Phylogeny and Geological History of the Cynipoid Wasps (Hymenoptera: Cynipoidea)

ZHIWEI LIU,[1] MICHAEL S. ENGEL,[2] AND DAVID A. GRIMALDI[3]

CONTENTS

[1] Department of Biological Sciences, Eastern Illinois University, 600 Lincoln Avenue, Charleston, IL 61920 (zliu@eiu.edu).
[2] Division of Invertebrate Zoology, American Museum of Natural History; Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive–Suite 140, University of Kansas, Lawrence, KS 66049-2811 (msengel@ku.edu).
[3] Division of Invertebrate Zoology, American Museum of Natural History (grimaldi@amnh.org).

ABSTRACT

The geological history of the wasp superfamily Cynipoidea is reviewed, with the description of various new taxa, being mostly in Late Cretaceous amber from New Jersey and Canada. The various fossil lineages are incorporated into a phylogenetic analysis of the superfamily, and their implications for understanding the evolution of the group are explored. The following new taxa or taxonomic changes are proposed (authorship of all taxa is Liu and Engel): **Protimaspidae**, new family; **Stolamissidae**, new family; *Stolamissus*, new genus; *Stolamissus mirabilis*, new species; **Prioliopterinae**, new subfamily; *Proliopteron*, new genus; *Proliopteron redactus*, new species; **Goeraniinae**, new subfamily; *Goerania*, new genus; *Goerania petiolata*, new species; *Micropresbyteria*, new genus; *Micropresbyteria caputipressa*, new species; *Anteucoila*, new genus; *Anteucoila delicia*, new species; *Jerseucoila*, new genus; *Jerseucoila plesiosoma*, new species; *Syneucoila*, new genus; *Syneucoila magnifica*, new species; *Tanaoknemus*, new genus; *Tanaoknemus ecarinatus*, new species; *Kinseycynips*, new genus; *Kinseycynips succinea* (Kinsey), new combination. The extinct family Rasnicynipidae is newly transferred to Figitidae and classified as a basal subfamily therein (Rasnicynipinae, status novus). The Gerocynipidae, its type genus *Gerocynips*, and the type species upon which they are founded, *Gerocynips zherichini*, are found to be nomenclaturally unavailable. *Gerocynips zherichini* is regarded as a nomen nudum; the genus as newly validated is *Gerocynips*, new genus (with *G. siberica* Kovalev as type species); and the family as validated is **Gerocynipidae**, new family. The fossil records of Cynipoidea are summarized.

INTRODUCTION

Wasps of the superfamily Cynipoidea (Apocrita: Proctotrupomorpha) are one of the more remarkable lineages among the parasitoid Hymenoptera. The superfamily is relatively small by comparison to the more diverse lineages of apocritan wasps, with presently ca. 3000 described species (Ronquist, 1999). However, Nordlander (1984) has estimated that there are may be as many as 20,000 cynipoid species, and intensive fieldwork and monographic studies are desperately needed, particularly in species-rich regions such as Mexico. Basal lineages of Cynipoidea are generally parasitoids of wood-boring insect larvae, such as immatures of various beetle families, oecophorid moths, or siricid wood wasps (Liu and Nordlander, 1994; Ronquist, 1995a; Liu, 2001; Liu et al., 2007). This primitive parasitoid biology is, indeed, the plesiomorphic condition for the parasitoid Hymenoptera (Euhymenoptera) as a whole (Grimaldi and Engel, 2005). Not surprisingly, the rather robust, parasitoid lineages of Cynipoidea (a.k.a. "macrocynipoids") form a grade to the so-called "microcynipoids." The microcynipoids consist of two extant families, the Figitidae and the Cynipidae. Figitids diverge biologically from the primitive syndrome of parasitizing wood-boring hosts and are instead parasitoids of various holometabolan larvae ranging from flies to lacewings, and some even victimize cynipids. Still other figitids are hyperparasitoids of braconid and chalcidoid primary parasitoids of aphids and psyllids (Buffington et al., 2005). Most remarkably, however, the Cynipoidea includes, aside from these parasitic lineages, secondarily phytophagous species, namely the gall wasps (family Cynipidae). Indeed, the gall wasps are one of the three most notable transitions within the Hymenoptera from a parasitoid or predatory life-history to a vegetarian habit (the other two being the fig wasps (Agaonidae) and the bees (Anthophila), although others do, of course, exist). Cynipids produce as larvae characteristic galls in angiosperm tissue, the most famous of which are the oak gall wasps developing in various tissues of species of the genus *Quercus* (Fagaceae). All cynipids feed on dicotyledonous angiosperms except for a single species, *Diastrophus smilacis* Ashmead, which induces galls on the monocotyledonous *Smilax* (Krombein et al., 1979; Ronquist and Liljeblad, 2001). Phytophagous inquilines of other cynipids have also evolved within the family (Ronquist, 1994). The Cynipoidea clearly encompasses an amazing range of

biological variation and significant evolutionary transitions making them worthy of investigation.

The Cynipoidea have long been assumed to be a natural group. Although not supported by any striking autapomorphy, recent studies have provided morphological evidence for monophyly. Ronquist (1999) listed the following features as synapomorphic for the superfamily: absence of radicle; forewing media (M) displaced anteriorly, approaching the posterior end of the marginal cell, distinctly angled and not running parallel to the posterior wing margin; abdominal sterna II (petiolar) and III (first postpetiolar) abutting or fused; metasoma distinctly laterally compressed; and forewing costa (C) absent. Ronquist (1999) also discussed several other possible autapomorphies for the superfamily while Ronquist (1995b, 1999), Ronquist and Nieves-Aldrey (2001), Vårdal et al. (2003), and Nieves-Aldrey et al. (2004) have summarized the phylogeny and classification.

Fossils of Cynipoidea are, unfortunately, rare and only a handful of species have been definitively assigned to the superfamily (see appendix 1). The first fossils assigned to Cynipoidea were described by Dr. Alfred C. Kinsey from material preserved in Baltic and Canadian amber (Kinsey, 1919, 1937). The latter fossil, *Protimaspis costalis* Kinsey, from the Late Cretaceous (Campanian) amber of Cedar Lake, Manitoba, Canada, was particularly notable as it was hitherto the oldest, definitive fossil cynipoid. For most of the 20th century Kinsey's species stood alone as the geological evidence for the Cynipoidea. Relatively recently, however, Oleg V. Kovalev (1994, 1995, 1996) described a small wealth of cynipoids from deposits of Eurasia, greatly expanding the fossil record of the superfamily. This work included several new Late Cretaceous species in mudstones of the Ola Formation (Cenomanian) along the banks of Obeshchayushchiy Creek in the Russian Far East and in amber from the Kheta Formation of the Taimyr Peninsula (Santonian), as well as additional taxa from Baltic amber (middle Eocene) (appendix 1). Herein we describe eight new North American fossils of Cynipoidea from the Late Cretaceous amber of Middlesex County in central New Jersey (Turonian) and from Medicine Hat, Alberta, Canada (Campanian). In addition, we provide critical new data for Kinsey's fossil species. Although many of the cynipoid fossils from Eurasia are well preserved and suitable for comparison with extant cynipoids, particularly those entombed in amber, these species were only recently placed into a phylogenetic framework (Ronquist, 1995b, 1999). None, however, was included in cladistic analyses with modern taxa, and we therefore have for the first time attempted to incorporate such paleontological data into analyses of higher level cynipoid phylogeny. With this wealth of new information we provide a new overview of the phylogeny and geological history of the Cynipoidea.

Terminology for the descriptions follows that of Ronquist and Nordlander (1989) and Ronquist (1995a), although wing vein terminology follows that more widely used across the Hymenoptera, and Pterygota at large, so as to highlight homologies (e.g., "first free abscissa of M" is used in place of "basalis" or "basal vein", although we denote the latter in parentheses to avoid confusion). Throughout we number segments according to their metasomal number rather than to abdominal count owing to the fusion of the first abdominal segment into the posterior of the thorax. Metrics are to be considered approximate because the optimal angle for specific measurements was not always attainable owing to the position of the specimen in the amber. The abbreviations F, S, and T are occasionally used for flagellomere, metasomal sternum, and metasomal tergum, respectively, and AMNH, RTMP, ROM, and CNC are used for American Museum of Natural History (New York), Royal Tyrell Museum of Paleontology (Drumheller, Canada), Royal Ontario Museum (Toronto, Canada), and the Canadian National Collection (Ottawa, Canada), respectively.

