30 Eurytomidae

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Abstract

The family Eurytomidae is a diverse monophyletic taxon defined by a suite of variable morphological characters. Eurytomid host associations are also highly variable, ranging from strict phytophagy to entomophagy, or both. The larvae of the majority of eurytomid species are seed eaters, gall inducers, parasitoids of phytophagous insects, and either primary or secondary parasitoids of the eggs, larvae or pupae of various arthropods (Diptera, Coleoptera, Hymenoptera, Lepidoptera, Orthoptera and Araneae). Hyperparasitic eurytomids mostly attack Ichneumonoidea. Four subfamilies are recognized, with Eurytominae the most diverse and common group. The chapter provides a diagnosis, discusses relevant morphology, summarizes their distribution, natural history, economic importance, and the taxonomy of important species groups, and provides a key to the subfamilies.

Diagnosis

Body length variable, typically ranging from 1.0 mm to 5.0 mm, but occasionally to 20 mm. Color usually black, brown, golden, or combination thereof (Fig. 30.1); rarely metallic blue and/or green with tinges of purple or red (Fig. 30.3A). Antenna with maximum of 11 flagellomeres, most commonly 9; a single anellus usually present, or 2–3 in Rileyinae (Couplet Fig. 30.C7); males often with whorls of setae on pedicellate flagellomeres (Fig. 30.4C) (not present in male Hembrinae, Buresiinae, some Rileyinae, and some Eurytominae), ventral plaque on male scape (Fig. 30.4C, inset) common. Pronotal collar quadrate in dorsal view. Mesosoma heavily sclerotized, sculpture often coarsely umbilicate (Fig. 30.3A–B), but can range to fine reticulation (Fig. 30.5A). Tarsi 5-segmented, except in male *Boucekiana tetracampoide* that have a 4-3-3 tarsal formula. Metasoma usually sessile or with a short petiole in females, but longer petioles occur (e.g., *Tenuipetiolus*, certain species of *Phylloxeroxenus*, *Aximopsis*, *Prodecatoma*, etc.). Males typically with distinctly petiolate metasoma (Figs 30.4A, cf. 30.5B).

Fig. 30.1. Eurytomidae. *Eurytoma collaris* (♀), habitus.

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Chalcidoidea of the World (eds John Heraty and James Woolley)

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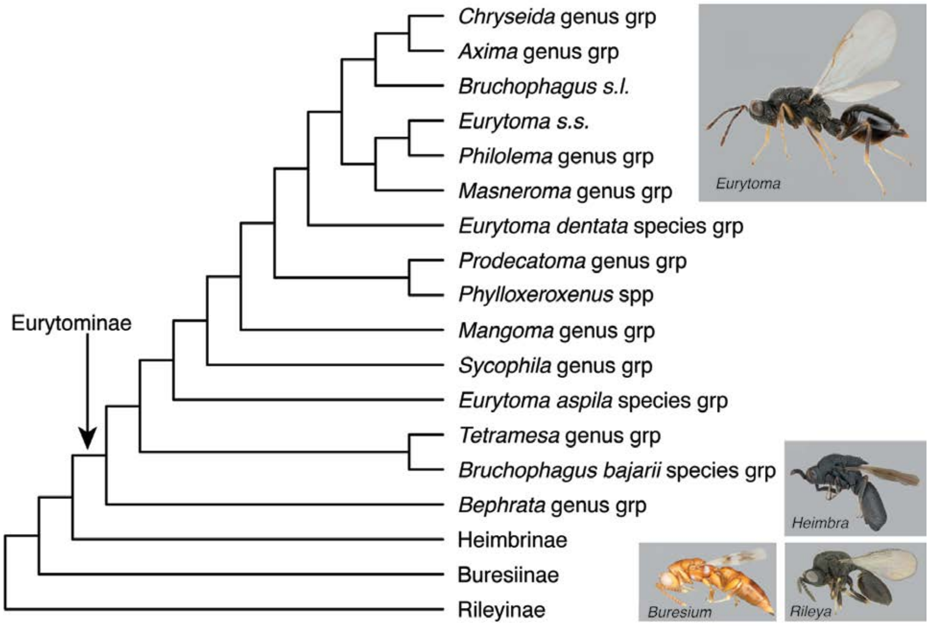


Fig. 30.2. Eurytomidae. Cladogram of relationships.

Morphology

Eurytomidae are currently not supported as a monophyletic group by morphological synapomorphies, and any unusual morphology exhibited within the family is either shared with other Chalcidoidea or of value only as diagnostic features of genera or species. As an example of the latter, many species of *Axima* and *Aximopsis* (Fig. 30.5C) have spines on the vertex between the eye and lateral ocellus or on the pronotum antero-medially. Other unusual morphology is seen in uncommon or very rare taxa: *Platyrileya cururipe* has a dramatically dorsally flattened mesosoma (Fig. 30.4B), a species of *Aximopsis* has a head capsule with distinct protuberances on the frons (Fig. 30.6A), females of known *Bruchodape* have Gt_4 with a protuberant dorsomedial 'button' (Fig. 30.6B), and *Masneroma angulifera* has a triangular pronotal projection extending posterad into an excavation of the mesoscutum (Fig. 30.6C). Heimbrinae have a robust mesoscutellar spine and fused Gt_{1+2} (Fig. 30.3B) that serves to diagnose this subfamily only. Mesoscutellar spines occur in other Eurytomidae, but are never as robustly produced (e.g., *Philolema spinifera*, certain *Aximopsis*). Eurytomids are most frequently confused with some Pteromalidae and Cleonymidae that have a quadrate pronotum. Pteromalidae often have the metasoma variously dorsoventrally compressed, whereas eurytomids are more commonly laterally compressed.

Many eurytomids, especially Eurytominae, have pedicellate and/or elongate flagellomeres or elongate flagellar setae in males (Fig. 30.4C), which may increase effective sensory surface area to aid in locating females. Males of some Eurytominae and Rileyinae also have many placoid sensilla on the scape, often in conjunction with a raised ventral plaque (Fig. 30.4C).

Wings are present and functional in all taxa, with rare exceptions such as the spring generation of *Tetramesa maderae* (Popescu, 2004). The metasoma is petiolate, with the petiole usually shorter than the metacoxa in females, and often much longer in males.

Diversity

Over 1600 described species in 73 genera are recognized in four subfamilies (Fig. 30.2) (Zhang, unpublished). There are currently no proposed tribes within eurytomid subfamilies, though Lotfalizadeh *et al*. (2007) provided evidence supporting numerous suprageneric groups in Eurytominae as part of their morphological phylogenetic analysis. Eurytominae contains 62 genera and ~1500 species. Heimbrinae contains two genera and eight species. Rileyinae contains seven genera and 78 species. Buresiinae contains two genera and nine species.

Distribution

Eurytomidae are found on all continents except Antarctica, with the highest diversity in tropical climates. Valuable regional treatments at the family group level include Burks (1971; World genera), Zerova (1976, 1995; Palearctic Eurytomidae, in part), Bouček (1988; Australasian Eurytomidae), and Narendran (1994; Indian Eurytomidae).

Classification and Relationships

Historical treatments

Walker (1832) included four genera in the family: *Eurytoma*, *Decatoma*, *Isosoma* and *Systole*. Ashmead (1904) described 23

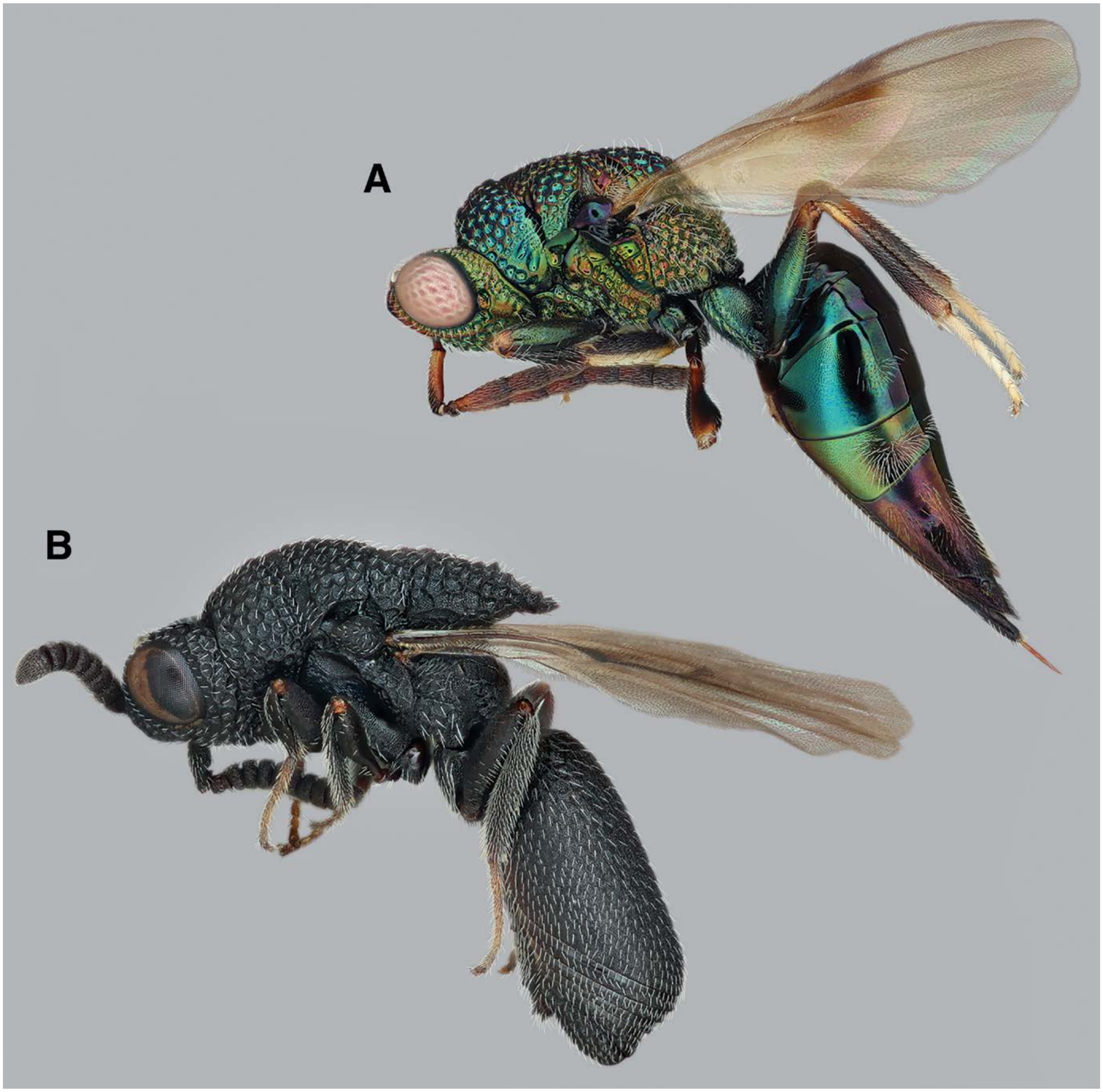


Fig. 30.3. Eurytomidae. **A**, Eurytominae: *Chryseida* sp. (♀), habitus. **B**, Heimbrinae: *Heimbra opaca* (♀), habitus.

