Phylogeny, classification and evolution of the Cynipoidea

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I review cynipoid phylogeny and evolution and present an improved higher classification of the superfamily, including the proposal of some nomenclatural changes at the family and genus level. There is convincing morphological evidence for cynipoid monophyly. Relationships with other apocritan wasps are unclear although some characters suggest that diapriids may form their sister group. Cladistic analysis based on adult morphology indicates that cynipoids fall into five monophyletic lineages arranged in a Hennigian comb or ladder: (Austrocynipidae (Ibaliidae (Liopteridae (Figitidae sensu lato, Cynipidae)))). The three first families comprise the macrocynipoids, the two latter the microcynipoids. Relationships among macrocynipoids have been analysed down to the genus or species level and considerable attention has been paid to their historical biogeography. In the microcynipoids, comprising the bulk of cynipoid diversity, phylogenetic research has focused on the gall wasps (Cynipidae). Higher-level relationships are well studied and this allows reconstruction of the early evolution of the gall wasp-host plant association and the origin of the inquilines. The Figitidae are by far the least known cynipoid family and their classification is chaotic; here, I present a first attempt at a cladistic analysis of their higher-level relationships. Biogeographic and fossil evidence, as well as a morphological clock estimate, suggest that the cynipoid crown-group initially diverged in the Jurassic but the earliest cynipoid fossils are from the mid Cretaceous. Existing cynipoid fossils are here tentatively placed in a phylogenetic context but explicit cladistic analysis is likely to shed more light on their exact relationships. Current phylogenetic estimates suggest that cynipoids went through three successive phases in their early evolution, each leaving a set of surviving lineages: first in the community of wood-boring insects, then in the gall community, and finally in the aphid community. The parasitic cynipoids have apparently shifted only four times between hosts in different insect orders, demonstrating extreme conservatism in host association as might be expected of koinobiont endoparasites.

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Introduction

Commonly mentioned diagnostic features of cynipoids include their small size, the characteristically reduced forewing venation, and the laterally compressed, short and rounded metasoma. However, there is considerable morphological variation in the superfamily. Broadly speaking, cynipoids fall into two groups: macrocynipoids and microcynipoids (Ronquist 1995b). Macrocynipoids are usually relatively large insects that are parasitoids of wood-boring or cone-boring insect larvae (Fig. 1A). When the host is consumed, the larva pupates inside the hard substrate and the adult insect chews its way out. For this reason, macrocynipoid adults have a number of adaptations for boring in wood, such as strongly sclerotized mandibles,

transversely ridged mesoscutum, distinct transverse pronotal crest and elongate body (Ronquist & Nordlander 1989). Many species also have legs with distinct processes, which apparently serve to brace the insect against the tunnel walls while it forces the mandibles into the wood at the end of the tunnel. Foveate or ridged sculpture, giving the sclerites extra strength, is common (Ronquist 1995a). Microcynipoids are smaller insects. With few exceptions, they are gall inhabitants or parasitoids of larvae living in soft substrates and lack the distinct modifications for making tunnels in wood. The mesosoma is characteristically high and compact and the metasoma is short and rounded, giving the insect a peculiar habitus (Fig. 1B). Microcynipoids constitute more than 90% of all cynipoid
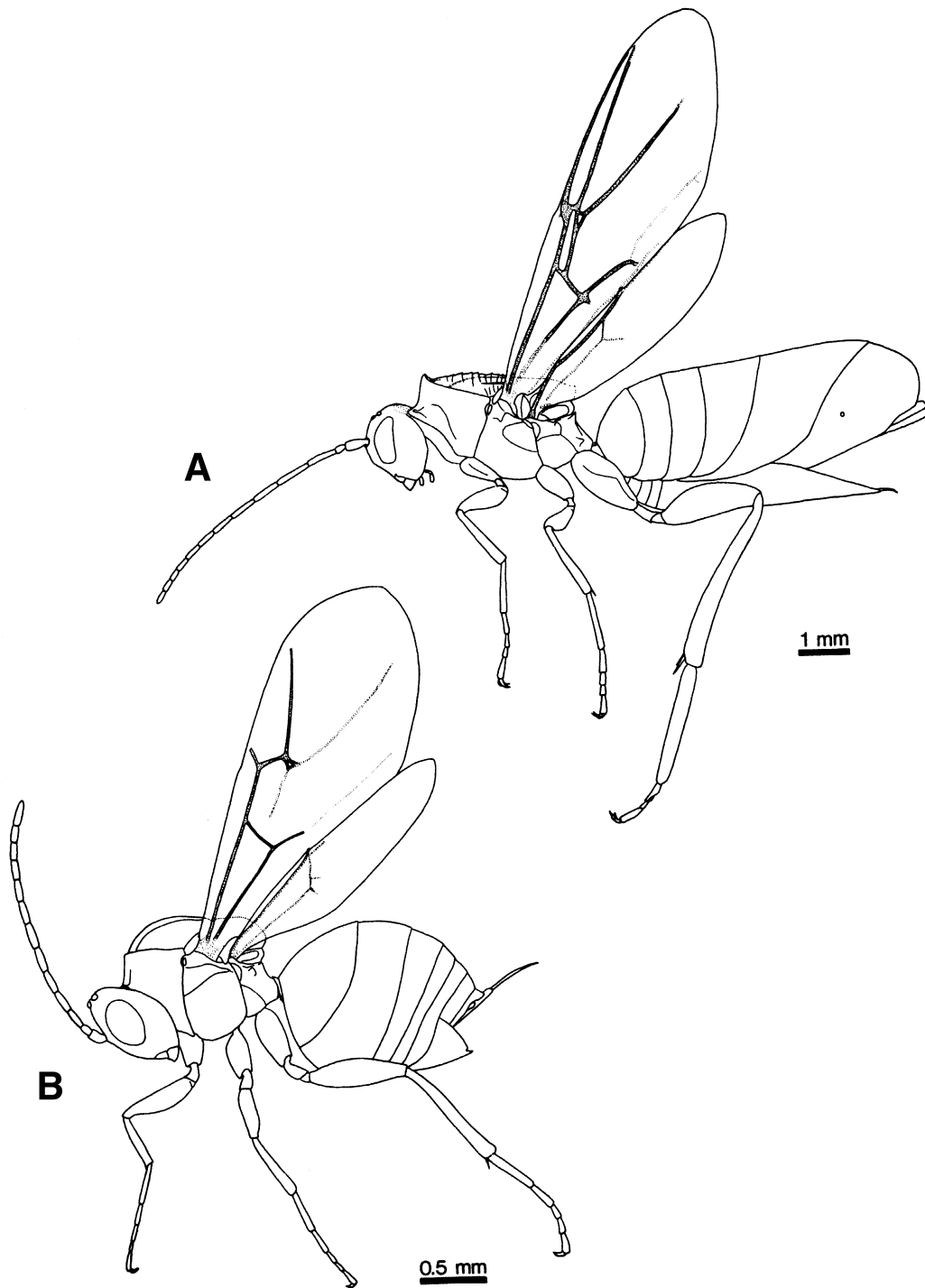
Fig. 1 Habitus drawings. —*A*. A macrocynipoid (Ibaliidae: *Ibalia rufipes*). —*B*. A microcynipoid (Cynipidae: *Isocolus rogenhoferi*). From Ronquist (1995b).

Table 1 Overview of the diversity of extant cynipoids. Largely based on Ronquist (1995b) and Liljeblad and Ronquist (1998).

Taxon	Genera	Species	Biology
AUSTROCYNIPIDAE	1	1	Parasitoids of oecophorid moth larvae tunnelling in *Araucaria* cones
IBALIIDAE	3	20	Parasitoids of siricid larvae in wood
LIOPTERIDAE	10	170	Parasitoids of buprestid, cerambycid and curculionid beetle larvae in wood
CYNIPIDAE			
Synergini	7	171	Phytophagous inquilines in galls of other cynipids
'Aylacini'	21	156	Gallers on eudicot herbs, one genus also on *Smilax* vines and *Rubus* bushes
Diplolepidini	2	63	Gallers on *Rosa*
Eschatocerini	1	3	Gallers on *Acacia* and *Prosopis* (Fabaceae)
Pediaspidini	2	2	Gallers on *Acer*
Cynipini	44	974	Gallers on Fagaceae and Nothofagaceae, mostly on *Quercus*
FIGITIDAE			
New subfamily	1	1	Parasitoid of cynipid gall inducer on *Papaver*
Thrasorinae	5	11	Reared from cynipid and chalcidoid galls, probably parasitoids of the gall inducers
Charipinae			
Alloxystini	5	128	Parasitoids of braconid and chalcidoid wasp larvae in aphids
Charipini	2	9	Parasitoids of chalcidoid wasp larvae in psyllids
Anacharitinae	8	63	Parasitoids of aphid-predating larvae of Hemerobiidae and Chrysopidae (Neuroptera)
'Figitinae'	13	138	Parasitoids of larvae of Diptera: Cyclorrhapha in various microhabitats
Aspicerinae	8	99	Parasitoids of aphid-predating larvae of Syrphidae and Chamaemyiidae (Diptera: Cyclorrhapha)
Emargininae	5	15	Associated with ants, probably parasitoids of Diptera larvae in ant nests or refuse deposits
Pycnostigminae	3	3	Biology unknown, presumably parasitoids of Diptera larvae
Eucoilinae	82	944	Parasitoids of Diptera: Cyclorrhapha
TOTAL	223	2971	

species (Table 1) and many supposedly diagnostic cynipoid features, such as the small size and the short metasoma, are actually microcynipoid features.

All macrocynipoids and the majority of microcynipoid species are parasitic on endopterygote insect larvae (Table 1). For the parasitic microcynipoids, the host records are restricted to larvae in the orders Hymenoptera, Diptera and Neuroptera, with the bulk of species being Diptera parasites. Macrocynipoids have been recorded as parasites of Lepidoptera, Hymenoptera, and Coleoptera larvae (Ronquist 1995b). All parasitic cynipoids have a similar life history (Haviland 1921; James 1928; Chrystal 1930; Huzimatu 1940; Wishart & Monteith 1954; Spradbery 1970; Rotheray 1979; Miller & Lambdin 1985). The egg is deposited inside a well-developed host embryo or a host larva, often a young larva. The cynipoid larva is initially a koinobiont endoparasitoid (living inside the host larva without halting normal activity and development of the latter), but eventually exits the moribund host and spends the last one or two instars feeding externally on the host remains.

The phytophagous gall wasps belong to the microcynipoids and include both gall inducers and inquilines (Table 1). The gall inducers form galls, inside which the larvae develop. The galls range from simple to complex and are induced on a variety of host plants, ranging from herbs to woody plants such as roses and oaks. The inquilines also have phytophagous larvae but cannot initiate gall formation on their own. Instead, their larvae develop inside the galls induced by other gall wasps (Ronquist 1994 and references cited therein).

For some years, the Cynipoidea have been subject to intense phylogenetic research based on morphological characters of adults. Here, I summarize this research and present a first analysis of the higher phylogeny of the Figitidae *sensu lato*, the only major cynipoid group that has not yet been treated cladistically. I also discuss the phylogenetic position of the described fossils and summarize research on the historical biogeography of cynipoids. Based on the best current estimate of higher cynipoid phylogeny, I propose an improved family and subfamily classification, including some nomenclatural changes at the family and genus level (Appendix). Finally, I briefly discuss some evolutionary implications of higher cynipoid relationships.

Monophyly of the Cynipoidea

There are no striking autapomorphies of the Cynipoidea but the superfamily has long been assumed to be a natural group and morphological evidence for its monophyly is slowly accumulating. I summarize the known autapomorphies below, including a discussion of all previously

proposed characters and some new ones. Although several of the commonly mentioned cynipoid autapomorphies are uncertain or have to be dismissed for various reasons, the first five characters or character complexes listed below together convincingly demonstrate cynipoid monophyly. In addition, a recent molecular analysis (of 16S mtDNA) of nonaculeate apocritan relationships strongly supported monophyly of the Cynipoidea, the superfamily being represented by one microcynipoid (a figitid) and one macrocynipoid (an ibaliid) (Dowton *et al.* 1997).

Cynipoid autapomorphies

1   Radicle absent (Ronquist 1995b: Fig. 3). All hymenopterans except cynipoids have a basal region, the radicle, distinctly differentiated from the rest of the scape. The lack of a radicle in cynipoids is unique within the Hymenoptera.

2   Media (M) of fore wing displaced anteriorly, approaching the posterior end of the marginal cell, distinctly angled and not running parallel to the posterior wing margin (Ronquist 1995b). Some ichneumonoids and formicids have the M vein slightly displaced anteriorly but the extreme displacement in cynipoids is unique in the Hymenoptera. The M vein is absent in many smaller parasitic wasps, but for each major group (Chalcidoidea, Platygastroidea, Ceraphronoidea) there are at least a few representatives with a distinct M vein and all of these have the M vein running in the posterior part of the wing, parallel to the posterior wing margin. The small areolet and broad costal cell, listed as putative cynipoid autapomorphies by Königsmann (1978), may be understood as consequences of the anterior displacement of M.

