one of the closest relatives and has often been used as an outgroup in phylogenetic studies of *Myrsidea* (e.g., Valim and Weckstein 2013, Kolencik et al. 2017, Madrid et al. 2020). However, a combination of morphological and genetic data indicated a new genus *Apomyrsidea* (previously known as "*Myrsidea*





Figs. 23 and 24. 23, Dorsal view of thorax of *M. sylviae*. 24, ventral view of thorax of *M. sylviae*.

from Formicariidae" in Valim and Weckstein 2013) should be separated from *Myrsidea*. Thus, these 2 genera are now considered as each other's closest relatives (Kolencik et al. 2021). Based on morphology, Kolencik et al. (2021) extended couplet 33 from the key to the genera of Menoponidae (Clay 1969) to indicate that *Apomyrsidea* (33a) differs from *Myrsidea* by the presence of *dorsocentral pronotal setae 2* (*dps 2*) and sternite I mostly surrounded by sternite II (which lies inside the wide notch on anterior margin

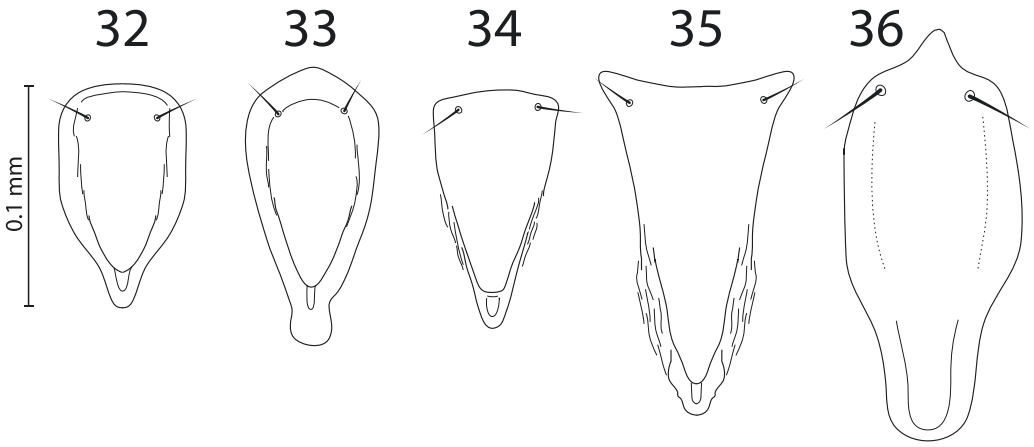


Figs. 25–31. 25–27, Dorsal view of thorax of females: 25, *M. bakeri*. 26, *M. pilosa*. 27, *M. bedfordi*. 28–29, lateral margin of prothorax: 28, *M. sylviae*. 29, *M. vincula*. 30–31, Posterior margin of metapleurite of female: 30, *M. sylviae*; 31, *M. hihi*. M = metanotum; ams = anterior metapleural setae; cms = central metanotal setae.

of sternite II). In addition, the genus *Oculomenopon* Price and Hellenthal, 2005 (33b), which is morphologically very close to *Myrsidea*, differs by the presence of posterior *dorsal head setae 23* (*dhs 23*). Unfortunately, there are no molecular data available for the genus *Oculomenopon* to resolve the phylogenetic relationships among these 3 genera.

Myrsidea can be distinguished from all other chewing lice genera with the combination of the following characteristics (modified from Clay 1966, 1969, Valim and Weckstein 2013):

(1) alveoli of *dorsal head setae* (*dhs*) 26 and 27 not closely associated (Fig. 19 vs. Fig. 21);
(2) *dhs 18* (outer mid-dorsal head seta by Clay 1966 or dorsal head seta "d" by Clay 1962) and *dhs 23* (posterior dorsal head seta "e" by Clay 1962) are missing (Fig. 19 vs. Fig. 21);
(3) head without sclerotized processes (oral spines) arising near the base of maxillary palpi (Fig. 20 vs. Fig. 22);
(4) dorsolateral margin of the head without lateral notch or slit (Figs. 11 and 19 vs. Fig. 21);



Figs. 32–36. Prosternal plate. 32, M. *sylviae*. 33, *M. mcleannani*. 34, *M. hihi*. 35, *M. eisentrauti*. 36, *M. bakeri*. All figures are drawn to the same scale.

(5) dorsal head sensilla 3–5 sensu Clay (1962; Figs. 9–12) or c–e sensu Clay (1969; Fig. 1c–e) absent (Fig. 19 vs. Fig. 21);
(6) characteristic gular plate with greater length and thickness of the posterior pair of setae compared to the rest (Fig. 14);
(7) pronotum without the 2 pairs of dorsal setae lying on or near the transverse carina (*dps 1* and *dps 2* by Clay 1962) (Fig. 19 vs. Fig. 21);
(8) prosternal plate well developed with 2 anterior setae (Fig. 20 vs. Fig. 22);
(9) strongly sclerotized ring-like mesothorax—sternum, pleura, and tergum fused to form a strongly sclerotized ring around the body (Fig. 20 vs. Fig. 22);
(10) mesonotum well defined with only 2 anterior setae (Fig. 19 vs. Fig. 21);
(11) femur III without combs of spine-like setae but with thick or sparse brushes of setae (Fig. 52);
(12) female ventral anal margin without lateral setae-bearing processes (see Clay 1969).

Morphological Characteristics Important for Species Descriptions

The characterization of the genus *Myrsidea* was originally made by Clay (1966). She indicated 20 morphological characteristics were a minimum for the description of species within this genus. Over the years, different authors have modified or added new characteristics. Here, we review all important characteristics and their variability inside the genus *Myrsidea*.

Head

(1) Lateral sides of preantennal region:

A. convex or rounded margin (Fig. 1);
B. slightly convex or straight margin (Figs. 2–4);
C. conspicuously concave margin (Fig. 5) as in *M. mcleannani*;

This character is especially prone to distortion in mounted specimens, and the shape of the anterior margin must be evaluated carefully. Thus, multiple specimens should be examined to clarify variation in this character.

(2) Anterior margin of preantennal region:

A. most species have rounded margins (Figs. 1–4);
B. preantennal region with an almost straight anterior margin (Fig. 6) as in *Myrsidea* from Hirundinidae.

(3) Hypopharynx—different types depending on degrees of reduction of esophageal sclerite:

A. most species have a fully or well-developed sclerite (called "strong" by some authors) with fully developed esophageal sclerite that almost completely overlaps sitophore sclerite (Fig. 7 and 16);
B. moderately reduced esophageal sclerite, sitophore sclerite is partially visible (Figs. 8 and 9);
C. completely reduced esophageal sclerite, i.e., only sitophore sclerite is visible (e.g., *M. quadrifasciata*, *M. wombei*, and *M. marksi* from Pycnonotidae, *M. sultanpurensis* from Turdidae; Fig. 10).

This is a very useful characteristic for species determination, but it has no phylogenetic value because closely related species can have different types of hypopharyngeal sclerites.

(4) Dorsal head setae (*dhs) 10/11* ratio:

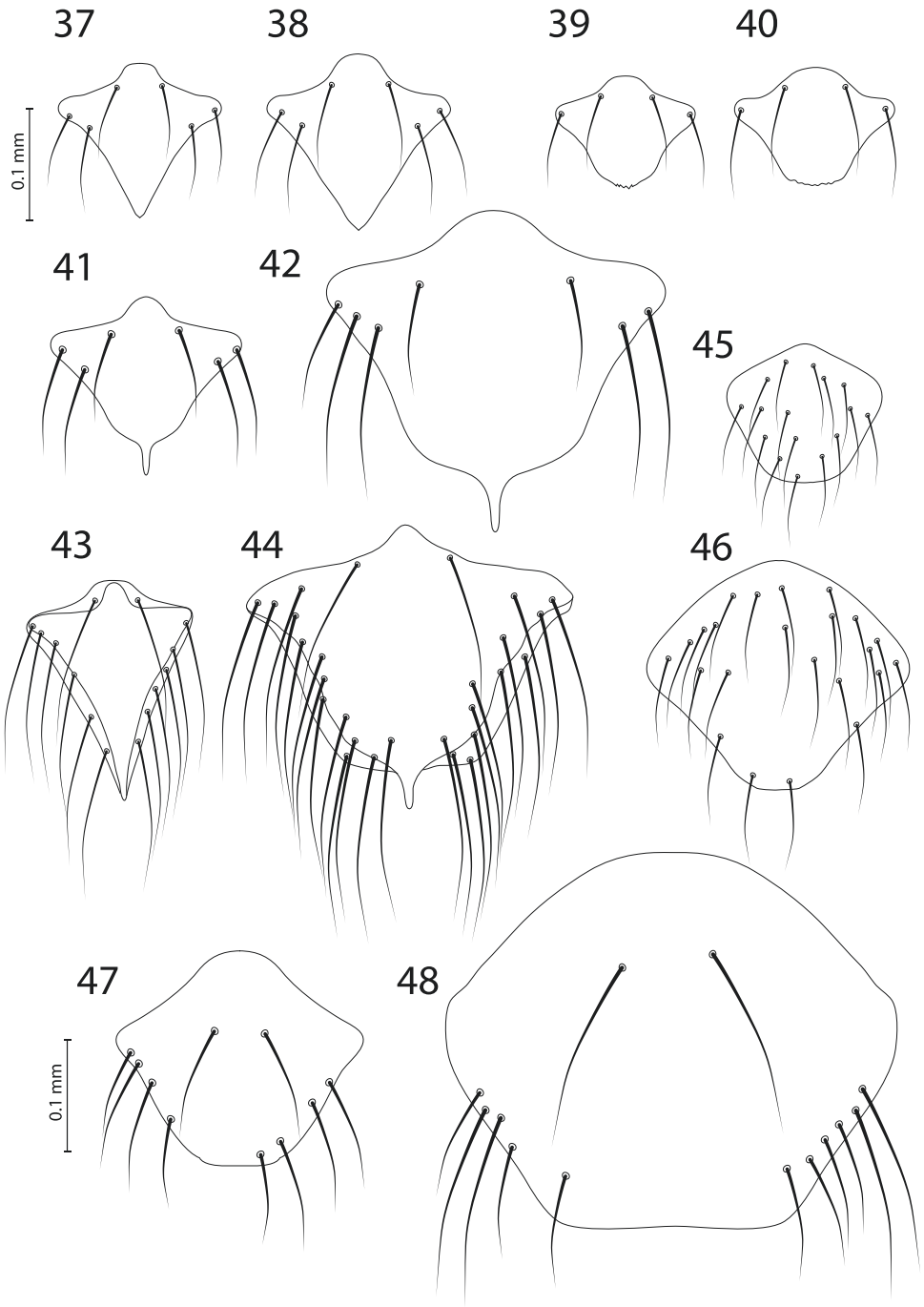
A. most species have *dhs 10* conspicuously shorter than *dhs 11*, i.e., *10/11* ratio of 0.4–0.6 (Fig. 11);
B. *dhs 10* as long as *dhs 11* or even longer, i.e., *10/11* ratio 0.7–1.2 (e.g., *M. srivastava* and *M. castanothorax* from Estrildidae, *M. bubalornis*, and *M. ledgeri* from Ploceidae, *Myrsidea* from Corvidae, *M. quadrifasciata*; Fig. 12).

This character may even show variation on both sides of the head on one individual, so it cannot be used alone to distinguish species if only a few specimens are available. The *10/11* ratio ranges are also only informative when they are consistent across many specimens, and they must be evaluated carefully for each species. Both sexes of the same species usually show the same value of the *10/11* ratio.

(5) Length of outer occipital seta *dhs 22* (posterior dorsal head seta "f" of Clay 1962):

A. Most species have *dhs 22* conspicuously shorter than *dhs 21* (Fig. 11);
B. A minority of species have *dhs 22* as long as inner occipital seta *dhs 21* (only known on some *Myrsidea* from toucans—formerly *Ramphasticola—M. aenigma*, *M. mirabile*, *M. moylei*; Fig. 13).

Clay (1966) considered the short length of outer occipital setae *dhs 22* as one of the generic characters of *Myrsidea*. However, Kolencik



Figs. 37–48. Metasternal plate. 37 and 38, M. *sylviae*: 37, Male; 38, Female. 39 and 40, *M. johnsoni*: 39, male; 40, female. 41 and 42, *M. hihi*: 41, male; 42, female. 43 and 44, *M. interrupta*: 43, male; 44, female. 45 and 46, *M. pilosa*: 45, male; 46, Female. 47 and 48, *M. bedfordi*: 47, Male; 48, Female. All figures are drawn to the same scale.

et al. (2022a) recently confirmed that *Ramphasticola* is a synonym of *Myrsidea*, so the variability of this character needs to be taken into consideration.

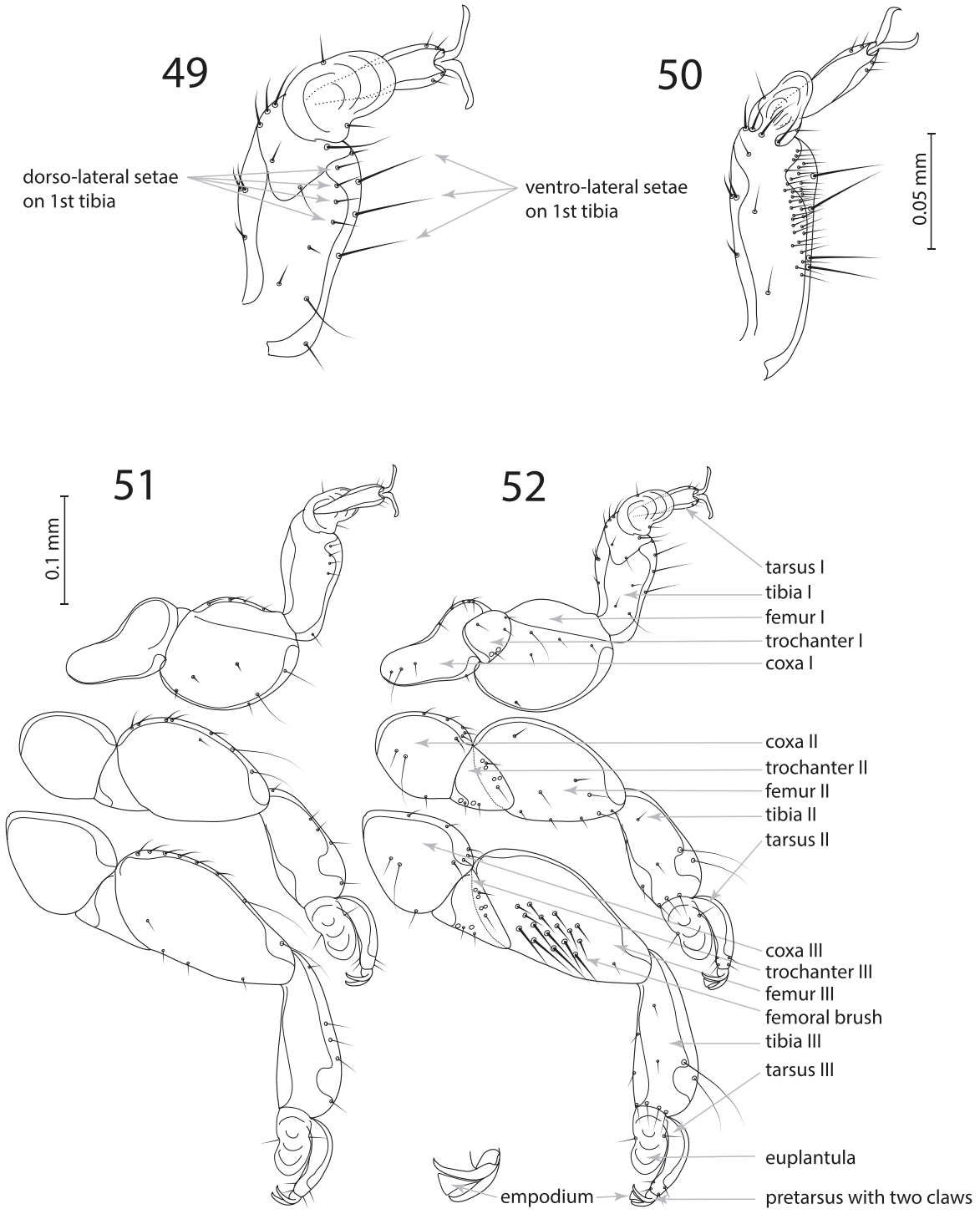
(6) Length of *labial seta 5* (*ls 5*) (or 3rd postmental seta according to Clay 1969; Fig. 14 and 15):

A. *ls 5* quite long, around 0.10 mm (e.g., 0.08–0.09 in *M. pitangi* from Tyrannidae, *M. seminuda* and *M. sayaca* from Thraupidae);
B. *ls 5* short (e.g., 0.03–0.04 in *M. oleaginei*, and *M. olivacei* from Tyrannidae).

(7) Ventrolateral fringe (or subocular comb row according to Clay 1969; Figs. 14 and 18):

A. Most species have 9–11 setae on each side (Figs. 14 and 18);
B. Conspicuously higher number of setae (e.g., *M. ivanliteraki* with 15–18, *M. vincula* with 13–15, or *Myrsidea* from Corvidae, e.g., *M. isostoma* or *M. anathorax* with 13–14 setae).

This character may show some variation even on both sides of the same specimen, so it cannot be used alone to distinguish species if only a few specimens are available.



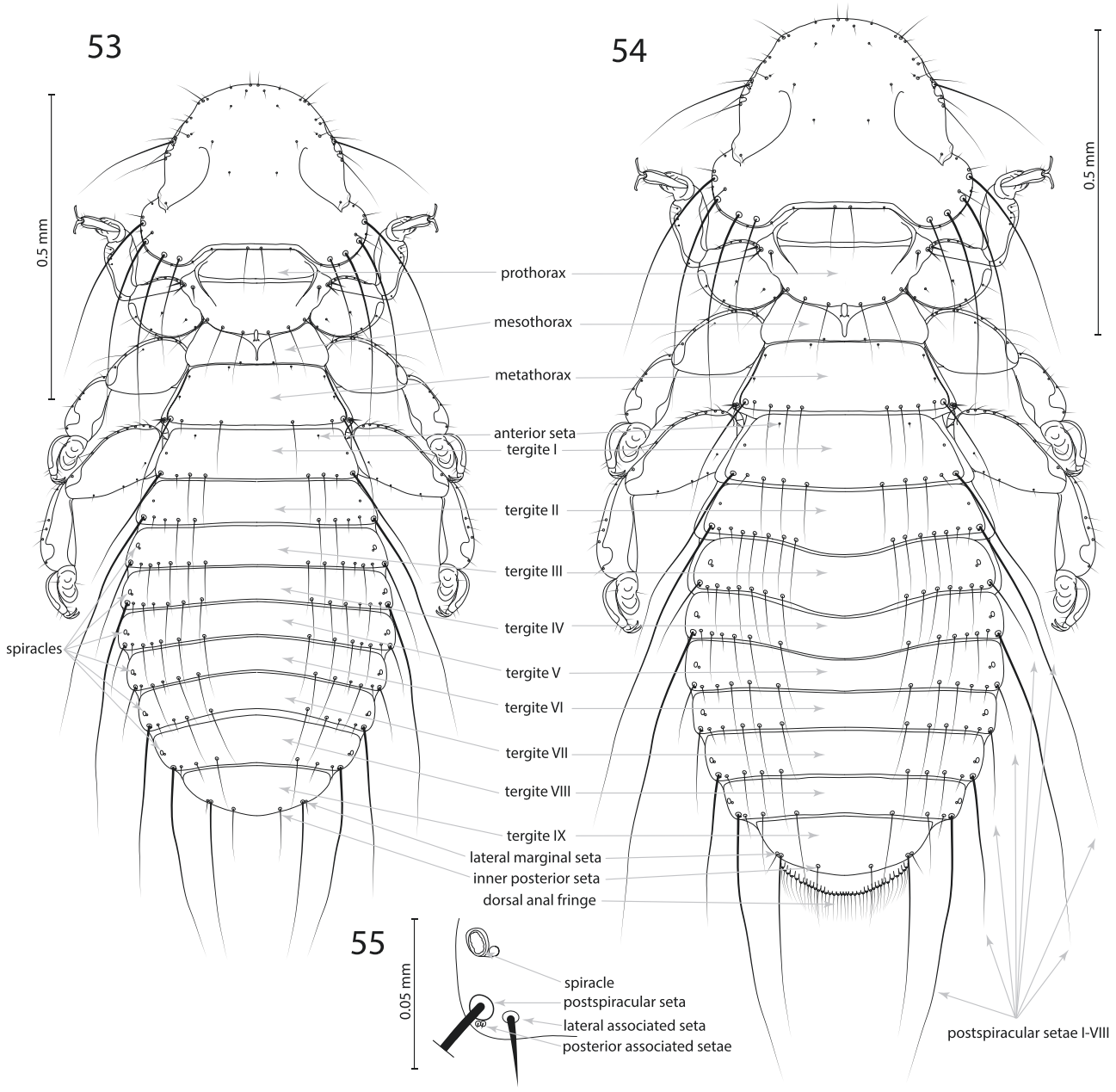
Figs. 49–52. 49–50, First tibia: 49, *M. sylviae*; 50, *M. ivanliteraki*. 51, Dorsal view of legs of *M. sylviae*. 52, Ventral view of legs of *M. sylviae* with detail of praetarsus III with 2 claws and empodium.

(8) Gula (gular plate):

A. Most species have 4–6 setae on each side (Fig. 14);
B. Higher number of setae (e.g., *M. isosotoma* from Corvidae with 7–9, *M. ivanliteraki* with 6–11, *M. sultanpurensis* 8–9 setae on each side);
C. Lower number of setae (e.g., *M. leucophtalmi*, *M. mcleannani* with 3–4).

This character may show variation even on both sides of a gular plate on one individual, so it cannot be used alone to distinguish species if only a few specimens are available.

(9) Characters of the antenna (Fig. 17)—Clay (1966: 338) stated that the characters of the antenna, especially the position of the 2 mushroom-like sensilla on the end of the flagellum, may prove to be of taxonomic value within the Menoponidae. The



Figs. 53–55. Dorsal view of *Myrsidea sylviae*: 53, male; 54, female. 55, Details of the postspiracular setal complex.

importance of this character for intraspecific and interspecific variability within *Myrsidea* is still questionable. Moreover, the antennal segments, especially the last one, are prone to distortion in mounted specimens. Thus, well-mounted specimens are necessary to evaluate differences in this character. More research is needed to evaluate the level of intraspecific and interspecific variability among antennal characters within the genus *Myrsidea*.

Thorax

(10) Shape of pronotum:

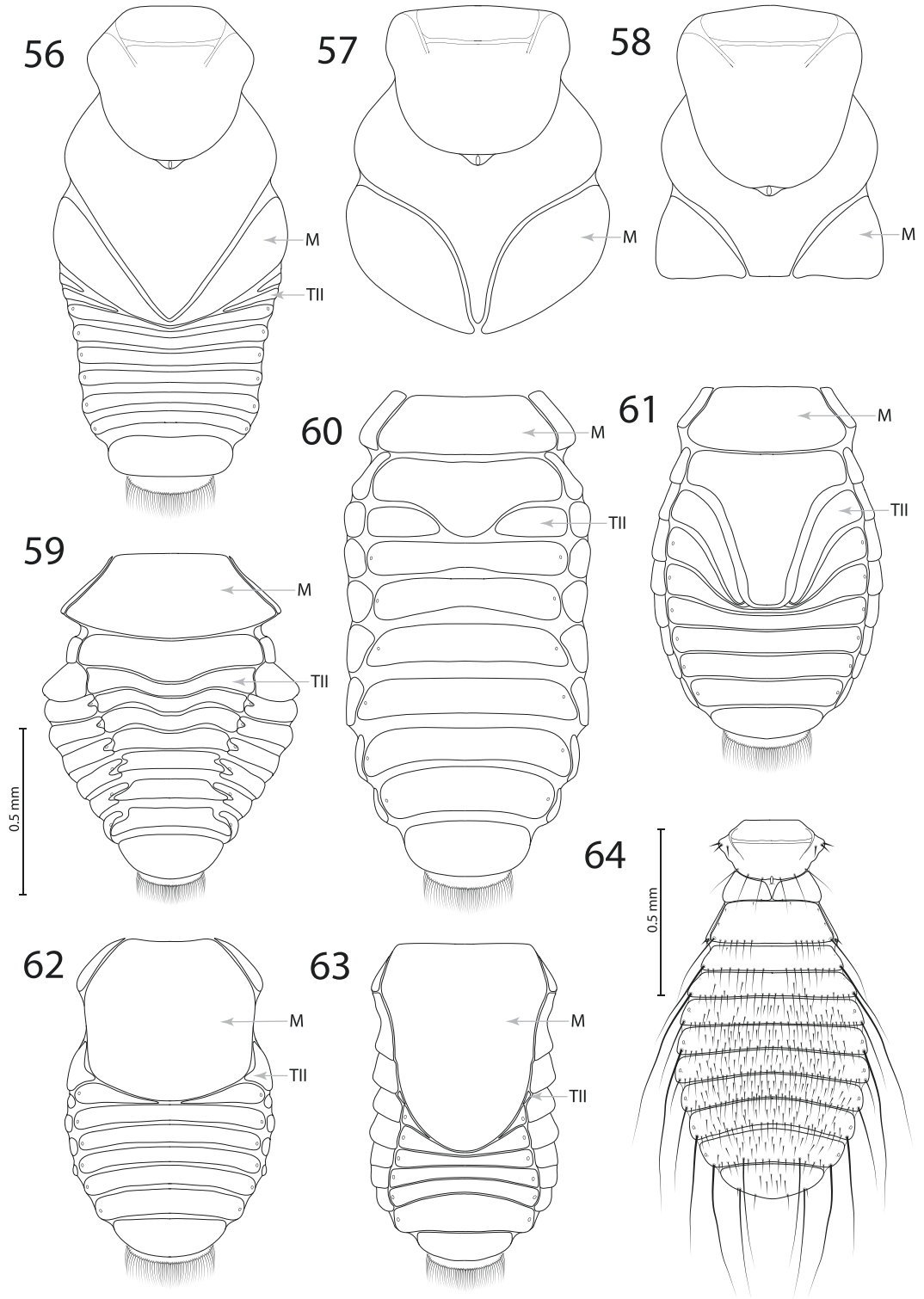
A. Almost all species have a pronotum of hexagonal shape with a straight or slightly rounded posterior margin (Fig. 23);

B. Enlarged pronotum with widely rounded posterior margin can be found on some *Myrsidea* from Corvidae (e.g., *M. bakeri*, Fig. 25), and some *Myrsidea* from toucans (former *Ramphasticola—M. aenigma*, *M. mirabile*, *M. moylei*; Figs. 56–58).

(11) Anterolateral marginal pronotal setae (*marginal prothoracic setae 1–3*, *mps 1–3* in Clay 1962):

A. Most species have 3 spine-like setae of the same length, usually with *mps 3* located submarginally next to *mps 2* (Figs. 23 and 28);

B. One (*mps 3*), 2 (*mps 2–3*), or all 3 anterolateral marginal setae (*mps 1–3*) longer and fine, not spine-like, with *mps 3* located submarginally next to *mps 2* (e.g., *M. vincula*, or *M. cornicis*, *M. isostoma* from Corvidae) (Fig. 29).

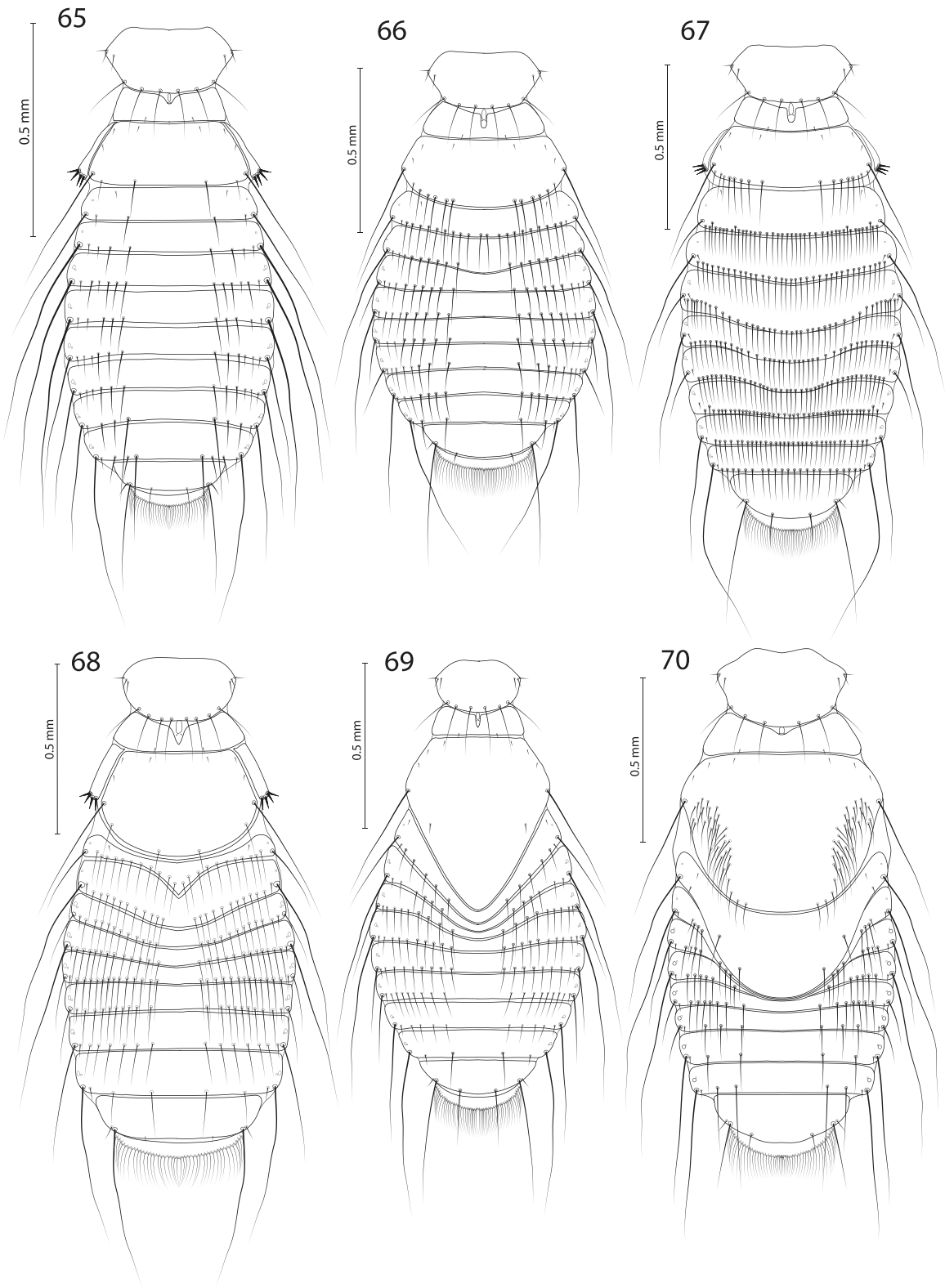


Figs. 56–64. Characters of dorsal thorax and abdomen. 56, Thorax and abdomen of a female of *M. moylei*. 57 and 58, Thorax of female: 57, *M. aenigma*; 58, *M. mirabile*. 59–63, Metathorax and abdomen of female: 59, *M. novaeseelandiae*; 60, *M. clayae*; 61, *M. montana*; 62, *M. grandiceps*; 63, *M. buxtoni*. 64, Thorax and abdomen of a male of *M. rustica*. Figs. 59–62, and 64 are drawn to the same scale. Figs. 56–58 are redrawn from Hellenthal et al. (2005), and Fig. 63 is redrawn from Waterston (1928). Figs. 56–63 are drawn without chaetotaxy, except anal fringe. Abdominal spiracula are present on abdominal segments III–VIII. M = metanotum, TII = tergite II.

(12) Posterior pronotal setae:

A. Most species with 6 setae (3 on each side, Fig. 23);

B. A minority of species with 8 or more setae (e.g., *M. vincula*, *M. ivanliteraki*, *Myrsidea* from *M. carrikeri* species group from Turdidae with 4 setae on each side; *Myrsidea* from Corvidae with 4–7; *M. bedfordi*, *M. malayensis* with 7–10 setae on each side, Fig. 27; and especially, *Myrsidea* from toucans—former *Ramphasticola*—*M. aenigma*, *M. mirabile*, *M. moylei* with a total of 43–90 setae).



