THE CYNIPOID FAMILIES

Introduction

The vast majority of cynipoids are small wasps, 1.0 to 5.0 mm in length, although a few species of the so-called macrocynipoids parasitizing wood-boring insects can reach 30 mm. They are usually brown or black in colour and never metallic. Both sexes are fully winged except in some brachypterous or apterous species of Cynipidae and Figitidae. Unlike most other Hymenoptera, females usually have 13 antennal articles (11 flagellomeres) and males 14 or 15. Males usually have the first flagellomere swollen and excavated laterally (exceptions include Anacharitinae (Figitidae), Liopteridae and *Heteribalia* (Ibaliidae)). Occasionally, the modifications of the male antenna may involve the second and third flagellomeres (some charipines and eucoilines). The pronotum reaches the tegulae. It is frequently equipped with an anterior plate, which may be raised off the surrounding pronotal surface (particularly prominent in many eucoilines). The forewing venation is characteristic (Figs. 4-7): the costa (C) is lacking, the pterostigma is reduced to a crossvein-like structure (other parasitic wasps with a reduced pterostigma usually have a linear remnant along the anterior wing margin), the media (M) is displaced anteriorly, and one of the few closed wing cells is the distinctive trapezoid marginal cell, which may be open (Figs. 4, 7) or closed (Figs. 5, 6) on the anterior wing margin. The Australian Austrocynipidae are exceptional in having a well-developed pterostigma but the other venational features are typical of cynipoids (Ronquist 1995*b*). Tarsi have five tarsomeres.

Rasnitsyn (1988) proposed a sister-group relationship between Cynipoidea and Diapriidae based on a number of characters. Although most of these characters are problematic, two deserve further consideration (Ronquist 1999): (1) hind wing vein *M* (+*Cu*) is concave above in diapriids and cynipoids but convex in other Hymenoptera; and (2) the basal flagellomere is modified similarly in males of Diapriidae and Cynipoidea. The latter modification consists of a ridge and an excavation, both of which are perforated with pores connected to an internal gland producing chemicals that are smeared onto the female antenna during courtship (Ronquist & Nordlander 1989; Ronquist 1995*b*; Isidoro *et al*. 1996; Isidoro *et al*. 1999). Male antennal glands occur in other parasitic Hymenoptera, but the external morphology and position of the gland-bearing article(s) is unique to cynipoids and diapriids. Finally, some fossil hymenopterans (Archaeocynipidae; Rasnitsyn & Kovalev 1988) from the early Cretaceous have a linear pterostigmal remnant and other venational characters suggesting diapriid affinities but a short and compressed metasoma and other features typical of cynipoids (Ronquist 1999). This could possibly provide additional evidence for a link between diapriids and cynipoids. The most recent molecular analyses of apocritan relationships (Dowton and Austin 2001) suggest cynipoids are sister to either Chalcidoidea or Heloridae + Vanhorniidae; unfortunately, the precise position of the cynipoid clade is highly dependent on analytical parameters.

The Cynipoidea consists of nearly 3,000 described species in 224 genera (Ronquist 1999). The phylogeny of the superfamily has been analysed in several recent papers (Ronquist 1994, 1995*a*, 1995*b*, 1999; Nordlander et al. 1996; Liljeblad & Ronquist 1998; Ros-Farré et al. 2000; Liu 2001; Fontal-Cazalla et al. 2002; Nylander et al. 2004) and this

has resulted in major rearrangements in the higher classification (reviewed by Ronquist 1999; see also Ronquist & Nieves-Aldrey 2001). The superfamily is now divided into five putatively monophyletic families: the Austrocynipidae, Ibaliidae, Liopteridae, Figitidae and Cynipidae. The Cynipidae comprise the phytophagous gall wasps; most of these are gall inducers but some of them develop as inquilines feeding on the plant tissue inside the galls of other cynipid species. The members of the other families are, as far as is currently known, all insect-parasitic. They develop initially as koinobiont endoparasitoids but spend the last one or two instars feeding externally on the host remains. They exclusively attack endopterygote insect larvae, usually as primary parasitoids. See Table 1 for a summary of host associations.

In terms of many morphological characters, the cynipoids fall into two groups: the "macrocynipoids" and the "microcynipoids". The macrocynipoids (Austrocynipidae, Ibaliidae and Liopteridae) (Fig. 2) are typically relatively large insects that develop as parasitoids of wood-, twig- or cone-boring insect larvae. The microcynipoids (Figitidae and Cynipidae) are typically smaller insects (Fig. 3). The mesosoma is higher and more compact and the metasoma is characteristically short, such that the wings project far beyond the posterior end of the body.

Phylogenetic analysis of 55 characters of adult morphology informative about inter-family relationships indicates that the microcynipoids form a monophyletic group whereas the macrocynipoids constitute a paraphyletic assemblage of more basal cynipoid lineages, with the Austrocynipidae being the sister group of all other Cynipoidea (Fig. 1; Ronquist 1995*b*). In the Figitidae, the figitoid inquilines (Parnipinae and Thrasorinae) constitute the most basal lineages, indicating that figitids originally developed inside galls, just like cynipids (Ronquist 1999). The Diptera-parasitic forms constitute a monophyletic core group of figitids, with the Hymenoptera and Neuroptera parasitoids in the aphid and psyllid communities as their sister group (Fig. 24). Details about the phylogenetic relationship among the Figitidae are not yet clear, but this situation is expected to change soon thanks to an ongoing project to build a comprehensive matrix of both morphological and molecular data spanning all the Figitidae (Buffington, unpublished data). .

There is some uncertainty concerning the exact position of liopterids: the most likely hypothesis has them as the sister group of microcynipoids (Fig. 1) but it cannot be excluded that they instead form a monophyletic group together with the ibaliids, as suggested originally by Rasnitsyn (1980) and later by Fergusson (1988, 1990). Except for this uncertainty concerning liopterids, the clades in the higher cynipoid phylogeny indicated in Fig. 1 are robust, with bootstrap confidence levels exceeding 95 % in parsimony analyses of the known morphological characters informative about these relationships (Ronquist 1995*b*, 1999). Alternative views on higher cynipoid relationships exist but are not well supported by data. They are either based on a narrow selection of the available characters or on unpublished analyses (for a detailed review, see Ronquist, 1999).

The five-family scheme outlined above, although similar to the system proposed by Rasnitsyn (1980, 1988), differs considerably from the traditional classification of the Cynipoidea and from alternative classifications proposed more recently (Kovalev 1994, 1996; Fergusson 1995). The most important differences concern the Figitidae, which are

often divided into a number of separate families by other authors. The most commonly recognised families are the Anacharitidae, Charipidae, and Eucoilidae but Kovalev (1994, 1996) raised many more figitid groups to separate family status. The major problem with these alternative classifications is that they minimally leave one heterogeneous group of unrelated lineages in the more narrowly circumscribed Figitidae (*sensu stricto*). Kovalev's scheme also adds a number of other figitid taxa that are clearly unnatural (e.g. Ros-Farré et al. 2000). Relationships among the subgroups of the Figitidae (*sensu lato*) are not known well enough to allow a complete division of the lineage into monophyletic subclades but the current knowledge does reveal major problems with the traditional classification. If deeply nested figitid lineages, such as the eucoilines, are recognised as separate families, then a large number of other figitid taxa will also have to be raised to family level, leading to an unnecessary proliferation of cynipoid families. For this reason, Ronquist (1999) defended a wide circumscription of the Figitidae and a system of relatively few, morphologically and biologically distinct subfamilies, where all but one (the Figitinae) are likely to be monophyletic. With this system, better understanding of figitid relationships in the future can be accommodated by classificatory changes at the subfamily rather than at the family level.

Some individual cynipoid taxa have recently been moved between families, particularly because of the better understanding of the distinction between the Figitidae and Cynipidae. For instance, the mainly South American genus *Myrtopsen*, reared from chalcidoid galls on *Acacia* and *Mimosa*, used to be placed among the inquilines in the Cynipidae but is now included among the gall-associated figitids in the subfamily Thrasorinae (Ronquist 1994, 1999). A new figitid subfamily, Parnipinae, was recently described for a Mediterranean species associated with poppy (*Papaver*) galls and originally placed in a genus (*Aulacidea*) of gall-inducing cynipids (Ronquist & Nieves-Aldrey 2001). The species is now known to be a parasitoid of the cynipid gall-inducer *Barbotinia oraniensis*, a life history consistent with its suggested phylogenetic position among the insect-parasitic figitids. The Pycnostigminae, previously placed in the Cynipidae, have been shown to be close relatives of the Eucoilinae, probably their sister group (Rasnitsyn 1980, 1988; Ronquist 1999; Fontal-Cazalla et al. 2002), and is now treated as a figitid subfamily. Their biology is still unknown. The genus *Himalocynips*, considered by Fergusson (1995) to be a separate cynipoid family and treated by others variously as a monotypic subfamily in the Cynipidae or in the Figitidae, has been shown to be deeply nested inside the gall-inducing cynipids and is now included in the cynipid tribe Pediaspidini (Liljeblad & Ronquist 1998; Ronquist 1999). For further details, see the recent review by Ronquist (1999).

FAMILY	# Genera/# spp.	Distribution	Biology
AUSTROCYNIPIDAE	1/1	Australia	Parasitoids of lepidopteran larvae in *Araucaria* cones
IBALIIDAE	3/19	Holarctic	Parasitoids of siricid larvae in wood
LIOPTERIDAE	10/170	Widespread, mostly Tropical	Parasitoids of coleopteran larvae in wood or in twigs
CYNIPIDAE	77/1400	Mostly Holarctic	Phytophagous gall inducers or inquilines
FIGITIDAE	132/1400	Cosmopolitan	Mostly parasitoids of Diptera larvae, also Hymenoptera and Neuroptera larvae

Table 1. Families of Cynipoidea: Their species richness, geographical distribution, and biology.

Currently, a large digital database of high-resolution scanning electron micrographs of representative cynipoids is available to the public. This image database forms a useful reference collection of correctly determined cynipoids, which should complement the keys in this chapter well. The URL of the image database is http://morphbank.net. The keys below consistently refer to metasomal segments by their true abdominal segment number. Since the first abdominal segment (the propodeum) is incorporated in the mesosoma, and the second segment forms a small and inconspicuous petiole in cynipoids, the first apparent (large) metasomal segment is the third abdominal segment (Figs. 13-14). In many other published cynipoid keys, the metasomal segments are numbered either starting from the petiole, or starting from the segment after the petiole. It is common among cynipoids that the anterior terga (abdominal terga 3 to 4 or 3 to 5) become fused to a syntergum. One of the best ways of identifying the terga correctly is to start counting from the posterior end. The eighth abdominal tergum is the only tergum with a functional spiracle, and the latter is almost always visible except in dried specimens where the abdomen has collapsed completely such that the posterior part of the metasoma is completely obscured by the anterior terga.

The family key does not include the Australian endemic *Austrocynips mirabilis*, the single representative of the family Austrocynipidae. This species is only known from three female specimens reared from *Araucaria* cones in tropical Australia. The family may conceivably occur in southern South America. They are easily distinguished from all other cynipoids by the presence of a large pterostigma, among many other characters (Riek 1971; Ronquist 1995*b*; Ronquist 1999). The families Figitidae and Cynipidae are difficult to separate unless one has considerable experience; figitid subfamilies and cynipid tribes are

easier to identify. If it is known, the biology is a quick guide: all cynipids are associated with galls whereas relatively few figitids are. Furthermore, cynipids are relatively less diverse in the Neotropics compared to figitids. Nevertheless, the beginner may find it useful to try a doubtful specimen both in the Cynipidae and the Figitidae key.

Key to the New World Families of the Cynipoidea

1 Mesoscutum with rough sculpture; either foveate, or with prominent transverse ridges, or both (Figs. 2, 18, 19); distinct pronotal crest (Figs. 2, 18, pc) present; large wasps, 5 to 30 mm in length, usually over 10 mm; largest metasomal tergum of female, in lateral view, usually the fifth, sixth, or seventh abdominal (Figs 2, 20 - 22). [Rarely collected; parasitoids of wood-boring insects.] 2

\- Mesoscutum smooth or with light sculpture, without strong transverse ridges or foveae but sometimes with weaker, irregular transverse ridges (Figs. 3, 26, 29, 31, 33, 36, 38); pronotal crest usually absent (Figs. 3, 26, 29, 31, 33, 36, 38); small wasps, 1 to 6 mm in length; largest metasomal tergum of both sexes, in lateral view, the third or fourth abdominal, or the third to fourth or third to fifth fused (Figs 13-14, 27, 30, 32, 34, 37, 40). 3

2 Marginal cell at least 9 times as long as broad (Figs. 2, 6); pronotum laterally without foveate sculpture (Fig. 2); hind femur short, about as long as hind coxa (Fig. 15); hind tibia much longer than hind femur (Fig. 15); hind tarsus with tarsomere 1 twice as long as combined length of tarsomeres 2-5 (Fig. 15); metasoma strongly laterally compressed, blade-like (in South American forms); both sexes with the largest metasomal tergum being the seventh abdominal (Fig. 2). [Introduced into parts of South America].
..... **Ibaliidae** (p. ***)

\- Marginal cell at most 6 times as long as broad; pronotum laterally with at least some foveate sculpture (Fig. 18); hind femur much longer than hind coxa; hind tibia slightly shorter than hind coxa (Fig. 16); hind tarsus with tarsomere 1 not as long as combined length of remaining tarsomeres in South American forms (Fig. 17); metasoma less strongly laterally compressed and more rounded in lateral view in South American forms (Figs. 20-22); largest metasomal tergum usually the fifth or sixth abdominal in females and the fourth or fifth in males. [Habitus Fig. 23].
..... **Liopteridae** (p. ***)

3 Mesoscutum usually with microsculpture making it dull; fore wing with innermost (proximal) trace of vein *Rs+M* pointing to the middle of the "basal vein" (the apparent cross-vein formed by portions of *Rs* and *M*) (Fig. 4); metasoma with the largest tergum being the third abdominal (gall-making forms; Fig. 14) or the fourth abdominal; in the latter case, the fourth abdominal is usually fused with the third (inquilines [the European gall-inducer *Xestophanes* also has the third and fourth abdominal terga fused in the female]; Fig. 13). [In South America associated with galls on *Quercus*, *Nothofagus*, *Acacia*, *Prosopis*, and *Hypochoeris*; possibly also *Rubus* and *Rosa*]. ..... **Cynipidae** (p. ***)

\- Mesoscutum usually shiny (exceptions occur in Thrasorinae, *Melanips* (Figitinae) and

Aspicerinae among South American forms); fore wing with innermost (proximal) trace of vein *Rs+M*, if present, pointing to the junction of the "basal vein" with *M+Cu* (Fig. 5); the vein *Rs+M* sometimes more or less completely absent (Fig. 7); metasoma with the largest tergum usually being the fourth abdominal (Figs. 32, 34, 37, 40), or the third to fourth or third to fifth fused (exceptions in some Charipinae (Fig. 27) and Anacharitinae (Fig. 30) among South American forms) [By far the most commonly collected family] ..... **Figitidae** (p. ***)

The Family Ibaliidae

DIAGNOSIS. Large (10-30 mm), heavily sclerotized cynipoids with transversely ridged mesonotum and prominent pronotal crest. Most similar to liopterids but easily distinguished from them based on a series of characters. The pronotal crest is incised medially in ibaliids but never in liopterids. The dorsal pronotal area (behind the pronotal crest) is wider in ibaliids than in liopterids. Liopterids have distinct foveate sculpture on the lateral surface of the pronotum and on the dorsal surface of the scutellum; this sculpture is lacking in ibaliids. All ibaliids except the Bornean genus *Eileenella* have a deep femoral groove on the mesopleuron; this groove is lacking in liopterids, which instead have a horizontal, rather superficial but broad impression on the mesopleuron (mi, Fig. 18). The marginal cell is extremely long in ibaliids (Fig. 6) but shorter in liopterids, even though liopterids often have a more elongate marginal cell than most microcynipoids. The proportions of the hind legs are different. Ibaliids have a uniquely short metafemur, hardly longer than the metacoxa and, except for *Eileenella*, an extremely long first tarsomere, twice as long as the combined length of tarsomeres 2-5 (Fig. 15). Liopterids have a much longer femur but a uniquely short tibia, shorter than the femur (Fig. 16). The first tarsomere of the metatarsus is usually much shorter (Fig. 16) and even in the most extreme cases it is never twice as long as the combined length of tarsomeres 2-5. The largest metasomal sclerite is the seventh abdominal in ibaliids but the third, fourth, fifth or sixth in liopterids. The metasoma of the only ibaliid genus known to occur in South America, *Ibalia*, is strongly laterally compressed and blade-like in lateral view, especially in females (Fig. 2). A detailed description of the morphology of *Ibalia rufipes* can be found in Ronquist and Nordlander (1989).

CLASSIFICATION AND DISTRIBUTION. Ibaliidae comprise three genera and 19 species (Liu & Nordlander 1994): the largely Holarctic *Ibalia*, *Heteribalia* from the eastern Palearctic and Asia, and *Eileenella* from New Guinea. Although *Eileenella* (Fergusson 1992; Kovalev 1994) and *Heteribalia* (Weld 1952) have previously been placed in the Liopteridae, all three ibaliids genera share several apomorphic features not present in Liopteridae *sensu stricto*, for example the short metafemur and the large seventh abdominal tergum (Ronquist 1995*a*, *b*; Nordlander *et al*. 1996).

The genus *Ibalia* (Fig. 2) is divided into two subgenera: *I*. (*Ibalia*), which parasitizse Siricinae in conifers, and *I*. (*Tremibalia*), which parasitizse Tremicinae (Siricidae) in hardwoods (Nordlander *et al*. 1996). Both subgenera occur in North America but only *I. (Ibalia) ruficollis* extends southwards into Mexico (Liu and Nordlander 1992). It is possible

that this species and several other closely related species known from southwestern United States could occur as far south as the natural distribution of Pinaceae in northern Nicaragua. *Ibalia l. leucospoides* has, apparently accidentally, been introduced into South America together with its host, *Sirex noctilio*. It has been recorded from Brazil and is likely to occur in Argentina and Chile as well (S. M. Ovruski, pers. comm.).

BIOLOGY. Species of *Ibalia* are koinobiont endoparasitoids of wood-boring sawflies of the family Siricidae (Chrystal, 1930; Cameron, 1965; Spradbery, 1970*c*).

ECONOMIC IMPORTANCE. Several species of *Ibalia* have been introduced into Australia and New Zealand for biological control of siricids (see Liu & Nordlander, 1994, for a review). Its role in controlling populations of *Sirex noctilio* in South America has not been studied. In Chile, researchers are starting a biological control program of *Tremex fuscicornis* using *Ibalia jakowlewi* (P. Parra, pers. comm.).

IDENTIFICATION. Liu and Nordlander (1994) provided keys to the genera and species of the world.

The Family Liopteridae

DIAGNOSIS. Large (5-15 mm), coarsely sculptured wasps. They are most similar to ibaliids but are easily separated from them on a series of characters discussed above under Ibaliidae.