3   Abdominal sternum 2 (petiolar) and 3 (first postpetiolar) abutting or fused (new character). Other hymenopteran families or superfamilies have, in their ground plans, the anterior end of the postpetiolar sternum telescoped inside the posterior part of the petiolar sternum, just like the remaining abdominal sterna and terga are telescoped into each other. The only known exception among parasitic wasps is found in the Proctotrupidae (including Vanhorniidae), in which the second and third sterna form part of a synsternum (Mason 1983; Naumann & Masner 1985), but this is unlikely to be homologous with the cynipoid state if proctotrupids are the sister group of pelecinids (with normal third sternum; Mason 1984). The state of this character has not been examined in platygastroids and ceraphronoids.

4   Metasoma distinctly laterally compressed (Königsmann 1978). Many other parasitic wasps have the metasoma laterally compressed but it is only the evaniids, austroniids and possibly also roproniids (depending on the inclusion or exclusion of *Renyxa* and some fossil forms) among superfamilies/families of parasitic wasps that are likely to have this character state in their ground plans.

5   Fore wing costa absent (Königsmann 1978). This is likely to be a cynipoid autapomorphy, although the costa is also absent in the ground plan of the Mymarommatidae + Chalcidoidea among parasitic wasps.

6   Venom gland unbranched (new character, D. L. J. Quicke, personal communication). Cynipoids are unusual among parasitic wasps in having an unbranched venom gland, a character state which appears to be associated with having a laterally compressed metasoma (Quicke *et al.* 1997). The structure of the venom gland has so far been described only for a few cynipoids (Frühauf 1924; Rizki & Rizki 1990) and venom gland morphology has not yet been comprehensively surveyed in other groups of parasitic wasps. Thus, this remains a promising but uncertain putative autapomorphy of the Cynipoidea.

7   Markedly developed scutellum (Königsmann 1978). The scutellum is more prominent in cynipoids than in most other apocritan wasps, and this feature may well be a good cynipoid autapomorphy. However, more detailed comparative studies of the apocritan scutellum, particularly with respect to internal anatomy, are needed to demonstrate that the cynipoid character state is apomorphic within the Apocrita.

Doubtful or erroneous cynipoid autapomorphies

1   Pterostigma absent (Königsmann 1978; Rasnitsyn 1988). Königsmann and Rasnitsyn were unaware of the description of *Austrocynips mirabilis*, a macrocynipoid with a true pterostigma (Riek 1971; Ronquist 1995b). Although loss of the pterostigma cannot thus be a cynipoid autapomorphy, it still holds as a putative synapomorphy of cynipoids excluding *Austrocynips*. There are other groups of parasitic wasps that lack a distinct pterostigma but the manner of reduction is different (Ronquist 1995b). In cynipoids excluding *Austrocynips*, the stigma has been reduced by lateral compression to a crossvein-like portion of the R_1 vein. Reduction of the stigma in other parasitic wasps has proceeded through anteroposterior compression, initially leaving a longitudinal, vein-like remnant along the anterior margin of the wing.

2   Antennal formula 13 : 14 (number of antennal articles of female antenna: male antenna) (Königsmann 1978). The antennal formula 13 : 14 (or possibly 13 : 15) is unusual among parasitic wasps but is likely to be the

ground-plan state in cynipoids excluding *Austrocynips* (Ronquist 1995b). However, *Austrocynips* females have 15 antennal articles (males unknown). Thus, it is possible that cynipoids including *Austrocynips* have the antennal formula 15 : 14 in their ground plan, just like monomachids, austroniids and diapriids.

3   Antennae having longitudinal placodeal sensilla (Rasnitsyn 1988). Placodeal antennal sensilla are common among apocritan wasps, and even longitudinal placodeal sensilla occur in some groups, notably ichneumonoids and chalcidoids (Basibuyuk & Quicke 1999). However, there are some structural differences among these taxa suggesting that the particular type of elongate placodeal sensilla in cynipoids may be independently derived (Gibson 1986). In *Austrocynips*, the placodeal sensilla are not distinctly defined, unlike the placodeal sensilla of other cynipoids (Ronquist 1995b). If *Austrocynips* is the sister group of other cynipoids, as indicated by many morphological characters, this may suggest an intermediate stage in a transformation series from antennae lacking distinctly defined elongate plate sensilla to having sensilla of the Cynipoidea type. Nonetheless, it is impossible to dismiss the alternative hypotheses that the cynipoid sensilla represent a retained plesiomorphy or form an intermediate stage in a more complex transformation series involving other types of sensilla.

4   Median mesoscutal line re-established (Rasnitsyn 1988). The alternative hypothesis of retained plesiomorphy cannot be dismissed.

5   Fore wing with $R_s + M$ and 2r-m re-established as nebulous veins from spectral precursors (Rasnitsyn 1988). The alternative hypothesis of retained plesiomorphy cannot be dismissed.

6   Reduction of the basal ring of the femur (Königsmann 1978). This character does not hold as a cynipoid autapomorphy (Ronquist *et al.* 1999).

Relationships between cynipoids and other parasitic wasps

Königsmann (1978) provided two putative synapomorphies in support of a sister-group relationship between chalcidoids and cynipoids: absence of cuspis in the male genitalia and the third valvulae being continuous with the second valvifer rather than separate. However, the presence of a distinct (albeit reduced) cuspis in *Ibalia* (Ronquist & Nordlander 1989) indicates that cynipoids have the cuspis present in their ground plans. Furthermore, the cuspis has been reduced or lost in the ground plan of many groups of parasitic wasps in addition to chalcidoids and cynipoids (Gibson 1986). Thus, reduction of the cuspis does not provide evidence of cynipoid + chalcidoid monophyly. The

ovipositor character has not yet been comprehensively surveyed among parasitic wasps and its status is therefore uncertain. Nevertheless, there is little compelling evidence that cynipoids and chalcidoids are closely related, particularly considering the major differences between these groups in a suite of mesosomal characters (Gibson 1986).

Rasnitsyn (1988) proposed a sister-group relationship between cynipoids and diapriids based on the following characters: (1) basal flagellar segments of male modified; (2) pronotum short medially, immovably connected with mesopleuron; (3) prepectus fused with pronotum forming internal pronotal inflection; (4) fore wing lacking tubular veins except those closing costal, basal and radial cells; (5) hind wing lacking tubular veins except those closing basal cell and R beyond basal cell; (6) hind-wing M(+ Cu) and r-m concave from above.

Most of these characters are problematic. A triangular pronotum rigidly attached to the mesopleuron (char. 2) occurs in the majority of parasitic wasps and a prepectus forming a posterior pronotal inflection (char. 3) is common among parasitic wasps (Gibson 1986). Reduced wing venation (chars. 4 and 5) also occurs in many groups of parasitic wasps and does not provide convincing evidence of cynipoid + diapriid monophyly.

The remaining two characters, however, are more difficult to refute. The concavity of the hind-wing vein M(+ Cu) is unique for the Cynipoidea and Diapriidae among major groups of nonaculeate apocritans and the vein is completely absent, making the state unknown, only in mymarommatids (Ronquist *et al.* 1999; Ronquist, unpublished data). Other hymenopterans have all longitudinal wing veins convex both in the fore and in the hind wing.

The male flagellar modification of diapriids and cynipoids consists of a ridge and an excavation of one or more of the basal flagellomeres. Both the ridge and the excavated surface are perforated with pores connected to an internal gland producing chemicals that are smeared onto the female antenna during courtship (Ronquist & Nordlander 1989; Ronquist 1995b; Isidoro *et al.* 1996; Isidoro *et al.* 1999). Male antennal glands occur in a variety of other parasitic wasps (Naumann & Masner 1985; Isidoro *et al.* 1996) but the external morphology and position of the gland-bearing articles is unique to cynipoids and diapriids. Unfortunately, there is some uncertainty concerning the ground-plan structure of the Cynipoidea because males are unknown for two of the most basal cynipoid lineages (i.e. *Austrocynips* and *Eileenella*; cf. Fig. 3).

There are no known putative synapomorphies that link cynipoids (and possibly diapriids) strongly with other groups of parasitic wasps. Cynipoids and diapriids are similar to monomachids and austroniids in the sexual

dimorphism in the number of flagellomeres (Rasnitsyn 1988), a possibly unique character among the nonaculeate apocritans. However, austroniids and monomachids have a prepectal and pronotal structure that is apparently more primitive than that found in diapriids, cynipoids and most other parasitic wasps. Parasitism of Diptera has been suggested as a synapomorphy of diapriids + monomachids + cynipoids (Rasnitsyn 1988) but dipterans are unlikely to be the primitive hosts of the Cynipoidea (see below). Cynipoids share a number of derived characters with a large portion of the nonaculeate apocritans, such as the absence of functional spiracles on abdominal segments 2-7, the presence of a posterior pronotal inflection, and the larvae being endoparasitic in early instars (Ronquist *et al.* 1999). Cynipoids also have a number of unusual features that are apparently plesiomorphic in the Apocrita, including the presence of some thoracic muscles that have been lost in most other groups (Gibson 1985).

Despite the two putative synapomorphies, the Cynipoidea and Diapriidae appeared as a monophyletic group only in some of the most parsimonious trees in the first morphology-based analysis of higher relationships among nonaculeate apocritans (Ronquist *et al.* 1999), stressing the existence of conflicting evidence. A recent molecular analysis (Dowton *et al.* 1997) placed the Cynipoidea as the sister group of all other apocritans, including diapriids, but the support for this placement was not convincing.

Higher cynipoid phylogeny

I have previously (Ronquist 1995b) surveyed cynipoid diversity, identified putative major lineages and analysed relationships among them based on external skeletal characters of adults. I concluded that the microcynipoids are monophyletic and fall into two monophyletic sister lineages, the phytophagous Cynipidae and the parasitic Figitidae (*sensu lato*), and that the macrocynipoids form a basal paraphyletic grade falling into three lineages, the Austrocynipidae (with a single species, *Austrocynips mirabilis*), Ibaliidae, and Liopteridae (Fig. 2A). Evidence is particularly strong for the sister-group relationship between *Austrocynips* and other cynipoids, the latter being supported as a monophyletic group by characters such as the loss of the pterostigma, the presence of a distinctly impressed mesopleural triangle, and the presence of the posterior subalar pit. The monophyly of the microcynipoids is also convincingly supported; the synapomorphies include meso- and metacoxae directed downwards instead of obliquely backwards, dorsal pronotal area absent, anterior pronotal flange short, head not distinctly impressed posteriorly, and transverse mesoscutal sculpture absent.

Of the five major cynipoid lineages I identified, the Figitidae *sensu lato* is the only one whose monophyly is contro-
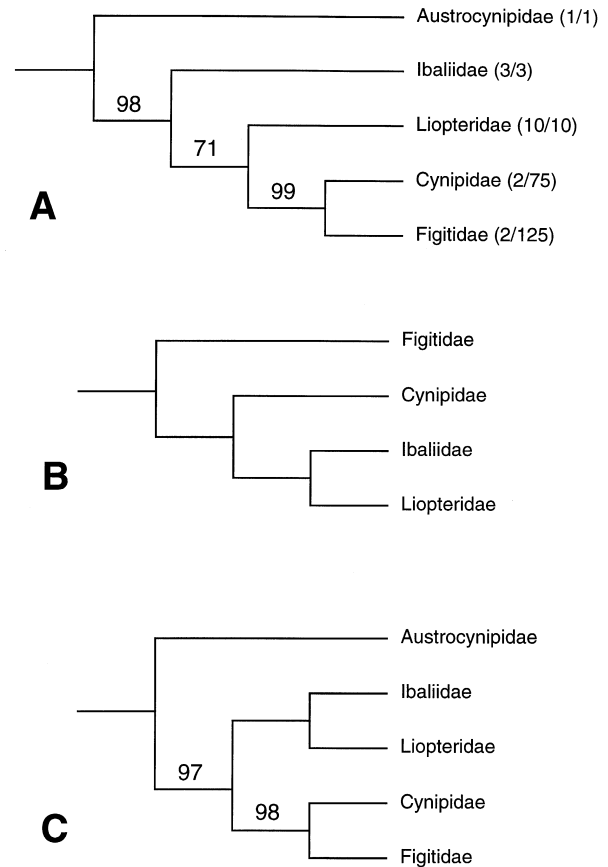

Fig. 2 Relationships among major cynipoid lineages. —*A.* According to analysis of Ronquist (1995b) based on 59 informative characters of external skeletal morphology. Numbers in parentheses are the number of genera studied for each family/the total number of genera in the family. —*B.* Phylogenetic hypothesis proposed by Rasnitsyn (1988). —*C.* One of two equally parsimonious trees (the other one is the tree shown in *A*) resulting from analysis of a modified matrix with characters coded in favour of Rasnitsyn's hypothesis (see text). Numbers on branches are bootstrap support values (as percentages) based on 1000 replications of branch-and-bound searches (published values for tree in *A*, original values for tree in *C*; only values above 50% given).

versial. However, my concept of the family agrees fully with that of Rasnitsyn (1980) both in the inclusion of three taxa of parasitic microcynipoids that are often treated by other authors as separate families (the Charipinae, Eucoilinae, and Anacharitinae) and in the inclusion of the Pycnostigminae, a poorly studied group with unknown biology, considered by all other workers to belong to the Cynipidae. I have slightly expanded Rasnitsyn's concept by transferring some gall-associated taxa from the Cynipidae to the Figitidae and loosely grouped them with other gall-inhabiting figitids under the name 'figitoid inquilines' (Ronquist 1994). The biology of the figitoid inquilines was unknown until recently, when it was shown that '*Aulacidea*'

nigripes is a parasite of a gall-inducing cynipid (Ronquist and J. L. Nieves-Aldrey, unpublished data).