new genera and erected the tribes Aximini, Eurytomini, Isosomini, Rileyini and Decatomini, which were accepted by Bugbee (1936). These tribes were raised to subfamily rank (Ferrière, 1950; excluding Aximini, Harmolitinae for Isosomini) and maintained by Nikol'skaya (1952). Claridge (1961b); replaced Decatominae with Eudecatominae and Peck (1963) followed Claridge (1961b). Burks (1971, 1979) added three new subfamilies (Heimbrinae, Prodecatominae and Philoleminae) without any diagnoses offered to distinguish these groups. According to Gates (2008), the proposed subfamily names above do not satisfy the criteria for availability set in Article 13 (ICZN, 1999) as they lacked diagnoses. Zerova (1988) used Ashmead's system but placed *Buresium* in a separate subfamily, Buresiinae. Subba Rao (1978) recognized only two subfamilies (Rileyinae and Eurytominae). Stage and Snelling (1986) revised Heimbrinae, added them to Subba Rao's classification and provided morphological support for the three subfamilies. This included formally synonymizing six subfamilies into Eurytominae (Aximinae, Decatominae, Philoleminae, Harmolitinae, Prodecatominae, and Eudecatominae. Stage and Snelling's (1986) classification was followed by Bouček (1988) in his monograph of the Australasian chalcidoid fauna and by DiGiulio for the Nearctic (1997). Gates (2008) tabulated the systems of classification previously used by different authors.

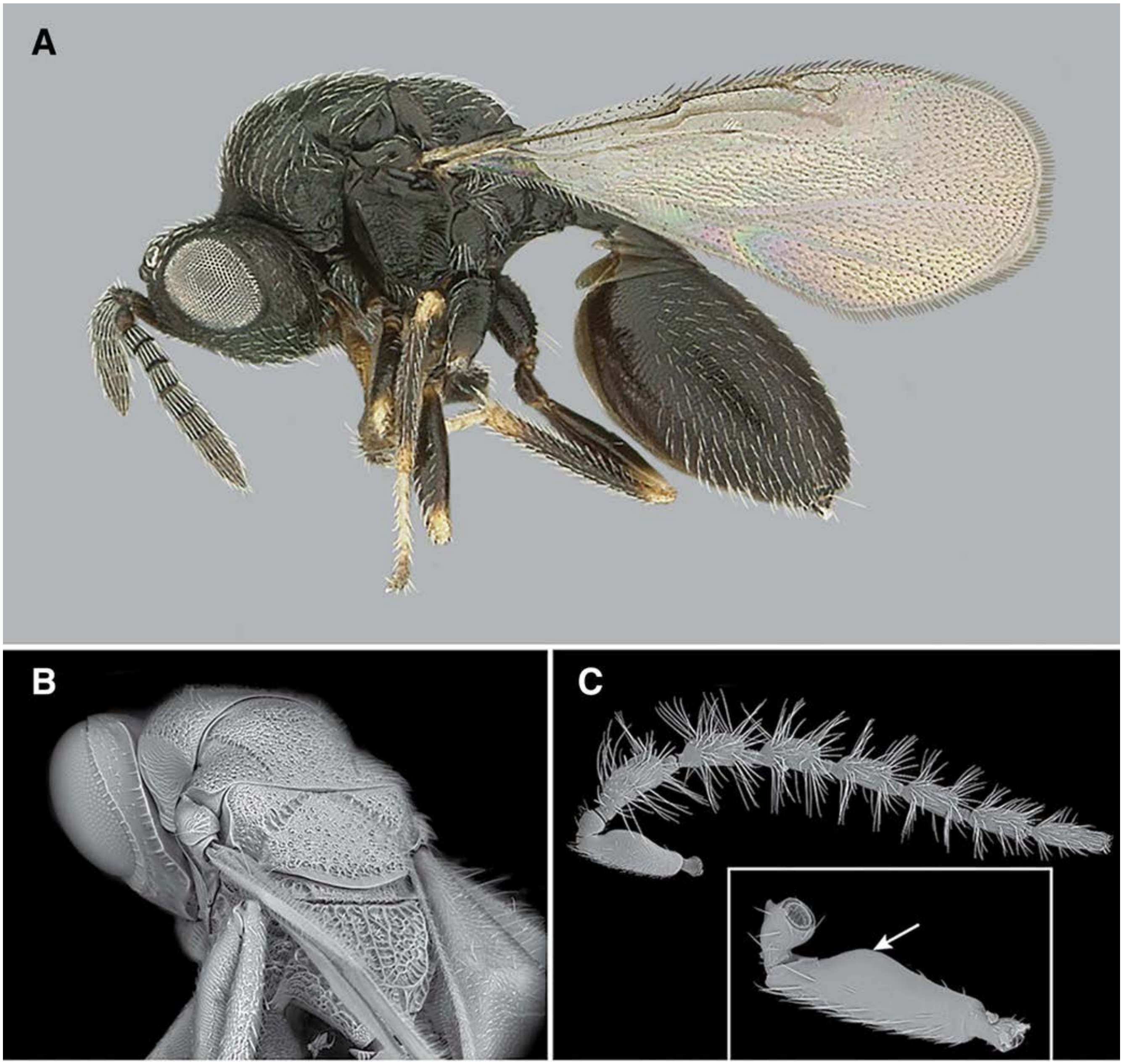


Fig. 30.4. Eurytomidae. **A**, **B**, Rileyinae: **A**, *Rileya pallidipes* (♂), habitus; **B**, *Platyrileya cururipe* (♀), head and mesosoma, dorsolateral view. **C**, Eurytominae: *Eurytoma* sp. (♂), antenna, inset: scape of *Eurytoma seminis* (♂), arrow: ventral plaque.

Buresiinae were synonymized with Eurytominae, and Rileyinae were revised and defined more narrowly, with the genera *Archirileya*, *Buresium* and *Macrorileya* excluded and transferred to Eurytominae (Gates, 2008). Lotfalizadeh *et al.* (2007) revived the status of Buresiinae, removing it from Eurytominae, based on having a flagellum with 11 flagellomeres, flagellomere 1 without MPS (Fig. 30.7A), flagellomeres 2–4 with MPS, pronotum at least as long as mesoscutum, prepectus long (Fig. 30.7B), metapleuron partly separated from propodeum, meso- and metafurcal pits quite small (the latter visible at high magnification), Gt_2 short and syntergum with a transverse carina in front of cerci (Fig. 30.12E).

Consequently, the two systems of classification conflict with each other: either Eurytominae are split into five tribes following Ashmead (1904), or the subfamily is undivided as proposed by Stage and Snelling (1986). Zerova (1988) carried out a character analysis and postulated groundplan features for Eurytomidae but she did not mention how she polarized the characters, nor did she distinguish between primitive and derived states to define eurytomid taxa.

