

Taxonomy

World Cynipoidea (Hymenoptera): A Key to Higher-Level Groups

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Abstract

While much has been learned regarding the phylogeny and evolution of cynipoid wasps, clearly illustrated diagnostic tools and identification keys have remained stagnant. So too, where keys do exist, they are often to genus or species, and there are no user-friendly keys to groups such as tribes, subfamilies, or families. This state of affairs leaves a knowledge gap for non-specialists and slows future research on the group. To address this, we provide a fully illustrated key to the higher-level groups of world Cynipoidea. We also provide summaries of all higher-level taxa with updated generic lists, biological data, distribution, and literature resources. The dichotomous key presented here is complimented with a multi-entry matrix-based key, created in Lucid, and served on www.waspweb.org with online versions of the dichotomous keys also available.

Key words: gall wasp, Cynipidae, Figitidae, parasitoid, Ibaliiidae

Cynipoid wasps are a relatively diverse lineage of Hymenoptera. Species range from being internal parasitoids of endopterygote insect larvae, including hyperparasitoids, to gall inducers on higher plants. To address the diversity of this group from an identification standpoint, Weld (1952), and later, Fergusson *in* Goulet and Huber (1993) have been the best resources for identifying families within the group. Since these publications came out, the general understanding of the evolution of cynipoids, and their classification, has changed significantly. Further, our taxonomic knowledge of many groups within the cynipoids has matured, while a taxonomic resource to higher groups (families, subfamilies, and tribes) has languished. We present here a fully illustrated identification key to the higher-level groups of Cynipoidea of the world. In addition, we provide a general overview of each group, taxonomic resources that are available for that group, comments on the biology and evolution of the group, and an updated list of genera currently assigned to that group.

The key allows identification to families, and further for the two common and species-rich families: Cynipidae into its constituent tribes, and Figitidae into its subfamilies. Thus, family-level taxa which the key does not allow identification of are the subfamilies of the rare Liopteridae, and the still somewhat preliminary tribes of the figiid subfamily Eucoilinae.

Key to Families, Subfamilies, and Tribes of World Cynipoidea

The skeleton of this key was devised by MB, MF, and JL while teaching The Hym Course in Tovetorp, Sweden, in 2012; later drafts were updated with student feedback from each subsequent Hym Course offering. Some key characters are modifications of the Hymenoptera of the World key (Goulet and Huber 1993). Additional characters and character state definitions presented here follow Ronquist *et al.* (2015) and van Noort *et al.* (2015). All morphological terms follow those used in Hymenoptera of the World (Goulet and Huber 1993) and are further defined on the Hymenoptera Anatomy Ontology project (<http://portal.hymao.org/projects/32/public/ontology/>). No new terminology is introduced here. Reviewers of earlier drafts of this paper helped in clarifying problematic characters and definitions. The key is illustrated using color photomicrographs of museum specimens. We are hoping this brings the user closer to the reality of working with specimens. For those interested in using a multi-entry matrix key, www.waspweb.org hosts the Lucid version of this key.

The key covers all Cynipoidea worldwide, and some of these groups are only found in certain areas or on certain plants. Some rarer taxa that may not be routinely collected worldwide

include Austrocynipidae, Liopteridae, and among the cynipids, the tribes Qwaqwaini, Phanacidini, Pediaspidini, Paraulacini, and Eschatocerini; among the figitids, Parnipinae, Thrasorinae, Pycnostigmata, Emargininae, Euceroptrinae, Plectocynipinae, and Mikeiinae. If the user arrives at any of these using the key, we suggest double-checking the characters before making a final decision.

The systematic overview following the key gives a general introduction to each group, especially in terms of diversity, geographical distribution, and biology. Diagnostic characters are usually not repeated in this section, but certain morphological key factors in evolution are highlighted. We list the most relevant literature, and the included genera in each group. The genera are ordered into any valid family-level taxa, the authorship of which are given (and in a few cases in informal groups of genera). For genera, authorship, species number, and geographical distributions are given. Geographical distributions are summarized in text or by abbreviations of biogeographic regions; AT for Afrotropical, AU for Australasian or Oceanic, NA for Nearctic, NT for Neotropical, OR for Oriental, PA for Palearctic (often divided into wPA and ePA for western and eastern Palearctic).

There is no single up to date, authoritative catalog for Cynipoidea. The closest to an updated online resource is Hymenoptera Online (<https://hol.osu.edu/>), which contains JL's personal cynipid catalog started in the late 1990s, as well as various other cynipoid taxa added over time. It contains a large number of problematic names, and changes made and taxa described since 2008 have been somewhat haphazardly maintained in HOL, as there is no one cynipoid curator of the data in that database. MF has kept a personal catalog focused mostly on Figitidae. Parts of this catalog have been published over time in smaller regional projects (e.g., [Forshage et al. 2013](#); [van Noort et al. 2015](#)). Charipinae have been cataloged by the Barcelona research group ([Ferrer-Suay et al. 2012](#)); however, these data are not yet present in HOL. Thus, here we have based classification and species numbers on our own lists, manually keeping track of the additions and subtractions from the last decades, referring back to HOL for comparison but including numerous changes from recent years alerted via Zoological Record and other sources, as well as making certain pragmatic considerations.

Identification Key to Families, Subfamilies, and Tribes of World Cynipoidea



Figs. 1 and 2. Fig. 1, *Paramblynotus virginianus* Liu, Ronquist and Nordlander, 2007, lateral view. USNM01231827. Fig. 2, *Ibalia anceps* Say, 1824, lateral view. USNM01231826.

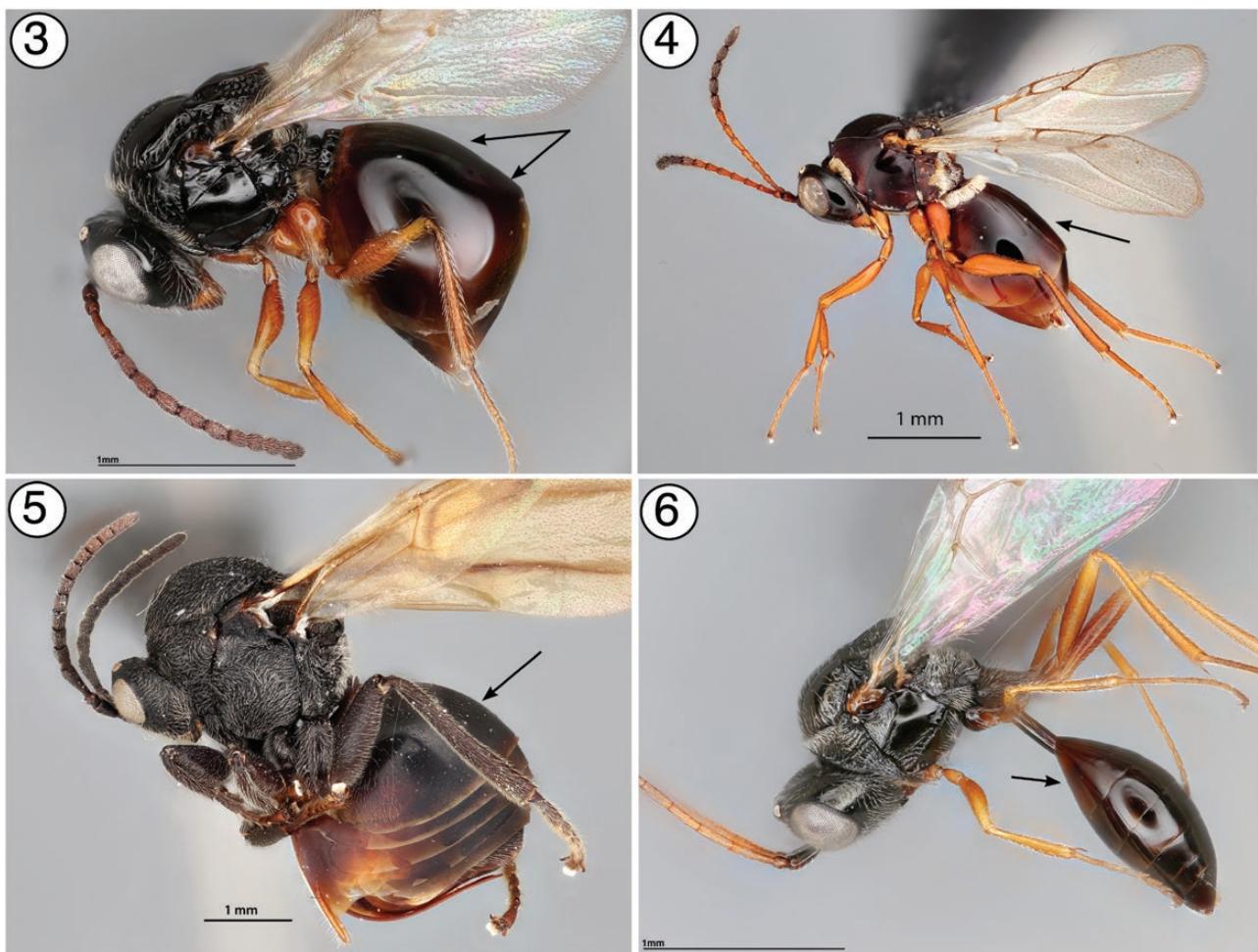
- Metasomal segment four, five or six the largest (in lateral view), with two to four small segments preceding largest segment (a, [Fig. 1](#)). Wings always fully formed, with marginal cell of forewing sometimes very elongate. Often large wasps, exceeding 10 mm in length. Mesoscutum with heavy sculpture (well-developed ridges or pits; b, [Fig. 1](#); arrows, [Fig. 2](#)) 2

There are still a rather large number of mystery names available, linked to lost or missing type specimens. In some cases, it is not clear if a particular name even belongs in Cynipoidea, or rather Chalcidoidea, Diapriidae or dipteran Cecidomyiidae. Further, some genera (e.g., *Eucoila*, *Ganaspis*, *Trybliographa*, *Andricus*, *Dryocosmus*) have had a large number of species assigned to them for seemingly arbitrary reasons. Keeping all these difficult circumstances in mind, we have presented species numbers that we have found documentation for and consider meaningful as preliminaries, while these numbers may still differ significantly from actual species numbers. In genera where these numbers are particularly problematic, we have mentioned this specifically, and also to indicate where particularly large number of undescribed species belong, as well as where large numbers of clearly misclassified or insufficiently known species reside. Hopefully, the data here will pinpoint where future research is most needed.

All specimens used here, except for Qwaqwaiini, are housed at the USNM (National Museum of Natural History, Washington, DC) and were often cleaned with a minute paintbrush and mounted to achieve the necessary views for each couplet. Unique specimen identifiers, in the form of USNM 'barcode' numbers, link images to specimens housed at the USNM. Images were captured using a Macroscopic Solutions 'microkit' (Tolland, CT) imaging station and stacked using Zerene Stacker LLC (Richland, WA). Please contact MB for additional details of this process.

We suggest the following to get the most out of using this key: 1) high-quality optics are a necessity for observing the pronotal plate and other small features throughout the key; 2) light dispersing film (in the United States, mylar is commonly used) should be installed if using fiber optic light sources with incandescent bulbs (the glare produced by these lights will obscure details of the cuticle). Lastly, having some biological and geographic data will make using the key easier.

As the basic identification of many of these groups is a general impediment to taxonomic progress, this key, and the taxonomic treatments that follow, provide a point of entry into cynipoid research not previously available. We hope this publication spurs renewed interest in cynipoid systematics, biology, and evolution.



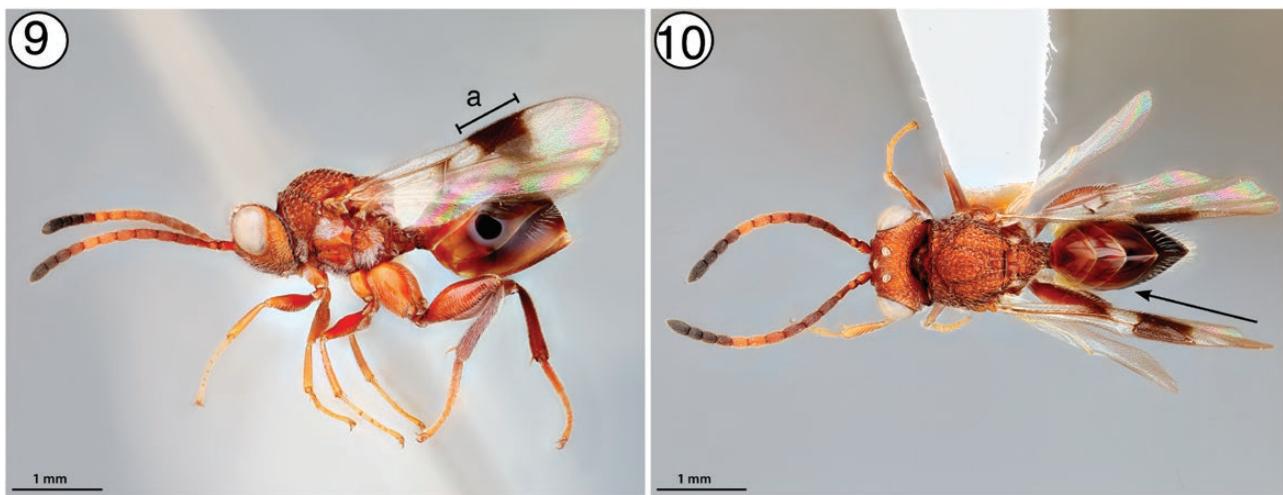
Figs. 3–6. Fig. 3, *Afstilba* sp., lateral view. USNMENT01022103. Fig. 4, *Dieucoila* sp., lateral view. USNMENT01231825. Fig. 5, *Amphibolips hidalgensis* Pujade-Villar and Melika, 2011, lateral view. USNMENT01231834. Fig. 6, *Anacharis melanoneura* Ashmead, 1887, lateral view. USNMENT01231833.

— Metasomal segment two or three the largest (in lateral view), or fused into a syntergum (arrows, **Figs. 3 and 4**), with at most one or two segments preceding the largest (arrows, **Figs. 5 and 6**). Wings usually fully formed; marginal cell of forewing usually shorter, rarely as long as $3\times$ as long as high. Adult wasps smaller than 10 mm in length. Deep ridges in mesoscutum less common; typically microcoriaceous or smooth



Figs. 7 and 8. Fig. 7, *Ibalia anceps*, lateral view. USNMENT01231826. Fig. 8, *Ibalia anceps*, dorsal view. USNMENT01231826.

2. Marginal cell of forewing extremely elongate ($9\times$ as long as high) (arrow, **Fig. 7**). Metasoma in dorsal view elongate and very laterally compressed, thin, blade-like (arrow, **Fig. 8**). Large, over 20 mm in lengthIbaliidae



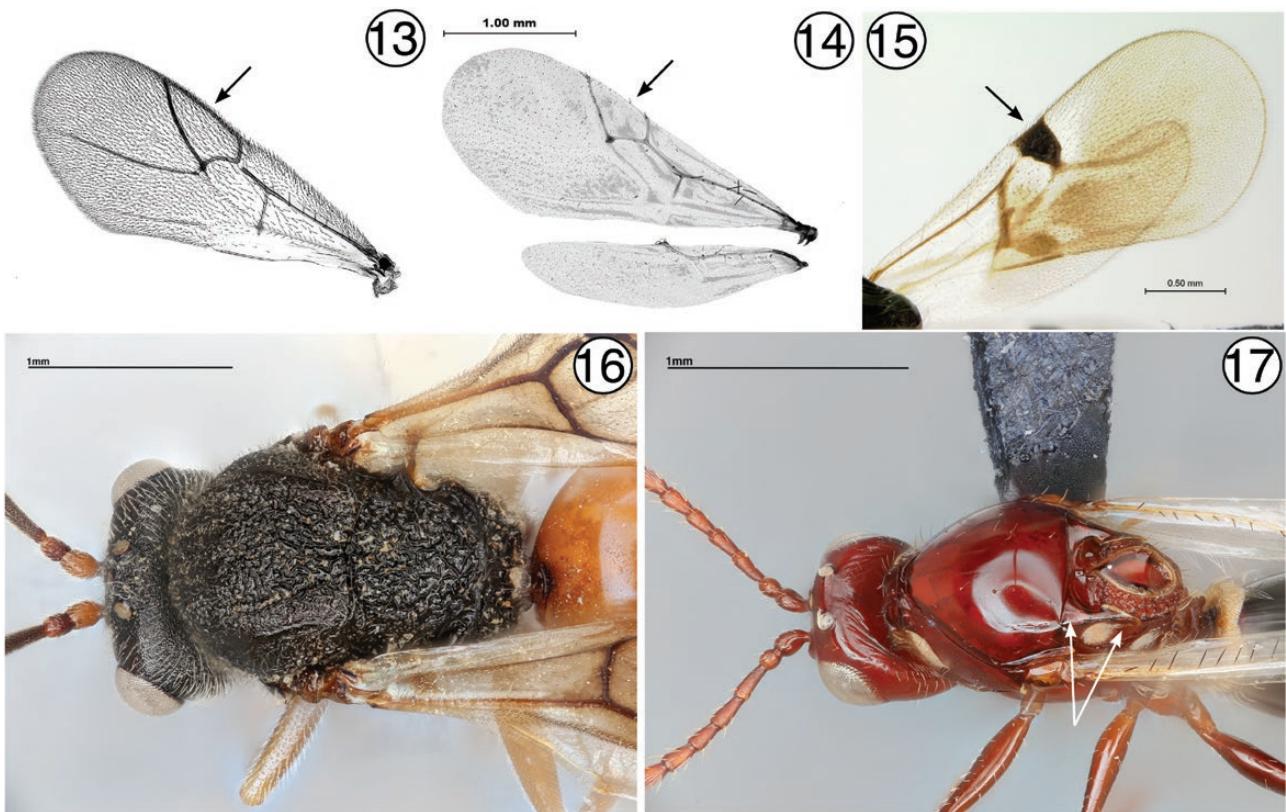
Figs. 9 and 10. Fig. 9, *Paramblynotus* sp., lateral view. USNMENT01231832. Fig. 10, *Paramblynotus* sp., dorsal view. USNMENT01231832.

— Marginal cell of forewing moderately elongate (3–4x as long as high) (a, Fig. 9). Metasoma in dorsal view rounded, ovate, subcylindrical (arrow, Fig. 10). Size varying, sometimes small, always under 20 mm Liopteridae



Figs. 11 and 12. Fig. 11, *Austrocynips mirabilis* Riek, 1971, lateral view. Holotype, ANIC. Fig. 12, *Austrocynips mirabilis*, lateral view. Holotype, ANIC.

3. With a pterostigma (arrow, Fig. 11), always fully winged. No foveae or lateral bars on scutellum (a, Fig. 12). Mesoscutum with well-developed transversal ridges (b, Fig. 12). Australia only, very rare Austrocynipidae



Figs. 13–17. Fig. 13, *Euceroptris maritimus* Weld, 1926, fore wings. USNMENT01525886. Fig. 14, *Odontosema anastrephae* Borgmeier, 1935, fore and hind wings. USNMENT00655913. Fig. 15, *Tylosema dayae* Buffington and van Noort, 2007, forewing. SAM-HYM-P0024394. Fig. 16, *Diplolepis bicolor* (Harris, 1852), dorsal view. USNMENT01231831. Fig. 17, *Striatovertex* sp., dorso-lateral view. USNMENT01231830.

— Without a pterostigma (arrows, Figs. 13 and 14) (very rarely the entire marginal cell is pigmented forming a pseudostigma; arrow, Fig. 15), rarely brachypterous/apterous. Usually with more or less developed foveae and lateral bars of scutellum (arrows, Fig. 17). Mesoscutum usually without well-developed transversal ridges (Figs. 16 and 17). Worldwide 4



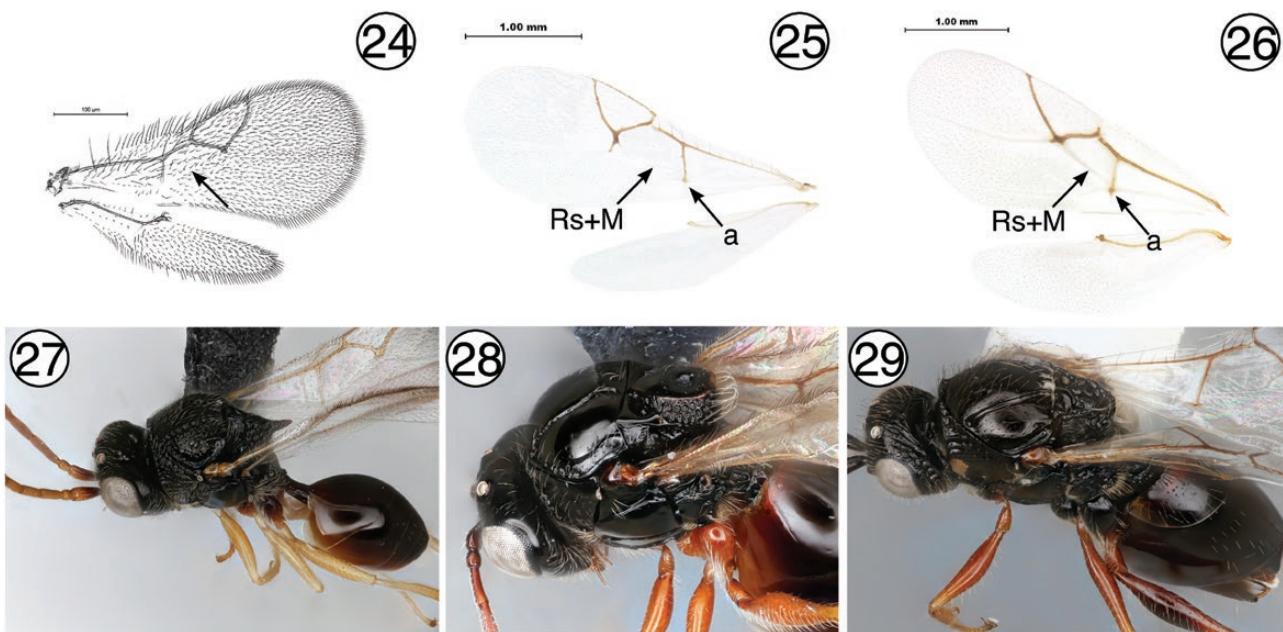
Figs. 18–20. Fig. 18, *Andricus quercusalifornicus* (Bassett, 1881), lateral view. USNMENT01231839. Fig. 19, *Striatovertex* sp., lateral view. USNMENT01231830. Fig. 20, *Trybliographa melanoptera* (Hartig, 1843), lateral view. USNMENT01231838.

4. Fully winged (Figs. 18–20). Note: brachypterous/wingless forms, or specimens with obscured, tangled or damaged wings, can be identified via this route too 5



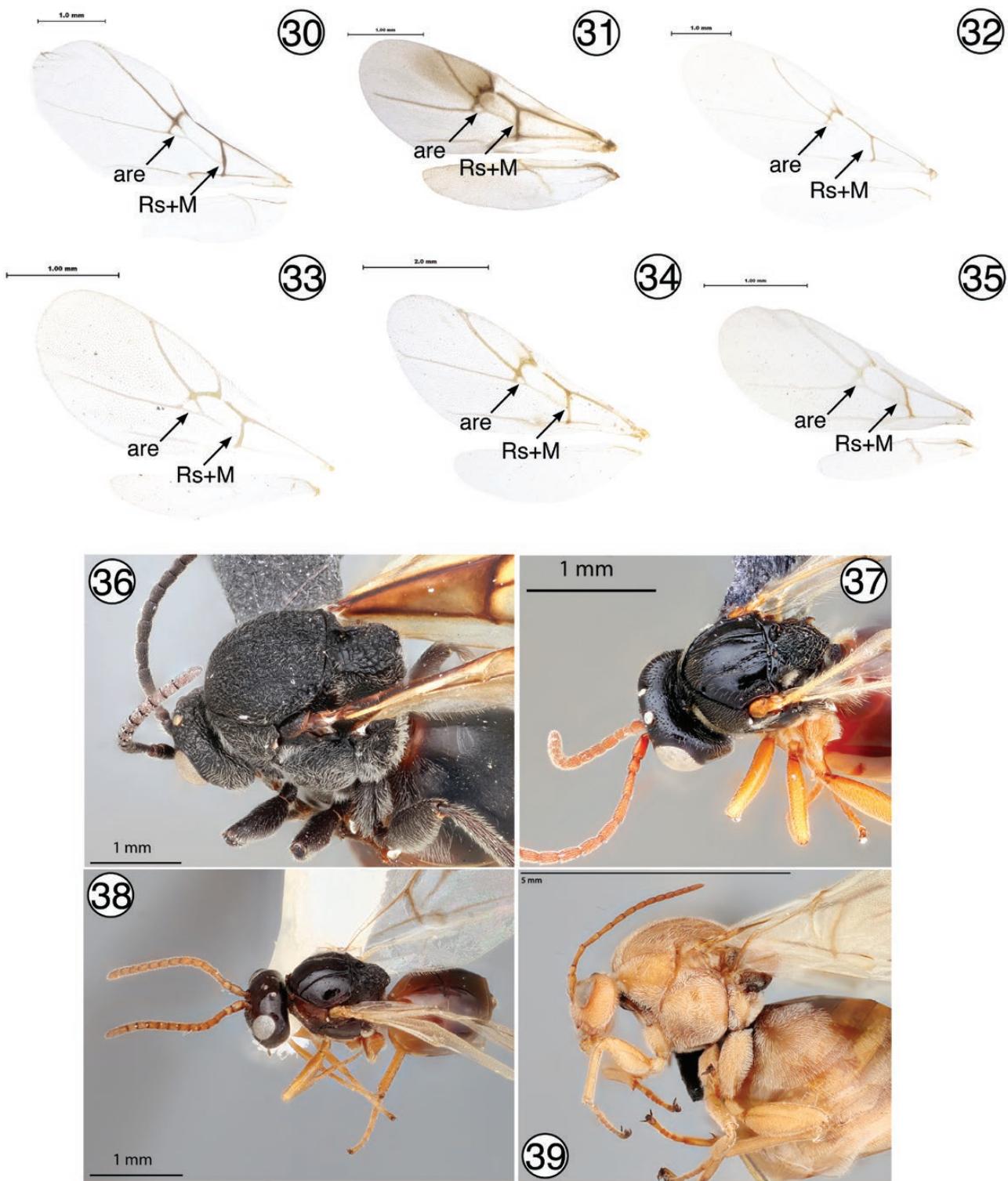
Figs. 21–23. Fig. 21, *Kleidotoma* sp., dorso-lateral view. USNMENT01231837. Fig. 22, *Lytoxysta brevipalpis* Kieffer, 1909, dorso-lateral view. USNMENT01231836. Fig. 23, *Phylloteras* sp., lateral view. USNMENT01231835.

— Brachypterous or apterous (Figs. 21–23) (shortcut route to groups where this feature is known) 33



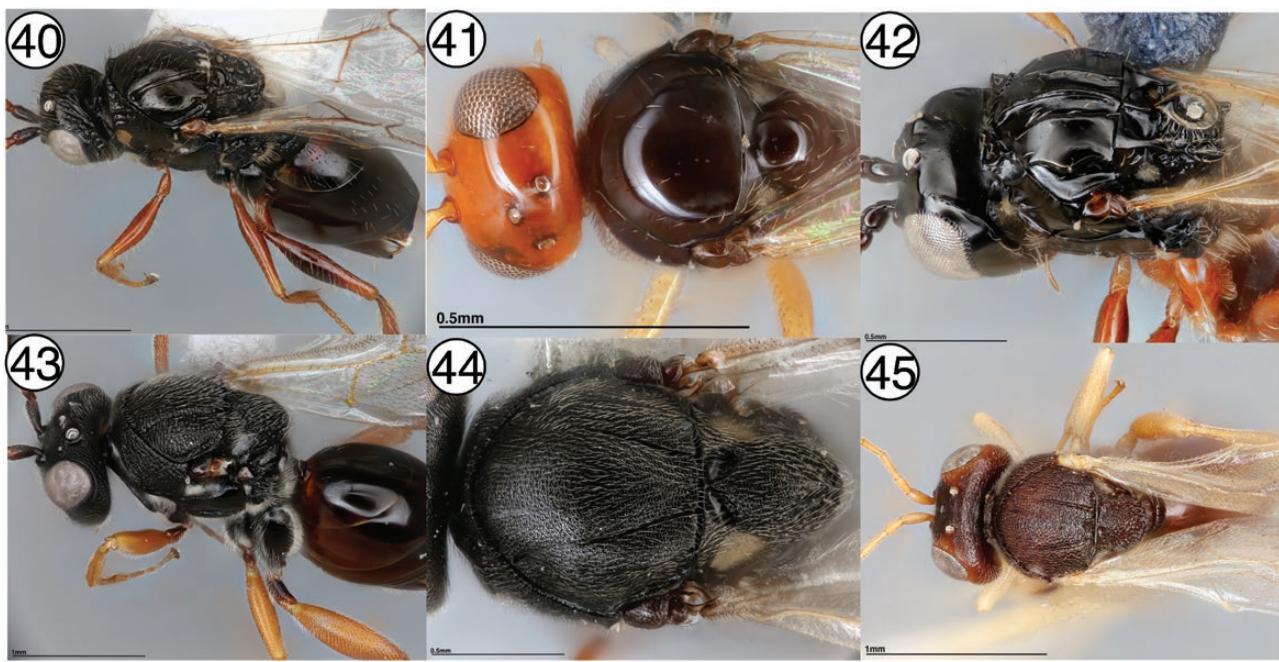
Figs. 24–29. Fig. 24, *Zaeucoila robusta* (Ashmead, 1896) fore and hind wings. USNMENT00993082. Fig. 25, *Figitessp.* fore and hind wings. USNMENT00764745. Fig. 26, *Paraspicera bakeri* Kieffer, 1907, fore and hind wings. USNMENT00764748. Fig. 27, *Xyalaspis flavipes* Ashmead, 1896, dorso-lateral view. USNMENT01231844. Fig. 28, *Gronotoma* sp., dorso-lateral view. USNMENT01231843. Fig. 29, *Figitessp.*, dorso-lateral view. USNMENT01231842.