My analysis (Ronquist 1995b) was based on 59 characters informative about relationships among cynipoid families and most interfamily relationships were strongly supported by the data as indicated by bootstrap support values (Fig. 2A). The characters were coded for a comprehensive sample of macrocynipoid species, including representatives of all genera, but only for four microcynipoid species representing two figitid and two cynipid genera. Thus, the analysis may be criticised for poor taxon sampling among microcynipoids. Monophyly of the phytophagous Cynipidae has since been strengthened in a study of cynipid relationships (Liljeblad & Ronquist 1998) but the monophyly the Figitidae *sensu lato* remains to be demonstrated in a formal cladistic analysis including a comprehensive sample of parasitic microcynipoids.

In his analysis of cynipoid relationships, which did not include *Austrocynips*, Rasnitsyn (1980, 1988) suggested that the Figitidae form the most basal lineage of cynipoids and that the Ibaliidae and Liopteridae are sister groups (Fig. 2B). These results were based on only two characters informative about higher cynipoid relationships, one venational and one metasomal feature. In my analysis of cynipoid relationships (Ronquist 1995b), the venational character was interpreted differently and the metasomal character was inadvertently omitted. To test Rasnitsyn's ideas against the other available morphological evidence, I took my character matrix and recoded the venational character according to Rasnitsyn's interpretation and added the metasomal character. I then changed the coding of the character referring to the male antennal ridge from a subsidiary character dependent on the presence of an excavation on the same flagellomere to an independent character. Although the presence of a ridge is strongly correlated with the presence of an excavation in cynipoids, the excavation and the ridge might theoretically evolve independently. Coding them as separate characters is a reasonable alternative coding that might give additional support for Rasnitsyn's grouping of the Liopteridae with the Ibaliidae (although possibly weighting the male antennal modification too strongly). Thus, the changed characters were as follows:

11. [Now independent of excavation on F1, char. 10] Longitudinal ridge on male F1: (0) present; (1) absent. Coded as in Ronquist (1995b), but inapplicable entries changed to 1.

46. [Character interpretation changed] Forewing veins $R_s + M$ and 1 m-cu: (0) basal part of $R_s + M$ absent, apparent $R_s + M$ consisting of $R_s + M$ and 1 m-cu; (1) $R_s + M$ complete, 1 m-cu present; (2) $R_s + M$ complete, 1 m-cu

absent. Coded 1 for hypothetical ancestor, 0 for Figitidae, and 2 for other cynipoids. Ordered 012.

59A. [New character]. Size of metasomal terga 5–7: (0) smaller than preceding terga; (1) larger than preceding terga. Coded 1 for Ibaliidae and Liopteridae, 0 for all other taxa.

The modified matrix represents, in my view, the most favourable coding of the available evidence with respect to Rasnitsyn's phylogenetic hypothesis. I ran the modified matrix with the branch-and-bound algorithm of PAUP 3.1.1 (Swofford 1993). The search resulted in two most parsimonious trees, one identical to that obtained in the original analysis with the unmodified matrix (Fig. 2A), the other one different only in grouping ibaliids with liopterids (Fig. 2C). Successive weighting of the modified matrix invariably resulted in the original tree (Fig. 2A), whether based on maximum values of character consistency indices, retention indices, or rescaled consistency indices. Support for the monophyly of microcynipoids and the sister-group relationship between *Austrocynips* and other cynipoids remained convincing, as indicated by bootstrap values (Fig. 2C). Constraining cynipoids excluding figitids to form a clade required 12 extra steps, a considerable increase over the 60 characters informative about family level relationships in the analysis.

In conclusion, there is a possibility that liopterids and ibaliids form a monophyletic group, as suggested by Rasnitsyn (and commented on by Ronquist 1995b), but current morphological evidence is slightly in favour of the liopterid + microcynipoid grouping (Fig. 2A). The evidence concerning figitid relationships is clearer. Even if figitids are considered unique among cynipoids in retaining the forewing crossvein 1 m-cu, an interpretation I have argued against elsewhere (Ronquist 1995b), the morphological evidence is strongly against a basal position of the Figitidae in the Cynipoidea.

Fergusson (1995) recently presented a revised higher classification of the Cynipoidea differing considerably from mine. For instance, Fergusson suggested that the macrocynipoids are monophyletic and placed the genus *Himalocynips* in a monotypic family. The latter is remarkable considering the large number of morphological features grouping *Himalocynips* with *Pediaspis* deep inside the gall-inducing Cynipidae (Liljeblad & Ronquist 1998) (cf. Fig. 4). Fergusson's classification is apparently backed by 'a phylogenetic reconstruction … robustly supported by morphological, palaeontological, biogeographical and biological evidence' (Fergusson 1995). The phylogenetic evidence has not yet been published except for a few putative synapomorphies supporting the monophyly of macrocynipoids (including *Austrocynips*) (Fergusson 1988, 1992). Parsimony analysis of

all the available morphological evidence, including these characters, suggests that the putative macrocynipoid synapomorphies are instead likely to be ground-plan characters of the Cynipoidea (Ronquist 1995b).

Kovalev presented a thorough revision of the higher classification of cynipoids in two recent papers on extinct and extant forms (Kovalev 1994; Kovalev 1996). With respect to extant cynipoids, the main difference compared with my arrangement is the elevation of a number of figitid genera and subfamilies to separate family status. In many cases, Kovalev's new families are likely to represent small apomorphic offshoots, the recognition of which as separate taxa leaves other groups paraphyletic. This has already been demonstrated for the Acanthaegilipidae (Ros *et al.* in press). Kovalev has not yet described his views on the phylogeny of the Cynipoidea in terms of an explicit phylogenetic hypothesis, nor has he presented synapomorphies supporting his groupings.

Macrocynipoid relationships

Macrocynipoids include three major monophyletic lineages: the Austrocynipidae, Ibaliidae, and Liopteridae. The Austrocynipidae comprise a single species, *Austrocynips mirabilis*, only known from three female specimens collected in Queensland, Australia (Riek 1971). The specimens were reared from cone-boring larvae of an undescribed oecophorid moth occurring in cones of *Araucaria cunninghamii*, a member of the archaic conifer family Araucariaceae (Ronquist 1995b).

Austrocynips is characterized by a number of autapomorphies including: (1) last flagellomere short, about as long as penultimate flagellomere; (2) antenna almost naked; (3) posterior margin of pronotum projecting over anterior margin of mesopleuron, not abutting; (4) mesothoracic spiracle covered by pronotum, not visible laterally; and (5) lateral bars absent. In addition, *Austrocynips* has a number of traits that are unique among cynipoids but are commonly found in the proctotrupoid complex and probably belong to the cynipoid ground plan. Thus, *Austrocynips* is a key taxon in linking cynipoids to other apocritan wasps.

Considering that *Austrocynips* was discovered only recently, there may well be additional members of the family. Systematic rearing of insects from *Araucaria* wood and cones from the Southern Hemisphere might reveal more about austrocynipid biology, distribution and diversity.

The Ibaliidae are characterized as a family by having a median notch in the pronotal crest, a pair of posterior scutellar processes, a short metafemur, and an enlarged seventh tergum in the female metasoma, among other characters (Ronquist 1995b). The family includes the largely Holarctic genera *Heteribalia* and *Ibalia* and the New

Guinean *Eileenella* (Fig. 3). *Eileenella* was placed in the Liopteridae by Fergusson (1992) and Kovalev (1994) but the single included species is undoubtedly an ibaliid (Ronquist 1995b). Kovalev proposed a separate subfamily for *Eileenella* but I have argued that a subfamily division of the Ibaliidae adds little information and should be avoided (Ronquist 1995b). Ibaliid taxonomy and biology have recently been reviewed (Liu & Nordlander 1994) and ibaliid relationships have been analysed to the species level (Nordlander, Liu & Ronquist 1996; Liu 1998b). As far as known, ibaliids are parasitoids of siricid woodwasp larvae in conifers and hardwoods. A few species of the genus *Ibalia* are the only macrocynipoids whose life history and early instars have been described in detail (Chrystal 1930; Spradbery 1970).

The Liopteridae share at least 12 synapomorphies including foveate pronotal sculpture, a mesopleural impression, a short metatibia, and dorsolateral scutellar processes (Ronquist 1995a, b). I have analysed liopterid relationships to the generic level and classified the family into four subfamilies: the Mayrellinae, Dallatorrellinae, Oberthuerellinae, and Liopterinae (Fig. 3) (Ronquist 1995a). I divided the Mayrellinae into three genera: *Kiefferiella*, *Decellea* and *Paramblynotus*. However, further studies of species relationships within the Mayrellinae (Liu 1998a) indicate that *Decellea* should be synonymised with *Paramblynotus*. The Mayrellinae predominantly occur in the Northern Hemisphere, the Dallatorrellinae are divided between South-east Asia and the Australian region, and the remaining subfamilies have a Gondwanian distribution (Fig. 3). Host records are only available for species in the Mayrellinae and include buprestid, cerambycid and curculionid beetle larvae boring in twigs and stems of deciduous trees and bushes (Ronquist 1995a; Liu 1998a). Two female specimens of *Decellea yangambicola* are claimed to have been reared from Lepidoptera (Ronquist 1995a) but this record needs confirmation. Other specimens of the same species have been reared from Coleoptera.

The historical biogeography of macrocynipoids is dealt with in a series of recent papers (Ronquist 1995a, b; Nordlander *et al.* 1996; Liu 1998a, b). Several cross-Beringian vicariance events that presumably date back at least to the terminal Eocene, about 33 million years ago (Ma), have been identified in ibaliids and liopterids associated with broad-leaved forests (Fig. 3). At the end of Eocene, previously continuous Asian and American broad-leaved forests became permanently separated in the Beringian area by other habitats through climatic deterioration (Nordlander *et al.* 1996 and references cited therein). Both the Ibaliidae and the Liopteridae show a basal split between Gondwanian and Laurasian groups, suggesting
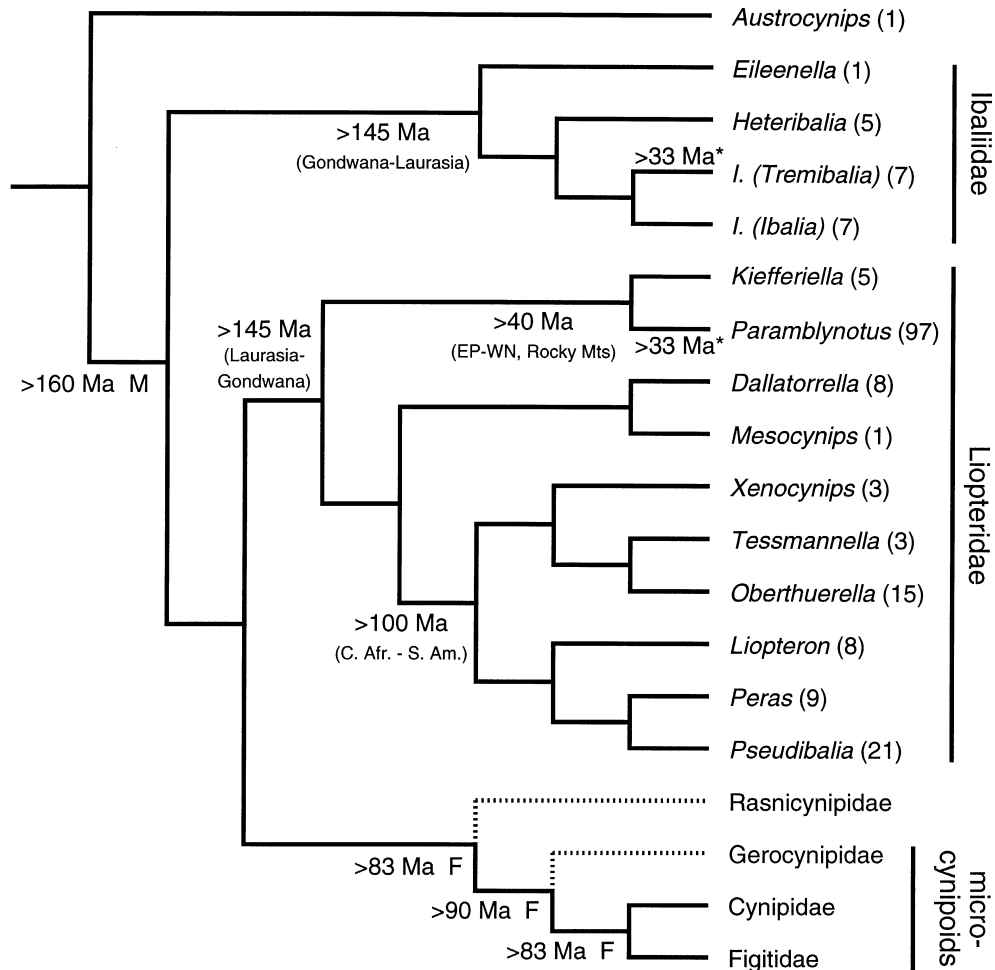
Fig. 3 Intergeneric relationships among macrocynipoids (based on Ronquist 1995b) and suggested position (dashed lines) of major fossil cynipoid lineages (see text). Minimum dates of cladogenetic events are based on vicariance events (vicariating areas in brackets), morphological clock (estimate followed by M) or fossils (estimate followed by F) (Ronquist 1995a, b; Nordlander *et al*. 1996; Liu 1998a, b). Number of known species (described and undescribed) of each terminal taxon in brackets. * = vicariance events within terminal taxa between eastern Nearctic and eastern Palaearctic deciduous forest elements.

that their earliest diversification goes back to the Jurassic (about 145 Ma) (Ronquist 1995b). This date agrees roughly with an estimate based on the amount of morphological character change in the phylogeny of the Ibaliidae before and after the cross-Beringian vicariance in *Ibalia (Tremibalia)* (Nordlander *et al*. 1996; Liu 1998b). In the Gondwanian liopterids, there is vicariance between a tropical South American lineage (Liopterinae) and a tropical African lineage (Oberthuerellinae) which presumably dates back to the rapid separation of the tropical parts of these continents about 100 Ma (Ronquist 1995a). In the liopterid genus *Paramblynotus*, there has been spectacular radiation in the eastern Palaearctic and Oriental regions, from which the genus colonized Africa and, more recently, the Americas (Liu 1998a).