Ronquist (1995*a*) proposed 12 autapomorphies for the family: 1) Foveate sculpture on lateral surface of pronotum and dorsal surface of scutellum (Figs. 18-19); 2) Acetabulum more or less vertical, divided into two furrows for the procoxae by a strong median keel, acetabular carina describing an ω-shape; 3) Metapleural sulcus reaches anterior metapectal margin far above mid-height of margin (Fig. 18, mps); 4) Intermetacoxal processes present; 5) Lateral pronotal carina reaching raised ventral pronotal margin (Fig. 18, lpc); 6) Laterodorsal process of scutellum present (Figs. 18-19, ldp); 7) Lateroventral carina of mesopectus present (Fig. 18, lc); 8) Nucha long (Fig.18, nu); 9) Metatibia shorter than metafemur (Fig. 16); 10) Petiolar annulus complete, tergal and sternal parts fused with no trace of a suture (Figs. 20-22); 11) Occipital carina present; 12) Mesopleural impression present (Fig. 18; mi). Particularly the characters 1, 3, 9 and 12 are useful in diagnosing the family.

CLASSIFICATION AND DISTRIBUTION. The Liopteridae comprise 11 genera and 170 known species, though less than half of these have been described (Ronquist 1995*a*). Most species are represented by very few specimens, suggesting that only a small fraction of the total world fauna has been collected. Liopterids occur primarily in tropical and subtropical regions of the world, with isolated species in Australia, eastern Asia and North America.

Ronquist (1995*a*) divided the family into four subfamilies: Mayrellinae (3 genera, widespread), Dallatorrellinae (2 genera, Australia and Asia), Oberthuerellinae (3 genera, Africa), and Liopterinae (3 genera, Neotropics). Two genera of Mayrellinae occur in the

New World, *Kiefferiella* in Western North America (Ronquist 1995a) and the widespread *Paramblynotus* (about 91 known species) with three closely related species in the New World, occurring from Texas south to southern Brazil and northern Argentina (Liu et al., unpubl. data). Liopterinae comprise *Liopteron* (8 described species, including those formerly placed in *Plastibalia*), *Peras* (11 described and 3 undescribed species), and *Pseudibalia* (12 described and 13 undescribed species). Thus, in tropical America there are two subfamilies, four genera, and about 50 species.

BIOLOGY. The available data indicate that Liopteridae are parasitoids of wood-boring coleopterous larvae, such as Buprestidae and Cerambycidae. In Argentina, "*Paramblynotus zonatus*" has been collected on a log of *Nectandra* sp. (Lauraceae) infected by the cerambycid genus *Oncideres* (Diaz 1973). In Costa Rica, a species of *Liopteron* was observed examining a fallen branch of *Pentaclethra macroloba* (Fabaceae) (H. Hespenheide, pers. comm.).

IDENTIFICATION. Ronquist (1995) provided a key to the world genera. Hedicke and Kerrich (1940) revised the species of Liopterinae and Liu (2001) revised the subfamily Dallatorrellinae, but most species are still undescribed so any species-level key has to be used with caution, and reliable species identification is usually not possible without access to type material. The four genera occurring in tropical America can be distinguished with the following key.

Key to the tropical American genera of Liopteridae

1 Petiole not or scarcely longer than broad, attached to remainder of metasoma horizontally (Fig. 20); tarsal claws simple. [Mayrellinae]. ..... *Paramblynotus*
- Petiole at least twice as long as medially broad and attached to remainder of metasoma tangentially to its dorsal curvature (Figs. 21-22); pro- and mesotarsal claws with basal, lamellate lobe. [Liopterinae]. 2

2 Mesoscutum at least medially with closely set, transverse costae (Fig. 19); antennae never widened apically; the body of the petiole anteriorly not separated from the articular bulb by a distinct collar; body length usually greater than 9.5 mm. ..... *Liopteron*
- Mesoscutum with costae less closely set; antennae slightly to distinctly widened towards the apex; the body of the petiole anteriorly separated from the articular bulb by a distinct collar (Figs. 21-22) body length less than 9.5 mm. 3

3 Lateral surface of petiole with broad, slightly impressed area broadening posteriorly (Fig. 21); dorsal surface of petiole with median ridge; scutellum without posterior processes; metasoma with terga 3 or 4 moderately reduced in size (Fig. 21). *Peras*
- Lateral surface of petiole with several narrower and deeper furrows (Fig. 22); dorsal surface with median furrow, occasionally with weak, short median ridge; scutellum with a pair of small but distinct posterior processes *or* metasoma with abdominal terga 3 and 4 more strongly reduced in size (Fig. 22). ..... *Pseudibalia*

The Family Figitidae

DIAGNOSIS. Insect-parasitic microcynipoids that are inherently difficult to separate morphologically from the phytophagous Cynipidae, the other family of microcynipoids. In some respects, it is far easier to diagnose cynipid tribes and figitid subfamilies than the families Cynipidae and Figitidae themselves. Ronquist (1999) listed three putative synapomorphies supporting the monophyly of the Figitidae: (1) an oblique posterior margin of the third abdominal tergum; (2) a secondary articulation in the ovipositor; and (3) the position of the Rs + M vein (directed towards the posterior end rather than the middle of the basal vein). The first character (oblique third tergum) is somewhat problematic because it also occurs in a few gall-inducing cynipids, primarily herb gallers, so the apomorphic nature of the figitid condition could be doubted. The second character (ovipositor articulation) appears to be a unique synapomorphy for the Figitidae It is present in all examined representatives of the family and is found nowhere else in the Cynipoidea. Critical support for its status as a figitid synapomorphy was provided by the documentation of its presence in the Parnipinae, the putative sister group of all other figitids (Ronquist and Nieves-Aldrey 2001). Nevertheless, relatively few figitids have been examined for the character to date and, even if it holds as a figitid synapomorphy without secondary reversals, it is not very useful for family identification because it requires dissection of female specimens. The state of the third character (Rs + M vein) is difficult to determine in many core figitids because the Rs+M vein is faint basally. However, critical taxa (Parnipinae, Thrasorinae) clearly have the apomorphic state expressed in their wing venation.

Fortunately there are several additional diagnostic characters that can be used to separate most cynipids and figitids. For instance, most figitids have a shining mesoscutum (exceptions in Parnipinae, some Thrasorinae and Charipinae, *Melanips* (Figitinae) and Aspicerinae) whereas almost all cynipids have a dull mesoscutum because of coriarious microsculpture. Gall-inducing cynipids typically have an open marginal cell whereas most inquilinous cynipids and many figitids have a closed marginal cell. Most cynipids lack a lateral pronotal carina, the most notable exception being the *Synergus* complex of inquilines and the anterior pronotal plate of cynipids is often incompletely defined laterally or even absent (many herb gallers, oak gall wasps) but when it is completely defined (inquilines and many herb gallers), it is never strongly raised above the rest of the pronotum. Figitidae often have either a prominent lateral pronotal carina (Figs. 26, 29, 31, 33, 36, lpc) or a well-defined, strongly raised pronotal plate (emarginines and eucoilines; Fig. 38, 46, pp). The largest metasomal tergum is usually the fourth abdominal in Figitidae (Figs. 32, 34, 37, 40) but occasionally the third (Parnipinae; some charipines, anacharitines and thrasorines; Figs. 27, 30). In gall-inducing cynipids, the largest metasomal tergum is the third abdominal (Fig. 14); in inquilinous cynipids (Synergini), however, the largest tergum is the fourth abdominal, which is typically fused with the third (Fig. 13).

CLASSIFICATION AND DISTRIBUTION. The cosmopolitan Figitidae, comprising 133 genera and about 1,400 described species, is the most species-rich and abundant cynipoid family. Relatively few taxonomic studies have been undertaken on the diverse tropical fauna and it is likely that only a small fraction of the world species has been described.

Ronquist (1999) divided the Figitidae into nine subfamilies (Table 2) and gave autapomorphies supporting the monophyly of eight of these. The problematic subfamily is the Figitinae, which is likely to be paraphyletic with respect to four other subfamilies, namely the Pycnostigminae, Eucoilinae, Emargininae, and Aspicerinae. Until figitine relationships have been studied in more detail, however, the assemblage is best classified as a single subfamily. Seven of the nine subfamilies are present in tropical America; absent are the two smallest subfamilies, Parnipinae and Pycnostigminae.

BIOLOGY. With respect to their biology, the figitids fall into three groups: the gall inhabitants (Parnipinae and Thrasorinae), which are probably parasitoids of gall-inducing cynipid and chalcidoid larvae, the forms associated with hymenopteran parasitoids or neuropteran predators in aphid and psyllid communities (Anacharitinae and Charipinae), and the parasitoids of Diptera larvae (Figitinae, Eucoilinae and Aspicerinae, probably also Pycnostigminae and Emargininae), usually attacking larvae developing inside plants or in decomposing organic matter. The Aspicerinae and *Melanips* (Figitinae) form a link between the two latter groups in that they attack aphid-predating Diptera larvae. In a preliminary analysis of higher figitid relationships, Ronquist (1999) found a correlation between the phylogeny and these biological groups: the gall-associated forms constitute the earliest figitid lineages, the forms associated primitively with aphid communities form an intermediate group, while the Diptera-parasitoids form a deeply nested monophyletic clade with the parasitoids of aphid predators as basal members (Fig. 24). More details concerning the biology are given below for each subfamily.

IDENTIFICATION. Generally speaking, figitids are difficult to identify. Part of the problem is that only a small fraction of the total fauna is known and that generic circumscriptions have, for the most part, not been worked out, leaving a number of isolated described taxa without relation to each other. Higher relationships have only recently become somewhat better understood (Ronquist 1999, Ros-Farré et al. 2000, Fontal-Cazalla et al. 2002) and the few existing keys to subfamilies and genera are completely outdated. The monograph by Weld (1952) can provide some guidance to the identification of figitid genera. In this chapter, we have dealt with figitid identification at the subfamily level, and when possible, to the generic level.

SUBFAMILY	# Genera/# spp.	Distribution	Hosts
Parnipinae	1/1	Mediterranean	Cynipid gall-inducer on *Papaver*
Thrasorinae	5/11	America, Australia	Presumably cynipid and chalcidoid gall inducers
Charipinae	7/140	Cosmopolitan	Braconid and chalcidoid parasitoids of Aphidoidea and Psylloidea (Homoptera)
Anacharitinae	8/63	Cosmopolitan	Neuropteran predators of aphids
Figitinae	13/140	Cosmopolitan	Diptera-Muscomorpha in plants or in decaying organic material Dipteran predators of aphids
Aspicerinae	8/100	Cosmopolitan	Dipteran predators of aphids
Emargininae	5/15	Tropical	Associated with ants, probably parasitoids of myrmecophilous Diptera
Pycnostigminae	3/3	Africa	Unknown, probably Diptera
Eucoilinae	83/1000	Cosmopolitan	Diptera-Muscomorpha

Table 2. Subfamilies of Figitidae with number of genera and species, geographic distribution, and biology (hosts of parasitoids are always larvae).

Key to subfamilies of Figitidae occurring in tropical America

1 Scutellum with an oval, tear-drop shaped, or elongate elevated plate dorsally; plate equipped with a glandular release pit medially or posteriorly (Figs. 43, 44, 45, grp); females with abdominal terga three to five, males with terga three to four, fused into a large syntergum. [By far the most commonly collected subfamily]. ..... Eucoilinae (p. ***)

- Scutellum occasionally with raised carinae defining a central area (Fig. 39) but never with an elevated plate dorsally; third abdominal tergum only very rarely fused with fourth tergum, never fused with fifth tergum (Fig 37, 40). 2

2 Lateral pronotal carina continuously distinct and evenly curved from lateroventral region on one side across dorsum to lateroventral region on other side (Fig. 29, lpc); head in anterior view triangular, mouth region small (Fig. 28); lateral propodeal carina absent (Fig. 29; cf. Fig. 26, ppc); scutellum smooth with a distinct marginal

carina (Fig. 29) or with a blunt to conspicuous, median scutellar spine; petiole without an anterior collar (Fig. 30) or with a collar ventrally and laterally but not dorsally.
..... Anacharitinae (p. ***)

- Lateral pronotal carinae, if present, separated from each other dorsally (Figs. 26, 31, 33, 36) (note that the lateral pronotal carina is not homologous with the lateral margin of the pronotal plate, which is a more anteriorly situated structure); head in anterior view squarish or rounded, mouth region broader (Figs. 25, 35); lateral propodeal carina present (Figs. 26, 31, 33, 36, 38); scutellum never smooth with a distinct marginal carina; petiole usually with a collar dorsally (Figs. 27, 32, 34, 37, 40) 3

3 Mesoscutum and mesopleuron smooth and shiny (except for a horizontal mesopleural carina, which is sometimes present), notauli absent (Figs. 26, 38); small insects, 1-3 mm long 4

- Mesoscutum and mesopleuron usually with some sculpture, notauli almost always present, at least partly (Figs. 31, 33, 38); usually larger insects 5

4 Fore wing deeply bilobed; scutellum elongate, with submedian carinae (Fig. 39); mesopleural triangle and posterior subalar pit absent (Fig. 37); propodeum posteriorly covered with dense, woolly pubescence (Fig. 40); antennae moniliform. Emargininae (p. ***)

- Fore wing not deeply bilobed; scutellum conspicuously convex, without sculpture (except sometimes for the posterior tip) (Fig. 26); mesopleural triangle and posterior subalar pit distinctly impressed (Fig. 26, mpt, psap); propodeal pubescence not extremely dense (Fig. 40); antennae connate.
..... Charipinae (p. ***)

5 Metasoma with abdominal tergum 3 saddle-shaped, with posterolateral margin concave and central part almost tongue-like (Fig. 37); lower face with a distinctly marked, usually depressed, area beneath the antennae, margined laterally by strong vertical carinae (Fig. 35); head posteriorly concave and equipped with transverse ridges; scutellum with three strong, longitudinal carinae (Fig. 9); hind tibia usually with a strong longitudinal ridge posteriorly (Fig. 8). ..... Aspicerinae (p. ***)

- Metasoma with abdominal tergum 3 not saddle-shaped, its posterolateral margin sometimes slightly concave (*Neralsia*; Fig. 34) but usually distinctly convex; head without margined area beneath antennae; head posteriorly usually convex but occasionally concave (*Neralsia*), without transverse ridges; scutellum without three strong longitudinal carinae (Fig. 10); ridge of hind tibia weaker or absent. 6

6 Hind coxa distinctly broad; female metasoma with fifth abdominal tergum enlarged, covering sixth and seventh tergum largely or wholly (in South American forms); lateral pronotal carina short, strongly curved and prominent (in South American forms); mesoscutum dull, equipped with irregular transverse ridges or almost smooth; posterior metatibial spine sometimes conspicuously long; associated with galls. ..... Thrasorinae (p. ***)

- Hind coxa more elongate; female metasoma with fifth abdominal tergum small, not much larger than sixth or seventh tergum; lateral pronotal carina usually longer; mesoscutum shining or dull; posterior metatibial spine not conspicuously long; parasitoids of Diptera larvae in various microhabitats but never in galls. ..... Figitinae (p. ***)

THRASORINAE. This is undoubtedly the figitid subfamily that is most difficult to separate from other figitids, particularly figitines. This is partly because of the few autapomorphies of the subfamily and partly because of the structural diversity within it. Several thrasorines also show distinct similarities with gall-inducing and inquilinous cynipids. These similarities include both apparent plesiomorphies (such as the dull mesoscutum) and convergences (such as the fused third and fourth tergum). Fortunately, the South American taxa form a subclade that is easy to identify (see below). Members of the Thrasorinae have the metacoxa distinctly swollen, although the difference compared to other figitids is small in some genera and may be difficult to appreciate. The mesopleuron usually has a horizontal mesopleural furrow, but this is a common figitid feature and a symplesiomorphy of all subfamilies except Parnipinae. The mesoscutum is dull or shiny and sometimes equipped with irregular transverse ridges (*Myrtopsen*). The scutellum is rather coarsely sculptured, at least on the sides.

Three of five genera occur in the Neotropics (Ronquist 1999): *Myrtopsen* (southwestern North America and South America), *Pegascynips* (South America), and *Plectocynips* (South America). All thrasorine genera except the North American *Euceroptres* share a series of derived features: lateral pronotal carina short, strongly curved and prominent; female with abdominal tergum 3 either reduced in size (most genera) or fused with fourth abdominal tergum (*Myrtopsen*), abdominal terga 5 and 8 enlarged, and tergum 7 reduced and more or less completely covered by tergum 6 (*Thrasorus*) or 5 (all South American representatives). *Pegascynips* and *Plectocynips* form a monophyletic group based on the shared presence of an extremely long posterior metatibial spur (Ronquist 1999).

The Thrasorinae have been reared from galls of cynipids and chalcidoids. They have previously been assumed to be phytophagous inquilines but the life history has not been studied in detail for a single species and their phylogenetic position predicts that they are parasitoids of some other hymenopteran gall inhabitant rather than gall-tissue feeders. Detailed and careful studies of their life history are dearly needed. *Myrtopsen mimosae* has been reared from galls on *Mimosa biuncifera* (Fabaceae) in the arid areas of the southwestern United States and adjoining Mexico together with the supposedly gall-inducing chalcidoid *Tanaostigmodes albiclavis* (Tanaostigmatidae). Dissection of a large number of such galls collected on *Mimosa biuncifera* in Arizona failed to reveal any visible host remains in gall chambers containing pupae of *Myrtopsen mimosae* (Liu, unpublished data). This suggests that *M. mimosae* may be a phytophagous inquiline and not a parasitoid, after all. However, the Parnipinae larva leaves miniscule remains of its host (Ronquist and Nieves-Aldrey, 2001), and such traces can easily be missed upon normal gall dissection. Therefore, confirmation of these observations by data on the early-instar larvae of *M. mimosae* would be extremely valuable. The four species of *Myrtopsen* described from southern South America were reared from galls on Myrtaceae (*Blepharocalyx* and *Eugenia*; Diaz 1975). *Plectocynips*

was described from specimens reared from *Nothofagus* galls (Diaz, 1976) and it is likely that *Pegascynips* is also associated with such galls given the close relationship between these two genera (Ronquist 1994) and the fact that specimens of *Pegascynips* are often collected in *Nothofagus* forests (Buffington, unpublished data; Ronquist, unpublished data). Similar *Nothofagus* galls have also produced the cynipid genus *Paraulax* and gall-inhabiting, perhaps gall-producing, chalcidoids of the genus *Aditrochus* (Pteromalidae: Ormocerinae) (De Santis, Fidalgo & Ovruski 1993).

Diaz (1981) gives a key to species of *Myrtopsen*.

