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, Ibaliidae

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 keys for identifying families within the group. Since these publications came out, the general understanding of the evolution of cynipooids, and their classification, has changed significantly. Further, our taxonomic knowledge of many groups within the cynipooids 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 Lioperidae, and the still somewhat preliminary tribes of the figitid 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

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include Austrocynipidae, Liopteridae, and among the cynipids, the tribes Qwaqwaini, Phanacidini, Pediaspidini, Paraaulacini, and Eschatocerini; among the figitids, Parnipinae, Thrasorinae, Pycnostigmiae, Emargininiae, Euceroptiniae, Plectocynipiniae, and Mikeiniae. 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). Charipiniae 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.

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., Eucola, 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 Qwaqwaini, 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 USNMENT ‘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.

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. USNMENT01231827. Fig. 2, Ibalia anceps Say, 1824, lateral view. USNMENT01231826.

1. 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
Figs. 3–6. Fig. 3, *Afrostilba* sp., lateral view. USNMENT0122103. 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× 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× 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 length .......................................................................................................................... Ibaliidae
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
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

— 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. 13–17. Fig. 13, Euceroptres maritimus Weld, 1926, fore wings. USNMENT01525886. Fig. 14, Odontosema anastrephae Borgmeier, 1935, fore and hind wings. USNMENT00656913. 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.

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

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Figs. 30–39. Fig. 30, Cerroneuroterus sp., fore and hind wings. USNMENT00655874. Fig. 31, Dipolepis rosae (Linnaeus, 1758) fore and hind wings. USNMENT00655959. Fig. 32, Biorhiza aburnea (Bassett, 1890), fore and hind wings. USNMENT00655850. Fig. 33, Synophromorpha sylvestris (Osten-Sacken, 1861), fore and hind wings. USNMENT00784705. 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, 1983, dorso-lateral view. USNMENT0148499. Fig. 38, Dryocosmus kuriphilus sp., dorso-lateral view. USNMENT01231850. Fig. 39, Andricus sternlichti Bellido, Pujade-Villar & Mélida, 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)
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

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 quercuscalifornicus, lateral view. USNMENT01231839. Fig. 58, Andricus quercuscalifornicus, antero-dorsal view. USNMENT01231839. Fig. 59, Andricus quercuscalifornicus, 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

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

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 inquilines in galls ........................................................................................................ 13
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

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

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

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 lacinatus Gillette, 1891, antero-dorsal view. USNMENT01448496. Fig. 86, Antistrophus lacinatus, 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. Gallers 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). Gallers on Asteraceae, rarely on other plants ......................... Phanacidini
— 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) ........................................................................................................................................................Aylacini

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
— 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
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
— 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. 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 quercuscalifornicus*, 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 Pycnastigminae

— Marginal cell not sclerotized (arrow, Fig. 119) ........................................................................................................................................................................20
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

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

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
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 Figitinae

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
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. 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. 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. Facial impression present (arrow, Fig. 155). First metasomal tergum saddle-like with concave posterolateral margin and more or less linguiform 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 Aspicerinae

— 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. 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 .................................................................

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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

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— 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)
31

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) ........................................................................................................ Eucolinae
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)
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 (*Auracaria 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 *Auracaria* were also surveyed but yielded no *Austrocynips*.

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

Distribution. Australia: Queensland.

Relevant literature. Riek, 1971; description. Paretas-Martinez et al., 2013; overview.

Classification.

Austrocynipidae Riek, 1971

*Austrocynips* Riek, 1971; 1 species in Australia.
Ibaliidae
Figs. 181–183
Ibaliids 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 Austrocynips, composing the ‘macrocynipoids’, represent the most pleiomorphic 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 strigate 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 Eilenellinae 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).
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, cPA

*Eileenella* Fergusson, 1992; 1 species Papua New Guinea

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**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 strigate 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.

**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.
Liopterids are found worldwide except the western Palearctic Region; most species are found in the tropics and subtropics. *Paramblynotus* is the most speciose of all liopterid genera, with an incredible diversity of species in southeast Asia. Most liopterids are rarely encountered in the field, though *Paramblynotus* 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, Mayrellinae 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 *Paramblynotus*. Buffington and van Noort (2012) revised the Oberthuerellinae; van Noort and Buffington (2013) revised Afro tropical Mayrellinae. Ronquist (1995a) provides a complete overview of the family, keys all the genera, and provides a world catalog. Liu et al. (2007) revises *Paramblynotus*, the most speciose of all liopterid genera. Van Noort et al. (2015) reviews all sub-Saharan Africa species and provides a key to genera.