Cynipidae

The higher phylogeny and early evolution of the Cynipidae are treated in several recent papers (Ronquist 1994; Liljeblad & Ronquist 1998; Ronquist & Liljeblad in prep). A detailed review of this work will appear elsewhere (Ronquist in press) and only a brief summary will be provided here.

The phytophagous gall inducers and inquilines have long been assumed to form a natural group. In addition to their unique phytophagous habit, a handful of synapomorphies in the skeletal morphology of adults are currently known, including the lack of a lateral pronotal carina and the medially narrowed dorsellum (Liljeblad & Ronquist 1998). However, all of the putative morphological synapomorphies have exceptions in the form of secondary reversal

within the Cynipidae or parallel gain in figitids. A larval character that may be a unique synapomorphy of the Cynipidae is the presence of two strong, blunt teeth in the mandibles of the last instar larva. Parasitic figitids and macrocynipoids have only one strong, sharp tooth (Haviland 1921; James 1928; Chrystal 1930; Huzimatu 1940; Wishart & Monteith 1954; Spradbery 1970; Rotheray 1979; Miller & Lambdin 1985; Ronquist, unpublished data). No exception to this character is currently known, but the survey of cynipoid larval diversity is yet very incomplete.

For our purposes, cynipids may be divided into three groups: the inquilines (tribe Synergini), the herb gallers (tribe Aylacini), and the woody rosid gallers (the tribes Diplolepidini (previously known as Rhoditini), Eschatocerini, Pediaspidini, and Cynipini). The woody rosid gallers comprise species exclusively associated with trees or bushes belonging to the eudicot subclass Rosidae, e.g. oaks and roses. The herb gallers are restricted to herbs, except for a few species in the genus *Diastrophus* that induce galls on *Rubus* bushes and *Smilax* vines (the latter being the only known monocot host of cynipids). Externally, the galls of the woody rosid gallers are generally more complex than those of the herb gallers. Internally, however, the galls are fundamentally similar, presenting the cynipid larva with a layer of nutritious cells, the nutritive tissue, on which it feeds.

The inquilines have larvae that develop inside cynipid galls induced on woody hosts by either woody rosid gallers or species of the genus *Diastrophus*. The inquiline larva is strictly phytophagous but the gall-inducing larva is often killed early in the development of the gall, either by being stabbed to death by the ovipositing inquiline female or through starvation (Shorthouse 1980; Brooks & Shorthouse 1998). The inquilines complete the formation of the host gall, sometimes conspicuously modifying the shape and size of it (Evans 1965; Wiebes-Rijks 1980; Brooks & Shorthouse 1997, 1998). Each inquiline species is usually restricted to the galls of one or a few related species of gall-inducing cynipids.

It was previously thought by some workers that the cynipid inquilines constitute an artificial, polyphyletic group with each inquiline being most closely related to its particular host gall inducer (Askew 1984; Gauld & Bolton 1988). Others have considered the possibility that cynipid inquilines represent primitive forms that never evolved the ability of inducing galls on their own (Malyshev 1968; Shorthouse 1980). It has now been convincingly shown that the inquilines evolved from cynipid gall inducers and that they share a common origin and have subsequently radiated to exploit different cynipid hosts (Ronquist 1994) (Fig. 4). Thus, the inquilines are gall inducers that have lost the ability to initiate galls but retain the capability of completing galls started by other species.

Phylogenetic analyses show that also the woody rosid gallers form a monophyletic group, and that these and the inquilines represent separate terminal offshoots of a paraphyletic basal assemblage of herb-galling lineages. The most recent analysis (Liljeblad & Ronquist 1998) suggests that there is a basal split in the cynipid phylogeny between one lineage leading to the inquilines and another (the *Barbotinia-Cynips* or B-C lineage) leading to the woody rosid gallers (Fig. 4). The tribe Cynipini (the oak gall wasps), a tremendously diverse group with more than 40 genera and about 1000 species, is likely to be monophyletic (Ronquist 1994; Liljeblad & Ronquist 1998) but intergeneric relationships within the group are poorly known. The current generic classification of the oak gall wasps includes several artificial or heterogeneous groups and it therefore seems likely that major classificatory changes will follow as future studies reveal higher relationships within the group.

Lower-level relationships have been analysed in European members of the Cynipini genus *Andricus* based on cytochrome *b* sequences (Stone & Cook 1998). Among the other tribes, lower-level relationships have so far only been studied in the inquiline genus *Synophromorpha* (Ritchie & Shorthouse 1987) and the Aylacini genus *Isocolus* (Baumann & Brandl 1993).

Parsimony mapping of biological and distribution characters on the higher cynipid phylogeny (Fig. 4) reveals a number of interesting features in the evolution of gall wasps and the gall wasp-host plant association (Ronquist and Liljeblad, in prep.). For instance, gall wasps apparently originated in the Western Palaearctic region, presumably in the Mediterranean basin or around the Black Sea. The first galls were single-chambered swellings induced in reproductive structures of herbs belonging to the family Papaveraceae or possibly the Lamiaceae. The species that induce cryptic galls, i.e. herb stem galls leaving no external sign on the attacked plant, evolved from species inducing more conspicuous galls and do not represent primitive forms as hypothesized by earlier workers (e.g. Kinsey 1920). For further details, see Ronquist (in press).

Cynipid classification

Extant cynipids are currently placed in the same subfamily (Appendix). Considering that cynipids fall into two monophyletic lineages (Fig. 4) that are easily separated on morphological characters (Liljeblad & Ronquist 1998), it seems likely that it will eventually be found advantageous to divide the extant members of the family into two separate subfamilies. The tribal classification of cynipids also needs revision; the best solution will probably be to subdivide the tribe Aylacini into a number of monophyletic
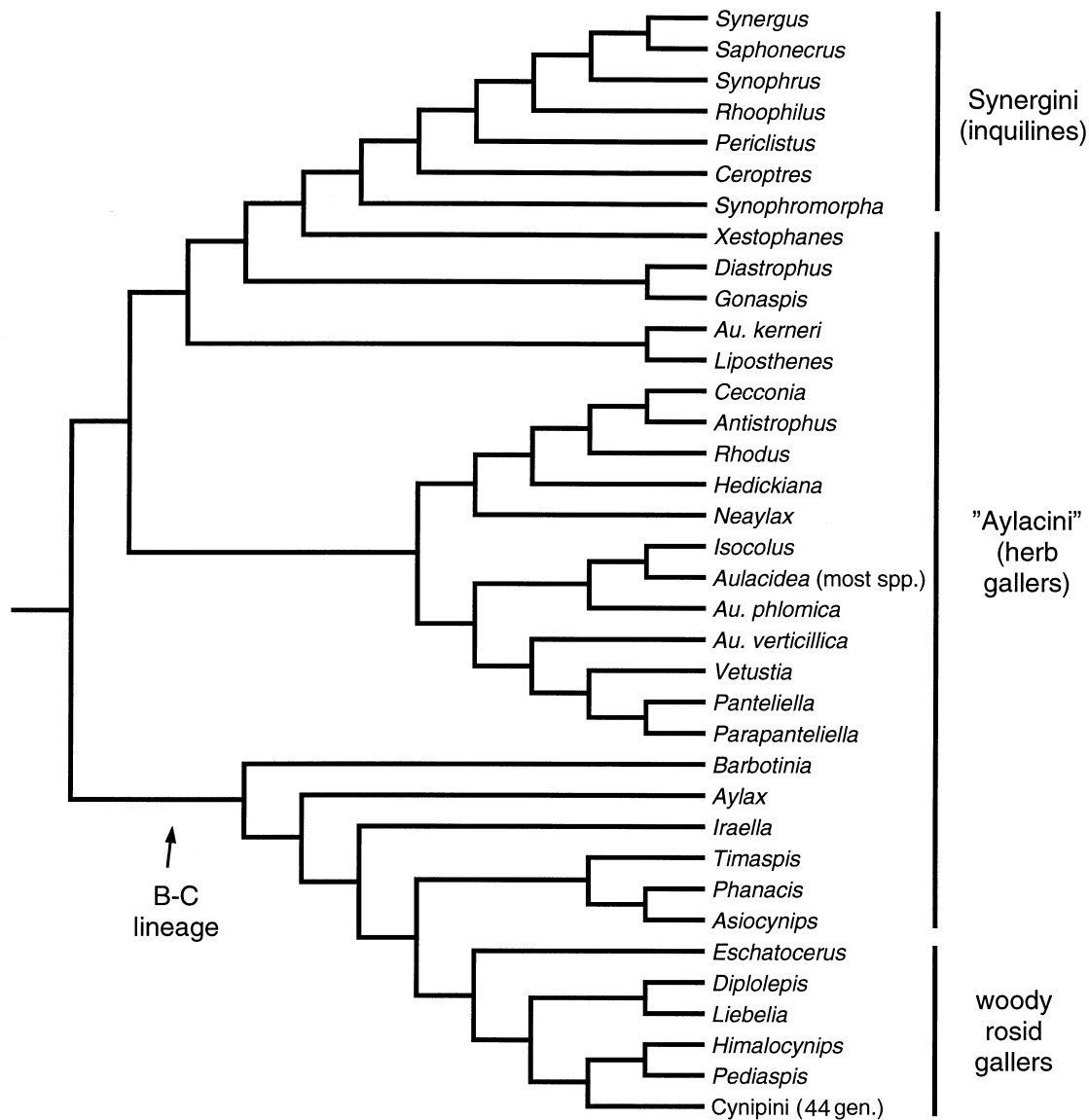
Fig. 4 Higher-level cynipid relationships (Ronquist 1994; Liljeblad & Ronquist 1998). The tree is a synthesis of two explicit cladistic analyses and *a posteriori* analyses of the position of five genera and hence no support values are given. The tree includes all cynipid genera of all tribes except the Cynipini and the following genera: *Zerovia* belongs to the *Timaspis-Phanacis-Asiocynips* lineage (Liljeblad & Ronquist 1998); *Poncyia* (original description insufficient for accurate placement, location of type unknown, no additional material available); *Australofigites* (likely synonym of *Phanacis*).

subgroups but retain the other tribes (Table 1, Fig. 4). However, since further studies of higher-level cynipid relationships are in progress, I consider it premature to revise the current classification of cynipids here.

Figitidae

The Figitidae are defined as a monophyletic group by having a distinct point of weakness in the ninth tergum of the female at the position of the base of the third valvula (Fig. 6A,B) (Ronquist 1995b). This structure allows some flexibility between the basal and distal parts of the ovipositor and has been the starting point for additional ovipositor modifications within the family (see below). The Figitidae are also characterized by having $R_s + M$ issuing from a point close to Cu, i.e. at the posterior end of the so called basal vein or basalis (Ronquist 1995b: Fig. 11). The vein $R_s + M$ is nebulous or spectral in some figitid subgroups, but there is almost always a distinct portion

directed towards the posterior end of the basal vein, not the middle or anterior part as in other cynipoids and other hymenopterans. Further possible figitid synapomorphies include a longitudinal carina on the posterior surface of the metatibia (also present in some macrocynipoids) and a third abdominal tergum with distinctly oblique posterior margin (the latter character also in some Cynipidae, presently with unclear polarity) (Ronquist 1995b; Liljeblad & Ronquist 1998).

The Figitidae remain the most poorly known cynipoid group phylogenetically and taxonomically. Higher figitid relationships have never been subject to formal cladistic analysis (but see Ros *et al*. in press), although a few relationships were suggested by Ronquist (1995b). Here, I divide the Figitidae into eight subgroups (Table 1) and present evidence that seven of these subgroups are monophyletic. I discuss the relationships within each subgroup and present an analysis of among-group relationships based largely on characters of the female metasoma.

New subfamily

A new genus and subfamily will be proposed elsewhere for the species '*Aulacidea*' *nigripes* Barbotin (1963). This species is a parasitoid of *Barbotinia oraniensis*, a cynipid inducing galls in seed capsules of *Papaver* in the Mediterranean region (Ronquist and J. L. Nieves-Aldrey, unpublished data). *A. nigripes* is superficially similar to cynipids and was placed in the cynipid genus *Aulacidea* by Barbotin. However, it shares the two principal figitid synapomorphies: (1) $R_s + M$ issuing from the posterior end of the basal vein; and (2) the ninth tergum of the female with a distinct point of weakness. *A. nigripes* also has possible figitid synapomorphies such as a longitudinal carina on the posterior surface of the metatibia and a third abdominal tergum with distinctly oblique posterior margin (Liljeblad & Ronquist 1998). Further, it possesses typical figitid plesiomorphies that are usually absent in cynipids, such as a lateral pronotal carina (cf. Fig. 5A: lpc) and a distinctly closed marginal cell. A likely autapomorphy of *A. nigripes* is the lack of a modified first flagellomere in the male antenna.