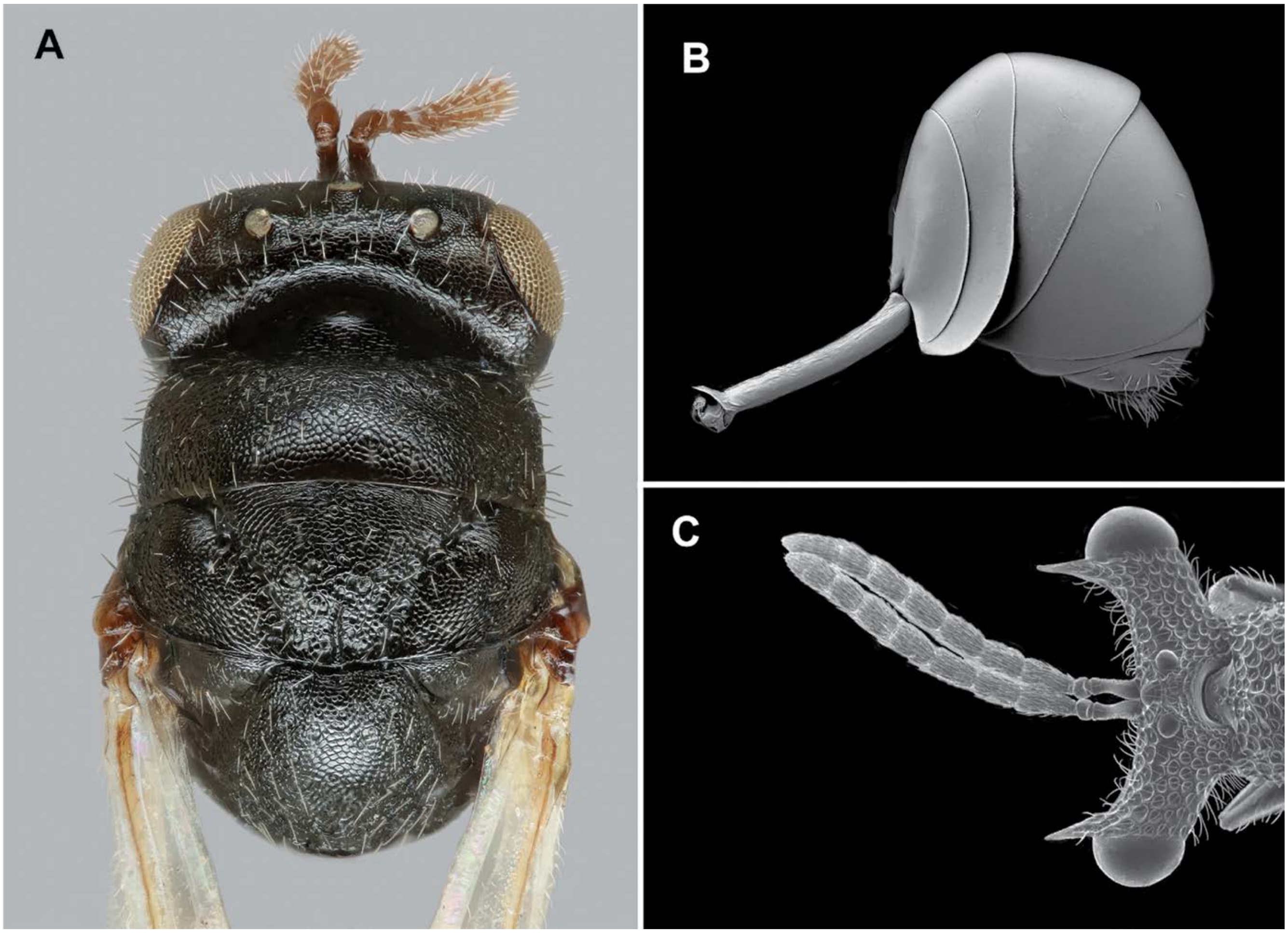


Fig. 30.5. Eurytomidae. **A**, **B**, Eurytominae: **A**, *Systole* sp. (♀), head and mesosoma, dorsal view; **B**, *Phylloxeroxenus* sp. (♂) metasoma. **C**, Aximinae: *Axima diabolus* (♀), head, dorsal view.

Recent classification

The genera of Eurytomidae are often poorly defined and rely on a suite of morphological characters for recognition. Over half of the species are described in the genus *Eurytoma* and, conversely, over 40 genera are monotypic. Genera are rarely clearly defined, despite recent attempts to improve our knowledge (e.g., Burks, 1971; Bouček, 1988; Narendran, 1994; Zerova, 1995; Lotfalizadeh *et al.*, 2007). Indeed, autopomorphies can be postulated for the monotypic genera but the largest genera are not based on shared derived characters. Burks (1971: 44) noted: 'Many species are placed in *Eurytoma* not because they are greatly like the type species, but because it has not yet been possible to place them elsewhere'. The problem is complicated by the apparently uniform habitus of the species and the intergradation of character states, which often form morphoclines.

The monophyly of Eurytomidae is still questioned because tangible morphological synapomorphies are lacking (Lotfalizadeh *et al.*, 2007; Gates, 2008). Wijesekara (1997) proposed two features that might support the monophyly of Eurytomidae: (1) genal bridge completely covering the hypostomal bridge (found also in some Chalcididae); and (2) anterior condyle of the petiole separated from the body only dorsally so that the anterior ventral margin of the petiole abuts the propodeal foramen, although his sampling of Eurytomidae was limited to two species belonging to *Eurytoma* and *Tetramesa*. The phylogenetic analysis of Gates (2008) used 50 characters to investigate the relationships between Cleonyminae (one species sampled), Leucospidae (two spp.), Chalcididae (ten spp.), Rileyinae *s.l.* (13 spp.), Heimbrinae (two spp.) and Eurytominae (nine spp.). Eurytomidae were monophyletic but weakly supported by states that were homoplastic.

Campbell *et al.* (2000) used 28S-D2 rDNA to explore the phylogeny of the Chalcidoidea and included five eurytomids. Despite this restricted sample the family was polyphyletic, comprising two disparate groups, Rileyinae and Eurytominae. Chen *et al.* (2004) carried out the first molecular phylogeny of the family using 24 species and four genes, 18S and 28S (rDNA) and 16S and COI (mtDNA). While most genes exhibited very low levels of variability and the domains analyzed strongly conflicted, the authors concluded that the family was not monophyletic, with Rileyinae sister to Dirhininae

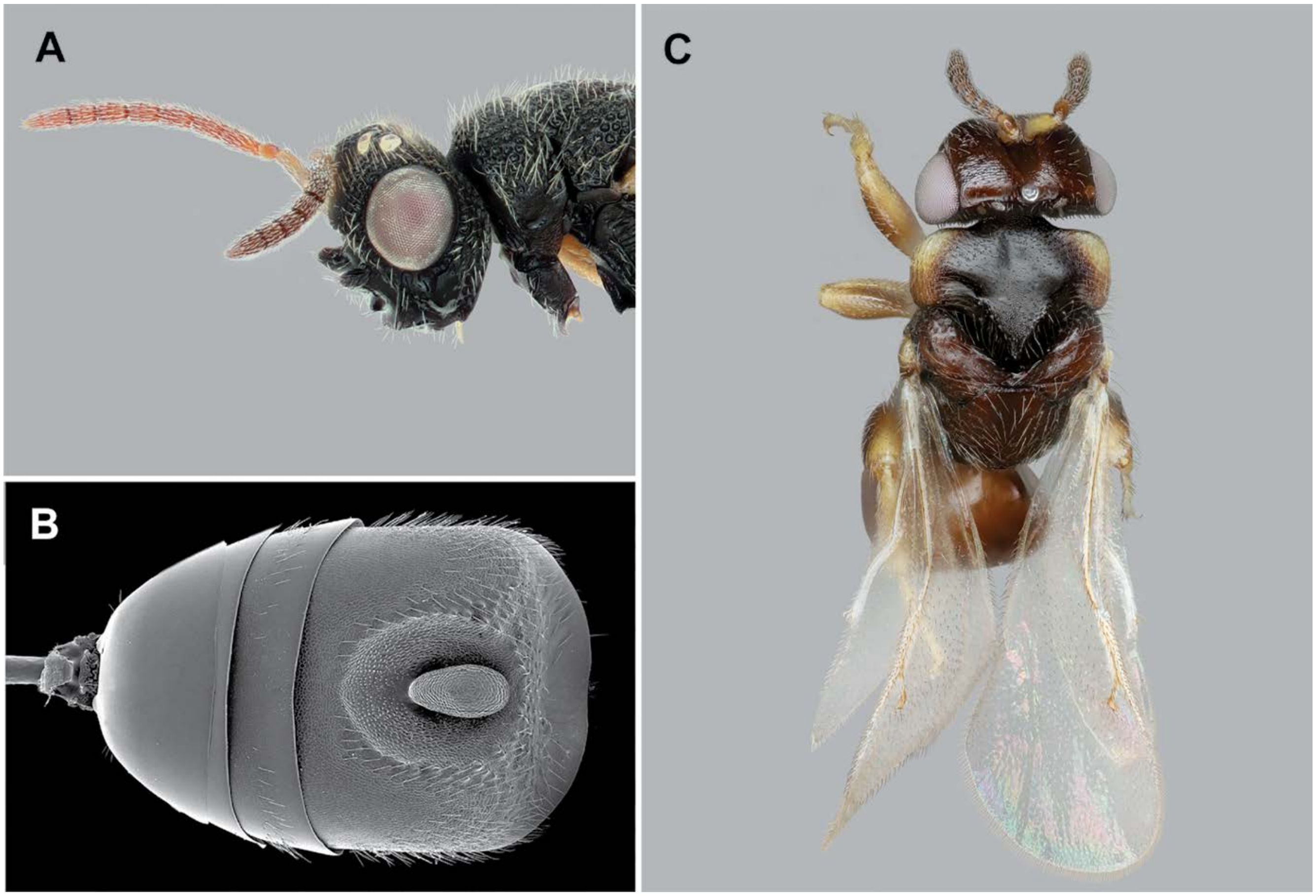


Fig. 30.6. Eurytomidae. Eurytominae: **A**, *Aximopsis* sp. (♀), head, lateral view; **B**, *Bruchodape ignota* (♀) metasoma, dorsal view; **C**, *Masneroma angulifera* (♀), habitus, dorsal view.

(Chalcididae) and nested within a clade containing Eunotidae, Perilampidae, and Eucharitidae. Munro *et al*. (2011) also did not recover a monophyletic Eurytomidae in their molecular analysis of Chalcidoidea. They did recover a monophyletic Rileyinae, but Buresiinae and Hemibrinae never grouped with the other Eurytomidae.

Heraty *et al*. (2013) recovered a monophyletic Eurytomidae, supported by 11 putative morphological synapomorphies, with all subfamilies monophyletic except for Heimbrinae which placed internally with *Neorileya* (Rileyinae). Peters *et al*. (2017) recovered a monophyletic Eurytomidae (but sampling only two genera of Eurytominae) as sister to Chalcididae using transcriptomic data and a reduced representation matrix. Based on a combination of AHE and UCE data (Cruaud *et al*., 2024), Eurytomidae (18 taxa representing all four subfamilies, but only one Heimbrinae) were monophyletic, with Chalcididae as sister-group. With the exception of the large morphological study on Eurytominae (Lotfalizadeh *et al*., 2007), other phylogenetic studies have focused more broadly on Hymenoptera and/or Chalcidoidea, but with few Eurytomidae (Branstetter *et al*., 2017; Zhang *et al*., 2020; Cruaud *et al*., 2021, 2024; Blaimer *et al*., 2023). Cruaud *et al.* (2024) also recovered the monophyly of Eurytomidae and its subfamily using UCE data. Conversely, the Blaimer *et al.* (2023) study used many of the same samples as Cruaud *et al.* (2024) but still did not recover Eurytomidae as monophyletic despite a wider sampling of 35 taxa with *Heimbra* sp. behaving as a rogue taxon by grouping either with the colotrechnine pteromalid *Colotrechnus* or within Chalcididae instead of within the otherwise monophyletic Eurytomidae.