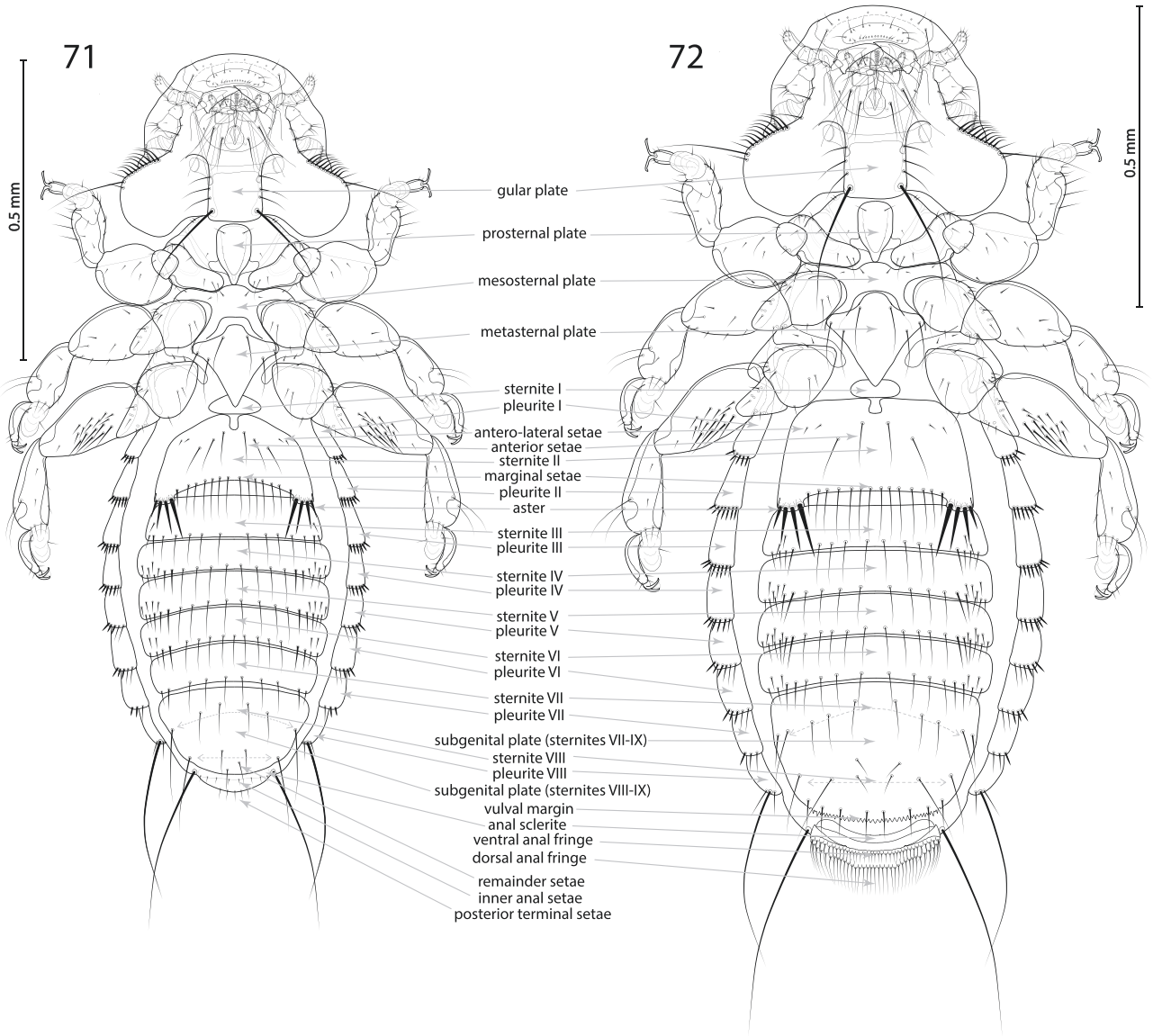
Figs. 65–70. Dorsal view of thorax and abdomen of females: 65, *M. pycnonoti*; 66, *M. leucophthalmi*; 67, *M. poliogasteri*; 68, *M. scleruri*; 69, *Myrsidea* sp. from *Erythrura trichroa*; 70, *M. chapensis*.

(13) Shape of prosternal plate:

A. Most species have prosternal plates with a rounded or convex anterior margin (Figs. 24, 32, and 33), rarely elongated, forming a distinct protuberance (Fig. 36);

B. A minority of species have plates with straight anterior margins, creating a triangle shape of the plate (e.g., *M. hibi*, Fig. 34);

C. Unique plate with concave anterior margin (*M. eisentrauti*, *M. pectinata*) (Fig. 35).



Figs. 71 and 72. Ventral view of *Myrsidea sylviae*: 71, male; 72, female. Dotted arrows show setal rows on the original sternite VII of females, sternite VIII of both males and females and the remainder of the setae of males.

The prosternal plate is always well-developed in *Myrsidea*, with well-defined sclerotized marginal borders around the plate. There are 2 anterolateral setae situated on the main body of the prosternal plate, submarginal to the anterolateral angles. Contrary to other menoponid genera, a pair of very small anterior prosternal setae are missing in *Myrsidea* (see also Marshall, 2003: 66).

(14) Latero-dorsal and latero-ventral setae on the first tibia:

A. Most species have 4(–6) latero-dorsal and 3(–4) latero-ventral setae (Figs. 49, 51, and 52);
B. A minority of species have a higher number of latero-dorsal setae (*M. ishizawai* from Turdidae with 11–21, *M. vincula* with 11–17, *M. ivanliteraki* with 23–35, Fig. 50).

(15) Shape of mesonotum:

A. Almost all species have narrow mesonotums of rectangular shape with straight posterior margins (Fig. 23);
B. Enlarged mesonotum can be found on females of some *Myrsidea* from Corvidae (e.g., *M. pilosa*, Fig. 26), and especially on some *Myrsidea* from toucans (e.g., former *Ramphasticola—M. aenigma*, *M. mirabile*, *M. moylei*) where the medio-posterior margin of mesonotum is strongly enlarged affecting the shape of metanotum and abdominal tergites (Figs. 56–58).

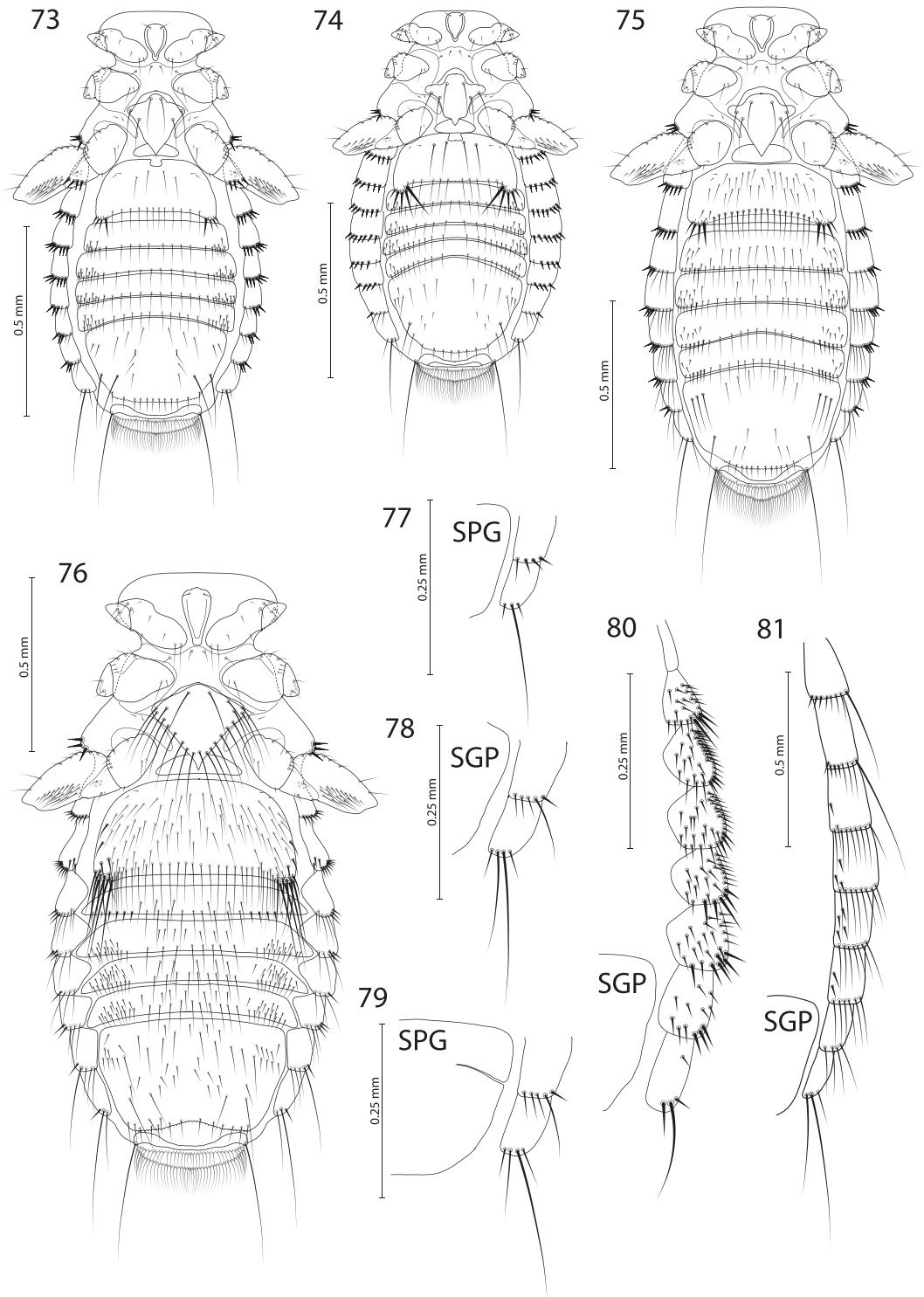
(16) Division of mesonotum:

A. Most species without median division of mesonotum (Figs. 25–27);
B. With a partial or complete median division of the mesonotum (e.g., *M. sylviae*, *Myrsidea* from Hirundinidae) (Figs. 23 and 64).

(17) Posterior mesonotal setae:

A. Almost all species have only 2 short posterior setae (Fig. 23);
B. A minority of species have 12–20 long additional setae are present (e.g., *M. karyi* and *M. pilosa* from Corvidae) (Fig. 26).

(18) Shape of the metanotum—this character can show sexual dimorphism, although almost all males have a nonenlarged



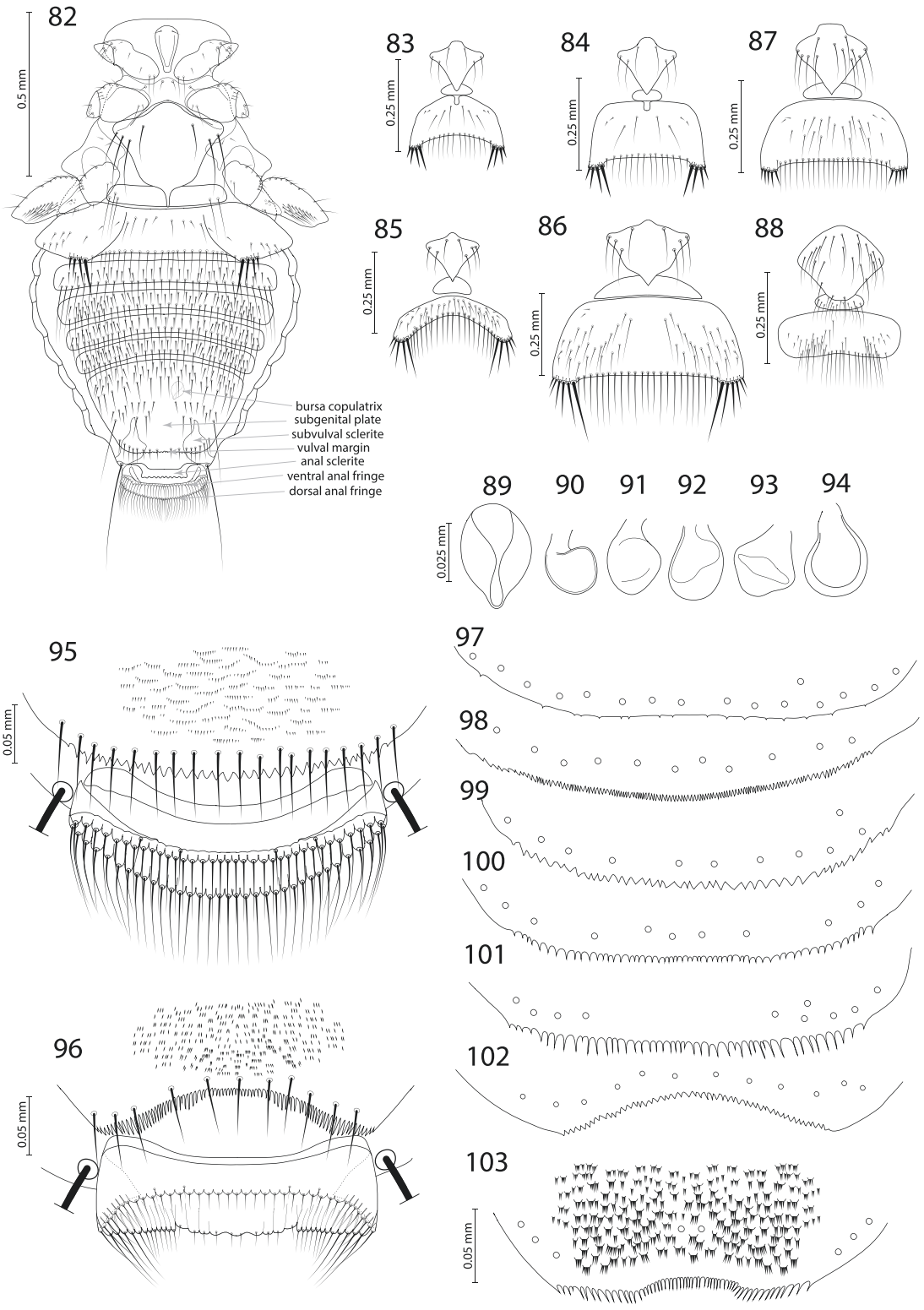
Figs. 73–81. 73–76, Ventral view of thorax and abdomen of females: 73, *M. pachyramphi*; 74, *M. capeki*; 75, *M. poliogasteri*; 76, *M. isostoma*. 77–79, pleurites VII and VIII: 77, *M. quadrifasciata*; 78, *M. rustica*; 79, *M. pycnonoti*. 80 and 81, pleurites I–VIII: 80, *M. pilosa*; 81, *M. ivanliteraki*.

metanotum with an almost straight posterior margin; in some species, the females show some modifications in metanotum:

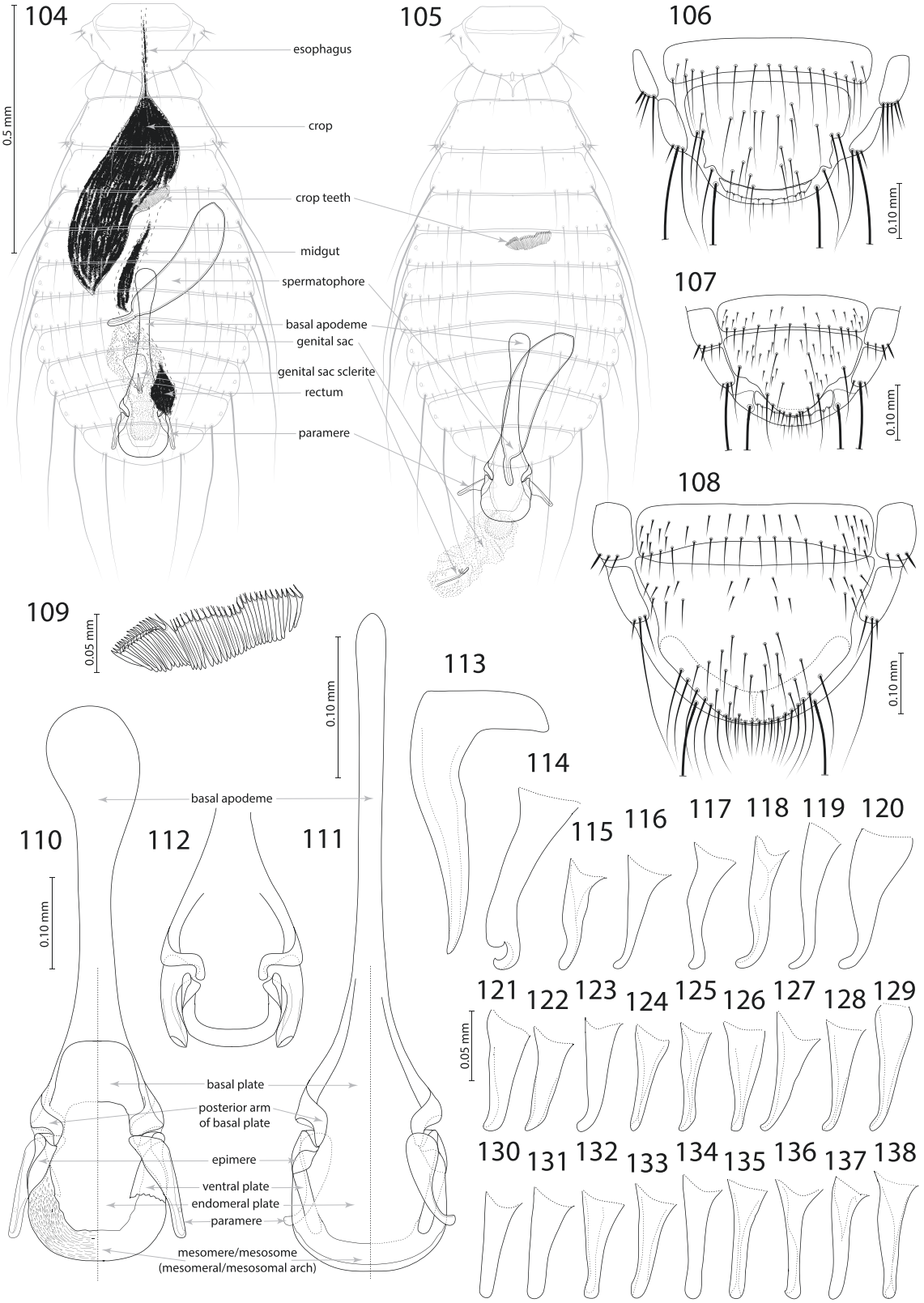
A. Females of most species have nonenlarged metanotum with almost straight posterior margin (Figs. 23 and 65);
B. Females and rarely also males (e.g., male of *M. chiapensis*) with slightly enlarged metanotum with rounded posterior margin (Fig. 66);
C. Females with strongly enlarged metanotum that affects the shape of subsequent abdominal tergites (Figs. 62, 63, 68–70).

(19) Division of metanotum:

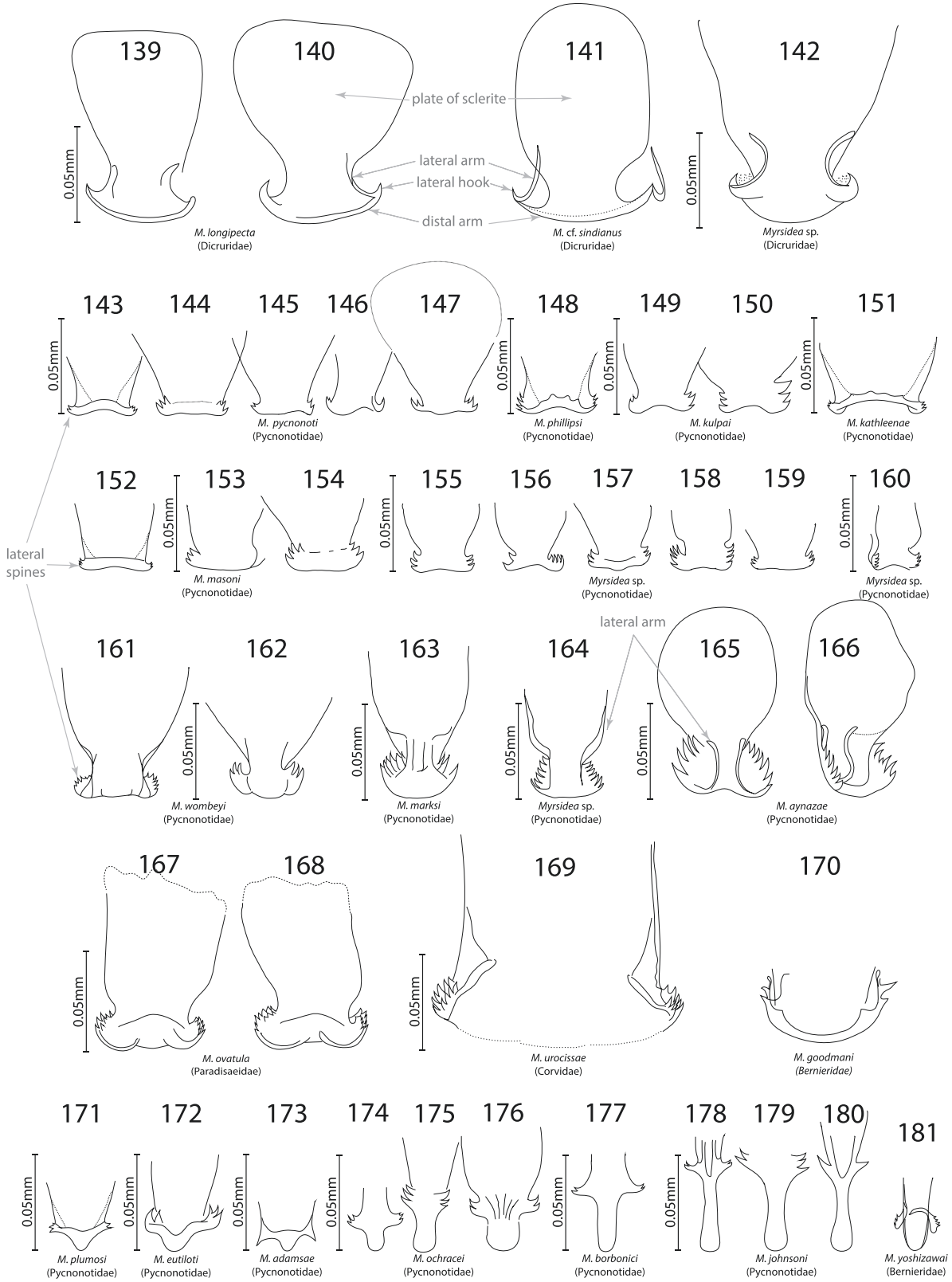
A. Most species without median division of metanotum (Figs. 23, 56, 59–63);
B. Complete median division of the metanotum is present on some *Myrsidea* from toucans (e.g., former



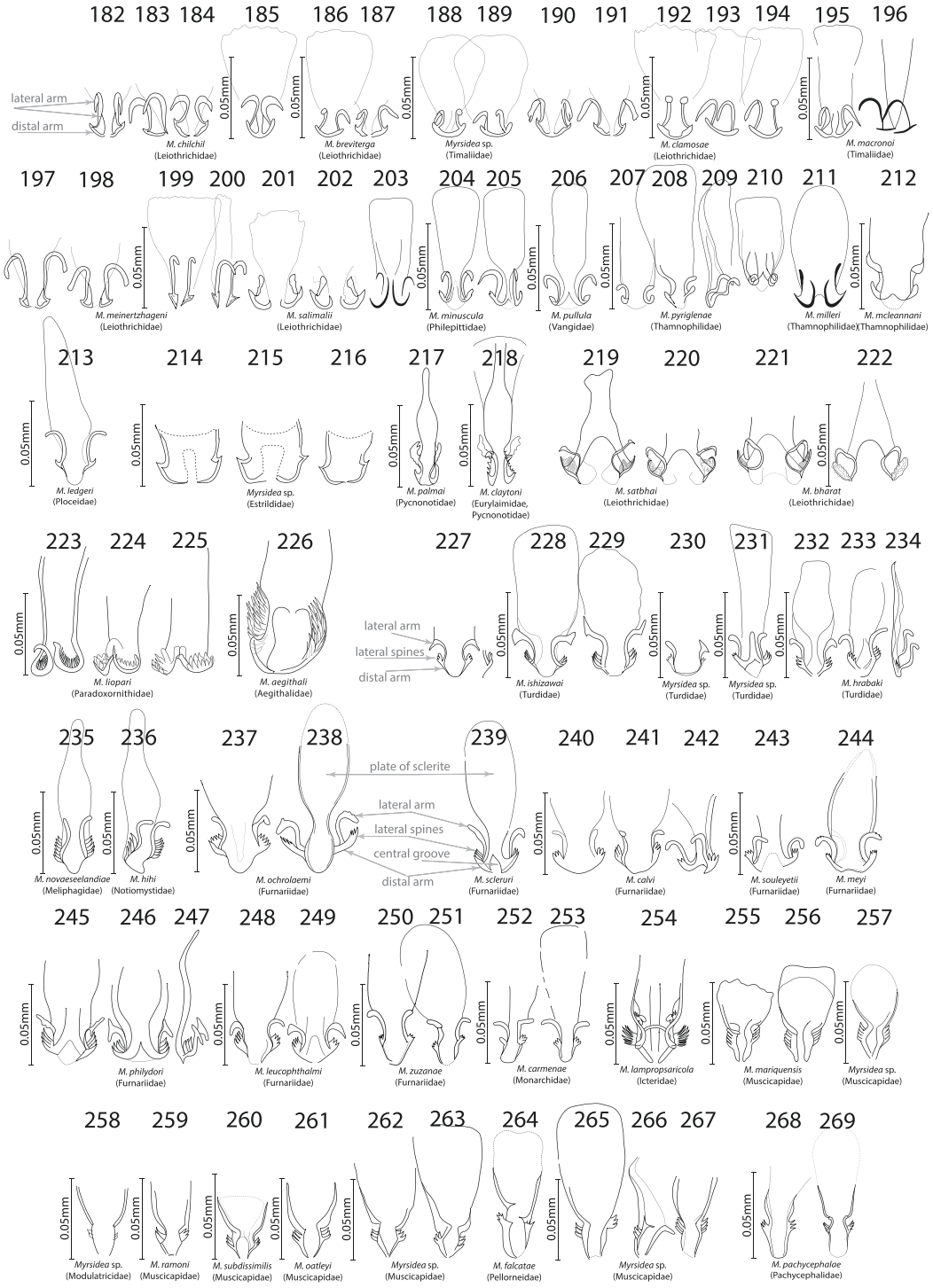
Figs. 82–103. 82, Ventral view of thorax and abdomen of a female of *M. hihi*. 83–88, Metasternal plate and sternites I–I: 83, Male of *M. sylviae*; 84, female of *M. sylviae*; 85, Male of *M. chiapensis*; 86, female of *M. chiapensis*; 87, female of *M. rustica*; 88, female of *M. pilosa*. 89–94, Bursa copulatrix: 89, *M. hihi*; 90, *M. spizae*; 91, *M. violaceae*; 92 and 93, *M. larvatae*; 94, *M. poliogasteri*. 95 and 96, Ventral terminalia—vulval margin, anal sclerite, and anal fringe of the female with microtrichia on the surface of the genital chamber: 95, *M. abidae*; 96, *M. srivastava*. 97–103 Vulval margin (small circles—alveoli of vulval setae are drawn to show its distribution): 97, *M. bakeri*; 98, *Myrsidea* sp. from *Lonchura ferruginosa*; 99, *M. quadrimaculata*; 100, *M. quadrifasciata*; 101, *M. estrildae*; 102, *Myrsidea* sp. from *Pseudonigrita arnaud*; 103, *Myrsidea* sp. from *Taeniopygia guttata* with comb-like projections on the surface of the genital chamber.



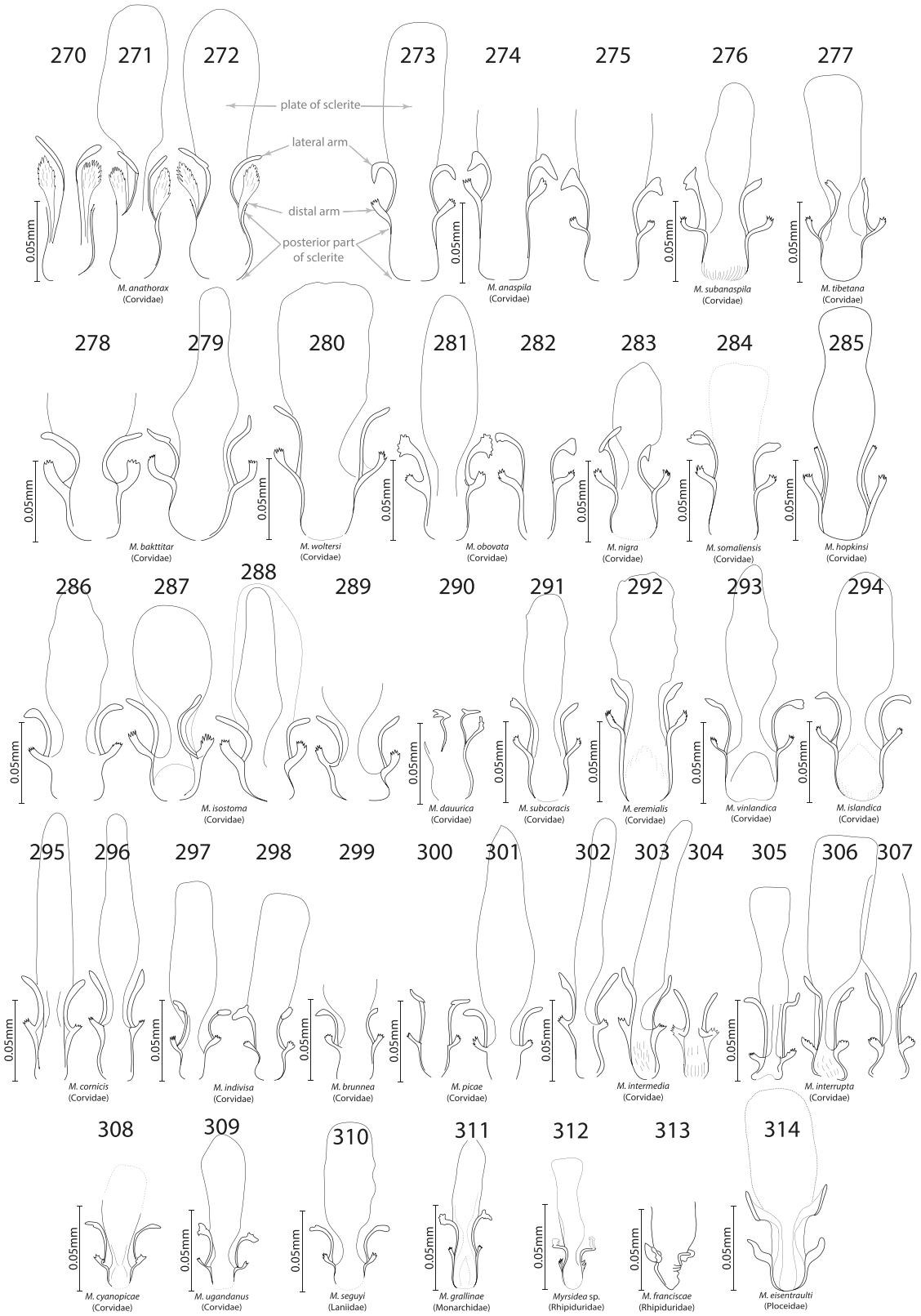
Figs. 104–138. 104 and 105, Dorsal view of thorax and abdomen of a male of *M. sylviae*: 104, approximate natural position of some internal organs; 105, extruded genitalia after dissection and/or slide mounting with distorted genital sac sclerite. 106–108, Male ventral terminalia (segments VII–X): 106, *M. ivanliteraki*; 107, *M. novaeseelandiae*; 108, *Myrsidea* sp. from *Pterorhinus vassali*. 109, Crop teeth of *M. ivanliteraki*. 110 and 111, dorso-ventral view of male genitalia: 110, *M. ivanliteraki*; 111, *M. hihi*. 112, Dorsal view of male genitalia of *M. comosa*. 113–138, Variability of shapes of parameres: 113, *Myrsidea* sp. from *Pterorhinus vassali*; 114, *Myrsidea* sp. from *Padda oryzivora*; 115, *Myrsidea* sp. from *Taeniopygia guttata*; 116, *M. srivastava*; 117, *Myrsidea* sp. from *Lonchura castaneothorax*; 118–120, *M. cyrtostigma*; 121 and 122, *M. q. quadrifasciata* from *Passer domesticus*; 123, *M. q. quadrifasciata* from *Passer montanus*; 124, *M. q. quelea*; 125, *M. q. textoris* from *Ploceus philippinus*; 126, *M. q. textoris* from *Ploceus nigricollis*; 127, *M. q. textoris* from *Ploceus cucullatus*; 128, *M. q. textoris* from *Euplectes progne*; 129, *M. q. textoris* from *Euplectes jacksoni*; 130, *M. pycnonoti*; 131, *Myrsidea* sp. from *Lonchura maja*; 132, *Myrsidea* sp. from *Lonchura ferruginosa*; 133, *Myrsidea* sp. from *Lonchura punctulata*; 134, *Myrsidea* sp. from *Erythrura trichroa*; 135, *M. estrildae*; 136, *Myrsidea* sp. from *Nigrita canicapillus*; 137, *Myrsidea* sp. from *Cryptospiza salvadorii*; 138, *M. quadrimaculata*. Figs. 113–138 are drawn to the same scale. Fig. 112 is redrawn from Clay (1968).