SYSTEMATIC PALEONTOLOGY

SUPERFAMILY CYNIPOIDEA LATREILLE

DIAGNOSIS: Small to medium-sized insects without metallic luster. Antenna filiform, usually with 11–12 and 12–13 flagellomeres in female and male, respectively; radicle absent. Pronotum posteriorly reaching tegula;

mesoscutellum in lateral view prominent. Forewing usually present and with distinctive triangular radial cell; C always absent; pterostigma always absent except in *Austrocynips*; M displaced anteriorly, approaching posterior end of marginal cell, distinctly angled and not running parallel to posterior wing margin. Tarsi pentamerous (i.e., 5-segmented). Metasoma almost always laterally compressed; metasomal sterna I (petiolar) and II (first postpetiolar) abutting or fused.

COMMENTS: The superfamily Cynipoidea presently comprises five extant and three extinct families, two of which are newly described herein. A summary of the classification of Cynipoidea is provided in table 1. Weld (1952) provided the most recent monograph of the world genera, but it is now largely out of date for most groups. Several works have examined the higher classification, establishing relationships and redefining the families, subfamilies, and tribes (e.g., Ronquist, 1995b, 1999; Nieves-Aldrey et al., 2004). In addition, some groups have been newly monographed to the level of species – e.g., Liu and Nordlander (1992, 1994) and Liu (1998b) for Ibaliidae; Ronquist (1995a), Liu (2001), and Liu et al. (2007) for Liopteridae, the first for world genera, the latter two for species of Dallatorrellinae and part of Mayrellinae; Nieves-Aldrey (2001) for Cynipidae of Iberia; and Ronquist and Nieves-Aldrey (2001) for Parnipinae (Figitidae).

Protimaspidae Liu and Engel, new family

TYPE GENUS: *Protimaspis* Kinsey, 1937.

DIAGNOSIS: The new family shares with Ibaliidae two unique characters that are not found in any other family of Cynipoidea: (1) mesopleuron with an oblique, strongly impressed femoral groove; (2) metacoxa dorsally strongly impressed longitudinally, anterolaterally with a triangular crest. The family can be easily distinguished from the Ibaliidae by the absence of a pair of submedian processes posteriorly on the mesoscutellum; the relatively small area of the pronotum behind the anterior vertical plate; the metafemur distinctly longer than the metacoxa; the short marginal cell of the forewing, about four times as long as wide; and the female tergum VII not enlarged.

TABLE 1
Hierarchical Classification of Superfamily Cynipoidea
(Updated from Ronquist, 1999, and Ronquist and Nieves-Aldrey, 2001)

Superfamily CYNIPOIDEA Latreille, 1802
"*macrocynipoids*" [paraphyletic]
  Family AUSTROCYNIPIDAE Riek, 1971
  Family IBALIIDAE Thomson, 1862
    Subfamily Eileenellinae Kovalev, 1994
    Subfamily Ibaliinae Thomson, 1862
  Family †PROTIMASPIDAE Liu and Engel, new family
  Family †STOLAMISSIDAE Liu and Engel, new family
  Family LIOPTERIDAE Ashmead, 1895
    Subfamily †Proliopterinae Liu and Engel, new subfamily
    Subfamily Mayrellinae Hedicke, 1922
    Subfamily Dallatorrellinae Kieffer, 1911
    Subfamily †Goeraniinae Liu and Engel, new subfamily
    Subfamily Liopterinae Ashmead, 1895
    Subfamily Oberthuerellinae Kieffer, 1903
"*microcynipoids*"
  Family †GEROCYNIPIDAE Liu and Engel, new family
  Family FIGITIDAE Thomson, 1862
    Subfamily †Rasnicynipinae Kovalev, 1996, new status
    Subfamily †Palaeocynipinae Kovalev, 1994
    Subfamily Parnipinae Ronquist and Nieves-Aldrey, 2001
    Subfamily Thrasorinae Kovalev, 1994
    Subfamily Charipinae Dalla Torre and Kieffer, 1910
      Tribe †Protocharipini Kovalev, 1994
      Tribe Alloxystini Hellén, 1931
      Tribe Charipini Dalla Torre and Kieffer, 1910
    Subfamily Anacharitinae Thomson, 1862
    Subfamily Figitinae Thomson, 1862
    Subfamily Eucoilinae Thomson, 1862
    Subfamily Pycnostigminae Cameron, 1905
    Subfamily Aspicerinae Dalla Torre and Kieffer, 1910
      Tribe †Palaeoaspicerini Kovalev, 1994
      Tribe Aspicerini Dalla Torre and Kieffer, 1910
    Subfamily Emargininae Kovalev, 1994
  Family CYNIPIDAE Latreille, 1802
    Subfamily †Hodiernocynipinae Kovalev, 1994
    Subfamily Cynipinae Latreille, 1802
      Tribe Aylacini Ashmead, 1903
      Tribe Diplolepidini Latreille, 1802
      Tribe Eschatocerini Ashmead, 1903
      Tribe Pediaspidini Ashmead, 1903
      Tribe Cynipini Latreille, 1802
      Tribe Synergini Ashmead, 1896

Fig. 1. Photomicrograph of holotype female of *Protimaspis costalis* Kinsey (ROM) in Canadian amber from Cedar Lake.

COMMENTS: Ronquist (1999) mentioned that the wing venation of *Protimaspis* is ''remarkably similar to that of *Rasnicynips*'', but this statement is obviously incorrect. The vein Rs+M is directed to the posterior end of the first free abscissa of M (= basalis vein) in *Rasnicynips* (Kovalev, 1994: as *Rasnitsynia* therein), but to the middle of the latter vein in *Protimaspis* (Kinsey, 1937) (figs. 1, 2).

Genus *Protimaspis* Kinsey

Protimaspis Kinsey, 1937: 22. Type species: *Protimaspis costalis* Kinsey, 1937.

DIAGNOSIS: As for the family (see above).

Protimaspis costalis Kinsey
figures 1, 2

Protimaspis costalis Kinsey, 1937: 22.

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: The placement of this taxon has historically been hindered by several factors. For example, Kinsey (1937) in his description of the species stated that the sex of the fossil ''is not quite clear'', but we have no doubt that this is a female. Certainly more details of the specimen can be observed owing to the advances in methods of preparation as well as in optical equipment available. Furthermore, Kinsey's original description used characters that are now understood to be superficial. We therefore provide the following new description for the species.