CHARIPINAE. These are very small wasps (1-3 mm in length) having an evenly rounded, smooth scutellum (Fig. 26). The subfamily is usually divided into two tribes, Alloxystini and Charipini (Kierych 1979a, b; Menke & Evenhuis 1991; like many other authors, they recognise the Charipinae as a separate family with the two tribes as subfamilies). Alloxystini are probably paraphyletic and comprise five genera (Menke & Evenhuis 1991; Ronquist, 1999). At least two of these, *Alloxysta* (without a mesopleural carina) and *Phaenoglyphis* (with a mesopleural carina; Fig. 26, mpc), occur in tropical America. Charipini is probably monophyletic, being characterized by synapomorphies such as the closely situated spiracles on the eighth abdominal tergum, the terminal club of the female antenna, a small carinate projection posteriorly on the scutellum, and the third abdominal tergum either being strongly reduced in size but still separated from the fourth tergum (*Apocharips*) or invisibly fused with the fourth tergum (*Dilyta*). *Apocharips* occur in Costa Rica (Menke 1993) and elsewhere in tropical and temperate South America. *Dilyta* occur in Africa and Australia and may be present in tropical America as well.

Species of Alloxystini are hyperparasitoids of Aphidoidea via aphidiine braconid or aphelinid primary parasitoids whereas Charipini are hyperparasitoids of Psylloidea via encyrtid primary parasitoids.

The two tribes of Charipinae can be separated by the following couplet, partly based on the keys to genera in Menke and Evenhuis (1991), which is a useful tool for determining most Neotropical genera.

- All flagellomeres separated by constrictions in female antenna; visible gaster represented by at least two large terga of approximately the same size (abdominal terga three and four) (Fig. 27) ..... Alloxystini
- Last two flagellomeres broadly joined in female antenna; visible gaster represented by a single tergal plate (abdominal tergum three and four fused) (*Dilyta*), or if two, then basal one much shorter than second (*Apocharips*) ..... Charipini

ANACHARITINAE. Members of this subfamily are relatively easy to identify on their habitus, particularly the triangular head with a small mouth (Fig. 28; a more primitive, broader head occurs in the Palearctic *Proanacharis*) and the characteristic pronotum with its large anterior plate delimited by a semicircular pronotal carina running continuously from

one side of the pronotum to the other (Fig. 29, lpc). The absence of the lateral propodeal carina is also a distinctive feature. Many genera have a smooth scutellum with a characteristic marginal carina (Fig. 29), unlike the scutellum of all other cynipoids. The sexes are more similar to each other than in most other cynipoids. This is because the females in all genera except *Anacharis* have the hypopygium (last abdominal sternum) secondarily modified such that it becomes similar to the last abdominal sternum of males (Ronquist 1999). Anacharitine males also lack the typical flagellomere modifications (first flagellomere swollen and excavated laterally) found in most other cynipoid males.

Of the eight genera in this subfamily at least five occur in tropical America. Three of the genera are endemic to South America and form a monophyletic group deeply nested within the subfamily (Diaz 1979; Ros-Farré et al. 2000). They can be distinguished on the presence of a malar sulcus, which often extends dorsally behind the eye, and on the small third abdominal tergum, which is much smaller than the fourth tergum. They also tend to have an open marginal cell (variable within *Acanthaegilips*), in contrast to the closed marginal cell of other anacharitines. The group includes *Solenofigites* and *Calofigites* (southern South America; scutellum without spine) and *Acanthaegilips* (Neotropical; apex of scutellum with long spine). In addition, the cosmopolitan genera *Anacharis* (petiole long, smooth and without a collar) and *Aegilips* (petiole shorter, sculptured and with collar laterally and ventrally) occur in South America, as well as *Xyalaspis* (Holarctic, extending south to Costa Rica; scutellum with blunt spine, otherwise similar to *Aegilips*).

Anacharitines are koinobiont endoparasitoids of the larvae of Hemerobiidae and Chrysopidae (Neuroptera).

Diaz (1979) gives a key to South American genera and Diaz (1983) reports *Acanthaegilips braziliensis* from Argentina. Ros-Farré et al. (2000) redescribe the genus *Acanthaegilips*, discuss its phylogenetic position, and list characters separating anacharitine and aspicerine genera.

FIGITINAE. This is an unresolved paraphyletic group, which forms part of the large clade of core figitids together with the emarginines, pycnostigmines, eucoilines and aspicerines (Ronquist 1999). As far as is known, this clade is exclusively Diptera-parasitic and it includes all figitids that are known to attack dipterans. The primary morphological synapomorphy of core figitids is the reduction in the size of the third abdominal tergum, which is smaller than the fourth tergum in the ground plan. However, this character evolved convergently in some charipines, some anacharitines and some thrasorines. Because figitines are not monophyletic, it is difficult to list good diagnostic features for them. Basically, figitines are core figitids that do not belong to any of the other four subfamilies in this clade.

The preliminary analysis of Ronquist (1999) suggests that *Melanips* is the sister group to Aspicerinae + (other figitines + Emarginae + Eucoilinae + Pycnostigminae) (Fig. 24) but relationships among the major groups of core figitids are still poorly known. Figitinae comprise 13 genera and 138 described species, with the majority of genera known only from temperate regions. Of the ten genera known from the New World, at least five occur in tropical America: *Melanips* (widespread, except in tropical Africa; mesoscutum

dull; Figs. 31-32), *Lonchidia* (cosmopolitan; small, scutellar foveae confluent, female antenna with club-like swelling apically), *Figites* (cosmopolitan, probably paraphyletic), *Neralsia* (New World, scutellum usually with a long spine; Figs. 33-34), and *Xyalophora* (Europe, Africa, New World; scutellum with short tooth; Fig. 10). The three latter genera are related and share features such as distinctly hairy eyes and wings usually with reduced pubescence. *Neralsia* show several similarities with aspicerines but it is currently unclear whether these similarities indicate close relationship. It is one of the most commonly collected figitine genera in South America. *Neralsia splendens* has been reported from Argentina (Diaz 1990; Diaz & Gallardo 1995) and Brazil (Marchiori & Linhares 1999); two unidentified species have been recorded from Panama (Nieves-Aldrey and Fontal-Cazalla, 1997).

Figitines are endoparasitic koinobionts of a wide range of Diptera larvae. The biology is similar to that of Eucoilinae and the species are often associated with flies in dung, carrion, or rotting fruit. Species of *Melanips* are atypical in that they parasitize dipterous larvae that prey on aphids, i.e. Syrphidae and Chamaemyiidae (Evenhuis 1968). The biology of *Lonchidia* is unknown. *Neralsia* and *Xyalophora* attack Sarcophagidae (Roberts 1935), while *Figites* have been reported from Anthomyiidae, Muscidae, Calliphoridae, Sarcophagidae, and other families of "Cyclorrhapha".

ASPICERINAE. The subfamily name is sometimes cited as "Aspiceratinae" (e.g. Ros-Farre et al. 2000) but the correct form is "Aspicerinae" (Ronquist 1999). Aspicerines form a distinctive monophyletic group of figitids. Characteristic features include the saddle-shaped third abdominal tergum (Fig. 37), the margined area beneath the antennae (Fig. 35), the concave and transversely ridged posterior surface of the head (shared with *Neralsia* in the Figitinae), the dull mesoscutum (Fig. 36), and the peculiar structure of the pronotum (Fig. 36): the raised ventrolateral pronotal margin is dorsally joined to the lateral pronotal carina at a distinct angle and beneath this angle there is a small and thin, window-like piece of chitin, which completely separates the pronotum into an anterior and a posterior part.

The subfamily consists of eight genera and 99 described species. Of the five genera known from the New World at least three occur in tropical America: *Balna* (Neotropical; mesoscutum with a median hump), *Callaspidia* (cosmopolitan; petiole long and third abdominal tergum with median hair patch) and *Prosaspicera* (New World; scutellum with a conspicuous, long apical spine; key to species in Diaz, 1984). Nieves-Aldrey and Fontal-Cazalla (1997) report *Balna nigriceps* and two unidentified species of *Prosaspicera* from Panama.

Aspicerines are parasitoids of larvae of Syrphidae (Diptera). Species of the Holarctic genera *Callaspidea* and *Omalaspis* have been reared from larvae of aphidophagous syrphids (see Fergusson 1986), and a Costa Rican species of *Balna* has been reared from an unidentified syrphid larva, which was preying on scale insects on citrus (P. Hanson, pers. comm.). Although detailed information is available only for *Callaspidea*, presumably all aspicerines are koinobiont endoparasitoids, like all other figitids.

EMARGININAE. Emarginines are minute cynipoids with highly characteristic features,

such as the deeply bilobed fore wing (this also occurs in a few eucoilines), a small, box-like marginal cell, the laterally compressed, entirely smooth, box-like mesosoma (Figs. 38-39), the lack of a lateral pronotal carina (Fig. 39), the lack of notauli (Fig. 38), the absence of the mesopleural triangle and the posterior subalar pit (Fig. 39) and the presence of woolly pubescence posteriorly on the mesosoma (Fig. 39) and anteriorly on the metasoma (Fig. 40). Some of these features are also commonly found in eucoilines, such as the hairy girdle anteriorly on the mesosoma and the lack of the posterior subalar pit and the lateral pronotal carina. However, unlike eucoilines the third tergum is free and not fused to the other terga (Fig. 40) in emarginines. The scutellum of emarginines has a pair of submedian ridges (Fig. 39) but lacks the eucoiline scutellar plate with its glandular release pit. Although many of the eucoiline and emarginine similarities appear to be convergences, emarginines are closely related to eucoilines (and pycnostigmines) (Fontal-Cazalla et al. 2002) (Fig. 24). The similarities between emarginines and charipines (the small body size and the lack of notauli) are only superficial and apparently do not indicate close relationship.

Emarginines are widespread in the Southern Hemisphere. The subfamily currently comprises five described, closely related genera: *Emargo*, *Bothriocynips*, *Thoreauella*, *Weldiola*, and *Quinlania*. *Thoreauella* is the oldest generic name in the subfamily; it was established by A. A. Girault in 1930 for an Australian species (Girault 1930). *Emargo* and *Bothriocynips* are based on South American species (Weld 1960; Diaz 1978), whereas *Weldiola* and *Quinlania* were proposed by Kovalev (1994) for some African species described by Quinlan (1988) in *Emargo*. Emarginines are associated with ants: they have been collected in army-ant refuse deposits (Weld 1960) and in *Camponotus* nests (Diaz 1978). They are presumably parasitoids of dipteran larvae developing in these environments.

EUCOILINAE. Eucoilines are easily distinguished from all other microhymenopterans by the raised plate or "cup" on the disc of the scutellum. Most species are fully winged but brachypterous individuals are known. It is the most speciose, abundant and omnipresent group of Cynipoidea and accounts for the vast majority of specimens encountered in most tropical situations. Worldwide there are 83 currently recognized genera with about 1000 described species, but it is probable that this subfamily contains more undescribed species than any other group of Cynipoidea. At this time it is impossible to estimate the diversity of eucoilines in tropical America.

Eucoilines are endoparasitoids of the larvae of a wide range of Diptera, ranging from those developing in living plant tissue (Tephritidae, Anthomyiidae, Chloropidae and Agromyzidae) to those being saprophagous (Sepsidae, Sphaeroceridae, Drosophilidae, Ephydridae, Phoridae, Muscidae, Calliphoridae and Sarcophagidae).
Association with animal dung appears to have resulted in the loss of pubescence on the propodeum and at the base of the second metasomal tergum (Nordlander, 1978*a*). Some species of *Eucoila*, *Kleidotoma* and *Trybliographa* associated with synanthropic flies have become very widespread. Male eucoilines are readily distinguished from females by their much longer antenna. In addition, the male antenna has either the third or fourth segment modified (the latter being apomorphic; Nordlander, 1982*b*).

The phylogenetic analysis of Fontal-Cazalla et al. (2002) suggested that attacking

leaf-mining flies in living plant tissue is the plesiomorphic condition in the subfamily, with more derived eucoilines attacking saprohpagous hosts in a variety of microhabitats. Further, their analysis indicated that there are two distinctly different groups of eucoilines that are entirely endemic to the Neotropical Region: the monophyletic *Zaeucoila* group of genera, which branch off early in the subfamily phylogeny, and a paraphyletic Neotropical grade of basal core eucoilines. The *Zaeucoila* group of genera specialize on leaf-mining flies and fruit infesting flies, while the Neotropical grade attack a variety of hosts in rotting fruit and other vegetation. Recent work on the Neotropical grade of genera by Buffington (unpublished) suggests that this group may constitute a monophyletic group rather than a paraphyletic grade.

Several Eucoilinae are economically important as parasitoids of dipterous pests, especially fruit flies (Tephritidae) and leaf miners (Agromyzidae). The Asian species *Aganaspis daci* (previously known as *Trybliographa daci*; see Lin 1987) was introduced into Florida, Mexico, and Costa Rica to control certain tephritid pests, but has apparently become established only in Florida. Native species reared from fruit-infesting Tephritidae in the Neotropics include *Aganaspis nordlanderi*, *A. pelleranoi*, *Diceratataspis flavipes*, *Lopheucoila anastrephae*, and *Odontosema anastephae* (Guimarães *et al*., 1999). However, there are still many unresolved taxonomic problems in the neotropical Eucoilinae associated with Tephritidae (Wharton *et al*., 1998). Among Eucoilinae that parasitize Agromyzidae, *Agrostocynips clavatus* has been reported from *Liriomyza huidobrensis* in Argentina (Diaz & Valladares, 1979; Valladares *et al*., 1982). A number of other genera have also been reared from leaf-mining Diptera, including *Tropideucoila* (Acosta & Cave, 1994), *Rhabdeucoela* (Buffington, unpublished data), *Aegeseucoela* (Buffington, 2002), and *Zaeucoila* (Acosta & Cave, 1994). Eucoilinae also parasitize dung flies, and in Brazil *Coneucoela brasiliensis*, *Ganaspis fulvocincta* and *Paraganaspis egeria* have been reared from Sarcophagidae associated with this habitat (Diaz & Gallardo, 1996*b*; Díaz *et al*., 2000).

The identification of genera of Eucoilinae is very difficult since the higher taxonomy of this subfamily has received so little attention. Keys are available for Britain (Quinlan, 1978), Hawaii (Beardsley, 1988, 1989), the Afrotropics (Quinlin 1986, 1988), and Taiwan (Lin, 1988) but they are not fully reliable even for the faunas they are intended to cover. Previously, the only key to genera that included the Neotropical fauna is that of Weld (1952), but it is completely outdated. Subsequent to Weld's work several genera have been redefined (Nordlander, 1976, 1978a & b, 1980, 1981, 1982a; Diaz & Gallardo 1997, 1998; Gallardo & Diaz, 1990, 1999; Buffington, 2002, in press) and a few new genera have been described (Buffington, 2002 ; Diaz, 1976; Lin, 1988; Quinlan, 1976, 1984, 1986, 1988). Nieves-Aldrey and Fontal-Cazalla (1997) list eucoilines collected in Panama, mostly at the generic level, but do not provide a key. The following key is the first attempt to provide generic level identification for the Neotropical Region since Weld (1952). The key focuses on commonly collected genera, and genera clearly circumscribed. The user should not be discouraged if a specimen cannot be identified unequivocally, since many taxa await description and proper circumscription.

Key to genera

Note: Correct lighting is essential in the examination of eucoilines; glare will prevent the

correct diagnosis of several features presented here. The user of this key should employ either fiber optic lamps in conjunction with light dispersing plastic film, or use fluorescent lamps (which have natural light dispersing properties).[Matt: Can you please edit this key so that it has the same style as the others? E.g. 1a and 1b should be 1 and -, respectively, there should be no complete sentences, and there should be no double spaces (so ", Fig. 44).double-spaceNotauli" should be ", Fig. 44);single-spacenotauli", for instance). If you wish, you can of course edit all the other keys and the rest of the text so that they fit in style with this one.]

1a. Parascutal impression present but incomplete (PI, Fig. 44). Notauli never present (Fig. 45)……..... **2**
1b. Parascutal impression present and complete (PI, Fig. 43). Notauli present (NOT, Fig. 43). .....***Gronotoma*** **(rarely collected)**

2a. Clypeal and malar spaces without conical projections or, if with small pyramidal protuberances, then the mesoscutum with sculpture present and pronotal plate nearly as wide as mesoscutum(PP, Fig. 46). **3**
2b. Clypeal and malar spaces each with a distinct conical protuberance; mesocutum lacking sculpture entirely (Fig. 45); pronotal plate narrow (PP, Fig 45).
..... ***Ganaspidium*** **(usually *G. utilis*)**

3a. Pronotal plate wide, nearly as wide as mesoscutum (PP, Fig. 44, 46). Mesoscutal keel often present (MSK, Fig. 44). Laterodorsal projections and/or posterior projections of the scutellum present (LDP, PPS, Fig. 44) or absent. Orbital furrows often present (OF, Fig. 41). Genal carina often present..... **4**
3b. Pronotal plate usually narrow (PP, Fig. 45). Mesoscutal keel always absent (Fig. 45). Laterodorsal projections absent (a few taxa may possess either posterior projections of the scutellum or a single posterior projection) (Fig. 45). Orbital furrows usually absent (fig. 42). Genal carina always absent (**Core Eucoilinae) 13**

4a. Posterior margin of scutellum rounded, occasionally with reduced laterodorsal projections (Fig. 43, 45)..... **5**
4b. Posterior margin of scutellum with distinct, paired, posterior and/or laterodorsal projections (LDP, PPS, Fig. 44) **8**

5a. Genal carina reduced; at most, extending to a point posterior to the midpoint of the compound eye . Mesoscutal keel absent. .....***Agrostocynips***
5b. Genal carina prominent, extending from the ventral margin of the malar space to the dorsal part of the head . Mesoscutal keel present, at least anteriorly (MSK, Fig. 44)... **6**

6a. Genal space coriaceous. Orbital furrows (OF, Fig. 41) removed from the inner margins of the eyes, extending instead across the lower face and originating dorsally from the lateral ocelli. Lateral propodeal carinae raised into blunt protuberances at junction with auxiliary propodeal carinae. Scutellum in lateral view meeting scutellar plate at a 90 degree angle…….....***Rhabdeucoela***
6b. Genal space smooth. Orbital furrows present along inner orbits of compound eyes, not

converging strongly across the lower face, and not originating dorsally at the lateral ocelli. Lateral propodeal carinae without protuberances. Scutellum in lateral view meeting scutellar plate at a distinctly acute angle..... **7**

7a. Dorsal margin of pronotal plate crested, deeply bifurcate (as in Fig. 44). Laterodorsal projections of scutellum occasionally present, usually reduced (LDP, Fig. 44). R_1 of forewing incomplete (marginal cell always open). Parapsidal hair line present. Orbital furrows (OF, Fig. 41) often extending to lateral ocelli (some species). Genal carina often flanged posterior to compound eye .....***Aegeseucoela***
7b. Dorsal margin of pronotal plate not crested (occasionally slightly bifurcate) (Fig. 43, 45, 46). Laterodorsal projections of scutellum always absent (Fig. 45). R_1 of forewing complete (marginal cell always closed). Parapsidal hair lines absent. Orbital furrows not extending to lateral margins of lateral ocelli. Genal carina not flanged. .....***Zaeucoila***