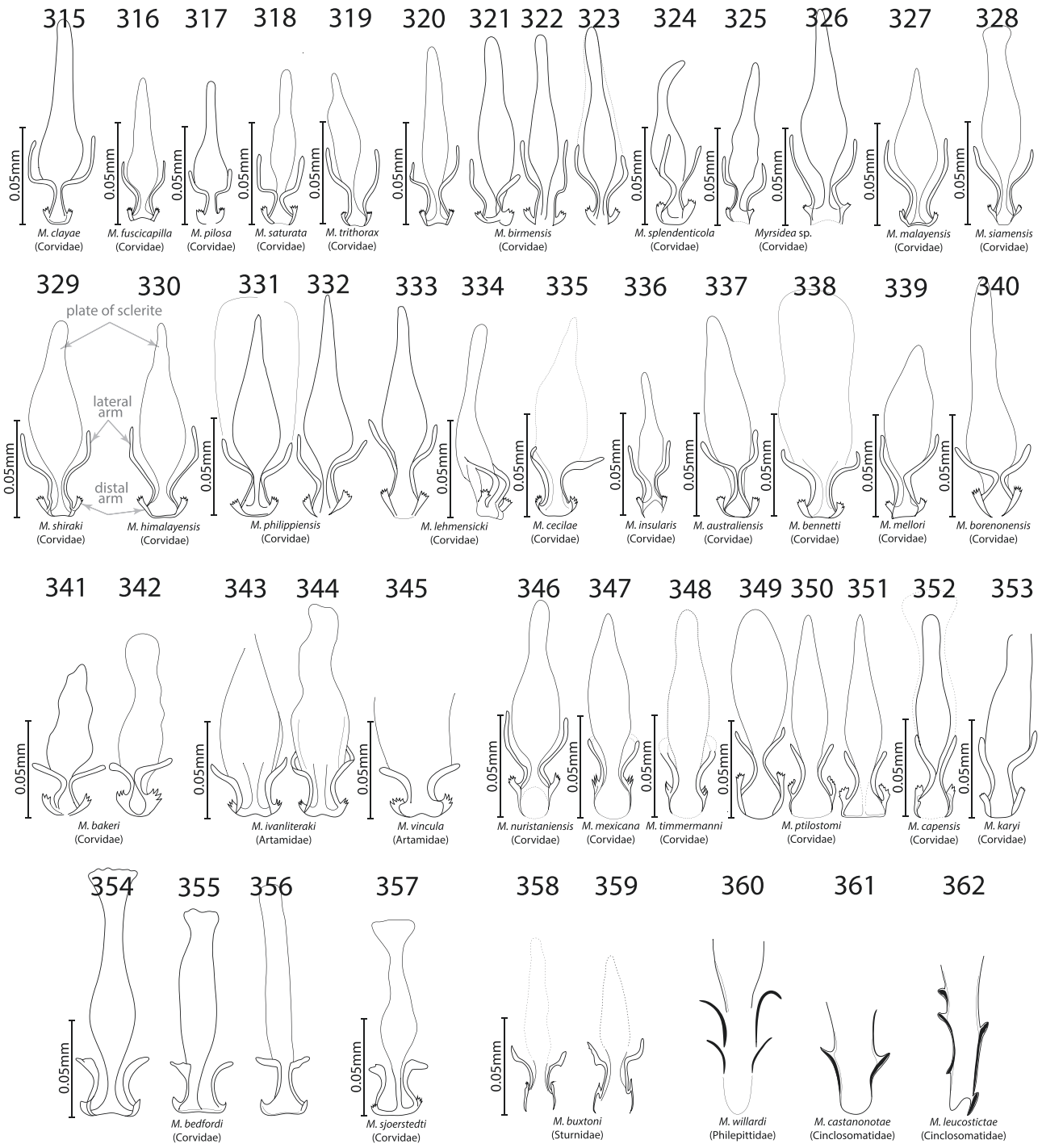
Figs. 139–181. Male genital sac sclerites. 139–140, *M. longipecta*. 141, *M.* cf. *sindianus* (from *Dicrurus paradiseus*). 142, *Myrsidea* sp. from *Dicrurus bracteatus*. 143–147, *M. pycnonoti*. 148, *M. phillipsi*. 149 and 150, *M. kulpai*. 151, *M. kathleenae*. 152–154, *M. masoni*. 155–159, *Myrsidea* sp. from *Bleda notatus*. 160, *Myrsidea* sp. from *Arizelocichla tephrolaema*. 161 and 162, *M. wombeyi*. 163, *M. marksi*. 164, *Myrsidea* sp. from *Eurillas latirostris*. 165 and 166, *M. aynazae*. 167 and 168, *M. ovatula*. 169, *M. urocissae*. 170, *M. goodmani*. 171, *M. plumosi*. 172, *M. eutiloti*. 173, *M. adamsae*. 174–176, *M. ochracei*. 177, *M. borbonici*. 178–180, *M. johnsoni*. 181, *M. yoshizawai*. Except for figures redrawn from other papers, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original papers. The following figures were redrawn from the following publications: Figs. 143, 148, 151, 171, 173, 174, 177, and 178 from Hellenthal and Price (2003); Figs. 152 and 161 Johnson and Price (2006); Figs. 170 and 181 from Price and Johnson (2006a).



Figs. 182–269. Male genital sac sclerites. 182–185, *M. chilchil*. 186 and 187, *M. breviterga*. 188, *Myrsidea* sp. from *Cyanoderma ruficeps*. 189, *Myrsidea* sp. from *Cyanoderma chrysaeum*. 190–194, *M. clamosae*. 195 and 196, *M. macronoi*. 197–200, *M. meinertzhageni*. 201 and 202, *M. salimalii*. 203–205, *M. minuscula*. 206, *M. pullula*. 220–223, *M. pyriglenae*. 224, *M. milleri*. 225, *M. mcleannani*. 213, *M. ledgeri*. 214 and 215, *Myrsidea* sp. from *Lonchura ferruginosa*. 216, *Myrsidea* sp. from *Lonchura maja*. 217, *M. palmai*. 218, *M. claytoni*. 219 and 220, *M. satbhai*. 221 and 222, *M. bharat*. 223–225, *M. liopari*. 226, *M. aegithali*. 227–229, *M. ishizawai* (with detail of slightly distorted lateral comb-like structure on Fig. 227). 230, *Myrsidea* sp. from *Geokichla citrina*. 231, *Myrsidea* sp. from *Zoothera marginata*. 232–234, *M. hrabaki*. 235, *M. novaeseelandiae*. 236, *M. hihi*. 237 and 238, *M. ochrolaemi*. 239, *M. scleruri*. 240–242, *M. calvi*. 243, *M. souleyetii*. 244, *M. meyi*. 245–247, *M. philydori*. 248–249, *M. leucophthalmi*. 250 and 251, *M. zuzanae*. 252 and 253, *M. carmenae*. 254, *M. lampropsaricola*. 255 and 256, *M. mariquensis*. 257, *Myrsidea* sp. from *Myiomela leucura*. 258, *Myrsidea* sp. from *Kakamega poliothorax*. 259, *M. ramoni*. 260, *M. subdissimilis*. 261, *M. oatleyi*. 262 and 263, *Myrsidea* sp. from *Chamaetylas poliocephala*. 264, *M. falcatae*. 265–267, *Myrsidea* sp. from *Alethe castanea*. 268 and 269, *M. pachycephalae*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publications: Figs. 182–184, 187, 190, 191, 197, 198, 201, 202, 219–221 from Tandan and Clay (1971); Figs. 196 and 264 from Price et al. (2006); Fig. 203 from Price and Johnson (2006b); Fig. 217 from Hellenthal and Price (2003); Fig. 223 from Lei et al. (2020); Fig. 224 from Price et al. (2008a); Fig. 227 from Clay (1966); Figs. 238 and 244 from Valim et al. (2011); Fig. 254 from Valim and Weckstein (2013); Fig. 268 from Palma and Klockenhoff (1988).



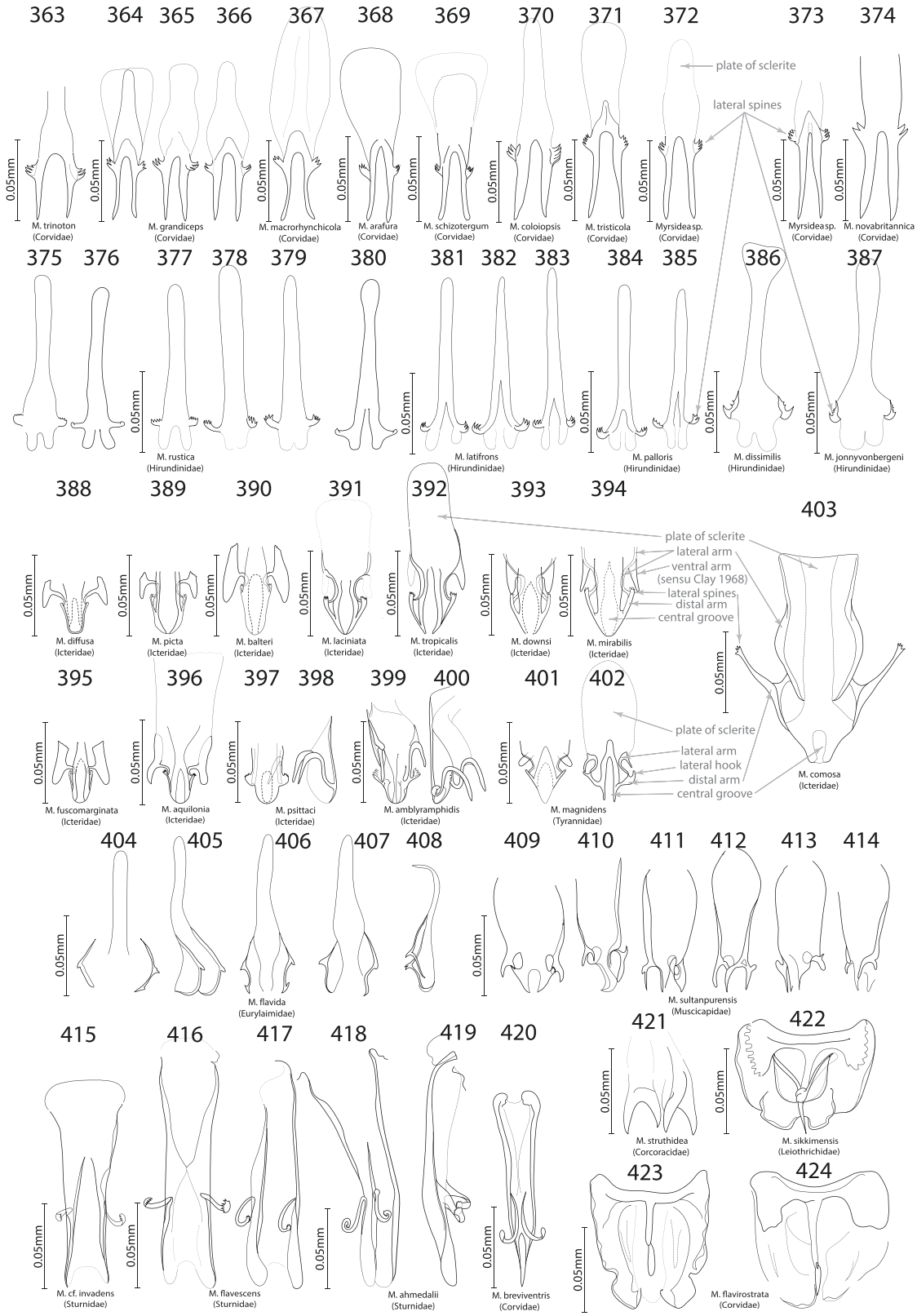
Figs. 270–314. Male genital sac sclerites. 270–272, *M. anathorax*. 273–275, *M. anaspila*. 276, *M. subanaspila*. 277, *M. tibetana*. 278 and 279, *M. bakttitar*. 280, *M. woltersi*. 281 and 282, *M. obovata*. 283, *M. nigra*. 284, *M. somaliensis*. 285, *M. hopkinsi*. 286–289, *M. isostoma*. 290, *M. dauurica*. 291, *M. subcoracis*. 292, *M. eremialis*. 293, *M. vinlandica*. 294, *M. islandica*. 295 and 296, *M. cornicis*. 297 and 298, *M. indivisa*. 299, *M. brunnea*. 300 and 301, *M. picae*. 302–304, *M. intermedia*. 305–307, *M. interrupta*. 308, *M. cyanopicae*. 309, *M. ugandanus*. 310, *M. seguyi*. 311, *M. grallinae*. 312, *Myrsidea* sp. from *Rhipidura* sp. 313, *M. franciscae*. 314, *M. eisentrauti*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publications: Fig. 285 from Klockenhoff (1981a).



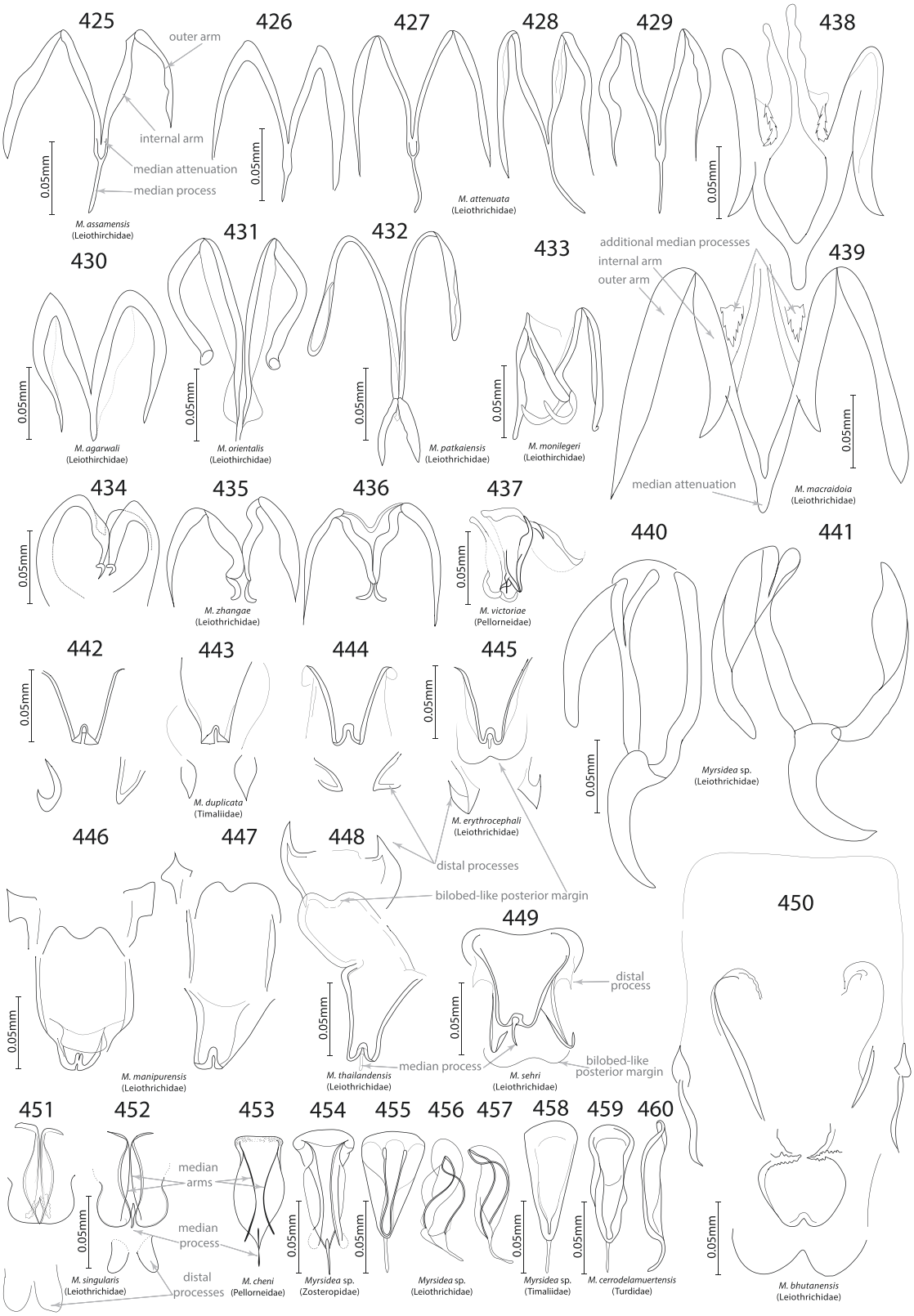
Figs. 315–362. Male genital sac sclerites. 315, *M. clayae*. 316, *M. fuscicapilla*. 317, *M. pilosa*. 318, *M. saturata*. 319, *M. trithorax*. 320–323, *M. birmensis*. 324, *M. splendenticola*. 325, *Myrsidea* sp. from *Corvus typicus*. 326, *Myrsidea* sp. from *Corvus meeki*. 327, *M. malayensis*. 328, *M. siamensis*. 329, *M. shirakii*. 330, *M. himalayensis*. 331–332, *M. philippinensis*. 333 and 334, *M. lehmensicki*. 335, *M. cecilae*. *336*, *M. insularis*. 337, *M. australiensis*. 338, *M. bennetti*. 339, *M. mellori*. 340, *M. borneonensis*. 341 and 342, *M. bakeri*. 343 and 344, *M. ivanliteraki*. 345, *M. vincula*. 346, *M. nuristaniensis*. 347, *M. mexicana*. 348, *M. timmermanni*. 349–351, *M. ptilostomi*. 352, *M. capensis*. 353, *M. karyi*. 354–356, *M. bedfordi*. 357, *M. sjoerstedti*. 358 and 359, *M. buxtoni*. 360, *M. willardi*. 361, *M. castanonotae*. 362, *M. leucostictae*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publications: Fig. 333 from Klockenhoff (1971b); Fig. 349 from Klockenhoff (1981a); Fig. 353 from Klockenhoff (1980a) Fig. 360 from Price and Johnson (2006b); Figs. 361 and 362 from Hellenthal and Price (2005).

Ramphasticola—*M. aenigma*, *M. mirabile*, Figs. 57 and 58).

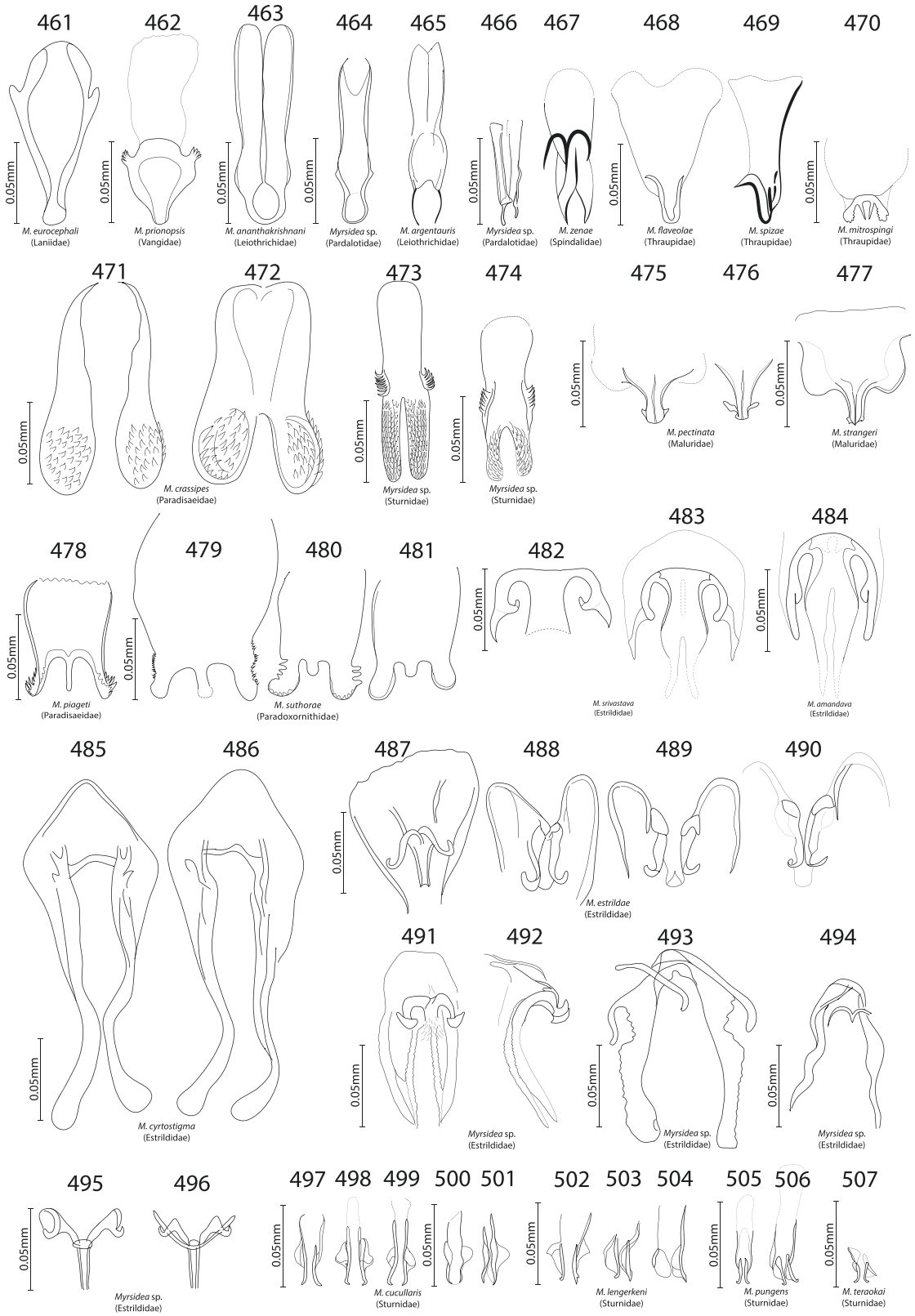
(20) Posterior metanotal setae—there can be a variable number of long setae on the posterior margin of the metanotum, usually with a median gap in the row of setae (Fig. 23). The pair of long and stout outermost posterolateral setae on each side of the metanotum are not included in the setal counts, due to their occurrence in all *Myrsidea* species. This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.



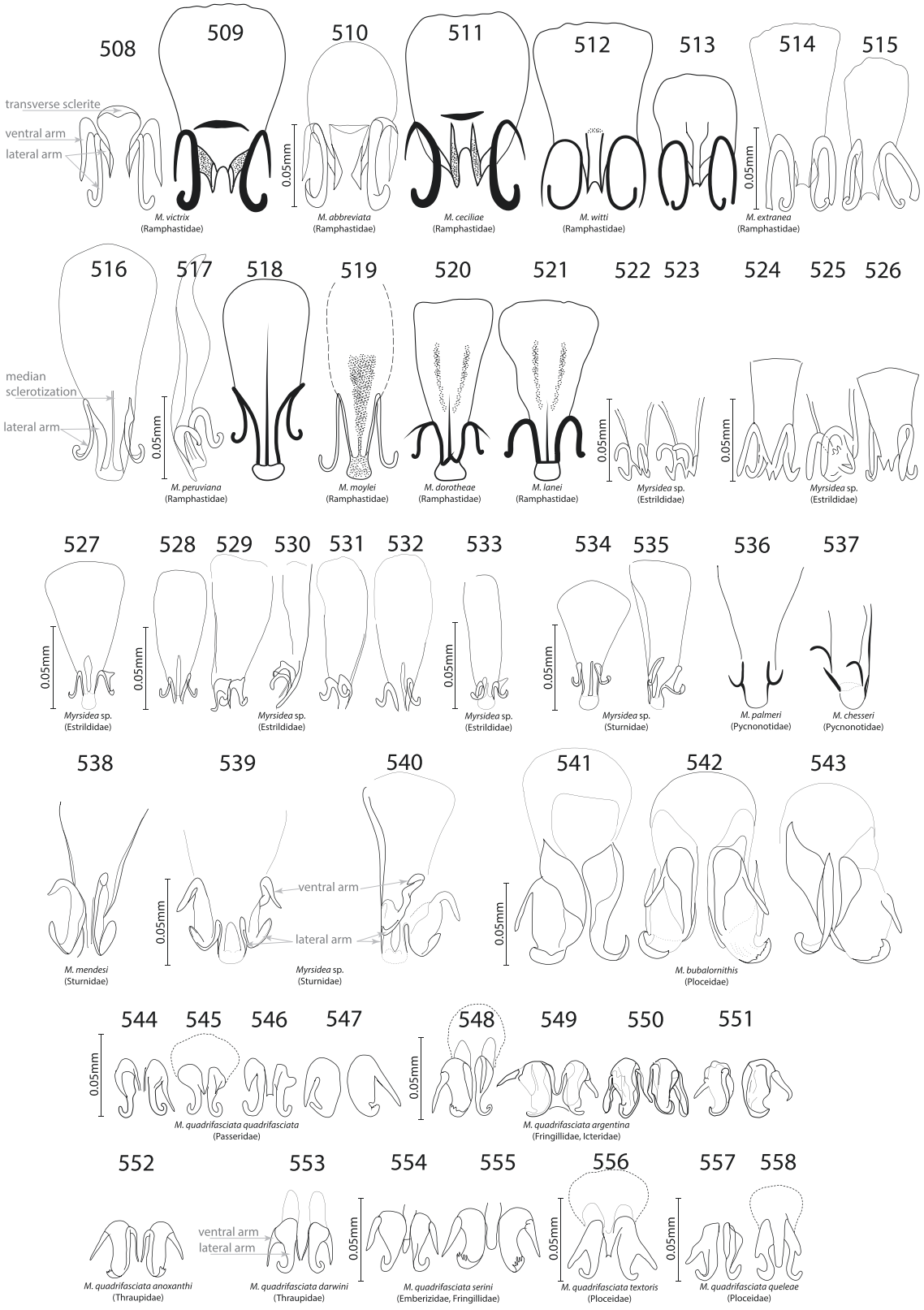
Figs. 363–424. 363, *M. trinoton*. 364–366, *M. grandiceps*. 367, *M. macrorhynchicola*. 368, *M. arafura*. 369, *M. schizotergum*. 370, *M. coloiopsis*. 371, *M. tristicola*. 372, *Myrsidea* sp. from *Corvus typicus*. 373, *Myrsidea* sp. from *Corvus woodfordi*. 374, *M. novabritannica*. 375–379, *M. rustica*. 380–383, *M. latifrons*. 384 and 385, *M. palloris*. 386, *M. dissimilis*. 387, *M. jonnyvonbergeni*. 388, *M. diffusa*. 389, *M. picta*. 390, *M. balteri*. 391, *M. laciniata*. 392, *M. tropicalis*. 393, *M. downsi*. 394, *M. mirabilis*. 395, *M. fuscomarginata*. 396, *M. aquilonia*. 397 and 398, *M. psittaci*. 399 and 400, *M. amblyramphidis*. 401 and 402, *M. magnidens* (Fig. 401 as approximate reconstruction). 403, *M. comosa*. 404–408, *M. flavida*. 408–414, *M. sultanpurensis*. 415, *M.* cf. *invadens*. 416–417, *M. flavescens*. 418 and 419, *M. ahmedalii*. 420, *M. vreviventris*. 421, *M. struthidea*. 422, *M. sikkimensis*. 423 and 424, *M. flavirostrata*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Fig. 374 from Klockenhoff (1980a); Fig. 375 from Conci (1942c); Figs. 376 and 380 from Clay (1949b). Figs. 388–390, 393–395, 397, 398, 401, and 403 from Clay (1968); Figs. 399 and 400 from Valim and Cicchino (2015a); Fig. 402 from Price et al. (2005).



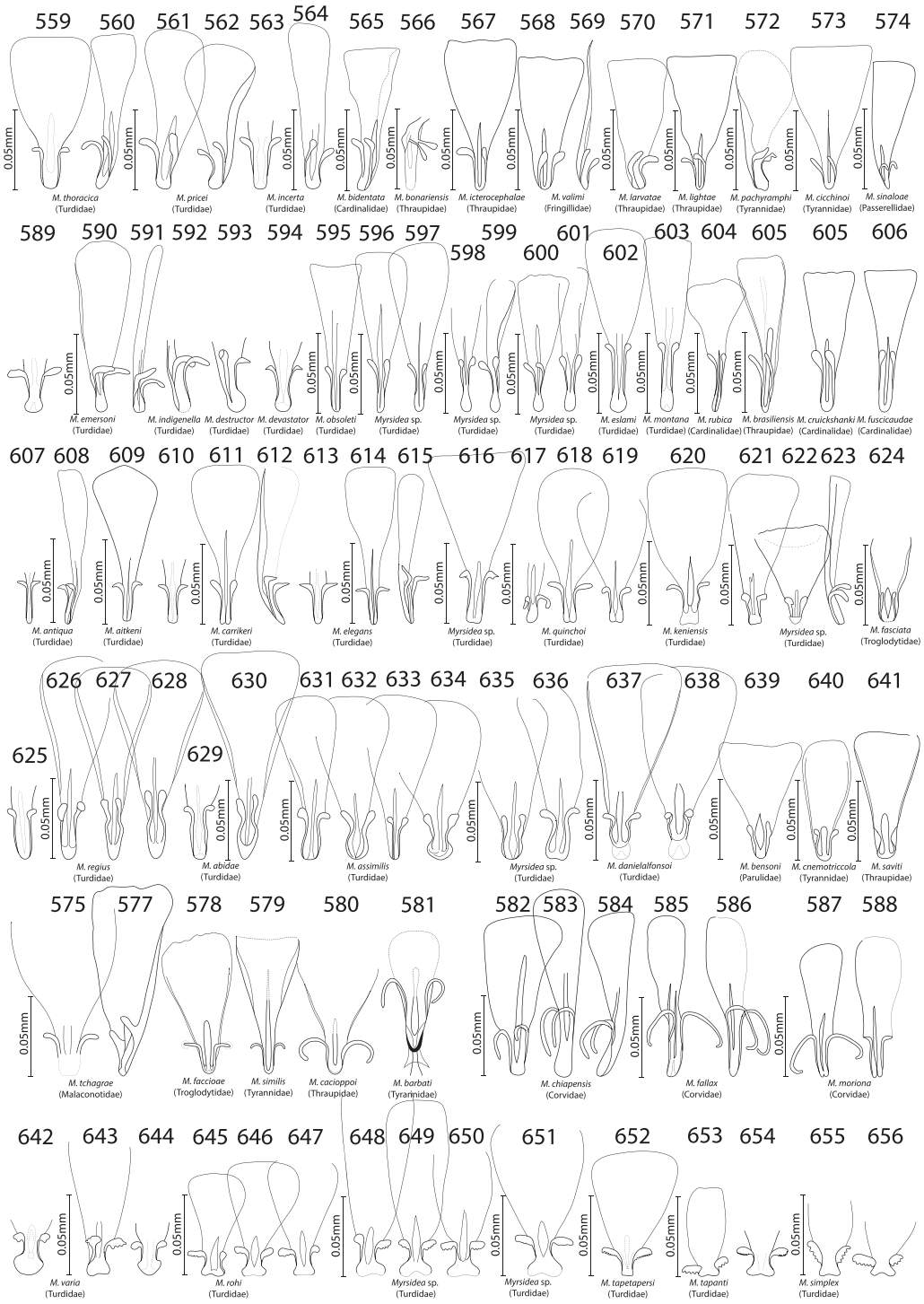
Figs. 425–460. Male genital sac sclerites. 425, *M. assamensis*. 426–429, *M. attenuata*. 430, *M. agarwali*. 431, *M. orientalis*. 432, *M. patkaiensis*. 433, *M. monilegeri*. 434–436, *M. zhangae*. 437, *M. victoriae*. 438 and 439, *M. macraidoia*. 440 and 441, *Myrsidea* sp. from *Pterorhinus vassali*. 442–444, *M. duplicata*. 445, *M. erythrocephali*. 446 and 447, *M. manipurensis*. 448, *M. thailandensis*. 449, *M. sehri*. 450, *M. bhutanensis*. 451 and 452, *M. singularis*. 453, *M. cheni*. 454, *Myrsidea* sp. from *Zosterops natalis*. 455–457, *Myrsidea* sp. from *Actinodura cyanouroptera*. 458, *Myrsidae* sp. from *Stachyris nigriceps*. 459–460, *M. cerrodelamuertensis*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Figs. 426 and 434 from Lei et al. (2020); Fig. 430 from Khan et al. (2009); Fig. 452 from Tandan (1972); Fig. 453 from Price et al. (2006).



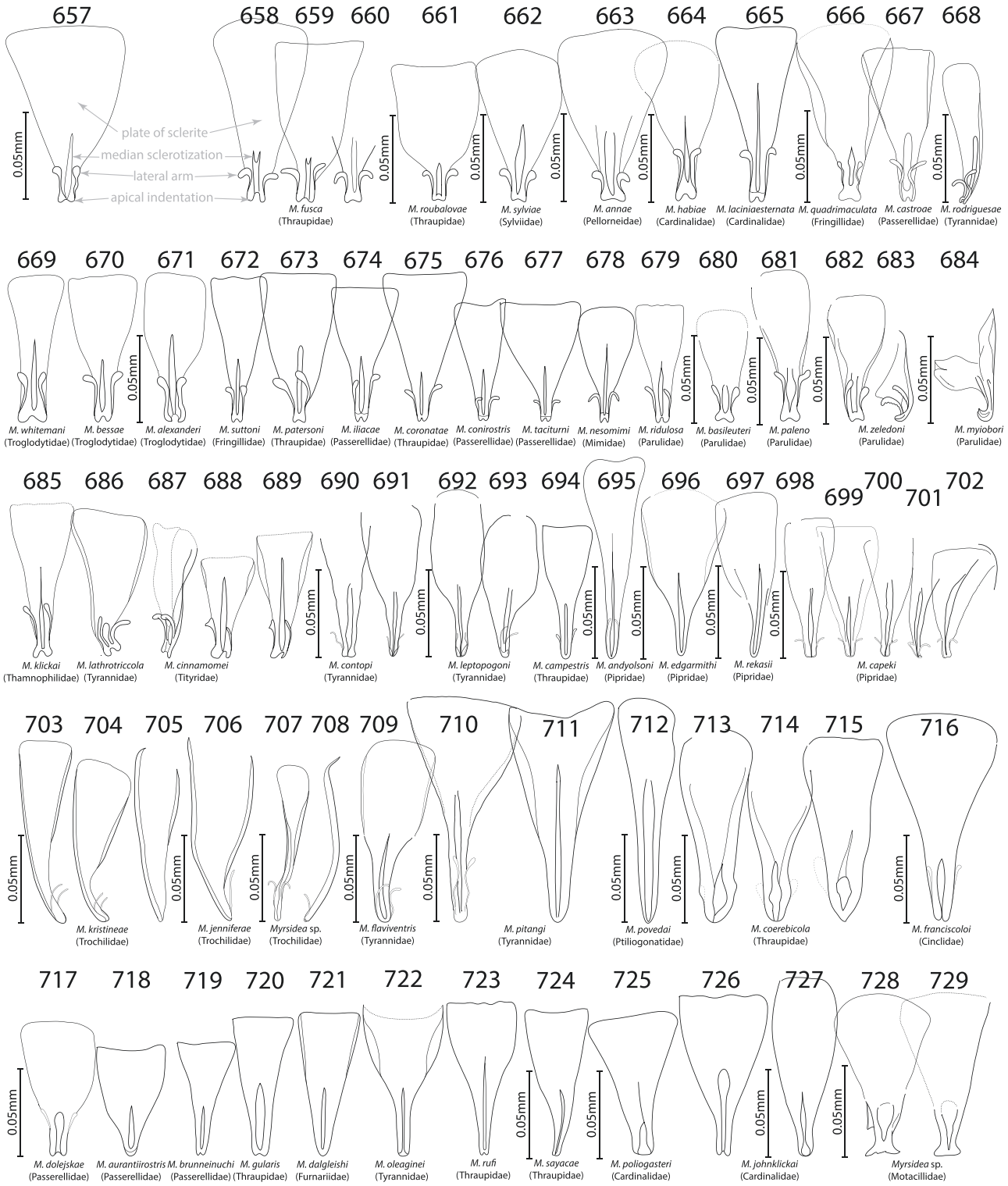
Figs. 461–507. Male genital sac sclerites. 461, *M. eurocephali*. 462, *M. prionopsis*. 463, *M. ananthakrishnani*. 464, *Myrsidea* sp. from *Pardalotus quadragintus*. 465, *M. argentauris*. 466, *Myrsidea* sp. from *Pardalotus punctatus*. 467, *M. zenae*. 468, *M. flaveolae*. 469, *M. spizae*. 470, *M. mitrospingi*. 471 and 472, *M. crassipes*. 473, *Myrsidea* sp. from *Gracula religiosa palawanensis*. 474, *Myrsidea* sp. from *Gracula religiosa*. 475 and 476, *M. pectinata*. 477, *M. strangeri*. 478, *M. piageti*. 479–481, *M. suthorae*. 482 and 483, *M. srivastava*. 484, *M. amandava*. 485 and 486, *M. cyrtostigma*. 487–490, *M. estrildae*. 491 and 492, *Myrsidea* sp. from *Estrilda nonnula*. 493, *Myrsidea* sp. from *Padda oryzivora*. 494, *Myrsidea* sp. from *Lonchura castaneothorax*. 495–496, *Myrsidea* sp. from *Taeniopygia guttata*. 497–501, *M. cucullaris* (500 and 501 formerly as *M. lyali*). 502–504, *M. lengerkeni*. 505 and 506, *M. pungens*. 507, *M. teraokai*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Fig. 463 from Rai (1978); Fig. 465 from Price et al. (2006); Figs. 467 and 469 from Price and Dalgleish (2006); Fig. 473 from Eduardo and Villa (2011); Fig. 479 from Lei et al. (2020); Fig. 499 from Fedorenko (1983); Fig. 500 from Klockenhoff (1984a).