Female. Body length 1.9 mm; forewing length 1.8 mm. Antenna 15-segmented, with distinct placodeal sensilla on all flagellomeres except F1; F1 slightly bent medially. Frons flat, without carinate structures. Lateral part of cranium distinctly expanded behind compound eye; gena broad; occipital carina
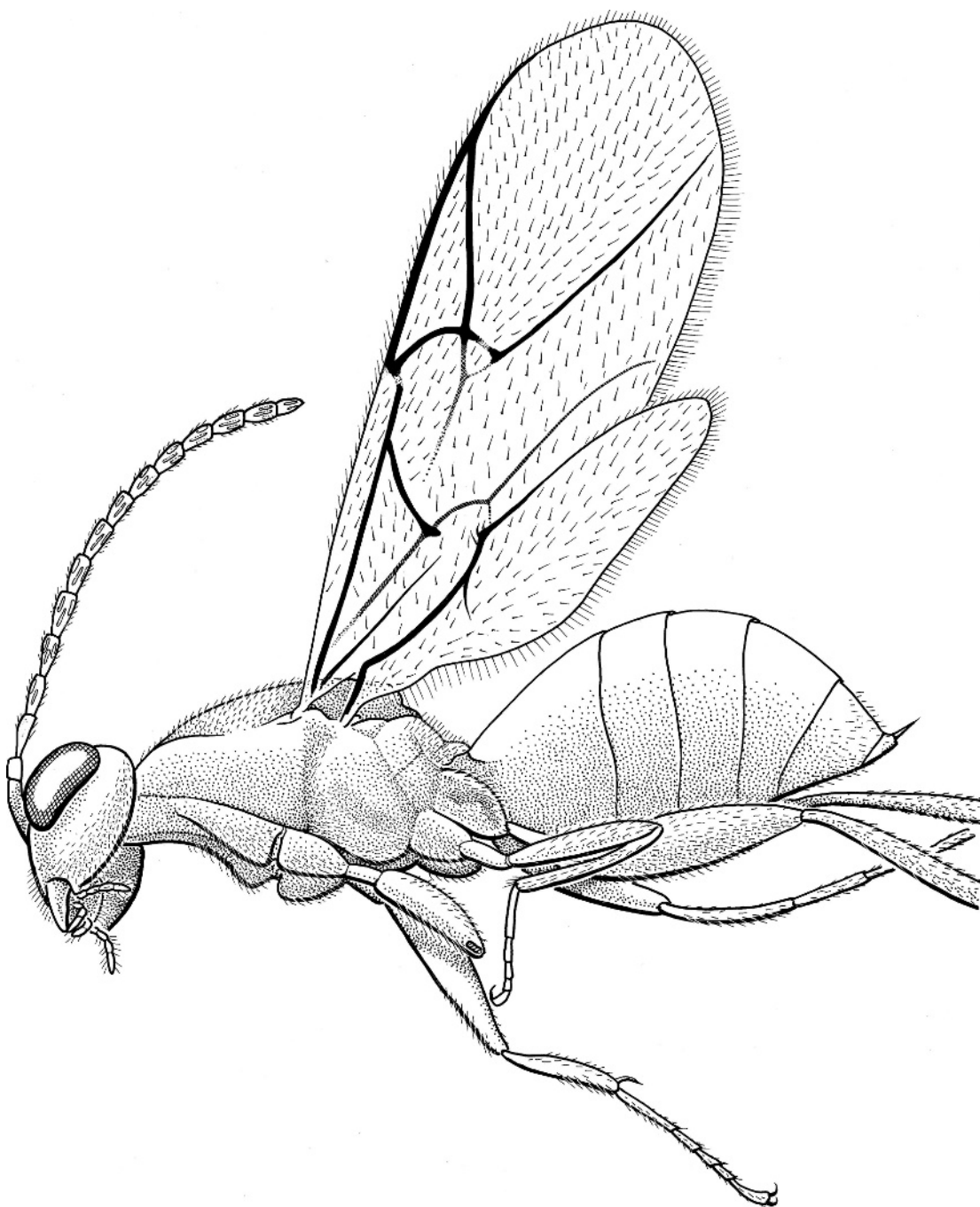
Fig. 2.   Holotype female of *Protimaspis costalis* Kinsey (ROM).

absent. Median dorsal length of pronotum behind anterior vertical plate short; pronotal carina absent; pronotal crest low and not incised medially, and dorsal pronotal area present and short; posteroventral margin of pronotum long and straight; lateral surface of pronotum glabrous. Mesonotum transversely costate; median mesoscutal impression and notauli absent; mesoscutellar suture transverse; mesoscutellum posteriorly sloped, without projection or process; mesopleuron ventrally protruding; mesocoxa directed obliquely backward, inserted on separate, oblique posterior area; median mesopleural impression and lateroventral mesopleural carina absent; mesopleural triangle slightly depressed with longitudinal striation; mesofemural groove present, granulate. Metapleural sulcus abruptly bent at middle; metepisternum subrectangular. Propodeal spiracular opening not completely covered by spiracular process, similar to extant *Ibalia* when observed laterally; lateral propodeal carina present; nucha short. Forewing lacking pterostigma; marginal cell closed, four times as long as wide; bulla in $Sc+R_1$ present; 2r-rs directed obliquely, sloping outward posteriorly; Rs+M with mesal end meeting first free abscissa of M (= basal vein) slightly behind the middle; areolet present. Metacoxa dorsally strongly depressed and lateroanteriorly with a triangular process. Petiolar annulus crescentic and glabrous; metasomal T4 largest among all terga, lateroposterior margin more or less vertical and straight; metasomal T3–6 subequal along middorsal line. **Male.** Unknown.

HOLOTYPE: Female, Late Cretaceous (Campanian), Cedar Lake, Manitoba, Canada; deposited in the Royal Ontario Museum.

Stolamissidae Liu and Engel, new family

TYPE GENUS: *Stolamissus* Liu and Engel, new genus.

DIAGNOSIS: This new family is distinguished from other cynipoids by the apomorphic combination of the following traits: (1) mesosoma short and high in lateral view; (2) pronotal crest and dorsal pronotal area absent; (3) mesocoxa directed vertically and downward; (4) lateral pronotal carina distinct; (5) pterostigma lacking (figs. 3, 4); (6) Rs+M of forewing with mesal end meeting the first

free abscissa of M (= basal vein) at about the middle; and, (7) posterior margin of metasomal T2 not distinctly oblique.

Stolamissus Liu and Engel, new genus

TYPE SPECIES: *Stolamissus mirabilis* Liu and Engel, new species.

DIAGNOSIS: As for the family (see above).

ETYMOLOGY: The new genus-group name is derived from the Latin *stolo* (meaning "branch") and *amissus* (meaning "lost"), which together mean "lost branch" (a reference to the fact that this clade was lost via extinction within Cynipoidea). The name is masculine.

COMMENTS: The genus has several of the symplesiomorphies that are shared among the macrocynipoids, including marginal cell of forewing relatively long and anteriorly closed, no bulla in $Sc+R_1$, remnant of pterostigma short and thick, and second metasomal tergum (= third abdominal tergum) large with succeeding abdominal terga narrow. In addition, the pronotum is distinctly raised dorsoanteriorly, a condition similar to that of Ibaliidae and Liopteridae, and the well-developed lateral pronotal carina resembles that of the liopterids. On the other hand, it appears that the mesocoxae are inserted vertically downward, a feature shared by the microcynipoids, but not obliquely on a ventrally protruding, separate, and oblique posterior area as in the macrocynipoids. The mesopectus appears not to protrude ventrally, a feature considered a synapomorphy for the microcynipoids (Ronquist, 1995a, 1999); however, we are somewhat cautious about this observation because of the presence of a bubble laterally above the mesopectal area, and our interpretation of this feature may be in error.

Stolamissus mirabilis Liu and Engel,
new species
figures 3, 4

Cynipidae sp.: Grimaldi et al., 2000: 73 [figured].

DESCRIPTION: **Female.** Body length 0.8 mm; forewing length 0.7 mm. Body entirely black; antennae and legs dark brown; wings hyaline, without any macula or band. Antenna 14-segmented; flagellum distinctly expanded

Fig. 3. Photomicrograph of holotype female of *Stolamissus mirabilis* Liu and Engel, new genus and species (NJ-709).

toward apex; scape and pedicel subequal in both length and thickness, slightly longer and much wider than F1; F1 distinctly longer than F2; apical and subapical flagellomeres somewhat fused with each other, other flagellomeres subequal to F1; elongate placodeal sensilla distinctly present on F8–12. Frons, vertex, and gena glabrous; median frontal carina absent; gena not expanded behind compound eye; length of compound eye about three times as long as malar space. Anterior plate of pronotum with dense punctures and posteriorly delimited by prominent lateral pronotal carinae; lateral surfaces of pronotum irregularly carinate in lower part and narrowly bridged medially. Mesoscutum transversely costate; median impression present in posterior two-thirds; notauli percurrent and prominent; mesoscutellar foveae transverse; mesoscutellum posteriorly sloped and without process; mesopleuron mostly glabrate, ventrally depressed along lower margin; median impression and lateroventral carina absent; mesopectus not distinctly protruding ventrally, mesocoxa directed vertically downward and not inserted on separate, oblique posterior

area (the mesopectal area is partly obscured by a large bubble and therefore our interpretation of the condition should be considered tentative). Propodeum devoid of processes. Wings hyaline, surface covered with appressed setae, margins ciliate. Forewing with marginal cell closed, slightly more than twice as long as wide; bulla in $Sc+R_1$ absent, 2r-rs oblique, sloping outward posteriorly; areolet present; Rs+M arising from about middle of first free abscissa of M (= basal vein). Mesofemur expanded dorsoventrally; first metatarsomere much shorter than combined length of second through fifth metatarsomeres; metapretarsal claw with basal lobe. Metasoma not distinctly compressed; metasomal T2 (= third abdominal tergum) relatively large, about one-third length of postpetiolar metasoma; metasomal T3–7 dorsally subequal. **Male.** Unknown.

HOLOTYPE: Female, AMNH NJ-709, Late Cretaceous (Turonian), White Oak Pit, Sayreville, Middlesex County, New Jersey, coll. AMNH expedition, 1996; deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, AMNH.

ETYMOLOGY: The specific epithet is the Latin word *mirabilis*, meaning "beautiful and good-looking".