**Classification.**

*Liopteridae* Ashmead, 1895

*Mayrellinae* Hedicke, 1922

*Kiefferiella* Ashmead, 1903; 2 species NA

*Paramblynotus* 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* Perry, 1833; 8 species NT

*Peras* Westwood, 1837; 10 species NT

*Pseudibalia* Kieffer, 1911; 13 species NT

**Cynipidae: Cynipini**

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 *Ceroptresini*. *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 Phanacidi. 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: Qwaqwauiini, including a single gall inducer on *Scolopia* (Salicaeae) in South Africa, and Paralucini, including two genera (*Paralux* and *Cecinobhagous*) of inquilines (or possibly parasitoids) in chalcidoid galls on *Notobagous* (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 gall ing insects of North America. Further, Coulianos 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 Papaveraeaceae (now Aylacini) or Rosaceae (now Diastrophini).

**Biology.** Gall inducers on various herbaceous plants in Asteraceae, Lamiaceae, Valerianaceae, and some Papaveraeaceae (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*. *Nearlax salviae* was detailed in Nieves-Aldrey (2002); Zerova et al. (2003) described the morphology and biology of *Salviella* 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 laciniiatus. 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
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).

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**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).
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

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.
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

Plate 2. Cynipini. Figs. 199 and 201, Andricus quercuscalifornicus, USNMENT01231839. Fig. 200, Melikaiella tumifica (Osten-Sacken, 1865), USNMENT01525885. Fig. 202, Zapatella daviae Buffington & Melika, 2016, USNMENT01231884. Fig. 203, Dryocosmus kuriphilus, USNMENT01231861. Fig. 204, Callicyrtis glandium, USNMENT01231862.
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 Zapateilla (Pujade-Villar et al. 2012b) and Melikaiella (Pujade-Villar et al. 2014). Two Palearctic genera, Belizinella Kovalev and Ussuruspis 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 Palearctic genera, Andricus and Callirhytis, are host alternators (heterocercy) 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 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 tarsigoni Kieffer and A. pseudofilos (Monzen), from Japan, Korea, China and Far East of Russia, are derived from their cyclically parthenogenetic ancestors A. mukaiyamai (Mukaiyamai) and A. kashiwaphilus Abe through the deletion of sexual generation (Abe 2007). Oak gall wasps have been very conservative on their host-plant choices, and host switches were extremely rare in the evolution of oak gall wasps (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 Palearctic 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 Palearctic and Oriental region. The most recent knowledge of Cynipini in Eastern Palearctic and Oriental region is reviewed in Pénzes et al. (2018).

Classification

Cynipini Billberg, 1820

Andricus 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
Aphelomyx Mayr, 1881; 3 species PA
Atrusca Kinsey, 1930; 59 species but taxonomy is uncertain NA, NT
Baruncynps 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
Discholcaspis 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
Eumyaria Ashmead, 1887; 6 species NA
Eumyariellia Melika and Abrahamson, 1997; 2 species NA
Femuros Kinsey, 1937; 7 species NA
Heterocercy Kinsey, 1922; 12 species NA
Holocynips Kieffer, 1910; 5 species NA
Kinseyella Pujade-Villar and Melika, 2010; 2 species NA
Kokkocyntis Pujade-Villar and Melika, 2013; 1 species NT
Latuspinsa 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
Phylloterus Ashmead, 1897; 9 species NA
Plagiotrochus Mayr, 1881; 22 species PA, OR
Protobaldinrictis Melika, Nicholls and Stone, 2018; 1 species NA
Pseudoneuroterus Kinsey, 1923; 4 species wPA
**Diastrophini**  
Figs. 205–207  
This tribe, circumscribed in Ronquist et al. (2015), contains the galler *Diastrophus* and *Xestophanes*, formerly included in the tribe Aylacini, and the inquilines *Periclistus* 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 (*Periclistus, 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  
*Periclistus* 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 galler 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 hybridzation among rose species can be common, confusing the taxonomy of the group, rose gellers seem to have adapted to intermediate species, much in the same way oak gellers 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
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

*Liebelia* Kieffer, 1903; 9 species PA
Eschatocerini

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
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 *Cecinothofagus*.

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

Distribution. Southern South America.

Plate 11. Paraulacini. Figs. 214 and 216, *Paraulax queulensis*, USNMENT01231854. Fig. 215, *Cecinothofagus* sp., USNMENT01231851.
Relevant literature. Nieves-Aldrey et al. (2009) summarizes the group completely.

Classification.

*Paraulacini* Nieves-Aldrey and Liljeblad, 2009

*Cecinotobagis* 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
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
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

*Qwaqwaia* Liljeblad, Nieves-Aldrey and Melika, 2011; 1 species
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

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. USNMENT0148497.
closely allied to S. iteensis 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. Pénczes 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 holometabolon 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 Pycnostigminae.