Figs. 508–558. Male genital sac sclerites. 508 and 509, *M. victrix*. 510, *M. abbreviata*. 511, *M. ceciliae*. 512, *M. witti*. 513–515, *M. extranea*. 516–518, *M. peruviana*. 519, *M. moylei*. 520, *M. dorotheae*. 521, *M. lanei*. 522 and 523, *Myrsidea* sp. from *Erythrura prasina*. 524–526, *Myrsidea* sp. from *Erythrura trichroa*. 527, *Myrsidea* sp. from *Cryptospiza salvadorii*. 528–532, *Myrsidea* sp. from *Cryptospiza reichenovii*. 533, *Myrsidea* sp. from *Nigrita canicapillus*. 534, *Myrsidea* sp. from *Notopholia corusca*. 535, *Myrsidea* sp. from *Lamprotornis ornatus*. 536, *M. palmeri*. 537, *M. chesseri*. 538, *M. mendesi*. 539, *Myrsidea* sp. from *Lamprotornis purpuroptera aenocephalus*. 540, *Myrsidea* sp. from *Lamprotornis caudatus*. 541, *M. bubalornithis*. 544–547, *M. quadrifasciata quadrifasciata*. 548–551, *M. q. argentina*. 552, *M. q. anoxanthi*. 553, *M. q. darwini*. 554 and 555, *M. q. serini*. 556, *M. q. textoris*. 557 and 558, *M. q. queleae*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Fig. 508 from Waterston (1915); Figs. 509, 511–513, 518, 520, and 521 from Price et al. (2004); Fig. 519 from Hellenthal et al. (2005); Figs. 536–537 from Johnson and Price (2006); Fig. 538 from Tendeiro (1993); Figs. 549–551 from Cicchino and Valim (2015); Fig. 552 from Price and Dalgleish (2007); Fig. 553 from Palma and Price (2010); Figs. 554 and 555 from Klockenhoff (1984c).



Figs. 559–656. Male genital sac sclerites. 559 and 560, *M. thoracica*. 561 and 562, *M. pricei*. 563 and 564, *M. incerta*. 565, *M. bidentata*. 566, *M. bonariensis*. 567, *M. icterocephalae*. 568 and 569, *M. valimi*. 570, *M. larvatae*. 571, *M. lightae*. 572, *M. pachyramphi*. 573, *M. cicchinoi*. 574, *M. sinaloae*. 575–577, *M. emersoni*. 578, *M. indigenella*. 579, *M. destructor*. 580, *M. devastator*. 581, *M. obsoleti*. 582 and 583, *Myrsidea* sp. from *Hylocichla mustelina*. 584 and 585, *Myrsidea* sp. from *Turdus aurantius*. 586 and 587, *Myrsidea* sp. from *Turdus jamaicensis*. 588, *M. eslami*. 589, *M. montana*. 590, *M. rubica*. 591, *M. brasiliensis*. 592, *M. cruickshanki*. 593, *M. fuscicaudae*. 594 and 595, *M. antiqua*. 596, *M. aitkeni*. 597–599, *M. carrikeri*. 600–602, *M. elegans*. 603, *Myrsidea* sp. from *Turdus albicollis*. 604–606, *M. quinchoi*. 607, *M. keniensis*. 608–610, *Myrsidea* sp. from *Neocossyphus poensis*. 611, *M. fasciata*. 612–615, *M. regius*. 616 and 617, *M. abidae*. 618–621, *M. assimilis*. 622 and 623, *Myrsidea* sp. from *Turdus ignobilis*. 624 and 625, *M. danielalfonsoi*. 626, *M. bensoni*. 627, *M. cnemotriccola*. 628, *M. saviti*. 629 and 630, *M. tchagrae*. 631, *M. faccioae*. 632, *M. similis*. 633, *M. cacioppoi*. 634, *M. barbati*. 635–637, *M. chiapensis*. 638 and 639, *M. fallax*. 640 and 641, *M. moriona*. 642 and 643, *M. varia*. 644–647, *M. rohi*. 648–650, *Myrsidea* sp. from *Turdus aurantius*. 651, *Myrsidea* sp. from *Turdus flavipes*. 652, *M. tapetapersi*. 653, *M. tapanti*. 654–656, *M. simplex*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Figs. 559, 563, 575, 578–580, 594, 597, 600, 612, 616, 642, 644, and 654 from Clay (1966); Fig. 566 from Clay (1968); Figs. 567 and 593 from Price and Dalgleish (2006); Figs. 568 and 592 from Price and Johnson (2009); Fig. 571 from Price et al. (2008b); Fig. 573 from Valim et al. (2011); Fig. 574 from Price and Dalgleish (2007); Figs. 638–641 from Valim and Cicchino (2015b); Figs. 632 and 634 from Price et al. (2005); Figs. 627, 628, 631, and 633 from Valim and Weckstein (2013); Figs. 629 and 630 from Klockenhoff and Tendeiro (1989); Fig. 627 from Valim and Reiley (2015).



Figs. 657–729. Male genital sac sclerites. 657–660, *M. fusca*. 661, *M. roubalovae*. 662, *M. sylviae*. 663, *M. annae*. 664, *M. habiae*. 665, M. laciniaesternata. *M. keniensis*. 666, *M. quadrimaculata*. 667, *M. castroae*. 668, *M. rodriguesae*. 669, *M. bessae*. 670, *M. whitemani*. 671, M. alexanderi. 672, *M. suttoni*. 673, *M. patersoni*. 674, *M. iliacae*. 675, *M. coronatae*. 676, *M. conirostris*. 677, *M. taciturni*. 678, *M. nesomimi*. 679, *M. ridulosa*. 680, *M. basileuteri*. 681, *M. paleno*. 682 and 683, *M. zeledoni*. 684, *M. myiobori*. 685, *M. klickai*. 686, *M. lathrotriccola*. 687 and 688, *M. cinnamomei*. 689–691, *M. contopi*. 692 and 693, *M. leptopogoni*. 694, *M. campestris*. 695, *M. andyolsoni*. 696, *M. edgarsmithi*. 697, *M. rekasii*. 698–702, *M. capeki*. 703–705, *M. kristineae*. 706, *M. jenniferae*. 707, *Myrsidea* sp. from "hummingbird." 708, *Myrsidea* sp. from *Amazilia tzacatl*. 709, *M. flvaviventris*. 710 and 711, *M. pitangi*. 712, *M. povedai*. 713–715, *M. coerebicola*. 716, *M. franciscoloi*. 717, *M. dolejskae*. 718, *M. aurantiirostris*. 719, *M. brunneinuchi*. 720, *M. gularis*. 721, *M. dalgleishi*. 722, *M. oleaginei*. 723, *M. rufi*. 724, *M. sayacae*. 725, *M. poliogasteri*. 726 and 727, *M. johnklickai*. 728, *Myrsidea* sp. from *Motacilla aguimp*. 729, *Myrsidea* sp. from *Motacilla alba*. Except for figures redrawn from other publications, all figures are drawn to the same scale. Scale is shown for redrawn figures if it was present in the original publications. The following figures were redrawn from the following publication: Figs. 667, 687, and 721 from Valim et al. (2011); Figs. 668, 683, and 709 from Valim and Weckstein (2013); Figs. 669 and 670 from Price et al. (2008c); Figs. 665–672, and 723 from Price and Dalgleish (2006); Fig. 673 from Price and Johnson (2009); Figs. 674–677, 694, 718–720 from Price and Dalgleish (2007); Figs. 678 and 679 from Palma and Price (2010); Fig. 685 from Price et al. (2008a); Fig. 688 from Dalgleish and Price (2005); Figs. 689, 711, and 722 from Price et al. (2005); Figs. 705 and 706 from Dalgleish and Price (2003b); Fig. 726 from Price et al. (2008b).

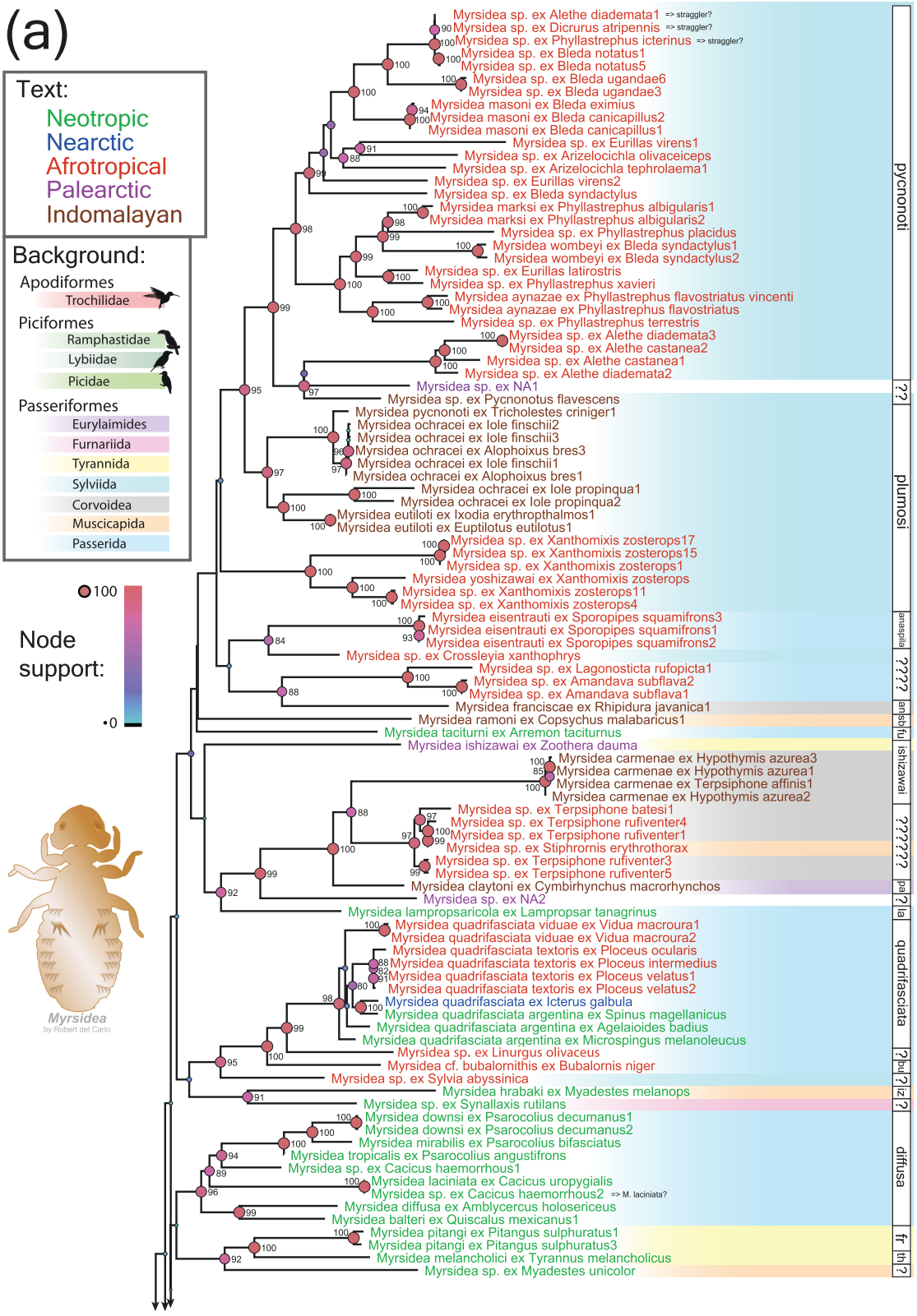


Fig. 730. A–D) Phylogenetic reconstruction based on an analysis of a 379-bp fragment of cytochrome oxidase subunit I for 330 unique *Myrsidea* specimens. Five additional specimens (*A. circumsternata, A. isacantha, Apomyrsidea klimesi, Menacanthus eurysternus,* and *Dennyus* sp.) were used as outgroups. "=>" highlights the specimens which were potentially misidentified or are stragglers or contaminants. The defined morphotype groups are labeled on the right of the tree ("?" labels the specimens where genital sclerite was not evaluated).

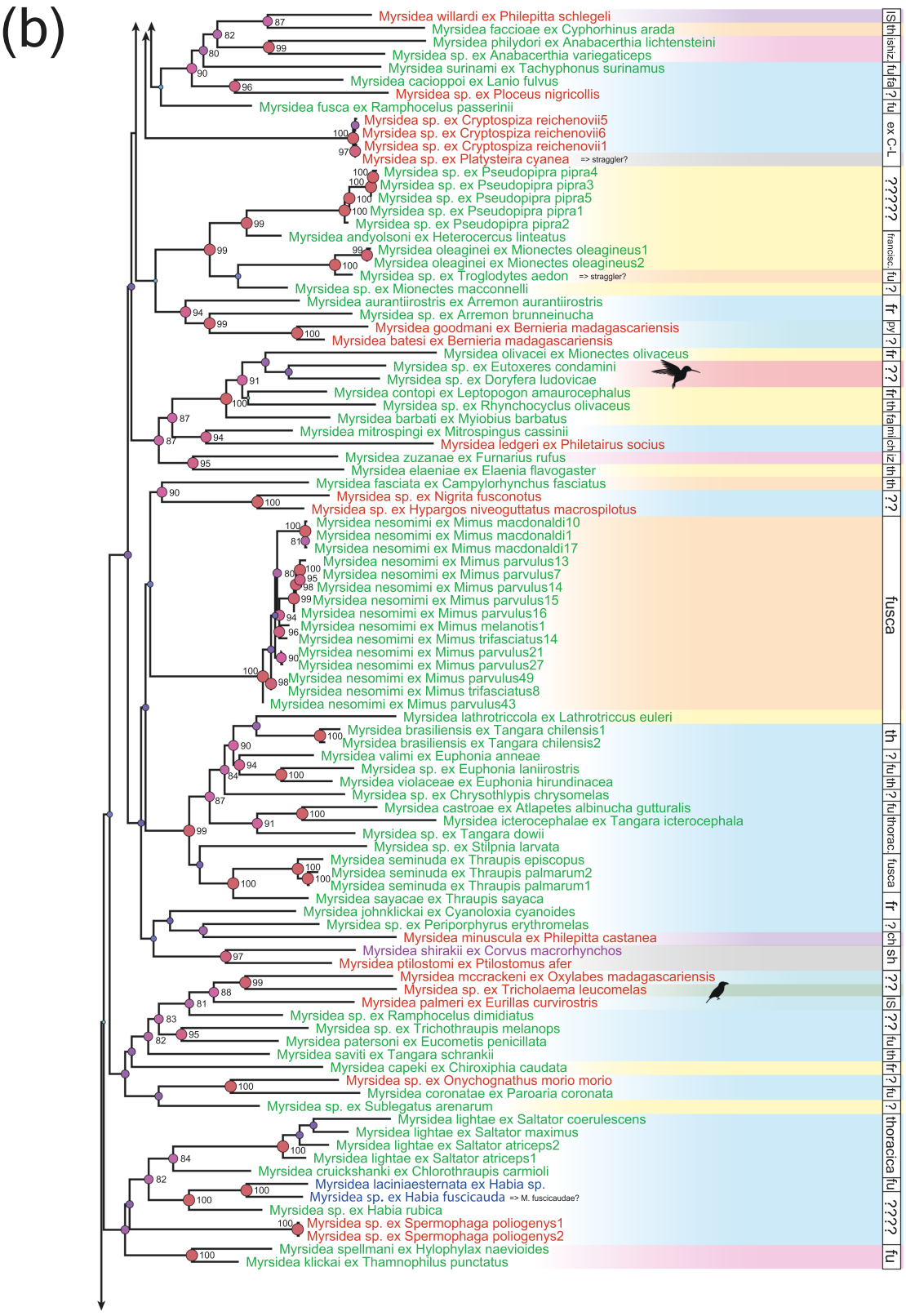


Fig. 730. Continued

(21) Presence of central metanotal setae (*cms*):

A. Most species have no central metanotal setae (Figs. 65–69); we name all setae on metanotum as central metanotal setae except setae on the posterior margin and pair of small anterior and 2 pairs of small anterolateral setae—these 6 small setae are always present and are therefore not included in setal counts;

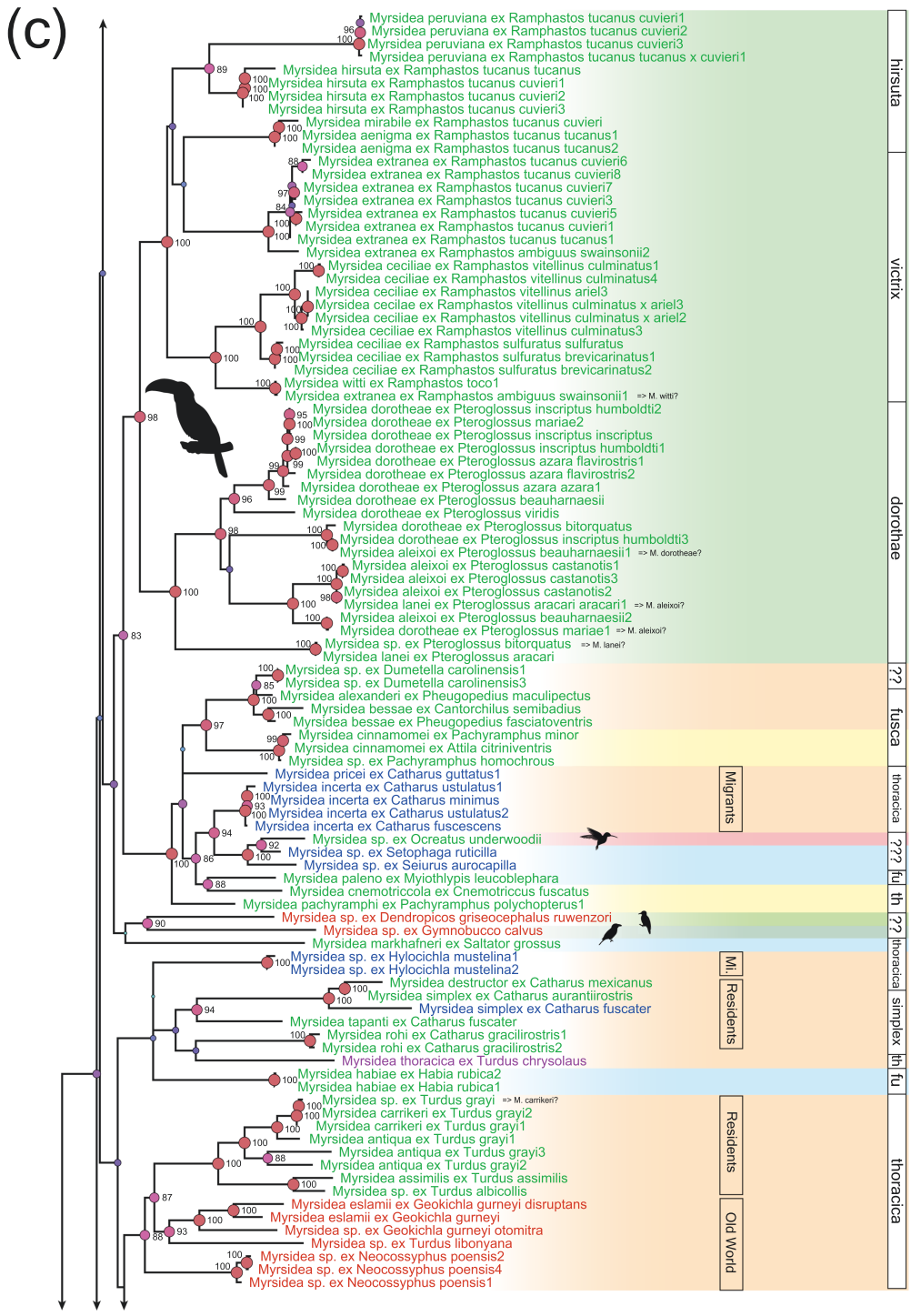


Fig. 730. Continued

B. A minority of species have some central metanotal setae; these setae can be located irregularly, or they can be arranged into a discrete patch on each side of the metanotum (especially in the case of females of *Myrsidea* from Corvidae, which have an enlarged metanotum, e.g., *M. bedfordi*, *M. chiapensis*, Figs. 27 and 70).

(22) Shape of metasternal plate:

A. Most species have a diamond-shaped metasternum (or shape of stingray) (Figs. 24, 37, and 38);

B. Metasternum not pointed posteriorly (e.g., *Myrsidea* from Pycnonotidae, Figs. 39 and 40 or some *Myrsidea* from Corvidae, e.g., *M. bedfordi*, *M. pilosa*, Figs. 45–48).

This character can show sexual dimorphism in size and shape (Figs. 41–48).

(23) Metasternal setae and their location:

A. Most species have 6–8 setae located on the margin of the plate (Figs. 37–42);

B. A minority of species have more setae (Figs. 43 and 44);

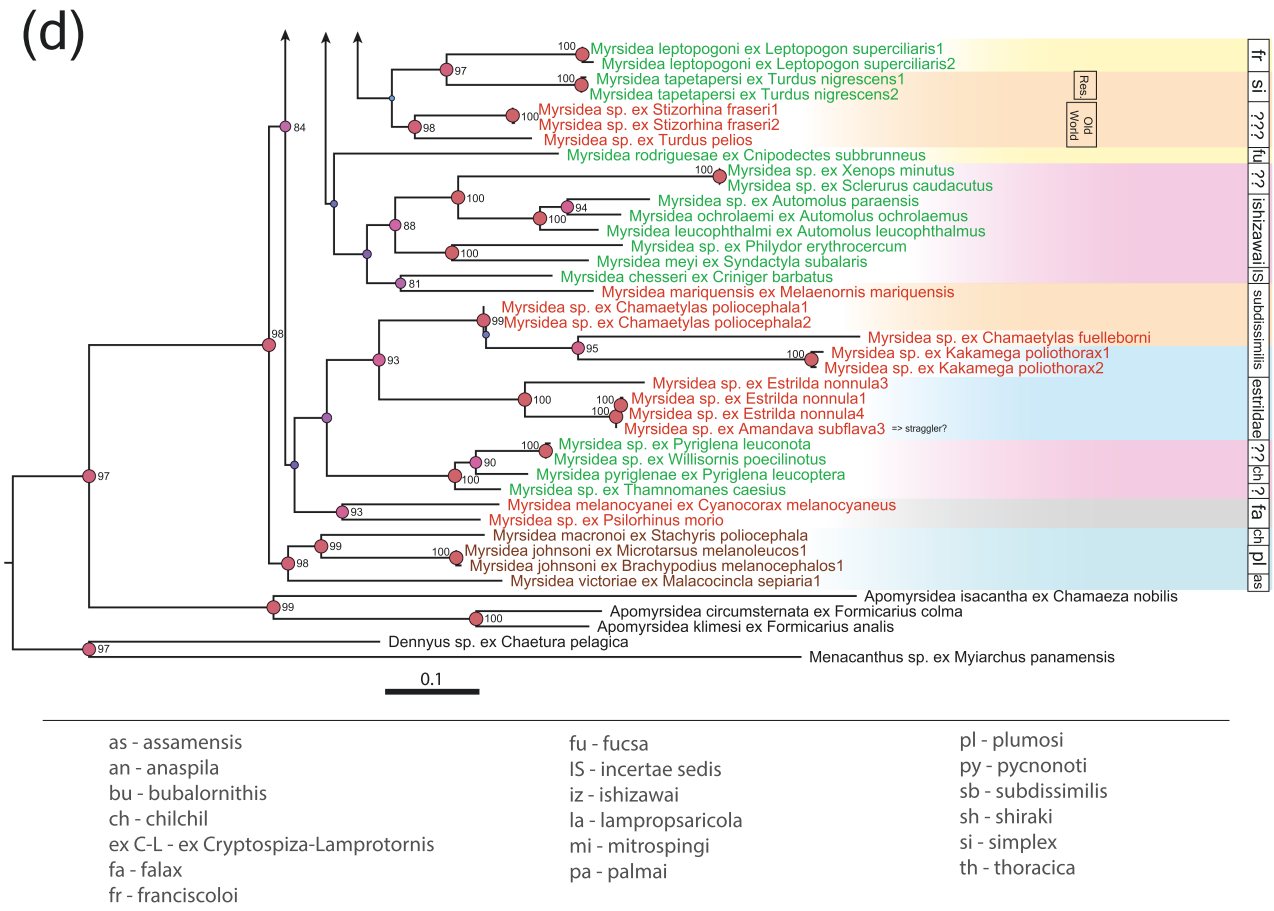


Fig. 730. Continued

C. very rarely with more setae, which are also located centrally on the plate (Figs. 45 and 46).

This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.

(24) Metapleural setae:

A. Most species have only (2–)3 spine-like setae of the same length on each metapleurite (Fig. 30);
B. Presence of some spine-like seta together with one or more conspicuously longer setae on each metapleurite (e.g., *M. hibi*, *Myrsidea* from Corvidae, Figs. 27 and 31).

This character, especially the presence and length of longer setae, may show variation within a species (they can be present on one side and absent on the second one), and cannot be used alone to distinguish species if only a few specimens are available.

(25) Presence of anterior metapleural setae (*ams*):

A. Most species have no anterior metapleural setae (Fig. 23);
B. A minority of species have anterior metapleural setae (especially in the case of female *Myrsidea* from Corvidae, for example, *M. pilosa*, Fig. 26).

(26) Brush of setae on 3rd femur (Fig. 52)—there can be different numbers of strong setae in the femoral brush. This character may show variation in both femoras in one individual, so it cannot be used alone to distinguish species if only a few specimens are available.

Abdomen

(27) Shape of tergites—this character can show sexual dimorphism, while almost all males have nonenlarged tergites with almost straight posterior margins, in most species, the females show some modifications of tergites (especially tergites I–IV):

A. Females with nonenlarged tergites with almost straight posterior margins (Fig. 65);
B. Females with some tergites slightly enlarged with rounded/tapered/convex medio-posterior margin (Figs. 54, 66–68);
C. Females with some tergites are strongly enlarged, affecting the shape of subsequent abdominal tergites (Fig. 70).

This is one of the most important characters for distinguishing species. The proposed categories can be used for each segment separately. These differences particularly concern tergites I–IV, which show the highest potential for modification, while tergites V–VIII are usually unmodified with a straight posterior margin.

(28) Division of tergites:

A. Most species without median division of tergites (Figs. 65–69); Even in cases where tergites are strongly compressed and distorted by an enlarged metanotum or preceding tergite, this does not mean that they need to be medianly divided (Fig. 70);
B. In a few species, partial or complete median division of some tergite is present (e.g., females of *M. clayae*, *M. montana*; Figs. 60 and 61);

C. Tergite I and II are greatly reduced in size (Fig. 56); in extreme cases, tergite I is absent (not apparent), and tergite II can be reduced to a small sclerite on each side of the body (*M. buxtoni*, *M. coloiopsis*, *M. grandiceps*; Figs. 62 and 63).

(29) Posterior tergal (tergo-central) setae—there is variation in the number and length of setae on the posterior margin of tergites. Therefore, posterior tergal (tergo-central) setae cannot be used alone to distinguish species if only a few specimens are available. The postspiracular setae on tergite I and the postspiracular setae and their lateral associated setae (setae b, of Clay 1970a; Fig. 55) on tergites II–VIII are not included in the setal counts due to their occurrence in all *Myrsidea* species. As noted by Clay (1966), the number of posterior tergal setae, especially those on VII–VIII is useful in separating species. Despite high variability in the number of these setae on particular segments, most species have only 4 posterior tergal setae on VIII.

(30) Length of tergal (tergo-central) setae:

A. Most species have tergal setae of approximately the same length;
B. Presence of short spine-like setae of variable number in the row of tergal setae (additional to aforementioned lateral seta associated with postspiracular seta), for example, *M. singularis*, *M. victoriae* from Leiothrichidae and Pellorneidae, respectively;
C. Presence of conspicuously longer setae in the row of tergal setae, e.g., inner tergal seta on tergite VII of females of *Myrsidea* from Pycnonotidae (Fig. 65), or pair of tergal setae on tergite VIII of the male of *M. rustica* (Fig. 64).

(31) Median gap in the row of posterior setae on tergites I–VIII:

A. Presence of a well-defined median gap in each row of tergal setae (Figs. 53, 54, and 65);
B. The absence of this gap—a continuous row of tergal setae across each segment (Fig. 67);

However, the absence or presence of this gap can vary between the tergal segments. In such cases, the continuous row of setae is usually only on segments 1–2, while other segments exhibit a well-defined median gap (Figs. 66 and 68). In such cases, this should be clarified in the descriptions (e.g., median gap present in tergites 3–8). The proposed categories can be used for each segment separately.

(32) Presence of anterior tergal setae:

A. Most species have no anterior tergal setae (Figs. 65–70); there is a pair of small anterior setae on tergite I that is always present; these setae are not included in setal counts (Figs. 53 and 54);
B. A minority of species have anterior setae scattered on tergites (e.g., males of *M. pectinata*, *M. rustica*, Fig. 64).

(33) Length of postspiracular setae:

A. Most species have postspiracular setae of different lengths on tergites I–VIII (Figs. 66–70);
B. A minority of species have very long setae of approximately the same length on tergites I–VIII (e.g., *M. ramphoceli*, *M. pycnonoti* (Fig. 65).

This characteristic can be evaluated for each abdominal segment separately. Because length is relative, it is always necessary to compare a particular seta with all others, as well as the total size of the evaluated specimen and species. In general, postspiracular setae on tergites II, IV, and VIII are usually the longest ones, whereas setae on tergites III, V, and VI are the shortest ones. Setae on tergites I and VII show high variability in their length in different species. Moreover, there can be variation in the length of these setae on both sides of a particular tergite, so this feature alone cannot be used to distinguish species if only a few specimens are available. Due to their position and length, these setae are often broken or missing. Thus, it is necessary to check the visible ending of these setae carefully, and we recommend not using measurements of obviously broken setae.

For categorization of the length of postspiracular setae (PSSL) we propose a simple approach using the ratio of the length of this seta to total length (TL) of the specimen (PSSL/TL): (i) very long seta (ratio < 5); (ii) long seta (ratio 5–9); and (iii) short seta (ratio > 9). This is only a simple tool, as there is great variability beyond any single classification. Thus, this characteristic should be carefully evaluated for each specimen and species.

(34) Spiracles (present on tergites III–VIII):

A. spiracles usually open on the tergites (Figs. 53, 54, 60–64);
B. in some species of *Myrsidea*, spiracles open on the pleurites or the membranous area between the tergite and pleurite (Fig. 59).

(35) Length of inner posterior seta of the last segment of the abdomen (Figs. 53 and 54)—2 categories can be distinguished, but only for females. The similar lengths of these setae are typically similar in males, but as males lack anal fringes, no direct comparison can be made.

A. seta not longer than anal fringe setae (Figs. 65–68);
B. seta is conspicuously longer than anal fringe setae (Fig. 69).

This character may show variation, even on both sides of the abdomen, so it cannot be used alone to distinguish species if only a few specimens are available.

(36) Length of short lateral marginal seta of the last segment of the abdomen (Figs. 53 and 54)—this short fine seta is always associated with one long stout seta on each side of the last tergite. This character may show variation, even on both sides of the abdomen, so it cannot be used alone to distinguish species if only a few specimens are available.

(37) Shape of pleurites:

A. mostly normal and squared-off (Figs. 71–75);
B. modified pleurites, e.g., the dorsolateral margin of some of pleurites III–VII divided, bilobed, and fitting together with modified lateral parts of tergites (*M. novaeseelandiae*, *M. hibi*, *M. hopkinsi*, Fig. 59).