Natural History

Eurytomidae exhibit a broad diversity of biology, host use and feeding behavior. A majority of the larvae occur inside plant tissues, either as seed-eaters or gall-formers, or as parasitoids of phytophagous insects. Most eurytomids are primary parasitoids, attacking eggs, larvae or pupae of various arthropod groups (Diptera, Coleoptera, Hymenoptera, Lepidoptera, Orthoptera and Araneae), while hyperparasitic eurytomids mostly attack Ichneumonoidea (Bouček, 1988; Noyes, 2019). Genera that include strictly phytophagous species include *Austrodecatoma*, *Ausystole*, *Cathilaria*, *Prodecatoma* (*sensu stricto*), *Risbecoma*, *Systole* and *Tetramesa*, with their larvae developing in stems of wild grasses, including cereal crops, or in seeds of Apiaceae, Fabaceae, Rosaceae, and other plant families.

Fig. 30.7. Eurytomidae. Eurytominae: **A**, *Buresium* sp. (♀), habitus, inset: antennal flagellum, arrow: anelliform first flagellomere; **B**, *Macrorileya* sp. (♀), mesosoma, lateral view; **C**, *Macrorileya* sp. (♀), syntergum, lateral view.

Others are thought to be gall formers in the roots and twigs of several plants: *Aranedra* and *Foutsia* develop in *Philodendron* spp. (Araceae) galls in the Neotropics (Bouček, 1988; Noyes, 2019; Gates, 2013, pers. obs.) and *Proseurytoma* spp. induce stem galls on *Geoffrea decorticans* (Fabaceae) and *Prosopis alba* (Fabaceae) in Argentina (Kieffer and Jörgensen, 1910; Brèthes, 1922; Gates, 2015, pers. obs.). There is even a reported myrmecophile, *Camponotophilus delvarei*, that develops as a gregarious, primary ectoparasitoid of the larvae and pupae of Microdontinae (Syrphidae) in arboreal nests of *Camponotus* (*Myrmobrachus*) sp. aff. *textor* (Pérez-Lachaud *et al*., 2013), which is the first report of their parasitization of Syrphidae. Previous ant associations include *Aximopsis aztecicida* and *A. affinis*, documented as ectoparasitoids of foundress queens of several species of *Azteca* (Formicidae: Dolichoderinae) (Brues, 1922; Lachaud and Pérez-Lachaud, 2012). The exact host–parasitoid relationships for most parasitoid species remain unknown. Some Eurytomidae that are thought to develop as parasitoids may in fact be inquilines (*Bruchophagus* in Habib, 1983). For example, various genera (*Sycophila*, *Ficomila*) reared from fruits of *Ficus* (Moraceae) may actually be inquilines in galls rather than parasitoids of Epichrysomallidae, but this still needs to be confirmed (see Chapter 25) (Compton *et al*., 2018). Moreover, some eurytomids such as *Eurytoma atripes* (Gahan, 1933), *Eurytoma parva* (Phillips, 1918), and *Eurytoma pachyneuron* are known to switch to phytophagy before or after consuming an insect host (Phillips, 1917; Phillips, 1927). Another case of biological plasticity involves the *Eurytoma rosae* species-group, in which adults are morphologically similar and impossible to segregate into morphospecies, although their eggs are diagnostic

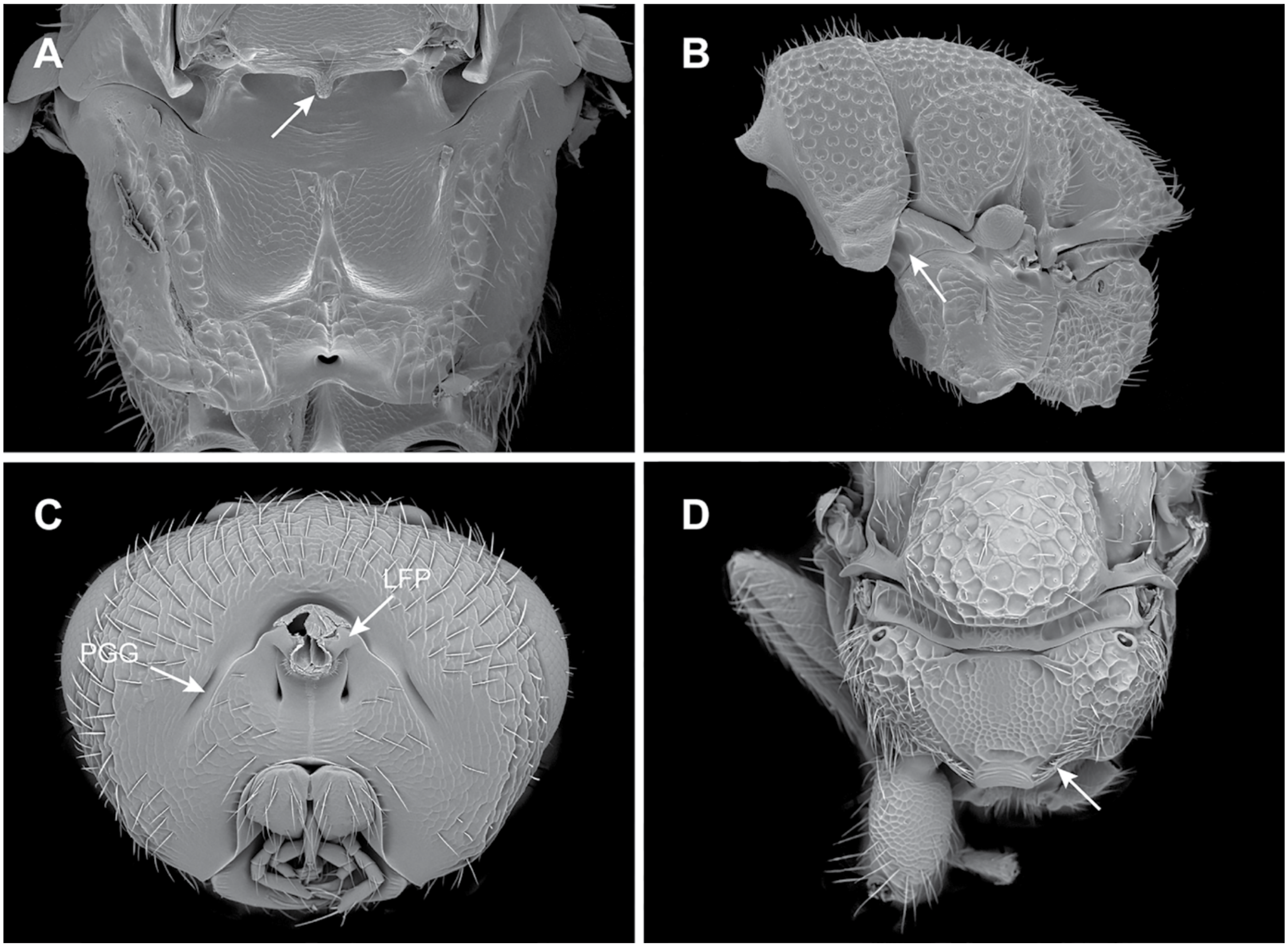


Fig. 30.8. Eurytomidae. Eurytominae: **A**, *Aximopsis* sp. (♀), mesosoma, ventral view, arrow: medioventral tooth; **B**, *Aximopsis* sp. (♀), mesosoma, lateral view, arrow: prepectal pit; **C**, *Bruchophagus* sp. (♀), head, posterior view, arrow: postgenal groove (PGG), arrow: lateral foraminal plate (LFP); **D**, *Bruchophagus* sp. (♀), scutellum and propodeum, dorsal view, arrow: brush of setae.

with *E. brunniventris* having the chorion setose versus smooth in *E. rosae* (Claridge and Askew, 1960). They may also be differentiated biologically, with larvae of *E. abrotani* (= *E. rosae*) predating inquiline Cynipidae associated with *Rosa* spp. (Rosaceae), whereas *E. brunniventris* larvae are associated with oaks and feed on the gall-forming cynipid larvae, its inquilines, and the gall tissue (Claridge and Askew, 1960). *Eurytoma parva* is reported to be entomophytophagous, consuming its gall-inducing host (*Tetramesa tritici*) before completing its development on host plant tissue (*Triticum aestivum*, Poaceae) (Phillips, 1927).