Thrasorinae

Kovalev (1994) proposed a new family for the single figitid genus *Thrasorus*, but this unit is too small to be useful even as a subfamily. As used here, the Thrasorinae include the genera *Euceroptres*, *Thrasorus*, *Myrtopsen*, *Pegacynips*, and *Plectocynips*, i.e. the 'figitoid inquilines' *sensu* Ronquist (1994) excluding '*Aulacidea*' *nigripes*. The Thrasorinae are defined as a group by having the metacoxa distinctly swollen. The species are associated with cynipid and chalcidoid galls on various trees and bushes. Nothing is known about

the biology but it seems likely that the Thrasorinae are parasites of the gall inducers or some other hymenopteran inhabitants in the galls they are associated with.

All thrasorine genera except *Euceroptres* share a series of derived features: female metasoma modified with the eighth and fifth tergum enlarged and the seventh tergum reduced and more or less completely covered by the sixth or fifth tergum; third abdominal tergum reduced in size; and lateral pronotal carina short, strongly curved and prominent. Among the derived thrasorines, the South American genera *Pegacynips* and *Plectocynips* appear to form a monophyletic group based on the shared presence of an extremely long posterior metatibial spur.

Charipinae

The Charipinae are defined as a monophyletic group by the evenly rounded scutellum without distinct sculpture (the superficial reticulate sculpture of *Lytoxysta* is undoubtedly secondarily derived). All other cynipoids have the scutellum at least partly with some distinct sculpture or puncture. The association with hymenopteran parasitoids of homopterans (aphids and psyllids) has been proposed as an additional synapomorphy of charipines (Menke & Evenhuis 1991) but the possibility that this feature is an intermediate stage in a more complex transformation series involving other hosts cannot be excluded.

The Charipinae are often divided into the Charipini and Alloxystini (or Charipinae and Alloxystinae if the subfamily is treated as a separate family) (Kierych 1979a, b; Menke & Evenhuis 1991). The Charipini are parasites of chalcidoids attacking psyllids (Menke & Evenhuis 1991) whereas the Alloxystini are parasites of braconids and chalcidoids attacking aphids. The Charipini, comprising the genera *Apocharips* and *Dilyta*, are defined as a monophyletic group by the derived position of the spiracles on the eighth abdominal tergum, the presence of an apical carina on the scutellum, and the reduction in size of the third abdominal tergum (Menke & Evenhuis 1991). The Alloxystini, on the other hand, are likely to be paraphyletic but the tribe is retained here for convenience until intergeneric relationships are clarified. *Hemicrisis* is currently synonymised with *Phaenoglyphis* but should be re-established as a valid genus. It has two features that are likely to be unique plesiomorphies in the Charipinae: distinct notauli and a partially sculptured mesoscutum. The remaining Alloxystini genera (*Carvercharips*, *Alloxysta* and *Lytoxysta*) and the Charipini appear to form a monophyletic group defined by absence of the mesopleural carina or ledge (cf. Figure 5B: f).

Kovalev (1994) proposed a separate family level taxon for *Lytoxysta*. This genus has a number of striking unique autapomorphies (Menke & Evenhuis 1991) but separation of the genus from the rest of the Alloxystini would leave an unna-
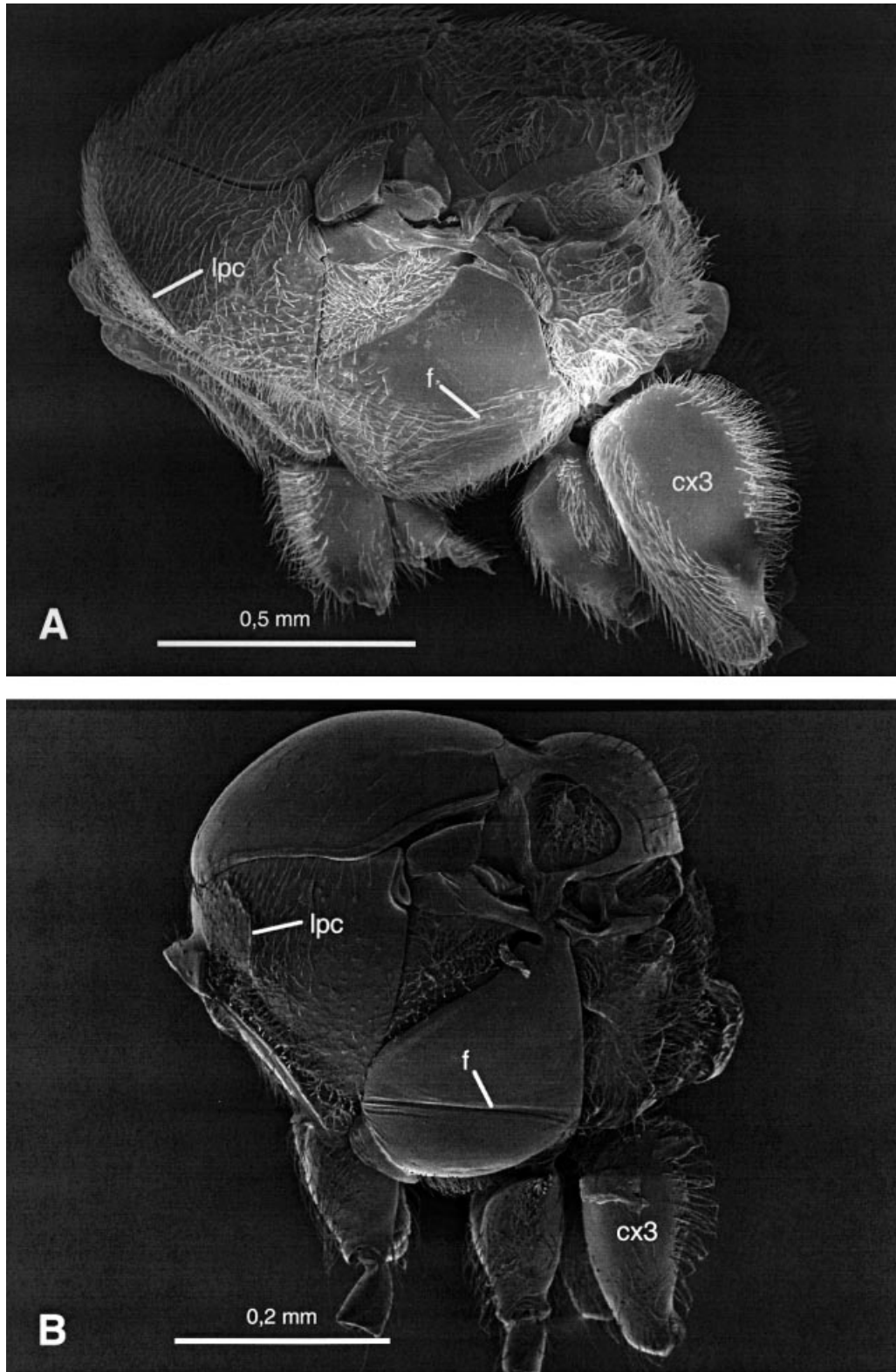
Fig. 5 Lateral view of female mesosoma illustrating important figitid characters. Scanning electron micrographs. —A. *Euceroptres montanus* (Thrasorinae). —B. *Phaenoglyphis villosa* (Charipinae). Abbreviations: cx3 = metacoxa; f = mesopleural furrow; lpc = lateral pronotal carina.

tural paraphyletic group, whose classification would eventually necessitate a number of additional new taxa at the same level as the one used for *Lytoxysta*. To avoid excessive splitting, I prefer to retain *Lytoxysta* in the Alloxystini.

Anacharitinae

The Anacharitinae (excluding *Petricynips*) are supported as a monophyletic group by a series of characters, including a unique anterior pronotal plate and a more or less elongate petiole that is largely derived from the petiolar neck instead of the petiolar annulus (Ros *et al.* in press). The position of *Petricynips* is uncertain. It may be a basal anacharitine but may also belong to the Diptera-parasitic figitids; definite clarification of its position must await collection of better material than the single defect female specimen currently known.

Anacharitines are parasitoids of aphid-feeding Neuroptera larvae. Kovalev (1996) considered the distinctive South American genus *Acanthaegilips* to fit poorly in the subfamily and erected a new family for it. However, parsimony analysis of the available morphological evidence indicates that *Acanthaegilips* is deeply nested within the Anacharitinae (Ros *et al.* in press). Kovalev (1996) further separated *Proanacharis* from the remaining Anacharitinae. Although it is likely that *Proanacharis* forms the sister lineage of other anacharitines (including *Acanthaegilips*), the morphological differences between these two lineages are so slight that recognition of a separate tribe or subfamily for *Proanacharis* appears unnecessary. The life history of *Proanacharis* is unknown and should be assumed to be similar to that of other anacharitines until observations prove otherwise. Thus, I find no reasons for maintaining *Proanacharis* in a separate higher taxon and therefore synonymise Proanacharitinae with Anacharitinae.

'Figitinae'

The Figitinae are defined by the lack of derived characters present in other figitid subfamilies and is an obvious classificatory wastebasket. Nevertheless, restricting the group to the Diptera parasites by exclusion of the 'figitoid inquilines', as proposed here, probably renders the subfamily paraphyletic only relative to the other Diptera-parasitic figitids, i.e. the Eucoilinae, Pycnostigminae, Aspicerinae and Emargininae.

Hellèn (1937) proposed a separate tribe for the figitine genus *Lonchidia*. However, formal division of the Figitinae makes little sense until higher relationships among the Diptera-parasitic figitids have been sorted out.

Aspicerinae

There is considerable morphological evidence supporting Aspicerinae monophyly, including presence of a facial depression, strongly ligulate third abdominal tergum, and a unique pronotal plate formed by lateral fusion of protruding dorsal and ventral elements (Ros *et al.* in press). Aspicerines are parasites of aphid-feeding syrphid and chamaemyiid larvae. Ros *et al.* (in press) give a preliminary analysis of intergeneric aspicerine relationships.

Emargininae

As used here, the Emargininae comprise the genera *Emargo*, *Bothriocynips*, *Thoreauella*, *Weldiola* and *Quinlania*. The group is well characterized by a number of apomorphic features, including a strongly laterally compressed mesosoma and a deeply bilobed fore wing. Many species have a scutellar carina of various shape but this structure is apparently not universally present in the group (Weld 1960). The carina has been interpreted as the margin of a reduced eucoiline-type scutellar plate and the group has consequently been placed in the Eucoilinae (Quinlan 1988; Menke & Evenhuis 1991). However, the scutellar carina of emarginines never assumes the form of a raised plate or cup, and there is apparently no gland associated with it. Furthermore, the Emargininae differ from eucoilines in lacking tergal fusions in the metasoma. Diaz (1978) placed emarginines (specifically the genus *Bothriocynips*) in the Charipinae but this is likely to be erroneous because: (1) emarginines lack the characteristic charipine scutellum; (2) emarginines have the antennae moniliform rather than connate as in the Charipinae; (3) emarginines have the third tergum reduced in size like the Charipini but lack all other synapomorphies of the Charipini (*viz.*, the closely situated spiracles on the eighth tergum and the posterior scutellar carina). Finally, the structure of the ovipositor (normal first valvula, ninth tergum with process) indicates that the Emargininae are related to the Diptera-parasitic figitids and not to the Charipinae.

Kovalev (1994) suggested division of the Emargininae (which he treated as a separate family) into two tribes. However, I do not consider tribal division of the Emargininae warranted at this point considering the morphological homogeneity of the group and the lack of knowledge of intergeneric relationships. One might even argue for treating the entire subfamily as a single genus.

Emarginines are associated with ants. Adults have been obtained through Berlese funnel extraction of refuse deposits of army ants (Weld 1960) and they have been collected in *Camponotus* nests (Diaz 1978). They are presumably parasitoids of myrmecophilous Diptera larvae.

Pycnostigminae

The Pycnostigminae are an isolated group comprising only three genera. The obvious apomorphy defining the Pycnostigminae is the secondarily sclerotized marginal cell

forming a pseudopterostigma (Königsmann 1978). Pycnostigmines are unique among figitids in having abdominal terga three to five fused in both the female and the male (Ronquist, unpublished data; see also Rasnitsyn 1980; Ronquist 1995b). The male state is likely to be apomorphic for the Pycnostigminae whereas the female condition is shared with the Eucoilinae. The biology of the Pycnostigminae is unknown but their phylogenetic position predicts parasitism of dipteran larvae in decomposing organic material or possibly inside plants.

Trjapitziniola is remarkable in having a polished scutellar area reminiscent of the eucoiline scutellar plate (Kovalev 1994: figs 24,25); this structure is absent in other pycnostigmines. The polished area in *Trjapitziniola* is not raised and not equipped with a gland as in eucoilines. Nevertheless, the presence of this structure raises the intriguing possibility that pycnostigmines are eucoilines with the scutellar plate strongly reduced (*Trjapitziniola*) or lost (other genera). If so, eucoilines may be paraphyletic relative to pycnostigmines. Further analyses of figitid relationships will be needed to determine whether this is the case.