In the females with modified abdomen, the pleurites may be reduced, absent, or modified in various ways. The shape of pleurites can be easily distorted during mounting. In slide-mounted specimens, the pleurites are typically compressed dorso-ventrally, so the shape and chaetotaxy may not be easily visible. Depending on the relative position and displacement of tergites and sternites, entire pleurites may be visible on one side of the abdomen from the dorsal view and on the other side from the ventral view.

(38) Posterior pleural setae on segments I–VII—there can be a variable number of setae of different lengths and thicknesses on the posterior margin of pleurites:

A. Most species have pleurites I–III with only short spine-like setae, whereas some slender and longer setae can be found together with spine-like setae on pleurites IV–VII. Setae are usually gradually lengthening from the dorsal end to the ventral end of the pleurite. Also, the thickness of setae changes gradually, so it is often difficult to distinguish those "slender and longer" setae from spine-like ones (Figs. 71 and 72);
B. With at least one conspicuously longer seta on the inner ventral angle of pleurite (e.g., *M. poliogasteri* with longer setae on sternites III–VII) (Fig. 75);
C. With at least one conspicuously longer seta on the inner dorsal angle of pleurite; e.g., *M. ivanliteraki* with long setae on sternites I–II (Fig. 81), *M. rustica*, *Myrsidea* from Pycnonotidae with long seta on sternite VII (Figs. 78 and 79).

This character, especially the presence and length of longer setae, may show variation within a species (they can be present on particular pleurite on one side of the body and absent on the second one), so it cannot be used alone to distinguish species if only a few specimens are available.

(39) Posterior pleural setae on segment VIII:

A. Most species with 3 setae, the central one is always long and stout (Figs. 71–76);
B. A minority of species with 4 or more setae, where only one seta is very long and stout (e.g., *Myrsidea* from Pycnonotidae, Fig. 79), or where 2 central setae are very long and stout (*Myrsidea* from Hirundinidae, Fig. 78).

(40) Ratio of length of inner/outer pleural setae on segment VIII:

A. Most species with inner seta longer than outer one (ratio > 1.5) (Figs. 73, 75, and 76), with some extreme examples in which inner seta being much longer than outer and almost as long as central one (e.g., *M. ivanliteraki*, Fig. 81);
B. Inner seta as long as outer one (ratio around 1; e.g., *Myrsidea quadrifasciata*, Fig. 77).

There is intraspecific variation in the lengths of these 2 setae, but the differences between some species are constant both in absolute length and in the ratio between the lengths of the inner and outer setae. This character may show some variation within a species (for example, there can be different ratios on each side of the body in some specimens), so it cannot be used alone to distinguish species if only a few specimens are available.

(41) Presence of anterior pleural setae:

A. Most species have no anterior pleural setae (Figs. 71–75);
B. A minority of species have anterior setae on pleurites (e.g., *M. comosa*, *M. ivanliteraki*, and especially, species from Corvidae, e.g., *M. intermedia*, *M. malayensis*, *M. pilosa*, Figs. 80 and 81).

(42) Presence of setae on sternite I:

A. Most species have no setae on sternite I (Figs. 71–76, 83–87);
B. A minority of species have setae on sternite I (*M. sultanpurensis*, *M. novaeseelandiae*, *M. hibi*, *M. pilosa*, Figs. 82 and 88).

(43) Shape of sternite II—this character can show sexual dimorphism. Almost all females have sternite II broad and almost rectangular-shaped, but males of some species have slender and strongly arched sternite II:

A. Broad, almost rectangular-shaped (Figs. 71–76, 86, and 87);
B. Slender, strongly arched (mostly presented in males) (Fig. 85).
C. Unique sternite II is present in *M. novaeseelandiae* and *M. hibi*, where the sternal plate is divided into 3 sections by 2 unpigmented oblique "sutures" (Fig. 82).

The proposed categories should be given for each sex separately in each description of species.

(44) Anterior margin of sternite II:

A. With a median notch (Figs. 71, 72, 83, and 84);
B. Without a median notch (Figs. 85–88).

(45) Anterior setae on sternite II (Figs. 71 and 72)—there can be a variable number of setae of variable lengths on the anterior part of sternite II. There is a pair of small anterolateral setae on each side of sternite II that is always present (anterolateral setae; Figs. 71 and 72); these setae are not included in the setal count. These setae are usually close together, but in some specimens, they can be separated on one or both sides of the sternite.

This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.

[1] Aster of stout spine-like setae or group of long setae on each posterolateral corner of sternite II:

[A] Most species have aster of 2–6 stout spine-like setae (Figs. 71–75); this morphotype can be named the "typical aster" (Price et al. 2004, Hellenthal et al. 2005, Kolencik et al. 2022a);
[B] A minority of species have only 1 stout spine-like seta (*M. pectinata*);
[C] In a few species, the "typical aster" is not developed—there is either a group of short setae without stout spine-like ones (e.g., some *Myrsidea* from toucans—former *Ramphasticola*—*M. aenigma*, *M. mirabile*, *M. moylei*) or groups of long setae (e.g., some *Myrsidea* from toucans—former *Ramphasticola*—*M. hirsuta*, or *Myrsidea* from Corvidae—*M. isostoma*; Figs. 76 and 88); this morphotype can be named the "atypical aster" (Price et al. 2004, Hellenthal et al. 2005, (Kolencik et al. 2022a).

This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.

(47) Length of spine-like setae in aster on each posterolateral corner of sternite II:

A. In most species, the innermost seta is the longest; other setae are consequently shorter, with the shortest outer one (Figs. 71–75);
B. In a few species, the aster consists of spine-like setae of approximately the same length (e.g., *M. rustica*, Fig. 87).

This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.

(48) Posterior marginal setae on sternite II—there can be a variable number of setae of variable lengths on the posterior margin of sternite II between the asters. The number of setae here may show variation and cannot be used alone to distinguish species if only a few specimens are available.

(49) Shape of sternites III–VI:

A. All sternites are broad and almost rectangular (Fig. 73);
B. All sternites are slender, arched, or narrowed medially (Fig. 74).
C. Some sternites are rectangular (usually sternites III–IV), and others are arched (at least sternite VI) (Fig. 75).

(50) Partial division of terminal sternites:

A. In most species, sternites VIII–IX of males and sternites VII–IX completely fused to form a subgenital plate (Figs. 71 and 72);
B. A partial lateral division or an indentation at posterolateral margin of sternum VII in females is known for some *Myrsidea*, e.g., *M. abbreviata*, *M. laciniata*, or some *Myrsidea* from bulbuls (Clay 1968, Hellenthal and Price 2003, Price et al. 2004; Fig. 79).

(51) Posterior sternal setae on segments III–VII—the number and length of setae on the posterior margin of sternites may differ between species. In addition, there may be latero-anterior setae, which on some segments, form a definite brush (Figs. 73 and 76). Sternite VII of females is fused with sternites VIII and IX to form the subgenital plate, but the row of posterior marginal setae of the original sternite VII is clearly visible and can easily be counted. The number of these setae may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available. Clay (1966) noted that the marginal setae of the brush may be distinguished from the central setae by being more spine-like and sometimes separated by a definite gap. In other cases, the marginal line of setae may be continuous, and the differences between the setae may be so slight that the division is a matter of opinion. We therefore recommend counting all these setae together.

(52) Presence of medio-anterior sternal setae on segments III–VII:

A. No medio-anterior sternal setae (Figs. 71–74);
B. A different number of medio-anterior sternal setae present (e.g., *M. poliogasteri*, *M. isostoma*, *M. hibi*; Figs. 75, 76, and 82).

The proposed categories can be used for each abdominal segment separately.

(53) Setae on the subgenital plate of female (sternites VIII–IX) (Fig. 72)—between the setal row associated with the posterior margin of the fused sternite VII and the vulval margin, there may be additional setae that vary in number and length. The number, length, and position of these setae may show variation within a species and cannot be used alone to distinguish species if only a few specimens are available. There is a long and stout seta on each side of the anal sclerite—this seta is not included in the setal count.

(54) Shape of the anal sclerite in females—there is variability in the shape of the anal sclerite (e.g., Figs. 82, 95, and 96). More research focused on this character is needed to evaluate its intraspecific and interspecific variability.

(55) Subvulval sclerite (sternite IX) of female (Fig. 82):

A. Usually not pigmented—not visible;
B. Clearly visible, e.g., *M. novaeseelandiae*, *M. hibi* (Fig. 82).

(56) Setae on the vulval margin of female:

A. Setae in a continuous row (Figs. 95–100);
B. With a median gap in the row of setae (Fig. 101).

There can be a different number of setae, usually of the same length, on the vulval margin. This character may show variation within a species, so it cannot be used alone to distinguish species if only a few specimens are available.

(57) Vulval margin of female (Fig. 72):

A. Most species have vulval margins with regular rows of small tips, which can be serrated to deeply serrated (Figs. 95, 96, 98, 99, and 102) or attenuated (Figs. 100, 101, and 103);
B. A minority of species have vulval margins with irregular rows of sparse tips (Fig. 97). This type of vulval margin is classified as smooth to slightly spiculated by some authors (e.g., Price 1977).

(58) The shape of the vulval margin of a female:

A. Most species have a straight or slightly rounded margin (Figs. 95, 97–101);
B. Concave medio-posterior margin (Figs. 96, 102, and 103).

(59) Sculpturing of the genital chamber:

A. Most species have inconspicuous projections on the surface of the genital chamber (Figs. 95 and 96);
B. Conspicuous comb-like projection present (*M. antiqua*, *Myrsidea* sp. from *Taeniopygia guttata*; Fig. 103).

(60) Setae in the dorsal, anal fringe of females (Fig. 72)—anal fringe consists of setae which are set on raised papillae. The number and lengths of setae in this fringe vary within a species and cannot be used alone to distinguish species if only a few specimens are available.

(61) Setae in the ventral anal fringe of females (Fig. 72)—The number and lengths of setae in this fringe vary within a species, and the ventral anal fringe itself cannot be used alone to distinguish species if only a few specimens are available. However, there may be additional setae in this region, which may be taxonomically important:

A. beside the longer setae set on raised papillae, there are usually some additional shorter setae (mostly 2–6) that are not set on raised papillae interspersed between these longer setae (Figs. 95 and 96);
B. In a minority of species, the ventral anal fringe has only setae set on raised papillae.

(62) Character of bursa copulatrix of female (Figs. 82, 89–94)—Clay (1966: 334) mentioned the morphology of the spermatheca as one of the important characteristics in separating *Myrsidea* species. Consequently, Clay (1968: 207) stated that the structure that she referred to as the spermatheca is in fact a bursa copulatrix. This structure is usually tiny, thin-walled, and sensitive to distortion in mounted specimens. In many species, it is pear-shaped, spherical, or oval. In mounted specimens,

especially those that are dissected, it is not possible to see the exact relationship of the spermatheca to the bursa. More research is needed to evaluate the importance of this character and assess whether intraspecific and interspecific variability is taxonomically meaningful.

(63) Setae on the subgenital plate of male (sternite VIII) (Fig. 71)—sternite VIII of the male is fused with sternite IX to form a subgenital plate, but the setae of the posterior margin of sternite VII are visible as a distinct line and can be counted separately. As the number and length of these setae can vary within a species, these characters cannot be used alone to distinguish species if only a few specimens are available. There is a long and stout seta on each side of the last segment—this seta is not included in the setal count.

(64) Setae on the remainder of the subgenital plate of male (sternite IX) (Fig. 71)—between the posterior row of setae on the fused sternite VII and the posterior margin of the subgenital plate, there may be additional setae. These setae differ in number, position, and length within a species and cannot be used alone to distinguish species if only a few specimens are available.

(65) Presence and size of setae on the posterior margin of the subgenital plate of male:

A. Usually there are no setae on the posterior margin of the subgenital plate, rarely there are 1–2 submarginal setae of the same type as on the remainder of the plate (Figs. 71 and 106);
B. A few species have a group of spine-like setae (*M. novaeseelandiae*, *M. hihi*, Fig. 107) or longer stout setae on this margin (*Myrsidea* sp. from *Pterorhinus vassali*, Fig. 108).

(66) Anal sclerite of male (Fig. 71):

A. Usually not pigmented—not visible (Fig. 71);
B. Well-pigmented—clearly visible, e.g., *M. ivanliteraki*, *M. hihi*, or *Myrsidea* sp. from *Pterorhinus vassali* (Figs. 106–108).

(67) Inner anal setae of males (Fig. 71)—there can be intraspecific variability in the number (8–10) of very short setae along the internal opening of the anus.

(68) Posterior terminal abdominal setae of males (Fig. 71)—there can be intraspecific variability in the number (mostly 3–4) of setae terminally on the posterior margin of the abdomen.

(69) Shape of parameres of male genitalia:

A. Most species have straight rod-like parameres (Figs. 130–138);
B. Parameres with apical portions curved outward (Figs. 111, 115–120);
C. Unique parameres can be found on *Myrsidea* sp. from *Pterorhinus vassali* (Fig. 113), *Myrsidea* from *Padda oryzivora* (Fig. 114), or *M. comosa* with inward curving parameres (Fig. 112).

Clay (1966) stated that the shape of parameres is constant in large groups of species. Due to the small size of parameres, their true shape can be easily distorted. That is the reason why well-mounted specimens are necessary to evaluate this character (see the variability of parameres of *M. quadrifasciata* complex, Figs. 121–129).

(70) Character of posterior inward projecting arms of the basal plate:

A. most species have curved or almost straight posterior arms (Figs. 104, 110, and 111);
B. angulated posterior arms are present in *M. psittaci* or *M. comosa* (Fig. 112).

(71) Shape of endomeral plate of male genitalia—Clay (1966: 334) mentioned the shape of endomeral plate as one of the important characteristics in separating species of *Myrsidea*. She also stated that the character of endomeral plate is constant in large groups of species. There is variability in mesosome (mesomere by Yoshizawa and Johnson 2006 or mesomeral arch by Marshall, 2003), epimere, and ventral plate (Figs. 110 and 111), but more research is necessary to evaluate the importance of these characteristics for intraspecific and interspecific variability.

(72) Type of male genital sac sclerite—the genital sac sclerite is a tiny structure connected with spiculate genital sac (Fig. 104). It mostly consists of (i) a distal part, usually with more or less sclerotized posterior and lateral structures, and (ii) an anterior, often almost transparent plate, usually with an inconspicuous outline that can be easily distorted and usually difficult to recognize. In its natural position, it is usually located close to or near the basal plate of the male genitalia. Due to the very small size of this sclerite, its true position and often its true shape can be easily distorted. Thus, well-mounted specimens are always necessary to evaluate this important character properly. Male genitalia can be easily extruded out of the abdomen during the dissection of the specimen and/or slide mounting. In such a case, the genital sac sclerite can be lost or confused with other internal structures, such as spermatophores or crop teeth. Spermatophores are conspicuous, bottle-shaped structures usually seen in the abdomen of nondissected specimens. A spermatophore can be lost, or its natural position can be distorted after the dissection of the specimen. If so, and especially if the genital sclerite is extruded, the posterior part of the spermatophore can be incorrectly identified as the genital sclerite (Fig. 105). Clay (1968) noted that probably all male *Myrsidea* produce spermatophores. She also stated that the form of the spermatophore may prove to be of taxonomic value within the Menoponidae. Its importance for assessing intraspecific and interspecific variability within *Myrsidea* is still unknown. Also, crop teeth (Fig. 109) could potentially be mistaken for genital sclerite. This structure is in the crop (Blagoveshtchensky 1959) and cannot be seen if the crop is full of food. It may be visible in the apical part of the abdomen of dissected specimens (Fig. 105). Clay (1969: 17) stated: "Although the presence of crop teeth has been used as a generic character, they seem to be present in all the Menoponidae: further dissections of suitable material are necessary to see whether they will show any taxonomic characters."

As most of the species of *Myrsidea* are best distinguished by females (e.g., significant variability in the shape of the abdominal tergites), the otherwise morphologically very similar males can be useful for the evaluation of phylogenetic relationships due to the differences in their genital sclerite type. Clay (1966) noted that: "Species of *Myrsidea* grouped together on the characters of the male genital sclerite are frequently found to be parasitic on a group of related hosts." Due to this fact, it may seem that the fastest way to revise this speciose genus is to make revisions following host families (Dalgleish and Price 2003a). However, in some cases, this is not true, as in the case of *M. claytoni* from Vietnam (Sychra et al. 2014c). Therefore, an improved method for broader taxonomic revision is not only to compare species from the same host family but also species from the

same biogeographical regions, with emphasis on the same type of genital sclerite.

Myrsidea Morphotypes

The term "species group" has often been used in *Myrsidea* publications to group species with similar morphological traits (e.g., Clay 1966, Tandan and Clay 1971, Klockenhoff 1984a, Price et al. 2004, Sychra and Palma 2021). Additionally, Klockenhoff (1984b) correctly stated that new species of *Myrsidea* should be placed into species groups according to male genital sac sclerite characters. Similarly, the morphological species groups described in this section (referred to as morphotypes; Supplementary Dataset S1; Fig. 730) are ordered according to the morphology of the male genital sclerite—from simple to more complex. Interestingly, the order of these groups partially corresponds to phylogenetic analyses (Fig. 1 in Kolencik et al. 2022a; Fig. 730), in which *Myrsidea* from *pycnonoti*, *plumosi*, *ishizawai*, and *anaspila* morphotype groups have simpler sclerites and *dorotheae*, *hirsuta*, or *victrix* morphotype groups have more complex sclerites. However, these morphotype group assignments are preliminary and based mainly on partial morphological data (genital sclerites). The main characters that we used to delimit morphotypes were: the character of (i) distal arm: if it is continuous across the entire distal margin of the sclerite; interrupted in the middle; convex or concave; or (almost) absent; (ii) distal part of the sclerite: straight, convex, concave, or elongated parallel-sided; (iii) lateral arm: undeveloped, short, prolonged, and outwardly curved, (iv) presence or absence of ventral arm—a pronounced and enlarged process of lateral arm; (v) presence or absence of lateral spines, and their number, i.e., single "hook" vs. larger number of spines; and (vi) presence or absence of median sclerotization. Considering the phylogeny, there may be some convergence in these traits. A thorough, comprehensive analysis of these characters and the molecular tree with well-supported clades are needed to verify if these morphologically defined groups could be further considered as species groups. According to the type of genital sac sclerite, *Myrsidea* species can be divided into the following 63 morphotypes:

(1) ***longipecta* morphotype** (Figs. 139–142): short and wide sclerite with an almost straight to slightly convex distal margin that can be somewhat thickened to form a distal arm (horizontal arm sensu Tandan and Clay 1971). The proximal ends of this margin form a simple hook-like projection. Short lateral arm (vertical arm sensu Tandan and Clay 1971) arises from these projections. The plate of the sclerite is wide and rounded proximally.

The genital sclerite of this morphotype is present in 2 species parasitizing 3 bird species (family Dicruridae) from Indomalaya and one yet undetermined *Myrsidea* from *Dicrurus bracteatus* from Australasia. Included species: *M. longipecta*, *M. sindianus*, *Myrsidea* sp. from *Dicrurus bracteatus*.

(2) ***pycnonoti* morphotype** (Figs. 143–170): usually short and wide sclerite similar to those of *longipecta* morphotype by having variable distal margin (roughly flat, slightly concave to rounded, or rarely slightly convex), with a more or less extensive lateral spinous area (lateral spines) located on the proximal ends of distal margin. The distal margin may have darker pigmentation, especially in the central part, in some specimens. This is probably not identical with the distal arm. On the other hand, thickened areas on each side of the distal margin of the sclerite of *M. ovatula* (Figs. 167–168) probably represent a medially divided distal arm. Lateral arms are usually undeveloped, but thin lateral arms can be present in some species (well-visible, e.g., on *M. aynazae*, Figs. 165–166). The plate of the sclerite, if visible, is wide and rounded proximally. Nevertheless, the proximal margin is usually difficult to recognize.

We named this morphotype *M. pycnonoti* because it is present mostly in *Myrsidea* parasitizing birds from the family Pycnonotidae. This morphotype is largely identical to the *pycnonoti* species group defined by Hellenthal and Price (2003).

The genital sclerite of this morphotype is present in 13 species, parasitizing 22 bird species (family Pycnonotidae) from Indomalaya (9 species) and the Afrotropics (4 species plus another yet undetermined *Myrsidea* from *Arizelocichla tephrolaema*, *Bleda notatus*, and *Eurillas latirostris*, Figs. 155–160, and 164). *Myrsidea ovatula* from 2 bird species from the family Paradisaeidae in New Guinea (Figs. 167–168), *M. urocissae* from *Urocissa caerulea* (Corvidae) from Taiwan (Fig. 169), and *M. goodmani* from *Bernieria madagascariensis* (Bernieridae) from Madagascar (Fig. 170) share the same or very similar sclerite, so we tentatively placed them to this morphotype group. More research is necessary to confirm the relationship of these species. Included species: *M. aynazae*, *M. finlaysoni*, *M. gieferi*, *M. goodmani*, *M. kathleenae*, *M. kulpai*, *M. marksi*, *M. masoni*, *M. mcclurei*, *M. ovatula*, *M. phillipsi*, *M. pycnonoti M. urocissae*, *M. warwicki*, *M. wombeyi*, *M. zeylanici*, *Myrsidea* sp. from *Arizelocichla tephrolaema*, *Bleda notatus*, *Eurillas latirostris*.

(3) ***plumosi* morphotype** (Figs. 171–181): small sclerite with lateral spines and having different medio-distal convexity in the range from slightly rounded convexity (Figs. 171–173) to distinct and prominent process (Figs. 177–180), with proximal ends of distal margin evenly tapered to a point or with several lateral spines. Lateral arms are apparently undeveloped; only on *M. johnsoni*, there are 2 more proximally sclerotized internal lines that can be analogous to lateral arms. The outline of the plate of the sclerite is unrecognizable.

This morphotype is identical to the *plumosi* species group defined by Hellenthal and Price (2003) and includes 6 species parasitizing 18 bird species (Pycnonotidae) from Indomalaya (5 species) and the Afrotropics (one species on Réunion). We tentatively placed also *M. yoshizawai* (Fig. 181) from *Xanthomixis zosterops* (Bernieridae) from Madagascar in this morphotype group because it shares similar medio-distal convexity and lateral serrated structures that can be analogous to lateral spines. More research is necessary to confirm the relationship of these species. Included species: *M. adamsae*, *M. borbonici*, *M. eutiloti*, *M. johnsoni*, *M. ochracei*, *M. plumosi*, *M. yoshizawai*.

(4) ***chilchil* morphotype** (Figs. 182–202): the genital sclerite of this group was well-described by Tandan and Clay (1971). It is quite small. The plate of sclerite is broad and rounded proximally or narrow with almost a rectangular outline (Fig. 195), tapering distally to a rather blunt end, with 2 associated arms on each side: (i) a distal arm, which is usually convex, having its median part associated with the plate; this arm can be continuous across the entire distal margin of the sclerite (e.g., Figs. 18–195) or it can be apparently interrupted in the middle (e.g., Figs. 184, 187, 199–202), medio-distal part of the sclerite of some species or specimens may be less sclerotized with inconspicuous outline to form a central pale area. In that case, the distal margin can appear rather concave at first view (Figs. 201, 211, and 216); (ii) a lateral arm arising from the outer ends of the distal arm. Lateral arms are prolonged and outwardly curved. The distal arm is basically similar, but the length and ending of lateral ones may show considerable interspecific differences (Figs. 182, 190, 195, and 201). Tandan and Clay (1971) also noted that, although the details of the sclerite could be delineated, in no 2 specimens did the distal arms appear identical—the difference was probably an artifact rather than due to individual variation (compare, e.g., Figs. 190–194, 195–198).

This morphotype is largely identical to the *chilchil* species group defined by Tandan and Clay (1971) and includes 6 species parasitizing

12 bird species from families Leiothrichidae and Timaliidae from the Afrotropics (3 species), Indomalayan and Western Palearctic (one species on 2 hosts—one in India and Pakistan, and the second in the Arabian Peninsula), and from Indomalaya (2 species plus another yet undetermined *Myrsidea* from *Cyanoderma chrysaeum* and *Cyanoderma ruficeps*, Figs. 188–189). *Myrsidea minuscula* and *M. pullula* from 2 bird species from families Philepittidae and Vangidae from Madagascar (Figs. 203–206), and 4 *Myrsidea* species parasitizing 4 bird species from the family Thamnophilidae from the Neotropics (Figs. 207–212) share the same or very similar sclerite, so we tentatively placed them to this morphotype group. Moreover, we tentatively placed *M. ledgeri* (Fig. 213) from *Philetairus socius* (Ploceidae) from the Afrotropics to this morphotype group because its distal arm has less sclerotized medio-distal part with proximal ends forming simple lateral hook-like (apparently not toothed) projection. More research is necessary to confirm the relationship of these species. Included species: *M. breviterga*, *M. clamosae*, *M. chilchil*, *M. ledgeri*, *M. macronoi*, *M. mayermae*, *M. mcleannani*, *M. meinertzhageni*, *M. milleri*, *M. minuscula*, *M. pullula*, *M. pyriglenae*, *M. salimalii*, *Myrsidea* sp. from *Cyanoderma chrysaeum* and *Cyanoderma ruficeps*.

(5) ***Myrsidea* from *Lonchura* spp.** (Figs. 214–216): this group has quite a small sclerite. It is similar to those of the *chilchil* morphotype. The distal arm is interrupted in the middle and curved laterally to form a simple hook-like projection at each proximal end. Lateral arms arise from these proximal ends of the distal arm. The plate of the sclerite is not developed. The medio-distal part of the sclerite is less sclerotized to form a central pale groove.

The genital sclerite of this morphotype is present in yet undescribed species of *Myrsidea* from 3 *Lonchura* host species (Estrildidae) from Indomalaya. Included species: *Myrsidea* sp. from *Lonchura ferruginosa*, *Lonchura maja*, *Lonchura punctulata*.

(6) ***palmai* morphotype** (Figs. 217–218): unique sclerite remotely similar to those of *M. salimali* from *chilchil* morphotype. Distal arms are strongly curved laterally to form conspicuous hook-like projections. Lateral arms with deeply serrated lateral margins and proximal part continuing to a quite large subapical projection of an irregular shape. The plate of the sclerite is long and narrow, especially in its proximal part.

This morphotype is identical to the *palmai* species group defined by Hellenthal and Price (2003) and includes 2 species parasitizing 5 bird species (Pycnonotidae and Eurylaimidae) from Indomalaya. Included species: *M. claytoni*, *M. palmai*.

(7) ***satbhai* morphotype** (Figs. 219–222): the genital sclerite of this group was well-described by Tandan and Clay (1971). It is composed of a plate of sclerite with 2 arms associated with each side of its distal end. The plate is feebly sclerotized and has a faint outline, even in well-preserved specimens, making interspecific comparison difficult. In general, it is narrow with 2 separate distal parts that are apparently not connected distally—it has the shape of an inverted letter "Y." Distal and lateral arms associated with the plate distally are thin, lateral ones with a tendency to be pronounced and outwardly curved (Fig. 221). There are tiny feebly sclerotized structures arising on the distal arms. Since both the arms and these structures can be easily distorted, it is hard to interpret their exact shape. Tandan and Clay (1971) wrote: "It was not possible to interpret the exact structure of the sclerites so that the figures are only approximations." (compare Fig. 219 vs. Figs. 220 and 221 vs. Fig. 222).

This morphotype is largely identical to the *satbhai* species group defined by Tandan and Clay (1971) and includes 2 *Myrsidea* species parasitizing 3 bird species (Leiothrichidae) from Indomalaya (one species) and both the Indomalayan and Afrotropical realms (second species). Included species: *M. bharat*, *M. satbhai*.

(8) ***liopari* morphotype** (Figs. 223–225): sclerite similar to those of *satbhai* morphotype with a long and narrow plate. The outline of the proximal margin of the plate is unrecognizable. The curved distal arms are hardly separated into horizontal and vertical arms (sensu Tandan and Clay 1971), with serrated or filiform structures apparently arising on the whole surface of these arms.

The genital sclerite of this morphotype is present in a single species *M. liopari* from *Lioparus chrysotis* (Paradoxornithidae) from China. More research is necessary to confirm whether it belongs to a separate morphotype group or if it rather belongs to the *satbhai* morphotype as supposed by Lei et al. (2020).

(9) ***aegithali* morphotype** (Fig. 226): sclerite quite large. The distal margin is broadly rounded. The lateral sides are strongly serrated. The medio-distal part of the sclerite is less sclerotized to form a central pale area. The outline of the proximal margin of the plate is unrecognizable.

The genital sclerite of this morphotype is present in *M. aegithali* from *Aegithalos caudatus* (Aegithalidae) from the Palearctic and another yet undetermined *Myrsidea* from *A. concinnus* (Aegithalidae) from Vietnam. Included species: *M. aegithali*, *Myrsidea* sp. from *Aegithalos concinnus*.

(10) ***ishizawai* morphotype** (Figs. 227–253): similar to those of *chilchil* morphotype but with the conspicuously toothed area located on proximal ends of the distal arm (with lateral comb-like structures sensu Clay 1966). Lateral arms are prolonged and outwardly curved. The plate of the sclerite, if visible, is narrow with a variable but usually an indistinct outline. The medio-distal part of the sclerite is often less sclerotized to form a central pale area or groove, so the posterior margin can appear concave (Figs. 239 and 243).

This morphotype is identical to the *ishizawai* species group defined by Clay (1966), who included only *M. ishizawai* from *Zoothera dauma* (Turdidae) from Japan and India. We also suggest including other species with very similar sclerites. In this view, it includes 15 species parasitizing on 20 bird species from families Furnariidae (10 species) in Neotropical Region; Notiomystidae (1 species) and Meliphagidae (1 species) from New Zealand; Monarchidae (1 species) in the Indomalayan realm and Turdidae (2 species)—one in Neotropical realm and second—*M. ishizawai*—in Indomalayan realm. Undetermined *Myrsidea* were found on 2 turdid hosts in China and Vietnam (Figs. 230 and 231) and on one furnarid host in Costa Rica. The placement of *Myrsidea* from distant host families and geographic areas to a single morphotype group is rather tentative, and more research is necessary to resolve the relationship of these lice. Included species: *M. calvi*, *M. carmenae*, *M. hibi*, *M. hrabaki*, *M. ishizawai*, *M. leucophthalmi*, *M. meyi*, *M. novaeseelandiae*, *M. ochrolaemi*, *M. philydori*, *M. scleruri*, *M. souleyetii*, *M. strobilisternata*, *M. waterstoni*, *M. zuzanae*, *Myrsidea* sp. from *Dendrocincla fuliginosa*, *Geokichla citrina*, *Zoothera marginata*.

(11) ***lampropsaricola* morphotype** (Fig. 254): sclerite similar to those of *ishizawai* morphotype group with conspicuous lateral serration on each side. The distal arm interrupted in the middle. Lateral arms are simple and lead up along the lateral margin of the plate of the sclerite. The outline of the plate is unrecognizable.

The genital sclerite of this morphotype is present in a single species *M. lampropsaricola* from *Lampropsar tanagrinus* (Icteridae) from Brazil.

(12) ***subdissimilis* morphotype** (Figs. 255–269): small slender sclerite. The distal part is elongated parallel-sided, with distal arms leading up along the latero-distal margin widened with the toothed area on the proximal ends of these arms. Lateral arms leading up along the lateral margin of the plate of the sclerite are not outwardly

curved. The proximal outline of the plate can be straight or widely rounded but often unrecognizable.

The genital sclerite of this morphotype is present in 5 *Myrsidea* species, parasitizing 5 bird species (Muscicapidae and Pellorneidae) from the Palearctic realm (one species from Japan), Indomalaya (2 species), and the Afrotropics (2 species). Four other undetermined *Myrsidea* were found on 2 muscicapid hosts from Cameroon (Figs. 262, 263, 265–267), one in Vietnam (Fig. 257), and one from *Kakamega poliothorax* (Modulatricidae) from Cameroon (Fig. 258).

Moreover, we tentatively placed also *M. pachycephalae* (Figs. 268 and 269) from 3 bird species from the family Pachycephalidae from Australasia (including New Guinea and Melanesia bioregion—Vanuatu and Fiji Islands) to this morphotype group because its distal arm is toothed on proximal ends and lateral arms are not outwardly curved. Palma and Klockenhoff (1988) wrote that the male genital sclerite of this species is similar to those of *M. karyi* (*shiraki* morphotype), *M. hopkinsi*, and *M. ptilostomi* (both from the *anaspila* morphotype; see below). They also noted that: "it could be argued that these morphological similarities are not, by themselves, an indication of the close phylogenetic relationship between these species." More research is necessary to confirm the relationship of these species. Included species: *M. falcatae*, *M. mariquensis*, *M. oatleyi*, *M. pachycephalae*, *M. ramoni*, *M. subdissimilis*, *Myrsidea* sp. from *Alethe castanea*, *Chamaetylas poliocephala*, *Kakamega poliothorax*, *Myiomela leucura*.

(13) ***anathorax* morphotype** (Figs. 270–272): sclerite is similar to members of the *anaspila* morphotype (see below). The distal part is elongated, usually with an inconspicuous or invisible medio-distal margin. Distal arms leading up along the latero-distal margin are enlarged proximally with extensively spiculated apical ends. Lateral arms are outwardly curved. The plate of the sclerite is long with a rounded proximal margin.

The genital sclerite of this morphotype is present in a single species, *M. anathorax*, from *Coloeus monedula* (Corvidae) from the Palearctic.

(14) ***anaspila* morphotype** (Figs. 270–314): large and long sclerite. The distal part is elongated, parallel-sided, usually with an inconspicuous or invisible medio-distal margin. Distal arms leading up along the postero-latero-distal margin are protruded proximally, and the protruding part has a toothed apical end. Lateral arms are outwardly curved. Their proximal parts can be variably enlarged (see, for example, Figs. 275, 281, and 290). The plate of the sclerite is long and narrow, with parallel lateral sides, rounded, or tapering proximally. The distal part of the plate can be narrowed and consequently enlarged and associated with proximal margins of distal arms (Figs. 296 and 301). Placement of *M. interrupta*, with the distal part of the sclerite with concave distal and lateral sides and with quite long lateral arms (Figs. 305–307), into this morphotype is rather tentative, and more research is necessary to resolve the relationship of these lice.