8a. Mesoscutal keel (MSK, Fig. 44) present or absent; parapsidal ridge absent (Fig. 2:E). Genal carina present or absent. Pronotal triangle (PT, Fig. 44) small, with the lateral side issuing from a point mesal to the laterodorsal margin of the pronotal fovea. Pronotal impression absent..... **9**
8b. Mesoscutal keel (MSK, Fig. 44) prominent; parapsidal ridge distinct (PR, Fig. 2: F). Genal carina always present. Pronotal triangle (PT, Fig. 2: C) large, with the lateral side issuing from near the laterodorsal margin of the pronotal fovea. Pronotal impression present **10**

9a. Mesoscutal keel absent. Posterior projections of scutellum elongate; laterodorsal projections of scutellum significantly smaller or absent. Orbital furrows joining with malar sulcus at clypeal margin, far from the compound eye. Ventral margin of mesopleural triangle rounded, indistinct (MPT, Fig. 18). ..... ***Diceratapsis***
9b. Mesoscutal keel present. Posterior and laterodorsal projections of the scutellum equally developed, resulting in four distinct lobes in dorsal view. Orbital furrows joining malar sulcus at the ventral margin of the compound eye. Ventral margin of mesopleural triangle distinct (MPT, Fig. 18) ***Moneucoela***

10a. Wings nearly devoid of setae, instead having small dots where setae are generally located. Metasoma slightly larger than the mesosoma. Parasitoids of fruit infesting cyclorrhaphous Diptera **11**
10b. Wings setose (basally bare in some species, but at least apically setose). Metasoma sub-equal in size to the mesosoma. When known, parasitoids of Agromyzidae..... **12**

11a. Scutellar plate (SCP, Fig. 43, 44) with a distinct spine overhanging midpit. Base of syntergum of metasoma with a distinct dorsoventral impression in lateral aspect. R_1 of forewing not reaching anterior margin of the wing. Apical fringe on forewing absent. ..... ***Lopheucoila***
11b. Scutellar plate (SCP, Fig. 43, 44) without a spine. Base of syntergum of metasoma without a dorsoventral impression. R_1 of forewing reaching the anterior margin of the wing. Apical fringe on forewing present.....***Dettmeria***

12a. Scutellar plate with a distinct spine overhanging midpit. Orbital furrows (OF, Fig. 41) extending to lateral ocelli ..... ***Penteucoila***
12b. Scutellar plate without a spine overhanging midpit (small tubercles often present). Orbital furrows extending only to lateral margins of the toruli..... ***Tropideucoila***

13a. Petiole elongate, as long as or longer than mesosoma. Head broader than mesosoma. **14**
13b. Petiole small, often difficult to see. Head narrower than mesosoma **15**

14a. Mesocutum transversly sculptured. ..... ***Perischus***
14b. Mesoscutum smooth, not transversely sculptured ..... ***Zamischus***

15a. Wings infuscate. Scutellar plate with prominent spine overhanging glandular release pit ..... ***Acantheucoela***
15b. Wings clear. Scutellar plate lacking a prominent spine..... **16**

16a. Glandular release pit (GRP, Fig. 47) facing posteriorly ..... ***Dieucoila***
16b. Glandular release pit facing dorsally (GRP, Fig. 45) **17**

17a. Mesopleural carina completely lacking ..... ***Glauraspidea***
17b. Mesopleural carina present, well developed (MPC, Fig. 26) **18**

18a. Posterior margin of scutellum bi-lobed (A, Fig. 49) **19**
18b. Posterior margin of scutellum evenly rounded or extended into a tapering spine (Fig. 43, 45, 47, 48, 50-52)..... **20**

19a. Frons lacking sculpture. Wings devoid of setae. Parasitoids of Tephritoidea ..... ***Odontosema***
19b. Frons with a distinct pair of parallel grooves issuing from base of toruli and extending toward dorsal margin of clypeus..... ***Caleucoela***

20a. Posterior margin of scutellum with a blunt, elongate spine directed posteriorly (A, Fig. 48) ..... ***Odonteucoila***
20b. Posterior margin of scutellum evenly rounded (occasionally with a posterior spike, but if present, not drawn out and tapering (e.g. Fig 45)..... **21**

21a. Wings completely bare except for a few large setae along marginal vein ..... ***Eucoila***
21b. Wings completely setose or nearly so **22**

22a. Dorsal surface of scutellum (area surrounding the scutellar plate) striate or smooth (A, Fig 50; A, Fig. 51)..... **23**
22b. Dorsal surface of scutellum crenulated or foveate (Fig. 45, Fig. 49)..... **25**

23a. Dorsal surface of scutellum distinctly striate (A, Fig. 50); scutellar plate occupying over half of the dorsal surface area of the scutellum (Fig. 50). Wings rounded at tips. ***Hexacola***
23b. Dorsal surface of scutellum usually striate but occasionally smooth (A, Fig. 51);

scutellar plate long and narrow, exposing much of the dorsal surface of the scutellum (Fig. 51). Wings emarginated to truncate at the tips **24**

24a. Propodeum and anterior area of syntergum covered in dense setae..... ***Kleidotoma***
24b. Propodeum and anterior area of syntergum completely devoid of setae.....***Eutrias***

25a. Base of syntergum nearly to completely devoid of setae. Parasitoids of Drosophilidae ..... ***Leptopilina***
25b. Base of syntergum with a complete ring of setae. Parasitoids of Drosophilidae and other Muscomorpha families.....**26**

26a. Posteroventral margin of metapleuron devoid of setae (A, Fig. 52). M vein (Fig. 4, 5) often present as spectral. Parasitoids of Callophoridae and Anthomyiidae ***Trybliographa***
26b. Posteroventral margin of metapleuron setose. Parasitoids of Drosophilidae or Agromyzidae.....**27**

27a. Dorsal surface of scutellar plate with a small, distinct point, immediately anterior to glandular release pit. Base of forewing devoid of setae.....***Nordlandiella***
27b. Dorsal surface of scutellar plate smooth and flat. Forewing entirely and evenly setose ..... ***Ganaspis***

The Family Cynipidae

DIAGNOSIS. Separation of the Cynipidae, or gall wasps as they are usually referred to, from the other microcynipoid family Figitidae is most conveniently based on the biology, if it is known: all cynipids are phytophagous, being either plant gall inducers or inquilines associated with cynipid galls while all figitids are insect-parasitic (except possibly for the Thrasorinae, see above). However, the challenge of placing some microcynipoids in either Cynipidae or Figitidae is real, and particularly concerns the gall-inhabiting Figitidae. For instance, the single species of the recently established figitid subfamily Parnipinae had long been placed in the cynipid genus *Aulacidea* and is morphologically remarkably similar to its gall-inducing cynipid host (Ronquist & Nieves-Aldrey 2001). The gall-inhabiting Thrasorinae are similar to cynipid inquilines both morphologically and perhaps also biologically (see above). Fortunately, the gall-inhabiting figitids and cynipids of the New World are easily separated based on host-plant preferences. The figitids are associated with galls on woody hosts in the family Fabaceae and in the genus *Nothofagus* (Nothofagaceae), whereas all cynipids are associated with other plants, notably in the family Rosaceae and in the genus *Quercus* (Fagaceae). Nonetheless, it must be borne in mind that the New World fauna of microcynipoids is poorly known so this situation may well reflect limited knowledge rather than true circumstances.

Several synapomorphies have been listed that support the monophyly of the Cynipidae, including an anteriorly open marginal cell, lack of a lateral pronotal carina, and the dorsal pronotal area being completely absent or hidden by the mesoscutum (Liljeblad and Ronquist, 1998; Ronquist, 1999). However, all of the putative morphological synapomorphies have

exceptions in the form of secondary reversal within the Cynipidae or parallel gain in Figitidae. Ronquist (1999) suggested that the presence of two strong, blunt teeth in the mandibles of the last instar larva might be a unique synapomorphy of the Cynipidae (parasitic figitids and macrocynipoids have only one strong, sharp tooth). This is largely confirmed in a recent survey of larval mandibles of the Cynipoidea (Nieves-Aldrey, Vårdal and Ronquist, unpublished data). Although some cynipid larvae have lost the second tooth, the main tooth is consistently stronger and more blunt in gall wasps than in their insect-parasitic relatives. Recent work has also shown autapomorphic features in the eggs of cynipids (Vårdal, Sahlén and Ronquist, 2003), including a thicker and less plastic shell. In addition to the putative cynipid synapomorphies, there is a large number of characters that are useful for separating cynipids and figitids. These include the dull mesoscutum (present in almost all cynipids but relatively rare in the Figitidae) and the large third abdominal tergum (common in Cynipidae, rare in Figitidae). For a more complete discussion, see the diagnosis of the Figitidae above.

CLASSIFICATION AND DISTRIBUTION. Current classification divides the family into two subfamilies: the Hodiernocynipinae (all extinct), and the Cynipinae, (all extant and several fossil species) (Ronquist, 1999). About 1369 extant species of cynipids in 77 genera are known to science and they are grouped into the gall-making tribesAylacini, Eschatocerini, Pediaspidini, Diplolepidini, and Cynipini, and the gall-inhabiting Synergini (inquilines) (Table 3; Fig. 53). The Aylacini primarily consists of herb gallers and is not monophyletic (Liljeblad and Ronquist, 1998; Ronquist 1999). The Eschatocerini, Pediaspidini, Diplolepidini, and Cynipini are each monophyletic and associated with woody host plants in the rosid lineage of eudicots. Together, these tribes form a monophyletic group referred to as the woody-rosid gallers (Liljeblad & Ronquist 1998). The inquilinous Synergini are also considered monophyletic (Ronquist 1994, 1999; Liljeblad and Ronquist, 1998).

Most cynipid tribes have their center of distribution in the temperate regions of the Holarctic but some of them extend into or are endemic to other regions (Table 3). The Central and South American cynipids are mostly oak gallers (Cynipini) and their inquilines (Synergini). These oak-associated species might be expected to occur wherever oaks are abundant, that is, throughout Central America and at high altitudes well into the northern parts of South America. The Aylacini are mostly European but a few important lineages are centered in North America, including the genus *Diastrophus*, and some of these lineages may extend into Central America although they have not been recorded there yet. The European Aylacini species *Phanacis hypochoeridis* occurs in temperate South America, obviously introduced there by man. To our knowledge, the Diplolepidini (gallers of *Rosa*) and their inquilines (in the genus *Periclistus*, Synergini) have not been recorded from Central or South America but may well occur in the region. The tribe Eschatocerini is endemic to South America; it only includes three closely related species that induce galls on twigs of *Acacia* and *Prosopis* (Fabaceae). It has been found in Uruguay and Argentina (Diaz, 1981). Another South American specialty is the genus *Paraulax*, reared repeatedly from complex galls on *Nothofagus* (Nothofagaceae) similar to those induced by Cynipini on oaks (De Santis, Ovruski and Fidalgo 1993; S. Ovruski, pers. comm.; J. L. Nieves-Aldrey, pers. comm.; Ronquist, unpublished data). The same galls yield a host of other hymenopterans, among them specimens belonging to the allegedly gall-inducing pteromalid genus

Aditrochus (De Santis, Ovruski and Fidalgo 1993). Thus, it is still uncertain whether *Paraulax* is the gall inducer or whether it is a guest (presumably phytophagous) in galls induced by chalcidoids. The genus *Paraulax* was implicitly placed in the Cynipini by Ronquist (1999) but a recent phylogenetic analysis based on adult morphology suggests that *Paraulax* belongs to the Pediaspidini instead (J. Liljeblad, pers. comm.). There are only two other genera in the Pediaspidini: *Pediaspis*, a European gall-inducer on maples (*Acer*), and the Himalayan *Himalocynips* with unknown biology. The addition of *Paraulax* would make this tribe even more heterogeneous. *Paraulax* has been found in Chile, Argentina and Tierra del Fuego and there are several undescribed and one described species (Nieves-Aldrey, pers. comm.; Pujade-Villar, pers. comm.; Ronquist, unpublished data).

Except for *Paraulax*, discussed above, it is unlikely that Cynipini occur naturally in temperate South America. However, *Plagiotrochus amenti* (synonyms *P. abdominalis* and *P. suberi*), a galler of the European cork oak (*Quercus suber*), has beeen introduced into at least Argentina (Diaz, 1972). Among the non-oak inquilines in the tribe Synergini, one species of the genus *Synophromorpha*, *S. kaulbarsi*, has been described from southern Mexico (Ritchie and Shorthouse, 1987). The biology of *S. kaulbarsi* is unknown but other members of the genus exclusively attack galls induced by the Aylacini genus *Diastrophus* on *Rubus* bushes (Rosaceae). Thus, the presence of *Synophromorpha* in southern Mexico could possibly indicate that *Diastrophus* occurs there as well (see above). Of course, it is also possible that the biology of *S. kaulbarsi* differs from that of other species of the genus.

About 147 species of cynipids, mostly Cynipini and a few species of oak-associated Synergini, have been reported from Guatemala and Mexico, especially southern Mexico (Kinsey 1936, 1937a, 1937b, 1938). Recent fieldwork has revealed a rich and diverse fauna of cynipids associated with oaks in Costa Rica (Prescott, unpublished data) and Panama and Colombia (Nieves-Aldrey, pers. comm.). The 90 species of oaks in North America support a Cynipini fauna of 640 known and probably many more unknown species. Considering the fact that there are 135 species of oaks (including 65 endemic) in Mexico alone (Nixon 1990), it is reasonable to believe the number of cynipid wasp species in the Neotropics to be upwards of 1000.

Tribe	**# Genera/# spp.**	**Distribution**	**Feeding Guild and Host**
Aylacini	21/156	Holarctic	Galler of Asteraceae, Rosaceae, Lamiaceae, Papaveraceae, Apiaceae, Valerianaceae, Brassicaceae, Smilacaceae
Cynipini[1]	44/974	Holarctic[2]	Galler of Fagaceae and Nothofagaceae, mostly on *Quercus*
Eschatocerini	1/3	S. America	Galler of *Acacia*, *Prosopis* (Fabaceae)
Pediaspidini	2/2	West Palearctic	Galler of *Acer* (Sapindaceae)
Diplolepini	2/63	Holarctic	Galler of *Rosa* (Rosaceae)
Synergini	7/179	Holarctic[3]	Inguilines in galls of *Diastrophus* (Aylacini) on *Rubus*, *Diplolepis* (Diplolepidini) on *Rosa*, and Cynipini on *Quercus*[4]

[Matt and Zhiwei: please make this table conform to the others in style (or make all tables conform to the required style in Sharkey's book)]

Table 3. Tribes of extant Cynipidae with number of genera and species, geographic distribution, and biology. (1 Including *Paraulax*; 2 mostly Holarctic, but extend into South America; 3 mostly Holarctic, but extend into Central America and probably South America as well); 4 one South African genus, *Rhoophilus*, is apparently an inquiline in Lepidoptera galls on *Rhus*, Anacardiacae; there is also a southern US species of *Periclistus* claimed to be an inquiline in *Diastrophus* galls on *Smilax*, Smilacaceae).

BIOLOGY. Females of gall-making cynipids lay their eggs into young, undifferentiated plant tissue. The normal developmental pattern of the host-plant tissue is altered such that a gall is formed around the cynipid larva. The presence of the larva is necessary for the continued growth of the gall (Bronner 1992), but the mechanism of gall formation is not yet understood. Cynipid galls are more complex than any other arthropod-induced plant galls (Cornell 1983). The galls are formed on all plant organs (i.e., flowers, leaves, buds, stems, twigs, and roots) and may contain from one to more than 100 larval chambers. The larva feeds on a layer of nutritious plant cells lining its chamber (Bronner 1992; Rohfritsch 1992). A hard layer of sclerenchyma, presumably serving to protect the larva from natural enemies, encloses this nutritive tissue and externally delimits what is referred to as the inner gall. Outside the sclerenchyma is a zone of parenchyma cells supplying the inner gall with water and nutrients. Externally, many galls are covered with specialized hairs or other structures foreign to the attacked plant organ but characteristic of the gall-inducing species. It is commonly believed that the evolution of the complexity and diversity of cynipid gall structure is driven by selection from natural enemies (Cornell, 1983; Stone and Cook, 1998). Cynipid gall inducers are specific both with respect to the host plant species and the plant organs they attack. The phylogeny and evolution of cynipids has been studied in a series of recent papers (Ronquist 1994; Liljeblad and Ronquist 1998; Stone and Cook 1998; Ronquist and Liljeblad 2001; Nylander et al. 2004; reviewed in Ronquist 1999). For a recent review on the population biology of oak gall wasps, see Stone et al. (2002).

The inquilines evolved from gall-making ancestors and are thus gall wasps that have lost the capability to induce galls (Ronquist 1994). The inquiline female lays eggs into young galls initiated by other gall wasps. The developing inquiline larvae feed on gall tissue. Some inquilines kill their host gall-inducers, either directly by the ovipositing inquiline female stabbing the host larva to death with her ovipositor, or indirectly through the inquiline larva starving the host larva to death by redirecting nutrients away from its gall chamber (Ronquist 1994 and references therein). However, many inquiline larvae form their own larval chamber in the parenchymal tissue of the host gall and do not seem to harm the host larva (Liu, unpublished data). Cynipid inquilines are usually specific in terms of both the gall and the host plant they attack. However, some inquilines may attack a range of similar galls or have two or more generations attacking different galls.

IDENTIFICATION. Cynipids are difficult to identify because there has been little traditional taxonomic work aimed at elucidating supraspecific relationships and working out natural generic classifications and keys for the most difficult groups, the Cynipini and Synergini. The situation is further complicated with respect to the Neotropical fauna because it is likely to include so many undescribed forms. Nevertheless, some guidance in the identification of neotropical cynipids may be provided by Weld (1950) and Kinsey (1936, 1937a, 1937b,

1938). Nieves-Aldrey's (2003) new volume on Cynipidae from the Iberian Peninsula may also be a good information source even though it only deals with a regional fauna of the family.

ECONOMIC IMPORTANCE. In general, cynipids are not considered to be a significant threat to their host plants. They do not defoliate their hosts and visible damage is restricted to the galls. However, cynipids often favor individual plants, on which galls can become extremely abundant, and it is likely that detailed studies of such heavily attacked plants would show a number of negative effects, including decreased growth and increased susceptibility to pathogens. The galls are highly complex structures and it must cost the plant water, nutrients, and energy to develop them. In a few cases, damage to the host plant and economic consequences are obvious. The best-known example is the Oriental chestnut gall wasp (*Dryocosmus kuriphilus*). Females of this wasp lay eggs in the vegetative and mixed buds of chestnut trees (*Castanea* spp.), inducing galls on the leaves, petioles, and catkins. The result is suppressed shoot elongation and reduced fruiting. Heavily infested trees can lose their vigor and die (Anagnostakis 1997). Since its introduction into Georgia (United States) in the 1970's on plant cuttings that did not go through quarantine, this species has nearly eliminated the chestnut industry (orchards of Chinese chestnuts) within the state and has now spread to other states, including Tennessee and North Carolina. Another species, *Neuroterus saltatorius*, has been listed as a pest of white oak, causing foliage discoloration and defoliation (e.g. Ohio Division of Forestry, 2003), although the significance of the damage to forestry needs to be quantified. Galls of this species are called jumping oak leaf galls. When they mature, they fall from the leaves onto which they are attached and onto the ground. If these detached galls are disturbed, the larva or pupa inside the gall can cause it to 'hop' to a height several times the gall's diameter.