Economic and Ecological Importance

Because of their diversified biology, Eurytomidae have contrasting economic importance. A handful of eurytomid species are economically important or potentially important biological control agents, while others would be considered pests. Select examples are discussed here. Many species are pestiferous seed-eaters of cultivated plants, for example *Bruchophagus* spp. on Fabaceae, including clover and alfalfa (Carrillo and Dickason, 1963; Aeschlimann and Vitou, 1989), and *Systole* spp. on Apiaceae, including coriander, fennel, and carrot (Lamborot *et al.*, 1995; Mittal and Butani, 1995). The *Eurytoma amygdali* species group consume stone-fruit seeds (Zerova and Fursov, 1991; Duval and Froment, 1998; An *et al.*, 1998), while *Eurytoma plotnikovi* feed on pistachio (Davatchi, 1956; Jaraya and Helali, 1978). *Eurytoma aloineae* is a seed predator of *Aloe* spp. (Burks, 1957; Prinsloo, 1980). Finally, species of *Bephratelloides* are in seeds of custard apples (Annonaceae) (Grissell and Schauff, 1990). Other species, such as *Bruchophagus fellis*, induce galls on citrus that can result in fruit yield loss (Smith *et al.*, 1997). However, some phytophagous species have been used very successfully for biological control of weedy invasive plants. *Eurytoma attiva* has been used for the control of invasive black sage (*Varronia curassavica*, Boraginaceae) in Malaysia (Burks, 1958; Simmonds, 1980), and in Mauritius (Fowler *et al.*, 2000). A biological control program using *Tetramesa romana*, a stem gall inducer, was attempted against the invasive *Arundo donax* (Poaceae) in the southern USA, but proved ineffective in spite of being

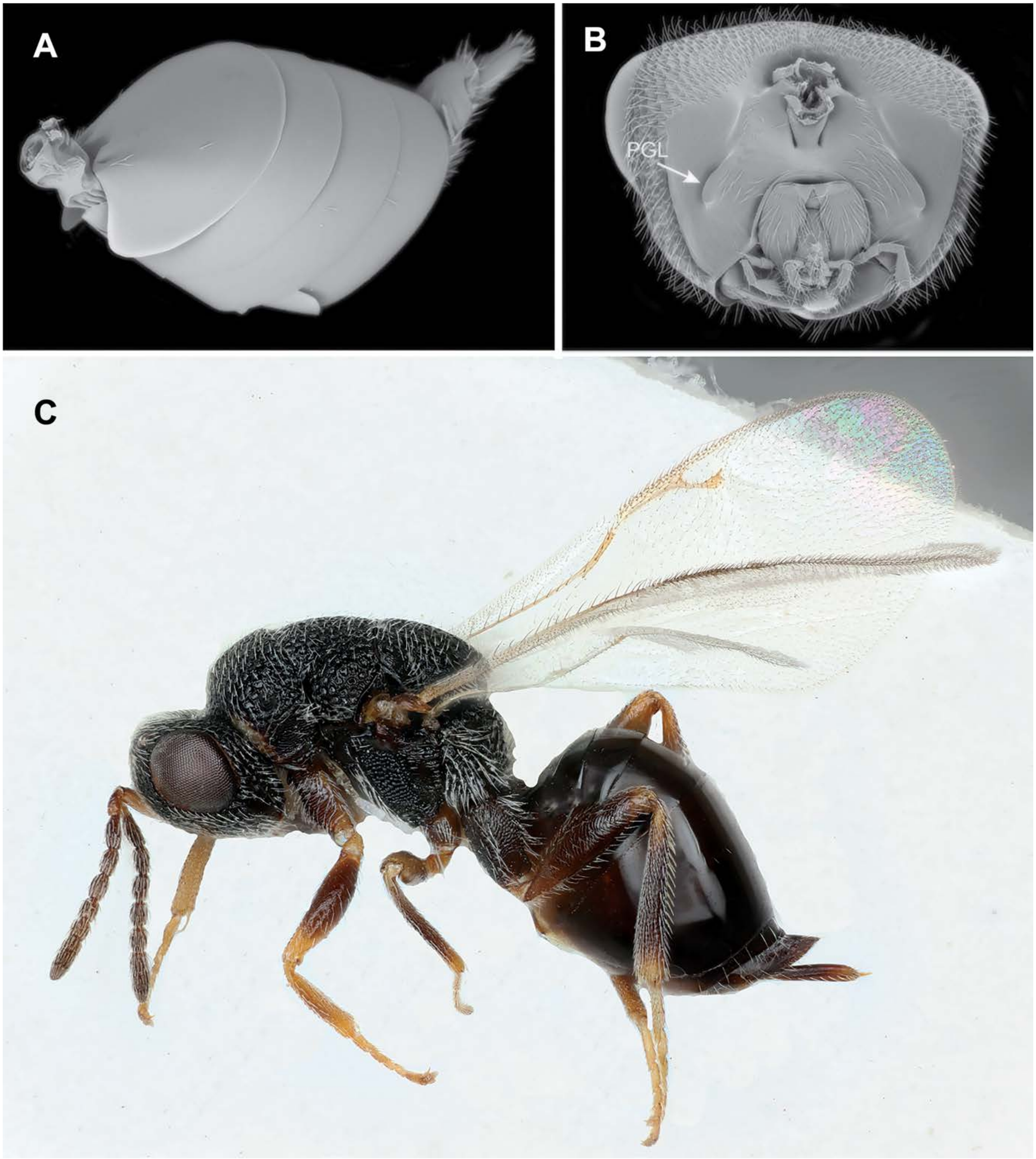


Fig. 30.9. Eurytomidae. Eurytominae: **A**, *Bruchophagus* sp. (♀) metasoma, lateral view; **B**, *Eurytoma maslovskii* (♀) head, posterior view, arrow: postgenal lobe (PGL); **C**, *Eurytoma morio* (♀), habitus.

established (Showler and Osbrink, 2018). Finally, some beneficial Eurytomidae are used as biological control agents of insects, e.g., *Aximopsis oryzivora*, a parasitoid of the stem borer *Maliarpha separatella* (Pyralidae) in tropical Africa (Delvare, 1988; Polaszek, 1998), and the successful introduction of *Eurytoma erythrinae* to control the invasive gall inducer *Quadrastichus erythrinae* (Eulophidae) in Hawaii, which was threatening the endemic tree *Erythrina sandwicensis* (Fabaceae) (Gates and Delvare, 2008).

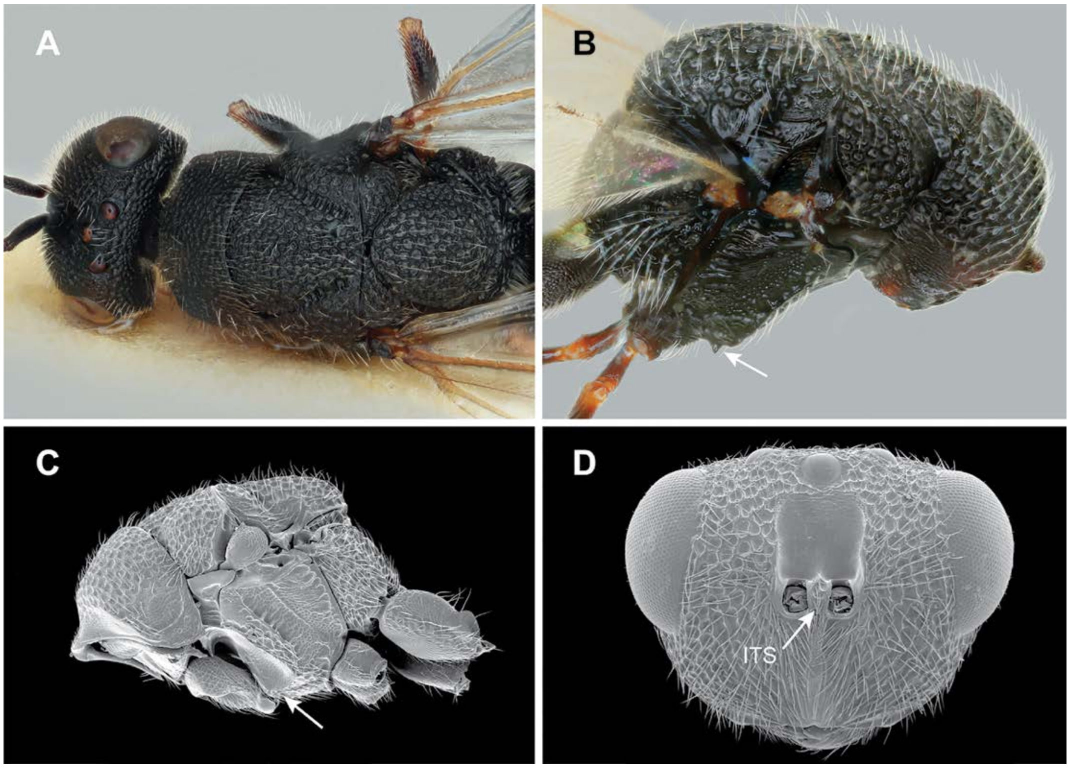


Fig. 30.10. Eurytomidae. Eurytominae: **A**, *Eurytoma amygdali* (♀), head and mesosoma, dorsal view; **B**, *Eurytoma brunniventris* (♀), mesosoma, lateral view, arrow: precoxal tooth; **C**, *Eurytoma robusta* (♀), mesosoma, lateral view, arrow: ventral shelf; **D**, *Eurytoma robusta* (♀), head, anterior view, arrow: intertorular space (ITS).