Clay (1968) noted that *Myrsidea* from the host family Laniidae has a sclerite similar to a *Myrsidea* species parasitic on some of the family Corvidae. Also, Tendeiro (1987) and Klockenhoff and Tendeiro (1989) noted that *Myrsidea* from 2 African laniid hosts have the same type of sclerite as that of *M. picae*. We agree with these morphological assessments and have placed *M. seguyi* and *M. ugandus* into this morphotype (Figs. 309 and 310).

This morphotype is largely identical to the *anaspila* species group defined by Klockenhoff (1981a) and includes 25 *Myrsidea* species parasitizing 28 bird species (Corvidae and Laniidae) from the Afrotropics (8 species), the Afrotropics and Palearctic (one species), Palearctic (12 species), Palearctic and Nearctic (one species), Nearctic (2 species), and Indomalaya (one species). *Myrsidea grallinae* from *Grallina cyanoleuca* from the family Monarchidae from the Australasian realm (Fig. 311) and an undetermined *Myrsidea* from *Rhipidura* sp. from Piaget's collection (Fig. 312) share the same or very similar sclerite. Due to this similarity, we suppose that the sclerite of *M. franciscae* from *Rhipidura javanica* (Rhipiduridae) from Borneo (Fig. 313) represents the distorted form of the same morphotype, so we tentatively placed them in this morphotype group. Moreover, we tentatively placed *M. eisentrauti* (Fig. 314) from *Sporopipes squamifrons* (Ploceidae) from the Afrotropics to this group, too, despite the protruding proximal part of the distal arm is "lobe-like," apparently not toothed. More research is necessary to confirm the relationship of these species. Included species: *M. anaspila*, *M. bakttitar*, *M. brunnea*, *M. cornicis*, *M. cyanopycae*, *M. dauurica*, *M. eisentrauti*, *M. elbeli*, *M. eremialis*, *M. franciscae*, *M. grallinae*, *M. hopkinsi*, *M. indivisa*, *M. intermedia*, *M. interrupta*, *M. islandica*, *M. isostoma*, *M. nigra*, *M. obovata*, *M. picae*, *M. seguyi*, *M. somaliensis*, *M. subanaspila*, *M. subcoracis*, *M. tibetana*, *M. ugandanus*, *M. vinlandica*, *M. woltersi*, *Myrsidea* sp. from *Rhipidura* sp.

(15) ***shiraki* morphotype** (Figs. 315–353): a rather small sclerite. The distal arm is usually curved laterally and toothed proximally. This arm can be continuous across the entire distal margin of the sclerite, or it can be interrupted in the middle. The lateral arm arising from the outer ends of the distal arm is long and thin, usually curved laterally near the base and proximally at about mid-length. The plate of the sclerite is long, narrow, tapering proximally, and usually well-pigmented; distally, it is associated with proximal margins of distal arms.

This morphotype is largely identical with the *shiraki* species group defined by by Klockenhoff (1969). It includes 26 species parasitizing 21 bird species (Corvidae) from Indomalaya (11 species), Australasia (9 species, 5 of them from New Guinea and Melanesia bioregion), the Nearctic (2 species), the Afrotropics (2 species), and Palearctic (1 species in Afghanistan and one species in Taiwan, Japan, and Korea). *Myrsidea ivanliteraki* and *M. vincula*, 2 bird species from the family Artamidae from Australasia (Figs. 343–345), share the same or very similar sclerite, so we tentatively placed them in this morphotype group. More research is necessary to confirm the relationship of these species. Included species: *M. australiensis*, *M. bakeri*, *M. bennetti*, *M. birmensis*, *M. borneoensis*, *M. capensis*, *M. cecilae*, *M. clayae*, *M. fuscicapilla*, *M. himalayensis*, *M. insularis*, *M. ivanliteraki*, *M. karyi*, *M. lehmensicki*, *M. malayensis*, *M. mellori*, *M. mexicana*, *M. nuristaniensis*, *M. philippinensis*, *M. pilosa*, *M. ptilostomi*, *M. saturata*, *M. shirakii*, *M. siamensis*, *M. splendenticola*, *M. timmermanni*, *M. trithorax*, *M. vincula*, *Myrsidea* sp. from *Corvus meeki*, *Corvus typicus*.

(16) ***bedfordi* morphotype** (Figs. 354–357): relatively broad sclerite with a long and thin plate generally similar to those of *shiraki* morphotype. The distal arm is straight and continuous across the entire distal margin of the sclerite. Contrary to *shiraki* morphotype, it is curved proximally to form a simple hook-like projection. The lateral arm arises from the outer ends of the distal arm and is slightly curved and enlarged apically.

This morphotype is identical to the *bedfordi* species group defined by Klockenhoff (1981a) and includes 2 *Myrsidea* species parasitizing 3 bird species from the family Corvidae from the Afrotropics. Included species: *M. bedfordi*, *M. sjoestedti*.

(17) ***buxtoni* morphotype** (Figs. 358 and 359): small sclerite with inconspicuous distal margin. Distal arms leading up along the latero-distal margin form a simple straight lateral projection. Lateral arms

are outwardly curved, with their apical parts enlarged upward. The outline of the plate of the sclerite is not visible.

The genital sclerite of this morphotype is present in a single species, *M. buxtoni*, from *Aplonis atrifusca* (Sturnidae) from Samoa.

(18) ***grandiceps* morphotype** (Figs. 363–374): unique sclerite with 2 narrow processes tapering distally and groups of lateral spines arising on the base of these processes. The plate of the sclerite, if visible, is long, narrow, rounded, or tapering proximally. Considerable interspecific differences can be recognized in the different lengths of the processes and the distance between them—from short, widely separated processes (*M. trinoton*, Fig. 363) to long processes separated only by a narrow groove (*Myrsidea* from *Corvus woodfordi*, Fig. 373).

This morphotype is largely identical to the *grandiceps* species group defined by Klockenhoff (1971b) and includes 9 *Myrsidea* species parasitizing 7 bird species (Corvidae) from Australasia (7 species, 5 of them from New Guinea and Melanesia bioregions) and Indomalaya (2 species). Two additional undetermined *Myrsidea* were found on corvid hosts in Sulawesi and Solomon Islands (Figs. 372 and 373). Included species: *M. arafura*, *M. coloiopsis*, *M. grandiceps*, *M. macrorhynchicola*, *M. novabritannica*, *M. robsoni*, *M. schizotergum*, *M. trinoton*, *M. tristicola*, *Myrsidea* sp. from *Corvus typicus*, *Corvus woodfordi*.

(19) ***rustica* morphotype** (Figs. 375–387): unique sclerite with 2 short processes rounded distally (the distal margin not always visible) and groups of well-sclerotized lateral spines arising at the base of these processes. The plate of the sclerite is long and narrow, usually with a posterior bifurcation (Figs. 380–385).

Clay (1968) already noted that *Myrsidea* from Hirundinidae have a characteristic sclerite but did not designate this as a separate species group. The genital sclerite of this morphotype is present in 5 species parasitizing 16 bird species (Hirundinidae) from the Neotropics (2 species), Nearctic and Neotropics (one species), Nearctic and Palearctic (one species) and nearly cosmopolitan distribution (one species—*M. rustica*). Included species: *M. dissimilis*, *M. jonnyvonbergeni*, *M. latifrons*, *M. palloris*, *M. rustica*.

(20) ***diffusa* morphotype** (Figs. 388–400): The genital sclerite of this group was well-described by Clay (1968). It comprises the distal arm that is divided in the middle and toothed proximally. This proximal part is well-visible from the dorsal view, which is why Clay (1968) named it the dorsal arm. The lateral arm continues to a pronounced and enlarged process (ventral arm sensu Clay 1968). Clay (1968) noted that: "In mounted specimens the ventral arms are usually pressed out laterally and their true shape distorted (see Figs. 397 and 398). The shape cannot, therefore, be used as a taxonomic character." The medio-distal part of the sclerite is less sclerotized to form a long, narrow central groove. The outline of the plate of the sclerite is usually unrecognizable, but Clay (1968) noted that: "There is also some minor individual variation in the length and breadth of the plate. Specific differences are shown in the general shape and length of the plate posterior to the dorsal arms and in the form of the dorsal arms."

The genital sclerite of this morphotype is present in 11 species, parasitizing 29 bird species (Icteridae) from the Neotropics (8 species), Nearctic (1 species), and in both Neotropics and Nearctic (2 species). Included species: *M. amblyramphidis*, *M. aquilonia*, *M. balteri*, *M. diffusa*, *M. downsi*, *M. fuscomarginata*, *M. laciniata*, *M. mirabilis*, *M. picta*, *M. psittaci*, *M. tropicalis*.

(21) ***magnidens* morphotype** (Figs. 401 and 402): quite a small sclerite similar to those of the *diffusa* morphotype. The distal part is prolonged with an inconspicuous medio-distal margin. The medio-distal part of the sclerite is less sclerotized to form a long, narrow central groove. The sides of this groove are more sclerotized than in the *diffusa* morphotype. Distal arms are not connected in the midline and are curved laterally to form simple hook-like projections. Lateral arms are outwardly curved with a tendency to be prolonged and proximally tapered. The plate of the sclerite, if visible, is as wide as sclerite, parallel-sided, with a rounded proximal margin.

This morphotype is identical to the *magnidens* species group defined by Price et al. (2005). It includes only *M. magnidens* from *Pitangus sulphuratus* (Tyrannidae) from Venezuela. Price et al. (2005) also placed *M. stenodesma* from *Empidonax atriceps* (Tyrannidae) from Costa Rica in *magnidens* species group according to abdominal chaetotaxy and shape of female abdominal tergites. Unfortunately, the male genital sac sclerite is obscured on an available male, so new fresh material from the type host is necessary to confirm the placement of this species into this morphotype.

(22) ***comosa* morphotype** (Fig. 403): unique large sclerite with long, narrow distal arms that are toothed proximally. In her description, Clay (1968) wrote: "what may be the ventral arms, are narrow, seem to be flattened and to lie on the ventral surface of the plate." The medio-distal part of the sclerite is less sclerotized to form a central pale groove.

The genital sclerite of this morphotype is present in a single species, *M. comosa*, from *Macroagelaius subalaris* (Icteridae) from the Neotropics.

(23) ***flavida* morphotype** (Figs. 404–408): long and narrow sclerite with poorly developed distal margin. Distal arms are short, forming a small lateral hook. Lateral arms also form a small lateral hook that continues up along the latero-distal margin. This sclerite can be easily distorted (compare Figs. 404–408).

The genital sclerite of this morphotype is present in a single species, *M. flavida*, from *Eurylaimus ochromalus* (Eurylaimidae) from Indomalaya.

(24) ***sultanpurensis* morphotype** (Figs. 409–414): quite a small sclerite similar to those of *magnidens* morphotype. Most available males have somewhat distorted sclerites with several distal and lateral processes that are hard to homologize with distal or lateral arms of sclerites of other morphotypes. It seems that it is naturally asymmetrical. In general, it can be characterized as follows: the distal part of the sclerite is prolonged, and the medio-distal part forms the central groove without the distal margin. Neither distal nor lateral arms have a well-defined outline. The structure that may be the distal arm is tapered laterally, whereas the structure that may be the lateral arm is in the form of an outwardly curved bifurcated process (Fig. 409). The plate of the sclerite has thickened lateral sides and an inconspicuous proximal margin.

This morphotype is identical to the *sultanpurensis* species group defined by Clay (1966), who wrote that: "In all available specimens, the male genital sclerite is somewhat distorted but appears to be the same as that of *ishizawai*." Contrary to Clay (1966), we placed *M. sultanpurensis* rather close to *magnidens* due to the absence of lateral comb-like structures typical for *ishizawai*. The genital sclerite of this morphotype is present in a single species, *M. sultanpurensis*, from *Myophonus caeruleus* (Muscicapidae) from Indomalaya.

(25) ***flavescens* morphotype** (Figs. 415–420): unique long and narrow sclerite with thin distally outwardly curved lateral arms. Lateral sides are slightly folded inward to form 2 converging "lines" (Figs. 415–416, and 420) or a long median line (Fig. 418). Distal part with a widely rounded or rather bilobed-like tip and concave medio-distal margin (Figs. 415–418). The proximal outline of the plate is usually poorly visible.

The genital sclerite of this morphotype is present in 3 species from 3 species of *Acridotheres* (Sturnidae) from Indomalaya and

Western Palearctic (Pakistan, Nepal, Sri Lanka, Taiwan, Thailand), and as introduced also in Hawaii, Tahiti, St. Helena Island, Chagos Archipelago, and Madagascar.

Note to *Myrsidea invadens*: *M. invadens* was described by Kellogg and Chapman (1902) based on only several females from *Acridotheres tristis* introduced in Hawaii. These authors provided only simple descriptions and a relatively good drawing. Consequently, Ferris (1932) redescribed this species from the same host species that was introduced to Tahiti. He provided adequate descriptions of both sexes, including more specific drawings. Unfortunately, he did not describe nor illustrate the male genital sac sclerite. The drawing of a female presented by Ferris (1932) shows tergites II–III with conspicuous medio-distal convexity, while that by Kellogg and Chapman (1902) has all the tergites with straight posterior margins. As such, it is questionable if these lice were really conspecific, and this group requires more evaluation.

It was well-documented that *Myrsidea* is common on *A. tristis* in its native range—India (Saxena et al. 2007) and Pakistan (Aslam et al. 2015). However, lice in these areas were most likely identified as *M. invadens* according to their host-association, so no information on the morphology of this species from its native range has been published to enable comparisons of these lice with those reported by Kellogg and Chapman (1902) and Ferris (1932). Recently, Eduardo and Villa (2011) redescribed "*M. invadens*" from *Gracula religiosa palawanensis* from Philippines. Unfortunately, these authors did not explain how they decided that their specimens were conspecific with *M. invadens*. Consequently, Bughio et al. (2018) reported that their *Myrsidea* from *A. tristis* in Pakistan differ from those described by Eduardo and Villa (2011) and described a new species *M. ahmedalii*. Due to the similarity of tergites of females of *M. ahmedalii* with those of *M. invadens* from Tahiti described by Ferris (1932), the question arises as to whether *M. ahmedalii* is indeed a new species or whether it is conspecific with *M. invadens*. We were able to examine *Myrsidea* from *A. tristis* from Nepal, Sri Lanka, Thailand, Hawaii, St. Helena Island, Chagos Archipelago, and Madagascar deposited at NHML, and we can confirm that they represent the same morphology of tergites as those byFerris (1932) and Bughio et al. (2018) from Tahiti and Pakistan, respectively. More research is necessary to resolve the true status of these lice. On the other hand, contrary to Eduardo and Villa (2011), we state that *Myrsidea* reported from *Gracula religiosa* represents a hitherto undescribed species belonging to a separate morphotype (see below). Included species: *M. ahmedalii*, *M. flavescens*, *M. invadens*.

(26) ***breviventris* morphotype** (Fig. 420): unique long and narrow sclerite generally similar to those of *flavescens* morphotype, with thin distally outwardly curved lateral arms. But, the distal part of the sclerite forms a narrow process-like tip (Fig. 420).

The genital sclerite of this morphotype is present in a single species, *M. breviventris*, from *Acridotheres melanopterus* (Sturnidae) from Java.

(27) ***struthidea* morphotype** (Fig. 421): very unique, quite a large sclerite remotely similar to those of *sultanpurensis* morphotype. The distal part has a pair of large well-sclerotized bifurcated claw-like processes. Other parts of sclerite are not apparent.

The genital sclerite of this morphotype is present in a single species, *M. struthidea*, from Struthidea cinerea (Corcoracidae) from Australia.

(28) ***flavirostrata* morphotype** (Figs. 422–424): unique large sclerite with T-shape antero-central structure and prolonged single medio-distal process. Lateral sides are rather membranous, lobe-like, with an inconspicuous outline.

The genital sclerite of this morphotype is present in 2 species parasitizing 2 bird species (Corvidae and Leiothrichidae) from Indomalaya. Included species: *M. flavirostrata*, *M. sikkimensis*.

(29) ***assamensis* morphotype** (Figs. 425–437): unique M-shaped sclerite consisting of a pair of long, slender arms that are recurved at about mid-length, with the distal half (outer arm in Fig. 425) being dorsal to the proximal half (inner arm in Fig. 425). Distally, these arms may be fused (Figs. 425–430) or separated (Fig. 431). Distal to these arms may be a median attenuation with either a single median process (which may be fused to the inner arms) (Figs. 425–429) or paired, broader extensions that are divided medially (as are the inner arms) (Fig. 431). To date, nothing has been homologized with the plate of the sclerite.

This morphotype shares some characters with the "species group B" defined by Tandan (1972) and includes 4 species parasitizing 4 bird species (Leiothrichidae) from Indomalaya. Contrary to Tandan (1972), we place *M. macraidoia*, and *M. monilegeri* together with *M. patakiensis* in their own morphotype group. More research is necessary to resolve the relationships of these lice. Included species: *M. agarwali*, *M. assamensis*, *M. attenuata*, *M. orientalis*.

(30) ***monilegeri* morphotype** (Figs. 432–437): M-shaped sclerite similar to those of the *assamensis* morphotype. Sclerites of this morphotype differ by the distal part of inner arms that is partly fused with 2 foliform, often curved processes (Figs. 432–437) and by the relative length of the outer arm vs. median attenuation, either with a median section shorter than outer lateral sections (Fig. 436) or with a median section longer than outer lateral sections (Fig. 432).

This morphotype group is partially identical to the "species group B" defined by Tandan (1972) and includes 4 species parasitizing 6 bird species (Leiothrichidae and Pellorneidae) from Indomalaya. Included species: *M. monilegeri*, *M. patkaiensis*, *M. victoriae*, *M. zhangae*.

(31) ***macraidoia* morphotype** (Figs. 438 and 439): unique, very large sclerite with a similar M-shape to those of the *assamensis* morphotype. Contrary to Tandan (1972), who included *M. macraidoia* in "species group B" together with other *Myrsidea* with an M-shaped sclerite, we place this species in a separate morphotype because of the presence of additional median serrated sclerites and pointed processes in median parts of the inner arms.

The genital sclerite of this morphotype is present in a single species, *M. macraidoia*, from *Pterorhinus albogularis* (Leiothrichidae) from Indomalaya.

(32) ***Myrsidea* from *Pterorhinus vassali* morphotype** (Figs. 440 and 441): unique, very large asymmetrical sclerite with 2 thick lateral arms, one of which is bifurcated proximally and is elongated to an "outer arm." Lateral arms are fused distally and elongated to a single large claw-like process.

The genital sclerite of this morphotype is present in an undescribed species of *Myrsidea* from *Pterorhinus vassali* (Leiothrichidae) from Vietnam.

(33) ***sehri* morphotype** (Figs. 442–450): unique tripartite sclerite consisting of (i) median W-shaped part with a well-sclerotized outline, with a single small and thin median process of indistinct outline that is often distorted or not apparent; (ii) outer sac-like structure with a featureless outline, often only with slightly apparent bilobed distal margin and invisible lateral margins; and (iii) distal processes, typically pointed, whose connection to the rest of sclerite is usually not apparent. This arrangement can be easily distorted during mounting, causing either the bilobed distal margin or distal pointed processes, or both, to be folded over the rest of the sclerite and located proximally (Figs. 446–448). The sclerite of *M. bhutanensis* (Fig. 450) represents a large sclerite consisting of a complex of several sclerites

generally analogous to those of other species in this group but with slightly different arrangements. Here we follow Tandan (1972), who placed this species into "species group A."

This morphotype group is almost identical to the "species group A" defined by Tandan (1972) and includes 6 species parasitizing 6 bird species (Leiothrichidae and Timaliidae) from Indomalaya. Contrary to Tandan (1972), we place *M. singularis* in its own morphotype group. More research is necessary to resolve the relationships of these lice. Included species: *M. bhutanensis*, *M. duplicata*, *M. erythrocephali*, *M. manipurensis*, *M. sehri*, *M. thailandensis*.

(34) ***singularis* morphotype** (Figs. 451–460): unique sac-like sclerite with 2 thin median arms and single medio-distal process. *Myrsidea singularis* has a pair of distal processes similar to members of the *sehri* morphotype. Other species in the *singularis* morphotype have no apparent processes distally.

The genital sclerite of this morphotype is present in 2 species parasitizing 3 bird species (Leiothrichidae and Alcippeidae) from Indomalaya. Other yet undetermined species were found on *Actinodura cyanouroptera* (Leiothrichidae; Figs. 455–457) and *Stachyris nigriceps* (Timaliidae) from Vietnam (Fig. 389), and *Zosterops natalis* (Zosteropidae) from Christmas Island (Fig. 454). Moreover, *M. cerrodelamuertensis* from *Catharus gracilirostris* (Turdidae) from Costa Rica also shares the same type of sclerite. More research is necessary to resolve this interesting case of the occurrence of almost identical genital sclerite in lice infesting unrelated hosts from distant geographic regions. Included species: *M. cerrodelamuertensis*, *M. cheni*, *M. singularis*, *Myrsidea* sp. from *Actinodura cyanouroptera*, *Stachyris nigriceps*, *Zosterops natalis*.

(35) ***eurocephali* morphotype** (Fig. 461): very distinctive sclerite; widened, rounded proximally, with a pair of short lateral processes in proximal third (when in situ), and elongated and attenuated distally.

The genital sclerite of this morphotype is present in only a single species, *M. eurocephali*, parasitizing 2 bird species (Laniidae) from the Afrotropics.

(36) ***prionopsis* morphotype** (Fig. 462): very distinctive sclerite, slightly swollen distally with lateral spines and rounded median part. Plate of the sclerite is narrow.

The genital sclerite of this morphotype is present in only a single species, *M. prionopsis*, from *Prionops plumatus* (Vangidae) from the Afrotropics.

(37) ***ananthakrishnani* morphotype** (Figs. 463–466): unique narrow and long sclerite, which is longitudinally divided with a posterior circular pale or unpigmented area (Fig. 463). Similar sclerite is also present in yet undetermined *Myrsidea* on *Pardalotus quadragintus* (Pardalotidae) from Australia (Fig. 464). We suggest that *M. argentauris* also belongs to this morphotype group. However, unlike *M. ananthakrishnani*, the medio-distal margin is not apparent in *M. argentauris*, and therefore, there are only postero-lateralr margins in the form of 2 thin processes (Fig. 465). A similar sclerite is also present in a yet undetermined *Myrsidea* infesting *Pardalotus punctatus* (Pardalotidae) from Australia (Fig. 466).

The genital sclerite of this morphotype is present in 2 species, parasitizing 2 bird species (Leiothrichidae) from Indomalaya and 2 as yet undetermined *Myrsidea* species from 2 bird species (Pardalotidae) from Australia. Included species: *Myrsidea ananthakrishnani*, *Myrsidea argentauris*, *Myrsidea* spp. from *Pardalotus punctatus*, *Pardalotus quadragintus*.

(38)***zenae* morphotype** (Fig. 467): unique narrow sclerite with a very short plate. The sclerite of this species seems to consist of 2 pointed parts distally and 2 curved processes that are hard to homologize with distal or lateral arms of sclerites of other morphotypes.

The genital sclerite of this morphotype is present in only a single species, *M. zenae*, from *Spindalis zena* (Spindalidae) from the Neotropics.

(39) ***spizae* morphotype** (Figs. 468 and 469): elongate sclerite with a broad, flattened triangular plate tapering distally, remotely similar to those of *thoracica* morphotype group (see below). Despite the original drawing of the sclerite of *M. spizae* by Price and Dalgleish (2006) looking distorted, Kolencik et al. (2017) found the same type of sclerite in *M. flaveolae*. The distal end of the sclerite is blunt with a rounded apical tip. It is asymmetrical in all available males, but we can only speculate that it is naturally asymmetrical. The median sclerotization, typical, for example, in *thoracica* morphotype group, is not developed. There is a continuous band across the entire distal margin of the sclerite, along the posterolateral margin, and on each side is pointed distally. The homology of this "band" with posterior and/or lateral arms of sclerites of other morphotypes is unclear. More research is necessary to confirm whether this group is indeed differentiated enough to consider it a separate morphotype or whether it is close to the *thoracica* morphotype group.

The genital sclerite of this morphotype is present in 2 species parasitizing 3 bird species (Thraupidae) from the Neotropics. Included species: *M. flaveolae*, *M. spizae*.

(40) ***mitrospingi* morphotype** (Fig. 470): small sclerite with 2 posterior spine-like processes and relatively large aliform lateral arms. It is hard to say if this is a natural form of the sclerite or if it is distorted. More research is necessary to confirm whether it represents a separate morphotype or belongs to another morphotype group.

The genital sclerite of this morphotype is present in only a single species, *M. mitrospingi*, from *Mitrospingus cassinii* (Mitrospingidae) from Costa Rica.

(41) ***crassipes* morphotype** (Figs. 471 and 472): unique large bilobed sclerite that consists of 2 sac-like structures separated by a long central groove. Distal parts of sclerite are strongly serrated and somewhat similar to those of the *aegithali* morphotype.

The genital sclerite of this morphotype is present in only a single species, *M. crassipes*, from *Epimachus fastosus* (Paradisaeidae) from New Guinea.

(42) ***Myrsidea* from *Gracula religiosa*** (Figs. 473 and 474): unique sclerite with 2 long wide processes rounded distally and extensive lateral spinous area arising on the base of these processes. Plate of the sclerite is relatively short and wide.

The genital sclerite of this morphotype is present in only a single species, recently described by Eduardo and Villa (2011) as "*M. invadens*," from *Gracula religiosa palawanensis* (family Sturnidae) from the Philippines. Since the sclerite conspicuously differs from those of *M. invadens* (see above), *Myrsidea* from *Gracula religiosa* represents a hitherto undescribed species belonging to a separate morphotype group.

(43) ***pectinata* morphotype** (Figs. 475–477): short and wide sclerite with narrowed medio-distal part with 2 small lateral projections and median longitudinal sclerotization. The outline of the plate is mostly unrecognizable.

The genital sclerite of this morphotype is present in 2 species parasitizing 3 bird species (Maluridae) from Australasia. Included species: *M. pectinata*, *M. strangeri*.

(44) ***piageti* morphotype** (Figs. 478–481): unique wide sclerite with a short, narrow medio-distal process and 2 lateral lobe-like structures with serrated lateral margins.

The genital sclerite of this morphotype is present in 2 species parasitizing 2 bird species (Paradisaeidae and Paradoxornithidae) from Indomalaya and New Guinea. Included species: *M. piageti*, *M. suthorae*.

(45) ***srivastava* morphotype** (Figs. 482–484): the complex sclerite with a well-sclerotized center, which is often the only portion readily visible during microscopic examination (compare Fig. 482 vs. Fig. 483). The sclerite has inwardly curved lateral processes that can be elongated as slightly sclerotized arms. The distal portion of the sclerite is elongated into 2 processes, tapering distally and separated by a narrow central groove. The outline of these processes, especially their distal tips, is typically difficult to visualize. The plate of the sclerite is apparently short and widely rounded, but the outline is difficult to recognize in most specimens.

The genital sclerite of this morphotype is present in 2 species parasitizing 6 bird species (Estrildidae) in the Afrotropics and Indomalaya. Included species: *M. amandava*, *M. srivastava*.

(46) ***cyrtostigma* morphotype** (Figs. 485 and 486): very large and unique sclerite with 2 long narrow lateral parts ending in rounded distal ends.

The genital sclerite of this morphotype is present in only a single species, *M. cyrtostigma*, which parasitizes 2 bird species (Estrildidae) from Indomalaya.

(47) ***estrildae* morphotype** (Figs. 487–492): a complex sclerite, similar to those of the *srivastava* morphotype, with a heavily sclerotized center and including 2 outwardly curved lateral processes and a central "process" that is as long as the lateral ones. The plate of sclerite is either not developed or easily distorted and difficult to recognize (compare Fig. 487 vs. Fig. 488). Instead, more sclerotized outer arms are present (forming the M-shaped sclerite similar to those of the *assamensis* morphotype). The sclerite of an undetermined *Myrsidea* from *Estrilda nonnula* shows elongated inner distal arms with serrated lateral margins that are distally connected with outer arms (Figs. 491 and 492). The placement of *Myrsidea* into this morphotype group is tentative, and more research is necessary to resolve the relationships of these lice.

The genital sclerite of this morphotype is present in only one species, *M. estrildae*, from *Estrilda astrild* (Estrildidae) from the Afrotropics. Another undetermined species, presumably from this group, was found on *Estrilda nonnula* from Cameroon. Included species: *M. estrildae*, *Myrsidea* sp. from *Estrilda nonnula*.

(48) ***Myrsidea* from *Padda oryzivora*** (Fig. 493): a relatively large and complex sclerite consisting of a proximo-central narrow rod-like sclerite that is slightly curved on both sides and 2 prolonged lateral plates with serrated lateral margins and narrow curved process on each proximo-lateral half.

The genital sclerite of this morphotype is present in an undescribed species of *Myrsidea* from *Padda oryzivora* (family Estrildidae) from Indomalaya. Placement of this *Myrsidea* to its own morphotype group is tentative, and more research is necessary to resolve its relationship to the *estrildae* morphotype. Moreover, a similar sclerite is found in an undetermined *Myrsidea* from *Lonchura castaneothorax* from New Guinea. The sclerite of this undetermined *Myrsidea* is more simple, with a curved antero-central sclerite and narrow and wavy, prolonged lateral plates (Fig. 494). Unfortunately, the sclerites of this undescribed species from New Guinea are distorted in both available male specimens, and therefore, more specimens are needed to resolve the relationships of this *Myrsidea* species to other *Myrsidea* from estrildid species.

(49) ***Myrsidea* from *Taeniopygia guttata*** (Figs. 495 and 496): unique small sclerite with a narrow posterior part and 2 groups of anterolateral sclerites.

The genital sclerite of this morphotype is present in an undescribed species of *Myrsidea* from *Taeniopygia guttata* (Estrildidae) from Australia.

(50) ***cucullaris* morphotype** (Figs. 497–507): very small, narrow sclerite consisting of 2 short, narrow lateral arms and a sac-like structure lateral to the lateral arms. This sclerite is often distorted and then appears similar to the sclerites of the *flavida* morphotype.

The genital sclerite of this morphotype is present in 4 species parasitizing 5 bird species (Sturnidae) from the Palearctics, Indomalaya, and Australasia.

We found that *M. lyali* described by Klockenhoff (1984b) from *Fringilla coelebs* (Fringillidae), has the same type of sclerite as *M. cucullaris* from *Sturnus vulgaris* (Sturnidae). When we compared the drawing of female abdominal tergites and the whole description, we found that they fall well within what we would consider the range of intraspecific variation of *M. cucullaris*. Klockenhoff (1984b) indicated that *M. lyali* cannot be included in any of the known species groups. Furthermore, Klockenhoff (1984b) noted that "Given that *M. lyali* is so far represented only by available material from *F. coelebs* from Ireland, it cannot be ruled out that this is a contamination or—perhaps a local—secondary infestation." We assume that Klockenhoff overlooked *M. cucullaris* in his revision, and we agree with Klockenhoff that specimens of *Myrsidea* from *F. coelebs* in his material were likely stragglers from *Sturnus vulgaris*, the type of host of *M. cucullaris*. Included species: *M. cucullaris*, *M. lengerkeni*, [*M. lyali*], *M. pungens*, *M. teraokai*.

(51) ***victrix* morphotype** (Figs. 508–515): a relatively large and broad sclerite with a broad plate that is rounded proximally and a conspicuously concave medio-distal margin. The distal arm is either absent or short and associated with the medio-distal margin of the plate. Lateral arms that follow the posterolateral margins of the plate are strongly bent at their midpoint, elongated beyond the distal margin of the plate, and curved laterally at their end. These arms are bifurcated at their midpoint with pronounced and enlarged processes that form the ventral arms (*sensu* Clay 1968). These arms vary in length and shape, with tapered or truncated proximal ends and either (i) not reaching the proximal part of the lateral arm (with a modest interruption in each lateral portion as described by Price et al. 2004; Figs. 508–510); or (ii) with much shorter ventral arms (with a wider gap in each lateral portion as described Price et al. 2004; Fig. 511); or (iii) ventral arms with parallel sides and truncated proximally reaching distal part of the lateral arm (with only narrow separation for each lateral portion as described by Price et al. 2004; Figs. 513–515); or (iv) with long lateral arms (ends of lateral portions overlapping to form oval as described by Price et al. 2004; Fig. 512). Conspicuous thin transverse sclerite medio-proximally to the basis of ventral arms is present in some species (Figs. 508–511).

Price et al. (2004) distinguished 3 species groups of *Myrsidea* from toucans: *victrix*, *extranea*, and *abbreviata*, which were based mainly on modifications of metanotum and/or tergites of females. They wrote that this arrangement introduces a degree of heterogeneity within 2 of these groups that include males with conspicuously different male genital sclerites: (i) the *victrix* species group with 2 species (*M. victrix*, *M. ceciliae*) that have sclerites with thin transverse sclerite medio-proximal to them and a third species (*M. witti*) that does not have this sclerite and has a whole sclerite appearing much as those in the *extranea* species group; (ii) the *extranea* species group with 2 species (*M. extranea*, *M. peruviana*) that are relatively homogeneous; and (iii) the *abbreviata* species group with 3 species from *Pteroglossus* hosts (*M. aleixoi*, *M. dorothae*, *M. lanei*) with one type of sclerite and a 4th species (*M. abbreviata*) from *Ramphastos* host that has a sclerite much as those from the *victrix* species group. Clay (1966) suggested that females show important characteristics that can be used to distinguish species, whereas the genital sclerites of males could be used to clarify the phylogenetic relationships among species within the genus *Myrsidea*. Recently, Kolencik et al. (2022) demonstrated that *Myrsidea* from toucan hosts form 3 separate

clades characterized by different types of genital sclerites—here named as *victrix* species group, *dorotheae* species group, and *hirsuta* species group, and therefore, confirmed Clay's (1966) suggestion.