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 Anacharisis, in conjunction with a very short ovipositor, is hypothesized to be an adaptation for ‘quick strike’ oviposition into predaceous 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 (Acanthaegilopsis). Anacharisis 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 Anacharisis (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
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
Solenogites Diaz, 1979; 1 species NT
Xyalaspis Hartig, 1843; 25 species worldwide but mostly Holarctic

Plate 16. Anacharitinae. Fig. 233–235, Anacharis melaneura, USNMMENT01231833. Fig. 236, Xyalaspis flavipes, USNMMENT01231844.
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 preying 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 Afrotropical Region and Northern Africa.

Relevant literature. Ros-Farré & Pujade-Villar revised Prosaspicera (2006), Callaspidia (2009a) Paraspicera (2011a), Omalaspis (2011b) and Aspicer (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
Aspicer Dahlbom, 1842; 54 species Holarctic but also found in India
Balha Cameron, 1883; 6 species NT
Callaspidia 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; 2 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 (Dilapo and Thoreuan) 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 Afrotopical species.

Classification.

Charipinae Dalla Torre and Kieffer, 1910

Alloxysta Förster; 137 species worldwide but mainly Holarctic, despite recent revisions many problems remain Apocharips Fergusson, 1986; 6 species NT, PA, AT
Dilapo 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  
*Thoreana* Girault, 1930; 4 species AU
Emargininae

Figs. 249 and 250

This unusual group of diminutive wasps has been variously classified, often as eucoilines. 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 figitid 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

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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

Euceroptres Ashmead, 1896; 4 species NA

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*Thoreauella* Girault, 1930; 15 species pantropical ePAePA
Eucoilinae

Figs. 253–258
Within the Figitidae, the vast majority of both species diversity, and abundance, occurs within Eucoilinae. Eucoelines 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 eucoelines 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

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.
groups of eucolines, including the Diglyphosematini (Buffington 2011), Zaeucoila (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 eucolines 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).

Eucolines are parasites 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). Drosophilidae parasites 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 eucolines that have been used in the biological control of pest flies include: Aganaspis species on tephritids; Trybiographa species on onion maggot; Banacuniculus; and Ganaspidium species on leafminers.

Biological. 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 Geronotoma micromorpha as an egg-larval parasite of Liriomyza trifoli; it is not known how widespread this type of biology is among Eucoilinae. Hosts are known 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 appear 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 Zaeucoila 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 Lenteran 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 Zaeucoila (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
Nordlandertia Quinlan, 1986; 4 species AT, PA
Paraglyphosema 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

Afrodontaspis Weld, 1962; 2 species AT
Botbrochus 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 cPA
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
Trybiographa 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
Areaaspis 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
Conucoela 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
Dieucoila 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
Epichresta 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
Gastraspida 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
Hexacola 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
Humboldteria Buffington 2017; 4 species NT
Hydrellaeucola Diaz & 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 Diaz, 1982; 2 species but 3 more need to be moved in and some described as new; NT, NA
Odontocoela Ashmead, 1903; 8 species NT
Odontosema Kieffer, 1909; 1 species NT
Paragranaspis Diaz & 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
Promiomeria 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
Stratovertex 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
Nanocoelbu 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
Stentorcorps Quinlan, 1984; 6 species AT
Trichoplaster 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
Lophuecoila 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
Penicoelbu Weld, 1951; 1 species NT
Presenecoela Buffington, 2004; 3 species NT, NA
Rhahemcoela Kieffer, 1907; 7 species NT
Tropidencoela Ashmead, 1903; 9 species NT
Zaeucolea Ashmead, 1903; 14 species NT, NA

‘Leptolamina group’, not currently assigned to a tribe
Leptolamina Yoshimoto; 16 species and more undescribed; OR, AU, AT, PA
Micrerioidea 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 inquienda

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 figitid 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 Eucoilinae, 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

**Mikeiinae**

Figs. 265 and 266

This small subfamily contains some unusual figitid species endemic to Australia. Mikeius was originally placed within Thrasorinae, a
subfamily containing *Thrasorus*, another gall-associated figitid from Australia. Following a phylogenetic analysis, Paretas-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 Paretas-Martinez et al. (2011). Phylogeny of the group by Buffington et al. (2012).

**Classification.**

 Mikeiinae Paretas-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 parasitoids 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.
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 Brèthes, 1928; 1 species NT
Plectocynips Díaz, 1976; 3 species NT
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 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, *Triapitziniola vanharteni* Buffington and van Noort 2007, USNMENT00764764.
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
Triapitziniola 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 pleiomorphic within Figitidae and forms a grade along with Euceroprinae and Plectocyphininae (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, Palmirella, Cicatrix).

Relevant literature. Paretas-Martinez et al. (2011) investigated Australian thraeserines; Ros-Farré and Pujade-Villar (2009b) revised Myrtopsen. Ros-Farré and Pujade-Villar 2007 described Scutimica. Ronquist (1999) discussed the so-called figitoid inquilines. 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
Palmirella 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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