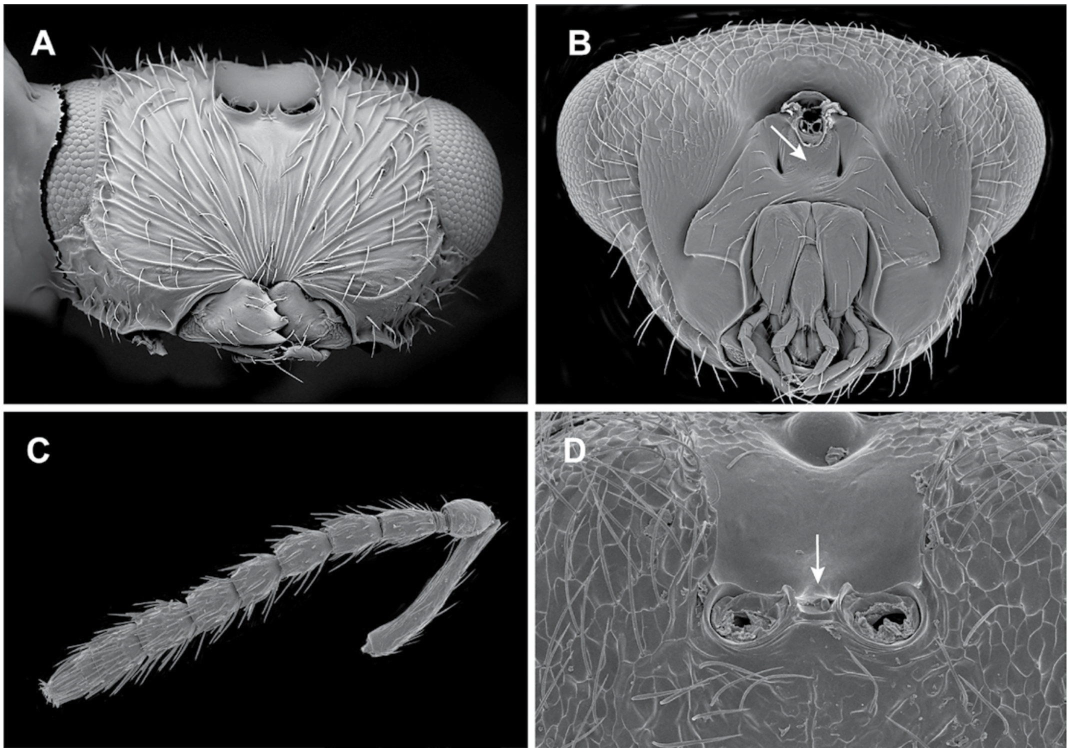


Fig. 30.11. Eurytomidae. Eurytominae: **A**, *Phylloxeroxenus* sp. (♀), head, anteroventral view; **B**, *Phylloxeroxenus* sp. (♀), head, posterior view, arrow: postgenal bridge; C, *Tetramesa hordei* (♀), antenna; D, *Tetramesa hordei* (♀), arrow: intertorular space.

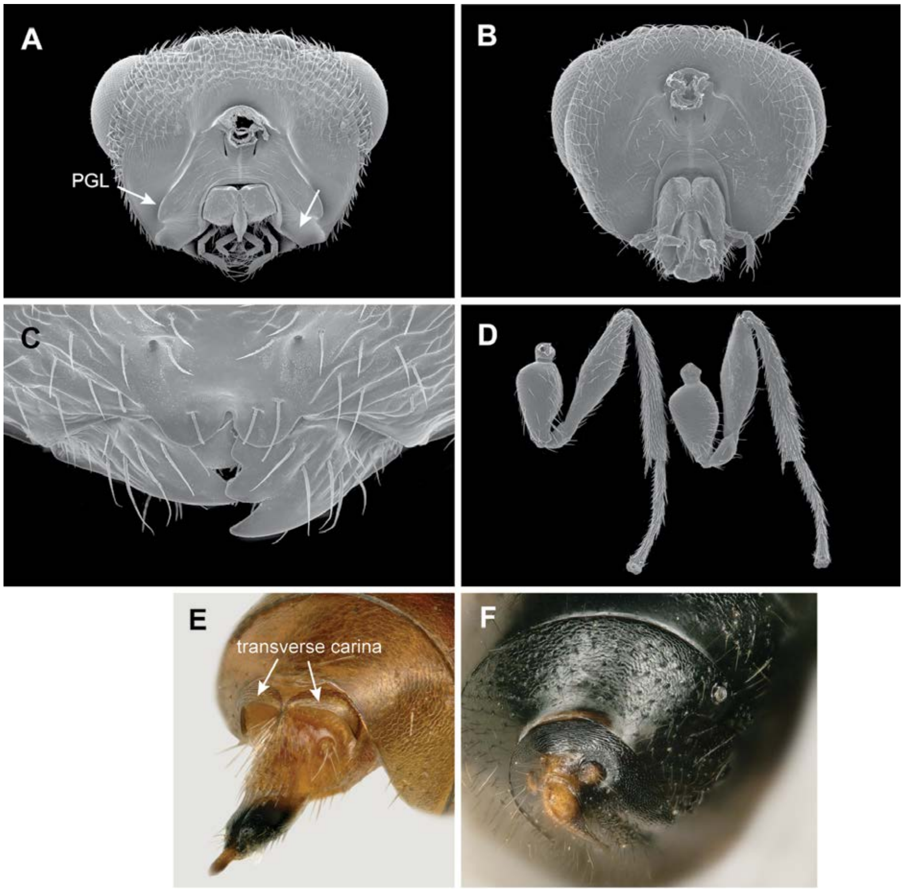


Fig. 30.12. Eurytomidae. Eurytominae: **A**, *Eurytoma bolteri* (♀), head, posterior view, arrow: postgenal lobe (PGL), arrow: ventral depression; **B**, *Sycophila smilax* (♀) head, posterior view; **C**, *Sycophila smilax* (♀), head, clypeus; **D**, *Sycophila smilax* (♀), hind legs; **E**, *Buresium rufum* (♀), metasoma, posterior view, arrows: transverse carina above cerci; **F**, *Tetramesa* sp. (♀), metasoma, posterior view.

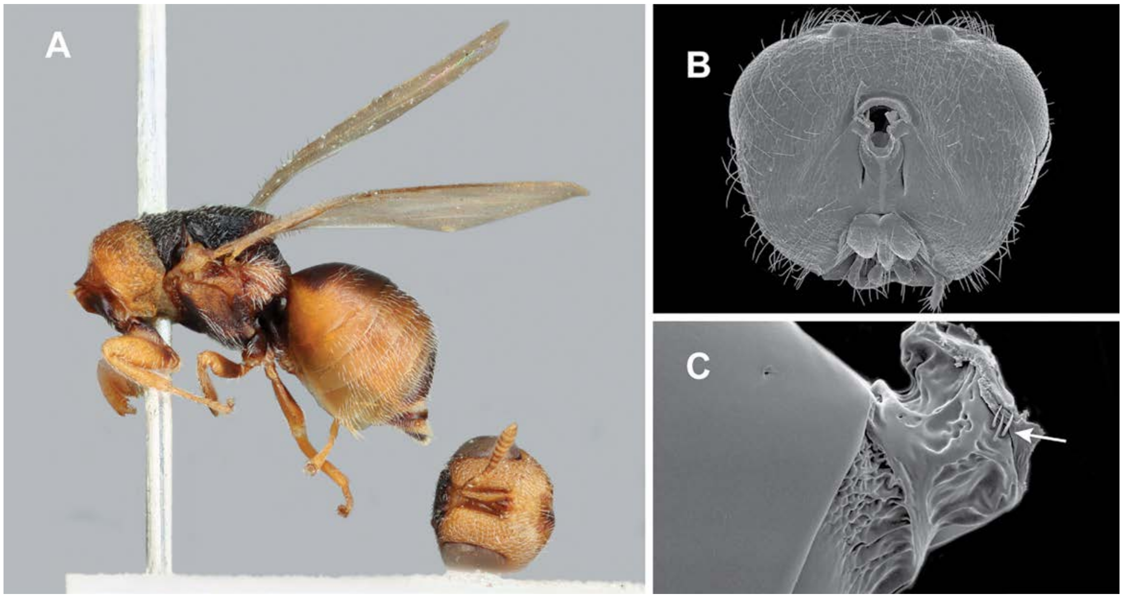
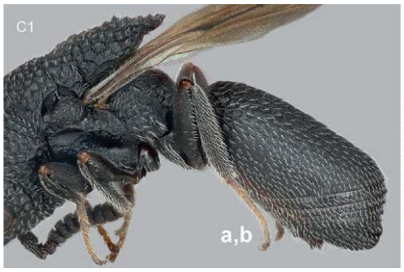


Fig. 30.13. Eurytomidae. Eurytominae: **A**, *Dougiola koebelei*, (♀), habitus, anterior head; **B**, *Tetramesa hordei* (♀), head, posterior view; **C**, *Tetramesa hordei* (♀), petiole, lateral view, arrow: lateral setae.

Key to subfamilies of Eurytomidae

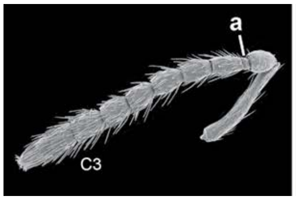
1) a. Scutellum produced apically as a robust spine-like process
b. Gastral terga 1 and 2 fused, carapace-like .... **Heimbrinae**

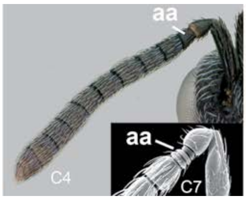
– aa. Scutellum not robustly produced as a spine
bb. Gastral terga 2 and 3 distinctly separate **2**

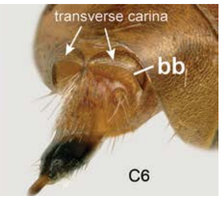


2) a. Antenna at most 11-segmented, including 1 anellus
b. Transverse carina on front of cercal plates on syntergum absent .... **Eurytominae**

– aa. Antenna 13-segmented, including 1–3 anelli
bb. Transverse carina on front of cercal plates on syntergum present **3**

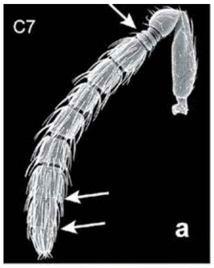


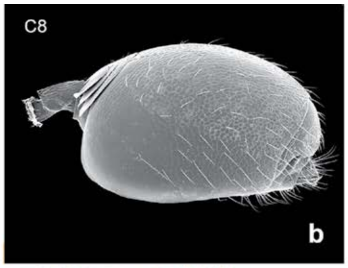


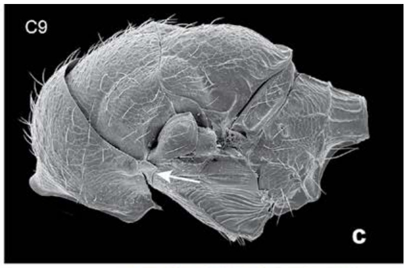


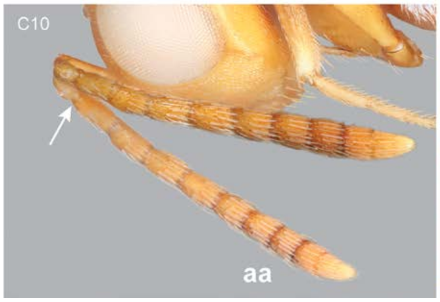
3) a. Antenna with 2 or 3 anelli
b. Basal 1–3 gastral terga (usually 1 or 1+2 or 1+2+3) reduced, **and**
c. Prepectus smaller than tegula .... **Rileyinae**

aa. Antenna with 1 anellus
bb. Basal 1–3 gastral terga not reduced
cc. Prepectus subequal to or larger than tegula .... **Buresiinae**