This morphotype is partially identical to the *victrix* species group defined by Price et al. (2004) and includes 5 species parasitizing 8 bird species in the genus *Ramphastos* (Ramphastidae) from the Neotropics. Included species: *M. abbreviata*, *M. ceciliae*, *M. extranea*, *M. victrix*, *M. witti*.

(52) ***hirsuta* morphotype** (Figs. 516–519): sclerite with long triangular plate with median sclerotization. The distal part of sclerite is narrow and elongated with a flattened distal margin. Distal arms apparently not developed or in the form of inconspicuous bands on the base of median sclerotization. Lateral arms following lateral margins of sclerite in the distal end are strongly bent at their midpoint and, elongated to the distal margin of the plate and curved laterally at their end. The length of lateral arms varies and may reach the distal end of the sclerite (Fig. 519), or these arms may be much shorter (Figs. 516–518).

The genital sclerite of this morphotype is present in 5 species parasitizing 2 Neotropical bird species in the genus *Ramphastos* (Ramphastidae). Included species: *M. aenigma*, *M. hirsuta*, *M. mirabile*, *M. moylei*, *M. peruviana*.

(53) ***dorotheae* morphotype** (Figs. 520 and 521): sclerite with long triangular plate with 2 central sclerotized areas rising from medio-distal sclerotization. The distal part of the sclerite is narrow and elongated with a flattened distal margin. Distal arms are apparently not developed or in the form of an inconspicuous band at the base of medio-distal sclerotization. Lateral arms leading up along the posterolateral margin are rounded or evenly bent, partially bifurcated at their midpoint, with longer arms curved laterally at their end.

The genital sclerite of this morphotype is present in 3 species parasitizing 5 bird species in the genus *Pteroglossus* (Ramphastidae) from the Neotropics. Included species: *M. aleixoi*, *M. dorotheae*, *M. lanei*.

(54) ***Myrsidea* from *Erythrura* spp.** (Figs. 522–526): a quite small sclerite with a short rectangular plate (if visible). Slightly similar to those of the *victrix* morphotype. The medio-distal margin is conspicuously concave. The distal arm is apparently not developed or very short and associated with the plate. Lateral arms following posterolateral margins of the plate, at proximal ends abruptly bent laterally. Distally, lateral arms extend beyond the distal margin of sclerite, forming curved processes of varying lengths.

The genital sclerite of this morphotype is present in yet undescribed species of *Myrsidea* from 2 *Erythrura* species from the family Estrildidae in Thailand, New Guinea, and Vanuatu.

(55) ***Myrsidea* from *Cryptospiza-Lamprotornis*** (Figs. 527–535): very small sclerite with a long, narrow, and parallel-sided, or triangular plate; overall similar to those of the *hirsuta* morphotype. The distal portion of the sclerite is narrow and prolonged, with a rounded distal margin and short median sclerotization. Distal arms are apparently not developed. Lateral arms follow posterolateral margin and are curved at an acute angle halfway along the length with a laterally curved end. The distal part of the lateral arm usually does not reach the tip of the sclerite. The apical part of the lateral arm has a tendency to continue to a lobe-like process—analogous to the ventral arm (Figs. 527, 533, and 535).

The genital sclerite of this morphotype is present in undescribed *Myrsidea* from 2 *Cryptospiza* species and *Nigrita canicapillus* (Estrildidae) and from *Notopholia corusca* and *Lamprotornis ornatus* (Sturnidae) from the Afrotropics.

(56) ***mendesi* morphotype** (Figs. 538–540): generally similar to those of the *hirsuta* morphotype and/or previous morphotype, but with conspicuously enlarged lateral arms that curve laterally in the distal end. The outline of the plate of the sclerite is usually poorly visible. The apical part of the lateral arms continues to a pronounced distally tapered ventral arm.

The genital sclerite of this morphotype is present in *M. mendesi* from *Onychognathus fulgidus* (Sturnidae) from São Tomé e Príncipe and another yet undetermined *Myrsidea* from *Lamprotornis caudatus* and *Lamprotornis purpuroptera aenocephalus* (Sturnidae) from Senegal and Sudan, respectively. Included species: *M. mendesi*, *Myrsidea* sp. from *Lamprotornis caudatus*, *Lamprotornis purputoptera aenocephalus*.

(57) ***bubalonrithis* morphotype** (Figs. 541–543): similar to those of *quadrifasciata* morphotype (see below), but conspicuously larger. The distal arm is apparently not developed. The lateral arm is conspicuously enlarged and distally outwardly curved. The apical part of the lateral arm continues to a pronounced distally tapered ventral arm. Similar to *quadrifasciata*, the shape of the distal part of the lateral arm is variable (from thin hook-like curved processes to thick serrated structures). This variability is most likely caused by a distortion of these structures as it may differ between sides in slide-mounted specimens; sometimes, both sides may overlap (Fig. 543). The outline of the plate of the sclerite is rounded.

The genital sclerite of this morphotype is present in only one species, *M. bubalornithis*, from *Bubalornis albirostris* (Ploceidae) from the Afrotropics.

(58) ***quadrifasciata* morphotype** (Figs. 544–558): unique, relatively small sclerite. The outline of the plate of the sclerite is usually not visible. If visible, then it is short and rounded with a central darker plate/process and 2 sublateral pale areas (Figs. 548, 553, and 556). The medio-distal margin is slightly concave. The distal arm is apparently not developed. Lateral arms following the posterolateral margin of the plate, bent at an acute angle, elongated beyond the tip of sclerite, and conspicuously enlarged with an outwardly curved end. The apical part of the lateral arm continues to a pronounced distally tapered process—ventral arm (sensu Clay 1968). There is variability in the shape of the distal part of the lateral arms, which range from thin hook-like curved processes (Figs. 545, 553, and 558) to thick serrated-like structures (Figs. 552 and 555). This variability is most likely caused in part by the distortion of these tiny structures, given that different sides of the same specimens may be different (Fig. 548).

This morphotype is identical to the *quadrifasciata* species group defined by Sychra et al. (2021) and includes *M. quadrifasciata* with 8 subspecies parasitizing 35 bird species from 8 families—Calcariidae, Emberizidae, Fringillidae, Icteridae, Passeridae, Ploceidae, Thraupidae, and Viduidae with an almost cosmopolitan distribution. Included (sub)species: *M. q. quadrifasciata* and *M. q. serini* from the Palearctic and Indomalaya but introduced with their hosts to the Nearctic (USA, Hawaii) and Australasia (New Zealand); *M. q. queleae*, *M. q. textoris*, and *M. q. viduae* from the Afrotropics; *M. anoxanthi*, *M. q. argentina*, and *M. q. darwini* from the Nearctic and Neotropics (see Sychra et al. 2021).

(59) ***thoracica* morphotype group**: It represents one of the most common types of genital sclerite in *Myrsidea*—an elongated sclerite with a broad, flattened triangular plate with distal tapering (Figs. 559–632). Genital sclerite morphology is as follows:

I. The general shape of the sclerite. Described by multiple independent authors (for example, Clay 1966, Price and Dalgleish 2006, 2007) as long, narrow, slender, elongate, slender

throughout the length, elongated triangular, or broadly triangular. The plate of the sclerite is pale or transparent—not sclerotized and its distal margin is often hardly visible and prone to distortion (see, for example, Figs. 608–610).

II. Presence of lateral arms. The terminal portion of the sclerite is usually divided into 2 by a lateral arm on either side (Clay 1966). These arms are described as: laterally projecting ventral arms (Clay 1966) or lateral subapical processes or projections (Price and Dalgleish 2007, Valim and Weckstein 2013). Posterior arms are apparently not developed.

III. The character of lateral arms. Lateral arms can be small, short (e.g., Fig. 606), slender (e.g., Fig. 611), or distinct, prominent, thin and long (e.g., Fig. 591). In mounted specimens, the arms are often found in a variety of positions, and therefore, it is not possible to assess their true size and shape (e.g., Figs. 608–610).

IV. Presence/absence of median sclerotization. This character is described as a median dark line (Clay 1966), dark median distal line, or darker medio-distal line (Price and Dalgleish 2007). This median sclerotization can be variable in its length, i.e., short (e.g., Figs. 626 and 627) to long (e.g., Figs. 582 and 583). Sometimes it is not apparent, but it is most likely due to distortion of the sclerite, or it is not developed (e.g., Figs. 570 and 572).

V. Character of the distal end. The distal section of the sclerite varies considerably in length in different species and tapers to a rounded, flattened, or bulbous end (Clay 1966). In *thoracica* morphotype, sclerite is tapered distally with a rounded tip (e.g., Fig. 626); blunt rounded distal tip (e.g., Fig. 568); with an elongated slender distal portion (e.g., Fig. 604); sclerite with a straight or slightly convex distal margin (e.g., Fig. 611); swollen distally (e.g., Fig. 619). In mounted specimens, the distal section of the sclerite can be easily distorted, which may obscure its true shape. Therefore, the tip of the male genital sac sclerite must be used for specific determination only very carefully. For example, Price and Dalgleish (2006), presented a figure of the sclerite for *M. laciniaesternata* and *M. suttoni* with a concave distal margin (Figs. 3 and 7 in Price and Dalgleish 2006) and *M. icterocephalae* with a rounded tip (Fig. 11 in Price and Dalgleish 2006). But they subsequently described sclerites of *M. bonariensis* and *M. suttoni* as similar to those in "Fig. 3 or Fig. 11" and "Fig. 7 or Fig. 11," respectively. As such, it can be interpreted that different specimens of particular species may appear to have a different shape of sclerite, i.e., with both concave distal margin and rounded tip (Fig. 610 vs. Fig. 611, or Fig. 617 vs. Fig. 618).

This morphotype is largely identical to the *thoracica* species group defined by Clay (1966), who included 19 species parasitized on birds from the family Turdidae. It is present in 48 species of *Myrsidea* parasitizing birds from 10 passerine families: Cardinalidae (4 species), Fringillidae (1), Malaconotidae (1), Parulidae (1), Passerellidae (2), Thraupidae (2), Tityridae (1), Troglodytidae (2), Turdidae (20), Tyrannidae (7). Other yet undetermined *Myrsidea* have been found on 5 turdid hosts: *Neocossyphus poensis* from Africa, *Hylocichla mustelina*, *Turdus aurantius*, and *Turdus jamaicensis* from the Nearctics; and *Turdus albicollis* from Neotropics. *Myrsidea* species with this sclerite morphotype occur all around the world (e.g., *M. thoracica* was introduced with *T. merula* to New Zealand). Included species: *M. abidae*, *M. aitkeni*, *M. antiqua*, *M. assimilis*, *M. bensoni*, *M. bidentata*, *M. bonariensis*, *M. brasiliensis*, *M. carrikeri*, *M. cayanae*, *M. cicchinoi*, *M. cnemotriccola*, *M. cruickshanki*, *M. danielalfonsoi*, *M. destructor*, *M. devastator*, *M. elaeniae*, *M. elegans*, *M. emersoni*, *M. eslamii*, *M. faccioae*, *M. fasciata*, *M. flaviventris*, *M. fuscicaudae*, *M. icterocephalae*, *M. incerta*, *M. indigenella*, *M. keniensis*, *M. larvatae*, *M. lightae*, *M. markhafneri*, *M. melancholici*, *M. montana*, *M. obsoleti*, *M. ophthalmici*, *M. pachyramphi*, *M. pittendrighi*, *M. pricei*, *M. quinchoi*, *M. regius*, *M. rubica*, *M. saviti*, *M. similis*, *M. sinaloae*, *M. spadicei*, *M. thoracica*, *M. tchagrae*, *M. valimi*, *Myrsidea* sp. from *Hylocichla mustelina*, *Neocossyphus poensis*, *Turdus aurantius*, *Turdus albicollis*, *Turdus jamaicensis*.

(60)***fallax* morphotype group**. Sclerite is similar to those of *thoracica* morphotype. Lateral arms are long and curved (e.g., Figs. 636–640). The median sclerotization is long.

The genital sclerite of this morphotype is present in 8 species, parasitizing 8 bird species from the family Corvidae from Neotropics. *Myrsidea barbati* from *Myiobius barbatus* (Tityridae) (Fig. 634) and *M. cacioppoi* from *Lanio fulvus* (Thraupidae) (Fig. 633) share the same or very similar sclerite, so we tentatively placed them in this morphotype group. More research is necessary to confirm the relationship of these species. Included species: *M. barbati*, *M. cacioppoi*, *M. chiapensis*, *M. cristatelli*, *M. daleclaytoni*, *M. fallax*, *M. lindolphoi*, *M. melanocyanei*, *M. moriona*, *M. pseudofallax*.

(61)***simplex* morphotype group**. Sclerite is generally similar to those of *thoracica* morphotype. Lateral arms are large aliform (Figs. 642–656). The median sclerotization is often not apparent (Figs. 653–656). The distal end of sclerite usually has a concave posterior margin, apparently enlarged and glossy bilobed (e.g., Figs. 649 and 654).

The genital sclerite of this morphotype is present in 5 species, parasitizing 8 bird species from the family Turdidae from the Neotropics. Two other undetermined *Myrsidea* were found on *Turdus aurantius* from Jamaica and *Turdus flavipes* from Trinidad. Included species: *M. rohi*, *M. simplex*, *M. tapanti*, *M. tapetapersi*, *M. varia*, *Myrsidea* sp. from *Turdus aurantius*, *Turdus flavipes*.

(62)***fusca* morphotype group** (Figs. 657–688). Sclerite is generally similar to those of *thoracica* morphotype. Lateral arms can be small, short (e.g., Figs. 666 and 677), slender (e.g., Fig. 675), or distinct, prominent (e.g., Fig. 673). The median sclerotization is usually well-visible and variable: from short and broad (e.g., Figs. 658–661) to slender and long (e.g., Fig. 665). The distal end of sclerite with a concave margin—with slight median indentation distally (slightly indented apex, e.g., Fig. 667); notched distally (e.g., Fig. 686); apparently enlarged and glossy bilobed tip (e.g., Figs. 680 and 681); with a parallel-sided terminally truncated distal portion (e.g., Fig. 673); incised distally (e.g., Fig. 668); distally bifurcate (e.g., Fig. 685); with pronounced distal asymmetry (e.g., Figs. 688 and 689).

The sclerite of this morphotype is present in 41 species of *Myrsidea* parasitizing birds from 12 passerine families: Cardinalidae (2 species), Fringillidae (4), Mimidae (1), Parulidae (5), Passerellidae (5), Pellorneidae (1), Sylviidae (1), Thamnophilidae (3), Thraupidae (11), Tityridae (2), Troglodytidae (4), Tyrannidae (2). Included species: *M. alexanderi*, *M. annae*, *M. basileuteri*, *M. bessae*, *M. blattae*, *M. castroae*, *M. cinnamomei*, *M. conirostris*, *M. coronatae*, *M. cyanocephalae*, *M. dacostai*, *M. diglossae*, *M. fusca*, *M. habiae*, *M. iliacae*, *M. klickai*, *M. laciniaesternata*, *M. lathrotriccola*, *M. melanopis*, *M. myiobori*, *M. nesomimi borealis*, *M. nesomimi nesomimi*, *M. pagei*, *M. paleno*, *M. patersoni*, *M. quadrimaculata*, *M. ramphoceli*, *M. ridulosa*, *M. rodriguesae*, *M. roubalovae*, *M. rozsai*, *M. seminuda*, *M. spellmani*, *M. surinami*, *M. suttoni*, *M. sylviae*, *M. taciturni*, *M. vincesmithi*, *M. violaceae*, *M. whitemani*, *M. zeledoni*, *M. zonotriciae*.

(63)***franciscoloi* morphotype group** (Figs. 690–729). Sclerite is generally similar to those of *thoracica* morphotype. Lateral arms are

either not developed (e.g., Figs. 712, 718–727), or rather they are too thin to be apparent (e.g., Figs. 695–697, 703–709, 716, and 717, or Fig. 710 vs. Fig. 711). The median sclerotization is very variable from short (e.g., Figs. 717 and 718), broad (e.g., Figs. 713 and 720) to slender and very long (e.g., Figs. 711 and 712). Sometimes, it is not apparent, but it is most likely due to distortion of the sclerite, or it is not developed (e.g., Figs. 705 and 706). The distal section of sclerite is usually tapered—with distal narrow tapering (e.g., Fig. 722); with a rounded tip (e.g., Fig. 718); with a straight margin (e.g., Figs. 728 and 729); but sometimes also with slight apical indentation (slightly indented apex, e.g., Figs. 716, 717, 719, and 720).

The sclerite of this morphotype is present in 30 species of *Myrsidea* parasitizing birds from 9 passerine families: Cardinalidae (3 species), Cinclidae (1), Furnariidae (1), Passerellidae (4), Pipridae (5), Ptiliogonatidae (1), Thraupidae (8), Tyrannidae (5), and also hummingbirds: Trochilidae (2). Another yet undetermined *Myrsidea* has been found on *Motacilla aguimp* and *Motacilla alba* (Motacillidae). Included species: *M. andyolsoni*, *M. aurantiirostris*, *M. baileyae*, *M. brunneinuchi*, *M. campestris*, *M. capeki*, *M. citrinae*, *M. coerebicola*, *M. contopi*, *M. dalgleishi*, *M. dolejskae*, *M. edgarsmithi*, *M. franciscoloi*, *M. gularis*, *M. jenniferae*, *M. johnklickai*, *M. kristineae*, *M. leptopogoni*, *M. marini*, *M. oleaginei*, *M. olivacei*, *M. phoenicii*, *M. pitangi*, *M. poliogasteri*, *M. povedai*, *M. rekasii*, *M. rufi*, *M. sayacae*, *M. sychrai*, *M. tangarae*, *Myrsidea* sp. from *Amazilia tzacatl*, *Motacilla aguimp*, *Motacilla alba*.

Species *Incertae Sedis*

In the case of 5 species, genital sac sclerites were drawn, but we were not able to check them personally, preventing us from placing them in any of the designated morphotypes.

1. *Myrsidea castanonotae* from *Ptilorrhoa castanonota* (Cinclosomatidae) from New Guinea. The sclerite of this species (Fig. 361) has an elongated and rounded distal part. The distal arm has a less sclerotized medio-distal part with proximal ends forming a simple lateral hook-like (apparently not toothed) projection. Lateral arms are either not present or only short and thin. The outline of the plate of the sclerite is not present in the drawing by Hellenthal and Price (2005).
2. *Myrsidea chesseri* from *Criniger barbatus* (Pycnonotidae) from Ghana. The sclerite of this species (Fig. 537) is generally similar to members of the *anaspila* morphotype or to those that we found in several *Myrsidea* from estrildid and sturnid hosts (Figs. 527–535).
3. *Myrsidea leucostictae* from *Ptilorrhoa leucosticte* (Cinclosomatidae) from New Guinea. The sclerite of this species (Fig. 362) seems to be asymmetrical, long, and narrow, with a concave distal margin and several lateral processes that are hard to homologize with distal and lateral arms of sclerites of other morphotypes. The outline of the plate of the sclerite is not present in the drawing by Price and Johnson (2006b).
4. *Myrsidea palmeri* from *Eurillas curvirostris* (Pycnonotidae) from Ghana (Fig. 536). The sclerite of this species is very similar to sclerites, as we found in several *Myrsidea* from estrildid and sturnid hosts (Figs. 527–535).
5. *Myrsidea willardi* from *Philepitta schlegeli* (Philepittidae) from Madagascar. The sclerite of this species (Fig. 360) is generally similar to members of the *anaspila* morphotype. The distal part is elongated and rounded. Distal arms leading up along the latero-distal margin are apparently not toothed proximally. Lateral arms are outwardly curved. The plate of the sclerite is not present in the drawing by Price and Johnson (2006b).

In the case of 3 other species, the genital sac sclerite is either strongly distorted—*M. neocinereae* (host family Tyrannidae) from the Neotropics or missing—on a single available male of *M. dukhunensis* (Motacillidae) from the Palearctic and on both available males of *M. cinerea* (Corcoracidae) from Australasia.

Due to the lack of access, we were unable to study male genital sac sclerites of the following species parasitizing birds from the following families and biogeographical regions/realms: **Palearctic**—*M. abhorrens* (Laniidae), *M. takayamai* (Campephagidae); **Afrotropics**—*M. guimaraesi* (Hirundinidae), and *M. mccrackeni* (Bernieridae) in Madagascar; **Indomalaya**—*M. insolita* (Corvidae), *M. peninsularis* (Dicruridae), and *M. takayamai* (Campephagidae); **Australasia**—*M. brevipes* (Paradisaeidae), *M. ptilorhynchi* (Ptilonorhynchidae); New Guinea and Melanesia bioregion—*M. albiceps* (Campephagidae); **Neotropics**—*M. luroris* (Hirundinidae), *M. stenodesma* (Tyrannidae), and *M. conspicua* (Fringillidae) in Hawaii.

Moreover, to our knowledge no known male specimens have been collected for the following 10 species: *M. proterva* (Muscicapidae) and *M. troglodyti* (Troglodytidae) from the Palearctic; *M. batesi* (Bernieridae) from Madagascar; *M. dukguni* (Timaliidae) and *M. insulsa* (Pittidae) from Indomalaya; *M. integra* (Paradisaeidae) from New Guinea and Melanesia bioregion; *M. seversoni* (Tyrannidae) from the Nearctic; *M. venustae* (Thraupidae), *M. imbricata* (Trochilidae), and *M. cayanensis* (Tyrannidae) from the Neotropics.

These species, therefore, cannot presently be placed in any morphotype group with confidence, and more collections and studies are necessary before they can be identified.

Based on the morphology of the male genital sac sclerite, we recognize 63 *Myrsidea* morphotype groups (morph. gr.), including 7 groups based on specimens of undescribed species. A total of 42 morph. gr. (67%, $n = 63$), including those based on undescribed species, are associated with a single host family. *Myrsidea* from 10 morph. gr. occur on hosts from 2 families (Supplementary Dataset S1). The remaining groups contain species of *Myrsidea* that were found on hosts from more than 2 different families and also from different biogeographic regions: *fallax* morph. gr. (from 3 host families), *pycnonoti* morph. gr., and *subdissimilis* morph. gr. (4), *anaspila* morph. gr., *ishizawai* morph. gr., and *singularis* morph.gr. (5), *chilchil* morph. gr. (6), *quadrifasciata* morph. gr. (8), *franciscoloi* morph. gr., and *thoracica* morph. gr. (10), and *fusca* morph. gr. (12). More research is necessary to resolve whether these morphotype groups are monophyletic or whether they, in fact, form separate species groups. This will also have a bearing on understanding the degree of host-switching of *Myrsidea* between distantly related hosts.

The highest numbers of *Myrsidea* from different morphotype groups were found infesting species in the following bird families: Leiothrichidae (10), Estrildidae (8), Corvidae (8), Sturnidae (7), Thraupidae (6), Icteridae, Ploceidae, Turdidae, Tityridae, and Tyrannidae (4), suggesting that there has been some level of host-switching among host families (Supplementary Figs. 2 and 3).

The highest diversity of morphotype groups was found in Indomalaya, where *Myrsidea* belonging to 37 (58%, $n = 63$) morphotype groups occur. A total of 39 (62%) morphotype groups occur in only one biogeographic region. On the other hand, 3 morphotype groups, *rustica*, *thoracica*, and *quadrifasciata*, have cosmopolitan distributions with occurrence in 6 regions (Supplementary Dataset S1; Supplementary Figs. 2 and 3).

In summary, the main goal of this study was to organize *Myrsidea* into broad groups that considered the diversity of the genus. While many morphotype groups currently include only a single species, given the diversity of this genus, it is likely that future species will be

discovered that would belong to what are currently smaller groups. An important issue to resolve concerns the status of the *thoracica* morphotype and other similar groups which are not monophyletic in the phylogenetic tree based on DNA sequence data (Fig. 730). One possibility could be that this morphotype group is a result of a retained ancestral (plesiomorphic) genital sac sclerite. However, a more strongly supported phylogenetic tree will provide definitive conclusions on the status of this group.

Different Values of Morphological Traits

We believe that not all morphological characteristics given above have the same value for species delimitation and assignment to morphotype groups. Some characteristics are highly variable within a single species. These considerations should form the basis for constructing diagnostic keys. Below, we divide morphological features into (A) primary, (B) secondary, (C) dimensions, and (D) eggs, which could be included as aspects of species descriptions or diagnostic keys.

A. Eleven primary characteristics have a higher value for species diagnosis and could also be useful for creating keys:

1. A degree of hypopharynx reduction (reduced, weak, strong).
2. Number of long posterior setae on the pronotum (normally 6 or 8).
3. Shape of metanotum (normal, enlarged).
4. Shape of tergites (straight, enlarged: concave, U-shaped, V-shaped, etc.).
5. Presence or absence of typical aster.
6. Presence or absence of setae on sternite I.
7. Shape of sternite II and presence (described as "notched") or absence of the depression on its anterior margin.
8. Presence or absence of median gap in the row of setae on all tergites.
9. Presence or absence of anterior setae on pleurites, tergites, and sternites.
10. Vulval margin in females (serrated, smooth).
11. Type of genital sac sclerite in males (GS).

B. Eighteen secondary characteristics have a lower value for diagnosis, but in some cases, they may be as useful as the primary characteristics above:

Head

1. Number of latero-ventral fringe setae (*lvfs*).
2. Size of labial seta 5 (*ls5*).
3. Size and ratio of head setae 10 (*dhs10*) and 11 (*dhs11*).
4. Number of gular setae (Gu/Gula).

Body

5. Shape of mesonotum (ME).
6. Shape of metanotum (MT) with its number of setae (except most posterolateral ones).
7. Shape of metasternum (MS) with its number of setae.
8. Number of setae on metapleurite (MP) and pleurite I–VIII (PI–PVIII).
9. Number of setae on tergite I–IX (TI–TIX).
10. Lengths of postspiracular setae on tergites I–VIII (*pssps1–pssps8*).
11. Number of setae on sternite I–VII and VIII + IX (SI–SIX).
12. Number and size of setae on aster (*a1*, *a2*, *a3*, etc.).
13. Size of inner and outer small posterior setae on tergite IX (*ipsIX*, *opsIX*).
14. Size of inner and outer posterior setae on pleurite VIII.
15. Shape of vulval margin (serrated, smooth) and the number of vulval setae (*vms*).
16. Number of dorsal and ventral setae on the anal fridge in females (*afd*, *afv*).

Legs

17. Outer dorsolateral and ventrolateral setae on the first tibia (*dts*, *vts*).
18. Number of setae in femoral brush (*fbs*).

C. Dimensions (Fig. 731) are here considered separate from discrete characteristics due to their often higher levels of variation and possible phenotypic plasticity. Clay (1966) indicates dimensions as potentially assisting in species determination beyond discrete characters. Also, some authors pointed out that Harrison's rule (Harrison 1915, Price et al. 2003, Harnos et al. 2017) may come into play, in which the size of a louse may correlate with the size of its host. Additionally, dimensions can also be slightly modified during the slide mounting process. In total, there are 13 useful dimensional characteristics for *Myrsidea* (Fig. 731):

1. Head length (along midline; HL).
2. Preocular width (at the level of alveoli of *dhs 11*; POW).
3. Head temple width (at the widest part, i.e., at the level of alveoli of *dhs 31*; TW).
4. Head length:width ratio (HLWR).
5. Prothorax width (PW).
6. Metanotum width (MW).
7. Abdomen width (measured on tergite IV; AWIV).
8. Anus width (in females; ANW).
9. Genital apparatus width (in males; GW).
10. Genital apparatus length (in males, GL).
11. Genital sclerite length (in males, GSL; only for species with a well-developed plate of sclerite and for well-prepared specimens).
12. Total length (along midline; TL).
13. Total length:width ratio (TLWR).

D. Louse eggs consist of 2 main external parts—the operculum and amphora and are glued to the feather with spumaline (Abrahamovich and Cicchino 1985, Valim and Cicchino 2015b). The general morphology of the louse egg was investigated by Abrahamovich and Cicchino (1985) based on the species *Vernoniella bergi* Kellogg, 1906 and *Osborniella guiraensis* Kellogg, 1906. Valim and Cicchino (2015b) described and illustrated the external chorionic architecture of the eggs for 6 *Myrsidea* species from corvid hosts (*M. picae*, *M. cornicis*, *M. isostoma*, *M. interrupta*, *M. fallax*, and *M. moriona*), with additional drawings of eggs and partial descriptions of 3 other passerine *Myrsidea*—*M. elegans*, *M. seminuda*, *M. psittaci* (Figs. 64–90 in Valim and Cicchino 2015b). Additionally, Cicchino and Valim (2015) demonstrated the value of using egg morphology for the taxonomic descriptions of *Myrsidea*. They compared and described the external chorionic egg architecture of the eggs from *M. serini* and *M. psittaci*. They found that although these 2 *Myrsidea* species occur on the same host individuals, they are readily distinguished by their egg morphology (Figs. 10–17 in Cicchino and Valim 2015).

Although these authors demonstrated the usefulness of eggs in *Myrsidea* taxonomy, the description methods were not fully consistent (Table 1 in Valim and Cicchino 2015b vs. Table 2 in Cicchino and Valim 2015), and some of the morphological traits and terminology were not explained sufficiently (e.g., opercular callus). Thus, a study that focuses more deeply on the morphology of *Myrsidea*

eggs (including additional illustrations), the nomenclature used, and larger taxonomic sample size is needed to further characterize the variation in traits that would be valuable for inclusion in taxonomic descriptions.

In conclusion, the increasing number of new species in the genus *Myrsidea* brings additional challenges to traditional (morphologically based) taxonomy, making complete revisions and identification keys for all *Myrsidea* species more difficult due to the robust amount of data required for the species comparisons. Some of the more complex revisions were partially made for the following host families: Cardinalidae, Emberizidae, and Thraupidae (Price and Dalgleish 2006, 2007, Price et al. 2008a), Corvidae (e.g., Klockenhoff 1974a, 1975), Estrildidae (Clay 1970c), Icteridae (Clay 1968), Parulidae (Kounek et al. 2011b), Pipridae (Dalgleish and Price 2003a), Ploceidae (Klockenhoff 1982, 1984a), Pycnonotidae (Hellenthal and Price 2003, Johnson and Price 2006), Thamnophilidae (Price et al. 2008b), Timaliidae *s. lat*. (Tandan and Clay 1971, Tandan 1972, Price et al. 2006), Troglodytidae (Price et al. 2008c), Turdidae (Clay 1966, Kounek et al. 2013), and Tyrannidae (Price et al. 2005).

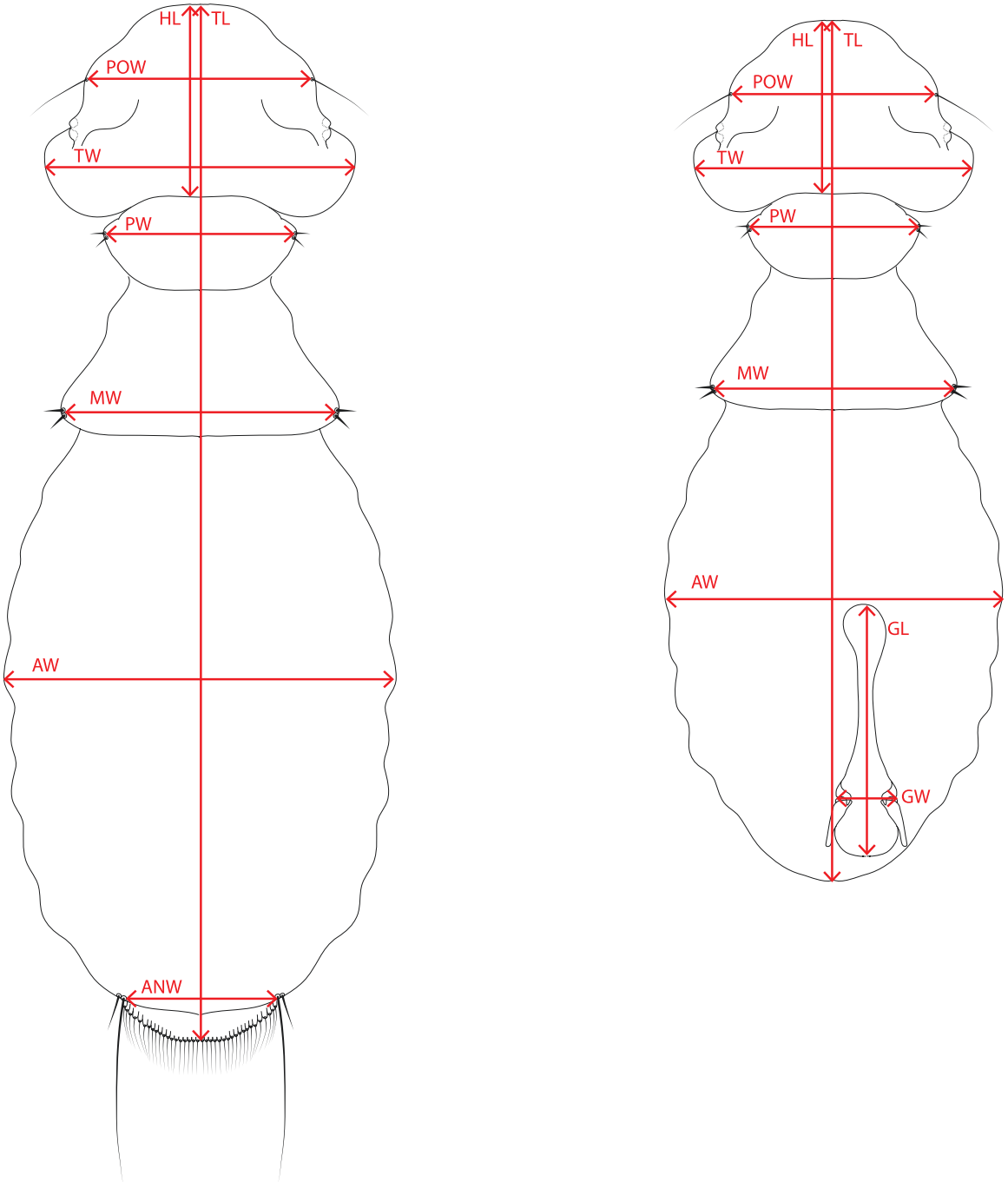


Fig. 731. Visualization of dimensional characteristics for *Myrsidea* (female left, male right): Head length (HL), Preocular width (POW), Head temple width (TW) Prothorax width (PW), Metanotum width (MW), Abdomen width (AW), Anus width (ANW), Genital apparatus width (in males; GW), Genital apparatus length (GL), Genital sclerite length (GL), Total length (TL).