5. Rs+M vein often indistinct or absent (arrow, Fig. 24); its proximal part, when present as a faint vein (Fig. 26) or a fold (Fig. 25) joins basal vein at ventral end of basal vein (a, Fig. 26). Areolet usually absent. Usually head and mesosoma shiny (Figs. 28 and 29), rarely rugose or matte (Fig. 27). Scutellum often complex, with differentiated structures such as, plates, spines etc 6



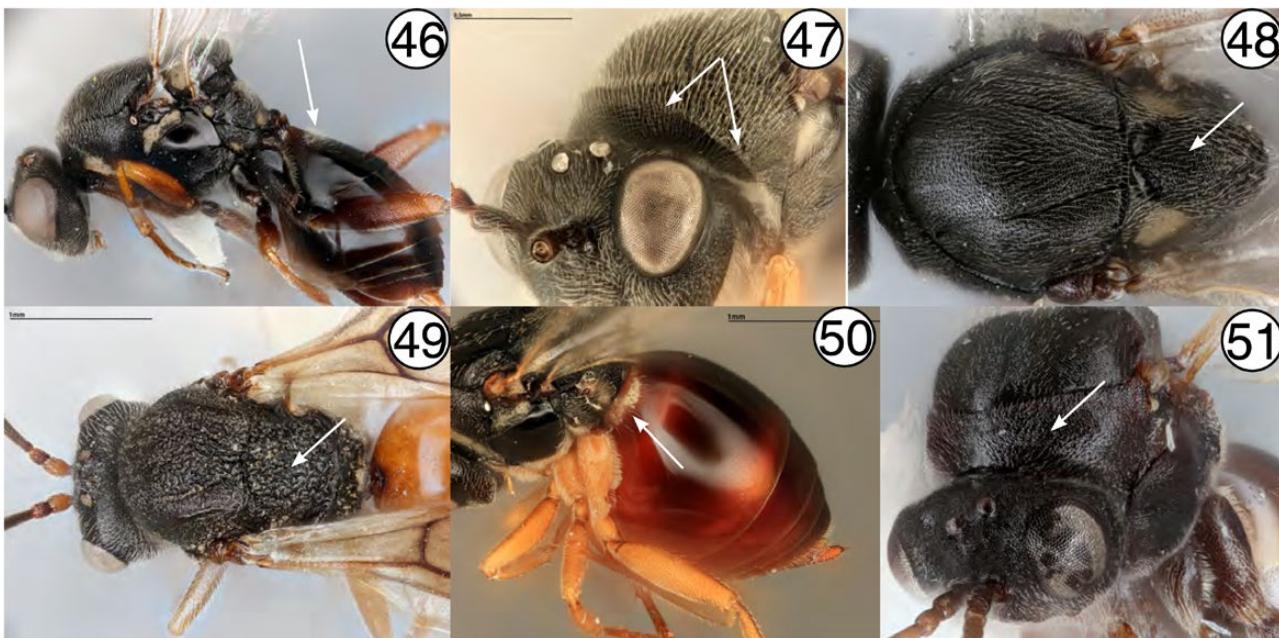
Figs. 30-39. Fig. 30, *Cerroneuroterus* sp., fore and hind wings. USNMENT00655874. Fig. 31, *Diplolepis rosae* (Linnaeus, 1758) fore and hind wings. USNMENT00655959. Fig. 32, *Biorhiza eburnea* (Bassett, 1890), fore and hind wings. USNMENT00655850. Fig. 33, *Synophromorpha sylvestris* (Osten-Sacken, 1861), fore and hind wings. USNMENT00764755. Fig. 34, *Plagiotrochus suberi* Weld, 1926, fore and hind wings. USNMENT00655825. Fig. 35, *Neuroterus quercusirregularis* (Osten-Sacken, 1861), fore and hind wings. USNMENT00655854. Fig. 36, *Amphibolips hidalgoensis*, dorso-lateral view. USNMENT01231834. Fig. 37, *Diastrophus kinkaidii* Gillette, 1893, dorso-lateral view. USNMENT01448499. Fig. 38, *Dryocosmus kuriphilus* sp., dorso-lateral view. USNMENT01231850. Fig. 39, *Andricus sternlichti* Bellido, Pujade-Villar & Melika, 2003, lateral view. USNMENT01231841.

— Rs+M starts at (or points towards) mid-length of basal vein (Rs+M, Figs. 30-35). Aerolet often present (are, Figs. 30-35). Usually large parts of head and mesosoma matte (Figs. 36 and 39), rarely smooth/shiny (Figs. 37 and 38). Scutellum distinct structure other than general fovea or rugosity (most of Cynipidae) 8



Figs. 40–45. Fig. 40, *Figitidae* sp., dorso-lateral view. USNMENT01231842. Fig. 41, *Alloxysta* sp., dorsal view. USNMENT01231840. Fig. 42, *Dettmeria* sp., dorso-lateral view. USNMENT01231849. Fig. 43, *Euceroptris maritimus*, dorso-lateral view. USNMENT01231848. Fig. 44, *Melanips* sp., dorsal view of mesosoma. USNMENT01231847. Fig. 45, *Synergus incisus* Gillette, 1896, dorsal view. USNMENT01231859.

6. Head, pronotum and mesoscutum shiny, more or less smooth, and usually not densely pubescent (**Figs. 40–42**) (most of Figitidae) 19
— Head, pronotum and mesoscutum matte from dense microsculpture, and more or less densely pubescent (**Figs. 43–45**) 7



Figs. 46–51. Fig. 46, *Melanips* sp., lateral view. USNMENT01231847. Fig. 47, *Euceroptris maritimus*, pronotum, antero-lateral view. USNMENT01231848. Fig. 48, *Melanips* sp., mesosoma, dorsal view. USNMENT01231847. Fig. 49, *Diplolepis bicolor*, dorsal view. USNMENT01231831. Fig. 50, *Diastrophus kinkaidii*, metasoma, lateral view. USNMENT01448499. Fig. 51, *Isocolus tinctorius* Melika & Gharaei, 2006, antero-dorsal view. USNMENT01231846.

7. With dense pubescence on base of metasoma (arrow, **Fig. 46**). Usually with distinct pronotal plate (arrows, **Fig. 47**). Often with complex structure on scutellum (arrow, **Fig. 48**) (some Figitidae) 19
— Usually without dense pubescence on base of metasoma (**Fig. 49**) but sometimes with small lateral patch (arrow, **Fig. 50**). Usually without distinct pronotal plate (arrow, **Fig. 51**). Always with a relatively simple scutellum dominated by evenly distributed fovea or rugosity (arrow, **Fig. 49**) (some Cynipidae) 8

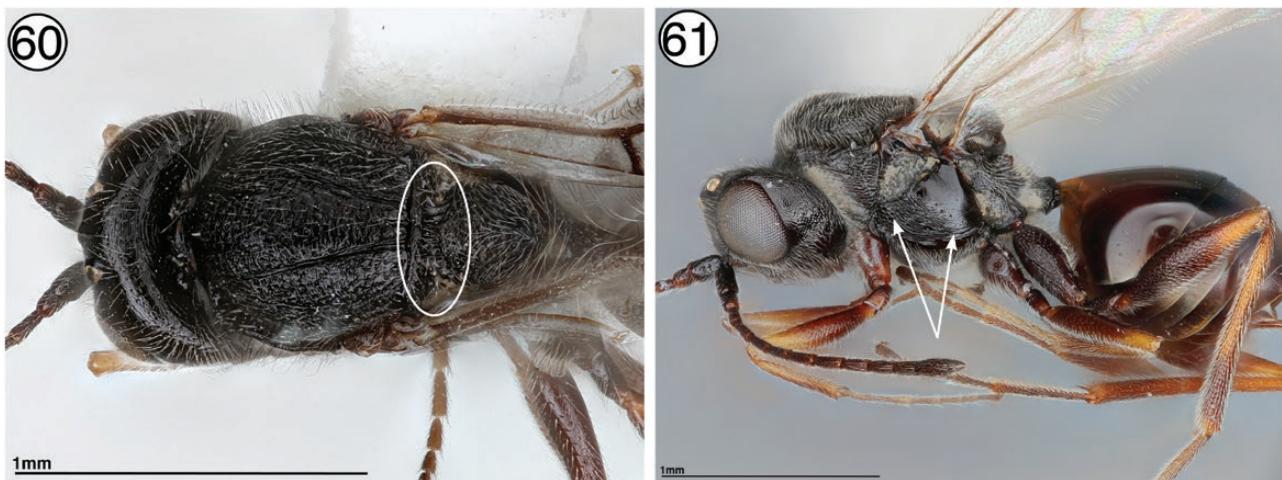


Figs. 52–55. Fig. 52, *Isocolus tinctorius*, antero-dorsal view. USNMENT01231846. Fig. 53, *Synergus atripennis* Ashmead, 1896, antero-dorsal view. USNMENT01231845. Fig. 54, *Isocolus tinctorius*, antero-dorsal view. USNMENT01231846. Fig. 55, *Synergus atripennis*, antero-dorsal view. USNMENT01231845.
8. Pronotum high, dorsomedially at least 1/5, usually 1/3, as long as greatest length of pronotum laterally (arrows, Figs. 52–55). The median area of pronotum with two submedian pits and often more or less sharply defined lateral demarcations. Pronotal plate present or absent 9



Figs. 56–59. Fig. 56, *Diplolepis bicolor*, antero-dorsal view. USNMENT01231831. Fig. 57, *Andricus quercusalifornicus*, lateral view. USNMENT01231839. Fig. 58, *Andricus quercusalifornicus*, antero-dorsal view. USNMENT01231839. Fig. 59, *Andricus quercusalifornicus*, antero-dorsal view. USNMENT01231839.

— Pronotum low, dorsomedially short, 1/7 or less compared to length of pronotum laterally (arrows, Figs. 56–59). Median area of pronotum without well-defined structures, at most with superficial depressions. Pronotal plate always absent 17

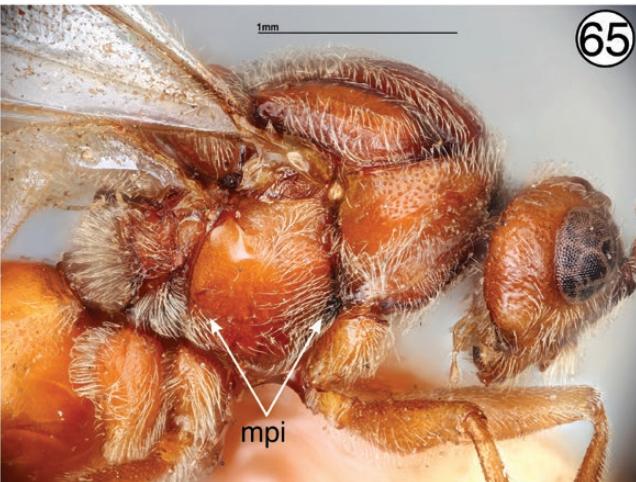


Figs. 60 and 61. Fig. 60, *Paraulax queulensis* Nieves-Aldrey and Liljeblad, 2009, dorsal view. USNMENT01231854. Fig. 61, *Paraulax queulensis*, lateral view. USNMENT01231854.

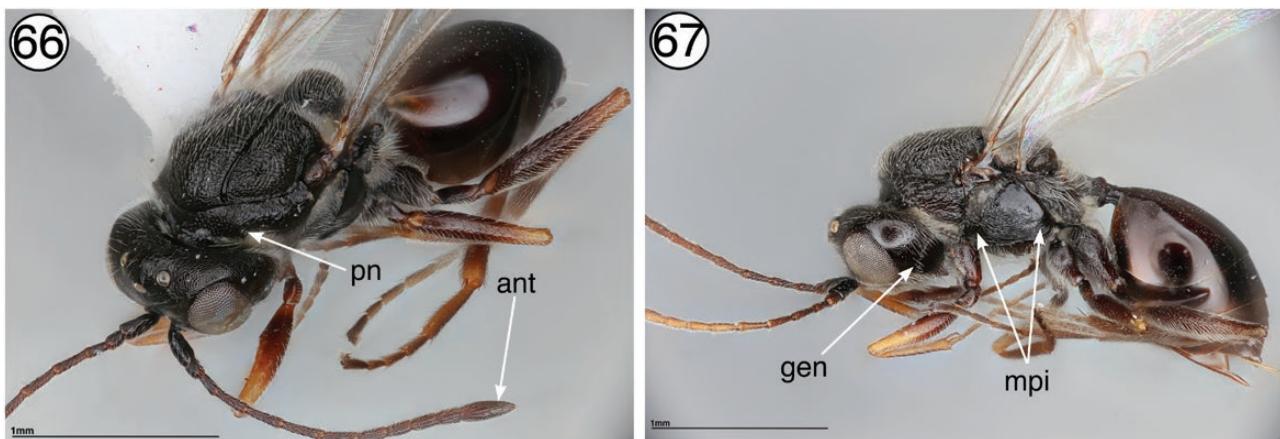
9. Scutellar foveae shallow, usually faint to completely absent (oval, Fig. 60). Mesopleuron with a median longitudinal mesopleural impression, sometimes very faint (arrows, Fig. 61) or absent. Inhabiting galls on *Nothofagus* or inducing galls on *Acer* (including the genus *Hymalocynips* from Nepal with biology unknown). Rarely encountered 10



Figs. 62 and 63. Fig. 62, *Aulacidea irani* Melika & Gharaei, 2006, dorsal view. USNMENT01231853. Fig. 63, *Aulacidea irani*, lateral view. USNMENT01231853. — Scutellar foveae usually well differentiated and deep, sometimes confluent and forming a transverse depression (circles, Fig. 62). Mesopleuron without a median longitudinal impression (arrow, Fig. 63) 11

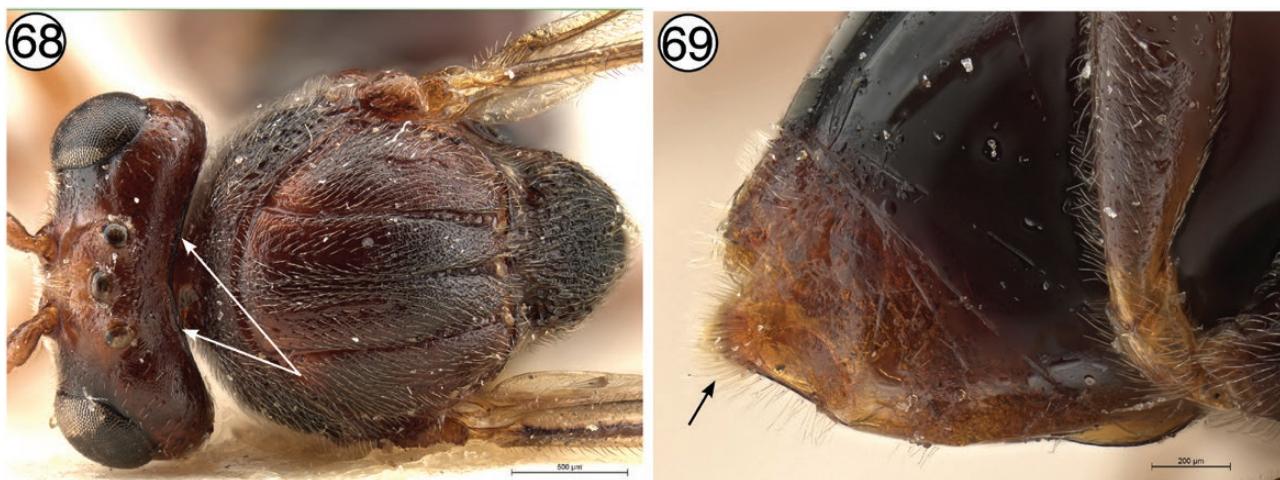


Figs. 64 and 65. Fig. 64, *Pediaspis aceris* (Gmelin, 1790), antero-lateral view. USNMENT01231852. Fig. 65, *Pediaspis aceris*, lateral view. USNMENT01231852. 10. Female antenna with 12 or more flagellomeres; last flagellomere not wider than the penultimate (ant, Fig. 64); male antenna without modified F1. Ventral area of gena without vertical carinae, genal carina absent. Ventral part of clypeus broadly projecting over mandibles (cly, Fig. 64). Dorsolateral margin of pronotal plate not projecting laterad (Fig. 65). Mesopleural impression absent or faint (mpi, Fig. 65). Profemur not modified. Palearctic gall-inducers on *Acer* or biology unknown Pediaspidini



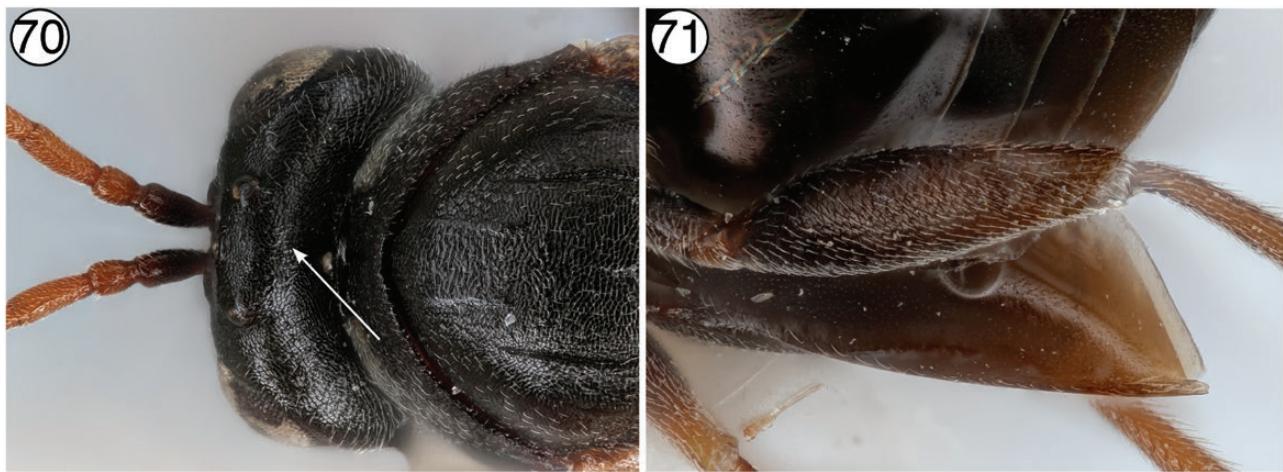
Figs. 66 and 67. Fig. 66, *Cecinothophagus* sp., antero-dorsal view. USNMENOT01231851. Fig. 67, *Cecinothophagus* sp., lateral view. USNMENOT01231851.

— Female antenna with 10 flagellomeres; last flagellomere wider than the penultimate (ant, Fig. 66); male antenna with either F2, F3 or both modified. Ventral area of gena with 5–9 vertical carinae (gen, Fig. 67). Genal carina present. Ventral part of clypeus at most slightly projecting over mandibles. Dorsolateral margin of pronotal plate strongly projecting laterad (pn, Fig. 66). Mesopleural impression present (mpi, Fig. 67). Profemur with ventral swelling composed of 4–5 rows of sharp, closely spaced, deep costulae. Associated with Neotropical galls on *Nothofagus* Paraulacini



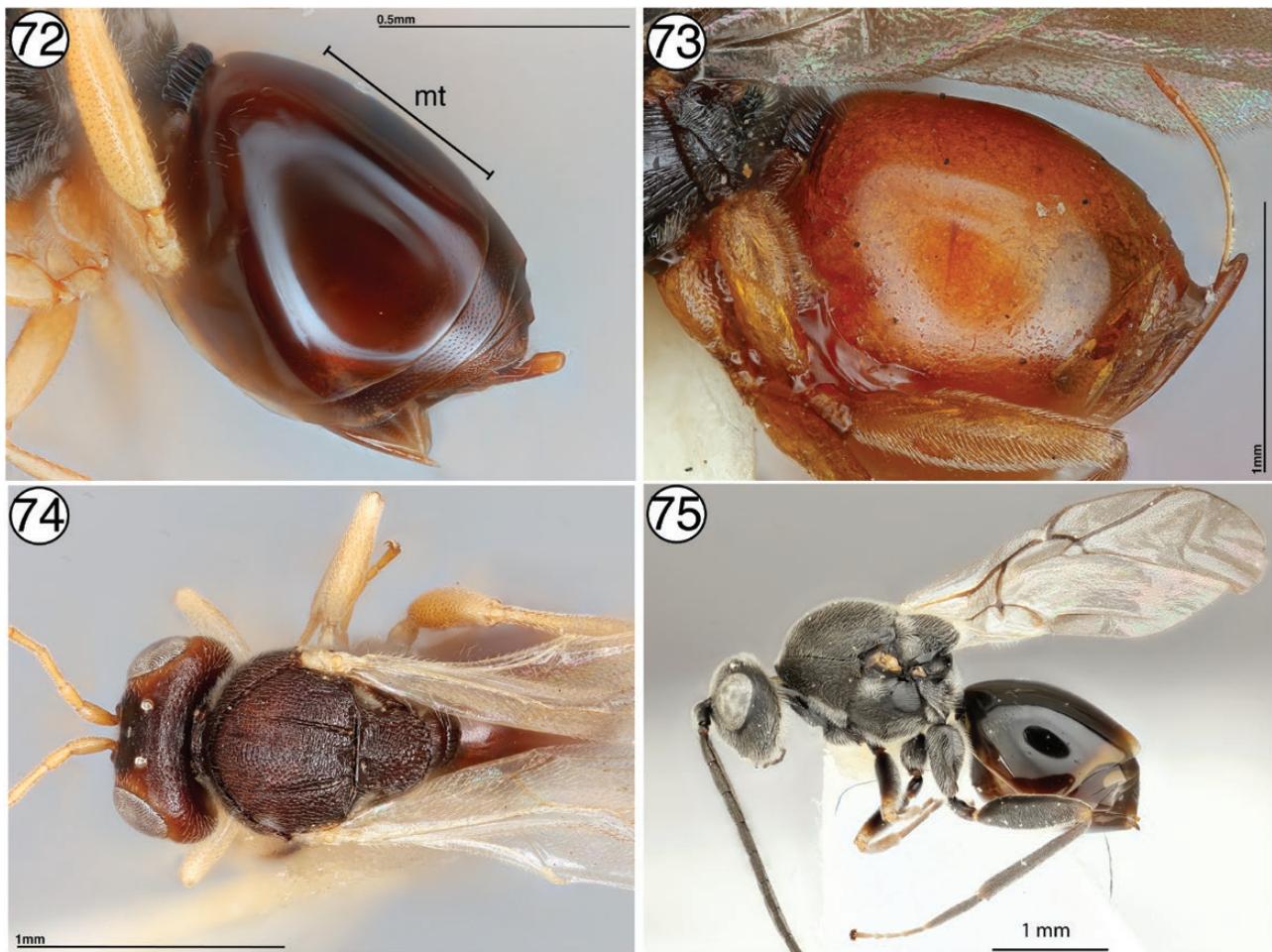
Figs. 68 and 69. Fig. 68, *Qwaqwai scolopiae* Liljeblad, Nieves-Aldrey & Melika, 2006, dorsal view. SAMHYMP044067. Fig. 69, *Qwaqwai scolopiae*, metasoma, lateral view. SAMHYMP044067.

11. Occiput with strong and sharp occipital carina (arrows, Fig. 68). Hypopygium abrupt, not prolonged into a ventral spine; with a dense tuft of long setae (arrow, Fig. 69). South African gall-inducers on *Scolopia*. Rarely encountered Qwaqwaiini



Figs. 70 and 71. Fig. 70, *Aulacidea irani*, head, dorsal view. USNMENT01231853. Fig. 71, *Aulacidea irani*, hypopygium, lateral view. USNMENT01231853.

— Occiput without distinct and sharp occipital carina (arrow, Fig. 70), sometimes with some strong parallel occipital rugae. Hypopygium with more or less distinct, elongated, needle-like ventral spine, with subapical setae never forming a dense tuft (Fig. 71) 12



Figs. 72–75. Fig. 72, *Synergus* sp., metasoma, lateral view. USNMENT01231858. Fig. 73, *Synergus atripennis*, metasoma, lateral view. USNMENT01231845. Fig. 74, *Synergus incisus*, dorsal view. USNMENT01231859. Fig. 75, *Synophrus politus* Hartig, 1843, lateral view. USNMENT01231857.

12. Metasomal terga 2 + 3 fused, or apparently fused, with or without a suture between terga 2 and 3; metasoma appears as one large segment (Figs. 72 and 73), sometimes with indistinct and continuous suture between these terga in either sex. Head and mesosoma almost always sculptured (Figs. 74 and 75). Metasoma anteroventrally angled, relative to midline, in lateral view (mt, Fig. 72). Holarctic and Oriental inquiline in galls 13



Figs. 76 and 77. Fig. 76, *Aylax papaveris* (Perris, 1841), lateral view. USNMENT01231856. Fig. 77, *Barbotinia oraniensis* (Barbotin, 1964), lateral view. USNMENT01448491.

— Terga 2–7 free in most cases (Fig. 76); if terga 2 + 3 fused in females into one large segment then head and mesosoma almost always smooth and shiny (otherwise, head and mesosoma sculptured) (Fig. 77). Metasoma usually more or less oval in lateral view (mt, Fig. 76). Holarctic gall-inducers on herbaceous plants or *Rubus* 14



Figs. 78 and 79. Fig. 78, *Ceroptres* sp., metasoma, lateral view. USNMENT00917016. Fig. 79, *Ceroptres* sp., head, anterior view. USNMENT00917016.

13. Metasomal T2 separated from T3 by suture; T2 much smaller than T3 (Fig. 78); first tergum hardly visible (Fig. 78). Depression present ventral of torulus (arrows, Fig. 79). Upper face, mesopleuron and vertex smooth. Metasoma hair patch often present. Pronotal plate complete Ceroptresini



Figs. 80 and 81. Fig. 80, *Synergus* sp. Metasoma, lateral view. USNMENT01231858. Fig. 81, *Synergus lignicola* (Osten-Sacken, 1862), head, anterior view. USNMENT01448497.

— Second and third tergum of metasoma fused into syntergum (T2 + 3, **Fig. 80**); no suture present between T2 and T3; first tergum relatively large, ring-like, longitudinally sulcate (arrow, **Fig. 80**). Depression absent ventral of torulus (though striae frequently present) (**Fig. 81**). Upper face, mesopleuron and vertex with various degrees of sculpture, not smooth. Pronotal plate incomplete dorsallySynergini



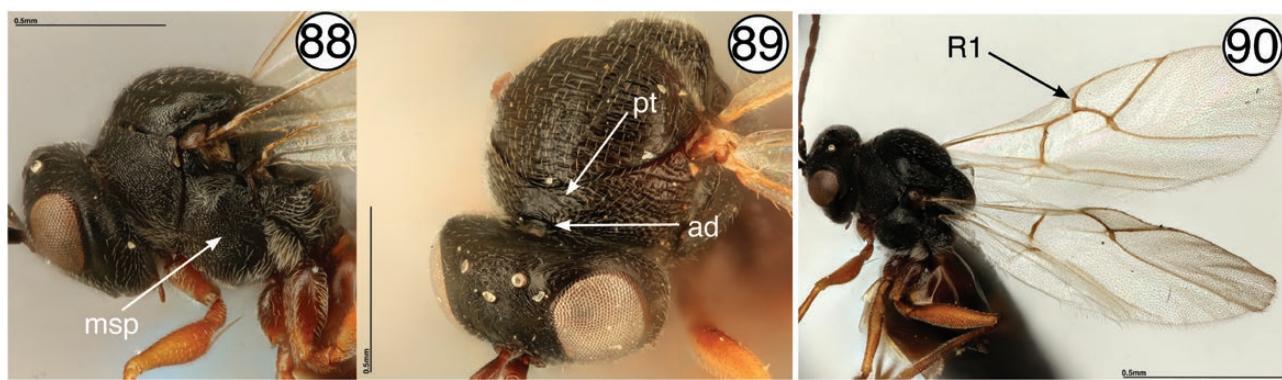
Figs. 82 and 83. Fig. 82, *Diastrophus kinkaidii*, antero-dorsal view. USNMENT01448499. Fig. 83, *Diastrophus kinkaidii*, lateral view. USNMENT01448499.

14. Pronotal plate present, defined dorsally and ventrally (pt, **Fig. 82**). Mesopleuron and mesosoma smooth (msp, **Fig. 83**). Most females with 10 flagellomeres in antenna. Metatarsal claws with distinct lobe. Gallers and inquilines on Rosaceae, or host unknown Diastrophini



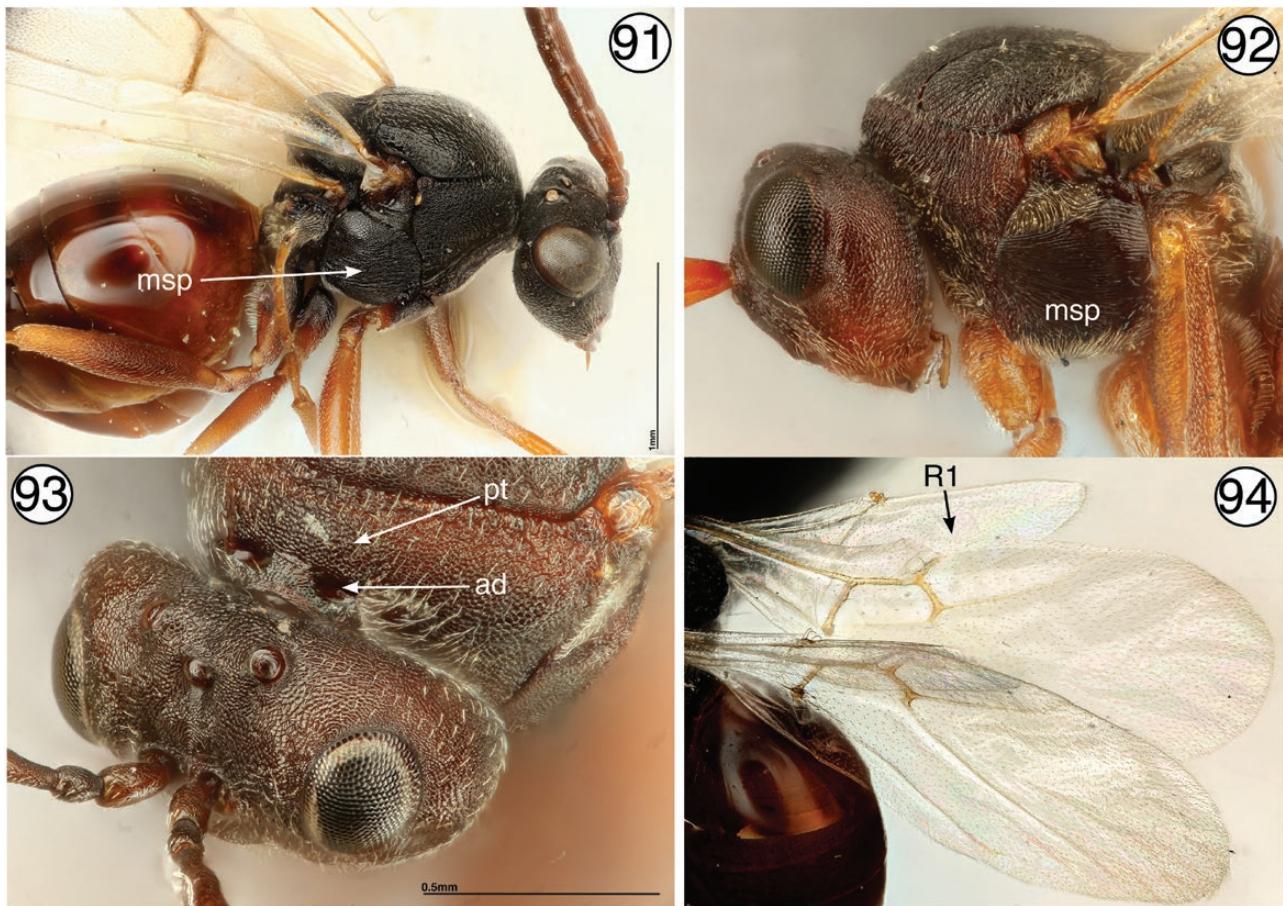
Figs. 84–87. Fig. 84, *Aulacidea podagrae* (Bassett, 1890), antero-dorsal view. USNMENT01448495. Fig. 85, *Antistrophus laciniatus* Gillette, 1891, antero-dorsal view. USNMENT01448496. Fig. 86, *Antistrophus laciniatus*, lateral view. USNMENT01448496. Fig. 87, *Aulacidea podagrae*, lateral view. USNMENT01448495.

— Pronotal plate incomplete, not defined dorsally (pt, Figs. 84 and 85). Mesopleuron and mesosoma sculptured to various degrees (msp, Figs. 86 and 87). Most females with more than 10 flagellomeres in antenna. Metatarsal claws simple. Gollers on various herbaceous plants 15



Figs. 88–90. Fig. 88, *Phanacis* sp., lateral view. USNMENT01448498. Fig. 89, *Phanacis* sp., antero-dorsal view. USNMENT01448498. Fig. 90, *Phanacis* sp., forewings. USNMENT01231855.