Eucoilinae

The monophyly of the Eucoilinae is supported by the universal presence of a scutellar cup or plate, a unique feature in the Cynipoidea. The scutellar plate has a deep depression centrally or posteriorly. The bottom of the depression is perforated with pores that are connected to outlet ducts of a large internal scutellar gland (Ronquist, unpublished data), the function of which is unknown. Another unusual character found in all eucoilines is the fusion of the third to fifth abdominal tergum in females, only shared with pycnostigmines among figitids (Ronquist 1995b). The Eucoilinae are by far the most species-rich figitid subfamily with some 80 genera and 1000 species recognized currently (Table 1). Many genera are poorly defined and phylogenetic analyses are desperately needed

to sort out generic limits and elucidate higher relationships in this important and cosmopolitan group of Diptera parasites. Nordlander (1982b) proposed a tentative classification of eucoilines into six informal genus groups. Unfortunately, apomorphic characters defining these groups have not been given and the circumscription of some groups remains uncertain. The relationships among them are also unknown. Kovalev (1994) treated the Eucoilinae as a separate family and raised Nordlander's genus groups to formal subfamilies. However, he did not provide apomorphic evidence supporting any of the groupings. I consider a formal division of the subfamily into tribes undesirable at present given the poor knowledge of higher eucoiline relationships, and therefore synonymise existing family group names. Eventually, however, division of the subfamily into tribes would be warranted given the enormous diversity of the group.

At a lower taxonomic level in the Eucoilinae, there have been a few cladistic analyses (Nordlander 1982a; Diaz 1990; van Alphen *et al.* 1991; Schilthuizen *et al.* 1998) and some discussion about possible phylogenetic relationships (Nordlander 1980, 1981, 1982a; Nordlander & Grijpma 1991). As far as is known, eucoilines are entirely restricted to hosts in the Diptera: Cyclorrhapha. Some easily cultivated *Drosophila* parasites have become important model organisms in experimental studies of parasitic wasp biology (e.g. Rizki & Rizki 1990; van Alphen 1993; Janssen *et al.* 1995; Combes 1996; Delpuech *et al.* 1996; Carton & Nappi 1997; Gemmil & Read 1998).

Characters informative about higher figitid relationships

The analysis of higher figitid relationships I present here is largely based on features of the female metasoma complemented with a few other morphological and biological characters. The characters requiring dissection were checked in a few exemplars of each subfamily (Table 2), other morphological characters were observed in specimens, or occasionally

Table 2 Species examined for female metasomal characters requiring dissection. Number of examined genera is given for each taxon; total number of genera in brackets.

Taxon	Genera	Examined taxa
Cynipidae	26 (77)	26 genera representing all tribes (see Liljeblad & Ronquist 1998)
Figitidae		
New subfamily	1 (1)	'*Aulacidea*' *nigripes*
Thrasorinae	2 (5)	*Euceroptres montanus, E. futilis, Myrtopsen mimosae*
Charipinae	3 (7)	*Phaenoglyphis villosa, Alloxysta victrix, Dilyta subclavata*
Anacharitinae	3 (8)	*Anacharis eucharioides, Xyalaspis* sp., *Calofigites* sp.
Figitinae	5 (13)	*Lonchidia clavicornis, Neralsia* sp., *Figites* sp., *Melanips alienus, Sarothrus tibialis*
Aspicerinae	3 (8)	*Callaspidia* sp., *Prosaspicera* sp.
Emargininae	1 (5)	*Thoreauella* sp.
Pycnostigminae	1 (3)	*Pycnostigmus rostratus*
Eucoilinae	5 (82)	*Disorygma depile, Trybliographa rapae, Eucoila crassinerva, Leptopilina heterotoma, Kleidotoma dolichocera*

published descriptions, of representatives of all valid genera of all subfamilies except for the Eucoilinae, for which only a small sample including all generic groups identified by Nordlander (1982b) was consulted. As outgroup state I used the likely ground-plan condition of cynipids (Liljeblad & Ronquist 1998). Since the Figitinae are likely to be paraphyletic, they were divided into subgroups having unique combinations of character states. This resulted in two figitine groups: *Melanips* and other figitines.

1   Structure of female antenna: (0) connate; (1) moniliform.

2   Sculpture of mesoscutum: (0) dull; (1) shining. There appears to be a general trend in figitids towards the loss of microsculpture on the mesoscutum producing a polished surface. The sclerite is dull in archaic representatives of Thrasorinae (*Euceroptres*), Charipinae (*Hemicrisis*) and Anacharitinae (*Proanacharis*), suggesting that this is the ground-plan state in these subfamilies. Other groups in the analysis are monomorphic for one of the states.

3   Mesopleural furrow/carina: (0) absent; (1) present. Most figitids have a horizontal mesopleural furrow or carina across the mesopleuron. In its plesiomorphic condition, the structure consists of a poorly defined furrow through which a few irregular, longitudinal carinae run (Fig. 5A). A derived condition that seems to have evolved twice independently (in the Charipinae and Eucoilinae) involves reduction to a single but very distinct horizontal carina or ledge (Fig. 5B). Although some figitids lack the structure completely, all figitid subgroups except the new subfamily are likely to have this structure in their ground plans, as indicated by the presence in archaic representatives. For instance, although most charipines lack the mesopleural furrow/carina, it is present in *Hemicrisis* and *Phaenoglyphis*. A similar structure is lacking in the ground plan of cynipids. Liopterids have a mesopleural impression in a similar position, but its structure is completely different (well-defined borders, evenly impressed, no longitudinal carinae) and is unlikely to be homologous with the mesopleural furrow of figitids (Ronquist 1995a).

4   Submedian petiolar pits (Ronquist & Nordlander 1989: figs 58, 59, structure 171): (0) present, deep and distinct; (1) absent or indistinct, shallow.

5   Size of third abdominal tergum of female: (0) larger than fourth tergum; (1) smaller than fourth tergum. Although there is a general trend towards reduction in size of the third abdominal tergum, the third abdominal tergum is likely to be larger than the fourth tergum in the ground plans of all figitid subgroups

except the Eucoilinae, Pycnostigminae, Emargininae, Figitinae (including *Melanips*), and Aspicerinae. The third tergum is part of a synsclerite in eucoilines and pycnostigmines but the position of spiracle remnants and the intertergal suture reveal that the third tergum is reduced in these subfamilies.

6   Structure of third to fifth abdominal tergum of females: (0) free; (1) fused.

7   Structure of ovipositor: (0) coiled in a spiral, without flexion point; (1) coiled in a spiral but with a marked discontinuity in the sclerotization of the ninth tergum,
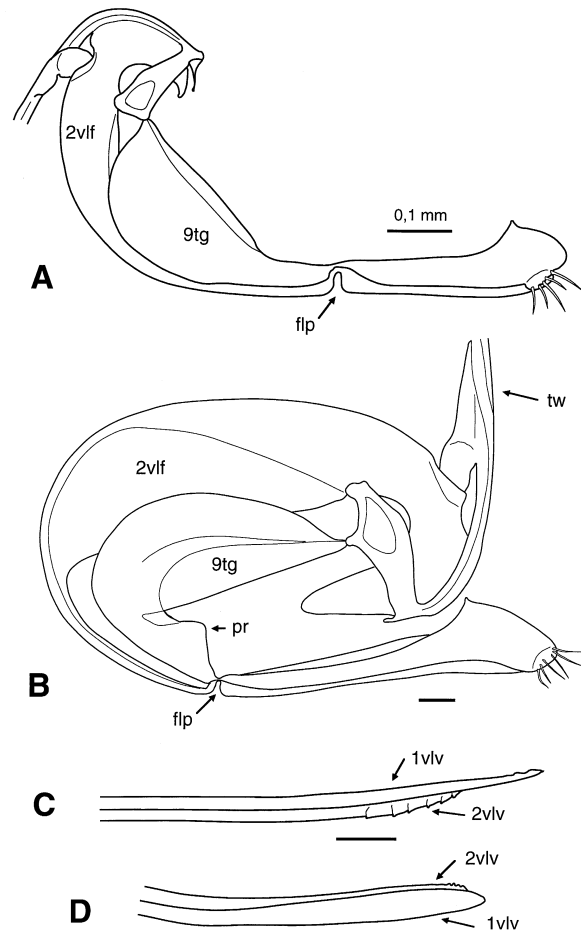

Fig. 6 Important ovipositor characters in the Figitidae. Drawings from slide mounts. —*A, B.* Basal part of ovipositor in lateral view. —*A. Phaenoglyphis villosa* (Charipinae). —*B. Trybliographa rapae* (Eucoilinae). —*C, D.* Apex of terebra in lateral view. —*C. Callaspidia* sp. Notice that the terebra is twisted 180°, shifting the positions of the first and second valvulae. —*D. Phaenoglyphis villosa* (Charipinae). The terebra is not twisted. Abbreviations: 1vlv = first valvula; 2vlv = united second valvulae; 2vlf = second valvifer; 9tg = ninth abdominal tergum; flp = ovipositor flexion point; tw = basal twist in terebra; pr = dorsal process of ninth tergum just anterior to flexion point. Scale bar is 0,1 mm in all cases.

giving a point of flexibility close to the base of the third valvula; (2) distinctly angled or elbowed with a well developed flexion point at the base of the third valvula separating a large basal, swinging part of the ovipositor from an apical part attached to the ventral margin of the eighth tergum (Fig. 6A,B) (Fergusson 1988; Ronquist, unpublished data). Ordered 012.

8　Ninth tergum of female (part of ovipositor): (0) without dorsal process; (1) with distinct dorsal process just anterior to the flexion point (Fig. 6B: pr).

9　Basal part of terebra: (0) twisted 180° so that the first valvulae are in dorsal position at the apex (Fig. 6B,C); (1) straight, not twisted 180°, first valvulae ventral at the apex (Fig. 6A,D). This character is variable in the Cynipidae and the ground-plan state is uncertain; the outgroup was therefore coded as having state unknown.

10　Shape of first valvula: (0) narrowing gradually, not broadened towards the apex (Fig. 6C); (1) distinctly broadened towards the apex (Fig. 6D).

11　Hosts belong to the insect order: (0) Hymenoptera; (1) Neuroptera; (2) Diptera. Unordered.

12　Larvae develop in: (0) galls; (1) aphid community; (2) decomposing organic material (carrion, dung, fungi, etc.) or inside plants but not in galls. Unordered.

Higher figitid relationships and classification

Running the matrix (Table 3) with the branch-and-bound algorithm of paup 3.1.1 (Swofford 1993) produced one most-parsimonious tree of length 12, CI = 0,92 and RI = 0,95 (Fig. 7). Although the analysis was based on relatively few informative characters, several groupings were well supported as indicated by bootstrap values. Pruning the biological characters from the matrix, leaving only morphological characters, produced the same shortest tree as the original matrix.

In the shortest tree, the sister-group relationship between the new subfamily and other figitids is supported by the presence of the mesopleural carina/furrow in the latter. The switch from hosts in the gall community to hosts in other microhabitats is a synapomorphy for figitids excluding Thrasorinae and the new subfamily. The same clade is supported by the development of a distinct flexion point in the ninth tergum of females (flp, Fig. 6A,B), separating a large basal, swinging part of the ovipositor from an apical part attached to the ventral margin of the eighth tergum. The derived structure allows the female to unfold the basal part of the ovipositor, increasing the action radius of the ovipositor and presumably also the speed with which the eggs can be deposited.

Charipines and anacharitines share a unique synapomorphy in having the first valvulae broadened apically (Fig. 6D). They also have the terebra straight basally (Fig. 6A,D) unlike all other figitids, which have the terebra
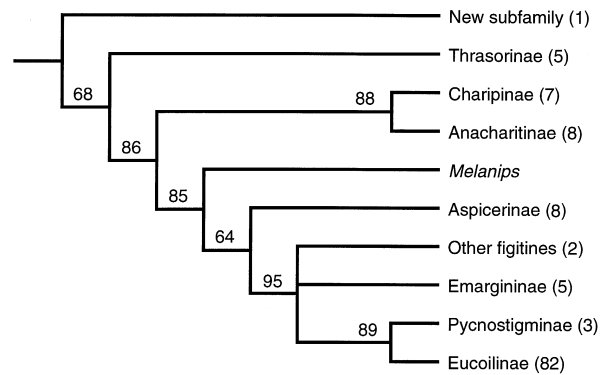

Fig. 7 Higher-level figitid relationships according to the analysis presented here. Numbers on branches are bootstrap support values (from 1000 replications of branch-and-bound searches). Numbers in brackets indicate the number of genera in each terminal taxon

Table 3 Observed states of morphological characters informative about higher figitid relationships. For character descriptions, see text. Character states in brackets are inferred ground-plan states of polymorphic taxa (see text).