However, there have been many advances in the taxonomy of the Passeriformes, which can be assessed by comparing, e.g., Clements (2000) and Gill et al. (2022). During the last 2 decades, bird species, genera, and even families have been split, lumped, or reclassified extensively (Boyd 2010). One example is the rearrangement of birds within the so-called nine-primaried oscines clade (Klicka et al. 2000, Ericson and Johansson 2003, Barker et al. 2004), which were considered the Fringillidae according to Sibley and Monroe (1990). As such, it is also important to know when analyzing older publications that the same host species might be named differently (e.g., belonging to different genera) across various publications. Interpreting overall ecological and evolutionary patterns in the host distribution of lice relies on having a classification of birds that reflects their phylogeny.

In studies of louse taxonomy, many authors have integrated data from DNA sequencing to supplement information from morphology (e.g., Johnson and Price 2006, Price and Johnson 2006a, b, 2009, Price et al. 2008a, 2008b, 2008c, Valim et al. 2011, Valim and Weckstein 2013, Kolencik et al. 2017, 2018, 2021, 2022a). Moreover, many species in this genus are included in more general studies of the phylogenetic relationships of genera inside Phthiraptera (Cruickshank et al. 2001, Johnson et al. 2003), population genetics (Štefka et al. 2011), or coevolution between chewing lice and their hosts (Balakrishnan and Sorenson 2007, Bueter et al. 2009). The main challenges in traditional taxonomy are the time-consuming work that involves searching through previously published morphological data and the crucial requirement of skilled taxonomists for morphological trait analysis and species identification.

Phylogenetics

Summary of Published Data

Several phylogenetic studies involving *Myrsidea* have been conducted over the last 2 decades (Johnson and Price 2006, Price and Johnson 2006a, b, 2009, Price et al. 2008a, Bueter et al. 2009, Valim et al. 2011, Valim and Weckstein 2013, Kolencik et al. 2017, 2018, 2021, 2022a, Gajdošová et al. 2020, Madrid et al. 2020, Sweet et al. 2021). However, only a few gene fragments have been examined for *Myrsidea*, including cytochrome oxidase subunit I (COI; e.g., Valim et al. 2011, Valim and Weckstein 2013, Kolencik et al. 2017, 2018, 2021, 2022a, Madrid et al. 2020), elongation factor 1-alpha (EF-1a; e.g., Kolencik et al. 2022a), wingless (Wg; Gajdošová et al. 2020), and 18s rDNA (Yoshizawa and Johnson 2003, Gajdošová et al. 2020). Most studies used either a single locus or a combination of a few loci. The majority of these trees have more highly supported terminal nodes and weakly supported basal nodes, suggesting that genomic-level data are necessary to reconstruct highly supported basal nodes (Allen et al. 2017, Johnson et al. 2018).

The most abundant gene sequenced for *Myrsidea* found on the Nucleotide database from GenBank (NCBI; data from 1st August 2022) is a 379 base pair (bp) fragment of the mitochondrial gene cytochrome oxidase subunit I (COI), which is the most commonly used barcode gene in louse studies (e.g., Johnson et al. 2002, Bush et al. 2016). There are 498 published COI sequences, including species previously known as *Ramphasticola* (Kolencik et al. 2022a) and excluding *Apomyrsidea* (Kolencik et al. 2021) species, plus 3 new sequences of *Myrsidea* from hummingbirds (Supplementary Table 1). Kolencik et al. (2017) proposed 12% uncorrected and above as sequence divergence in COI that is sufficient to delimit species in *Myrsidea*. This locus exhibits a high level of overall divergence between species (overall mean *p*-distance of 498 sequences = 21%). A second sequenced locus from COI is a longer fragment of the gene (COI-L; ~671 bp). COI-L is represented in GenBank either as unique or combined with the smaller COI fragment for a total of 228 available COI-L *Myrsidea* sequences.

The second most common gene sequence for *Myrsidea* species is a fragment of the nuclear gene EF-1a (~349 bp), with 243 *Myrsidea* sequences in GenBank (NCBI). EF-1a generally exhibits lower divergence between species (overall mean uncorrected *p*-distance of 243 sequences = 5%). There are only a few sequenced *Myrsidea* for a ~385 bp fragment of Wg (37 GenBank sequences; overall uncorrected mean *p*-distance = 6%), a fragment of 18S rDNA ($n = 18$; mean uncorrected *p*-distance = 1%), 15 sequences of variable microsatellite loci (Martinů et al. 2015), and one sequence for each 12s and 16s ribosomal rDNA loci.

Phylogenetic Reconstruction

In this review, we focus on an analysis of the 379 bp fragment of COI, which, to date, is the most commonly used locus in phylogenetic studies of *Myrsidea*. Here, we present a phylogenetic reconstruction of all unique (excluding duplicates) *Myrsidea* COI sequences from GenBank ($n = 320$; Fig. 730A–D). An additional 5 specimens were used as outgroups. As expected, due to the use of only one fragment of one gene, the backbone of the tree is poorly supported. Our analysis does not fully resolve the uncertainty in relationships between the different clades of *Myrsidea*, but we believe that this could serve as a starting point for the inclusion of whole genomic data in future studies. The following caution in the interpretation of our phylogenetic analysis needs to be taken into consideration, as many clades remain still poorly supported (UF bootstraps values <90%). The phylogeny presented here serves the purpose of visualization of available data and the differences, which may appear when using larger sampling, and/or to show possible future directions. As some of the most common problems in science are lack of resources and lack of time, these data could be used to help prioritize future specimen choices for whole genome sequencing.

As part of our process, we assessed the validity of these sequences and indicated any potential issues. For example, in one case, a terminal taxon is labeled as *M. extranea* but is found in a separate clade from all other *M. extranea* specimens. This specimen appears to be closest to *M. witti* with only a 0.53% difference, suggesting a possible misidentification of this specimen. We highlighted these kinds of cases across our phylogenetic tree with "=>" and added their expected species names next to the original names (Fig. 730A–D). We highlight 6 specimens that most likely represent stragglers or even contaminations where a louse from another host is accidentally transferred to a new host during collection (Palma and Peck 2013). Alternatively, they could be real biological events where a louse is colonizing a novel host (see Sychra et al. 2014b for the explanation of the occurrence of *Myrsidea* sp. from *Troglodytes aedon*).

The structure of our phylogenetic tree has similarities in the terminal nodes with the most recently published phylogenetic study of *Myrsidea* (Kolencik et al. 2022a). Not surprisingly, our tree differs in the weakly supported basal rearrangements, but it confirmed the separation of species from the recently erected genus *Apomyrsidea* (Kolencik et al. 2021). This further suggests *Apomyrsidea* is sister to, and thus, the closest relative of *Myrsidea* (UFboot = 97; Fig. 730D).

Host-Switching Events

recently reported a case of incomplete host-switching (sensu Clayton et al. 2015) for *Myrsidea claytoni* between 2 unrelated hosts. *Myrsidea claytoni* was first described based on specimens collected from 2 bulbuls (Pycnonotidae), *Pycnonotus eutilotus* from Sarawak and *Pycnonotus sinensis* from Hong Kong (Hellenthal and Price 2003). Sychra et al. (2014c) collected *M. claytoni* from

32 Black-and-Red Broadbills—*Cymbirhynchus macrorhynchos* (Eurylaimidae) in Vietnam. Interestingly, Sychra et al. (2014c) explained that although *P. eutilotus* does not occur in Vietnam, in most of its geographical distribution, it is sympatric with *C. macrorhynchos*, and all 3 bird species share similar habitats, possibly providing opportunities for ongoing dispersal of parasites between sympatric hosts in different families. Furthermore, Weckstein (2004), in a study of cophylogenetic history among toucans and their chewing lice, suggested that incomplete host-switching or ongoing dispersal between unrelated hosts may have been possible in locations where birds with similar behavior and ecology coexist (Johnson et al. 2011, Gustafsson and Olsson 2012, Gustafsson et al. 2019).

Host-shifts may have also led to the complete host-switching of *Myrsidea*. This is the case between migratory birds and tropical resident birds, as reported by Kolencik et al. (2022a), where lice parasitizing the Neotropical migrant *Catharus* thrushes were closely related to *Myrsidea* species from distantly related, nonmigratory hosts of the families Tityridae (tityras) and Parulidae (wood warblers) (Jetz et al. 2012, Kolencik et al. 2022a). In this case, the parasites likely shifted to new host lineages and then underwent divergence. Interestingly, our broader sampling confirms these findings (Fig. 730C and D) and, additionally, this clade includes birds from other host families—Mimidae (catbirds), Troglodytidae (wrens), Tyrannidae (tyrant flycatchers), and even Trochilidae (hummingbirds, Apodiformes). Similarly to Kolencik et al. (2022a), we found 2 clades of *Myrsidea* species from thrushes and other birds (Fig. 730C and D). Our results further confirm the statement from Kolencik et al. (2022a) that at a macroevolutionary scale, there have likely been multiple host-switching events between both migratory thrushes and tropical residents and tropical resident thrushes and other tropical resident birds. The main question remains whether the inclusion of whole genomic data will continue to support the basal relationships reconstructed only with partial DNA sequence data.

Although most *Myrsidea* species parasitize passerine birds (order Passeriformes), the genus was originally described based on specimens from piciform hosts, and several other species of *Myrsidea* have subsequently been described from nonpasseriform hosts from the orders Apodiformes and Piciformes (Supplementary Dataset S1). Similarly, as reported by Kolencik et al. (2022a), we found a few separate lineages of nonpasserine lice across our phylogenetic tree. Kolencik et al. (2022a) found toucan lice (Piciformes: Ramphastidae) in 2 separate nonsister clades, whereas our analysis lumped them together into one large clade consisting of lice exclusively parasitizing hosts in the family Ramphastidae (UFboot = 98; Fig. 730C). Thus, here we suggest that lice from toucans (*Ramphastos*) are the sister group to those parasitizing araçaris (*Pteroglossus*). More distantly from this clade, we recovered a clade consisting of 2 *Myrsidea* specimens from piciform hosts, one from a host in the family Picidae and the other from a host in the family Lybiidae. Lastly, another well-separated clade including nonpasserine louse *Myrsidea* sp. from *Tricholaema leucomelas* (Lybiidae) was previously reported by Kolencik et al. (2022a) as sister to *Myrsidea pagei* from the tanager *Ramphocelus dimidiatus* (Thraupidae), but it is sister to lice parasitizing birds from the families Bernieridae and Pycnonotidae (parvorder Sylviida) in the analysis from this study (Fig. 730B).

Several factors might explain these differences between Kolencik et al. (2022a) and the present study, including different methodologies applied to a more taxon-rich dataset here (330 vs. 152 taxa) but based on fewer gene fragments (1 vs. 3) and only partially overlapping taxon samples. However, more importantly, both studies generally agree that there appear to be some major host-switching events between different orders of birds as well (Kolencik et al. 2022a; present study).

For instance, our present phylogenetic reconstruction includes 3 new sequences of *Myrsidea* from hummingbirds (Apodiformes) from Peru. To date, these are the only published genetic data for *Myrsidea* from hummingbird hosts, which have been rarely collected in the field (Oniki-Willis et al. 2023); further morphological analyses and more specimens are necessary to confirm their identities and to describe these species. However, these 3 specimens from hummingbirds were placed in 2 different clades in our phylogeny (marked with hummingbird outlines in Fig. 730B and C). Two specimens of *Myrsidea* sp., from *Eutoxeres condamini* and *Doryfera ludovicae*, are nested inside of a well-supported clade consisting of *Myrsidea* from the host family Tyrannidae (Tyrannida, UFboot = 100, Fig. 730B). Another hummingbird *Myrsidea* sp. from *Ocreatus underwoodii* was placed in another well-supported clade together with 2 *Myrsidea* from the host family Parulidae (Passerida, UFboot = 100, Fig. 730C). This pattern is consistent with transfer between different host orders and has been found for other groups of bird lice (Johnson et al. 2001, Catanach and Johnson 2015, Bush et al. 2016, Kolencik et al. 2022b).

Myrsidea Species Limits

Understanding the interspecific limits is one of the most complicated and difficult aspects of louse biology and plays a key role in understanding this megadiverse genus. In particular, understanding how the value of the intra- and interspecific sequence divergences has an impact on the estimate of operational taxonomic units (OTUs). OTUs are groups of closely related individuals and are often used in studies to cluster species by their similarity (e.g., Bush et al. 2016, Kolencik et al. 2022a). For example, Kolencik et al. (2022a) combined interspecific limits made by Kolencik et al. (2017) based on a 379-bp fragment of COI as a molecular delimitation of OTUs using *mothur* (Schloss et al. 2009). Kolencik et al. (2017) reviewed 15 previously published molecular studies of *Myrsidea* and found that the interspecific variation in COI ranged from 10.7% to 34.3% for diagnosable morphospecies. Meanwhile, intraspecific differences ranged from 0% to 11.4%. From the data available, Kolencik et al. (2017) proposed 12% uncorrected divergence as a reliable limit for species delimitation in *Myrsidea*. It appears that a unique approach for each genus might be necessary as, e.g., Bush et al. (2016) assessed COI with only a 5% cutoff value for *Brueelia*.

However, it is unlikely that all species are evolving at the same rate, and therefore, including both morphological and host-association data will likely be important for validating these molecular estimates of differentiation. Kolencik et al. (2022a) tested the validity of this method (12% cutoff in *mothur*) by comparing these results with the results from a bGMYC analysis (Reid and Carstens 2012), which uses a conspecific probability threshold value to calculate the number of OTUs. In general, Kolencik et al. (2022a) found that a 12% cutoff from the *mothur* analysis, which calculated 83 OTUs, differed a little from the bGMYC analysis, which estimated 98 OTUs. bGMYC examines the tree topology and branch lengths to determine population level to species level processes and identifies OTUs, while *mothur* assigned sequences to the OTUs based on the defined cutoff value—in our case, a 12% value estimated by Kolencik et al. (2017). This process could be useful in finding potential new subspecies or cryptic species, which might be diagnosable with detailed morphological analysis (Kolencik et al. 2022a: Fig. 1, Table S1).

Although *Myrsidea* is known to be highly host-specific (e.g., Price et al. 2003, Valim and Weckstein 2013; present study), at a finer

taxonomic scale, there are cases where the same *Myrsidea* species is found on more than one host species or alternatively, multiple louse species are found on the same avian host species. For example, 4 individuals of *M. lightae*, identified on the basis of morphology, parasitize 3 different saltator host species (*Saltator atriceps*, *S. coerulescens*, *S. maximus*; Fig. 730B, bottom). However, specimens from *S. atriceps* and *S. coerulescens* are sufficiently divergent in COI that they were identified as separate OTUs by Kolencik et al. (2022a). We expect a similar scenario for the specimen from *S. maximus*. One possibility is that one can account for both host and geographic distribution data as limited support for molecular divergence to help define the upper limits of intraspecific variation. For example, *Myrsidea lightae* shows a higher genetic distance corresponding with geographic distance. In this case, the uncorrected *p*-distance between specimens collected in Honduras (GenBank A/N KY113134) and Panama (EU289211) is 8.2%, and the *p*-distance between those collected in Panama and Paraguay (KY113135) is 11.1%, and between those collected in Honduras and Paraguay is 11.4%. However, these specimens exhibit only minimal morphological differences (Kolencik et al. 2017, 2022a). The *M. lightae* sample from Nicaragua (MZ574042) falls well into this pattern, where compared with the sample from Honduras, *p*-distance is 7.1%, with Panama is 9%, and with Paraguay is 11.7%. Conclusively, by increasing the cutoff *p*-distance based on diagnosable morphology, we might underestimate the real, possibly cryptic, diversity. Herein, we agree with Kolencik et al. (2017) that a 12% cutoff is a reasonably conservative starting place for COI species delimitation, and *M. lightae* from Central and South America could be 2 subspecies on the cusp of interspecific divergence.

By contrast, the *Myrsidea* from Red-crowned Ant-Tanager (*Habia rubica*, Passerida) exhibit a different scenario with 2 different well-separated *Myrsidea* clades parasitizing this host taxon. One clade of *Myrsidea* from *Habia rubica* (Fig. 730C, bottom) consists of 2 specimens of *M. habiae* (from *Habia rubica*) collected from South America (Paraguay), and a second clade (Fig. 730B, bottom) includes 3 lice from different host individuals collected from Central America—*M. laciniesternata* (from *Habia* sp.) from Mexico, *Myrsidea* sp. (from *Habia fuscicauda*) from Panama and *Myrsidea* sp. (from *H. rubica*) from Nicaragua. Interestingly, *M. laciniesternata* and *M. habiae* are morphologically similar (see Price and Dalgleish 2006: Figs. 1–4, Kolencik et al. 2017: Fig. 2). However, the uncorrected *p*-distance between *M. habiae* COI sequences and all other *Myrsidea* species parasitizing the host *H. rubica* is well above the 12% cutoff, with *Myrsidea* species from *H. rubica* appearing to be significantly genetically distinct (Paraguay vs. Mexico—18.2%, Paraguay vs. Panama –19.2%, Paraguay vs. Nicaragua—19.8%).

Geographic distribution patterns can also be important for delimiting *Myrsidea* species found on toucan hosts. Interestingly, the bGMYC analysis calculated double the numbers of OTU for toucan lice in comparison with *mothur* (22 vs. 11) (Kolencik et al. 2022a). Based on general morphology, this is likely an overestimate. However, in some cases, these OTUs differ in their host species/subspecies or in the locality where they were collected (Kolencik et al. 2022a: Fig. 1, Table S1). For example, *M. dorothae* with 3 OTUs in *mothur*'s analysis differ in their hosts, and in only one case, they were collected from the same locality. Similarly, 5 of 6 OTUs identified by bGMYC from the single morphospecies *M. dorothae* were each collected from a different host species or subspecies (Kolencik et al. 2022a: Table S1). Kolencik et al. (2022a) also reported 3 additional *Myrsidea* species with multiple OTUs in bGMYC analysis—*M. lanei* (2 OTUs), *M ceciliae* (3), and *M. extranea* (3) (Kolencik et al. 2022a: Table S1). In the case of both *M. extranea* and *M. ceciliae*, 2 divergent OTUs were collected from different host taxa and from different regions (Central vs. South America; Kolencik et al. 2022a: Table S1). Interestingly, like in the case of *M. extranea*, this division could be associated with variability in the morphology of the male genital sclerite (Figs. 513–515).

There is also one case where both analyses failed to identify morphospecies as separate OTUs. In this case, *Myrsidea aenigma* and *Myrsidea mirabile* were not diagnosed by either molecular OTU analysis (Kolencik et al. 2022a: Table S1). The females of these louse species can be easily distinguished based on their morphological differences—e.g., the size of the metanotum, the shape of tergites I and II, and their chaetotaxy (Hellenthal et al. 2005: Figs. 2 and 3). However, our phylogenetic analysis put *M. aenigma* and *M. mirabile* into the same clade (Fig. 730C) with only minimal genetic distance between them (*p*-distance in COI = 2.64–2.9%). These parasites were collected from different hosts and localities. All 3 specimens of *M. aenigma* were collected from *Ramphastos tucanus tucanus* in eastern Amazonian Brazil (Belém and Portel, State of Pará), whereas a specimen of *M. mirabile* was collected from a different subspecies, *Ramphastos tucanus cuvieri*, in western Amazonian Brazil (Japurá, State of Amazonas). Thus, the host, geographic range, and morphological diagnosis, coupled with low genetic divergence, suggest that these taxa might be in the early stages of divergence. Genomic scale data will help to better characterize divergence among these close relatives to determine whether there is still ongoing gene flow between them.

Male Genital Sclerite Morphology as a Phylogenetic Tool

Clay (1966) suggested that male genital sclerites could be used to clarify the phylogenetic relationships among *Myrsidea* species. Fifty-seven years later, Kolencik et al. (2022a) used their phylogenetic reconstruction to assess the value of these characters in delimiting clades of *Myrsidea* from toucans (Kolencik et al. 2022a: Fig. 1). Their results vindicated Clay's suggestion that closely related *Myrsidea* species had the same type of male genital sclerites. Furthermore, in this study, we have erected new or validated the previously proposed species groups as morphotypes according to the type of male genital sclerite and, where possible, included labels with morphotype names in the figure of our phylogenetic reconstruction for comparison (Fig. 730). However, due to the use of only one fragment of one gene, which often results in low support values in the backbone of the tree, caution is needed when interpreting the phylogenetic reconstruction of morphotype groups in Fig. 730A–D. Genomic data are necessary to further resolve the relationships among morphotype groups and assess whether or not they are monophyletic. Still, we believe that these results shed more light on the importance of this morphological feature. In most cases, it appears that morphotype groups correspond well with clades in the molecular tree. The most speciose morphotype groups in both our morphological and genetic analysis are the *fusca* morph. gr. and *thoracica* morph. gr. However, members of these groups are found all across the tree and biogeographic regions.

The phylogenetic analysis presented here suggests that the *Myrsidea* species with the most common genital sclerite morphology (i.e., *franciscoloi*, *fusca*, *thoracica* morphotypes) do not form monophyletic groups and are likely to consist of many independent groups. Thus, this particular shape of the sclerite could be a plesiomorphic character and not a signal of phylogenetic structure. Similar cases can be found in other groups; for example, *M. johnsoni* here placed in the *plumosi* morphotype, probably represents a unique lineage separate from that of the *plumosi* species group. The *ishizawai*

morphotype is present in species from distant host families and geographic areas, and it is not monophyletic in our phylogenetic analysis. Thus, the similarity of sclerites in these groups can also be a result of convergence.

Interestingly, the most diverse biogeographic region with respect to genital sclerite-defined morphotype groups is Indomalaya with representatives of 37 (58%, $n = 63$) morphotype groups reported in our checklist data (Supplementary Dataset S1), followed by Australasia with 20 representatives, then the Neotropics with 19, the Afrotropics with 18, Palearctic with 12, and lastly, Nearctic with 10 representatives (Supplementary Fig. 3). Unfortunately, our phylogenetic data do not include equal sampling effort from all biogeographic regions as most of the specimens are either from the Neotropics or Afrotropics, with the Nearctic, Palearctic, and Indomalaya regions highly underrepresented, and with a lack of any molecular data from Australasia.

The Checklist

The most recent world checklist, which includes *Myrsidea* species, is The Chewing Lice World Checklist and Biological Overview published by Price et al. (2003). Over the last 20 years, there have been many new species described (Supplementary Dataset S1), and recent publications have changed some of the taxonomy and nomenclature of *Myrsidea* (Kolencik et al. 2021, 2022a, Sychra et al. 2021). Furthermore, after 2003, molecular methods have become more prevalent and sophisticated in taxonomic studies of lice; together with morphological descriptions, this has provided an important and necessary new tool for characterizing biological diversity in this group.

This study focuses on the review of *Myrsidea* and includes a checklist of taxa and host associations with a comprehensive dataset from all available publications to date. This *Myrsidea* checklist contains data from more than 250 publications, (Supplementary Dataset S1; included in References) with the oldest one from Linnaeus (1758) and the most recent from Bassini-Silva et al. (2023). We include data from previously published checklists: Harrison (1916), Ferris (1916), Hopkins and Clay (1952), Ledger (1980), and Price et al. (2003). In several cases, due to published errors, we have made changes in both bird and louse taxonomy, including the validity of some host-louse associations. The cases that were removed from our checklist are presented in the "Questionable_Myrsidea" tab of the Supplementary Dataset S1 with all explanations included.

The *Myrsidea* checklist (Supplementary Dataset S1) is divided into 3 parts. The first part is a list of all valid and described *Myrsidea* species and contains (i) the *Myrsidea* species name, (ii) the authors, (iii) the publications mentioning these species, (iv) their bird hosts (both species and subspecies), (v) the host breeding biogeographic regions; and (vi) the localities of occurrence from where *Myrsidea* species were reported.

The second part of the *Myrsidea* checklist focuses on *Myrsidea*, which has been mentioned in all previous publications without formal species descriptions. These were identified to the genus level and are written as "*Myrsidea* sp." ($n = 333$). We believe in the importance of these generic occurrence records for novel information and present these in hopes of demonstrating where additional taxonomic work is needed. For example, in most cases ($n = 269$; 81%), these unidentified *Myrsidea* reveal new louse-host associations.

The third part of the *Myrsidea* checklist includes all of the questionable cases of *Myrsidea* host associations, where further research is needed to assess their validity. Usually, these are cases where a *Myrsidea* was reported from an uncommon host and, thus, may have been a straggler or a contaminant. These are cases where a parasite species is found on a host that it does not normally parasitize due either to natural host-switching (straggling) or a human-induced mistake (contamination). Contamination is known to happen when collectors use the same bags for the collection of different host specimens or during the manipulation of birds (Palma and Peck 2013). We are hopeful that more data in the future could clarify these records.

We report a total of 382 known and recognized *Myrsidea* species described to date (390 taxa, including subspecies; Supplementary Dataset S1). When taking into account the recent synonymy of species into the *Myrsidea quadrifasciata* complex, this means almost 100% growth in the last 2 decades (as corrected $n = 197$ in Price et al. 2003), and a mean number of new species descriptions of over 9 new species every year. Of the known *Myrsidea* species ($n = 382$), 366 species can be found on a total of 488 passeriform host species from 57 families. The 16 remaining species of *Myrsidea* parasitize nonpasserine birds from 2 additional families—13 *Myrsidea* species from 13 host species in the family Ramphastidae (toucans, order Piciformes) and 3 species of *Myrsidea* from hosts in the family Trochilidae (hummingbirds, order Apodiformes). There are 15 additional reports as *Myrsidea* sp. from nonpasserine avian orders: 10 reports from Apodiformes (family Trochilidae) and 5 reports from Piciformes (families Capitonidae, Lybiidae, and Picidae) (Supplementary Dataset S1).

In general, species of *Myrsidea* are highly host-specific, with 78% of *Myrsidea* species ($n = 297$) restricted to a single host species (Supplementary Dataset S1). Most of the remaining species ($n = 68$; 17.8%) are known to occur on 2–3 closely related host species, and a few *Myrsidea* species ($n = 9$; 2.4%) occur on 4–5 different host species from the same host family. Only 7 *Myrsidea* species (1.8%) were reported from more than 5 host species: *M. fuscomarginata* and *M. dissimilis* from 6 host species, *M. ochracei* from 7 host species, *M. rustica* from 8 host species, *M. psittaci* from 10 host species, and *M. thoracica* from 11 host species. Two *Myrsidea* species were reported from 2 different but phylogenetically closely related families (Ohlson et al. 2013, Oliveros et al. 2019): *M. cinnamomei* from the avian families Tyrannidae and Tityridae and *M. violaceae* from Passerellidae and Fringillidae. These avian hosts live in sympatry and are even syntopic, often traveling together in feeding flocks, which could result in horizontal nonspecific transport of chewing lice to new hosts (Balakrishnan and Sorenson 2007, Bueter et al. 2009).

The only extreme case of a generalist *Myrsidea* seems to be the *M. quadrifasciata* species complex, which has been reported from 35 host species belonging to 8 passerine families (Calcariidae, Emberizidae, Fringillidae, Icteridae, Passeridae, Ploceidae, Thraupidae, and Viduidae). The recognition of this complex is relatively new and is the result of a combination of morphological and molecular data (Sychra et al. 2021), where all individuals studied to date fall well under the 12% intraspecies variability limit in the 379-bp segment of COI proposed by Kolencik et al. (2017). In addition to *M. quadrifasciata*, 9 previously known species (*M. anoxanthi*, *M. argentina*, *M. balati*, *M. darwini*, *M. major*, *M. serini*, *M. queleae*, *M. textoris*, and *M. viduae*) were synonymized (Sychra et al. 2021). Sychra et al. (2021) further divided *M. quadrifasciata* complex into 8 subspecies based on their geographic distribution and host preferences (*M. quadrifasciata*, *M. balati*, and *M. major*, all belonging to *M. q. quadrifasciata*); we have also included these in our checklist presented here (Supplementary Dataset S1).

Sychra et al. (2014c) also reported the first confirmed case of *Myrsidea* species found naturally on 2 phylogenetically distantly related bird species—*M. claytoni* from *Cymbirhynchus macrorhynchos* (Eurylaimidae) in south Vietnam. This species was originally

described based on specimens from *Pycnonotus eutilotus* and *P. sinensis* (Pycnonotidae) from Sarawak and Hong Kong, respectively (Hellenthal and Price 2003). We believe that the occurrence of *M. claytoni* on *C. macrorhynchos* is the result of successful natural secondary colonization of a new host.

Of the 488 bird species known to be parasitized by *Myrsidea* (Supplementary Dataset S1), 88.5% ($n = 432$) harbor only one species of *Myrsidea*. Synoxenic distribution of *Myrsidea*, i.e., the presence of more than one *Myrsidea* species on the same host species, has been reported for 58 bird species, of which 43 host species are known to harbor only 2 *Myrsidea* species (Price et al. 2003, 2008a, Kounek et al. 2011a, 2013, Valim et al. 2011), and another 12 host species harbor 3–6 *Myrsidea* species. One host, the Large-billed Crow—*Corvus macrorhynchos* Wagler, 1827, is known to harbor 9 *Myrsidea* species (Price et al. 2003). However, most of these hosts, including *C. macrorhynchos*, are characterized by a large geographic area of occurrence, with different host subspecies likely harboring different *Myrsidea* species (Supplementary Dataset S1). There are only a few reports of the "sympatric" occurrence of 2 different species of *Myrsidea* on the same bird individual at the same time, e.g., *M. johnklickai* and *M. sychrai* on *Cyanocompsa cyanoides* (Price et al. 2008b) and *M. serini* and *M. psittaci* on *Chrysomus thilius petersii* (Cicchino and Valim 2015). Interestingly, Cicchino and Valim (2015) reported that the sympatric *Myrsidea* species always oviposited on different feathers.

Conclusions

The checklist of *Myrsidea* (Supplementary Dataset S1) represents a comprehensive look at the current state of knowledge of *Myrsidea* diversity. This list is meant to enable an understanding of the gaps in our knowledge and to target areas for future research.

For example, by listing collecting locations for all *Myrsidea* species from publications and the number of species mentioned in each publication, we were able to examine the spatial distribution of the state of knowledge of *Myrsidea* research (Supplementary Fig. 4). Some countries are clearly understudied with no or few publications (Supplementary Fig. 4). A similar situation applies to the available sequence data (see Map in Supplementary Table S1). This lack of knowledge, in combination with information on that country's avian host diversity (as in Valim and Weckstein 2013), could reveal countries or regions that might be ideal places for future collections to discover additional diversity. For example, although Brazil appears on the surface to be a well-studied region, Valim and Weckstein (2013) pointed out that there are potentially still over 900 *Myrsidea* species that have yet to be described. A different example is the Caribbean island of Hispaniola. The online database Avibase—Bird Checklists of the World (Lepage 2023) indicates that the avifauna of Hispaniola comprises 323 bird species, of which 121 are passerines—the most common avian host order of *Myrsidea*. However, there is only one published record of *Myrsidea*—*M. imbricata* from the hummingbird, *Riccordia swainsonii* (Apodiformes) from Hispaniola (Neumann 1891). However, both the host and the locality for this record are questionable (Price et al. 2003). It is very likely that sampling ectoparasites from birds in Hispaniola will lead to the discovery of new species of *Myrsidea*. A similar scenario applies to many other countries, which have relatively high avian diversity, but no confirmed records of *Myrsidea* up to date (e.g., Cuba, Côte d'Ivoire, Kazakhstan, etc.; Supplementary Dataset S1).

Lastly, we emphasize the importance of future work toward morphology-based (or rather integrative) online databases, which could not only serve as a source of previously published data but, together with this publication, would also help train future louse taxonomists.

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

Acknowledgments

We would like to thank everyone who helped us with field and laboratory work. Our special thanks go to the following persons and institutions for the loan of specimens used in this study: P. A. Brown (Natural History Museum, London, UK), Donald C. Arnold (K.C. Emerson Entomology Museum, Oklahoma State University, Stillwater, OK, USA), Dirk Rohwedder (Zoological Research Museum Alexander Koenig, Bonn, Germany), Ricardo L. Palma (Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand), Alexandra Marcal (Museu Bocage, Museo Zoologico da Universidade de Lisboa, Lisboa, Portugal), Anna Lindholm (Department of Zoology, Cambridge, UK), Igor Malenovsky (Moravian Museum, Brno, Czech Republic), Vladimir Jansky (Slovak National Museum, Bratislava, Slovakia), Patricia Gentili-Poole and David Furth (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA), Tomi Trilar (PMSL = Slovenian Museum of Natural History, Ljubljana, Slovenia). We thank Jill Jankowski for providing the specimens of *Myrsidea* from hummingbirds. We are also grateful to 2 anonymous reviewers who provided very detailed and helpful comments and suggestions to improve this article.

Funding

This work was supported in part by NSF DEB-1925312 and DEB-1902031 to J.M.A., NSF DEB-1925487 and DEB-1926919 to K.P.J., NSF DEB-1855812 and DBI-1901935 to J.D.W., and VetUni grant number 2023ITA22 to O.S.

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