15. Mesopleuron with reticulate or rugulose sculpture (msp, Fig. 88). Submedian depressions on pronotal plate effaced, shallow, and indistinct (ad, Fig. 89). Dorsal part of pronotal plate not reaching mesoscutum (pt, Fig. 89). R1 in forewing reaching anterior margin of wing (R1, Fig. 90), and marginal cell at least partially closed (Fig. 90). Gollers on Asteraceae, rarely on other plants Phanacidini



Figs. 91–94. Fig. 91, *Barbotinia oranensis*, lateral view. USNMENT01448491. Fig. 92, *Aulacidea podagrae*, lateral view. USNMENT01448495. Fig. 93, *Antistrophus laciniata*, antero-dorsal view. USNMENT01448496. Fig. 94, *Antistrophus laciniata*, forewings. USNMENT01448496.

— Mesopleuron longitudinally striate, striate-reticulate, or smooth, never rugulose (msp, Figs. 91 and 92). Submedian depressions of pronotal plate present, typically separated (ad, Fig. 93). Dorsal part of pronotal plate typically reaching mesoscutum. R1 of forewing reaching or not reaching wing margin (R1, Fig. 94). Marginal cell open or closed (Fig. 94)..... 16



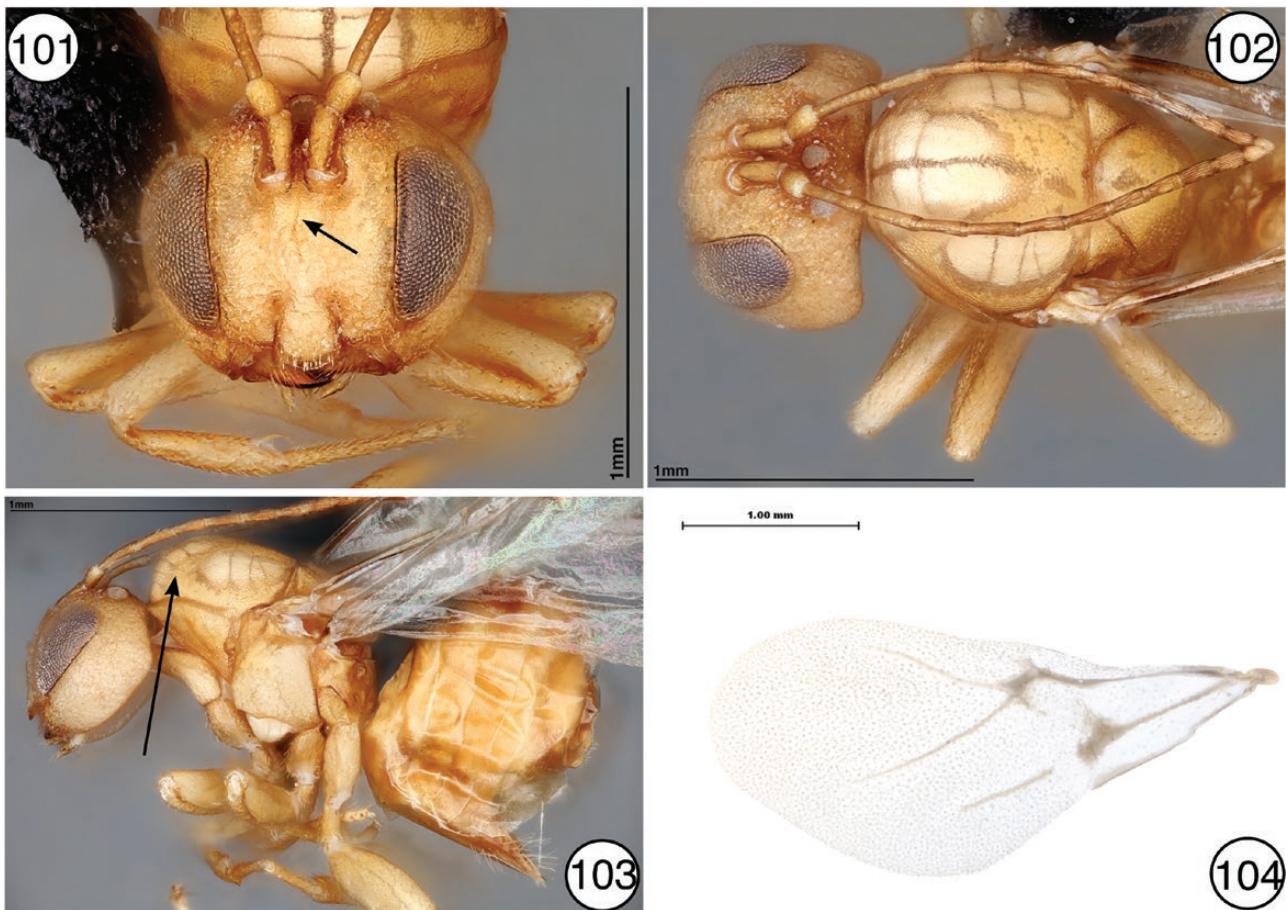
Figs. 95 and 96. Fig. 95, *Iraella ionescui* Pujade-Villar & Schiopu, 2015, lateral view. USNMENT01231864. Fig. 96, *Iraella ionescui*, antero-dorsal view. USNMENT01231864.

16. Mesopleuron striate-reticulate or reticulate (msp, Fig. 95); female antenna with 12 flagellomeres; pronotum (in dorsal view) short, about 1/5 as long as greatest length of outer margin (pt, Fig. 96); admedian depressions narrowly separated and strongly transverse (ad, Fig. 96); gallers on *Papaver* (Papaveraceae)Aylacini



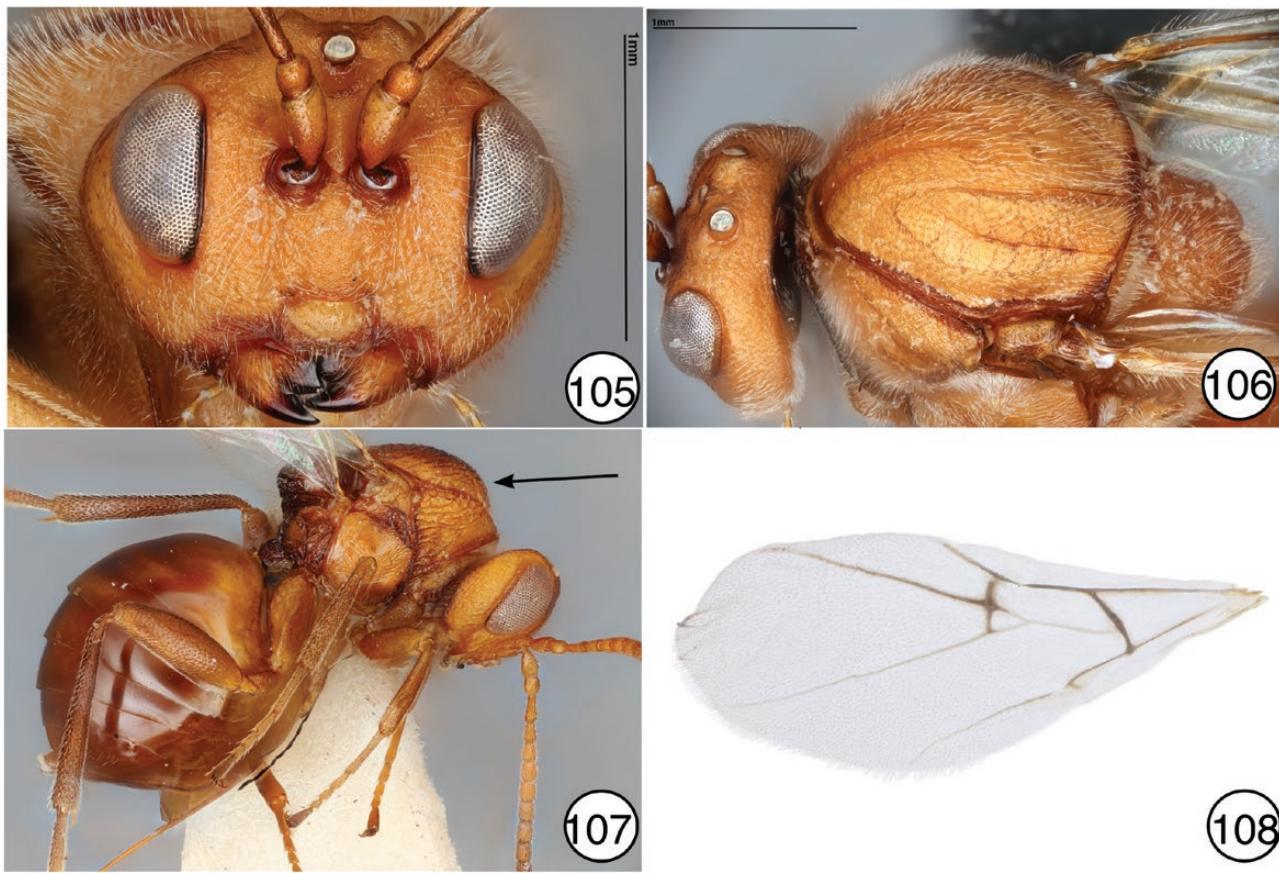
Figs. 97–100. Fig. 97, *Antistrophus laciniata*, lateral view. USNMENT01448496. Fig. 98, *Aulacidea podagrae*, lateral view. USNMENT01448495. Fig. 99, *Aulacidea podagrae*, antero-dorsal view. USNMENT01448495. Fig. 100, *Antistrophus laciniata*, antero-dorsal view. USNMENT01448496.

— Mesopleuron longitudinally striate (msp, Figs. 97 and 98); female antenna with 10–11 flagellomeres; pronotum (in dorsal view) longer, about 1/3 to 1/4 as long as greatest length of outer margin (pt, Figs. 99 and 100); admedian depressions oval or round, usually more widely separated (ad, Fig. 100); gallers on Asteraceae, Lamiaceae, Valerianaceae, and Papaveraceae Aulacideini



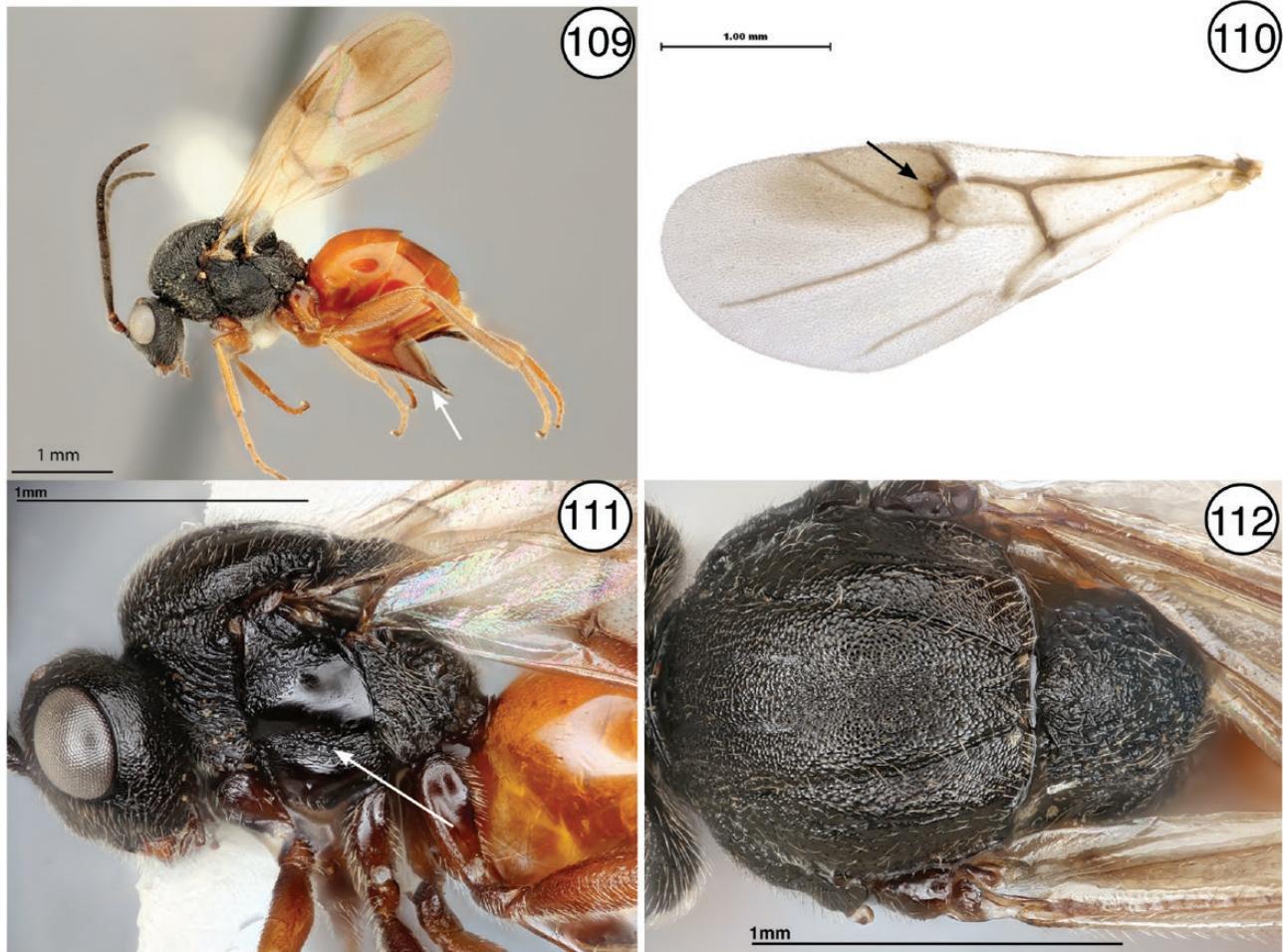
Figs. 101–104. Fig. 101, *Eschatocerus acaciae* Mayr, 1881, head, anterior view. USNMENT01231863. Fig. 102, *Eschatocerus acaciae*, dorsal view. USNMENT01231863. Fig. 103, *Eschatocerus acaciae*, lateral view. USNMENT01231863. Fig. 104, *Eschatocerus acaciae*, forewing. USNMENT00655966.

17. Frons between antennal toruli with strong longitudinal carina (arrow, Fig. 101); notauli and scutellar foveae absent (Fig. 102); mesoscutum bulging above pronotum (arrow, Fig. 103); Rs+M and R1 of forewing inconspicuous, marginal cell with Rs separate from anterior wing margin; basal vein absent (Fig. 104); Neotropical gall-inducers on *Acacia* or *Prosopis* *Eschatocerini*



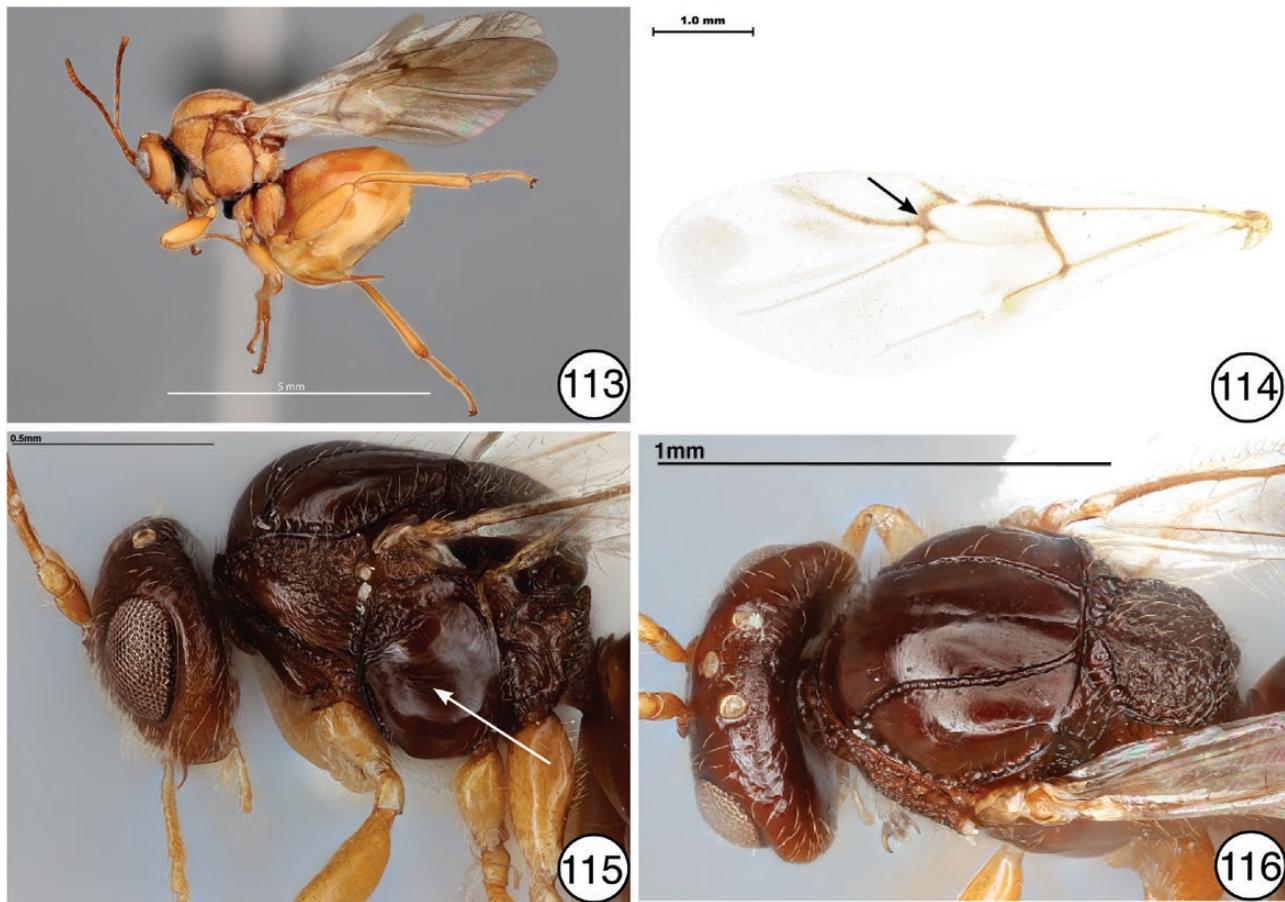
Figs. 105–108. Fig. 105, *Andricus quercusalifornicus*, head, anterior view. USNMENT01231839. Fig. 106, *Andricus quercusalifornicus*, dorsal view. USNMENT01231839. Fig. 107, *Callirhytis glandium* (Giraud, 1859), lateral view. USNMENT01231862. Fig. 108, *Cerroneuroterus* sp., forewing. USNMENT00655874.

— Frons usually without median carina (Fig. 105); if present, (some *Plagiotrochus*) then it is not so strong and cannot be readily differentiated from Fig. 101. Notauli complete, incomplete or absent (Fig. 106). Scutellar foveae present or confluent, forming shallow transverse depression in lateral view. Mesoscutum not bulging above pronotum (arrow, Fig. 107); Rs+M and R1 of forewing usually present and visible, Rs reaching or almost reaching anterior wing margin. Basal vein present (Fig. 108) in forewing. Gall-inducers on Fagaceae or *Rosa* 18



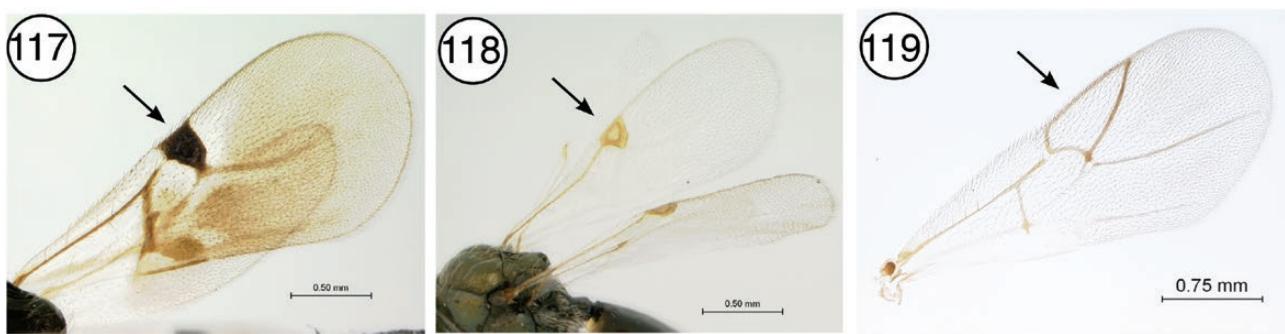
Figs. 109–112. Fig. 109, *Diplolepis bicolor*, lateral view. USNMENT01231831. Fig. 110, *Diplolepis rosae*, forewing. USNMENT00655959. Fig. 111, *Diplolepis bicolor*, lateral view. USNMENT01231831. Fig. 112, *Diplolepis bicolor*, dorsal view. USNMENT01231831.

18. Mesopleuron with a broad, crenulate mesopleural impression (arrow, Fig. 111). Usually with a combination of the following character states: hypopygium plough-shaped (arrow, Fig. 109); lateral propodeal carinae indistinct; scutellar foveae faint or absent (Fig. 112); 2r of forewing with a median vein stump projecting distad (arrow, Fig. 110); Holarctic gall-inducers on *Rosa*Diplolepidini



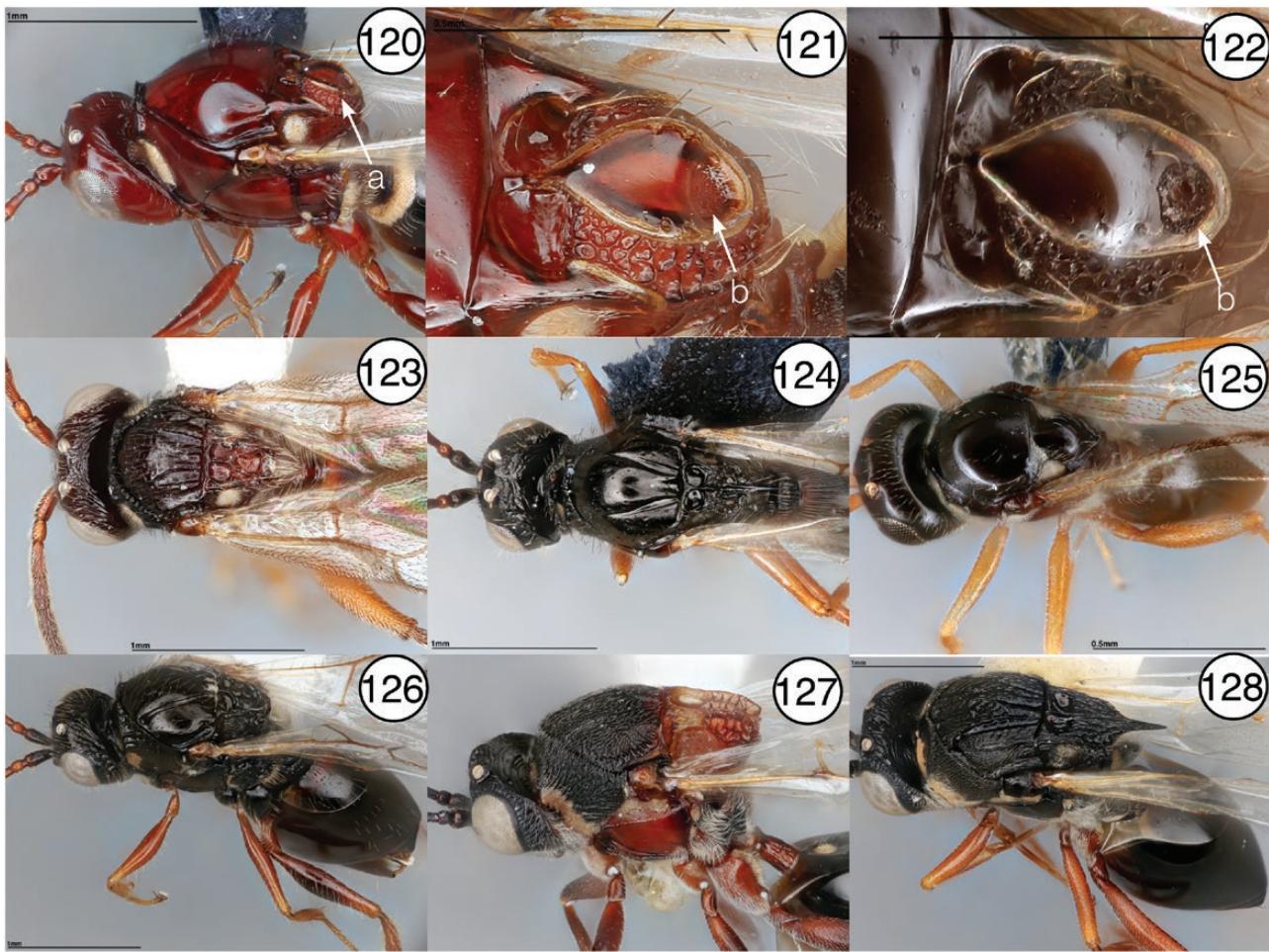
Figs. 113–116. Fig. 113, *Andricus quercusalifornicus*, lateral view. USNMENT01231839. Fig. 114, *Andricus cornigerus* (Osten-Sacken, 1862), forewing. USNMENT00655954. Fig. 115, *Dryocosmus kuriphilus* Yasumatsu, 1951, lateral view. USNMENT01231861. Fig. 116, *Dryocosmus kuriphilus*, lateral view. USNMENT01231861.

— Mesopleuron usually without a mesopleural impression (Fig. 113; arrow, Fig. 115). Without other characters combined (Figs. 113–116). Holarctic and Oriental gall-inducers on Fagaceae, mainly *Quercus* Cynipini



Figs. 117–119. Fig. 117, Forewing, *Tylosema dayae*, SAM-HYM-P0024394. Fig. 118, *Pycnostigmus mastersonae* Buffington and van Noort, 2007, forewing. SAM-HYM-P0024397. Fig. 119, *Melanips* sp., forewing. USNMENT00655980.

19. Marginal cell sclerotized into a pseudostigma (arrows, Figs. 117 and 118). Afrotropical and southeastern Palearctic/Middle East Pycnostigminae
— Marginal cell not sclerotized (arrow, Fig. 119) 20



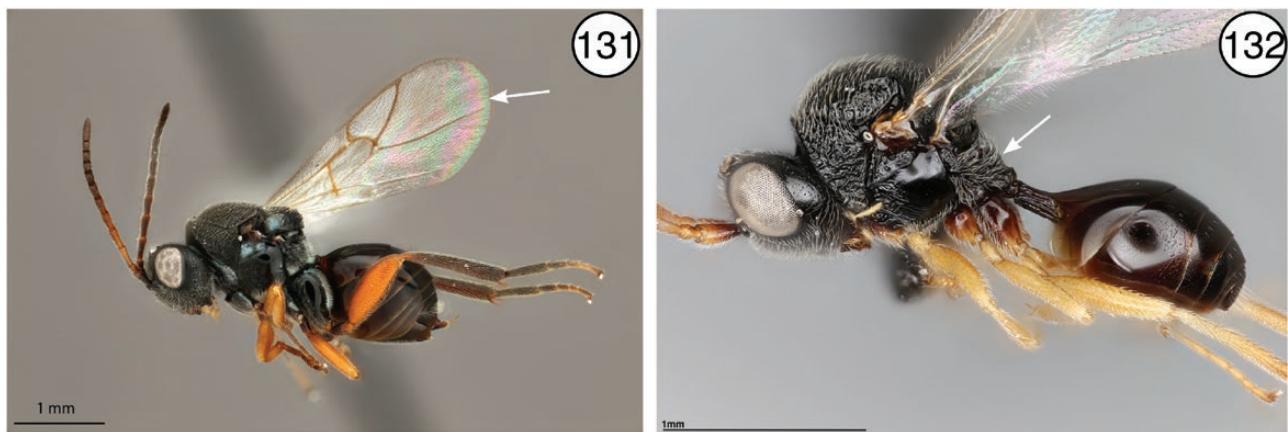
Figs. 120–128. Fig. 120, *Striatovertex* sp., dorso-lateral view. USNMENT01231830. Fig. 121, *Afrostilba* sp., dorso-lateral view. USNMENT01022103. Fig. 122, *Trybliographa melanoptera*, dorsal view. USNMENT01231838. Fig. 123, *Scutimica* sp., dorsal view. USNMENT01231860. Fig. 124, *Neralsia* sp., dorsal view. USNMENT01231869. Fig. 125, *Alloxysta* sp., dorsal view. USNMENT01231868. Fig. 126, *Figitis* sp., dorso-lateral view. USNMENT01231842. Fig. 127, *Callaspidea* sp., lateral view. USNMENT01231867. Fig. 128, *Aspicera hartigi* Dalla Torre, 1843, dorso-lateral view. USNMENT01231866.

20. Scutellum with an elevated scutellar plate (a, **Fig. 120**); with a glandular release pit (b, **Figs. 121** and **122**) Eucoilinae
— Structure of scutellum variable, posterior surface relatively flat or evenly convex, never with a distinct elevated plate and associated posterior release pit (**Figs. 123–128**) 21



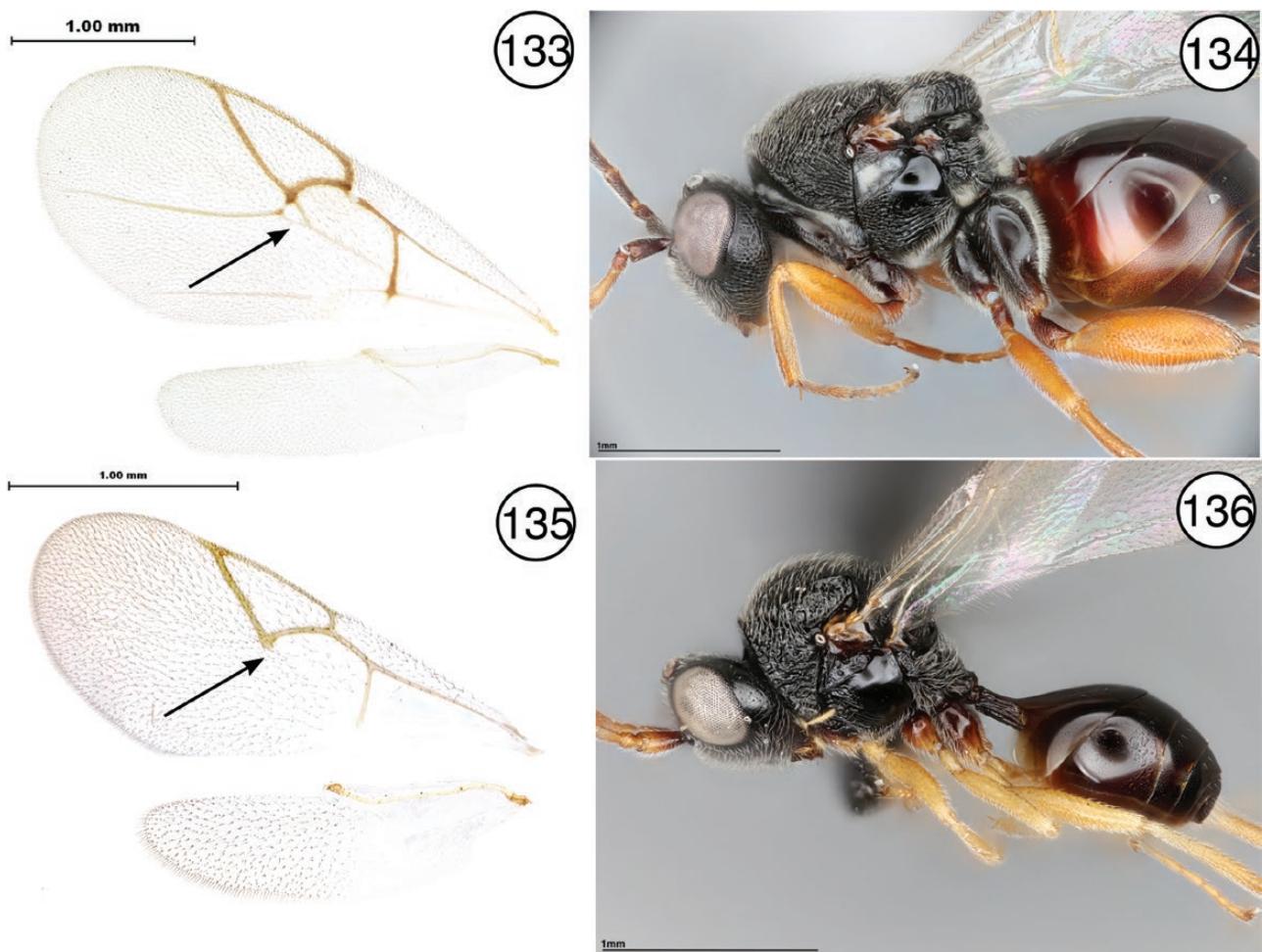
Figs. 129 and 130. Fig. 129, *Thoreauella* sp., lateral view. USNMENT01525887. Fig. 130, *Thoreauella* sp., lateral view. USNMENT01022106.