[Matt and Zhiwei: I think we need a special couplet for *Paraulax* and I also believe we should stress how to separate Syergini from Aylacini using characters not requiring removal of the head; I have introduced these changes below]

Key to tribes of Cynipidae occurring in tropical America

1 Head with a well-defined, strongly carinate area just above the mandible, otherwise without carinate or striate sculpture; female antenna with 12 articles, apex widened and forming a distinct club. In galls on *Nothofagus*; belongs to Cynipini or possibly Pediaspidini. ..... *Paraulax*

- Head without a restricted, strongly carinate area just above the mandible, if striate then over a larger and less well-defined region; female antenna never with a club. 2

2. Pronotum not strongly shortened toward the middle; median length (height) of pronotum at least one sixth, and usually one third, of the length (height) along its posterolateral margin(fig.8a); ventral spine of 7th abdominal sternum (hypopygium) of female short (fig. 8b); species usually fully-winged; vein Rs+M of forewing, when present or indicated, reaching the basal vein well below the middle (fig. 5). Gall makers of herbaceous host plants and inquilines. 3

- Pronotum strongly shortened toward the middle; median length (height) of pronotum at most one seventh of the length (height) along the posterolateral margin (fig. 9a); ventral spine of 7th abdominal sternum (hypopygium) of female longer than broad in lateral view (fig. 9b); vein Rs+M of forewing, when present or indicated, reaching the basal vein at or above the middle (fig. 4); some species with apterous agamic generation. Gall makers of woody rosids. 4

3 Abdominal terga 3 and 4 always fused in females and often in males (fused in males of *Synergus*, *Saphonecrus*, and *Synophrus*, but free in other genera), fusion line marked with a distinct suture in females of *Ceroptres* (fig. 9b) but not visible externally in other genera; syntergum or abdominal tergum 4 often covering most of the remaining part of the postpetiolar metasoma in dried specimens; face, vertex and mesosoma at least partly sculptured, never entirely smooth and shining; marginal cell usually closed on anterior margin; occipital foramen widely separated from oral cavity; shortest distance between margin of occipital foramen and hypostomal carina at least as long as (usually distinctly longer than) the height of hypostomal cavity measured as the maximal distance between hypostomal carina and a line across lower margins of genae (fig. 8c); gula completely reduced and gular sulci united throughout or reduced to a narrow median strip (except in *Synophromorpha* having gular sulci meeting near hypostomata); maxillary palps 4-segmented (the two basal segments partly fused). Inquilines in galls on *Quercus* (Fagaceae), *Rosa*, and *Rubus* (Rosaceae). ..... **Synergini**

- Abdominal terga 3 and 4 always free, if fused (females of *Xestophanes*, a galler of *Potentilla* that is not known to occur in South America), then face, vertex and mesosoma smooth and shining; abdominal tergum 4 usually not covering most of the remainder of the metasoma in dried specimens; marginal cell usually open on anterior margin; occipital foramen close to oral cavity, shortest distance between margin of occipital foremen and hypostomal carina distinctly shorter than (usually less than half) the height of the hypostomal cavity(fig. 10); gula either distinctly present with gular sulci separated from each other or reduced with gular sulci meeting near hypostomata (fig. 10); maxillary palps 5-segmented (two basal segements free). Gall makers attacking herbaceous plants, particularly of the families Asteraceae, Lamiaceae, Papaveraceae, and Rosaceae (only *Phanacis hypochoeridis*, a gall inducer of *Hypochoeris*, definitely known to occur in South America). ..... **Aylacini**

4 Antennae inserted high on face, upper margin of antennal sockets at the same level as the upper margin of eyes; antennal sockets very close to each other, distance between sockets distinctly narrower than width of anterior ocellus; frons with a strong median keel; dorsal axillar area large, triangular, and situated in the same plane as the scutellum (fig. 11a); scutellar foveae absent; notuli absent (fig. 11b); wing venation reduced: forewing Rs+M almost completely invisible, R1 hardly traceable, and Rs not reaching anterior margin of wing (fig. 7). Only one genus known from Uruguay and Argentina making galls on *Acacia* and *Prosopis* (Fabaceae). .....

..... (*Eschatocerus*) **Eschatocerini**

- Antennae inserted on the middle of the face, upper margin of antennal sockets below the upper margin of the eyes by at least 1.5 times vertical diameter of the sockets; antennal sockets widely separated from each other, distance between sockets distinctly wider than width of anterior ocellus; frons without a strong keel; dorsal axillar area not as described as above; scutellar foveae present and distinct from each other or forming a shallow transverse median depression; notauli present; forewing Rs+M at least partly present, R1 distinct, and Rs reaching or almost reaching anterior margin of wing (figs.4 and 5). 5

5 Mesopleuron with longitudinal depression; hypopygium of female ploughshare-shaped (fig. 12); radial cell of forewing usually closed anteriorly. Gall makers of *Rosa.* ..... **Diplolepidini**

- Mesopleuron without longitudinal depression; hypopygium of female never ploughshare-shaped; radial cell of forewing open anteriorly. Gall makers of Fagaceae, mostly on *Quercus,* with a few species on *Castanea*, *Castanopsis*, and *Lithocarpus.* ..... **Cynipini**

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Fig. 1. Phylogeny of the Cynipoidea (from Ronquist, 1999).

Figs. 2-7. Cynipoidea. Figs. 2 - 3. Habitus; 2, A macrocynipoid (Ibaliidae: *Ibalia rufipes*); 3, A microcynipoid (Cynipidae: *Isocolus rogenhoferi*). Figs. 4-7. Fore wings; 4, Cynipidae; 5, Figitidae; 6, *Ibalia* sp. (Ibaliidae); 7, *Dilyta* sp. (Figitidae: Charipinae: Charipini). Explanation of abbreviations: mc = marginal cell.

Figs. 8-12. Cynipidae. 8. *Synergus gallaepomiformis* (Synergini): 8a. Mesosoma, lateral view, 8b. Metasoma, lateral view, 8c. occiput; 9. *Biorhiza pallida* (Cynipini): 9a. Mesosoma, lateral view, 9b. Metasoma, lateral view; 10. *Diastrophus nebulosus* (Aylacini), occiput; 11. *Eschatocerus acaciae* (Eschatocerini), 11a. Face, 11b. Mesosoma, dorsal view; 12. *Diplolepis rosae* (Diplolepidini), metasoma, lateral view.

Figs. 13-17. Cynipoidea. Figs. 13-14. Metasoma in lateral view; 13, *Synergus* sp. (Cynipidae: Synergini); 14, *Neuroterus* sp. (Cynipidae: Cynipini). Fig. 15. Hind leg of *Ibalia rufipes* (Ibaliidae). Fig. 16. Hind femur and tibia, *Liopteron apicale* (Liopteridae: Liopterinae). Fig. 17. Hind tarsus, *Paramblynotus braziliensis* (Liopteridae: Mayrellinae). Explanations of abbreviations: 3tg = third abdominal tergum; 4tg = fourth abdominal tergum.

Figs. 18-23. Liopteridae. Fig. 18. Mesosoma in lateral view, *Paramblynotus braziliensis* (Mayrellinae). Fig. 19. Mesosoma in dorsal view, *Liopteron nigripenne* (Liopterinae). Figs. 20-22. Female metasoma in lateral view; 20, *Paramblynotus braziliensis* (Mayrellinae); 21, *Pseudibalia* sp. (Liopterinae); 22, *Peras fenestratum* (Liopterinae). Fig. 23, general habitus. Explanation of abbreviations: 5tg = fifth abdominal tergum; mi = mesopleural impression; lc = lateroventral carina of mesopleuron; ldp = laterodorsal process of scutellum; lpc = lateral pronotal carina, mps = metapleural sulcus; mpt = mesopleural triangle; nu = nucha; pc = pronotal crest.

Fig. 24. Phylogeny of the Figitidae (modified from Ronquist, 1999).

Figs. 25-30. Scanning electron micrographs of Figitidae. Figs. 25-27, *Phaenoglyphis villosa* (Charipinae: Alloxystini); 25, head in anterior view; 26, mesosoma in lateral view; 27, metasoma in lateral view. Figs. 28-30. *Anacharis eucharioides* (Anacharitinae); 28, head in anterior view; 29, mesosoma in lateral view; 30 metasoma in lateral view. Explanation of abbreviations: lpc = lateral pronotal carina; mpc = mesopleural carina; mpt = mesopleural triangle; psap = posterior subalar pit; ppc = lateral propodeal carina.

Figs. 31-34. Scanning electron micrographs of Figitidae: Figitinae. Figs. 31-32. *Melanips opacus*; 31, mesosoma in lateral view; 32, metasoma in lateral view. Figs. 33-34. *Neralsia* sp.; 33, mesosoma in lateral view; metasoma in lateral view. Explanation of abbreviations: lpc = lateral pronotal carina.

Figs. 35-40. Scanning electron micrographs of Figitidae. Figs. 35-38. *Aspicera scutellata* (Aspicerinae); 35, head in anterior view; 36, mesosoma in lateral view; 37, metasoma in lateral view. Figs. 38-40. *Thoreauella* sp. (Emargininae); 38, mesosoma in lateral view; 39, mesosoma in dorsal view; 40, metasoma in lateral view. Explanation of abbreviations: lpc = lateral pronotal carina; pp = pronotal plate.

Figs. 41-46. Scanning electron micrographs of Figitidae: Eucoilinae. Fig. 41. *Tropideucoila rufipes*, head in anterior view. Fig. 42. *Trybliographa rapae*, head in anterior view. Fig. 43. *Gronotoma* sp., mesosoma in dorsal view. Fig. 44. *Tropideucoila rufipes*, mesosoma in dorsal view. Fig. 45. *Trybliographa rapae*, mesosoma in dorsal view. Fig. 46. *Zaeucoila* sp., mesosoma in antero-dorsal view. Explanation of abbreviations: grp = glandular release pit; ldp = latero-dorsal projections; msk = mesoscutal keel; not = notaulus; of = orbital furrow; pi = pronotal impression; pp = pronotal plate; pps = posterior projection of scutellum; pt = pronotal triangle; scp = scutellar plate.

Figs. 47-52. Scanning electron micrographs of Figitidae: Eucoilinae. Fig. 47. *Dieucoila* sp., mesosoma in lateral view. Fig. 48. *Odonteucoila chapadae*, mesosoma in lateral view; arrow A: posterior scutellar process. Fig. 49. *Odontosema anastrephae*, mesosoma in dorsal view; arrow A: bifurcate posterior scutellar margin. Fig. 50. *Hexacola* sp., mesosoma in dorsal view; arrow A: striate scutellar disc. Fig. 51. *Kleidotoma dolichocera*, mesosoma in dorsal view; arrow A: striate scutellar disc. Fig. 52. *Trybliographa rapae*, mesosoma in lateral view; arrow A: posteroventral margin of metapleuron devoid of setae.

Fig. 53. Phylogeny of the Cynipidae (modified from Liljeblad and Ronquist, 1998). Some European genera of Aylacini omitted; taxa known to occur in South America given in bold. The tribe Pediaspidini will be represented in South America if *Paraulax* is moved there from the tribe Cynipini. *Diastrophus* and Diplolepidini have not yet been recorded from Central or South America but might be expected to occur there.

Literature Cited [Matt: The formatting needs a complete overhaul, many inconsistencies now in detail (usage of "and" or ampersand(&), order of initials, space or not between initials, parentheses or not around publication year, etc), errors, double spaces, lack of space etc.]

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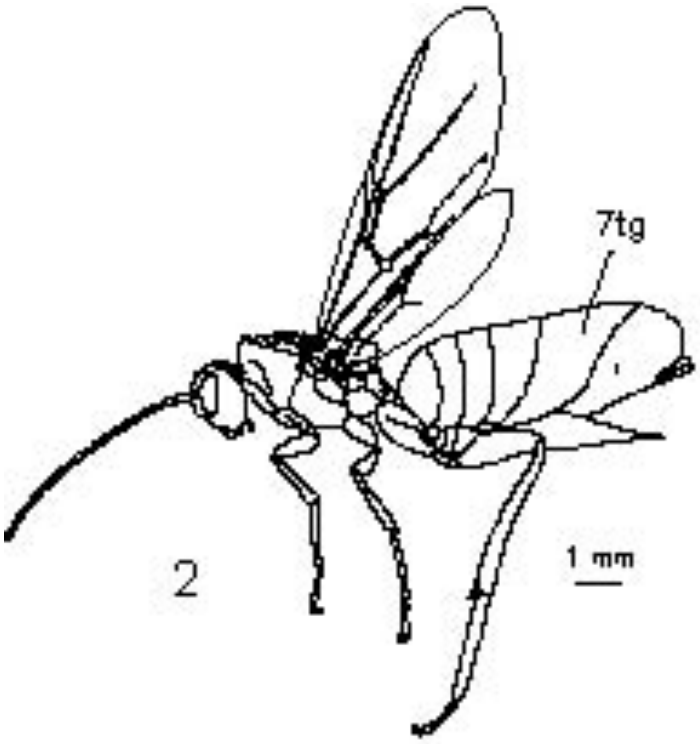
Austrocynipidae
Ibaliidae
Liopteridae
Macrocynipoids
Cynipidae
Figitidae
Microcynipoids

Fig. 1



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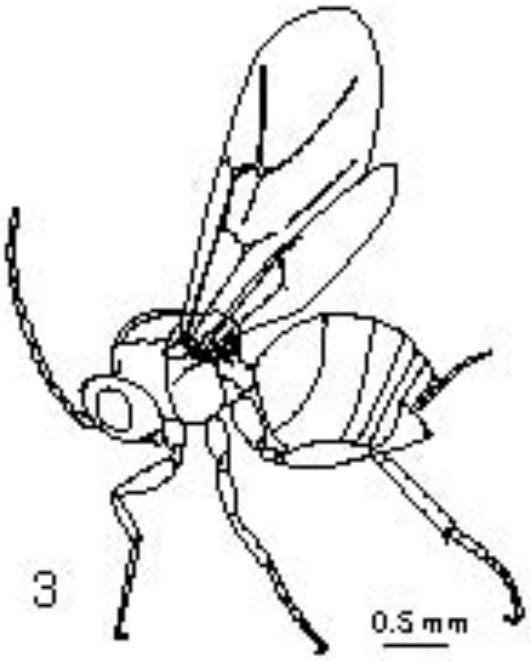

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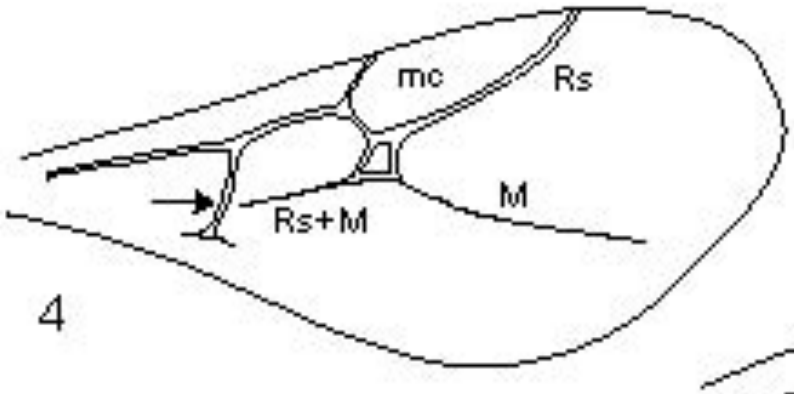

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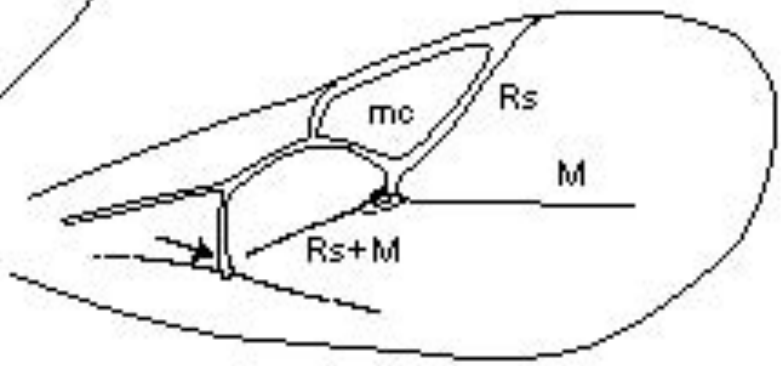

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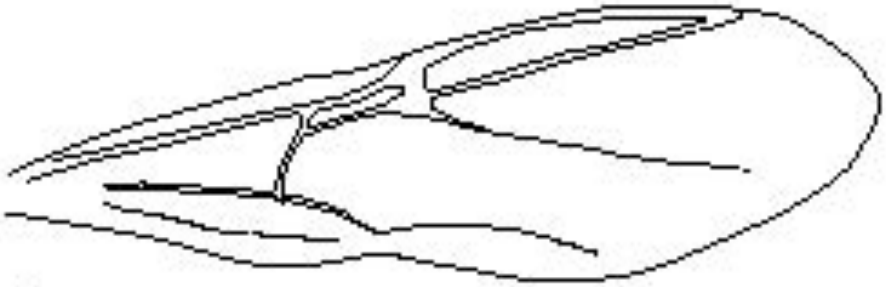

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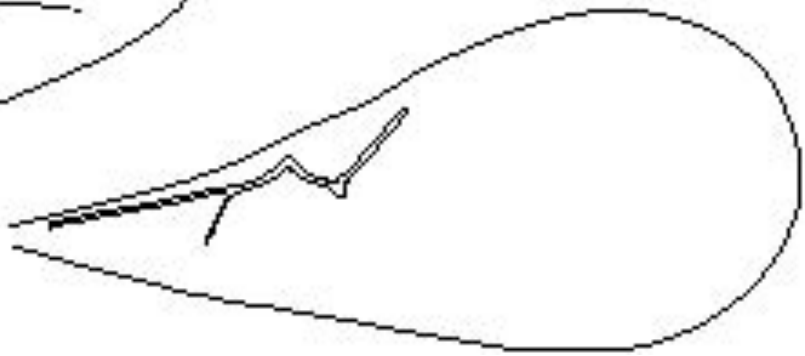