FAMILY LIOPTERIDAE ASHMEAD

DIAGNOSIS: Ronquist (1995a) recently revised the family and suggested the following characters as apomorphies: lateral surface of pronotum and dorsal surface of mesoscutellum foveate; acetabulum more or less vertical, divided into two furrows for procoxa by a strong median keel; acetabular carina describing a ω-shape; metapleural sulcus reaching anterior metapectal margin far above the midheight; intermetacoxal processes present; lateral pronotal carina reaching the raised ventral pronotal margin; laterodorsal process of mesoscutellum present; lateroventral carina of mesopectus present; nucha long; metatibia shorter than metafemur; petiolar annulus complete, tergal and sternal parts fused completely; occipital carina present; and mesopleural impression present.

COMMENTS: Where known, extant Liopteridae are parasitoids of wood-boring beetles of families such as Buprestidae, Cerambycidae, and Curculionidae (Ronquist, 1995a; Liu et al.,
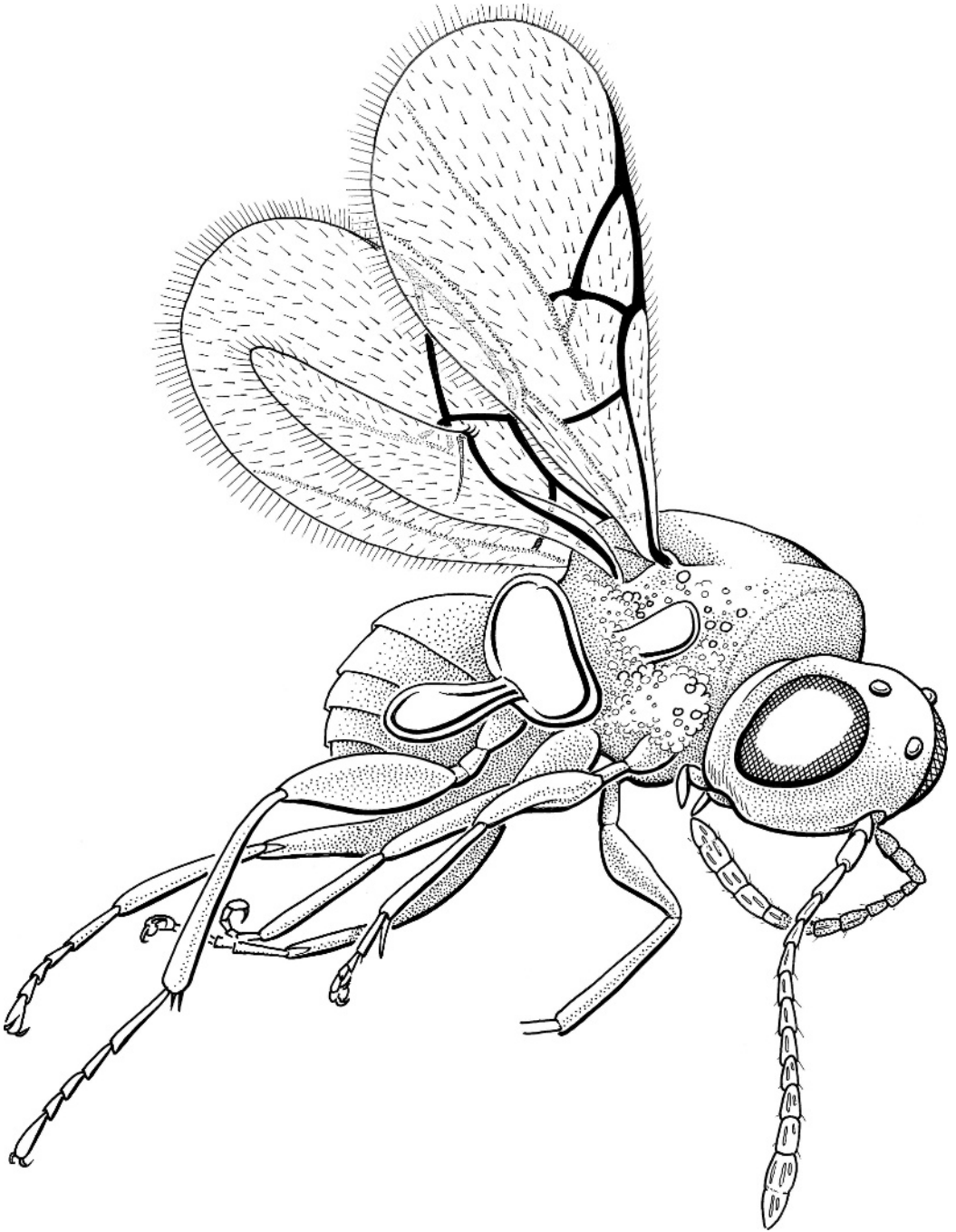
Fig. 4.   Holotype female of *Stolamissus mirabilis* Liu and Engel, new genus and species (NJ-709).

2007). The genera of Liopteridae were revised by Ronquist (1995a) and an analysis of their relationships was undertaken. The genera of the family are presently segregated into four subfamilies: the Liopterinae (New World) and Oberthuerellinae (African) are sisters, with Dallatorrellinae (Asian and Australian) as sister to them, and the Mayrellinae (cosmopolitan except the Australian region) basal.

According to our cladistic analyses the new fossil genus *Proliopteron* is basal to a clade consisting of all other Liopteridae (see below). In addition, the genus *Goerania*, described below, obviously belongs to the clade consisting of the subfamilies Oberthuerellinae + Liopterinae, although we have decided not to include it in the cladistic analysis owing to the limited number of observable characters. Both genera are characterized by an array of distinct features and therefore we herein erect two new subfamilies, as Proliopterinae and Goeraniinae, to accommodate them.

Proliopterinae Liu and Engel, new subfamily

TYPE GENUS: *Proliopteron* Liu and Engel, new genus.

DIAGNOSIS: As for the genus (see below).

Proliopteron Liu and Engel, new genus

TYPE SPECIES: *Proliopteron redactus* Liu and Engel, new species.

DIAGNOSIS: The genus can be easily distinguished from all other genera in the family by a combination of: (1) characteristic liopterid-like sculpture on gena and lateral surface of pronotum absent, (2) lateral pronotal carina dorsally very reduced, (3) posterior mesoscutellar processes absent, (4) metatibial lobe absent, (5) pubescence of wings reduced such that it is represented by mere dots, and (6) mesocoxa inserted to mesopectus vertically, not on a separate, projected area (a few modern species of *Paramblynotus* also have this feature).

COMMENTS: *Proliopteron* is the sister clade to all other liopterids. The genus lacks several of the synapomorphic features shared by other liopterids, including the characteristic foveate integumental sculpturing of the pronotum and mesoscutellum, the median mesopleural impression, the posterior mesoscutellar pro-

cess, and the metatibial lobe. Some of the features of the genus are also shared by *Mesocynips*, including the lack of foveate sculpturing on the pronotum and mesoscutellum and the absence of the posterior mesoscutellar process.

ETYMOLOGY: The genus-group name is a combination of *pro-* (Latin, meaning "before") and *Liopteron*, the type genus of the family. The name is masculine.

Proliopteron redactus Liu and Engel, new species
figures 5, 6

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body length 1.0 mm; forewing length 0.9 mm. Body mostly black to dark brown; antenna and legs dark brown; wings hyaline, without any macula or band. Antennae cylindrical and slightly expanded toward apex, 12-segmented; pedicel almost spherical, half as long as scape; F1 as long as F2; other flagellomeres subequal to F1, except apical flagellomere is twice as long as preceding one; elongate placodeal sensilla present on all flagellomeres. Frons, vertex, and gena glabrous; lower face with flat but distinct median carina complete to clypeus, otherwise without apparent sculpture; gena not expanded behind compound eye; compound eye longer than malar space by one-third. Lateral surfaces of pronotum glabrous; lateral pronotal carina dorsally reduced. Mesoscutum glabrate, without transverse costa; mesoscutellum posteriorly sloped without process; mesopleuron glabrous and ventrally bordered by straight lateroventral carina; mesopectus not protruding ventrally, mesocoxa directed vertically and not inserted on separate, oblique posterior area. Propodeum devoid of processes; lateral propodeal carina dorsally raised into a distinct right-angular lobe. Wings entirely hyaline, all wing margins ciliate except anterior margin of forewing; pubescence of wings reduced and represented by mere dots. Forewing with marginal cell closed, four times as long as wide; bulla in Sc+R$_1$ present; 2r-rs oblique, sloping outward posteriorly; areolet absent; Rs+M arising from somewhat anterior to middle of first free abscissa of M (= basal vein). First metatarsomere slightly shorter than combined length

Fig. 5. Photomicrograph of holotype female of *Proliopteron redactus* Liu and Engel, new genus and species (CAS-409).

of second through fifth metatarsomeres; meta-prestaral claws simple, without basal lobe. Metasoma inserted high on propodeum, post-subpleuron long; metasomal T2–4 (= abdominal T3–5) subequal in size, metasomal T5 largest; metasomal T7 exposed, not completely covered by metasomal T6; metasomal S3–5 (= abdominal S4–6) exposed, not covered by metasomal S2; ovipositor exserted, apically with ventral serrations (fig. 6). **Male.** Unknown.