21. Apex of forewing deeply bilobed (arrow, **Fig. 129**). Often raised median area on scutellum. Densely packed (foamy) setae present on propodeum (arrow, **Fig. 130**). Typically 1.5 mm in length Emargininae



Figs. 131 and 132. Fig. 131, *Euceroptris maritimus*, lateral view. USNMENT01231848. Fig. 132, *Xyalaspis flavipes*, lateral view. USNMENT01231844.

— Apex of forewing rounded (arrow, Fig. 131). Propodeum variously setose to glabrous, never with densely packed setae (Fig. 132) 22



Figs. 133–136. Fig. 133, *Euceroptris maritimus*, forewing. USNMENT00655937. Fig. 134, *Euceroptris maritimus*, lateral view. USNMENT01231848. Fig. 135, *Xyalaspis* sp., forewing. USNMENT00655972. Fig. 136, *Xyalaspis flavipes*, lateral view. USNMENT01231844.

22. Areolet present (arrow, Fig. 133); base of metasoma setose or glabrous (Fig. 134) 23

— Areolet absent (arrow, Fig. 135); base of metasoma glabrous (Fig. 136) 25



137



138

Figs. 137 and 138. Fig. 137, *Euceroptres maritimus*, dorso-lateral view. USNMENT01231848. Fig. 138, *Figites* sp., lateral view. USNMENT01231842.

23. Head and mesoscutum generally coriaceous to foveate, and frequently setose (Fig. 137) 24
 — Head and mesoscutum generally smooth, lacking dense setal patterns, but some stout setae present (Fig. 138) some Figitiniae



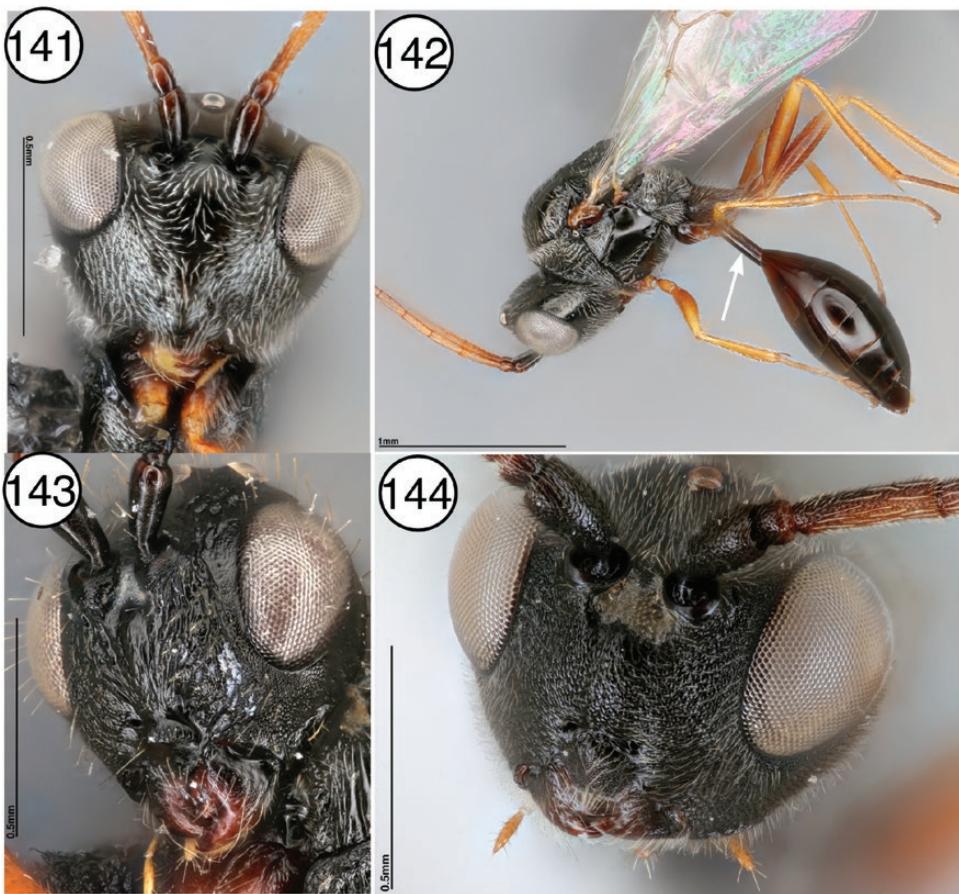
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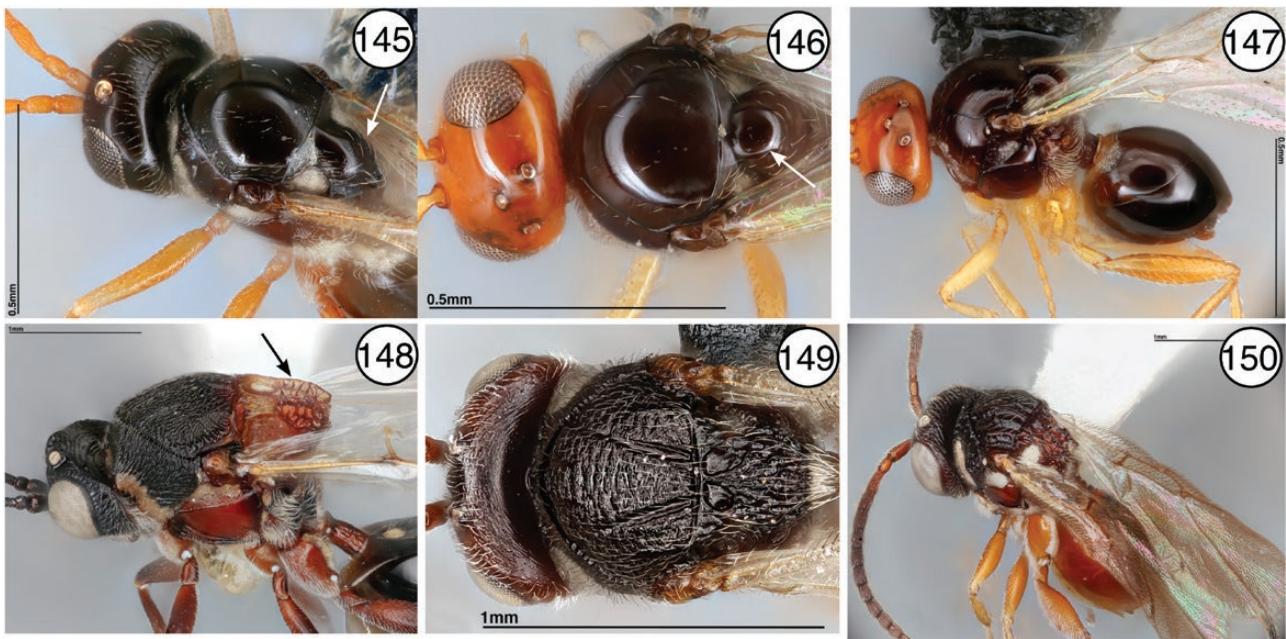
Figs. 139 and 140. Fig. 139, *Parnips nigripes* (Barbotin 1964), lateral view. USNMENT01231874. Fig. 140, *Euceroptres maritimus*, lateral view. USNMENT01231848.

24. Mesopleuron striate, with no indication of distinct mesopleural furrow (arrow, Fig. 139). Lateral pronotal carina absent. Mediterranean, on *Papaver* Parnipinae
 — Mesopleuron dorsally smooth, ventrally striate along the distinct mesopleural furrow (arrow, Fig. 140). Lateral pronotal carina present. Nearctic, on *Quercus* Euceroptrinae



Figs. 141–144. Fig. 141, *Anacharis melanoneura* Ashmead, 1887, head, anterior view. USNMENT01231833. Fig. 142, *Anacharis melanoneura*, lateral view. USNMENT01231833. Fig. 143, *Callaspidea* sp., head, anterior view. USNMENT01231867. Fig. 144, *Neralisia* sp., head, anterior view. USNMENT01231869.

25. Head generally triangular in anterior view; mouth small, with broadly overlapping mandibles (Fig. 141). Petiole often long (arrow, Fig. 142). First metasomal tergum subequal in length to second, sometimes longer *Anacharitinae*
 — Head oval to round in anterior view (Figs. 143 and 144); mouth region broadened, mandibles larger and not extensively overlapping. Petiole typically not elongate 26



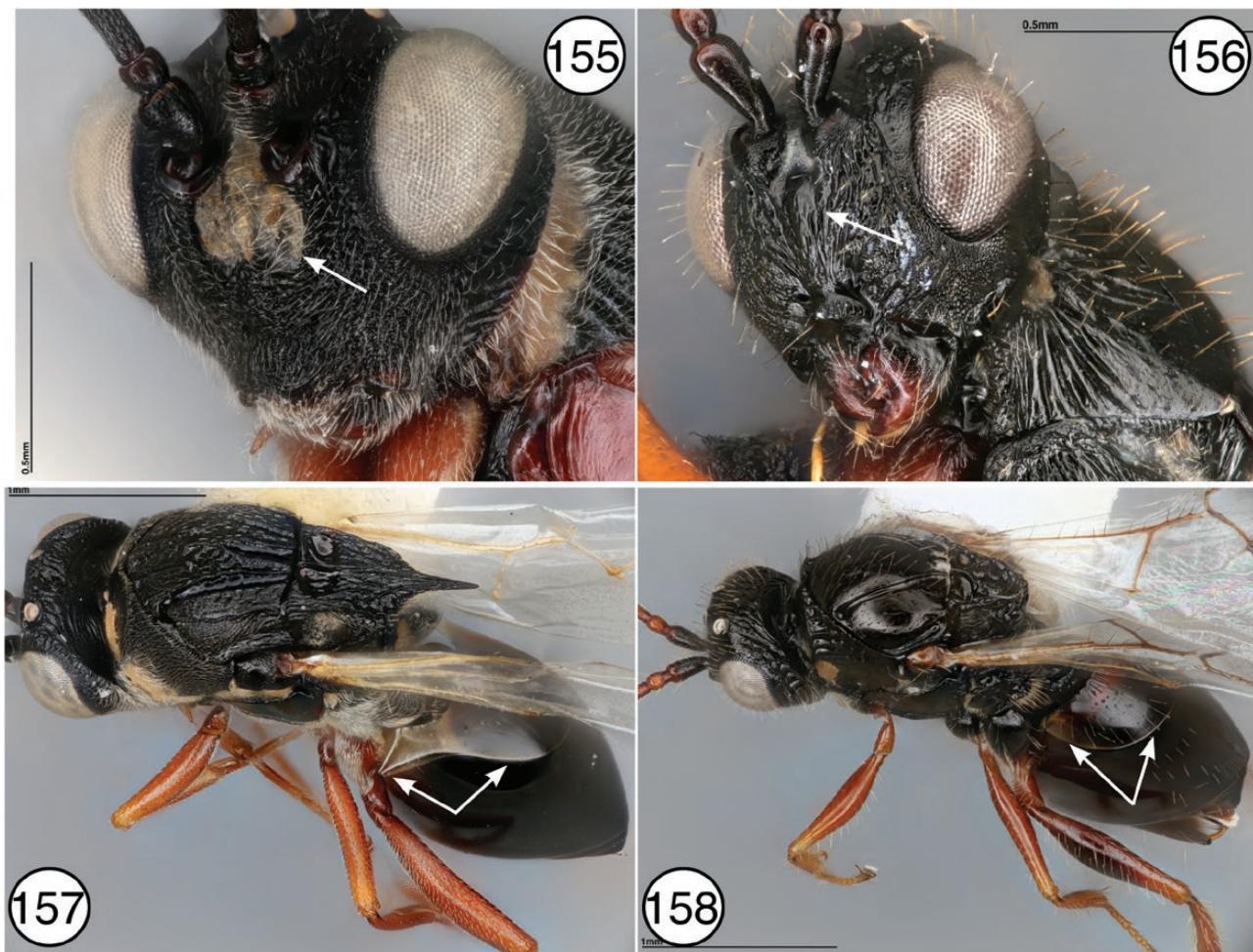
Figs. 145–150. Fig. 145, *Apocharisps trapezoidea* (Hartig, 1841), dorso-lateral view. USNMENT01231873. Fig. 146, *Alloxysta* sp. dorsal view. USNMENT01231840. Fig. 147, *Alloxysta* sp. lateral view. USNMENT01231840. Fig. 148, *Callaspidia* sp., lateral view. USNMENT01231867. Fig. 149, *Myrtopsen mimosae* Weld, 1926, dorsal view. USNMENT01525867. Fig. 150, *Scutimica* sp., dorso-lateral view. USNMENT01231860.

26. Scutellum evenly convex, rounded, smooth (arrows, Figs. 145 and 146). Usually tiny, very often pale in color (Fig. 147). Mesoscutum usually shiny and smooth (Figs. 145–147), rarely matte Charipinae
— Scutellum flat or weakly convex, and sculptured (Figs. 148–150). Usually darker, typically black. Mesoscutum usually with transverse ridges or distinct microsculpture (Figs. 148–150) 27



Figs. 151–154. Fig. 151, *Plectocynips lago* Buffington and Nieves-Aldrey, 2011, lateral view. USNMENT01231872. Fig. 152, *Araucocynips* sp., hind leg. USNMENT01231865. Fig. 153, *Plectocynips lago*, hind leg. USNMENT01231872. Fig. 154, *Callaspidia* sp., hind leg. USNMENT01231867.

27. Metatibial spur remarkably long, more than half the length of basal tarsomere (arrows, Figs. 151–153). Neotropical; associated with *Nothofagus* forests. Rarely encountered Plectocynipinae
— Metatibial spur not remarkably long, at most a quarter of length of first tarsomere (arrow, Fig. 154) 28



Figs. 155–158. Fig. 155, *Callaspidea* sp., head, anterior view. USNMENT01231867. Fig. 156, *Neralsia* sp., head, anterior view. USNMENT01231869. Fig. 157, *Aspicera hartigi*, dorso-lateral view. USNMENT01231866. Fig. 158, *Figites* sp., dorso-lateral view. USNMENT01231842.

28. Facial impression present (arrow, Fig. 155). First metasomal tergum saddle-like with concave posterolateral margin and more or less lin-guiform median part (arrows, Fig. 157). Often relatively large, with a well sculptured body, often red color, and wings with strongly reduced pubescence and accessory veins core Asicerinae
— Facial impression absent (arrow, Fig. 156). First metasomal tergum rounded, usually with a convex margin (arrows, Fig. 158). Size varying from relatively large to very small 29



Figs. 159 and 160. Fig. 159, *Mikeius hartigi* (Girault, 1929), lateral view. USNMENT01231871. Fig. 160, *Melanips* sp., mesosoma, lateral view. USNMENT01231847.
29. Short petiole, no flange or collar (arrow, Fig. 159). Inquilines, mostly in Australia and Neotropical region, very rare in Nearctic and East Palearctic regions. Rarely encountered 30
— Longer petiolar region, with a reduced basal metasomal tergum forming a collar or sheath over petiole (arrow, Fig. 160) 31



Figs. 161–163. Fig. 161, *Myrtopsen mimosae*, head, anterior view. USNMENT01525867. Fig. 162, *Scutimica* sp., head, dorsal view. USNMENT01231860. Fig. 163, *Mikeius hartigi*, head, anterior view. USNMENT01231871.
30. With a circumtorular impression (an impression above antennal insertion) (cti, Figs. 161 and 162). Often with a well-developed pronotal plate (pt, Fig. 162) Thrasorinae
— Without a circumtorular impression (arrow, Fig. 163). Without a well-developed pronotal plate, just visible laterally (pt, Fig. 163). Australia only Mikeiinae



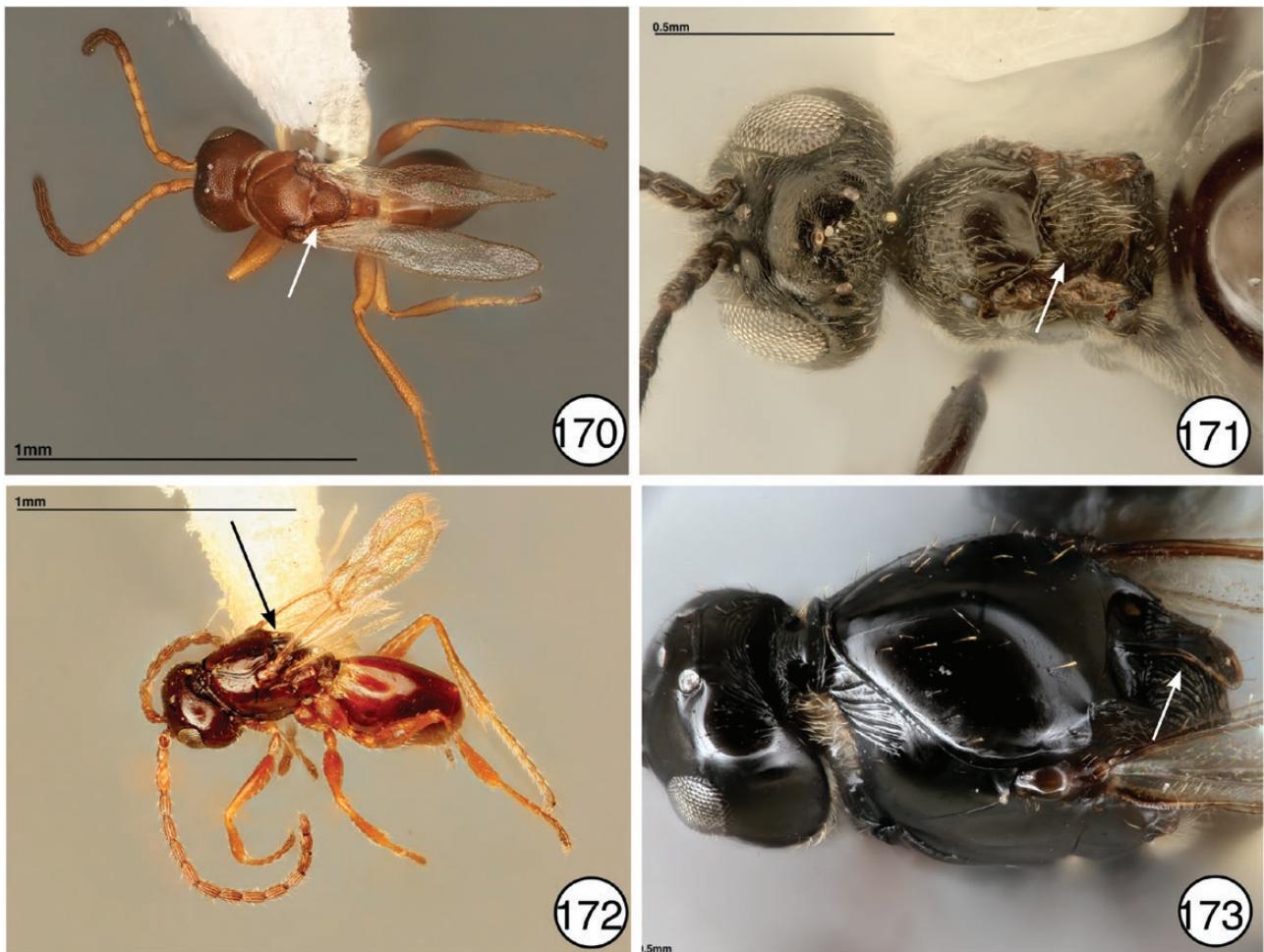
Figs. 164–167. Fig. 164, *Neralsia* sp., lateral view. USNMENT01231869. Fig. 165, *Melanips* sp., mesosoma, lateral view. USNMENT01231847. Fig. 166, *Neralsia* sp., head, anterior view. USNMENT01231869. Fig. 167, *Melanips* sp., head, anterior view. USNMENT01231847.

31. Without a metasomal hairpatch (arrow, Fig. 164). Eyes commonly setose (arrow, Fig 166) core Figitinae
— With a metasomal hair patch (arrow, Fig 165). Eyes typically glabrous (arrow, Fig. 167) 32



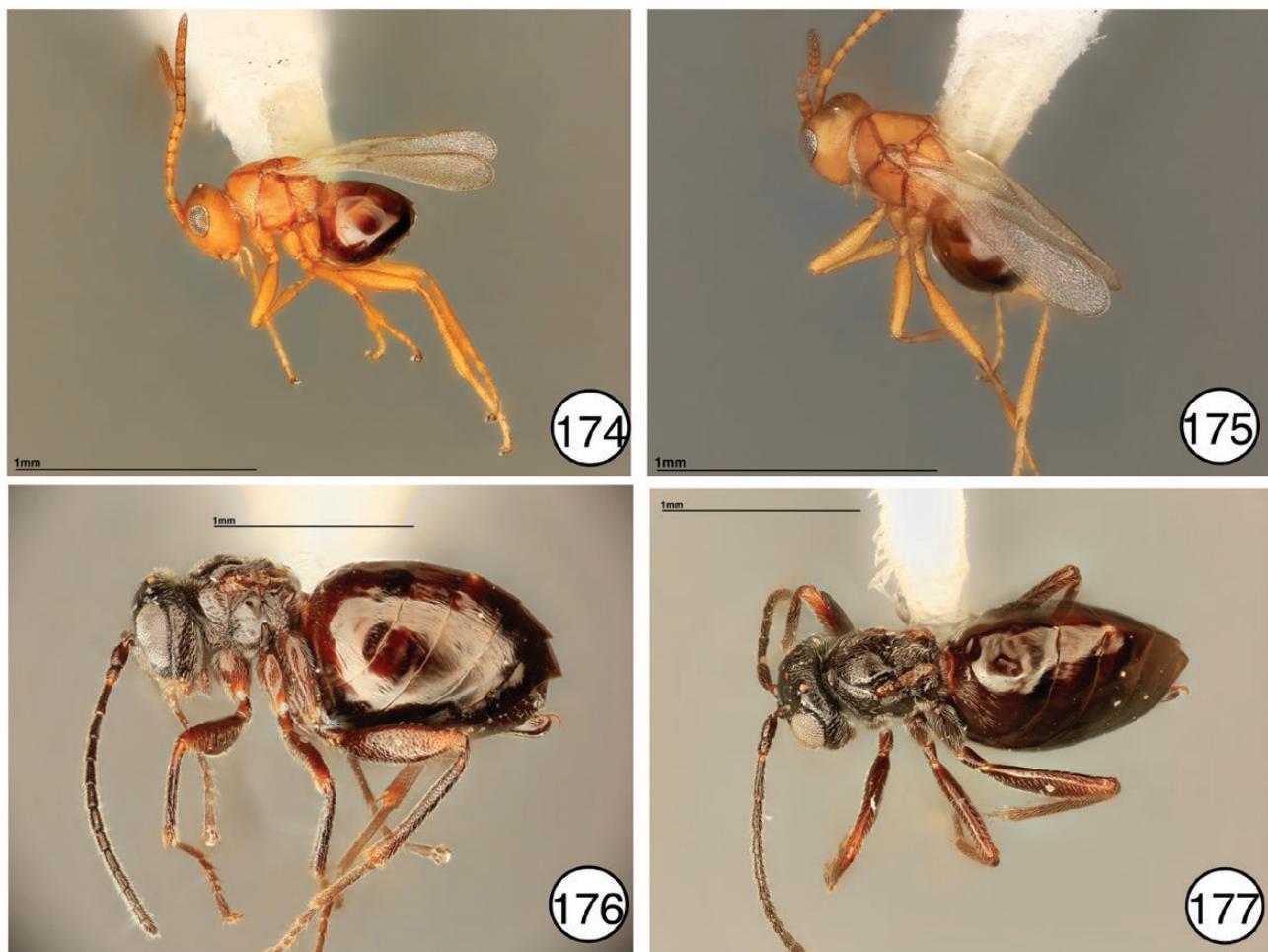
Figs. 168 and 169. Fig. 168, *Lonchidia* sp., dorsal view. USNMENT01525866. Fig. 169, *Melanips* sp., mesosoma, dorsal view. USNMENT01231847.

32. Mesoscutum typically shining, lacking microsculpture (Fig. 168), frequently with long setae present several Figitinae
— Mesoscutum matte and leathery with dense microsculpture (Fig. 169) *Melanips* (Aspicerinae)



Figs. 170–173. Fig. 170, *Lytoxysta brevipalpis*, dorsal view. USNMENT01231836. Fig. 171, *Phylloteras* sp., dorsal view. USNMENT01231835. Fig. 172, *Kleidotoma* sp., dorso-lateral view. USNMENT01231837. Fig. 173, *Kleidotoma* sp., head and mesosoma, dorso-lateral view. USNMENT01525865.

33. Scutellum simple, without a distinct scutellar plate (arrows, Figs. 170 and 171) 34
 — Scutellum surmounted by distinct scutellar plate (arrows, Figs. 172 and 173) Eucoilineae



Figs. 174–177. Fig. 174, *Lytoxysta brevipalpis*, lateral view. USNMENT01231836. Fig. 175, *Lytoxysta brevipalpis*, dorso-lateral view. USNMENT01231836. Fig. 176, *Phylloteras* sp., lateral view. USNMENT01231835. Fig. 177, *Phylloteras* sp., dorsal view. USNMENT01231835.

34. Metasoma about the size of the mesosoma (Figs. 174 and 175); brachyptery (Figs. 174 and 175) more common than aptery. Color variable but very often pale. Mesosoma usually not strikingly narrow. Scutellum evenly convex. Mainly in summer in the Holarctic Region
..... Charipinae
- Metasoma at least twice the size of mesosoma (Figs. 176 and 177), both segments the same size; apterous (Figs. 176 and 177) to brachypterous. Color from pale to dark brown. Mesosoma usually strikingly narrow. Scutellum rather flat. Mainly in the winter half of the year in the Holarctic Region..... Cynipini (alternate generation of winged forms)

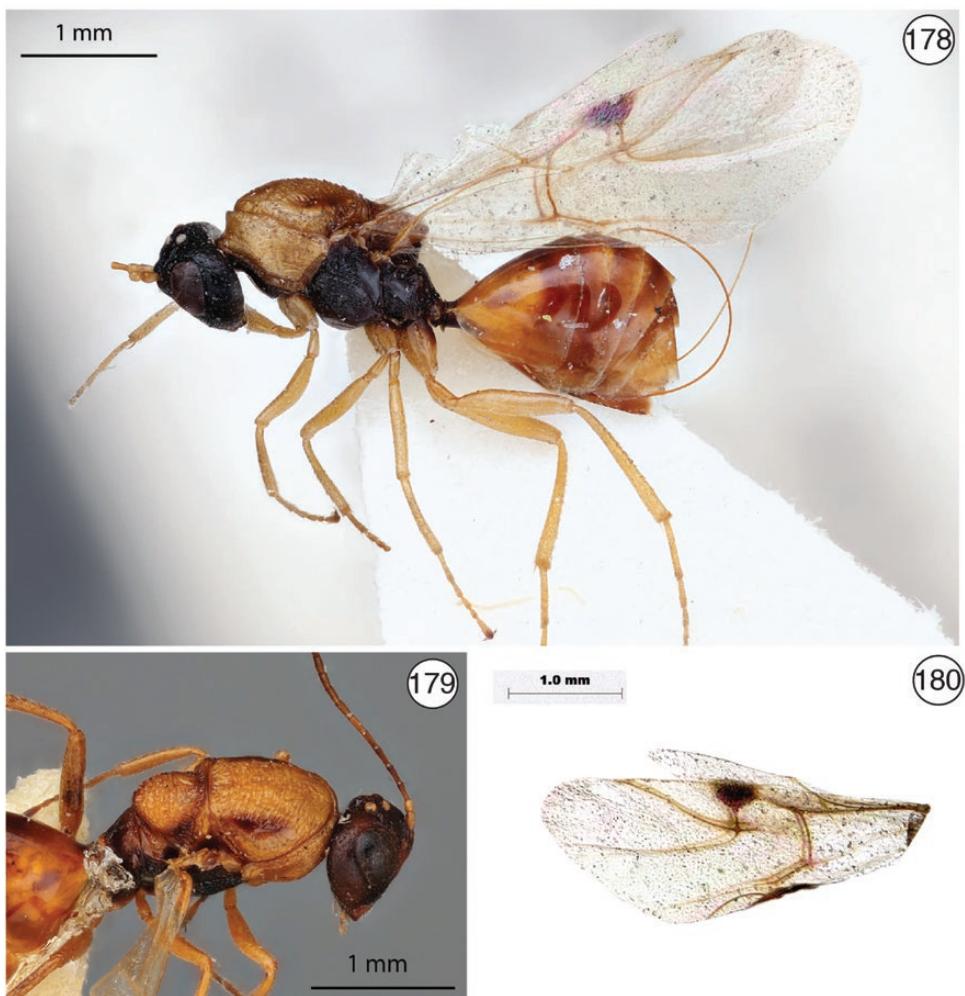


Plate 1. Figs. 178–180. *Austrocynipidae*. *Austrocynips mirabilis*. Holotype, ANIC.

Systematic Overview

Austrocynipidae

Figs. 178–180

This monotypic family is one of the rarest within the Hymenoptera. *Austrocynips mirabilis* Riek, 1971 was reared from cones of hoop pine (*Araucaria cunninghamii* Aiton ex D. Don) in Australia that were infested with oecophorid moths. Previously, cones from these trees were collected for propagation and timber production; this is now achieved through other means, and cones are not regularly collected. As these cones are difficult to access, *Austrocynips* has not been collected again since the original description. Riek (1971) reports that other species of *Araucaria* were also surveyed but yielded no *Austrocynips*.

Biology. Host Unknown. Collected from *Araucaria* cones infested with oecophorid moths (Ronquist 1999).

Distribution. Australia: Queensland.

Relevant literature. Riek, 1971; description. Páretas-Martínez et al., 2013; overview.

Classification.

Austrocynipidae Riek, 1971

Austrocynips Riek, 1971; 1 species in Australia.