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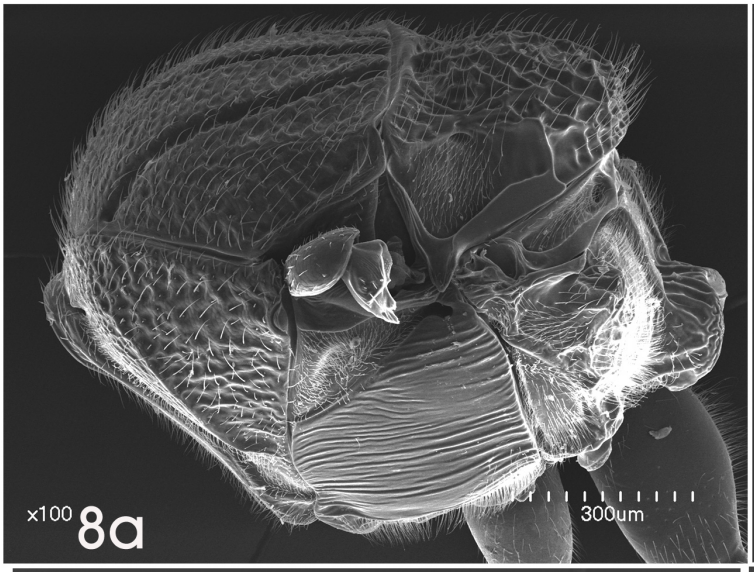
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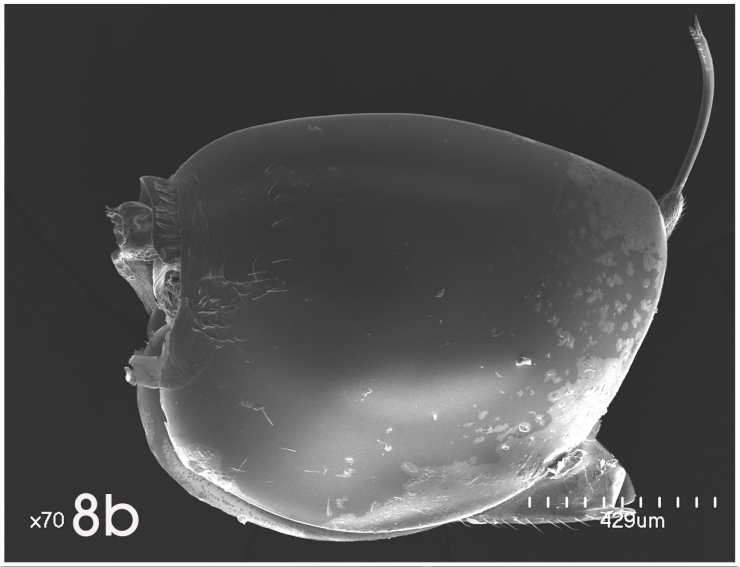
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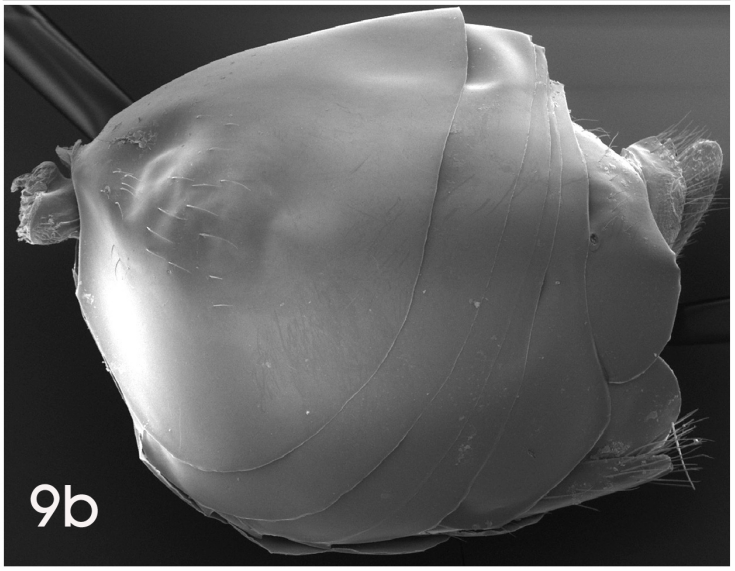
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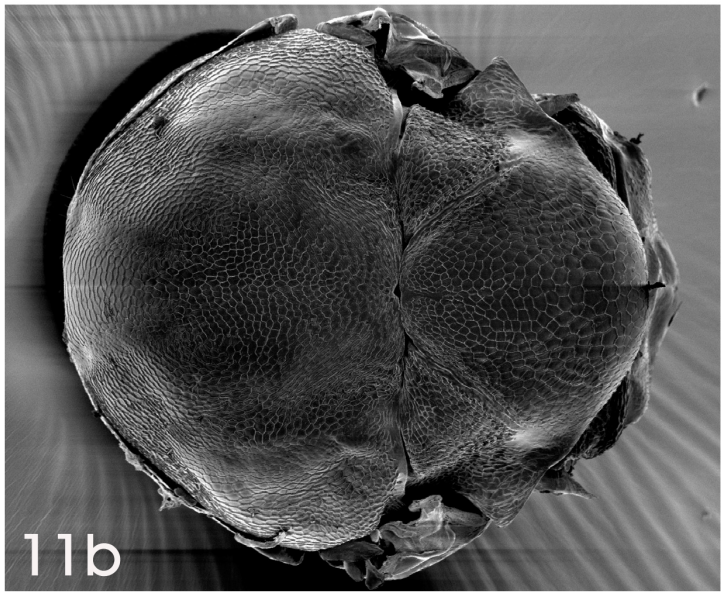
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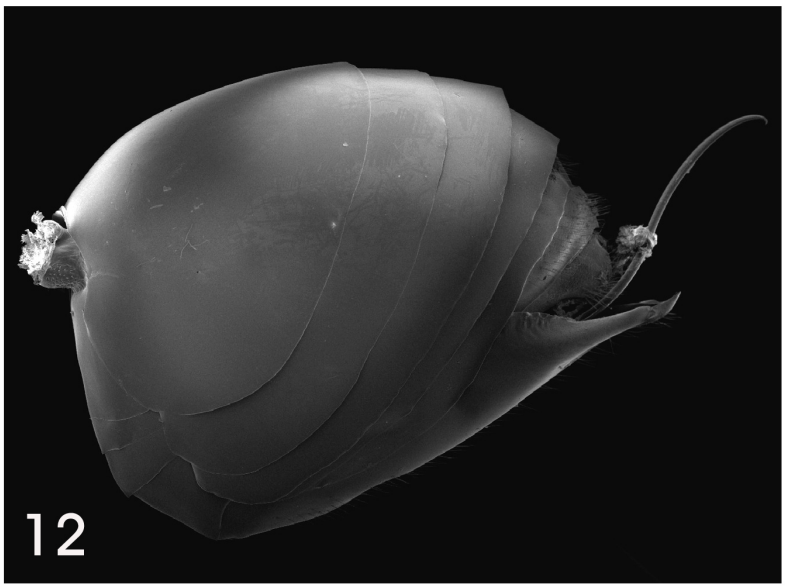
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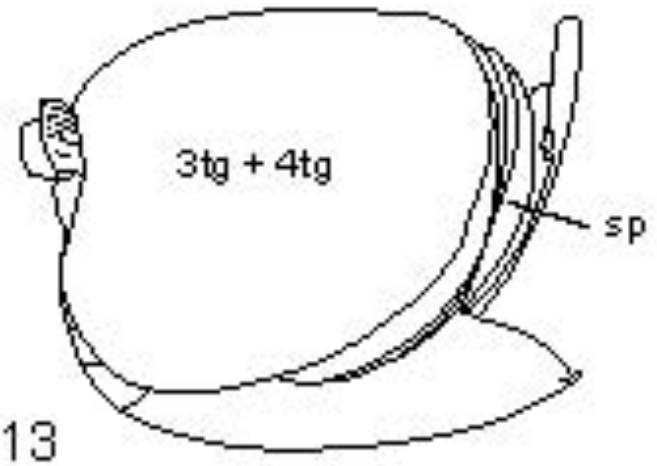

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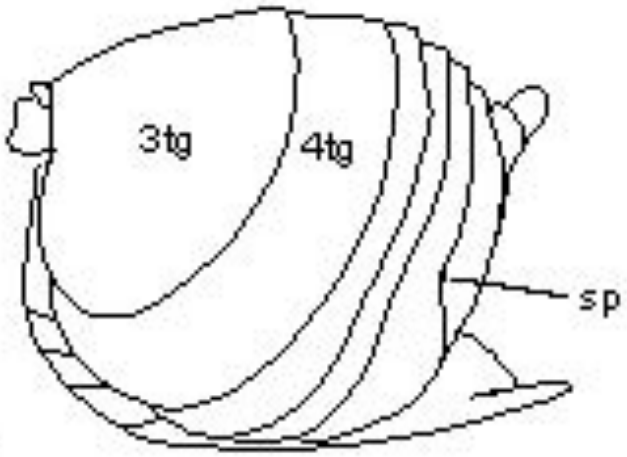

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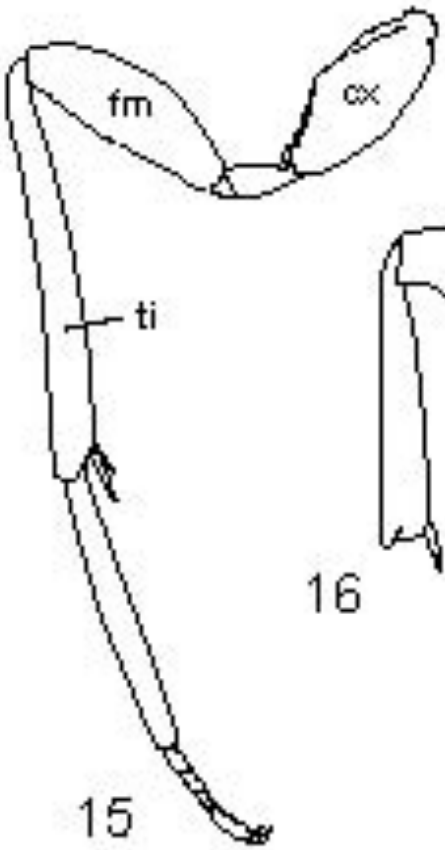

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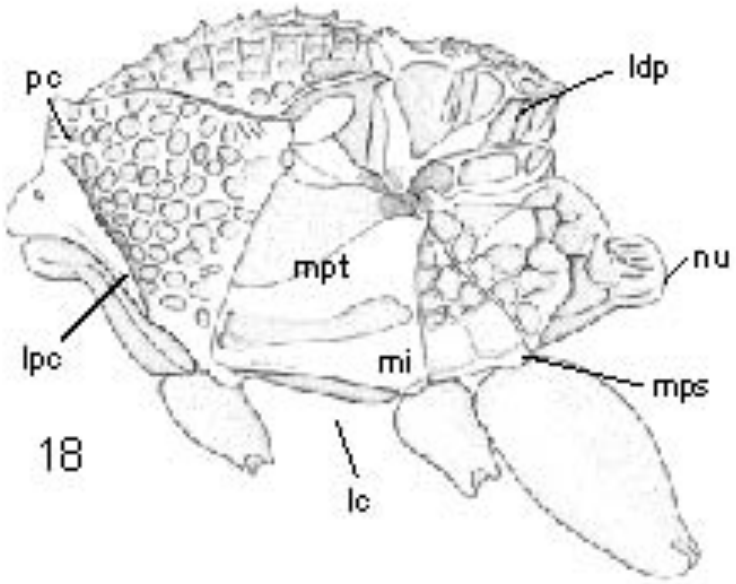

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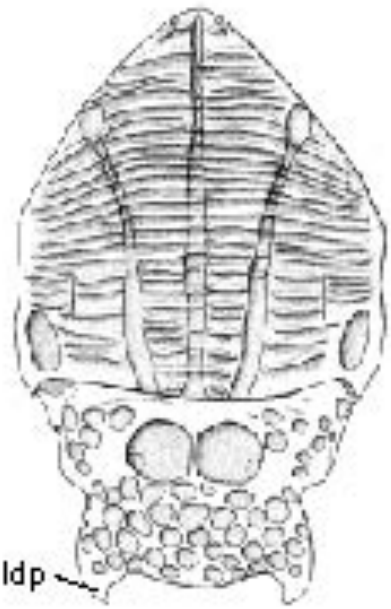

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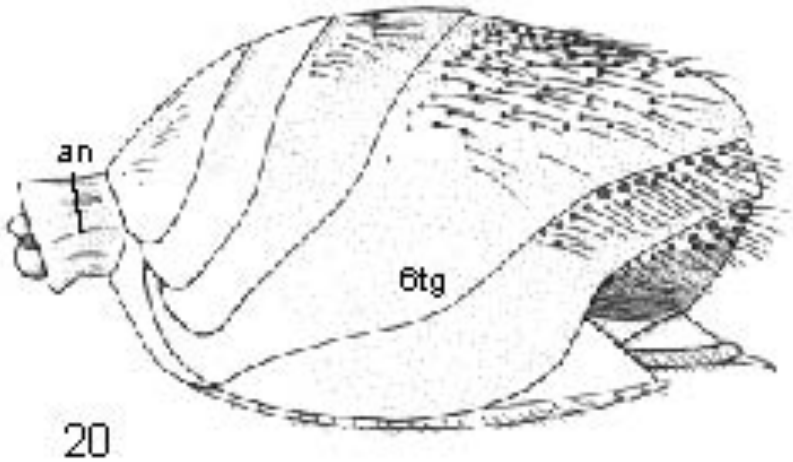

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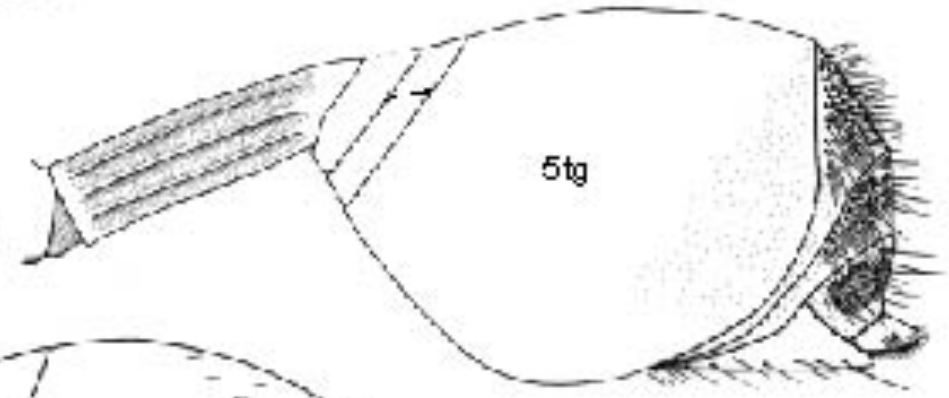

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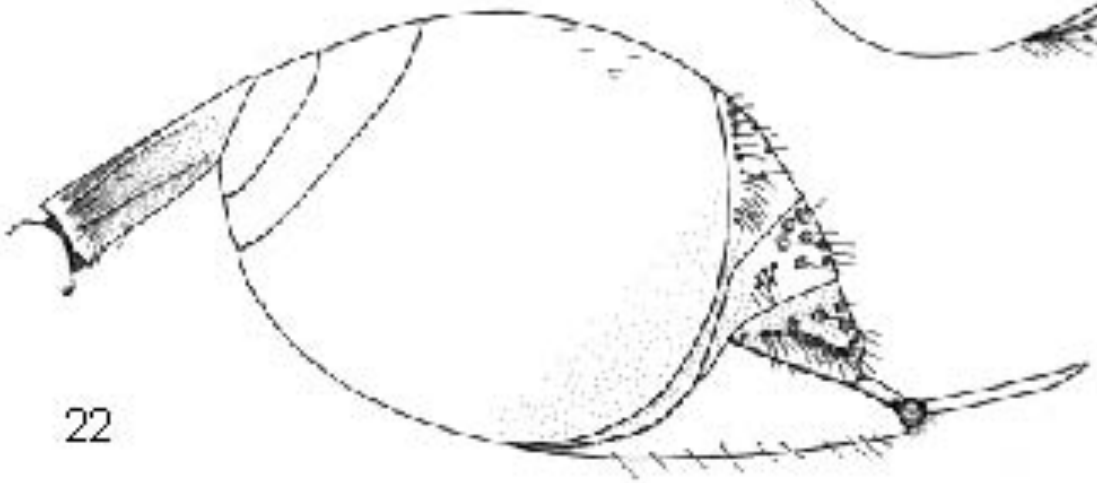

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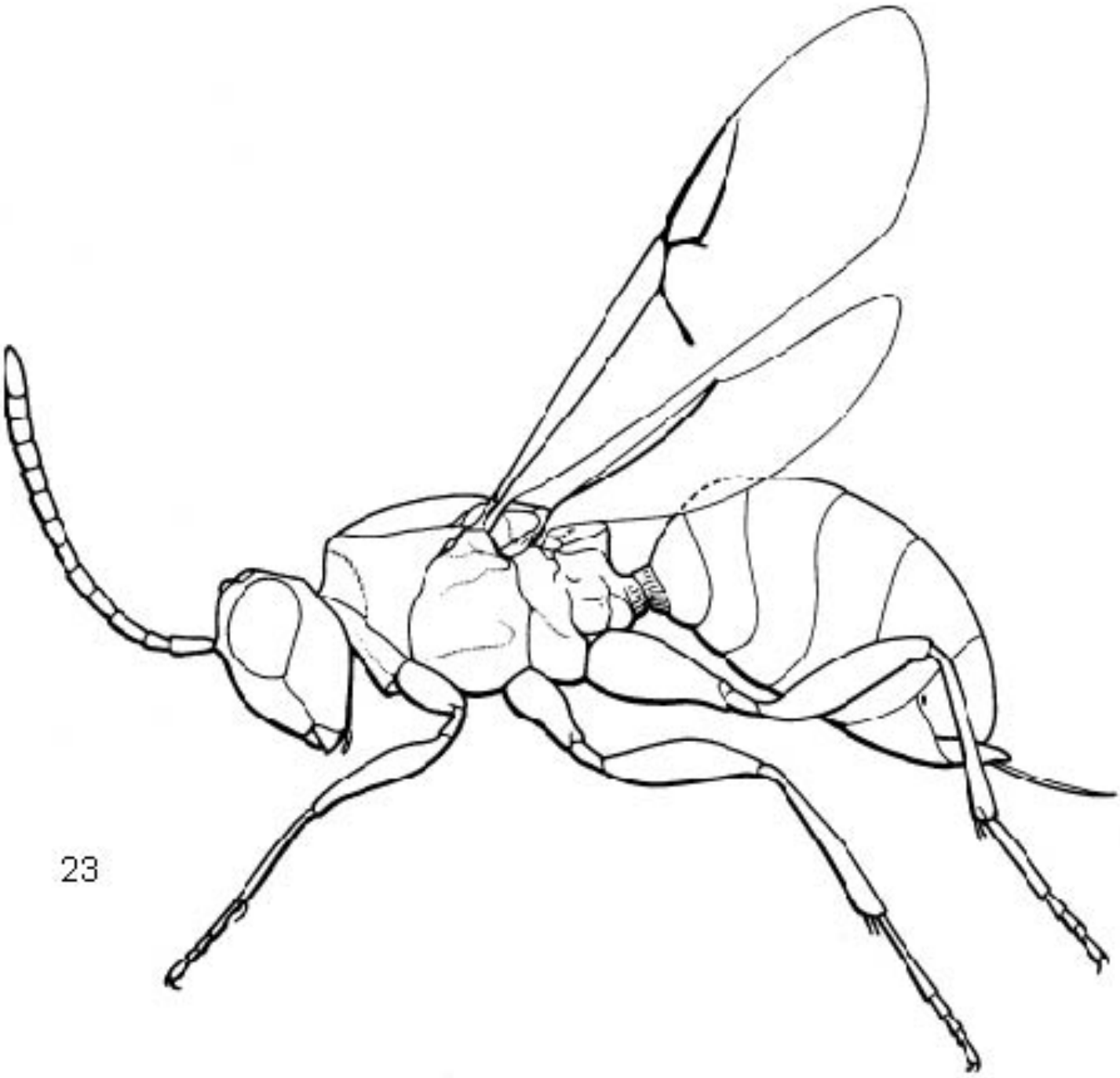