HOLOTYPE: Female, CNC CAS-409, Late Cretaceous (Campanian), Medicine Hat, Alberta, Canada, coll. J.F. McAlpine, 1971-VII-8–10 [8–10 July 1971]; deposited in the CNC.

ETYMOLOGY: The specific epithet is derived from the Latin word *redactus* meaning "reduced" and refers to the reduced pubescence on the wing membranes.

Goeraniinae Liu and Engel, new subfamily

TYPE GENUS: *Goerania* Liu and Engel, new genus.

DIAGNOSIS: As for the genus (see below).

Goerania Liu and Engel, new genus

TYPE SPECIES: *Goerania petiolata* Liu and Engel, new species.

DIAGNOSIS: Median flagellomere of antenna cylindrical, with very dense longitudinal placodeal sensilla. Head distinctly impressed posteriorly in dorsal view; gena expanded behind compound eyes; vertex, gena, and occiput glabrous. Anterior pronotal flange long; submedian depression of pronotum present and open laterally; dorsal pronotal area distinct; pronotal crest not observable; lateral surface of pronotum sloped evenly, without foveate sculpture. Mesoscutum transversely
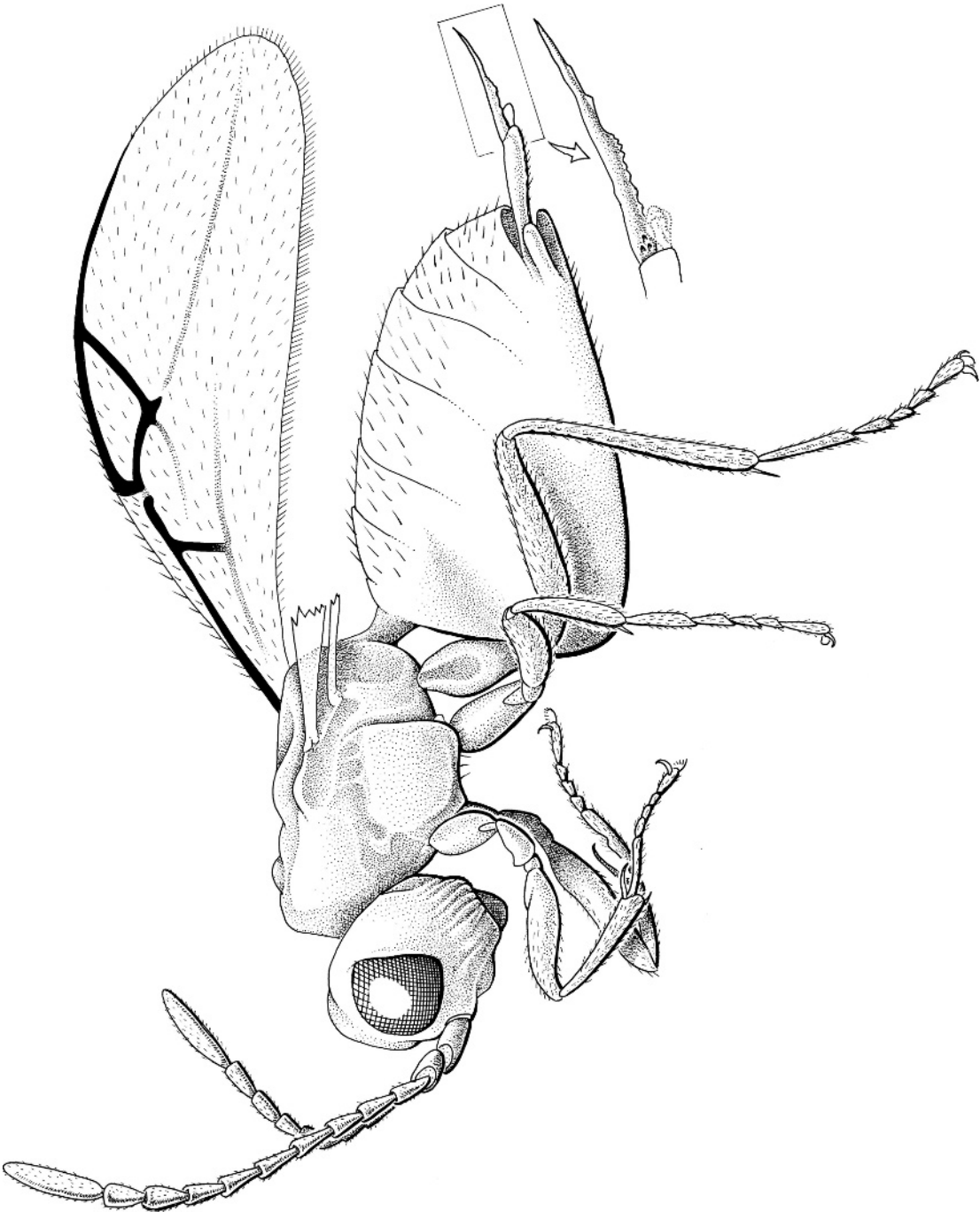
Fig. 6. Holotype female of *Proliopteron redactus* Liu and Engel, new genus and species (CAS-409).

costate; median impression and lateral notauli distinct; lateral margin of axilla conspicuously raised anteriorly. Forewing without pterostigma; 2r-rs long and perpendicular to anterior wing margin; marginal cell closed; bulla in Sc+R$_1$ present; Rs+M issuing from close to posterior two-thirds of first free abscissa of M (= basal vein). Mesocoxa inserted vertically; metatibia distinctly longer than metafemur and with a longitudinal carina on dorsal surface. Metasoma strongly compressed laterally; nucha low; petiolar annulus positioned low, long; petiole at least twice as long as wide, longitudinally carinate; posterior margin of petiole and anterior margin of metasomal T1 abutting, dorsal margins of the two more or less continuous (i.e., without constriction between segments); metasomal T2–7 of female visible and subequal in length along middorsal line.

ETYMOLOGY: The genus is named after Dr. Göran Nordlander, Uppsala, Sweden, who has significantly contributed to our current understanding of cynipoid relationships and mentored several of the most active cynipoid researchers worldwide.

COMMENTS: The new genus belongs to the clade consisting of the subfamilies Oberthuerellinae and Liopterinae. Although it is difficult to collect sufficient characters to incorporate the species into the analysis of cynipoid phylogeny, several observable features strongly indicate its placement within this clade, including the following: (1) lateral margin of axilla conspicuously raised anteriorly; (2) petiolar annulus long, median dorsal length at least twice as long as minimum dorsal width (estimated from lateral view); and (3) posterior margin of petiole (= metasomal T1) and anterior margin of metasomal T2 abutting, dorsal margins of the two more or less continuous (i.e., without constriction between segments).

Goerania can be easily separated from genera in the Oberthuerellinae and Liopterinae by the absence of foveate sculpture on the lateral surface of the pronotum and the postpetiolar terga of the metasoma being subequal in length.

Goerania petiolata Liu and Engel, new species
figures 7, 8

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body length 3.0 mm, forewing length 2.5 mm. Antenna filiform, 14-segmented. Anterior plate of pronotum transversely costate. Mesoscutum transversely weakly costate; median impression distinctly present in posterior one-third; notauli percurrent; parascutal carina posterolaterally smooth and not raised; mesoscutellum foveate-reticulate, posteriorly broadly rounded; dorsal lateral process present; scuto-scutellar suture transverse and separated into two foveae by a median carina. Forewing marginal cell closed, 3.8 times as long as wide; Rs+M proximally directed toward posterior two-thirds of basal vein; areolet distinct. First metatarsomere slightly shorter than combined length of second through fifth metatarsomeres. Petiolar annulus long, median dorsal length at least two times as long as minimum dorsal width (estimated from lateral view). **Male.** Unknown.