Plate 2. Figs. 181–183. Ibaliiidae. *Ibalia anceps*. USNMENT01231826.

Ibaliiidae

Figs. 181–183

Ibaliiids are generally a holarctic group with the highest species richness in North America (Liu and Nordlander 1992). These are very distinct cynipoids, often brightly colored, and several times larger in body size than any other cynipoids (some liopterids are also large). Ronquist (1995a,b) hypothesized that this group, along with liopterids and *Astrocytips*, composing the ‘macrocynipoids’, represent the most plesiomorphic forms of cynipoids, and further suggesting that the ground-plan biology for cynipoids is parasitizing wood boring insect larvae. This argument is supported by the fact that all members of macrocynipoid families possess horizontally striate mesoscuta, putatively an adaptation to chewing out of woody substrates where their hosts dwell. Indeed, ibaliids are known to be koinobiont endoparasitoids of siricid woodwasps (Hymenoptera: Siricidae)

(Hurley et al. 2020). Species of *Ibalia* are typically not very rare in the eastern Nearctic Region and parts of the Palearctic Region; species in the desert southwest of the United States are more rarely encountered. Species of *Heteribalia* are not common in the wild, but one species is regularly intercepted from wood products entering the United States from China (Buffington, personal observation). *Eileenella* has not been collected since its description. *Eileenella* has been placed in its own monotypic subfamily Eileneellinae Kovalev, 1994, which appears not to have been formally synonymized in the literature, even though its usefulness is obviously limited and has not been commonly cited.

Biology. Koinobiont endoparasitoids of Siricidae (Hymenoptera).

Distribution. Holarctic and Oriental, one genus extends into Papua New Guinea; Introduced to Australia, New Zealand, and South Africa for biological control (Hurley et al. 2020).



Plate 3. Liopteridae. Fig. 184, *Liopteron* sp., USNMENT01231879. Fig. 185, *Oberthuerella lenticularis* Saussure, 1890, USNMENT00764775. Fig. 186, *Peras* sp., UFES68459. Figs. 187 and 189, *Paramblynotus virginianus*, USNMENT01231827. Fig. 188, *Paramblynotus* sp., USNMENT01231878.

Relevant literature. Ronquist and Nordlander (1989) provided an exhaustive study of the morphology of *Ibalia rufipes* that remains the basis of all morphological studies among cynipoids; Liu and Nordlander 1994, revision; Nordlander et al. 1996, phylogeny; Ronquist 1999, review.

Classification.

Ibaliidae Thomson, 1862

Ibalia Latreille, 1802; 14 species NA, PA, OR, introduced AT, AU

Heteribalia Sakagami, 1949; 5 species OR, ePA

Eileenella Fergusson, 1992; 1 species Papua New Guinea

Liopteridae

Figs. 184–189

As with the ibaliids, most members of this family are rather striking in appearance, often to be found outside the cynipoids in museum collections of Hymenoptera. Some are brightly colored, though most species have a dark, black, and shiny appearance. As mentioned elsewhere, liopterids are among the macrocynipoids: large in size, with horizontally striate mesoscuta. There are no definitive host records, only anecdotal evidence that they are parasitoids of wood-boring insect larvae (Ronquist 1995a, Buffington et al. 2012). Four subfamilies are recognized, and species/genera have been often been classified in Cynipidae and other groups.

Loipterids are found worldwide except the western Palearctic Region; most species are found in the tropics and subtropics. *Paramblynnotus* is the most speciose of all loipterid genera, with an incredible diversity of species in southeast Asia. Most loipterids are rarely encountered in the field, though *Paramblynnotus* can be very abundant in Malaise traps during certain times of the year.

Biology. Associated with wood; presumably parasitoids of wood-boring insect larvae.

Distribution. Worldwide except western Palearctic Region. Of the subfamilies, Mayellinae has the same distribution as the entire family, whereas the other are more restricted: Dallatorrellinae: Paleotropical; Oberthuerellinae: Afrotropical; Liopterinae: Neotropical.

Relevant literature. Hedicke and Kerrich (1940) and Ronquist (1995a) revised the family. Liu et al. (2007) revised *Paramblynnotus*. Buffington and van Noort (2012) revised the Oberthuerellinae; van Noort and Buffington (2013) revised Afrotropical Mayellinae. Ronquist (1995a) provides a complete overview of the family, keys all the genera, and provides a world catalog. Liu et al. (2007) revises *Paramblynnotus*, the most speciose of all loipterid genera. Van Noort et al. (2015) reviews all sub-Saharan Africa species and provides a key to genera.

Classification.

Liopteridae Ashmead, 1895

Mayellinae Hedicke, 1922

Kiefferiella Ashmead, 1903; 2 species NA

Paramblynnotus Cameron, 1908; 106 species worldwide except wPA

Dallatorrellinae Kieffer, 1911

Mesocynips Cameron, 1903; 1 species OR

Dallatorrella Kieffer, 1911; 8 species OR, AU

Oberthuerellinae Hedicke, 1903

Xenocynips Kieffer, 1910; 3 species AT

Tessmannella Hedicke, 1912; 6 species AT

Oberthuerella Saussure, 1903; 18 species AT

Liopterinae Ashmead, 1895

Liopteron Perty, 1833; 8 species NT

Peras Westwood, 1837; 10 species NT

Pseudibalia Kieffer, 1911; 13 species NT

Cynipidae: Cynipinae

Note: Most commonly in recent years, authorship of family-group names based on *Cynips* has been quoted from Latreille (1802). However, Alonso-Zarazaga and Nieves-Aldrey (2002) corrected the authorship of the family since Latreille did not include any actual cynipids in his family, and the name was not made available until later, making 'Billberg, 1820' the correct authorship.

The current classification of the Cynipidae places all extant forms in a single subfamily, with the majority of species falling into one of four tribes: the oak gallers (Cynipini), the herb gallers (Aylacini), the

rose gallers (Diplolepidini), and the inquilines (Synergini). *Ceroptres*, previously classified within Synergini, have recently been placed into their own tribe, the Ceroptrresini. *Diastrophus*, gallers on rosaceous herbs, were previously classified within Aylacini, are now in their own tribe, Diastrophini, which includes some inquiline genera. Many herb galling genera, previously classified within Aylacini, have been moved to Aulacideini and Phanacidini. Rarer tribes include the Pediaspidini (maple gallers), and the Eschatocerini (gallers of *Acacia* and *Prosopis* in the Fabaceae). Lastly, two additional rare tribes have been recently described based on morphologically divergent forms from the Southern Hemisphere: Qwaqwaaiini, including a single gall inducer on *Scolopia* (Salicaceae) in South Africa, and Paraulacini, including two genera (*Paraulax* and *Cecinothofagus*) of inquilines (or possibly parasitoids) in chalcidoid galls on *Nothofagus* (Nothofagaceae) in southern South America (Chile).

Nieves-Aldrey (2001) provides an overview of the Iberian fauna and provides keys to tribes. Ronquist et al. (2015) established several new tribes and provided an illustrated key. Pujade-Villar (2019) follows the same classification of Ronquist et al. (2015) and provides an alternative identification key. Unlike many other insect groups, cynipids can also be readily identified by the gall left behind after the adult wasp has emerged. Weld (1957, 1959, 1960a) pioneered this form of identification, and summarized what was known about gall morphology and host plant records in series of privately printed pamphlets. In addition, Weld's own collection of galls are located at the USNM and have undergone recuration recently. More recently, Russo (2006) has updated much of Weld's work, and includes not only color images of galls, but also covers other galling insects of North America. Further, Coulianov and Holmåsen (1991) provide an overview of galls in Scandinavia.

Aulacideini

Figs. 190–192

This recently circumscribed tribe includes many taxa formerly treated in Aylacini, many species of which are treated by Nieves-Aldrey (1994). Members moved to Aulacideini include species that are gallers on Lamiaceae and Asteraceae (Ronquist et al. 2015), but do not include the gallers of Papaveraceae (now Aylacini) or Rosaceae (now Diastrophini).

Biology. Gall inducers on various herbaceous plants in Asteraceae, Lamiaceae, Valerianaceae, and some Papaveraceae (Ronquist et al. 2015). *Aulacidea subterminalis* have been used in the biological control of invasive weeds in North America (APHIS 2011) and New Zealand (Syrett et al. 2001).

Distribution. Holarctic.

Relevant literature. Ronquist et al. (2015) described the tribe; Ronquist (1994) and Liljeblad and Ronquist (1998) treated species in this group phylogenetically using morphology. Melika (2006) reviewed the western Palearctic fauna. Buffington et al. (2017) reported on *Antistrophus* on *Silphium*. *Neaylax salviae* was detailed in Nieves-Aldrey (2002); Zerova et al. (2003) described the morphology and biology of *Salviela* Melika. Life cycle of *Aulacidea subterminalis* has been studied in depth by Syrett et al. (2001) and introduced into New Zealand and North America for weed control.

Classification.

Aulacideini Nieves-Aldrey, Nylander and Ronquist, 2015 (the availability and authorship of this name is disputed and will hopefully be settled soon)

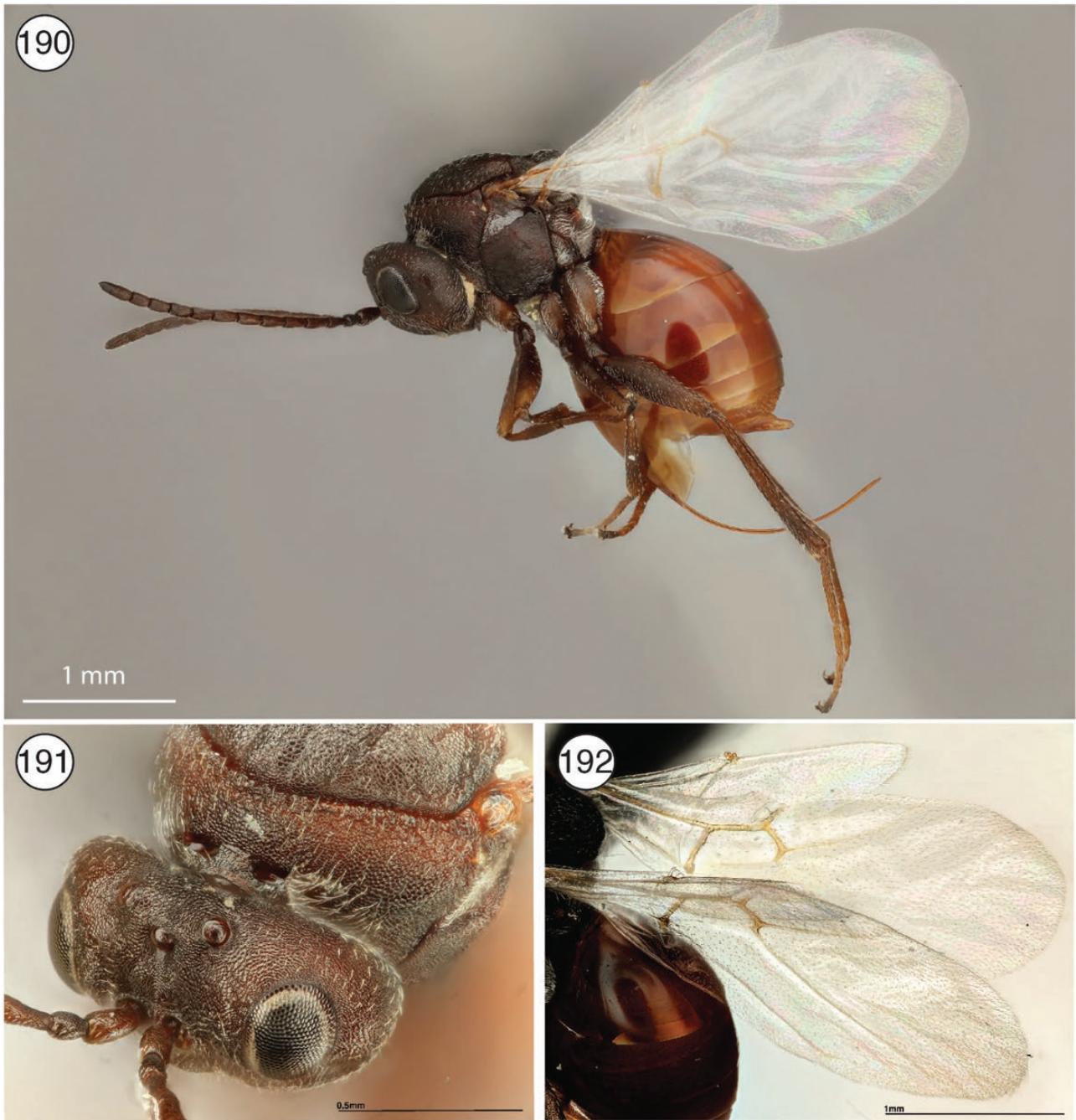


Plate 4. Aulacideini. Figs. 190–192. *Antistrophus laciniatus*. USNMENT01448496

Antistrophus Walsh, 1869; 10 species NA

Aulacidea Ashmead, 1897; 38 species PA, NA

Cecconia Kieffer, 1902; 1 species wPA

Hedickiana Nieves-Aldrey, 1994; 1 species wPA

Isocolus Förster, 1869; 26 species PA

Liposthenes Förster, 1869; 3 species PA, introduced NA

Neaylax Nieves-Aldrey, 1994; 4 species PA

Panteliella Kieffer, 1902; 3 species PA

Rhodus Quinlan, 1968; 1 species wPA

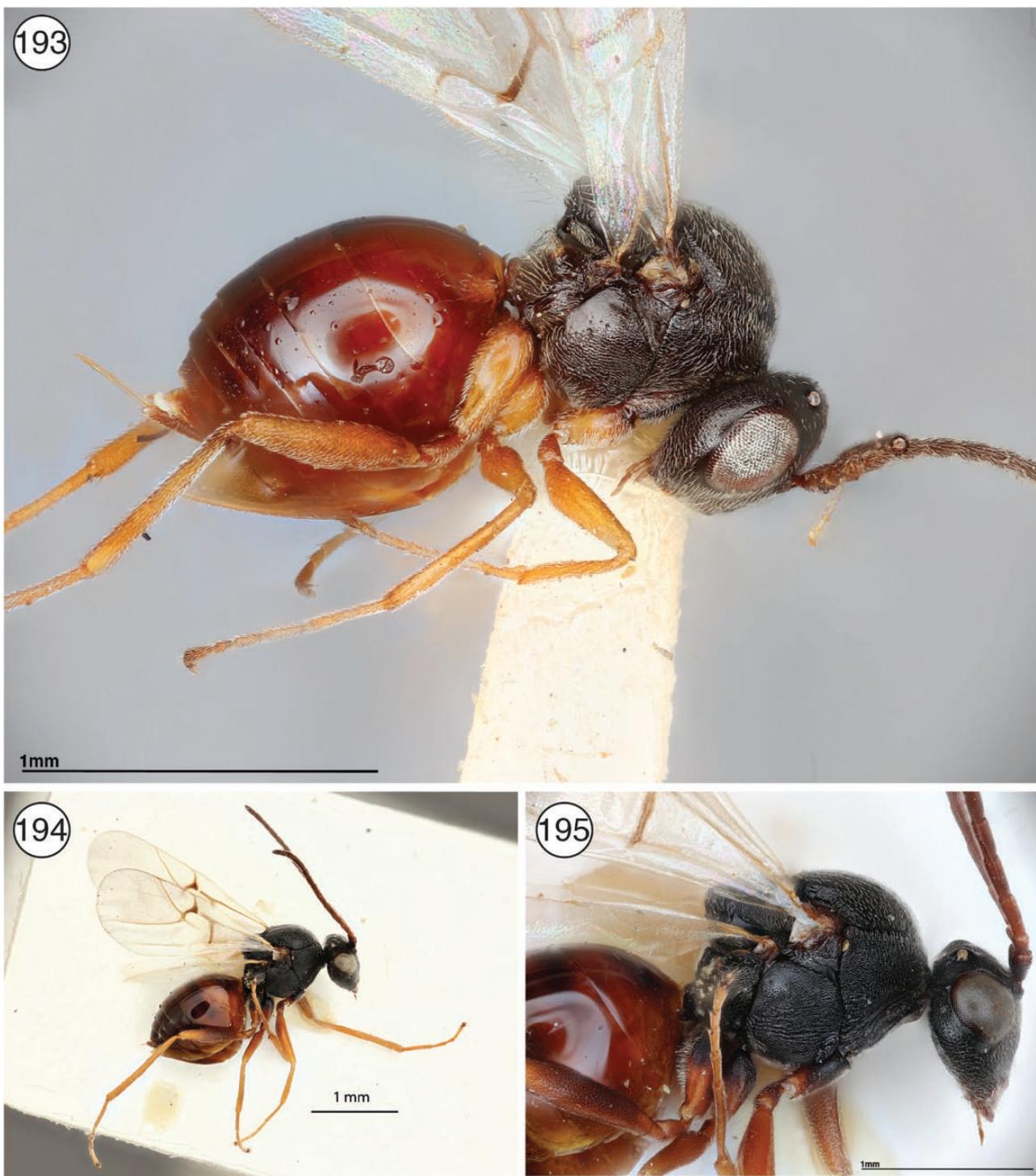


Plate 5. Aylacini. Fig. 193. *Aylax papaveris*, lateral view, USNMENT01231856. Figs. 194 and 195. *Barbotinia oranienis*, USNMENT01448491.

Aylacini

Figs. 193–195

Ronquist (1994) argued that this tribe, as it was circumscribed, was not monophyletic, and formed the basal lineages of Cynipidae. Following this, Liljeblad and Ronquist (1998) presented more robust data to support splitting up Aylacini, but no action was taken until Ronquist et al. (2015). We now recognize this tribe as being restricted to species galling *Papaver* in the Palearctic region. Several taxa previously classified in this tribe can now be

found in Aulacideini, Phanacidini, and Diastrophini. These taxa all shared the trait of being gallers of herbs and other non-woody plants; Ronquist et al. (2015) concluded that these are unrelated host shifts.

Biology. Gall inducers on *Papaver* in the Palearctic Region.

Distribution. Palearctic Region. Occasionally intercepted on plants being imported to North America; possibly introduced into other regions (Buffington, personal observation).



Plate 6. Ceroptresini. Figs. 196–198. *Ceroptres* sp. USNMENT00917016

Relevant literature. Ronquist et al. (2015) circumscribed our current recognition of this tribe and summarized the biology; Ronquist (1994) and Liljeblad and Ronquist (1998) treated the group phylogenetically based on morphology. Nieves-Aldrey (1994) treated Thomson's Aylacini, many of which are now in Aulacideini. Melika (2006) reviewed the western Palearctic fauna.

Classification.

Aylacini Ashmead, 1903

Aylax Hartig, 1840; 20 species PA, introduced NA
Barbotinia Nieves-Aldrey, 1994; 1 species wPA
Iraella Nieves-Aldrey, 1994; 3 species wPA

Ceroptresini

Figs. 196–198

This very small tribe was erected as the species contained here render *Synergus* paraphyletic. As a result of the topology recovered in Ronquist et al. (2015), *Ceroptres* was moved to the novel tribe Ceroptresini.

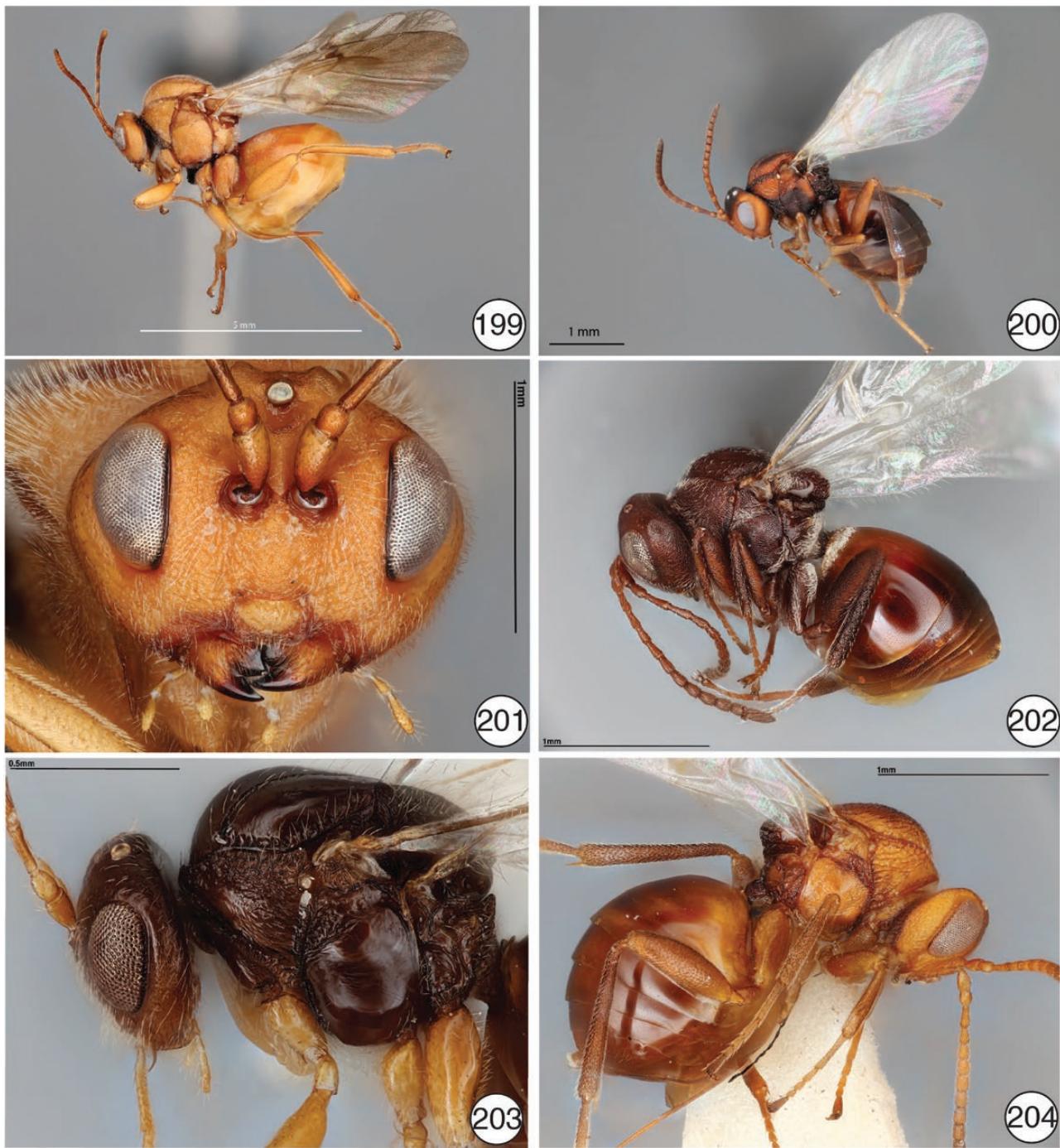


Plate 7. Cynipini. Figs. 199 and 201, *Andricus quercusalifornicus*, USNMENT01231839. Fig. 200, *Melikaiella tumifica* (Osten-Sacken, 1865), USNMENT01525885. Fig. 202, *Zapatella davisae* Buffington & Melika, 2016, USNMENT01231884. Fig. 203, *Dryocosmus kuriphilus*, USNMENT01231861. Fig. 204, *Callirhytis glandium*, USNMENT01231862.

Biology. Possibly inquilines of Cynipini on oaks (Ronquist et al. 2015).

Distribution. Holarctic.

Relevant literature. Tribe circumscribed in Ronquist et al. (2015); revised by Lobato-Vila and Pujade-Villar (2019).

Classification.

Ceroptresini Nieves-Aldrey, Nylander and Ronquist, 2015

Ceroptres Hartig, 1840; 21 species NA, PA

Buffingtonella Lobato-Vila and Pujade-Villar, 2019; 1 species
NA

Cynipini

Figs. 199–204

The majority of cynipid species belong to this single tribe. Members of the tribe are gall inducers on species of *Quercus*, *Castanea*, *Castanopsis*, *Chrysolepis*, and *Lithocarpus* (Fagaceae), by far the largest number on oaks. Many more species and genera are expected to be discovered and described from Asia where Fagaceae

generic diversity is relatively high and little work has been done on the Cynipini fauna until recently (e.g., Tang et al. 2009; Ide et al. 2010; Tang et al. 2011; Melika et al. 2011; Ide et al. 2012; 2013; Melika et al. 2013b; Ide and Abe 2015; Tang et al. 2016). New genera and new species have also been continuously discovered in the Nearctic and Neotropics (e.g., Medianero and Nieves-Aldrey 2011; Medianero et al. 2011; Nieves-Aldrey et al. 2012; Pujade-Villar et al. 2012a, b; Pujade-Villar et al. 2013; Medianero and Nieves-Aldrey 2013), highlighting the fact that the taxonomy of Cynipini is still far from complete. Taxonomy of Cynipini has been controversial, including several species previously classified in *Andricus* and *Callirhytis* having been moved between these two genera (Burks 1979), and several Nearctic *Callirhytis* species transferred to newly erected genera *Kinseyella* (Pujade-Villar et al. 2010) and *Zapatella* (Pujade-Villar et al. 2012b) and *Melikaiella* (Pujade-Villar et al. 2014). Two Palaearctic genera, *Belizinella* Kovalev and *Ussuraspis* Kovalev, were synonymized with *Trigonaspis* (Melika and Abrahamson 2002), but then reestablished as valid genera (Melika 2012). Three Nearctic genera, *Dros* Kinsey, *Erythres* Kinsey, and *Femuros* Kinsey, were synonymized with *Andricus* (Melika and Abrahamson 2002) but then reestablished as valid genera (Pujade-Villar and Melika 2014; Pujade-Villar and Ferrer-Suay 2015; Pujade-Villar et al. 2017). Lastly, *Sphaeroteras*, synonymized with *Biorhiza* by Melika and Abrahamson (2002), was reestablished as a valid genus (Pujade-Villar et al. 2018).

Biology. The life cycle of Cynipini involves cyclical parthenogenesis (heterogony), with a sexual generation where males and females mate to produce an asexual generation of only females, that reproduce parthenogenetically and gives rise to a new bisexual generation. The two generations differ in terms of the gall phenology, galling positions, gall structure, and adult morphology and size. These biological distinctions have been led the two generations of the same species classified as different species and even as different genera in the past. Two Palaearctic genera, *Andricus* and *Callirhytis*, are host alternators (heteroecy) that their life cycles alternate between two host-plant subgroups, section *Cerris* and section *Quercus* sensu stricto in the genus *Quercus*. Although in some species, the two alternating generations have been associated, for many species they have not yet been matched. Field observation is a firm approach to associate the two generations, however, DNA barcoding is another useful tool to pair the two generations (e.g., Ács et al. 2007; Melika et al. 2013a; Nicholls et al. 2018). There are only three exceptions in Cynipini known to reproduce purely parthenogenetically. The first case is the global pest, the chestnut gallwasp *Dryocosmus kuriphilus* Yasumatsu (Aebi et al. 2006). This species has one generation per year and has been introduced into Europe, North America, and some countries in Asia outside its native region in China. The other two species, *Andricus targionii* Kieffer and *A. pseudoflos* (Monzen), from Japan, Korea, China and Far East of Russia, are derived from their cyclically parthenogenetic ancestors *A. mukaigawae* (Mukaigawa) and *A. kashiwaphilus* Abe through the deletion of sexual generation (Abe 2007). Oak gallwasps have been very conservative on their host-plant choices, and host switches were extremely rare in the evolution of oak gallwasps (Stone et al. 2009).

Distribution. Holarctic, Neotropical, and Oriental Regions.

Relevant literature. Nieves-Aldrey (2001) reviews the Iberian fauna. Melika and Abrahamson (2002) made a world revision of Cynipini on the basis of Weld's Cynipoidea monograph (Weld 1952). Stone et al. (2002) and Csóka et al. (2005) reviewed the general biology, ecology,

and evolution of Cynipini, and Abe et al. (2007) reviewed species richness, host-plant diversity, and background on the hypotheses of geographic origin of Cynipini. The Western Palaearctic fauna of Cynipini is reviewed in Melika (2006) on the basis of the Ukrainian fauna. Melika et al. (2010) made a taxonomic revision of species, particularly those that gall section *Cerris* of *Quercus* in the Palaearctic and Oriental region. The most recent knowledge of Cynipini in Eastern Palaearctic and Oriental region is reviewed in Pénzes et al. (2018)

Classification

Cynipini Billberg, 1820

Acraspis Mayr, 1881; 20 species NA

Amphibolips Reinhard, 1865; 53 species NA, NT

Andricus Hartig, 1840; ca 375 species but taxonomy is uncertain and far from stable with many more or less dubious taxa
NA, PA, OR, NT

Aphelonyx Mayr, 1881; 3 species PA

Atrusca Kinsey, 1930; 59 species but taxonomy is uncertain
NA, NT

Barucynips Medianero and Nieves-Aldrey, 2013; 1 species NT
Bassettia Ashmead, 1887; 9 species NA

Belizinella Kovalev, 1965; 2 species ePA

Belonocnema Mayr, 1881; 2 species NA

Biorhiza Westwood, 1840; 6 species PA, NA

Callirhytis Förster, 1869; 80 species but taxonomy is uncertain and far from stable NA, PA

Cerroneuroterus Melika and Pujade-Villar, 2009; 9 species
PA, OR

Chilaspis Mayr, 1881; 2 species wPA

Coffeikokkos Pujade-Villar and Melika, 2012; 2 species NT

Cyclocynips Melika, Tang and Sinclair, 2013; 2 species OR

Cycloneuroterus Melika and Tang, 2011; 17 species OR, ePA

Cynips Linnaeus, 1758; ca 75 species but taxonomy is uncertain and far from stable with many more or less dubious taxa
NA, PA, NT

Disholcaspis Dalla Torre and Kieffer, 1910; 55 species NA, NT
Dros Kinsey, 1937; 5 species NA

Dryocosmus Giraud, 1859; 50 species but diagnostic characters need to be revised and new genera will be erected; PA, NA, OR
Erythres Kinsey, 1937; 2 species NA

Eumayria Ashmead, 1887; 6 species NA

Eumayriella Melika and Abrahamson, 1997; 2 species NA

Femuros Kinsey, 1937; 7 species NA

Heteroecus Kinsey, 1922; 12 species NA

Holocynips Kieffer, 1910; 5 species NA

Kinseyella Pujade-Villar and Melika, 2010; 2 species NA

Kokkocynips Pujade-Villar and Melika, 2013; 1 species NT

Latuspina Monzen, 1954; 9 species ePA, OR

Loxaulus Mayr, 1881; 17 species NA, NT

Melikaiella Pujade-Villar, 2014; 14 species NA

Neuroterus Hartig, 1840; 79 species but taxonomy is uncertain and far from stable including more or less dubious taxa;
PA, NA, NT

Odontocynips Kieffer, 1910; 3 species NA, NT

Philonix Fitch, 1859; 7 species NA

Phylloteras Ashmead, 1897; 9 species NA

Plagiotrochus Mayr, 1881; 22 species PA, OR

Protobalandricus Melika, Nicholls and Stone, 2018; 1 species NA

Pseudoneuroterus Kinsey, 1923; 4 species wPA



Plate 8. Diastrophini. Figs. 205–207, *Diastrophus kinkaidii*, USNMENT01448499.