Taxon	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
New subfamily	0	0	0	0	0	0	1	0	0	0	0	0
Thrasorinae	0	(0)	1	(0)	0	(0)	1	0	0	0	?	0
Charipinae	0	(0)	(1)	(0)	0	(0)	2	0	1	1	0	1
Anacharitinae	0	(0)	1	(0)	0	0	2	0	1	1	1	1
Melanips	0	0	1	1	0	0	2	0	0	0	2	1
Other Figitinae	1	1	1	1	0	0	2	1	0	0	2	2
Aspicerinae	0	0	1	1	0	0	2	1	0	0	2	1
Emargininae	1	1	0	1	1	0	2	1	0	0	?	2
Eucoilinae	1	1	1	1	1	1	2	1	0	0	2	2
Pycnostigminae	1	1	1	1	0	1	2	1	0	0	?	?
Outgr.: Cynipidae	0	0	(0)	(0)	0	(0)	0	0	0	0/1	–	0

twisted 180° basally so that the first and second valvulae shift positions (Fig. 6B,C). The Diptera-parasitic figitids are supported as a monophyletic group by the association with dipteran hosts and the reduction in the size of the third abdominal tergum in females. Except for *Melanips*, all Diptera-parasitic figitids have moniliform antennae (least distinct in Pycnostigminae) and the female ninth tergum bears a distinct process serving as attachment for a muscle from the eighth tergum (pr, Fig. 6B). The Pycnostigminae and Eucoilinae share a unique synapomorphy in having the third to fifth abdominal terga fused to a synsclerite in the female metasoma. The first tergum after the synsclerite is set at a distinct angle to the latter and has a unique, rounded sclerotization in the median part of its anterior margin. The eucoilines and pycnostigmines also lack the anterior submedian petiolar pits present in all other cynipoids.

The analysis presented here is by no means comprehensive. In addition to the included characters, there is a long suite of morphological features varying within the Figitinae and indicating that individual figitine genera, parts of genera or groups of genera scatter among the major lineages of Diptera-parasitic figitids. For instance, *Figites* and *Neralsia* share some derived features with the Aspicerinae; *Amphitectus* (which should be removed from synonymy with *Sarothrus*) and *Seitneria* (which should be removed from synonymy with *Figites*) show some presumably symplesiomorphic similarities with *Melanips*; *Lonchidia* displays affinities with emarginines and possibly eucoilines + pycnostigmines. The phylogenetic implications of this character variation are likely to be restricted to the relative position of figitine genera within the assemblage of Diptera-parasitic figitids and this problem can only be elucidated in a comprehensive analysis of figitid relationships in which each figitine genus or species group is treated as a separate terminal taxon. Further study of figitid morphology is also likely to reveal a wealth of additional morphological characters informative about higher figitid relationships.

Nevertheless, the analysis of figitid relationships presented here suggests that the common recognition of the Eucoilinae as a separate family may be difficult to defend since it is likely to eventually necessitate division of the parasitic microcynipoids (the Figitidae *sensu lato*) into at least nine different families, possibly more depending on the relationships of the paraphyletic Figitinae. If several families were used for the parasitic microcynipoids, it would seem more reasonable to keep all the Diptera parasites in a single unit, the Figitidae *sensu stricto* (this grouping would still be wider than the traditional circumscription of the Figitidae, which excludes the eucoilines and pycnostigmines). For the time being, however, I prefer grouping all parasitic microcynipoids in a single family.

Cynipoid fossils

Recent work has revealed a rich diversity of cynipoid fossils from the Cretaceous and Tertiary, including both impression fossils and beautifully preserved amber specimens (Rasnitsyn & Kovalev 1988; Kovalev 1994, 1995, 1996). Most fossils have not been placed in the context of a phylogenetic hypothesis (for exceptions, see Ronquist 1995a, b) and none of them has been included in a cladistic analysis. Here, I review the evidence available in published descriptions and illustrations and discuss likely relationships of all described cynipoid fossils. Nevertheless, it is evident that more careful examination of the specimens and explicit cladistic analysis is likely to shed more light on the phylogenetic position and evolutionary significance of the fossils.

Kovalev (1994) separated cynipoid-like parasitic wasps into the Archaeocynipoidea and the Cynipoidea, the former comprising the extinct families Archaeocynipidae, Gerocynipidae, Rasnicynipidae and Palaeocynipidae and the latter all extant cynipoids and some fossil taxa of subfamily rank or lower. According to Kovalev, the Archaeocynipoidea differ from the Cynipoidea in having the metapectus free and not fused to the propodeum. Since all extant apocritan wasps have the metapectus fused to the propodeum and the Archaeocynipoidea are obviously not the most basal apocritans, I consider it extremely unlikely that these fossils actually have the metapectus free. It seems more plausible that the apparently free metapectus is an observational or optical artefact or is due to physical distortion of the specimens. Therefore, I see no need to distinguish the superfamily Archaeocynipoidea.

Archaeocynipidae from the lower Cretaceous are supposedly the oldest cynipoid fossils (Rasnitsyn & Kovalev 1988). However, it has not been possible to verify the presence of a single putative cynipoid autapomorphy in them, except possibly for the shape of the scutellum (Ronquist 1995b). In contrast to cynipoids, archaeocynipids have a linear pterostigmal remnant formed by anteroposterior compression, the costa is present, the areolet is comparatively large and the media is in the plesiomorphic posterior position. The wing venation thus suggests diapriid affinities. The position of archaeocynipids will remain uncertain until we know more about the relationships among extant parasitic wasps and how various morphological characters map onto this phylogeny.

There are only two described macrocynipoid fossils: *Kiefferiella connexiva* (Liopteridae) from the upper Eocene (34 Ma) of Florissant, Colorado (Ronquist 1995a) and *Ibalia* sp. from the upper Miocene of France (5.5 Ma) (Nel 1996). None of these fossils are old enough to push other

age estimates of cladogenetic events further back in time but the liopterid fossil reinforces the minimum age of the *Kiefferiella-Paramblynotus* split determined from biogeographic evidence (cf. Fig. 3).

The Rasnicynipidae are represented by a single amber fossil, a female specimen, from the upper Cretaceous (Santonian, 83–87 Ma) (Kovalev 1994). According to Kovalev, *Rasnicynips* is an intermediate link between the Archaeocynipidae and the Ibaliidae and he specifically compares it with the superficially similar ibaliid genus *Eileenella*. However, the fossil lacks all known ibaliid synapomorphies (Ronquist 1995b). Most characters mentioned in the original description or illustrated in the accompanying drawings (Kovalev 1994: figs 14–19) are macrocynipoid symplesiomorphies: body elongate, dorsal pronotal area present, no bulla in $R_1 + Sc$, pterostigmal remnant short and thick, third abdominal tergum large, posterior abdominal terga narrow. However, the vertical rather than oblique position of the meso- and metacoxae is a microcynipoid feature and this, in combination with the absence of any ibaliid or liopterid synapomorphies, indicates that *Rasnicynips* represents a basal branch on the lineage leading to microcynipoids (Fig. 3).

The family Gerocynipidae was proposed for a set of impression fossils from the mid Cretaceous (Cenomanian, 90–97 Ma) (Kovalev 1994). These are obviously microcynipoids, having a number of putative microcynipoid synapomorphies: pronotal crest absent, dorsal pronotal area absent, meso- and metacoxae directed vertically, mesosoma short and high, and metasoma rounded in lateral view. Kovalev concluded that gerocynipids were gall inducers because only females are known. Among now living cynipoids, strongly female-biased sex ratios and thelytokous parthenogenesis are decidedly more common in gall inducers than in inquilines and parasitoids. Furthermore, the extremely large and rounded metasoma of gerocynipids is reminiscent of that of several archaic extant lineages of gall-inducing cynipids. If gerocynipids are gall inducers then they probably belong to the Cynipidae. However, the published descriptions and illustrations of gerocynipids do not allow the identification of a single cynipid synapomorphy and gerocynipids appear to have three apparently plesiomorphic characters that are not found in microcynipoids, namely a transversely carinated mesosoma (at least in some species), a continuous $R_1 + Sc$ (without bulla) (one specimen), and a comparatively large areolet (one specimen). Therefore, gerocynipids are tentatively placed here basal to extant microcynipoids (Fig. 3).

Kovalev (1994) erected the family Palaeocynipidae for two amber fossils from the upper Cretaceous (Santonian, 83–87 Ma). Although placed in the Archaeocynipoidea, Kovalev considered palaeocynipids to be immediate ancestors of modern figitids like charipines, anacharitines and figitines/aspicerines. Palaeocynipids are obviously microcynipoids and share with the Figitidae (*sensu lato*) the derived character of having the $R_s + M$ vein issuing from the posterior end of the basal vein (Kovalev 1994: figs 11, 13). However, palaeocynipids lack the transverse mesopleural furrow and the associated carinae found primitively in all major figitid lineages except the new subfamily. This suggests that the palaeocynipids form a basal lineage in the Figitidae, and they are treated here as a subfamily in this group.

Kovalev (1994) proposed the monotypic subfamily Hodiernocynipinae of the Cynipidae for a number of recently discovered and previously described cynipoid impression fossils from the upper Eocene to upper Oligocene (34–24 Ma). Several of these fossils were previously provisionally placed in the Figitidae (Statz 1938). I agree with Kovalev that the hodiernocynipines are microcynipoids and that they do not belong to the crown-group of the Figitidae. No synapomorphies of the Cynipidae can be identified in the published descriptions of hodiernocynipines but there is no evidence suggesting that they are more basal microcynipoids or more closely related to the crown-group of the Figitidae, so they may tentatively be left in the Cynipidae.

Several fossils are likely to be phylogenetically nested deep within modern cynipids. *Aulacidea succinea*, for instance, described from a well-preserved specimen in Baltic amber (presumably of Eocene age, about 45 Ma) (Kinsey 1919), is apparently an inquiline belonging to the *Synergus-Saphonecrus* complex. One of two fossils described by Cockerell (1921) from the Oligocene (33–23 Ma) may well have been correctly placed in the Diplolepidini, whereas the identity of the other fossil, supposedly belonging to Cynipini, appears more uncertain.

Kovalev erected the new subfamily Protocharipinae of his Charipidae (corresponding to my Figitidae: Charipinae) for *Protocharips evenhuisi* and *Protimaspis costalis*, both described from amber fossils of upper Cretaceous age (about 80–85 Ma). The specimen of *Protocharips* is very small, like many charipines. Otherwise, there is no compelling evidence in the description to either confirm or reject the placement of *Protocharips* in the Charipinae and the genus is here provisionally retained in a separate tribe in this subfamily. The specimen of *Protimaspis costalis* is larger and the wing venation with the $R_s + M$ vein issuing from the middle of the basal vein suggests that it is misplaced in the Figitidae (Kinsey 1937). Kinsey considered the specimen to be a cynipid but the pterostigmal remnant is short and thick, a macrocynipoid symplesiomorphy that is not found in microcynipoids. The wing venation is remarkably similar to that of *Rasnicynips* and *Protimaspis* is here tentatively transferred to the Rasnicynipidae.

Palaeofigites balticus was described recently from Baltic amber (of Eocene age, about 45 Ma) and placed in a separate subfamily of the Figitidae (Kovalev 1995). The species was compared with the extant genera *Figites* and *Zygosis* but the description and the figure (Kovalev 1995) clearly suggests a member of *Amphitectus*. Further work will have to confirm this placement; here, I tentatively synonymise

Palaeofigitinae with Figitinae and retain *Palaeofigites* as a valid genus.

Palaeoaspicera orientalia was described from amber of lower Palaeocene age (about 60–65 Ma) (Kovalev 1994) and placed in a new subfamily. The drawing and the description do not allow reliable identification of a single synapomorphy of the Aspicerinae. However, the habitus of
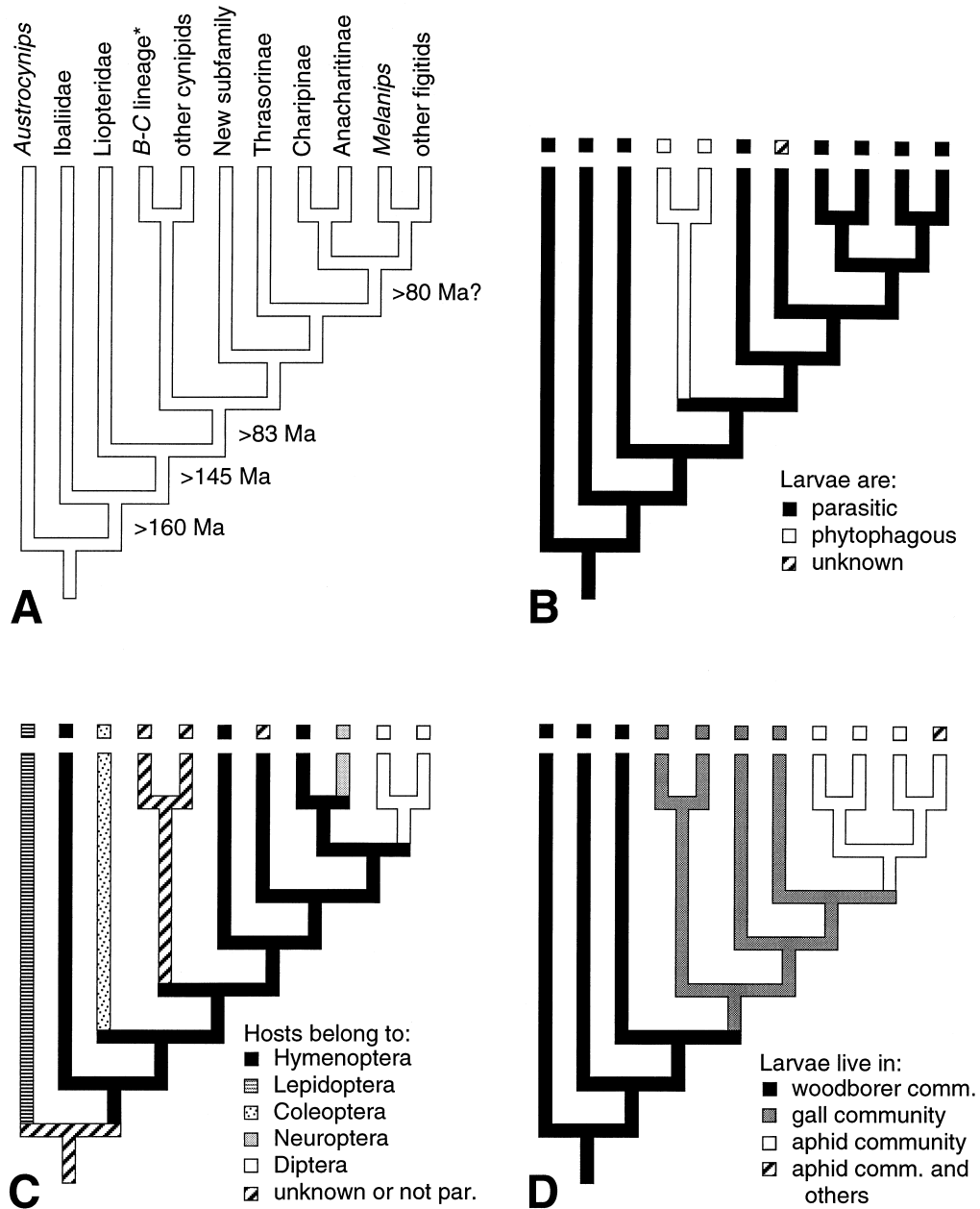