HOLOTYPE: Female, CAS, Late Cretaceous (Campanian), Medicine Hat, Alberta, Canada; deposited in the CNC.

ETYMOLOGY: The specific epithet is taken from Latin, *petiolata*, meaning "stalked", and is a reference to the long petiolar segment of the species. Indeed, this is the oldest species with an extended petiole in the Cynipoidea.

FAMILY FIGITIDAE THOMSON

DIAGNOSIS: Figitids are morphologically diverse, making unifying traits a challenge to identify. Ronquist (1995b, 1999) suggested that the Figitidae are supported by two apomorphies: presence of a distinct point of weakness in the eighth metasomal tergum of the female at the position of the gonoplac (= third valvula), and forewing Rs+M situated close to the end of the first free abscissa of M (= basal vein). Further potential apomorphies include a vertical posterior margin of metasomal T2 and the presence of a longitudinal carina on the posterior surface of the metatibia. Although each of the above characters except for the first has similar states in other lineages of Cynipoidea, the unique combination of these traits supports the separation of Figitidae from other cynipoids.

COMMENTS: Species of Figitidae are relatively small and are primary parasitoids, principally on Diptera, but hosts also include

Fig. 7. Photomicrograph of holotype female of *Goerania petiolata* Liu and Engel, new genus and species (CAS).

chrysopid and hemerobiid lacewings (Neuroptera) or Cynipidae. In addition, some species are hyperparasitoids of braconid and chalcidoid primary parasitoids of aphids and psyllids. Ronquist (1995b, 1999) considerably altered the concept of Figitidae. Ronquist was able to demonstrate from his analyses that figitids were paraphyletic, and he incorporated into Figitidae some groups that historically had been regarded as distinct families. The current classification of Figitidae is summarized in table 1.

SUBFAMILY INCERTAE SEDIS

Micropresbyteria Liu and Engel, new genus

TYPE SPECIES: *Micropresbyteria caputipressa* Liu and Engel, new species.

DIAGNOSIS: F1 of male antenna medially not flattened and not twisted. Head distinctly compressed longitudinally and not impressed posteriorly; lateral occipital carina laterally strongly expanded into a broad lobular structure; lower face glabrate, with a simple,

more or less complete median carina. Anterior pronotal flange short; anterior submedian depression open laterally; dorsal pronotal area narrow but distinct; lateral pronotal carina present; lateral pronotal surface without foveate sculpture. Mesoscutum glabrous; median longitudinal impression and lateral notauli distinct; mesoscutellum posteriorly extended into a prominent horizontal process; lower mesopleuron ventrally strongly expanded into a broad lobular structure, posteriorly covering basal part of mesocoxa. Forewing with bulla present in $Sc+R_1$; $Rs+M$ issuing from close to posterior end of first free abscissa of M (= basal vein). Mesocoxa inserted almost vertically; metacoxa distinctly dorsomedially swollen and dorsolaterally distinctly depressed. Petiolar annulus low and without longitudinal carina; petiole slightly shorter than wide, with distinct longitudinal carinae.

ETYMOLOGY: The specific epithet is derived from the Greek words *mikros* (meaning "little" or "small") and *presbytrion* (meaning "an assemblage of elders"). The name is feminine.

Fig. 8. Holotype female of *Goerania petiolata* Liu and Engel, new genus and species (CAS).

COMMENTS: The extensive lobular expansion of the upper part of the lateral occipital carina and massively expanded ventrolateral carina of the mesopectus separate *Micropresbyteria* from all other cynipoids. The longitudinally distinctly compressed head, the lack of distinct sculpture on the head and mesosoma, the short anterior pronotal flange, and the downward insertion of the meso- and metacoxae strongly indicate that the fossil belongs to the microcynipoids. The presence of an obvious dorsal pronotal area, the position of the proximal end of Rs+M close to the posterior end of the first free abscissa of M (= basal vein), and the presence of the longitudinal carina dorsolaterally on the metatibia further suggest that the genus belongs to the family Figitidae. Because of a lack of information for female characters, which are more crucial in cynipoid phylogeny, we only provisionally place the genus in Figitidae.

Micropresbyteria caputipressa Liu and Engel, new species
figures 9, 10

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Male.** Body length 1.00 mm; forewing length 0.90 mm. Body mostly black to dark brown; wings hyaline, without any macula or band. Antenna cylindrical, 14-segmented; pedicel almost spherical, one-half as long as scape; F1 medially not flattened and not twisted as in male of most known species of cynipoids, slightly longer than F2 (F2 seven-sixths length of F1) and much thicker than the latter; elongate placodeal sensilla present on all flagellomeres. Head compressed longitudinally, attached high to mesosoma; frons, vertex, gena, and malar space glabrous; compound eye prominent, distinctly produced in front of gena, and vertically much extended; malar space reduced to narrow strip beneath compound eye; gena not expanded behind compound eye. Lateral surface of pronotum glabrous. Mesoscutum curved dorsally in lateral view and glabrous, with sparse pubescence; without transverse costa; median impression and lateral notauli distinct; mesoscutellum flat dorsally and posteriorly projected into a blunt process (an artifact of preservation?); mesopleuron glabrous; lower meso-

pleuron ventrally expanded; mesosoma across mesopleuron almost as high as long, excluding mesoscutellar process. Mesocoxa inserted almost vertically, not obliquely at posterior area. Propodeum devoid of processes; nucha short and broad in lateral view. Wings entirely hyaline, with sparse pubescence; all wing margins ciliate. Forewing with marginal cell closed, about 2.6 times as long as wide; bulla in Sc+R_1 present, 2r-rs oblique, sloping outward posteriorly; areolet large; Rs+M nebulous, arising from posterior end of first free abscissa of M (= basal vein). Anterior margin of hind wing with three hamuli. Metabasitarsus shorter than combined lengths of second to fifth metatarsomeres; metacoxa dorsally distinctly depressed; metatibia dorsolaterally with a distinct longitudinal carina; all pretarsal claws simple, without basal lobe. Petiolar annulus relatively long, attached low to propodeum; segmentation of metasoma indistinct owing to imperfect preservation. **Female.** Unknown.

HOLOTYPE: Male, RTMP 96.9.170, Late Cretaceous (Campanian), Grassy Lake (110° 40′W, 49°45′N), Alberta, Canada; deposited in RTMP.

ETYMOLOGY: The specific epithet is derived from Latin *caputa* (meaning "head") and *pressus* (meaning "pressed"). The name refers to the longitudinally compressed head.

SUBFAMILY EUCOILINAE THOMSON

DIAGNOSIS: The subfamily is easily distinguished from all other cynipoids by the presence of a mesoscutellar cup or plate with a deep depression centrally or posteriorly. In addition, eucoiline females, except for two of the new fossil genera described below, have the second through fourth metasomal terga (= abdominal T3–5) fused, a feature shared only with the Pycnostigminae (Figitidae) among cynipoids.