Sphaeroteras Ashmead, 1897; recently resurrected with 5 species; NA, NT
Striatoandricus Pujade-Villar, 2020; 6 species NA
Trichagalma Mayr, 1907; 3 species ePA, OR
Trigonaspis Hartig, 1840; 22 species PA, NA
Ussuraspis Kovalev, 1965; 1 species ePA
Zapatella Pujade-Villar and Melika, 2012; 13 species NA, NT
Zopheroteras Ashmead, 1897; 6 species NA

Diastrophini

Figs. 205–207

This tribe, circumscribed in Ronquist et al. (2015), contains the gallers *Diastrophus* and *Xestophanes*, formerly included in the tribe Aylacini, and the inquilines *Perclistus* and *Synophromorpha*, formerly included in the Synergini. Both the gallers and the inquilines are associated with host plants in the family Rosaceae. With respect to the inquilines, this appears to be a case of agastoparasitism, where the inquiline of a gall inducer is a close relative. Hence, including these inquilines in Synergini rendered that tribe paraphyletic.

Biology. Species are associated with Rosaceae (Rosa, Rubus), with both gall-inducers (*Diastrophus*, *Xestophanes*) or inquilines (*Perclistus*, *Synophromorpha*). A very common host plant are species of *Rubus*. Records of association with the monocot *Smilax* (Ashmead 1896, Ronquist et al. 2015) are probably erroneous (Buffington and Gates, pers. obs.).

Distribution. Holarctic, transgressing into the Neotropics.

Relevant literature. Tribe is circumscribed and diagnosed in Ronquist et al. (2015). Ronquist (1994) first investigated the group phylogenetically and recognized the Aylacini where these genera previously were classified as paraphyletic. Ritchie and Shorthouse (1987) revised *Synophromorpha*.

Classification.

Diastrophini Nieves-Aldrey, Nylander and Ronquist, 2015

Diastrophus Hartig, 1840; 19 species NA, PA, NT

Perclistus Förster, 1869; 16 species NA, PA

Synophromorpha Ashmead, 1903; 6 species NA, ePA

Xestophanes Förster, 1869; 4 species PA, ePA

Diplolepidini

Figs. 208–210

Members of this tribe are all gallers of *Rosa* in the Holarctic Region. The wide variety of galls produced by these species, and the relative ease of locating them in the field, has led to a rather extensive literature on the biology and ecology of these wasps. A very thorough review by Shorthouse (1993) describes in detail the research on the diplolepidine wasps, including gall induction, larval feeding, life cycle aspects, and parasitoids. As hybridization among rose species can be common, confusing the taxonomy of the group, rose gallers seem to have adapted to intermediate species, much in the same way oak gallers in the Cynipini seem to have ‘specialized’ on intermediate oak species.

Morphologically, these wasps all share a rather unique hypopygium that extends ventrally, and has been described as ‘plough-share shaped’ in literature. Phylogenetically, Liljeblad and Ronquist (1998) recovered this group as sister to *Eschatocerus*, with

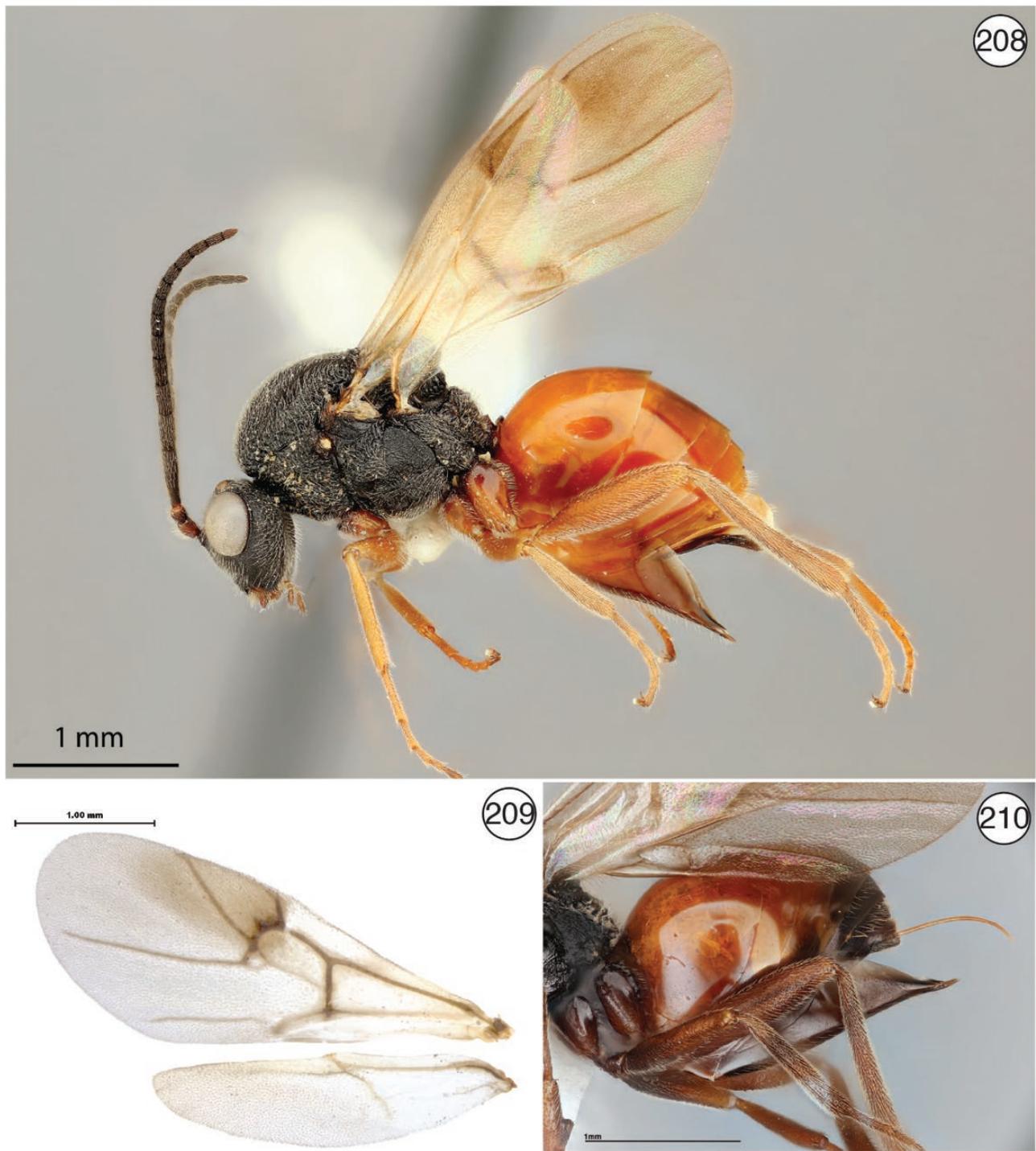


Plate 9. Diplolepidini. Fig. 208, *Diplolepisspp.*, USNMENT01231850. Fig. 209, *Diplolepis rosae*, USNMENT00655959. Fig. 210, *Diplolepis bicolor*, USNMENT01231831.

low support. More recently, Ronquist et al. (2015) found the group sister to Pediaspini and Eschatocerini.

Biology. Gall inducers on *Rosa* (Rosaceae).

Distribution. Holarctic. Could be moved into non-native areas with horticultural products.

Relevant literature. Shorthouse (1993, 2001) are the most comprehensive reviews to date; Ronquist (1994, 1999), Liljeblad

and Ronquist (1998), and Ronquist et al. (2015) investigated the phylogenetics of the group.

Classification.

Diplolepidini Latreille, 1802

Diplolepis Geoffroy, 1762; 52 species but taxonomy is uncertain and far from stable with many more or less dubious taxa; NA, PA
Lielbelia Kieffer, 1903; 9 species PA



Plate 10. Eschatocerini. Figs. 211–213, *Eschatocerus acaciae*, USNMENT01231863 and USNMENT00655966.

Eschatocerini

Figs. 211–213

This monotypic tribe may feel unsatisfactory for taxonomy, but its erection is based on phylogeny (Ronquist et al. 2015). This unusual group can be readily collected when host plants are located; otherwise, the taxon is rarely collected.

Biology. Species are gall inducers on *Prosopis* spp. and *Acacia* spp. (Fabaceae) in South America.

Distribution. Arid regions of the Neotropics.

Relevant literature. Nieves-Aldrey and San Blas (2015) revised the tribe and described the biology in depth; Ronquist (1995b) and Ronquist et al. (2015) studied the phylogenetic placement of the group.

Classification.

Eschatocerini Ashmead, 1903

Eschatocerus Mayr, 1881; 3 species NT

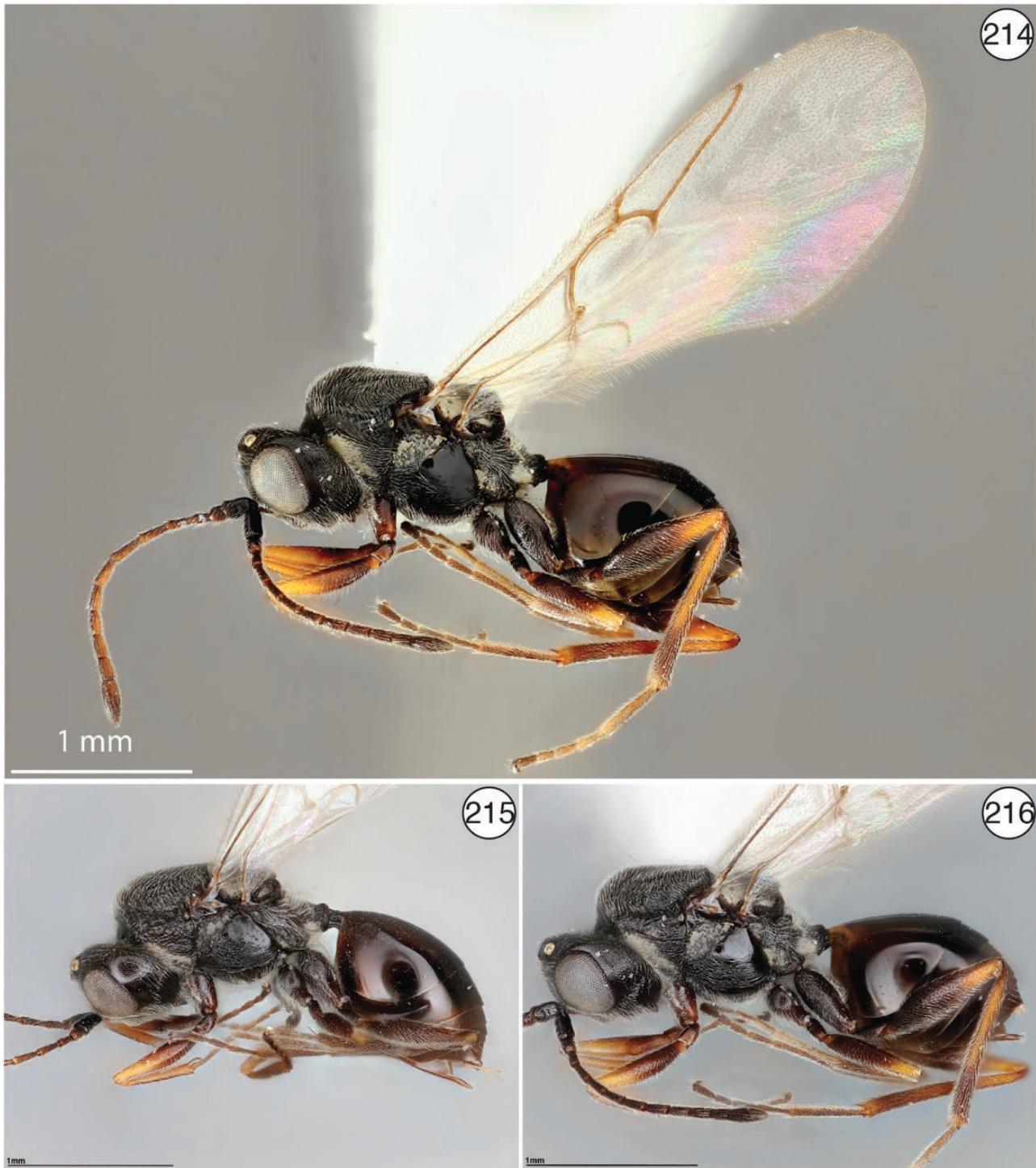


Plate 11. Paraulacini. Figs. 214 and 216, *Paraulax queulensis*, USNMENT01231854. Fig. 215, *Cecinothophagus* sp., USNMENT01231851.

Paraulacini

Figs. 214–216

Species of Paraulacini have been reared from galls on *Nothofagus* spp. in southern Chile and Argentina. However, it is unclear whether these wasps are gall inducers, inquilines of chalcidoid gall inducers, or parasitoids of chalcidoid gall inducers (Ronquist et al. 2015). *Paraulax* was described by Kieffer (1904) and was tentatively placed in Aylacini (Dalla Torre and Kieffer 1910; Weld 1952), later

in Cynipini (Ronquist 1999), then in Pediaspidini (Liljeblad et al. 2008). Nieves-Aldrey et al. (2009), based on biology and phylogeny, circumscribed Paraulacini to accommodate species in *Paraulax* as well as the new genus *Cecinothophagus*.

Biology. Unknown. Reared from galls on *Nothofagus* trees (Nothofagaceae).

Distribution. Southern South America.



Plate 12. Pediaspidini. Figs. 217 and 218. *Pediaspis aceris*, USNMENT01231852.

Relevant literature. Nieves-Aldrey et al. (2009) summarizes the group completely.

Classification.

Paraulacini Nieves-Aldrey and Liljeblad, 2009

Cecinothofagus Nieves-Aldrey and Liljeblad, 2009; 3 species NT

Paraulax Kieffer, 1904; 3 species NT

Pediaspidini

Figs. 217 and 218

The name has been rendered alternately as Pediaspini and Pediaspidini in literature. Pediaspidini is the linguistically correct, and there is no prevailing usage that speaks for the other option. This tribe of Palearctic species gall *Acer* spp. *Himalocynips* (biology

unknown) was originally described in its own family (Yoshimoto 1970).

Biology. Gall inducers on maple trees (*Acer* spp; Sapindaceae).

Distribution. Palearctic Region. *Himalocynips* only known from Nepal (Yoshimoto 1970).

Relevant literature. Ronquist (1995b) suggested the inclusion of *Himalocynips* within Pediaspidini, and has been followed since.

Classification.

Pediaspidini Ashmead, 1903

Himalocynips Yoshimoto, 1970; 1 species Himalaya

Pediaspis Tischbein, 1852; 1 species wPA, NT

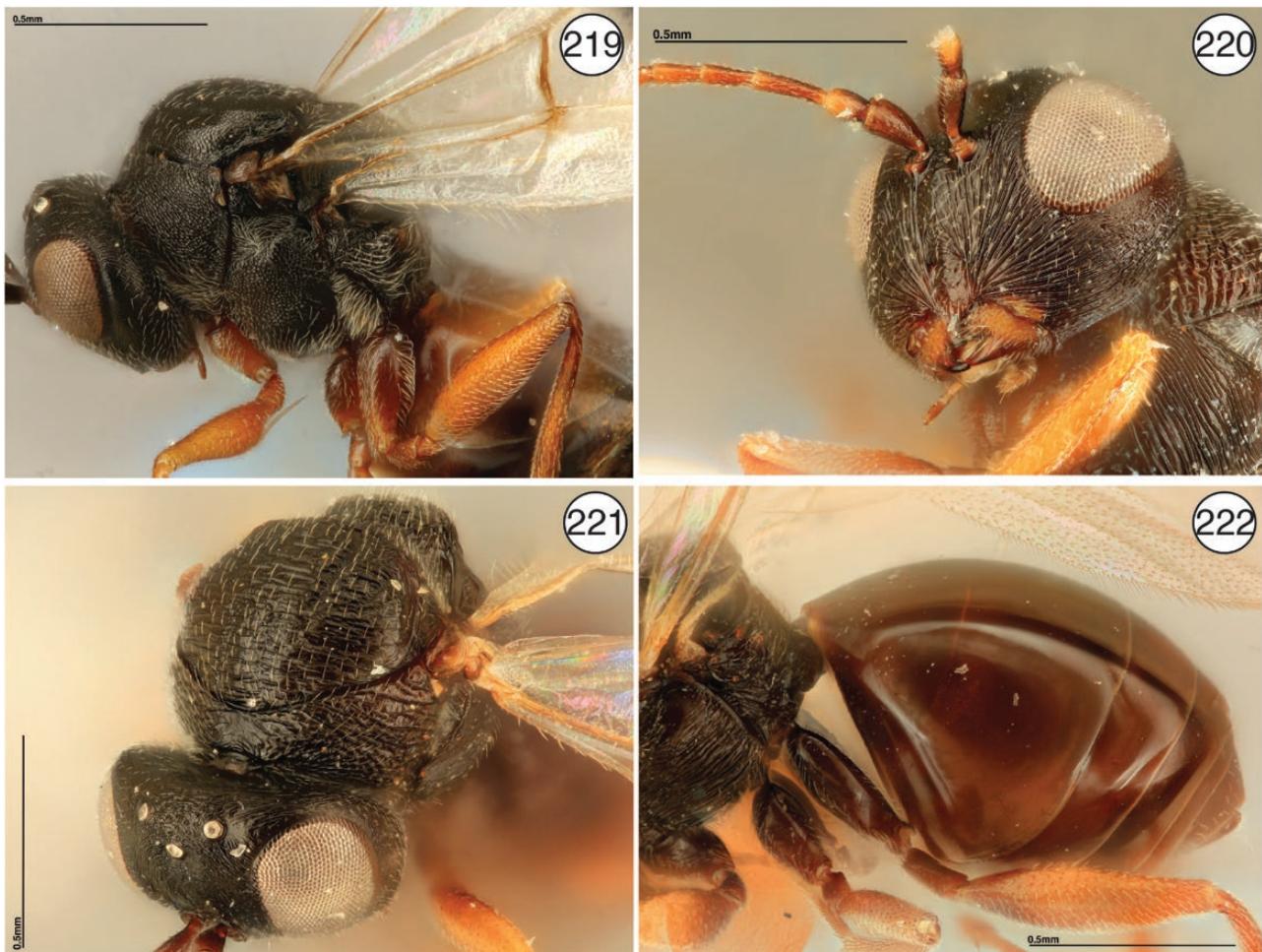


Plate 13. Phanacidini. Figs. 219 through 222. *Phanacis* sp., USNMENT01448498.

Phanacidini

Figs. 219–222

Much like the Aulacideini, members of Phanacidini are herb gallers on Asteraceae. The phylogenetic analysis of Ronquist et al. (2015) found these species, previously included in Aylacini, rendered that tribe polyphyletic. Hence, these species were removed into the novel tribe Phanacidini.

Biology. Mostly stem gall inducers on Asteraceae, with a few species on Lamiaceae and Apiaceae.

Distribution. Palearctic Region, most species in arid Southwest & Central Asia. *Phanacis* recorded from Kenya presumably introduced; intentionally introduced into Australia and South Africa for weed biological control.

Relevant literature. Ronquist et al. (2015) is the most recent treatment of the group; Ronquist (1995b, 1999) discusses issues with the placement of genera now found in this tribe.

Classification.

Phanacidini Nieves-Aldrey, Nylander & Ronquist, 2015

Asiocynips Kovalev, 1982; 4 species central Asia

Diakontschukia Melika 2006; 1 species ePA

Phanacis Förster, 1869; 30 species PA, introduced AT, NA

Zerovia Dyakontshuk, 1988; 1 species central Asia

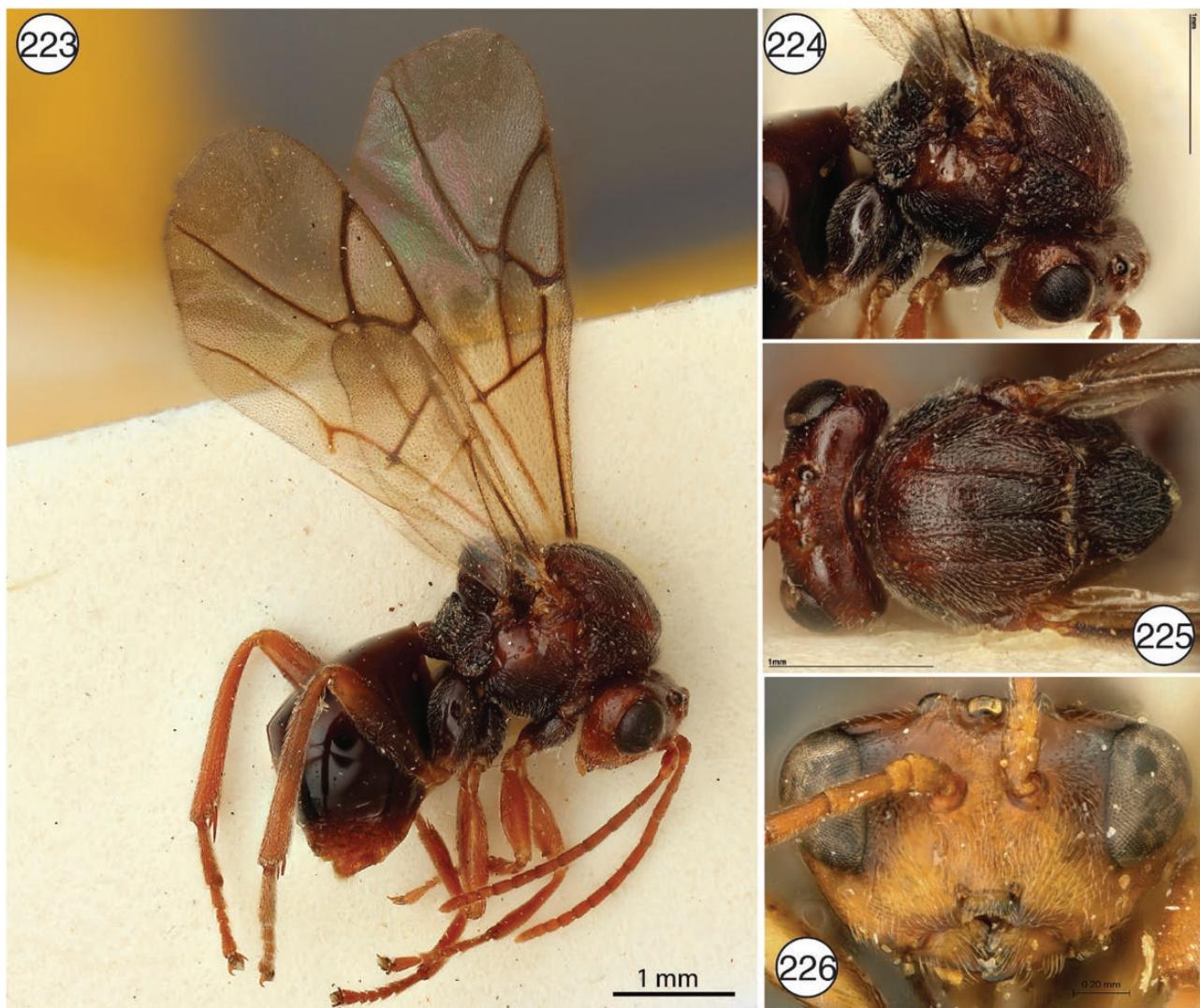


Plate 14. Qwaqwaiini. Figs. 223 through 226. *Qwaqwaiini scolopiae*, SAMHYMP044067.

Qwaqwaiini

Figs. 223–226

This unusual group is another example of a monotypic tribe in the Cynipinae. Species are gallers on *Scolopia* (Salicaceae) in South Africa. In fact, this tribe appears to be endemic to South Africa, where a single species galls *Scolopia mundii*, forming unilocular stem galls (Liljeblad et al. 2011).

Biology. Gall inducer on *Scolopia mundii* (Eckl. & Zeyh.) Warb. (Salicaceae), a tree in the eudicot subclass Rosidae (Liljeblad et al. 2011).

Distribution. South Africa: KwaZulu-Natal; Mpumalanga.

Relevant literature. Tribe and its only species recently described by Liljeblad et al. (2011); treated again in Ronquist et al. (2015).

Classification.

Qwaqwaiini Liljeblad, Nieves-Aldrey and Melika, 2011

Qwaqwaiini Liljeblad, Nieves-Aldrey and Melika, 2011; 1 species AT

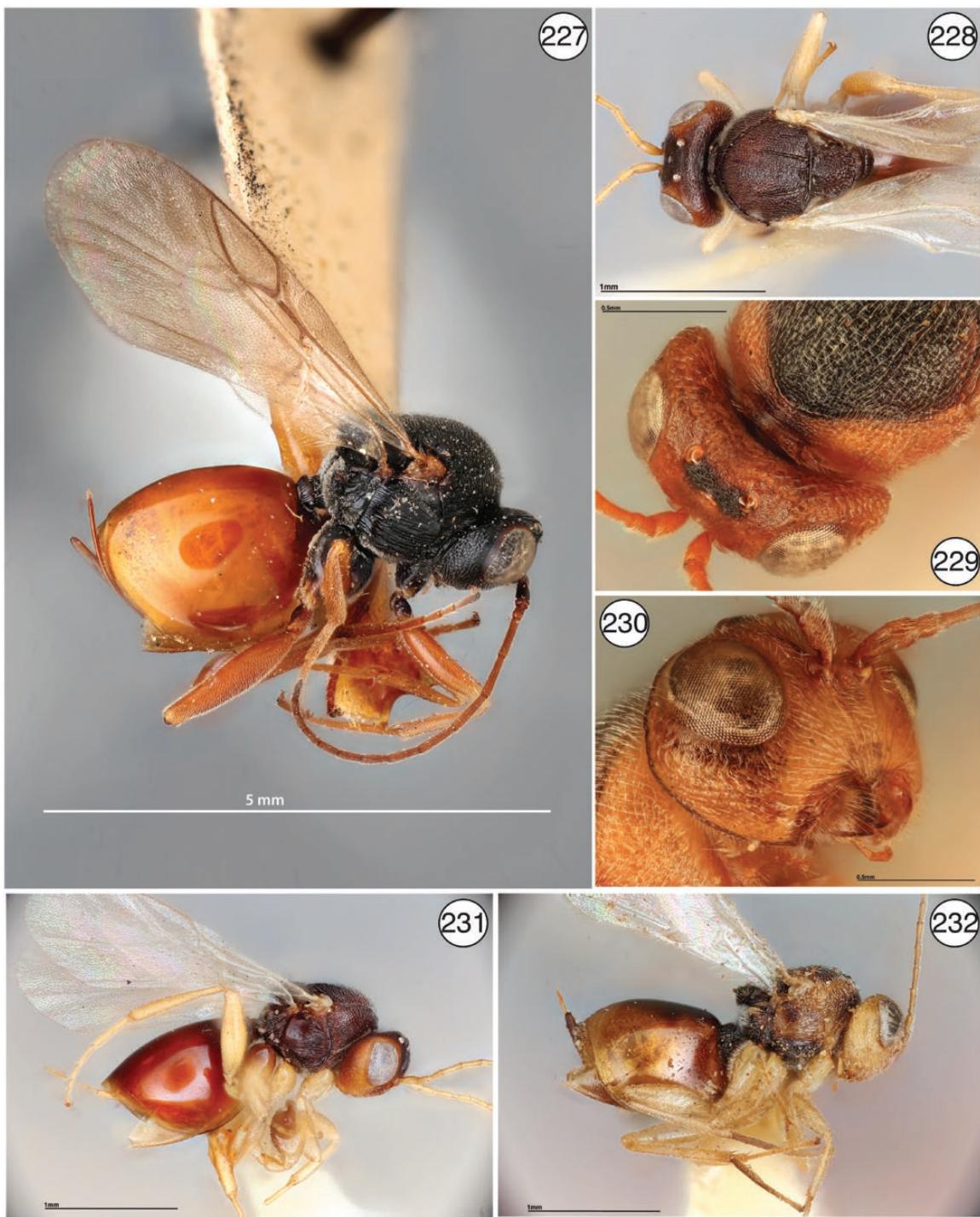


Plate 15. Synergini. Fig. 227, *Synergus distinctus* McCracken & Egbert, 1922, USNMENT01081301. Figs. 228 and 231, *Synergus incisus*, USNMENT01231859. Figs. 229, 230, and 232, *Synergus lignicola* Osten-Sacken, 1862. USNMENT01448497.

Synergini

Figs. 227–232

The traditional composition of this tribe turned out to be polyphyletic, and included any cynipid that was known or presumed to be an inquiline. However, Ronquist et al. (2015) demonstrated that inquilinism has evolved numerous times, and as a result, some members of Synergini s.l. were moved to other tribes (see Ceroptresini, Diastrophini, above). *Synergus*

is readily identified by the presence of a syntergum on the metasoma, and is by far the most readily collected and speciose genus in the tribe.

Biology. Mainly inquilines of gall-inducing Cynipini on Fagaceae. In some cases, inquilinism reaches a degree where gall inducers do not survive and hatch. It was recently discovered that *Synergus itoensis* Abe, Ide & Wachi (Abe et al. 2011) is able to induce galls *de novo*. Further, this species is found alongside other undescribed species

closely allied to *S. itoensis* from Japan, which lead to [Ide et al. \(2018\)](#) arguing that the Synergini gall inducers have independently arisen from other inquilines.

Rhoophilus is wholly unique being an inquiline forming secondary cells in galls induced by *Scyrotis* moths (Cecidosidae) on *Searsia* (formerly *Rhus*) (Anacardiaceae) shrubs and trees. Larval cells expand into the hollow interior of the host gall resulting in death of the gall-inducing moth larva ([van Noort et al. 2007](#)).

Distribution. Mostly Holarctic, but single taxa present in all regions; *Rhoophilus* endemic to South Africa.

Relevant literature. [Ronquist \(1999\)](#) reviewed the data for and against the monophyly of Synergini s.l.; tribe recently treated in [Ronquist et al. \(2015\)](#). The term *agastoparasitism* coined in [Ronquist \(1994\)](#) to describe some inquiline biology. [Van Noort et al. \(2007\)](#) thoroughly studied *Rhoophilus loewi*. [Péñez et al. \(2012\)](#) reviewed the world oak associated inquilines.

Classification.

Synergini

Agastoroxenia Nieves-Aldrey and Medianero, 2010; 1 species NT

Lithosaphonecrus Tang, Melika and Boszó, 2013; 9 species OR plus Papua New Guinea

Rhoophilus Mayr, 1881; 1 species South Africa

Saphonecrus Dalla Torre and Kieffer, 1910; 40 species but taxonomy is uncertain; PA, NA, OR

Synergus Hartig, 1840; 137 species but taxonomy is uncertain and far from stable with many more or less dubious taxa; PA, NA, NT

Synophrus Hartig, 1843; 7 species wPA

Ufo Melika and Pujade-Villar, 2005; 5 species ePA, OR

Unplacable Nomina dubia Poncyia Kieffer, 1903; 1 species

Figitidae

This family is the most speciose group within the Cynipoidea. Members of this family are, when biology is known, internal parasitoids of other holometabolous insects, and in at least one group, hyperparasitoids. [Buffington et al. \(2012\)](#) reviewed all the host records of the family and summarized the reliable host records. With some 157 genera and more than 1,700 species, subfamilies and tribes have been erected to bring some order to this diversity. In fact, it is typically easier to identify the lower groups of Figitidae than the family itself, and this is reflected in the key here. In terms of biology,

the subfamilies fall into three categories: some are parasitoids of muscomorphan Diptera (Eucoilinae, Figitinae); some are inquilines or parasitoids inside galls (Euceroptrinae, Mikeiinae, Parnipinae, Plectocynipinae, Thrasorinae: all species-poor); some are parasitoids of various insects attacking aphids (Anacharitinae, Aspicerinae, Charipinae). Finally, hosts are unknown for Emargininae and Pycnostigmata.