Buresiinae

Two genera, *Buresium* and *Macrorileya*, are currently recognized in Buresiinae, totaling nine species. The subfamily is supported as monophyletic by having: an 11-segmented flagellum with F1 elongate or transverse but lacking MPS (Fig. 30.7A, Couplet Fig. C4), flagellomeres 2–4 elongate or anelliform, but with elongate MPS; pronotum about as long as mesoscutum; prepectus long; metapleuron partly separated from propodeum; gastral tergum 2 short; syntergum with a transverse carina anterad of the cerci (Fig. 30.12E) (Lotfalizadeh *et al.*, 2007). *Buresium naso* is associated with *Mordellistena* sp. (Mordellidae) in stems of *Cannabis sativa* (Cannabaceae) (Bouček, 1983). *Macrorileya* spp. are predators of tree cricket (Gryllidae) (Silvestri, 1920; Smith, 1930) or cicada (Cicadidae) eggs inserted in twigs (Delvare, 2016, pers. obs.).

Eurytominae

This is the largest and most diverse subfamily of Eurytomidae. There is a lack of consensus of tribal classification within Eurytomidae and Eurytominae (but see Lotfalizdeh *et al.*, 2007).

Characterization of Large Genera of Eurytominae

Aximopsis

This genus of 36 species is distributed primarily in tropical regions, though several species occur in temperate and arid habitats in the Palearctic region. Historically confused with *Eurytoma*, *Aximopsis* is more speciose than currently indicated. Collections from extensive Malaise trapping and canopy fogging in Costa Rica and Ecuador, respectively, have yielded ~60 new species. Therefore, its size may be expected to eventually number in the hundreds of species globally. Gates *et al.* (2006) reported on *Aximopsis s.s.*, a more narrowly defined monophyletic lineage within the larger *Aximopsis s.l.* The latter is recognized by a suite of morphological characters that are homoplastic: postgenal laminae raised, prepectus with a strong medioventral tooth (Fig. 30.8A), subventral carinae of prepectus delimiting a raised surface (Fig. 30.8A), subventral prepectus with a deep pit (Fig. 30.8B), mesopleuron with a horizontal ventral shelf and a completely delimited epicnemium (Fig. 30.8B). Unpublished molecular studies indicate non-monophyly of the genus and several species groups have been discerned morphologically.

Aximopsis are parasitoids of endophytic insects living in branches, stems or leaf-mines, including xylophagous Coleoptera (mainly Cerambycidae and Buprestidae), aculeate Hymenoptera nesting in twigs (Gates, 2009) or leaf-mining Buprestidae. Lotfalizadeh *et al.* (2007) postulated a host shift from Coleoptera to Hymenoptera associated with the common use of beetle galleries by nesting wasps. A second shift possibly involves coevolution with some Buprestidae (*Taphrocerus* spp. and *Pachyschelus* spp.) which, in the Neotropical region, became leaf miners on Arecaceae (Gates *et al.*, 2006).

Bruchophagus

Lotfalizadeh *et al.* (2007) characterized seven species groups in *Bruchophagus*. Over 170 species are described globally, primarily from the northern hemisphere. *Bruchophagus s.l.* is supported by: (1) intertorular space (ITS) raised above the surface of the antennal scrobes, ending dorsally in a sharp or blunt tooth (Fig. 30.10D) (with further reversals in the *metallica* and *gibba* species groups); (2) postgenal grooves (PGG) with inner edge step-like on upper part, separated from the dorsal margin of lateral foraminal plate (LFP) by a very slight emargination (Fig. 30.8C); (3) propodeum with a brush of hairs on each side of the petiolar cavity (Fig. 30.8D) (hairs sometimes reduced); (4) metacoxa dorsally hairy at base (Fig. 30.8D); and (5) first gastral tergite with sublateral lines of hairs on each side of the submedian pits (Fig. 30.9A). Characters 1–2 are rarely visible in mounted specimens and require high magnification to see, thus 3–5 are better for recognition. Some of these states are sometimes reversed, particularly in small species, or otherwise fainter (sculpture, carinae, sulci, hairs). The genus is variable and can be difficult to identify, but usually the posteriorly and rounded gena and absence of a postgenal lamina are useful for recognizing *Bruchophagus*. Lotfalizadeh *et al.* (2007) recovered the genus as monophyletic but with low branch support. but an unpublished molecular study offers stronger support.

Bruchophagus are most commonly associated with seeds, especially Fabaceae, but other smaller species groups are associated with gall inducers of plants in saline habitats (Zerova, 1978) or with *Tetramesa* galls on grasses (Szelényi, 1968, 1974).

Eurytoma sensu stricto

The largest genus in the family with over 700 species described. All species with a carinate gena and no other outstanding characters have been included in this genus. Claridge (1961a) was first to use the habitus of the postgena to characterize *Eurytoma*, followed by Bouček (1988). The genus is here redefined in the narrower sense of Lotfalizadeh *et al.* (2007): (1) postgenal lamina present and raised ventrally over the surface of the postgena (Figs 30.9B, 30.12A), such that the postgenal lamina is therefore visible as a tooth in lateral view; (2) postgena with a ventral depression between the posterior margin of the gena and the hypostomal fossa, and the depression delimited dorsally by a ridge or a step (Fig. 30.12A); and (3) gena with posterior margin slightly angulate above oral fossa (Fig. 30.12A). These characters are shared by all members of the *abrotani* species group, to which *Eurytoma abrotani*, the type species of the genus, belongs (Delvare, 2016, pers. obs.; Noyes, 2019). The presence of a postgenal lamina is shared with some Neotropical species belonging to *Bephratoides*, *Chryseida* or *Eurytoma* 'Peru' (*sensu* Lotfalizadeh *et al.*, 2007). *Eurytoma* includes the following species groups.

- The *stenostigma* **species-group** includes at least four described Palearctic species with the clava truncate at the apex in females (Zerova, 1995) and the flagellum 6-segmented in the male; in both sexes the postmarginal vein forms a very acute angle with the stigmal vein; nothing is known about their biology.

- The ***appendigaster*** **species group** is highly diverse in the Holarctic region; its members are parasitoids of *Tetramesa* spp. that induce galls in grass stems (Claridge, 1959b). The group is characterized by the fusiform shape of the flagellomeres (Fig. 30.11C), a relatively long marginal vein (at least 1.4× as long as stigmal), a deep median groove on the propodeum and a horizontal ovipositor (ascending backwards in most eurytomids) (Lotfalizadeh *et al*., 2007).
- The ***morio*** **species group** includes parasitoids of xylophagous beetles, especially Scolytinae (Curculionidae) (Delvare *et al*., 2014). It is supported by a hairy metacoxa (Fig. 30.9C), a relatively inflated marginal vein, and a distinctive costal cell bearing numerous white hairs on its ventral surface. It is supported as monophyletic (Lotfalizadeh *et al*., 2007). Most species lack the characteristic postgenal depression of *Eurytoma*. Most diverse in temperate regions, it occurs less commonly in the Afrotropical and the Neotropical regions.
- The ***amygdali*** **species group** only occurs in the Palearctic region. It includes seed-feeders associated with Rosaceae (Zerova and Fursov, 1991). This group is characterized by long setation on the head (Fig. 30.10A) and broad notauli (Fig. 30.10A), the female antenna has a 6-segmented funicle and a 1-segmented clava; they also lack a postgenal depression.
- ***E. plotnikovi*** is a species associated with *Pistacia vera* (Anacardiaceae), sharing the long pilosity on the head and mesosoma, and broad notauli with the members of the *amygdali* species group. It displays the typical postgenal depression of *Eurytoma*. *Eurytoma plotnikovi* was found as the sister-group of *E. amygdali* (Lotfalizadeh *et al*., 2007).
- The ***abrotani*** **species group** is most diverse in the Holarctic region (at least 40 European spp.) and includes parasitoids of gall-making cynipids, and tephritids or weevils developing in stems and flowers of Asteraceae (Claridge, 1961b). Members of the *abrotani* species group are recognized by the precoxal tooth visible in lateral view and formed by the raised adscrobal carina (Fig. 30.10B). It is supported as monophyletic if the *appendigaster* species group is included (Lotfalizadeh *et al*., 2007).
- The ***verticillata*** **species group** is mostly Afrotropical but also includes the Palaearctic *E. verticillata*. Species are parasitoids or hyperparasitoids of Lepidoptera (Delvare, 1988). They resemble the *abrotani* species group, but lack the ventral depression of the postgena. The mesopleuron is distinctive, with the epicnemium completely delimited and the elbowed adcrobal carina incompletely delimiting a ventral shelf.
- The ***robusta*** **species group** is distributed in the Palearctic and Afrotropical regions. In the Palearctic, species parasitize Tephritidae associated with the same habitat as the *abrotani* species group; in Africa, species are mostly parasitoids of bruchine Chrysomelidae developing in seeds of Fabaceae (Delvare, 1988; Rasplus, 1988). The group is monophyletic in all cladograms (Lotfalizadeh *et al*., 2007). It is supported by the following derived states: an emarginate clypeus (Fig. 30.10D), a strigose lower face (Fig. 30.10D), a narrow ITS, a medioventral tooth on the prepectus (cf. Fig. 30.8A), a ventral shelf on the mesopleuron (Fig. 30.10C), and its completely delimited epicnemium (Fig. 30.10C, arrow).
- ***Eurytoma crotalariae*** consumes seeds of *Crotalaria* spp. (Fabaceae) in West Africa (Delvare, 1988) and is found simultaneously with species of the *Eurytoma robusta* species group parasitizing bruchids. Its postgena has no ventral depression. It shares many derived states with the *robusta* species group.
- The ***fumipennis*** **species group** includes seed-eaters of *Euphorbia* species (Zerova, 1994). They are distributed only in the Palaearctic region. The group is supported by the protruding ventral margin of the clypeus, sometimes with short median tooth, a squat mesosoma, and the propodeum strongly sloping and flat.