COMMENTS: The presence of the mesoscutellar plate undoubtedly supports the monophyly of the subfamily, a feature exhibited by all three of the taxa treated herein. The new genera *Anteucoila* and *Jerseucoila* (see below), however, lack the fusion of metasomal T2–4 and are therefore obviously basal to all other eucoilines, representing a stem group to the subfamily as it is understood based on modern
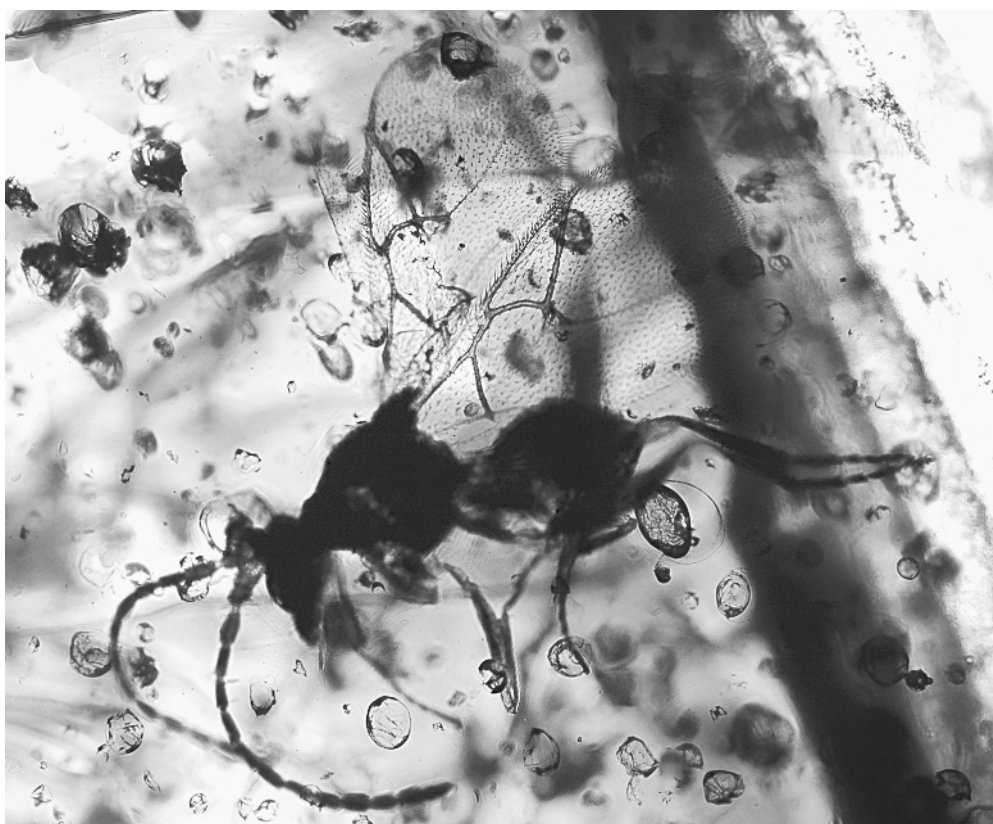
Fig. 9. Photomicrograph of holotype male of *Micropresbyteria caputipressa* Liu and Engel, new genus and species (RTMP-96-9-170).

taxa. However, as already noted, *Anteucoila* and *Jerseucoila* possess a well-developed mesoscutellar cup, indicative of their placement as eucoilines. The third genus, *Syneucoila*, is a typical crown-group eucoiline and is, in fact, apparently related to the clade consisting of the *Zaeucoila* generic group and the core + higher eucoilines (Fontal-Cazalla et al., 2002; see below).

The Eucoilinae is the most species-rich figitid subfamily, currently with about 80 genera and 1000 species. Where known, eucoilines are restricted to hosts of the cyclorrhaphan Diptera (Ronquist, 1999, and references therein). The other Cretaceous genus, *Syneucoila* (see below), is more typical of modern Eucoilinae (yet still rather plesiomorphic for its clade), attesting to the antiquity of the lineage.

Anteucoila Liu and Engel, new genus

TYPE SPECIES: *Anteucoila delicia* Liu and Engel, new species.

DIAGNOSIS: The new genus is easily distinguished from all other members of the subfamily (except *Jerseucoila*, see below) by absence of the characteristic fusion of metasomal T2–4 and by the postpetiolar terga of about equal length along the middorsal line. The only other genus exhibiting these plesiomorphies is *Jerseucoila,* from which *Anteucoila* can be differentiated by the strongly sculptured mesoscutellar plate (weakly carinate and weakly granulose in *Jerseucoila*), straight path of Rs on the apical border of the marginal cell (distinctly arched apically in *Jerseucoila*), the shorter metabasitarsus (elongate in *Jerseucoila*), the shorter second
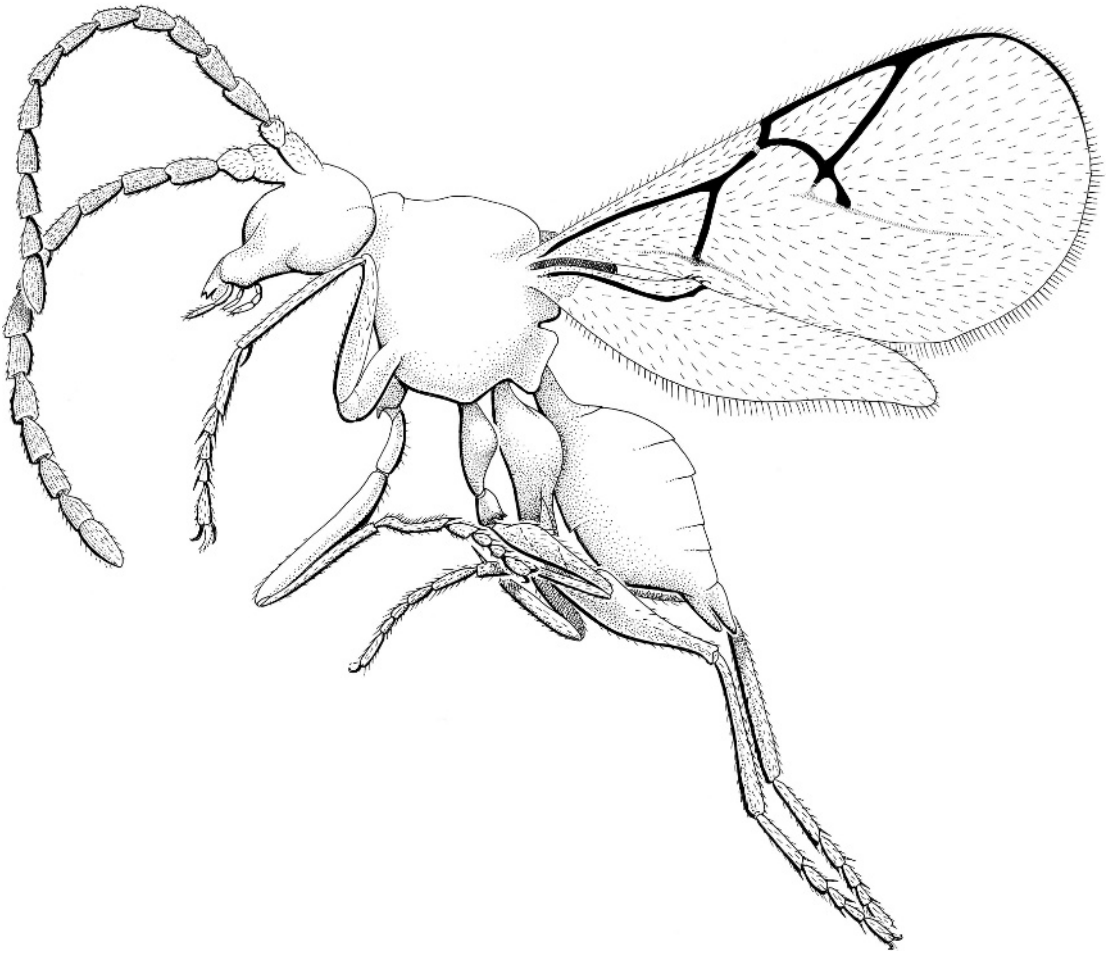
Fig. 10.   Holotype male of *Micropresbyteria caputipressa* Liu and Engel, new genus and species (RTMP-96-9-170).

metasomal tergum (more elongate in *Jerseucoila*), and the narrower petiole (fig. 11) (broader in *Jerseucoila*).

ETYMOLOGY: The new genus-group name is a combination of *ante-* (Latin, meaning "before") and *Eucoila*, type genus of the subfamily. The name is feminine.

Anteucoila delicia Liu and Engel, new species figures 11, 12

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body length 0.63 mm; forewing length 0.6 mm. Body mostly black to dark brown; wings hyaline, without macula or band. Antenna cylindrical, 12-segmented, with distal three flagellomeres conspicuously expanded; pedicel almost spherical, two-thirds as long as scape; F1 distinctly longer than F2; elongate placodeal sensilla distinct on at least distal flagellomeres. Frons, vertex, gena, and malar space glabrous; lower face somewhat elevated in upper part; gena not expanded behind compound eye; compound eye longer, slightly more than twice length of malar space. Lateral surface of pronotum glabrous; lateral pronotal carina present. Mesoscutum slightly curved dorsally in lateral view; mesoscutellum posteriorly sloped and dorsally with a central plate; mesopleuron glabrous; mesopectus not

Fig. 11. Photomicrograph of holotype female of *Anteucoila delicia* Liu and Engel, new genus and species (RTMP-96-9-785).

protruding ventrally, mesocoxa directed vertically and not inserted on separate, oblique posterior area. Propodeum devoid of processes; lateral propodeal carina distinct. Wings hyaline, with sparse pubescence; all wing margins, especially outer margin, ciliate. Forewing with marginal cell closed, about three times as long as wide; bulla in Sc+R_1 absent; 2r-rs oblique, sloping outward posteriorly; areolet absent; Rs+M reduced, hardly traceable, arising from posterior end of first free abscissa of M (= basal vein). Metabasitarsus about half as long as combined lengths of second to fifth metatarsomeres; pretarsal claws simple, without basal lobe. Postpetiolar metasomal terga not fused, all subequal in length along middorsal line; hypopygium of female long and slender. **Male.** Unknown.