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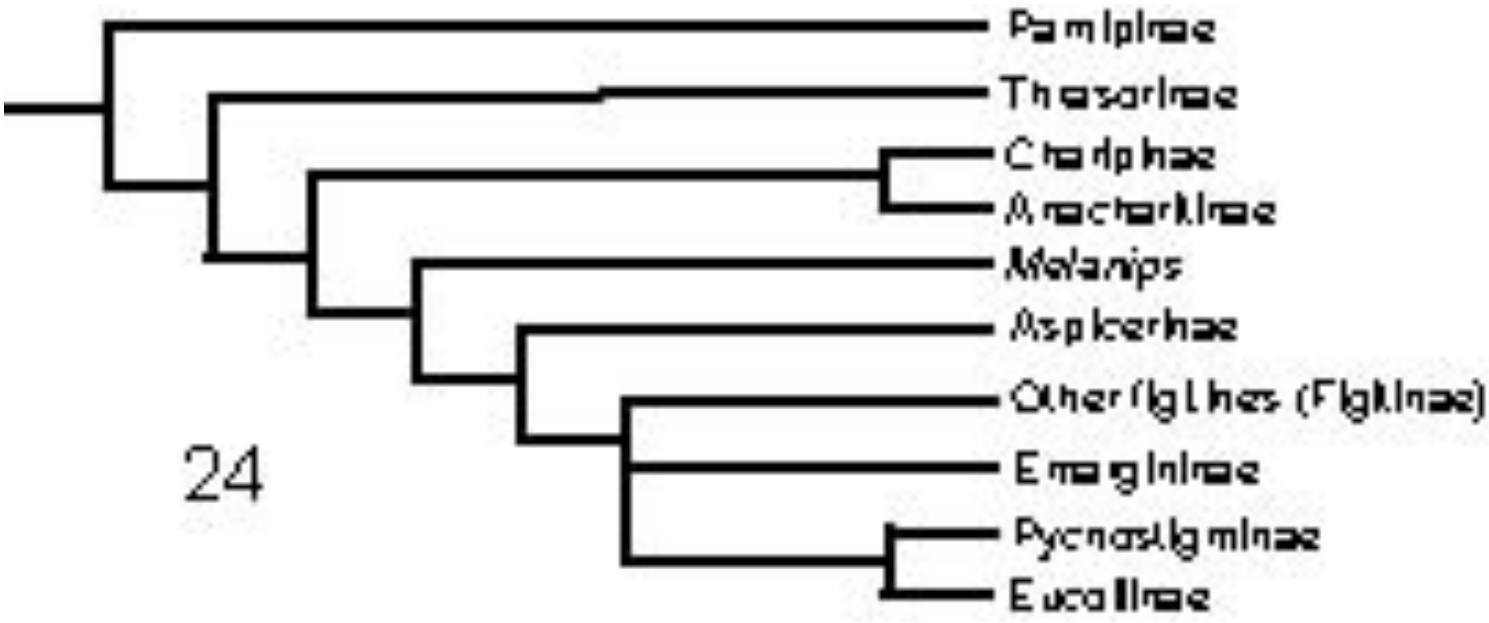
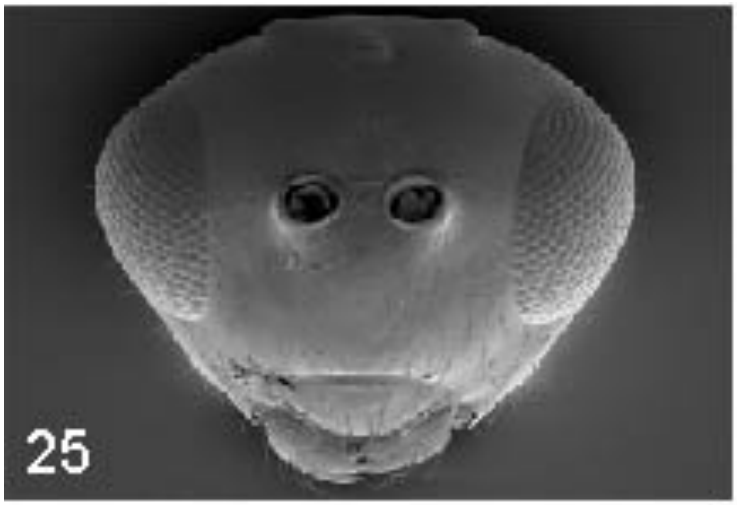