Phylloxeroxenus

This genus of nine described species is distributed primarily in tropical regions of the New World, where they have been often misidentified as *Eurytoma* because species also have a carinate gena; only a few species extend into temperate habitats (Noyes, 2019; Gates *et al*., 2020). They are most commonly associated with galls, often Cecidomyiidae, and they are likely parasitoids of the gall inducer. Some Neotropical species are associated with various plant seeds (e.g., Orchidaceae). *Phylloxeroxenus cressoni* is known from seeds of *Varronia* (as *Cordia) curassavica* (Boraginaceae) galled by *Eurytoma attiva*, while *P. phylloxerae* are associated with *Phylloxera* (Phylloxeridae) galls. *Phylloxeroxenus* is more speciose than currently indicated. Collections from extensive Malaise trapping and canopy fogging in only two countries, Costa Rica and Ecuador, have yielded ~80 new species. Therefore, the number of species may be expected to eventually be in the hundreds globally.

Species in this genus have been confused as *Eurytoma, Bruchophagus,* or *Prodecatoma*. The raised genal carina is shared with *Eurytoma*, but *Phylloxeroxenus* lack the postgenal groove constantly diverging downwards, a raised postgenal lamina (sometimes faint ones present that converge ventrally), and a ventral depression on the postgena (Fig. 30.11B).

The group was weakly supported as monophyletic (Lotfalizadeh *et al*., 2007) by the following apomorphies: (1) lower face strigose (Fig. 30.11A); (2) postgenal bridge with median strip of ornamentation vestigial or even absent (Fig. 30.11B, arrow); (3) prepectus with subventral carinae diverging strongly, carinae joining the medioventral tooth when present; (4) metapleuron with precoxal carinae close to its anterior margin; enlarged Gt_4 mostly covering Gt_5 (shared with *Prodecatoma s.s.* and *Tenuipetiolus*); (6) petiolar part of Gs_1 enlarged, often greatly so. (Note that there was no '5' in the original publication.) An in-depth study incorporating many additional taxa is needed to resolve generic limits for these closely related genera.

Sycophila

This cosmopolitan genus consists of 120 described species that are either associated with cynipid and chalcidoid galls in the Holarctic (Balduf, 1932; Claridge, 1959a; Gates *et al*., 2020; Zhang *et al*., 2022), or as inquilines or parasitoids associated with figs in the tropics (Li *et al.*, 2010). Lotfalizadeh *et al.* (2007) defined *Sycophila* and its sister-group *Ficomila* as monophyletic based on the following: (1) clypeus bilobed (Fig. 30.12C); (2) lateral foraminal plate with dorsal margin forming, together with the inner edge of postgenal grooves, a strong wavy line (Fig. 30.12B); (3) postgenal groove somewhat curved in the upper parts; (4) dorsal metatibia with enlarged setae (Fig. 30.12D); (6) thickened margin vein; (7) fore wing with infumate spot behind marginal vein; and (8) lack of ring-like process on the epicnemium and broad areola on the prepectus (synapomorphies of *Ficomila*). With the exception of (2) and (3) as possible synapomorphies, the other characters are considered homoplastic.

Tetramesa

This genus of over 200 species is distributed primarily in the Holarctic (Zerova, 1976; Noyes, 2019). The presence of three hairs on each side of the articular area of the petiole (Fig. 30.13C) (two in other Eurytominae) is the only synapomorphy characterizing the genus (Lotfalizadeh *et al.*, 2007). The clade of *Cathilaria* + *Tetramesa* is sometimes found as the sister-group of *Systole* (Lotfalizadeh *et al.*, 2007), a result independently corroborated by Heraty *et al.* (2013) and in the initial UCE results (also including *Aiolomorphus rhopaloides*) of Blaimer *et al.* (2023). The genera *Cathilaria* + *Tetramesa* + *Systole* may be characterized by: (1) flagellar segments with suberect hairs (Fig. 30.11C); (2) flagellar segments with few elongate sensilla (Fig. 30.11C); (3) notauli deep and broad. *Tetramesa* and *Cathilaria* share the following derived states: (1) head and mesosoma with long, thin and erect setation; (2) intertorular space with a transverse carina (Fig. 30.11D, arrow); (3) lateral foraminal plate completely delimited dorsally and laterally (Fig. 30.13B) (several reversals in *Tetramesa*) (Lotfalizadeh *et al.*, 2007). *Tetramesa* have an elongate body with the wings narrow, the axillar grooves narrowly separated at the transscutal articulation, and the propodeum moderately sloping. In *Cathilaria*, the body is compact with the wings relatively broader, the axillar grooves widely separated at the transscutal articulation and the propodeum strongly sloping. Larvae of both genera develop within stems of Poaceae (Claridge, 1961c; Zerova and Seregina, 1994); *Cathilaria* is restricted to *Hilaria* (Poaceae) (Zerova, 1999).

Rileyinae

This subfamily contains one larger genus, *Rileya*, and six smaller genera. Most rileyines have two to three anelli (rare case of one in *Platyrileya*), five or six funiculars, and a three-segmented clava. The prepectus is usually smaller than the tegula (except *Platyrileya*). This subfamily is primarily New World, ranging from tropical to arid regions, but two species are known from the Palearctic (Zerova, 1976; Cam, 2003) and five from Australasia (Thien *et al.*, 2003; Gates, 2008). The subfamily is supported as monophyletic by: (1) 13-segmented antenna in both sexes (plesiomorphic) (Couplet Fig. C7); (2) sexual dimorphism in antennal shape (males often with ventral sensory plaque on scape) (apomorphic) (cf. Couplet Fig. C4, inset); (3) gaster with terga 1, 1 and 2 or 1–3 reduced/fused and positioned anterodorsally (apomorphic) (Figs 30.4A, 30.13A, Couplet Fig. C8); (4) highly reduced prepectus (apomorphic) (Couplet Fig. C9); and (5) two or three anelli (apomorphic) (Couplet Fig. C7) (Lotfalizadeh *et al.*, 2007). *Platyrileya* is a very unusual taxon morphologically, having Gt_{1-3} foreshortened and a mesepimeral–metapleural junction similar to that of *Rileya* (albeit smaller and less distinctly produced); however, it has larger ‘anelli’ than other Rileyinae except *Dougiola*. It is difficult to differentiate the basal three flagellomeres of *Platyrileya*, but they appear to lack MPS and are only slightly smaller than subsequent funiculars. Species of *Platyrileya*, which are provisionally included, also possess a large, triangular, anteroventrally deflected prepectus. *Boucekiana* are also slightly aberrant by possessing three ring-like ‘anelli’ that lack MPS, a slightly foreshortened Gt_1, and a small triangular prepectus. *Dougiola* have a reduced prepectus, but possess three larger, non-ring-like ‘anelli’ that lack multiporous plate sensilla, and Gt_1 is not significantly reduced.

Rileyinae are parasitoids of Cecidomyiidae gall inducers with the exception of *Neorileya*, which parasitize exposed eggs of Heteroptera (Gates, 2008). Kraus and Tanoue (1999) reported root gall development ostensibly caused by *Rileya* (as *Calorileya*) *nigra* on the aerial roots of *Cattleya guttata* (Orchidaceae) in Brazil. They cited Gomes (1943) although that reference offers no details about gall initiation, and particularly the oviposition behavior. Molliard (1903) and Gagne (1994) both reported orchid roots galls being caused by Cecidomyiidae and one of us (Gates, 2013, pers. obs.) has reared cecidomyiids from orchid root galls, thus it may not form galls but rather parasitize the gall-maker.

Heimbrinae

This smallest subfamily of Eurytomidae consists of two genera, *Heimbra* and *Symbra*, totaling eight species. Stage and Snelling (1986) subdivided *Heimbra* into a North American (two spp.) and a South American (four spp.) species group. The subfamily is supported as monophyletic by: (1) presence of robust scutellar spine (Fig. 30.3B, Couplet Fig. C1); and (2) gastral terga 1+2 fused and carapace-like (Fig. 30.3B, Couplet Fig. C1). This subfamily is strictly New World, occurring primarily in arid to temperate climates. Hosts are unknown but one of us (MWG) swept three specimens from perennial bunchgrass in the Mojave Desert that had numerous broken, hollow stems exposed. Label data from *Heimbra bicolor* in USNM indicates rearing from buprestid and curculionid infested stems of *Sida* sp. (Malvaceae).

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Appendix 30.1

Couplet Figures. Eurytomidae: **C1,** *Heimbra opaca,* Heimbrinae (mesosoma and metasoma); **C2,** *Aximopsis balajasi* (♀), Eurytominae (mesosoma and metasoma); **C3,** *Tetramesa hordei* (♀), Eurytominae (antenna); **C4,** *Macrorileya* sp. (♀), Buresiinae (antenna); **C5,** *Tetramesa* sp. (♀), Eurytominae (metasoma); **C6,** *Buresium rufum* (♀), Buresiinae (metasoma, posterior view); **C7,** *Rileya pulchra* (♀), Rileyinae (antenna); **C8,** *Rileya* sp. (♀), Rileyinae (metasoma, lateral view); **C9,** *Rileya* sp. (♂), Rileyinae (mesosoma, lateral view); **C10,** *Buresium* sp. (♀), Buresiinae (antenna, lateral view); **C11,** *Buresium* sp. (♀), Buresiinae (mesosoma and metasoma, lateral view).