Anacharitinae

Figs. 233–236

The moderately diverse anacharitines are often among the more easily recognizable wasps within the cynipoids. They tend to be elongate, with a subtriangular head (in anterior view). In fact, the head is frequently the widest part of the animal (when viewed dorsally). The narrow petiole, so characteristic of the common *Anacharis*, in conjunction with a very short ovipositor, is hypothesized to be an adaptation for ‘quick strike’ oviposition into predatory Neuroptera ([Buffington 2007](#)). The narrow petiole allows for maximum flexibility in directing the ovipositor tip; the short ovipositor requires the slightest insertion into the larval body to deposit an egg. Together, this allows the wasp to successfully oviposit before the host can mount a counter-attack. The limits of some genera are poorly circumscribed.

Biology. Primary parasitoids of aphidophagous Hemerobiidae, and possibly Chrysopidae.

Distribution. Main genera are widespread but mostly Holarctic, while the Neotropical region has several endemic genera and the Afrotropics one (*Acanthaegilips*). *Anacharis* is the most widespread with at least one species common in Australia.

Relevant literature. The research group at the University of Barcelona (led by Juli Pujade-Villar) has been very active in this taxon. [Ros-Farré et al. \(2000\)](#) revised *Acanthaegilips* and characterized the aspicerines and anacharitines; [Mata-Casanova et al. \(2015a\)](#) revised *Xyalaspis*; other species-level treatments of *Aegilips* ([Mata-Casanova et al. 2017](#); [Mata-Casanova et al. 2019](#)) and *Anacharis* ([Mata-Casanova et al. 2015b](#)); [Restrepo-Ortiz and Pujade-Villar \(2010\)](#) provide a key to genera of the world. [Van Noort et al. \(2015\)](#) reviewed the Afrotropical species of the subfamily. [Buffington et al. \(2007, 2012\)](#) provided phylogenetic data on the group.

Classification.

Anacharitinae Thomson, 1862

Acanthaegilips Ashmead, 1897; 17 species NT

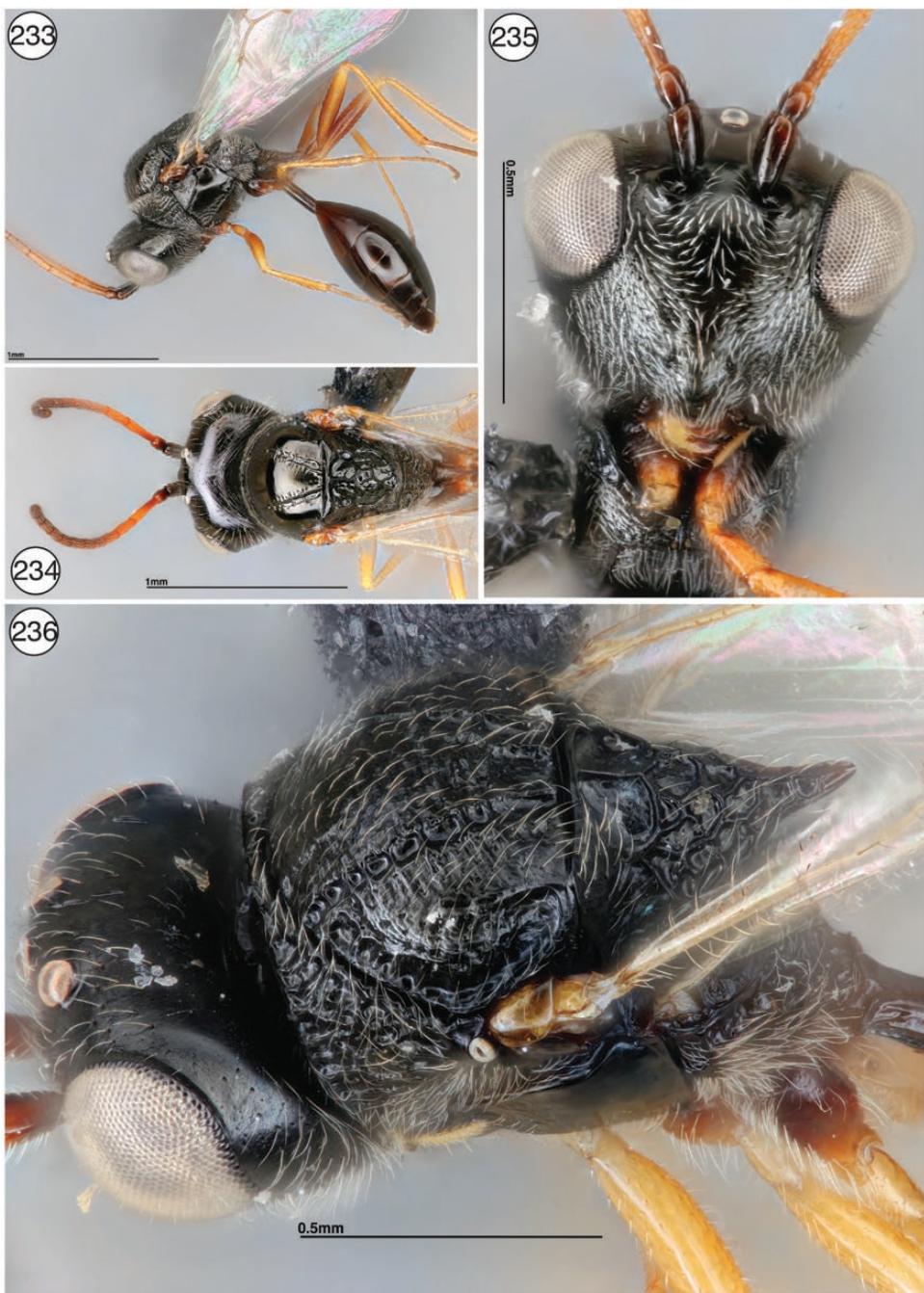


Plate 16. Anacharitinae. Fig. 233–235, *Anacharis melaneura*, USNMENT01231833. Fig. 236, *Xyalaspis flavipes*, USNMENT01231844.

Acanthaegilopsis Pujade-Villar, 2013; 2 species AT
Aegilips Haliday, 1835; 30 species worldwide but mostly Holarctic
Anacharis Dalman, 1823; 25 species worldwide but mostly Holarctic

Calofigites Kieffer, 1909; 2 species NT
Hexacharis Kieffer, 1907; 1 species NA
Solenofigites Díaz, 1979; 1 species NT
Xyalaspis Hartig, 1843; 25 species worldwide but mostly Holarctic

Aspicerinae

Figs. 237–242

With respect to general morphology, Aspicerinae are among the most spectacular of all figitids. They are typically stout with very little in the way of sexual dimorphism. While a majority of figitids are shiny black, several species of *Aspicera*, *Callaspidia* and *Anacharoides* are bright

orange to red in color. Their wings are glabrous and shimmer in the right light. Several genera, including *Aspicera*, *Prosaspicera*, and *Paraspicera* have well-developed scutellar spines. Most aspicerines have stout hind legs and an extremely petiolate metasoma. Like the anacharitines, aspicerines are quick-strike parasitoids, attacking syrphid larva that themselves provide a significant threat to the wasp during oviposition.

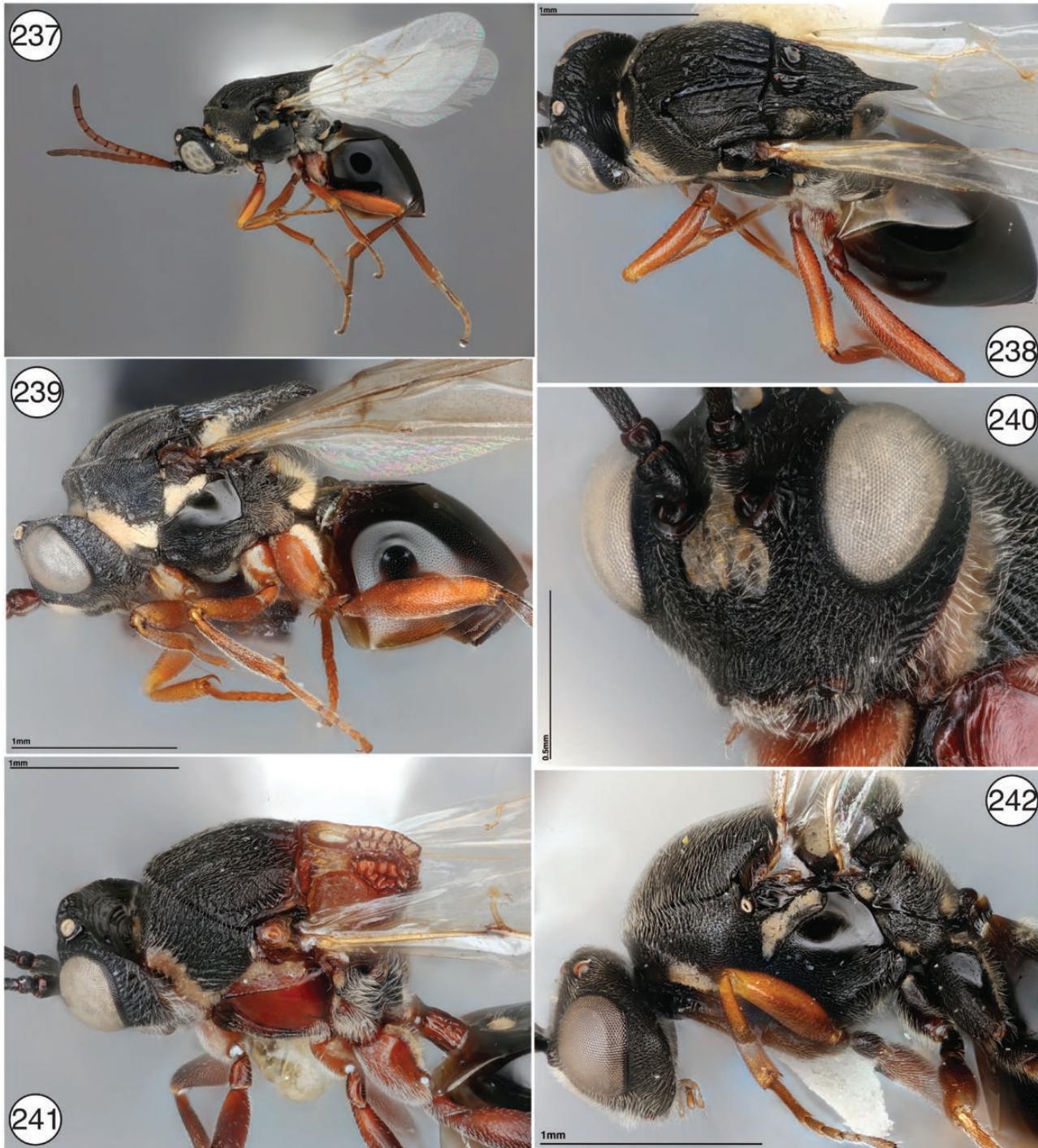


Plate 17. Aspicerinae. Figs. 237 and 238, *Aspicera hartigi*, USNMENT01231866. Fig. 239, *Prosaspicera* sp., USNMENT01231883. Figs. 240 and 241, *Callaspidia* sp., USNMENT01231867. Fig. 242, *Melanips* sp., USNMENT01231847.

A very short ovipositor, coupled with a highly flexible metasoma and strong hind legs, allow the wasp to attack the host before the host can mount a counter attack (Buffington 2007). *Melanips* is taxonomically problematic with respect to Figitinae and Aspicerinae. *Melanips* lacks morphological characters that can positively associate the genus with either subfamily; however, species of *Melanips* have been reared from Chamaemyiidae larvae predating on aphids, and this biology coincides with Aspicerinae. Further, Buffington et al. (2007, 2012) recovered *Melanips* as sister-group to the remaining Aspicerinae, and suggested moving *Melanips* to that subfamily. The group is currently being evaluated as its own subfamily (Mata-Casanova et al. personal communication). Despite recent revisions, several species remain undescribed and some regional faunas largely unexplored.

Biology. Koinobiont endoparasitoids of aphidophagous syrphid and chamaemyiid flies (summarized in Buffington et al. 2012).

Distribution. Mostly Holarctic; *Anacharoides* is indigenous to the Afro-tropical Region and Northern Africa.

Relevant literature. Ros-Farré & Pujade-Villar revised *Prosaspicera* (2006), *Callaspidea* (2009a) *Paraspicera* (2011a), *Omalaspis* (2011b) and *Aspicera* (2013); Buffington and van Noort (2009) revised *Anacharoides*. Ros-Farré (2007) provides a key to genera.

Classification.

Aspicerinae Dalla Torre and Kieffer, 1910

Anacharoides Cameron, 1904; 7 species AT

Aspicera Dahlbom, 1842; 54 species Holarctic but also found in India

Balna Cameron, 1883; 6 species NT

Callaspidea Dahlbom, 1842; 8 species PA, NA, NT

Melanips Walker in Haliday, 1835; 31 species PA, NA, OR, NT, but the genus is poorly known and the number means very little
Omalaspis Giraud, 1860; 14 species PA, NA

Paraspicera Kieffer, 1907; 2 species NA

Prosaspicera Kieffer, 1907; 32 species worldwide except wPA and AU

Pujadella Ros-Farré, 2007; 2 species OR

Charipinae

Figs. 243–248

This is an extremely diverse group known exclusively as hyperparasitoids in aphid and psyllid systems. While not particularly

diverse at the genus level, the species diversity in *Alloxysta* is remarkable, and it is possible numerous cryptic species complexes are present in the genus. The small size and smooth cuticle of charipines make them easily recognized at the subfamily level. While genera are relatively approachable with respect to identification, species limits are still being addressed, and in some cases, species-level identification is difficult if not impossible. The research group at the University of Barcelona (Pujade-Villar Lab) is the most active in the world and has produced the most recent research on the group, spearheaded by Mar Ferrer-Suay. The volume of papers and new taxa in recent years is remarkable, and has been particularly valuable in making the types accessible. Up to a point, nomenclatural issues, as well as distribution knowledge and practical identification have benefitted significantly from this. But this is not definitive since species circumscriptions are still often uncertain, as revisions have usually been made on the basis of rather small numbers of specimens and a set of preferred morphological characters, not considering biological or molecular evidence nor phylogenetic considerations. Particularly troublesome was the erection of all wingless forms into separate species.

Biology. Hyperparasitoids of aphidiine braconids and aphelinid chalcidoids through aphids and psyllids. Data summarized online at <http://www.charipinaedatabase.com>.

Distribution. Worldwide, but with the largest number of species in the Holarctic, while two unusual groups (*Dilapothor* and *Thoreauana*) are from Australia.

Relevant literature. Menke and Evenhuis (1991) provided the first modern update of the group. Ferrer-Suay et al. (2012) provided a world catalog, which has also been merged into an online database (Ferrer-Suay et al. 2014); Ferrer-Suay et al. (2013a) review Neotropical species, Oriental species (Ferrer-Suay et al. 2013b) and Palearctic species (Ferrer-Suay et al. 2018); van Noort et al. (2015) reviewed the Afrotropical species.

Classification.

Charipinae Dalla Torre and Kieffer, 1910

Alloxysta Förster; 137 species worldwide but mainly Holarctic, despite recent revisions many problems remain

Apocharisps Fergusson, 1986; 6 species NT, PA, AT

Dilapothor Paretas-Martinez and Pujade-Villar, 2006; 1 species AU

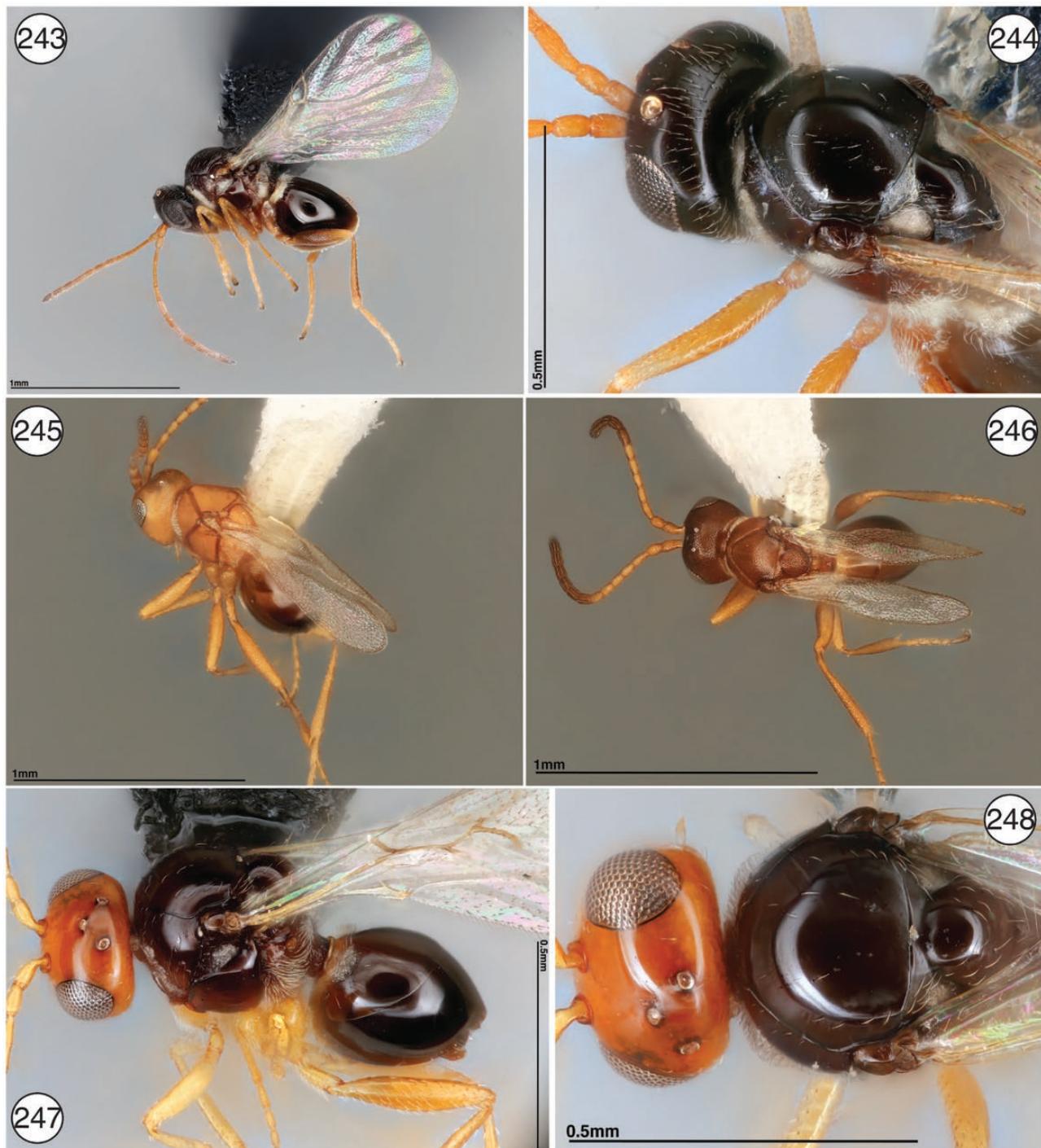


Plate 18. Charipinae. Figs. 243 and 244, *Apocharips trapezoidea*, USNMENT01231873. Figs. 245 and 246, *Lytoxysta brevipalpis*, USNMENT01231836. Figs. 247 and 248, *Alloxysta* sp., USNMENT01231840.

Dilyta Förster, 1869; 14 species AT, PA, NA, OR
Lobopterocharips Paretas-Martinez and Pujade-Villar, 2008; 1 species OR
Lytoxysta Kieffer, 1909; 1 species NA

Phaenoglyphis Förster, 1869; 44 species, worldwide but mainly Holarctic, despite recent revisions many problems remain
Thoreauana Girault, 1930; 4 species AU



Plate 19. Emargininae. Fig. 249, *Thoreauella* sp., USNMENT01022106. Fig. 250, *Thoreauella* sp., USNMENT01525887.



Plate 20. Euceroptrinae. Figs. 251 and 252, *Euceroptris maritimus*, USNMENT01231848.

Emargininae

Figs. 249 and 250

This unusual group of diminutive wasps has been variously classified, often as eucoelines. Ronquist (1999) clarified the circumscription of the group and recognized them as their own subfamily (reviewed by Pujade-Villar 2019). While typically rare in most parts of the world, they are a dominant figtid group in Madagascar (van Noort et al. 2015). Several genera have been described, but all have been synonymized under *Thoreauella* Girault; considering that, nothing less than a world-wide revision would be able to find phylogenetically meaningful groups.

Biology. Host unknown, but adults have been collected from formicid refuse piles (Weld 1960b).

Distribution. Pantropical and transgressing into Eastern Palearctic, but rarely collected outside Madagascar.

Relevant literature. Ronquist (1999) circumscribed the group; Weld (1960b) suggested species are ant associates. Van Noort et al. (2015) reviewed the Afrotropical species and moved all species into *Thoreauella*.

Classification.

Emargininae Kovalev, 1994

Thoreauella Girault, 1930; 15 species pantropical ePAePA

Euceroptrinae

Figs. 251 and 252

This small group has been variously classified, most frequently as cynipids. Species are gall associates, presumably gall wasp parasitoids. Ronquist (1999) grouped them as members of the ‘figitoid inquilines’, but Buffington and Liljeblad (2008) revised the genus and recognized the group as a distinct subfamily; Buffington et al. (2007) phylogenetically recovered the group outside of the other gall-associated figitids.

Biology. Parasitoids or inquilines of *Andricus* spp. (Cynipini) on *Quercus* spp.

Distribution. Holarctic Region; mostly Nearctic, with one recent specimen seen from Serbia (Buffington, pers. obsv.)

Relevant literature. Ashmead (1896) described the genus; Buffington and Liljeblad (2008) revised the genus and described the subfamily.

Classification.

Euceroptrinae Buffington and Liljeblad, 2008

Euceroptris Ashmead, 1896; 4 species NA

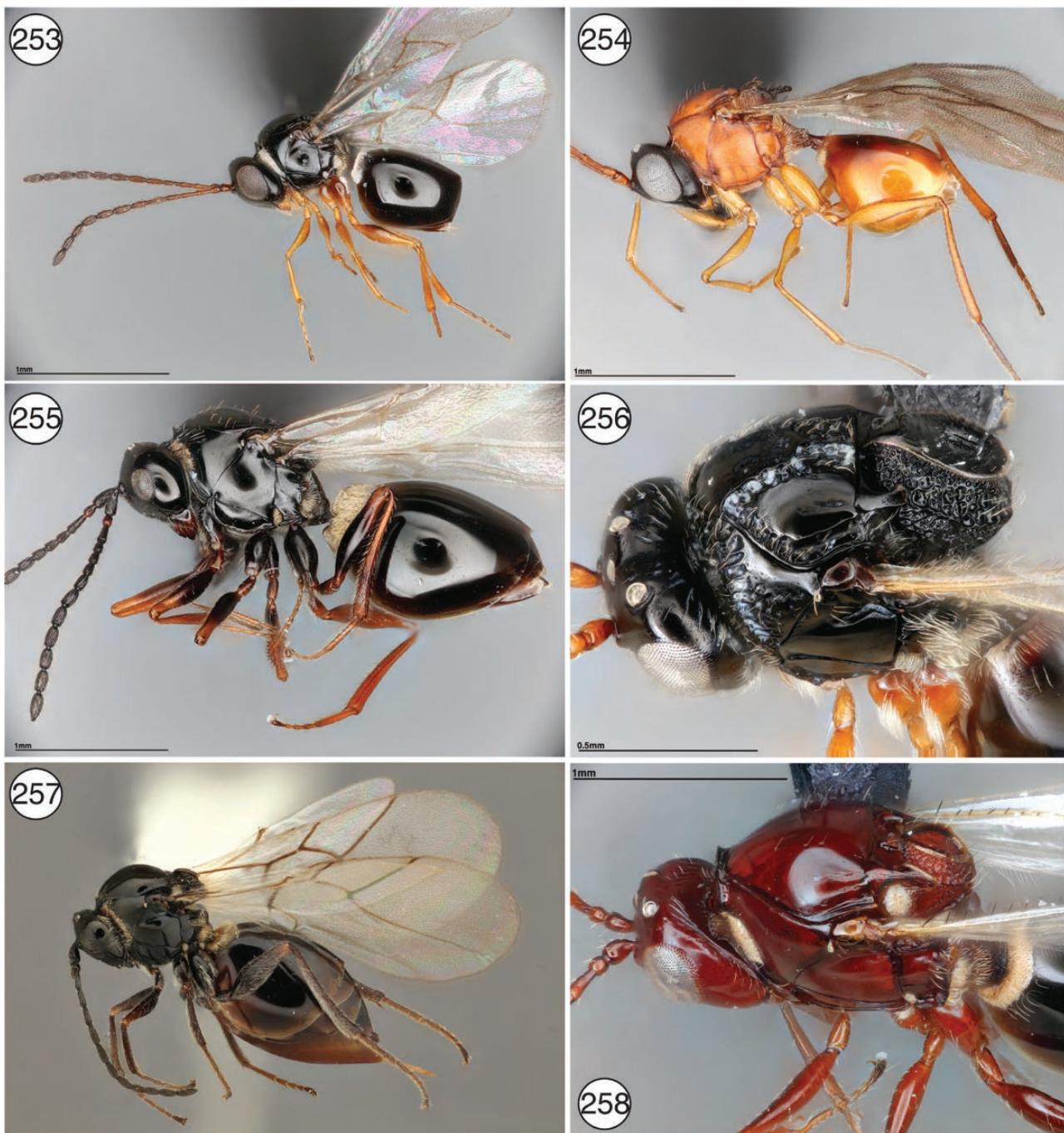


Plate 21. Eucoilinae. Fig. 253, *Ganaspis brasiliensis* (Ihering, 1905), USNMENT01520001. Fig. 254, *Odonteucoila* sp., USNMENT01231882. Fig. 255, *Kleidotoma* sp., USNMENT01525865. Fig. 256, *Gronotoma* sp., USNMENT01231843. Fig. 257, *Trybliographa melanoptera*, USNMENT01231838. Fig. 258, *Striatovertex* sp., USNMENT01231830.

Eucoilinae

Figs. 253–258

Within the Figitidae, the vast majority of both species diversity, and abundance, occurs within Eucoilinae. Eucoilines can be collected very easily on all continents (they are even found on Antarctic islands), and many species do very well in the suburban to urban environments, as well as around farms. Unlike most other cynipoids, the eucoilines are immediately recognizable by a single morphological feature: the scutellar plate. This feature is a structure holding up a glandular release pit the function of which is currently unknown. The feature is often referred to as a cup, a plate, a teardrop, or a disk. Because

of their commonness, and being immediately recognizable from all other cynipoids, many species have been more or less haphazardly described. As a result, this large group became an impenetrable taxonomic morass for decades until Nordlander's work in the late 70s and early 80s began to make some sense of the diversity. Nordlander (1982b) summarized his work and generated generic groups that remained relevant well into the 2000s. Fontal-Cazalla et al. (2002) ignited renewed interest in the phylogeny of the group, and set the stage for an expanded analysis at the core of Buffington et al. (2007). The resulting phylogenies and recognition of phylogenetically informative characters have helped motivate addressing the taxonomy of larger

groups of eucoilines, including the Diglyphosematini (Buffington 2011), Zaeucoilini (Buffington 2009) and Eucoilini (Forshage 2009). The most comprehensive regional treatment of the Eucoilinae was published by van Noort et al. (2015) and establishes a format for future projects on eucoilines at other regional scales. In order to make sense of the genera within the group, tribes have recently been established. However, this is very much a work in progress and many genera currently lack tribal placement.

In all regions, the majority of species remain undescribed, and the described species are very often in completely wrong genera (due to the mentioned earlier lack of knowledge of phylogenetically informative characters). The latter problem (but not the former) has been addressed and largely rectified for some regions (Europe, North America, the Afrotropics) but remains at large elsewhere (the Oriental, Oceanic, and Neotropical regions all have a majority of described species still misplaced).

Eucoilines are parasitoids of cyclorrhaphous flies (Buffington et al. 2012), with most host associations still unknown but spanning over a wide diversity of flies (Ronquist 1999, Buffington 2007, Buffington et al. 2012). *Drosophila* parasitoids in the genera *Ganaspis* and *Leptopilina* have been used in lab studies since the 1960s. Their biology has thus been studied in remarkable detail, and they are currently being considered for use in the biocontrol of *Drosophila suzukii* ("SWD"). Other eucoilines that have been used in the biological control of pest flies include: *Aganaspis* species on tephritids, *Trybliographa* species on onion maggot; *Banacuniculus*; and *Ganaspidium* species on leafminers.

Biology. Koinobiont endoparasitoids of cyclorrhaphous flies. Early instar maggots are parasitized; and then after the host fly forms a puparium, the wasp kills the host, and completes its own pupation within the host puparium. Abe (2009) documented *Gronotoma micromorpha* as an egg-larval parasitoid of *Liriomyza trifolii*; it is not known how widespread this type of biology is among Eucoilinae. Hosts are unknown for most species, and the records we have are very often anecdotal, but several preliminary patterns can be observed. First, that almost all reliable host records are indeed of muscomorphan (cyclorrhaphous) flies; some exceptional records of *Kleidotoma* on Sciaridae appears to us to be correct, whereas numerous, unisolated host records from Mycetophilidae are probably all erroneous. Second, that probably at least half of the Eucoilinae species attack saprophagous flies in more or less ephemeral habitats (dung, carrion, compost, debris, fermenting fruit and mushrooms) whereas another good portion attack phytophagous flies (leaf miners etc.). Thus, Diglyphosematini and Zaeucoilini are mostly but not exclusively on leafmining Agromyzidae, while Kleidotomini and Eucoilini are mostly but not exclusively on various saprophagous flies. Third, a "rule of thumb" that has been used among workers in the group for decades is to expect any genus of Eucoiline wasp to attack one particular family of flies. This is not valid in any strict sense but a mere pragmatic guidance, but with our limited data it works in a large number of cases. Large eucoiline genera tend to include exceptions (host switches), and two large genera (*Kleidotoma* and *Hexacola*) are known to have a wide range of hosts. The fly families attracting the largest number of eucoiline genera are Drosophilidae and Agromyzidae. Very little is known about host specificity of individual eucoiline species.

Distribution. Worldwide. Particularly speciose in the Neotropical Region.

Relevant literature. Weld (1952) remained dominant until the publications of Nordlander established a new standard of thoroughness and phylogenetic thinking in eucoiline research (Nordlander, 1976, 1978, 1980, 1981, 1982a, summarized in Nordlander [1982b]). Van Lenteren

et al. (1998) and van Alphen et al. (1991) investigated biology and host use. Forshage and Nordlander (2008) provided basic circumscription of tribes and keyed western Palearctic genera, Buffington revised Diglyphosematini (Buffington 2011) and the new tribe Zaeucoilini (Buffington 2009). Forshage (2009) summarized global overview of the subfamily and especially Eucoilini. Van Noort et al. (2015) provided a substantial overview of the Afrotropical fauna, and Forshage et al. (2013) cataloged Nearctic taxa. A combination of the Afrotropical key and the European key (Van Noort et al. 2015 and Forshage and Nordlander 2008) will allow generic recognition of most Eucoilinae worldwide, except in the utterly diverse Neotropics (cf Buffington et al. 2006) and highly aberrant Pacific islands (cf Beardsley 1989). Species-level identification is very often not possible, but many common European species can still be keyed with Quinlan (1978) even though taxonomy is obsolete, and odd taxa globally can be recognized using Weld (1952). Useful generic treatments are available for *Ganaspidium* (Buffington 2010a), *Banacuniculus* (Buffington 2010b), *Zaeucoila* (Buffington et al. 2018), European *Rhoptromeris* (Nordlander 1978, Costa Baião and Forshage 2018), *Leptopilina* in different regions (Nordlander 1980, Allemand et al. 2002, Novkovic et al. 2011, Lue et al. 2016), and several genera in Taiwan (Lin 1987, 1988), as well as for several lesser, recently described genera or regional assemblies thereof, while many recent studies still await publication. Fontal-Cazalla et al. (2002) and Buffington et al. (2007) provided phylogenies.