Pamipinae
Thrasorinae
Charipinae
Anacharitinae
Melanips
Aspicerinae
Other figitines (Figitinae)
Emargininae
Pycnostigminae
Eucoilinae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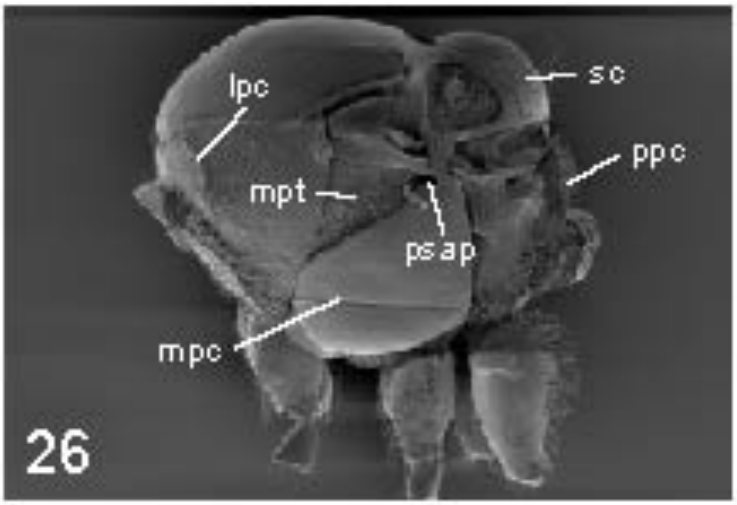
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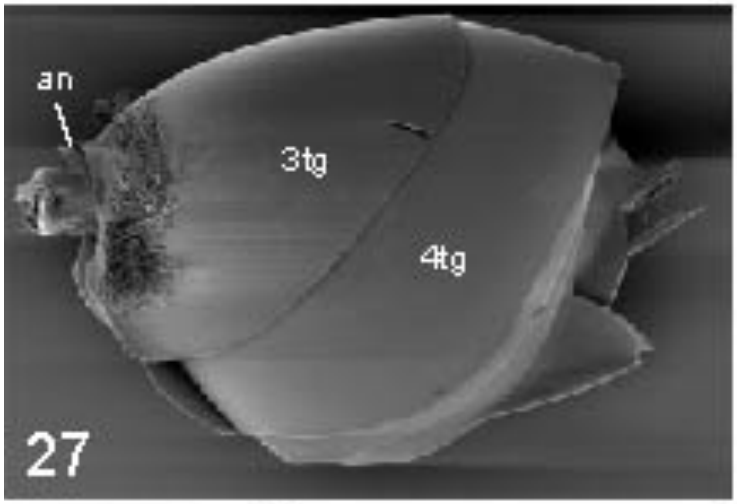
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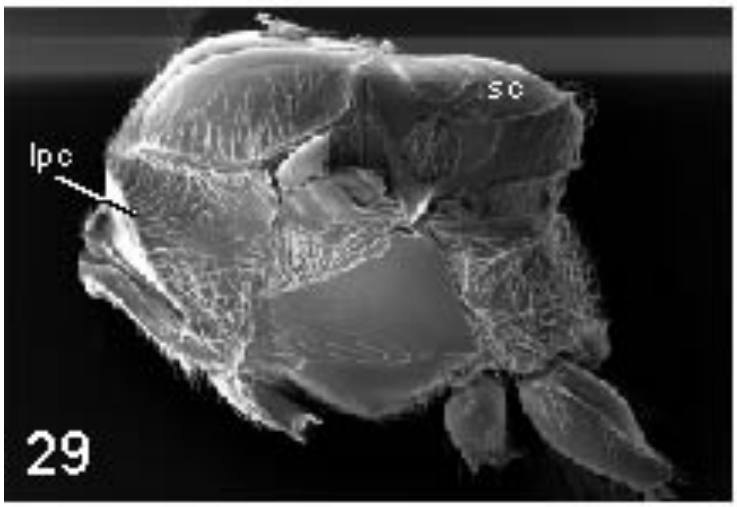
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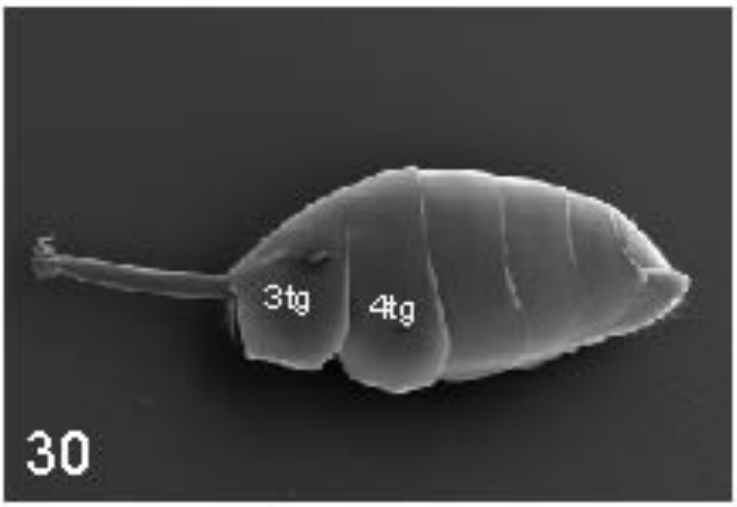
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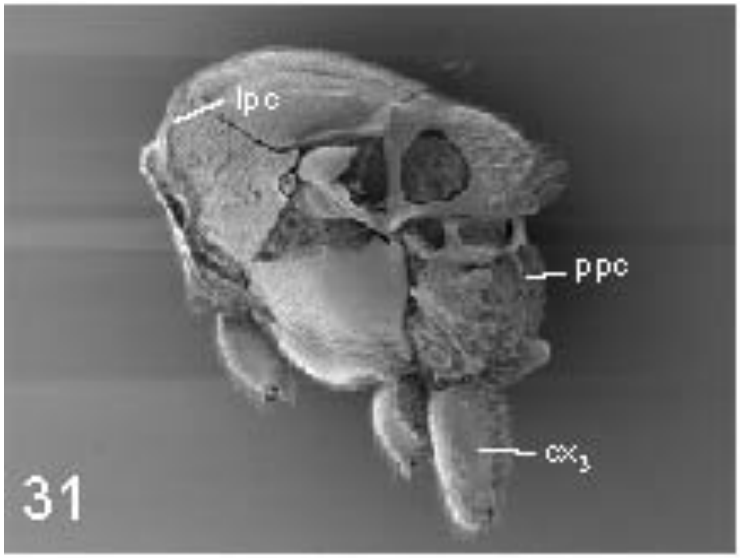
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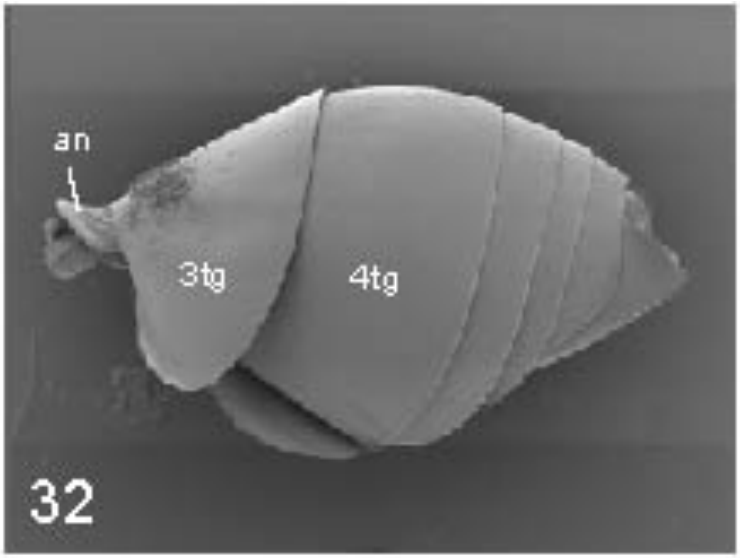
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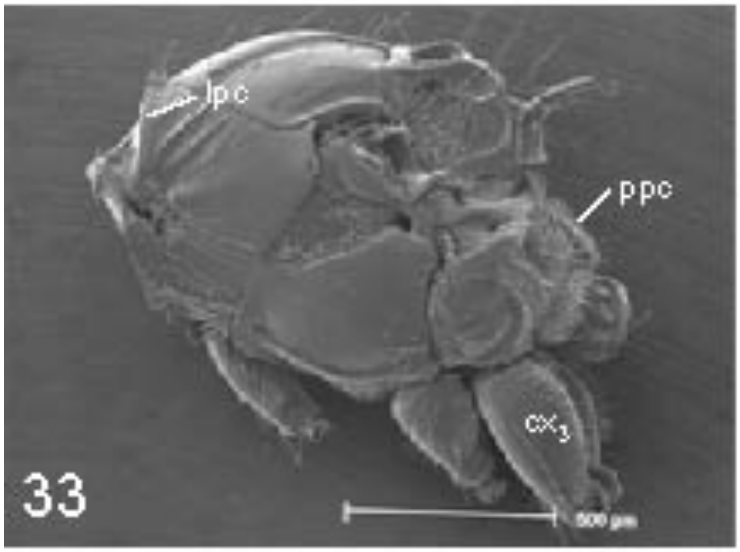
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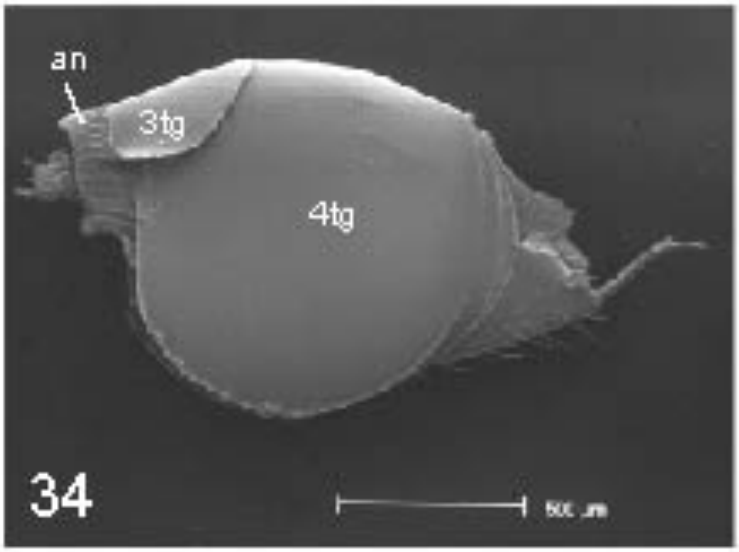
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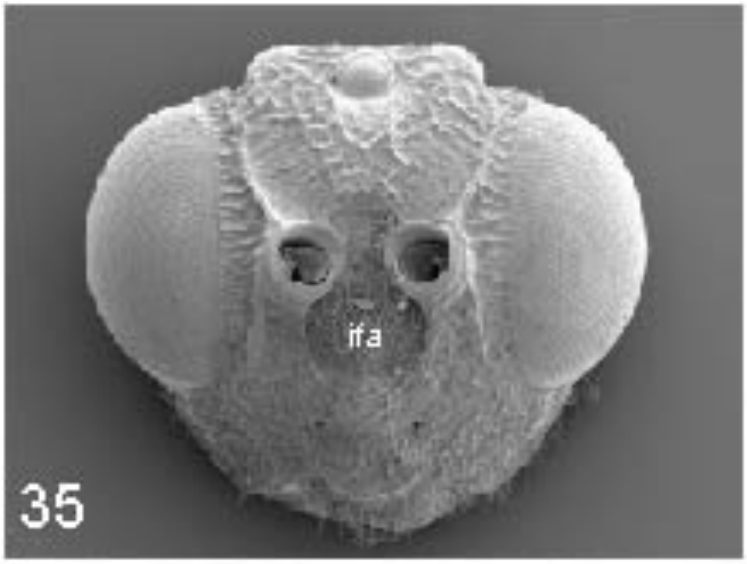
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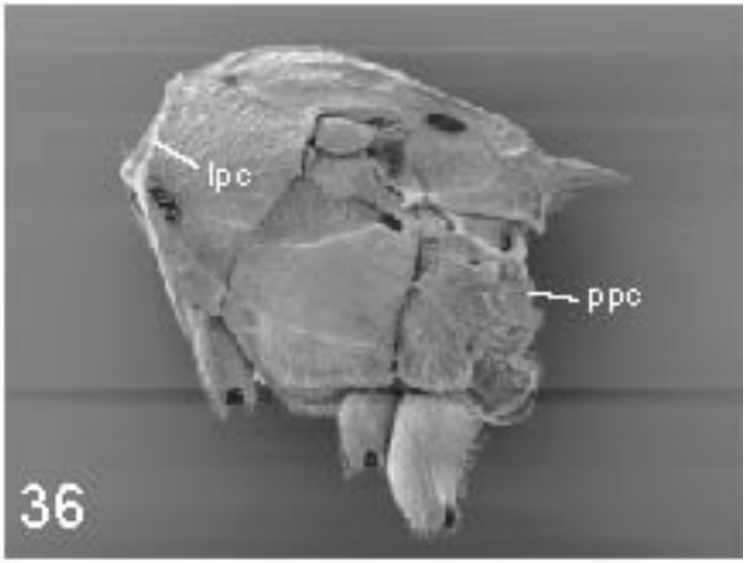
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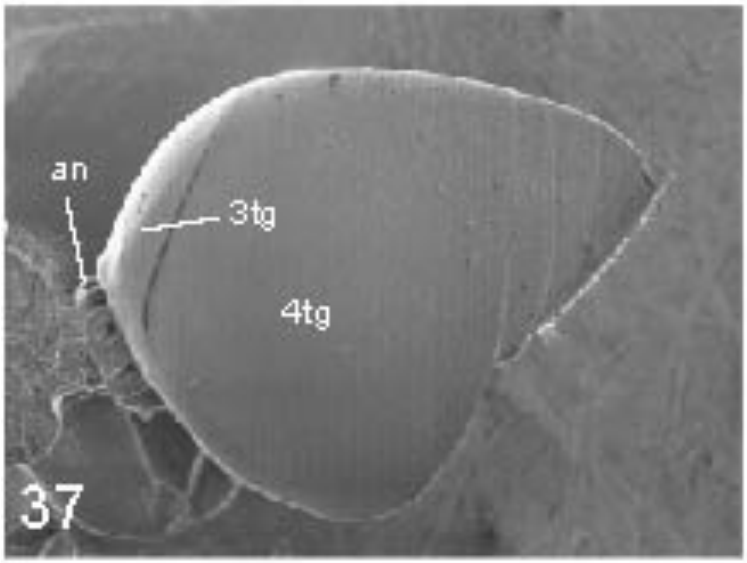
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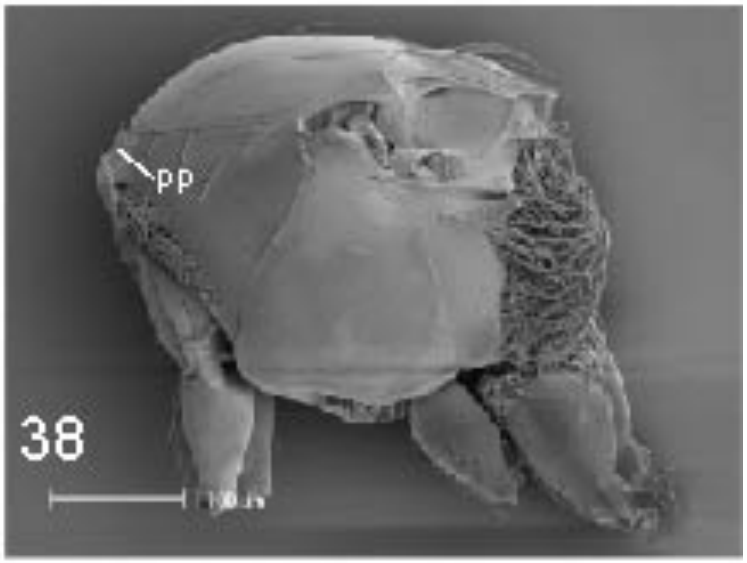
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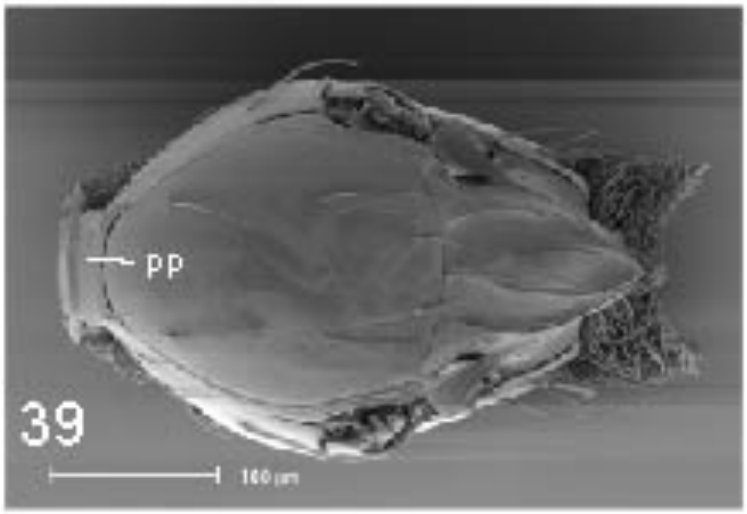
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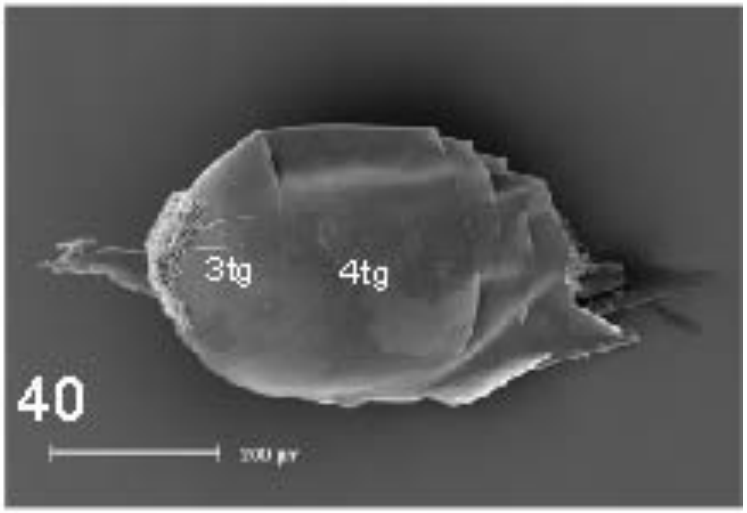
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of
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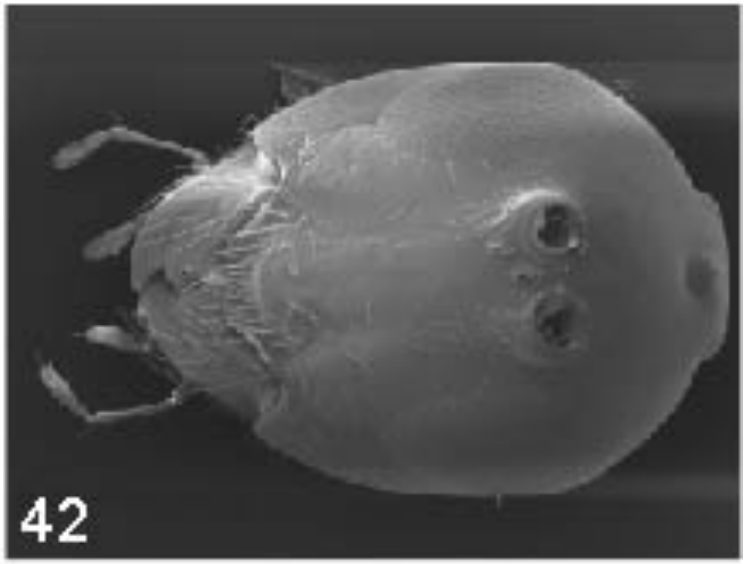
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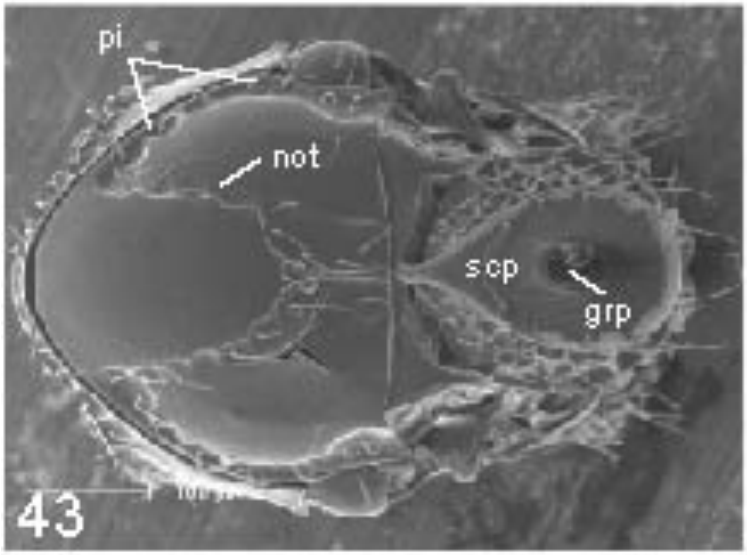
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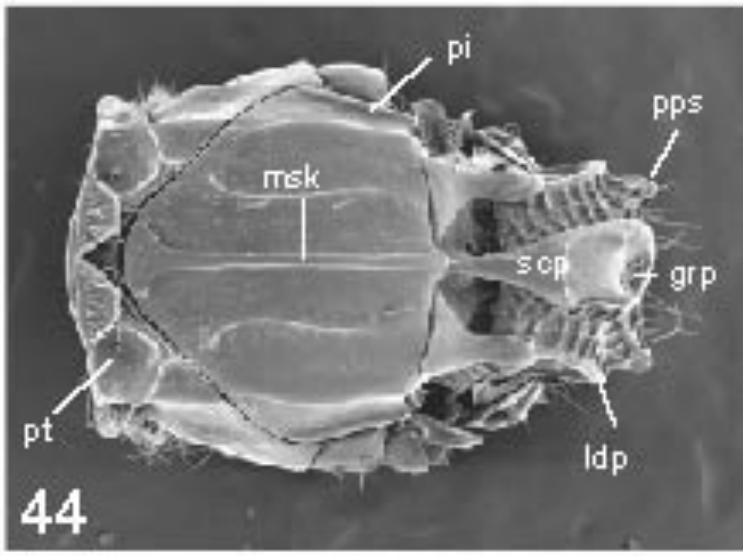
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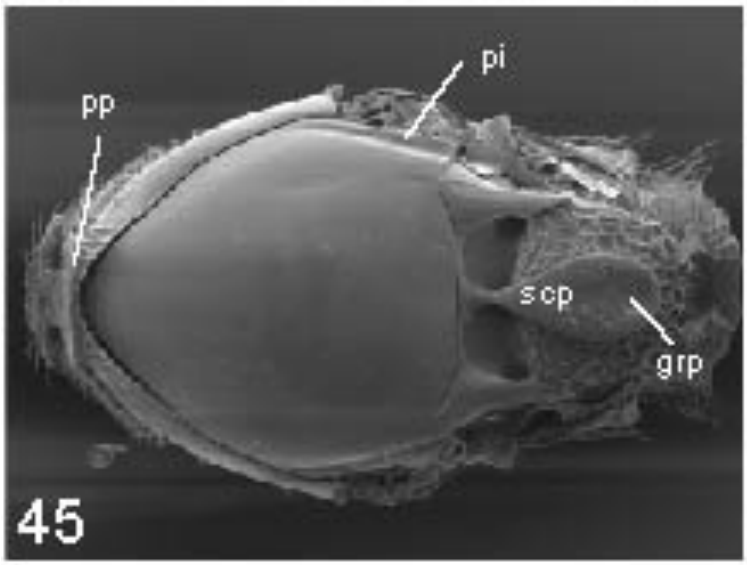
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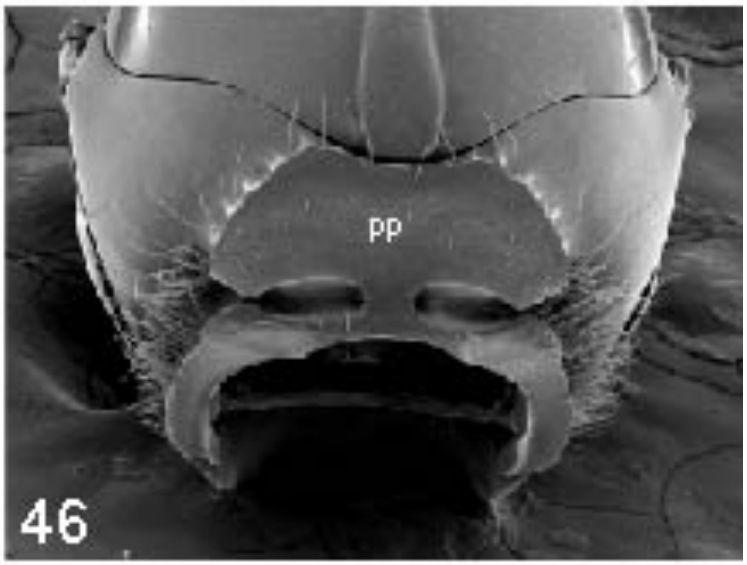
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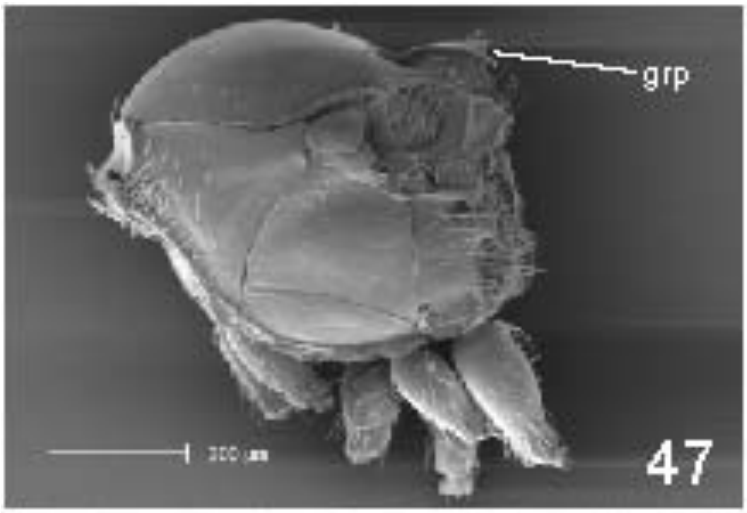
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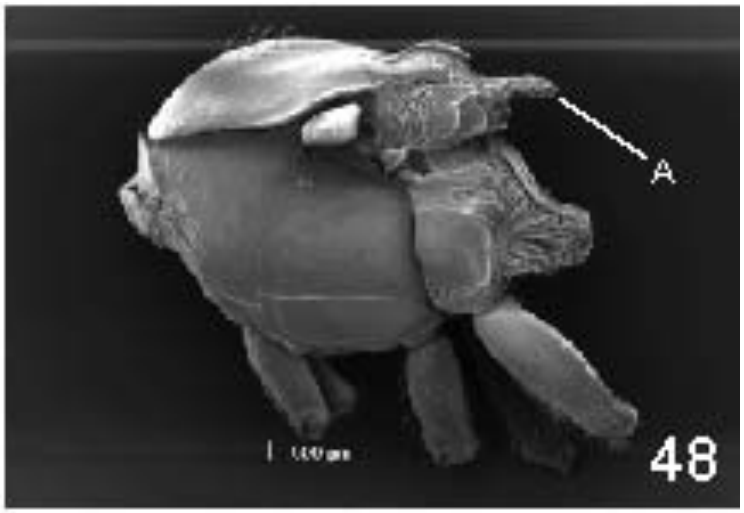
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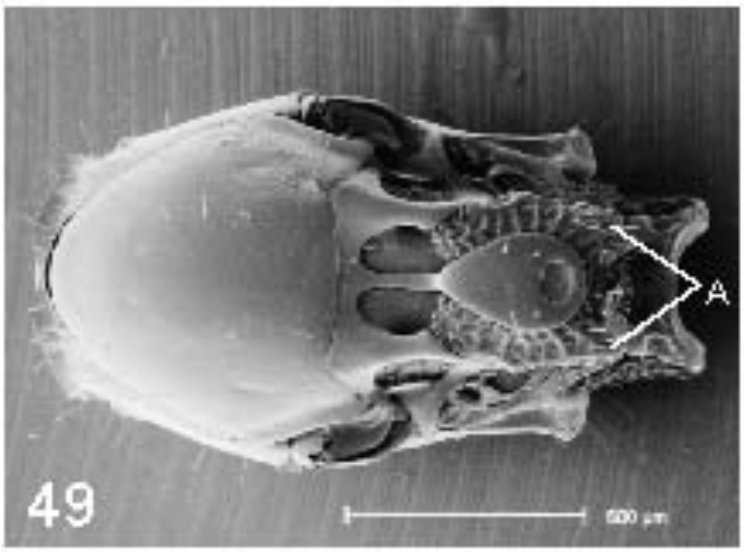
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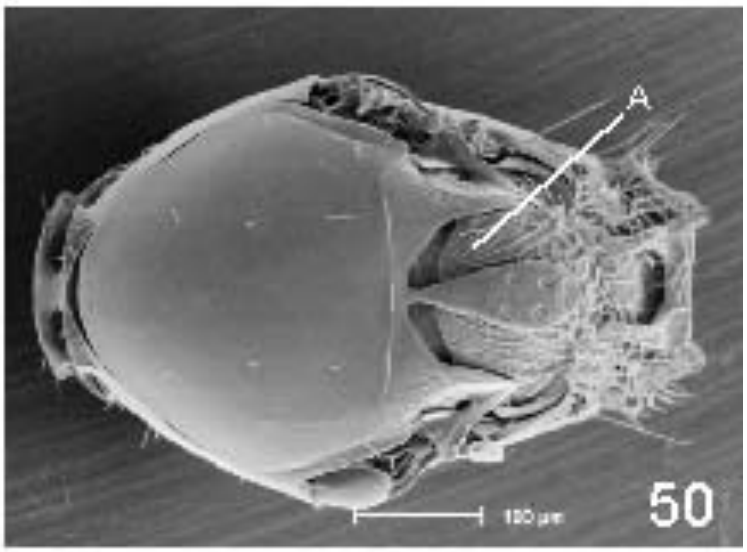
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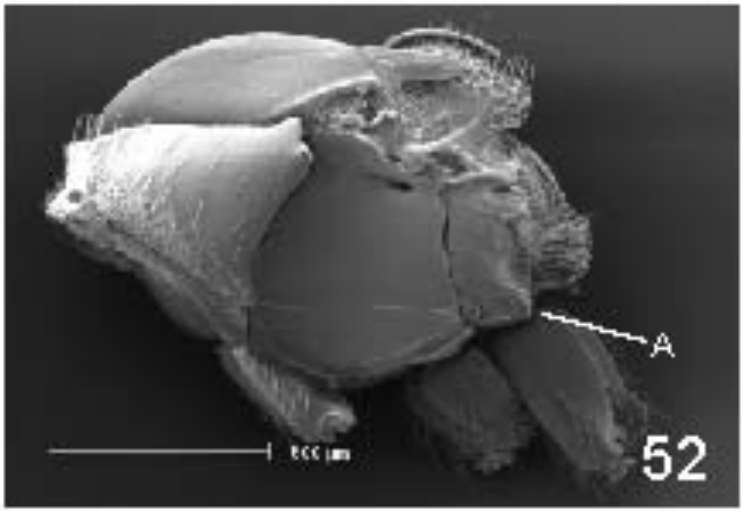
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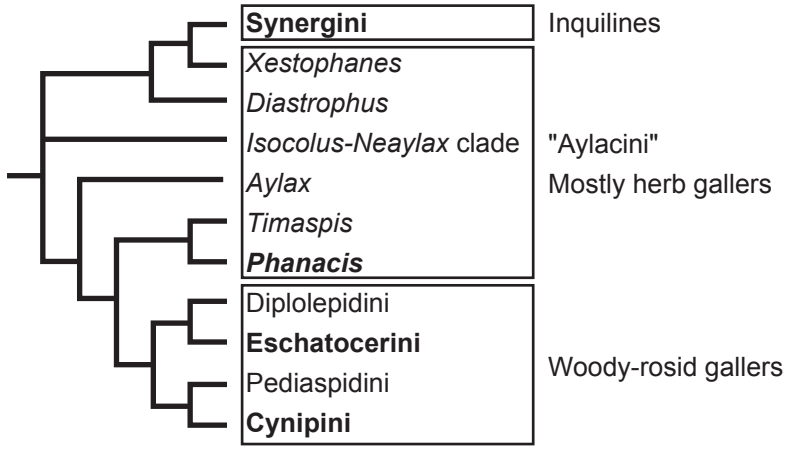
Synergini
Inquilines
Xestophanes
Diastrophus
Isocolus-Neaylax clade
"Aylacini"
Aylax
Mostly herb gallers
Timaspis
Phanacis
Diplolepidini
Eschatocerini
Pediaspidini
Woody-rosid gallers
Cynipini

Fig. 53