Fig. 8 Parsimony mapping of biological traits onto the higher-level phylogeny of the Cynipoidea. —*A*. Phylogeny used for mappings with estimated dates of cladogenetic events. —*B*. Mapping of the larval life mode. —*C*. Mapping of the insect order attacked by parasitic larvae. —*D*. Mapping of larval microhabitat suggesting that cynipoids have passed through three evolutionary stages, each leaving a set of surviving lineages: (1) in the community of wood-borers; (2) in the gall community; and (3) in the aphid community.

the insect suggests Aspicerinae and I therefore tentatively place the genus in a separate tribe in this subfamily.

Evolution of cynipoids

Mapping of biological characters onto the current estimate of cynipoid phylogeny suggest that there were three important phases in the evolution of cynipoids, each phase leaving a set of surviving lineages (Fig. 8). During the first phase, cynipoids were koinobiont endoparasitoids of wood-boring endopterygote insect larvae (Fig. 8D). The macrocynipoids represent surviving lineages from this early phase, which presumably goes back to the Jurassic or possibly the late Triassic (Fig. 8A). One lineage (the ancestor of microcynipoids) shifted to parasitizing gall-inducing endopterygote larvae, perhaps gall-inducing parasitic wasp larvae. This occurred at least before the late Cretaceous and presumably before the mid Cretaceous (Fig. 8D). Two archaic figitid lineages (the Thrasorinae and the new subfamily) represent remnants of these early gall inhabitants, an offshoot of which produced the spectacular radiation of phytophagous gall inducers and inquilines in the Cynipidae (Fig. 8B). The third phase was initiated when one lineage shifted from attacking gall-inducing hymenopteran larvae to utilizing aphid-parasitic hymenopteran larvae as hosts (similar to the biology of extant Charipinae: Alloxystini). Radiation within the aphid community then followed, producing parasites of aphid-feeding Neuroptera larvae (Anacharitinae) and aphid-feeding Diptera larvae (remaining Figitidae) (Evenhuis 1971). The parasites of Diptera larvae eventually shifted to dipteran hosts in other microhabitats and underwent spectacular radiation, producing among others the immensely successful eucoiline lineage.

The parasitic cynipoids have been extremely conservative in their host choice, as may be expected of koinobiont endoparasites. All victims are endopterygotes and there have apparently been only three shifts between hosts belonging to different insect orders (Fig. 8B). Judging from the number of described species, there are at least 2000 internal branches and equally many terminal lineages in the parasitic part of the cynipoid phylogeny. Thus, less than 1‰ of cynipoid species (lineages between nodes) have apparently succeeded in shifting to a host belonging to a different insect order.

Conclusion

In the past decade we have seen tremendous progress in the understanding of higher cynipoid relationships. Nevertheless, many important problems remain, particularly in the phylogeny of the Figitidae. Until now, phylogenetic analyses of cynipoids have been based largely on external skeletal characters of adults, particularly analyses of higher-level relationships. External morphological characters are still likely to provide a wealth of new information for groups in which they have not yet been studied extensively, e.g. the Figitidae and Cynipini. For other groups, exploration of novel character sources, such as internal anatomy, larval anatomy and molecular sequences, is more likely to contribute important new information in reconstructing cynipoid phylogeny and evolution. New insights are also likely to result from careful and explicit cladistic analysis of the phylogenetic position of cynipoid fossils. The variety of life modes and host associations found in cynipoids and the availability of hypotheses of relationships for many groups present a unique opportunity for studying phylogenetic patterns in the evolution of parasitic insects.

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Appendix. Classification and nomenclature

Summary of the proposed higher classification of the Cynipoidea and suggested nomenclatural changes. For characters defining each group see text, Ronquist (1995 a,b,) and Liljeblad & Ronquist (1998). Extinct taxa are followed by '+'. Taxa that are demonstrably paraphyletic are surrounded by quotation marks. All nomenclatural references appear in the reference list.

AUSTROCYNIPIDAE
Austrocynipinae Riek, 1971
Included genus: *Austrocynips*

IBALIIDAE
Ibaliinae Thomson, 1862
Eileenellinae Kovalev, 1994
Included genera: *Eileenella, Ibalia, Heteribalia*

LIOPTERIDAE
Mayrellinae
Mayrellinae Hedicke, 1922
Included genera: *Kiefferiella, Paramblynotus*

Dallatorrellinae
Dallatorrellinae Kieffer, 1911
Mesocynipinae Kerrich in Hedicke & Kerrich, 1940
Included genera: *Dallatorrella, Mesocynips*

Oberthuerellinae
Oberthuerellinae Kieffer, 1903
Included genera: *Xenocynips, Tessmannella, Oberthuerella*

Liopterinae
Liopterinae Ashmead, 1895
Included genera: *Liopteron, Peras, Pseudibalia*

RASNICYNIPIDAE +
Rasnitsyniidae Kovalev, 1994 preocc.
Rasnicynipidae Kovalev, 1996
Included genera: *Rasnicynips* + , *Protimaspis* +

GEROCYNIPIDAE +
Gerocynipidae Kovalev, 1994
Included genera: *Gerocynips* + , *Arctogerocynips* + , *Antiquecynips* +

CYNIPIDAE
Hodiernocynipinae +
Hodiernocynipinae Kovalev, 1994
Included genus: *Hodiernocynips* +

Cynipinae

'Aylacini'

Aulacini Ashmead, 1903

Aulacideini Fergusson in Gauld & Bolton, 1988 : 143.
    Incorrect emendation of Aulacini Ashmead, 1903.

Included genera: *Barbotinia, Aylax, Iraella, Phanacis, Timaspis, Asiocynips, Zerovia, Panteliella, Parapanteliella, Vetustia, Aulacidea, Isocolus, Neaylax, Rhodus, Hedickiana, Antistrophus, Cecconia, Liposthenes, Diastrophus, Gonaspis, Xestophanes*

Diplolepidini

Diplolepariae Latrielle, 1802. corrected to Diplolepidae.
Rhoditini Hartig, 1840. **New synonymy**.

Included genera: *Diplolepis, Liebelia*

Eschatocerini

Eschatocerini Ashmead, 1903

Included genus: *Eschatocerus*

Pediaspidini

Pediaspidini Ashmead, 1903

Himalocynipinae Yoshimoto, 1970

Included genera: *Himalocynips, Pediaspis*

Cynipini

Cynipsera Latreille, 1802. Corrected to Cynipidae.

Included genera: about 40 valid genera, not listed here

Synergini

Synerginae Ashmead, 1896

Included genera: *Synophromorpha, Ceroptres, Periclistus, Rhoophilus, Synophrus, Saphonecrus, Synergus*

Cynipidae *incertae sedis*
Poncyia, Australofigites

FIGITIDAE

Palaeocynipinae +

Palaeocynipidae Kovalev, 1994. **New status**.

Included genera: *Palaeocynips* + , *Palaeocynipiana* +

New subfamily (to be described elsewhere)

Included genus: New genus (for *Aulacidea nigripes* Barbotin, 1963)

Thrasorinae

Thrasoridae Kovalev, 1994. **New status**.

Included genera: *Euceroptres, Thrasorus, Myrtopsen, Pegacynips, Plectocynips*

Note: Kovalev (1994) proposed the genus *Riekcynips* in this subfamily. The name is not valid since the type species of the genus is a *nomen nudum* (no type specimen designated).

Charipinae

Protocharipini +

Protocharipinae Kovalev, 1994. **New status**.

Included genus: *Protocharips* +

'Alloxystini'

Allotriina Thomson, 1862. Unavailable because *Allotria* is
    preoccupied.

Alloxystinae Hellén, 1931

Lytoxystinae Kovalev, 1994. **New synonymy**.

Included genera: *Hemicrisis, Phaenoglyphis, Alloxysta, Lytoxysta, Carvercharips*

Charipini

Charipinae Dalla Torre & Kieffer, 1910

Dilytinae Kierych, 1979

Included genera: *Apocharips, Dilyta*

Anacharitinae

Anacharitinae Thomson, 1862

Megapelmidae Förster, 1869

Acanthaegilipidae Kovalev, 1996. **New synonymy**.

Proanacharitinae Kovalev, 1996. **New synonymy**.

Included genera: *Acothyreus, Proanacharis, Anacharis, Aegilips, Xyalaspis, Calofigites, Solenofigites, Acanthaegilips*

'Figitinae'

Figitina Thomson, 1862. Corrected to Figitini.

Lonchidini Hellén, 1937

Palaeofigitinae Kovalev, 1996. **New synonymy**.

Included genera: *Melanips, Amphitectus, Seitneria, Sarothrus, Figites, Zygosis, Neralsia, Xyalophora, Lonchidia, Trischiza, Homorus, Paraschiza, Sarothrioides*

Eucoilinae

Eucoilidae Thomson, 1862. **New status**.

Dieucoilini Belizin, 1961. **New status**.

Ganaspini Belizin, 1961. **New status**.

Glauraspidini Belizin, 1961. **New status**.

Kleidotomini Belizin, 1961. **New status**.

Cothonaspinae Belizin, 1961. **New status**.

Diglyphosemini Belizin, 1961. **New status**.

Trichoplastini Kovalev, 1989. **New status**.

Note: Several additional family group names were proposed by Kovalev (1994), but they are not available since they were not accompanied by a diagnosis (ICZN, 3rd ed., Article 13a).

Included genera: about 80 valid genera, not listed here

Pycnostigminae

Pycnostigmusinae Cameron, 1905. Emended to
    Pycnostigminae.

Tyloseminae Kieffer, 1905

Note: The name of the subfamily is sometimes incorrectly spelt Pycnostigmatinae. The second part of *Pycnostigmus* is latinized from the Greek *stigma* with a change of ending. In deriving the subfamily name, the stem is that appropriate to the latinized form (ICZN, 3rd ed., Article 29b(iii)). The correct subfamily name is thus Pycnostigminae and not Pycnostigmatinae. The latter would have been correct given that the original Greek form, *stigma*, had been used in the genus name on which the subfamily was based.

Included genera: *Pycnostigmus, Tylosema, Trjapitziniola*

Aspicerinae

Note: The name of the subfamily is sometimes incorrectly spelt Aspiceratinae. The second part of *Aspicera* is latinized from the Greek *keras* with a change of ending. In deriving the subfamily name, the stem is that appropriate to the latinized form (ICZN, 3rd ed., Article 29b(iii)). The correct subfamily name is thus Aspicerinae and not Aspiceratinae. The latter would have been correct given that the original Greek form had been used in the genus name on which the subfamily was based.

Palaeoaspicerini +

   Palaeoaspicerinae Kovalev, 1994. **New synonymy**.
Included genus: *Palaeoaspicera +*

Aspicerini

   Aspicerinae Dalla Torre & Kieffer, 1910
   Onychiina Thomson, 1862
Included genera: *Paraspicera, Aspicera, Prosaspicera, Balna, Omalaspis, Anacharoides, Callaspidia, Ceraspidia*

Emargininae

   Emarginidae Kovalev, 1994. **New status**.
   Weldiolini Kovalev, 1994. **New synonymy**.
   Quinlanini Kovalev, 1994. **New synonymy**.
Included genera: *Emargo, Thoreauella, Bothriocynips, Weldiola, Quinlania*

Figitidae *incertae sedis*
Petricynips

PROPOSED CHANGES IN GENERIC CLASSIFICATION
Hemicrisis Förster, 1869 **removed from synonymy** with
   Phaenoglyphis Förster, 1869
Amphitectus Hartig, 1840 **removed from synonymy** with
   Sarothrus Hartig, 1840
Seitneria Tavares, 1928 **removed from synonymy** with
   Figites Latreille, 1802