Classification.

Eucoilinae Thomson, 1862

Diglyphosematini Belizin, 1961

- Afrostilba* Benoit, 1956; 18 species AT
- Banacuniculus* Buffington, 2010; 8 species NA, NT plus Hawaii
- Diglyphosema* Förster, 1869; 7 species PA
- Disorygma* Förster, 1869; 7 species PA, OR
- Ealata* Quinlan, 1986; 5 species AT, OR
- Ganaspidium* Weld, 1955; 6 species NA, NT, AT but mainly arid North American Southwest
- Gronotoma* Förster, 1869; currently 35 species but a few more described species belong here, worldwide
- Microstilba* Förster, 1869; 6 species, wPA
- Nordlanderia* Quinlan, 1986; 4 species AT, PA
- Paradiglyphosema* Lin, 1988; 3 species but at least 1 more described and some undescribed belong here, mostly OR but also AT
- Sinatra* Buffington, 2011; 1 species around the Pacific
- Tobiasiana* Kovalev, 1979; 4 species arid southern Palearctic

Eucoilini Thomson, 1862

- Afrodonaspis* Weld, 1962; 2 species AT
- Bothrocachis* Cameron, 1904; 8 species currently in genus but a few more belong here, mostly AT but also OR and Hawaii
- Eucoila* Westwood, 1833; only 3 described species currently are classified as *Eucoila* in a meaningful sense, while many need to be removed elsewhere and yet a few others need to be moved in or described as new, PA, NAPA, NA
- Leptopilina* Förster, 1869; 41 described species currently in the genus in a meaningful sense but more are currently being described and still ca 12 need to be moved in from other genera, worldwide
- Linaspis* Lin, 1988; 1 species ePA
- Linoeucoila* Lin, 1988; 11 species, OR but undescribed species also AT

Maacynips Yoshimoto, 1963; 3 described species and numerous undescribed in Australia and throughout the Pacific and East Asia

Quasimodoana Forshage, Nordlander & Ronquist, 2008; 2 species PA, NA

Trybliographa Förster, 1869; 43 described species currently in the genus in a meaningful sense but some 20 more need to be moved in from other genera and far more described as new, worldwide but mainly Holarctic

Ganaspini Belizin, 1961

Acantheucoela Ashmead, 1900; 6 species NT

Aganaspis Lin, 1987; 7 described species currently in the genus in a meaningful sense but ca 10 more need to be moved in and more described as new; worldwide but mainly Oriental and Neotropic

Areaspis Lin, 1988; 2 species but 2 more need to be moved in and additional ones described as new, OR, AT

Aspidogyrus Yoshimoto, 1962; 4 species Hawaii

Caleucoela Kieffer, 1909; 1 species NT

Chrestosema Förster, 1869; 3 described species currently in the genus in a meaningful sense but more will soon be moved in, and described as new, while remaining others will be moved out; mainly OR, PA

Coneucoela Kieffer, 1909; 1 species NT

Didyctium Riley, 1879; 12 described species currently in the genus in a meaningful sense but ca 10 need to be moved in and many more described as new; worldwide

Dieuoila Ashmead, 1903; 7 described species currently in the genus in a meaningful sense but ca 10 need to be moved in and more described as new; NT, NA

Discaspis Lin, 1988; 1 species OR

Ditanyomeria Yoshimoto, 1963; 4 nominal species AU, to be synonymized

Endecameris Yoshimoto, 1963; currently 2 species but many undescribed, PA, OR, AT, AU

Epicoela Borgmeier, 1935; 2 species NT

Epochresta Lin, 1988; 1 species OR

Euxestophaga Gallardo, 2017; 1 species NT

Fontaliella Pujade-Villar, 2013; 1 species NT

Ganaspis Förster, 1869; 25 described species currently in the genus in a meaningful sense, but ca. 40 more need to be moved in and yet more described as new; worldwide

Gastraspis Lin, 1988; 2 species OR, AT

Glauraspida Thomson, 1862; 3 described species currently in the genus in a meaningful sense, but a few more are being moved in or described as new; PA, rare in NA, NT

Hexacula Förster, 1869; 43 described species currently in the genus in a meaningful sense but ca 25 more need to be moved in and many more described as new; worldwide

Humboldtaria Buffington 2017; 4 species NT

Hydrelliaeucoila Díaz & Gallardo, 2009; 1 species NT

Hypodiranchis Ashmead, 1901; 9 described species currently in the genus in a meaningful sense but a few more need to be moved in or described as new: Pacific and East Asian

Lispothyreus Yoshimoto, 1962; 2 species Hawaii

Mirandicola Belizin, 1968; 8 described species currently in the genus in a meaningful sense but some more are currently being described and many remain undescribed, OR, PA

Nesodiranchis Perkins, 1910; 6 species Hawaii

Nordlandiella Díaz, 1982; 2 species but 3 more need to be moved in and some described as new; NT, NA

Odonteucoila Ashmead, 1903; 8 species NT

Odontosema Kieffer, 1909; 1 species NT

Paraganaspis Díaz & Gallardo, 1996; 2 species but 6 more need to be moved in and some described as new; NT, NA

Pentamerocera Ashmead, 1896; 1 species but very poorly known; NT

Perischus Weld, 1931; 2 species NT

Promiomera Ashmead, 1903; 1 species NT

Pressia Belizin, 1968; 1 nominal species PA, to be synonymized

Pseudodiranchis Yoshimoto, 1962; 10 nominal species, but poorly known, real species number might be smaller or larger; Hawaii

Sinochresta Lin, 1988; 2 species OR

Steleucoela Kieffer, 1908; 2 species NT

Striatovertex Schick, Forshage & Nordlander, 2011; 13 species but some are synonyms NT, NA and Hawaii

Trissodontaspis Ashmead, 1903; 1 species NT

Weldia Yoshimoto, 1962; 6 species, but poorly known, real species number might be smaller or larger; Hawaii

Zamischus Ashmead, 1903; 3 species NT

Kleidotomini Hellén, 1960

Cothonaspis Hartig, 1840; 7 species, mainly Holarctic and AT, as well as a cosmopolitan species

Eutrias Förster, 1869; 1 species, Holarctic

Garudella Buffington & Forshage, 2014; 4 species, OR, AT

Kleidotoma Westwood, 1833; 137 species worldwide, but by far most are still undescribed

Muhaka Buffington & Copeland, 2015; 1 species AT

Triplasta Kieffer, 1901; 4 species NT

Trichoplastini Kovalev, 1989

Angustocorpa Quinlan, 1988; 4 species AT

Nanocthulhu Buffington, 2012; 1 species AT

Nordlanderiana Kovalev, 1989; 1 species PA

Rhoptromeris Förster, 1869; 46 described species currently in the genus in a meaningful sense, but ca. 10 more need to be moved in and several more described as new, worldwide but mainly AT & PA

Stentorceps Quinlan, 1984; 6 species AT

Trichoplasta Benoit, 1956; 27 described species currently in the genus in a meaningful sense, but a few need to be moved in and several more described as new, worldwide but mainly AT, PA, NA

Zaeucoilini Buffington, 2009

Dettmeria Borgmeier, 1935; 2 species NT

Dicerataspis Ashmead, 1896; 2 species NT

Lopheucoila Weld, 1951; 2 species NT

Marthiella Buffington, 2009; 2 species NT

Moneucoela Kieffer, 1907; 2 species NT

Moritiella Buffington, 2006; 2 species NT

Paradettmeria Gallardo & Díaz, 2011; 1 species NT

Penteucoila Weld, 1951; 1 species NT

Preseucoela Buffington, 2004; 3 species NT, NA

Rhabdeucoila Kieffer, 1907; 7 species NT

Tropideucoila Ashmead, 1903; 9 species NT

Zaeucoilala Ashmead, 1903; 14 species NT, NA

'Leptolamina group', not currently assigned to a tribe

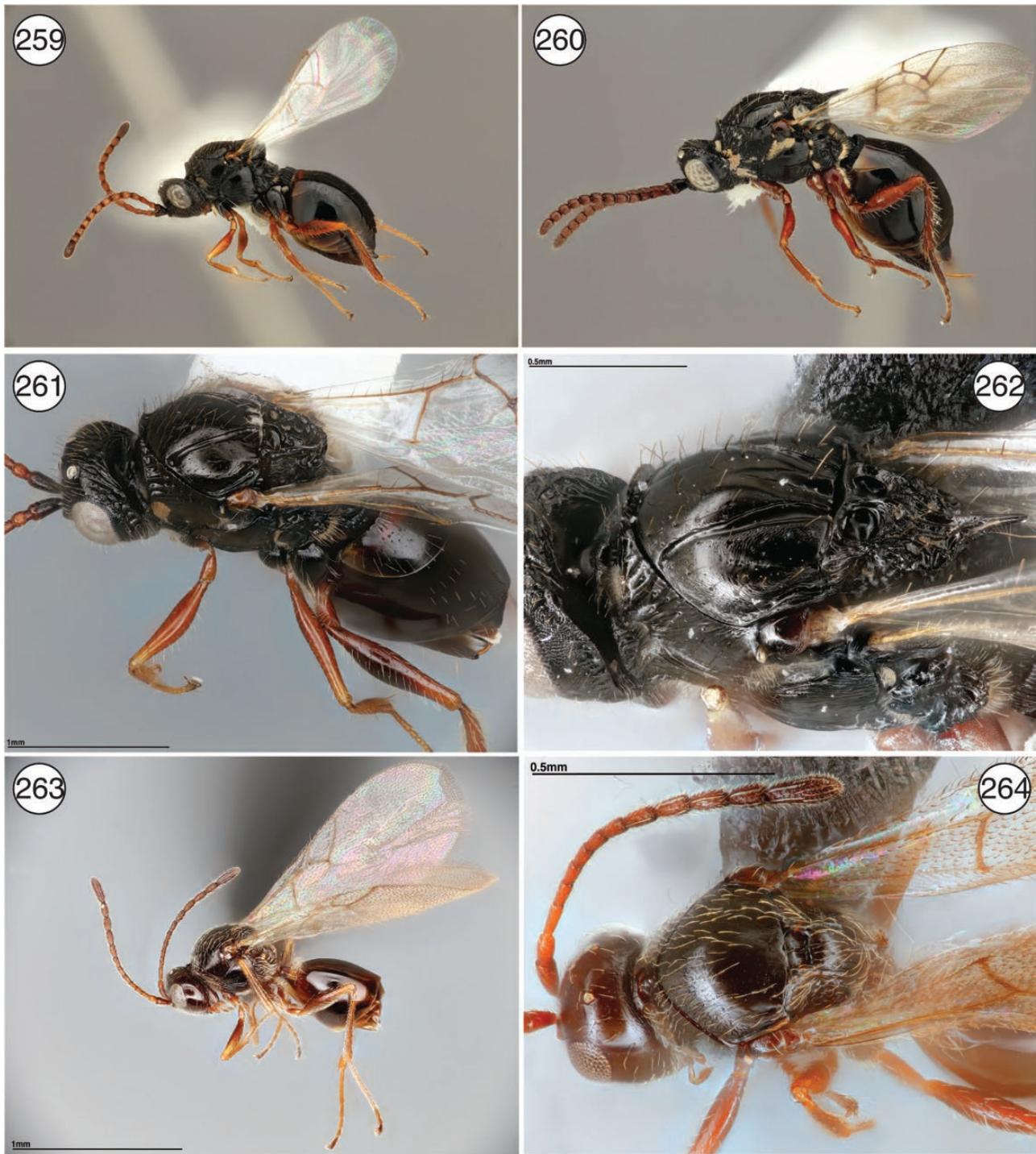


Plate 22. Figitinae. Figs. 259 and 261, *Figites* sp., USNMENT01231842. Fig. 260, *Neralsia* sp., USNMENT01231881. Fig. 262, *Neralsia* sp., USNMENT01231869. Figs. 263 and 264, *Lonchidia* sp., USNMENT01525866.

Leptolamina Yoshimoto; 16 species and more undescribed; OR, AU, AT, PA

Micreriodes Yoshimoto, 1962; 1 species currently in genus, a few need to be moved in and some more described as new; mainly PA, OR, AU but single specimens found in AT, NA

Unplaced *Nomina inquierenda*

Delomeris Diaz & Gallardo, 1996; 1 species NT

Unplacable *Nomina dubia*

Macrocereucoila Ashmead, 1887; 1 species
Tetraplasta Ashmead, 1903; 1 species

Figitinae

Figs. 259–264

No subfamily within Figitidae has been taxonomically abused as much as Figitinae. Historically, cynipoids that were clearly not

gall wasps, but also not recognizably eucoilines, anacharitines, or aspicerines, have been placed here. Hence, Figitinae has been a classic ‘dustbin’ concept. The phylogenetic research started by Ronquist (1999), and carried on by Buffington et al. (2007), recovered a core group of ‘obvious’ figitine genera (*vis.* *Neralsia*, *Xyalophora*, *Figites*), demonstrating that at least at a basic level, the group may be monophyletic. These core genera are some of the largest of all species of figitids, and are typically glabrous except for some stout setae, also having glabrous wings (apparently an adaptation to their often sticky host habitats, i.e., dung and carcasses). More peripheral genera, such as *Melanips* and *Lonchidia*, have been much more difficult to confine to Figitinae; this is reflected in this very paper, where these two taxa come out at the end of the figtid key to groups. Some figitines can be quite common, especially in Malaise traps and in sweepnet samples of pastureland.

Biology. Figitinae are parasitoids of muscomorphan Diptera, but for most taxa there are no known host associations. The available records show a similar pattern as in Eucolinae, a dominance for attacking saprophagous flies in ephemeral habitats (dung, carrion, compost), but several attacking phytophagous flies. The species-rich and more common genera are all focused on large, quick-developing calyptrate flies, while some notable forms parasitize, i.e., Anthomyiidae in conifer cones. While they have been included in surveys for natural enemies of species such as horn fly and face fly (Muscidae) in the United States, the parasitism rate has been too low for actual impact. Similarly, in Europe and Asia, *Amphithectus* (under very varying names) have been studied searching for natural enemies of cone seed predators, but no practical application has been developed.

Distribution. Worldwide. Some species of *Neralsia* and *Xyalophora* move with muscoid flies associated with livestock.

Relevant literature. Van Noort et al. (2014) revised the Afrotropical members of the subfamily. Paretas-Martínez and Pujade-Villar (2010) reviewed the Australian species; Pujade-Villar et al. (2008) reviewed the species limits of *Xyalophoroides quinquelineata*; Jimenez et al. (2008d) revised *Xyalophora* and Jimenez et al. (2008a, 2008b, 2008c) North American *Neralsia*. Forshage and Nordlander (2018) clarified the circumscription and biology of the *Amphithectus* group. Buffington et al. (2007, 2012) investigated the phylogeny of the group.

Classification.

Figitinae Hartig, 1840

Figites group

Figites Latreille, 1802; 54 species, but taxonomy is uncertain with many more or less dubious taxa, probably worldwide
Foersterhomorus Pujade-Villar, Petersen-Silva & Paretas-Martinez, 2011; 1 species PA

Neralsia Cameron, 1883; 61 species worldwide but most species NT

Paraschiza Weld, 1944; 1 species NA

Trischiza Förster, 1869; 5 species PA, NA

Xyalophora Kieffer, 1901; 14 species worldwide but not yet reported from the Oriental region



Plate 23. Mikeiinae. Figs. 265–266, *Mikeius hartigi*, USNMENT01231871.

Xyalophoroides Jiménez and Pujade-Villar, 2008; 1 species NA
Zygosis Förster, 1869; 2 species PA

Lonchidia group

Lonchidia Thomson, 1862; 7 species PA, NA, rare AT

Sarothrus group

Amphithectus Hartig, 1840; 2 species PA, NA, several undescribed

Sarothrioides Belizin, 1961; 1 species ePA

Sarothrus Hartig, 1840; 8 species PA, NA

placement uncertain

Ferpereira Pujade-Villar, 2012; 1 species NT

Nebulovenia Pujade-Villar and Paretas-Martinez, 2012; 1 species PA

Mikeiinae

Figs. 265 and 266

This small subfamily contains some unusual figtid species endemic to Australia. *Mikeius* was originally placed within Thrasorinae, a



Plate 24. Parnipinae. Figs. 267–268, *Parnips nigripes*, USNMENT01231874.

subfamily containing *Thrasorus*, another gall-associated figitid from Australia. Following a phylogenetic analysis, [Parejas-Martinez et al. \(2011\)](#) removed *Mikeius* from Thrasorinae and placed it in its own subfamily, Mikeiinae. Very rare in collections, but large numbers can be reared from *Ophelimus* (Eulophidae) infested *Eucalyptus* trees in Australia.

Biology. Primary parasitoid of *Ophelimus* spp. (Eulophidae: Chalcidoidea) on *Eucalyptus* spp.

Distribution. Australia.

Relevant literature. *Mikeius* described by [Buffington \(2008\)](#); Mikeiinae by [Parejas-Martinez et al. \(2011\)](#). Phylogeny of the group by [Buffington et al. \(2012\)](#).

Classification.

Mikeiinae [Parejas-Martinez and Pujade-Villar, 2011](#)

Mikeius [Buffington, 2008](#); 5 species AU

Parnipinae

Figs. 267 and 268

This monotypic subfamily has been the focus of a great deal of research on the evolution of Figitidae and Cynipidae. Originally classified as a cynipid, *Parnips* was later elevated to its own subfamily of Figitidae, and has been hypothesized as being the sister-group to the rest of Figitidae ([Ronquist and Nieves-Aldrey 2001](#); [Buffington et al. 2007](#)). This unusual genus are parastoids of gall wasps (Aylacini) in *Papaver* (Papaveraceae) flowers in the Mediterranean. While usually rare in collections, *Parnips* can be readily obtained from *Barbotinia*-infested *Papaver* flowers.

Biology. Primary parasitoid of Aylacine gall wasps in *Papaver*.

Distribution. Palearctic Region; Mediterranean.

Relevant literature. [Ronquist and Nieves-Aldrey \(2001\)](#) described the subfamily; [Buffington et al. \(2007, 2012\)](#) provided phylogenetic data. [Ronquist et al. \(2018\)](#) summarized and added new knowledge.

Classification.

Parnipinae [Ronquist and Nieves-Aldrey, 2001](#)

Parnips [Ronquist and Nieves-Aldrey, 2001](#); 1 species described from the Mediterranean, 1 undescribed known.



Plate 25. Plectocynipinae. Figs. 269, 272, and 273, *Plectocynips lago*, USNMENT01231872. Figs. 270 and 271, *Araucocynips* sp., USNMENT01231865.

Plectocynipinae

Figs. 269–273

This is another small group of gall-associated Figitidae that were considered members of the informal ‘figitoid inquiline’ group of Ronquist (1994; 1999). Ros-Farré and Pujade-Villar (2007) moved both *Plectocynips* and *Pegascynips* to Plectocynipinae. The group is very small, and is strongly associated with galls on *Nothofagus* forests in temperate South America. While rare in collections, relatively large numbers can be obtained from careful rearing of galls, or canopy fogging *Nothofagus*.

Biology. Associated with *Aditrochus* species (Chalcidoidea: Pteromalidae: Ormocerinae) and unidentified hymenopterous gallers on *Nothofagus* spp. (Fagaceae).

Distribution. Neotropical Region; temperate South America.

Relevant literature. Weld (1952) moved *Pegascynips* from Liopteridae to Figitidae. Ros-Farré and Pujade-Villar (2007) described the subfamily. Buffington and Nieves-Aldrey (2011) revised the subfamily. Buffington et al. (2007, 2012) investigated the phylogeny of the group.

Classification.

Plectocynipinae Ros-Farré and Pujade-Villar, 2007

Araucocynips Buffington and Nieves-Aldrey, 2011; 2 species NT

Pegascynips Brêthes, 1928; 1 species NT

Plectocynips Díaz, 1976; 3 species NT

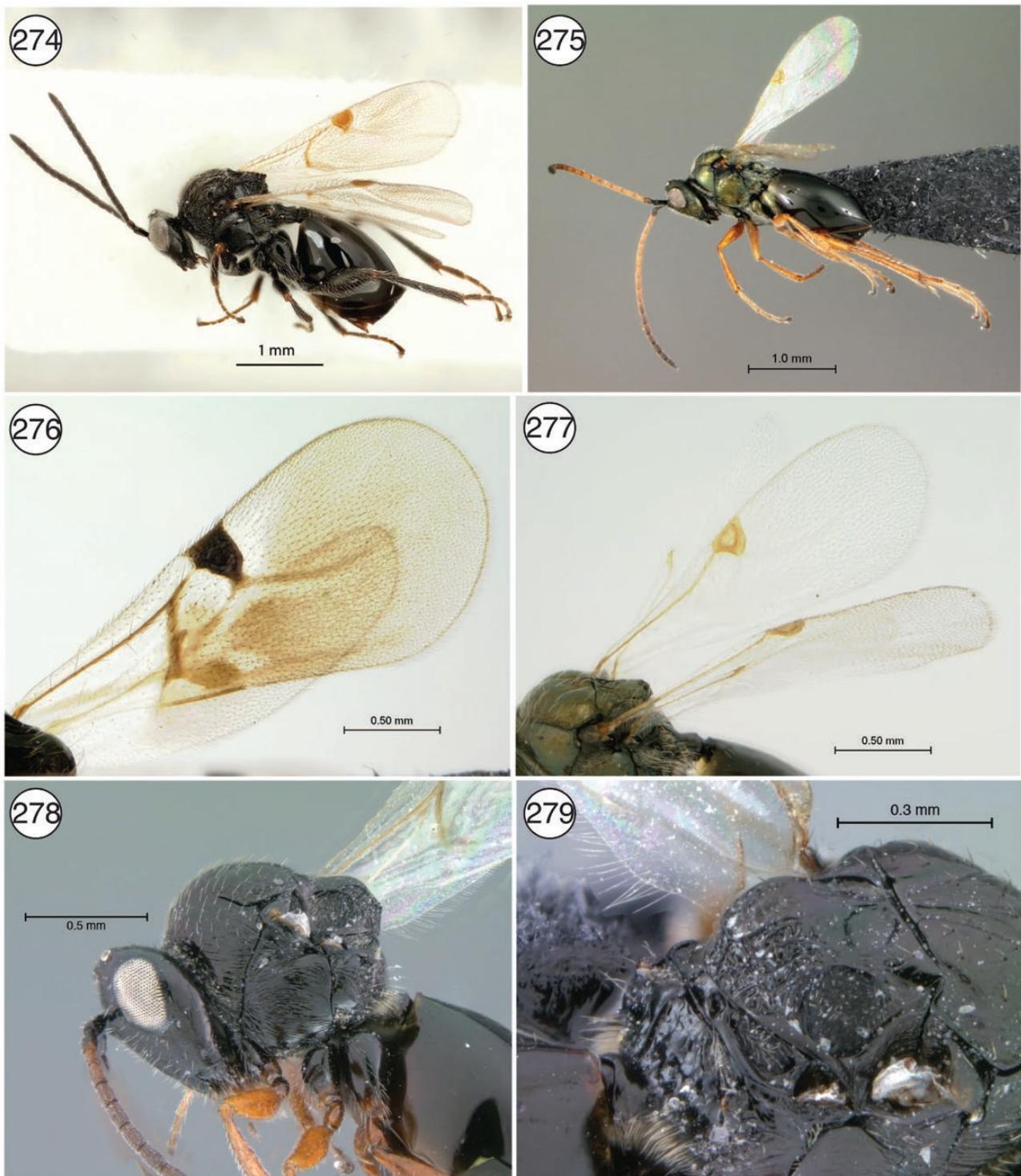


Plate 26. Pycnostigminae. Fig. 274, *Pycnostigmus rostratus* Cameron, 1905, USNMENT01231880. Figs. 275 and 277, *Pycnostigmus mastersonae* Buffington and van Noort, 2007, SAM-HYM-P0024397. Fig. 276, *Tylosema dayae* Buffington and van Noort, 2007, SAM-HYM-P0024394. Figs. 278 and 279, *Trijapitziniola vanharteni* Buffington and van Noort 2007, USNMENT00764764.

Pycnostigminae

Figs. 274–279

This charismatic and poorly known figitid group has a unique vein structure in the forewing; the veins of the marginal cell are heavily expanded, nearly closing the marginal cell, resulting in a pseudopterostigma. The only known metallic-colored figitid (*Pycnostigmus mastersonae*) belongs to the pycnostigmines. Their

biology is unknown; all known specimens have been passively collected in Malaise traps

Biology. Hosts unknown.

Distribution. Afrotropical and Palearctic; most species from Western Cape Province, RSA. Rarely collected in arid southern Palearctic (North Africa and Southwest Asia).

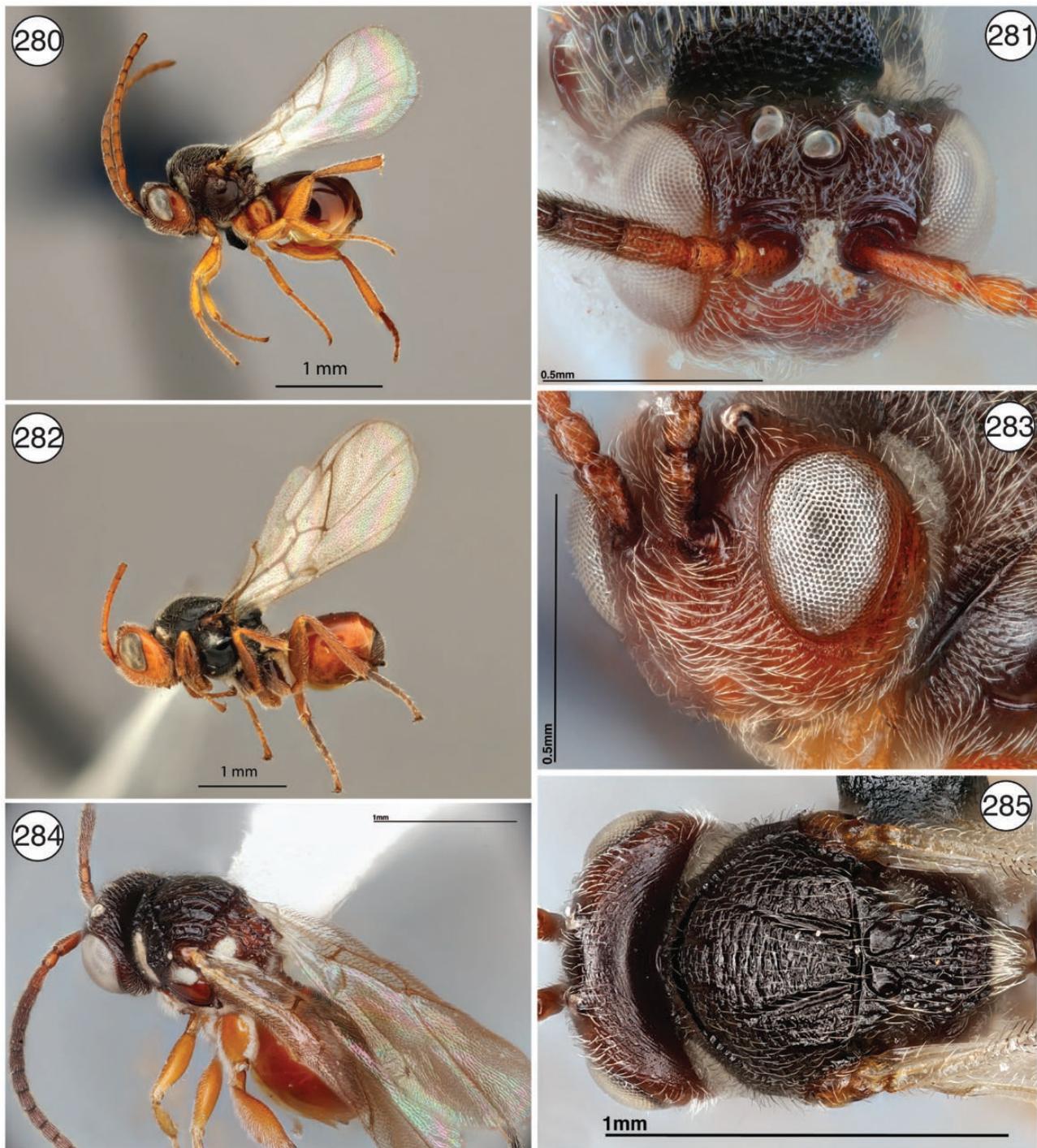


Plate 27. Thrasorinae. Figs. 280, 283, and 285, *Myrtopsen mimosae*, USNMENT01525867. Figs. 281 and 284, *Scutimica* sp., USNMENT01231860. Fig. 282, *Thrasorus pilosus* Weld, 1944, USNMENT01231876.

Relevant literature. Buffington and van Noort (2007) revised the genus. Buffington et al. (2007, 2012) investigated the phylogeny of the group.

Classification.

Pycnostigminae Cameron, 1905

Pycnostigmus Cameron, 1905; 5 species South Africa
Tryapitziniola Kovalev, 1995; 2 species Southwest Asia
Tylosema Kieffer, 1905; 3 species South and North Africa

Thrasorinae

Figs. 280–285

The majority of genera that have been previously treated by Ronquist (1994, 1999) as ‘figitoid inquilines’ are now members of this small subfamily. All members of this group are associated with galls; however, the species are from various regions, and in some cases, details of their biology is unknown. In most cases, very few specimens of these species are in collections. The outlier here is *Myrtopsen*, which can readily be reared from tanaostigmatids on Fabaceae in the Nearctic and Neotropical Regions. Phylogenetically, the group

is relatively plesiomorphic within Figitidae and forms a grade along with Euceroptrinae and Plectocynipinae (Buffington et al. 2007).

Biology. In most cases, unknown but presumably associated with galls. *Myrtopsen* is a primary parasitoid of Tanaostigmatidae (Chalcidoidea) on Malvaceae and Fabaceae (Buffington et al. 2012).

Distribution. Fragmented: Nearctic Region (*Myrtopsen*); Neotropical Region (*Myrtopsen*, *Scutimica*); Austral-Asian Region (*Thrasorus*, *Palmiriella*, *Cicatrix*).

Relevant literature. Paretas-Martinez et al. (2011) investigated Australian thrasorines; Ros-Farré and Pujade-Villar (2009b) revised *Myrtopsen*. Ros-Farré and Pujade-Villar (2007) described *Scutimica*. Ronquist (1999) discussed the so-called figitoid inquines. Buffington et al. (2007, 2012) investigated the phylogeny of the group.

Classification.

Thrasorinae Kovalev, 1994

- Cicatrix* Paretas-Martinez, 2011; 3 species AU
- Myrtopsen* Rübsaamen, 1908; 12 species NT, NA, ePA
- Palmiriella* Pujade-Villar and Paretas-Martinez, 2011; 1 species AU
- Scutimica* Ros-Farré, 2007; 2 species AU
- Thrasorus* Weld, 1944; 3 species AU

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