HOLOTYPE: Female, RTMP 96.9.785, Late Cretaceous (Campanian), Grassy Lake (110° 40′W, 49°45′N), Alberta, Canada; deposited in RTMP.
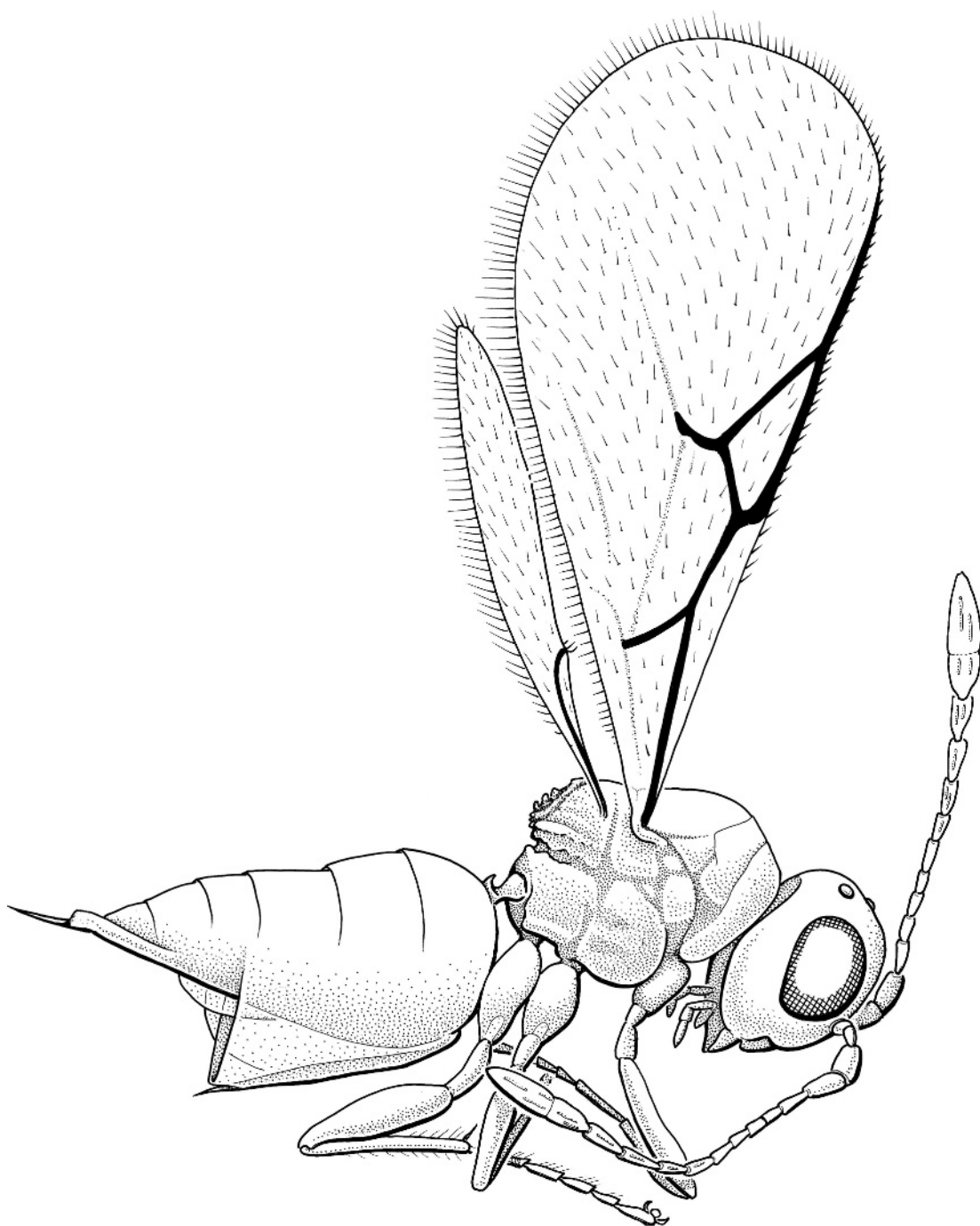
Fig. 12. Holotype female of *Anteucoila delicia* Liu and Engel, new genus and species (RTMP-96-9-785); note that the right antenna (lower one in image) is partially pulled from the head capsule and so the basalmost sclerites depicted are not portions of the antenna but are instead sclerotic debris.
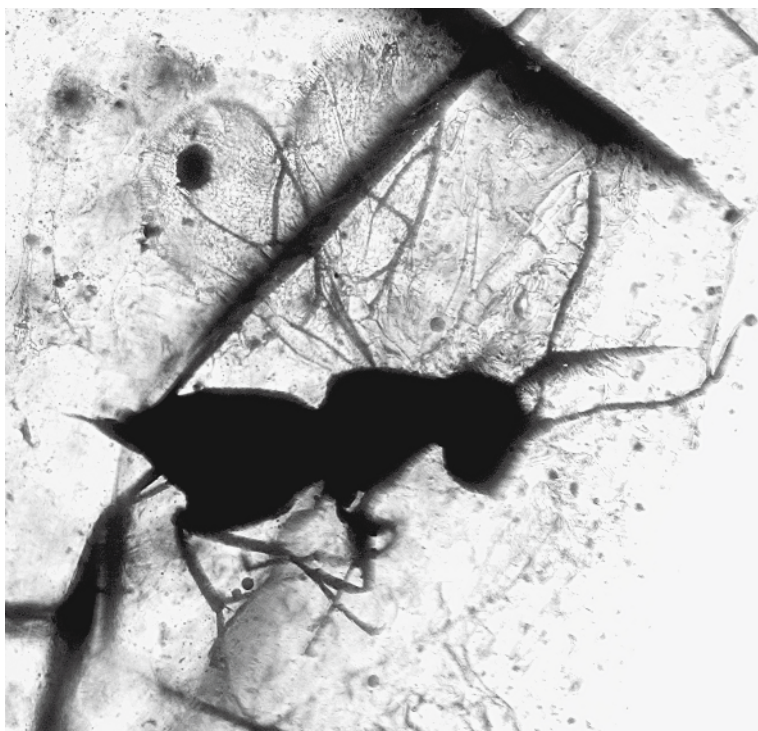
Fig. 13. Photomicrograph of holotype female of *Jerseucoila plesiosoma* Liu and Engel, new genus and species (NJ-1006).

ETYMOLOGY: The specific epithet is derived from the Latin word *delicia* (meaning "favorite" or "lovely").

Jerseucoila Liu and Engel, new genus

TYPE SPECIES: *Jerseucoila plesiosoma* Liu and Engel, new species.

DIAGNOSIS: Like *Anteucoila* (see above) with freely articulated metasomal T2–4, this new genus can be readily excluded from crown-group Eucoilinae. The presence of a mesoscutellar plate, as in the former genus, supports its position as a stem-group eucoiline. *Jerseucoila* differs from *Anteucoila* by the apically less expanded antenna, the weakly carinate and sculptured mesoscutellar plate, the arching of the distal abscissa of Rs, the elongate metabasitarsus, the larger second metasomal tergum, and the broader petiole (fig. 13) (refer also to the Diagnosis for *Anteucoila*).

ETYMOLOGY: The new genus-group name is a combination of Jersey (a reference to the amber deposit in which it was discovered) and *Eucoila*, type genus of the subfamily. The name is feminine.

Jerseucoila plesiosoma Liu and Engel, new species
figures 13, 14

Cynipoid sp.: Grimaldi and Engel, 2005: 422 [figured].

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body length 0.60 mm; forewing length 0.51 mm. Body mostly black; wings hyaline, without macula or band. Antenna cylindrical, with distalmost flagellomeres more elongate than preceding flagellomeres; pedicel almost spherical, two-thirds as long as scape; F1 about as long as F2; elongate placodeal sensilla distinct on nearly all flagellomeres except basal two. Frons, vertex, gena, and malar space apparently glabrous (difficult to integument in holotype owing to layer of microscopic bubbles); gena not expanded behind compound eye; com-
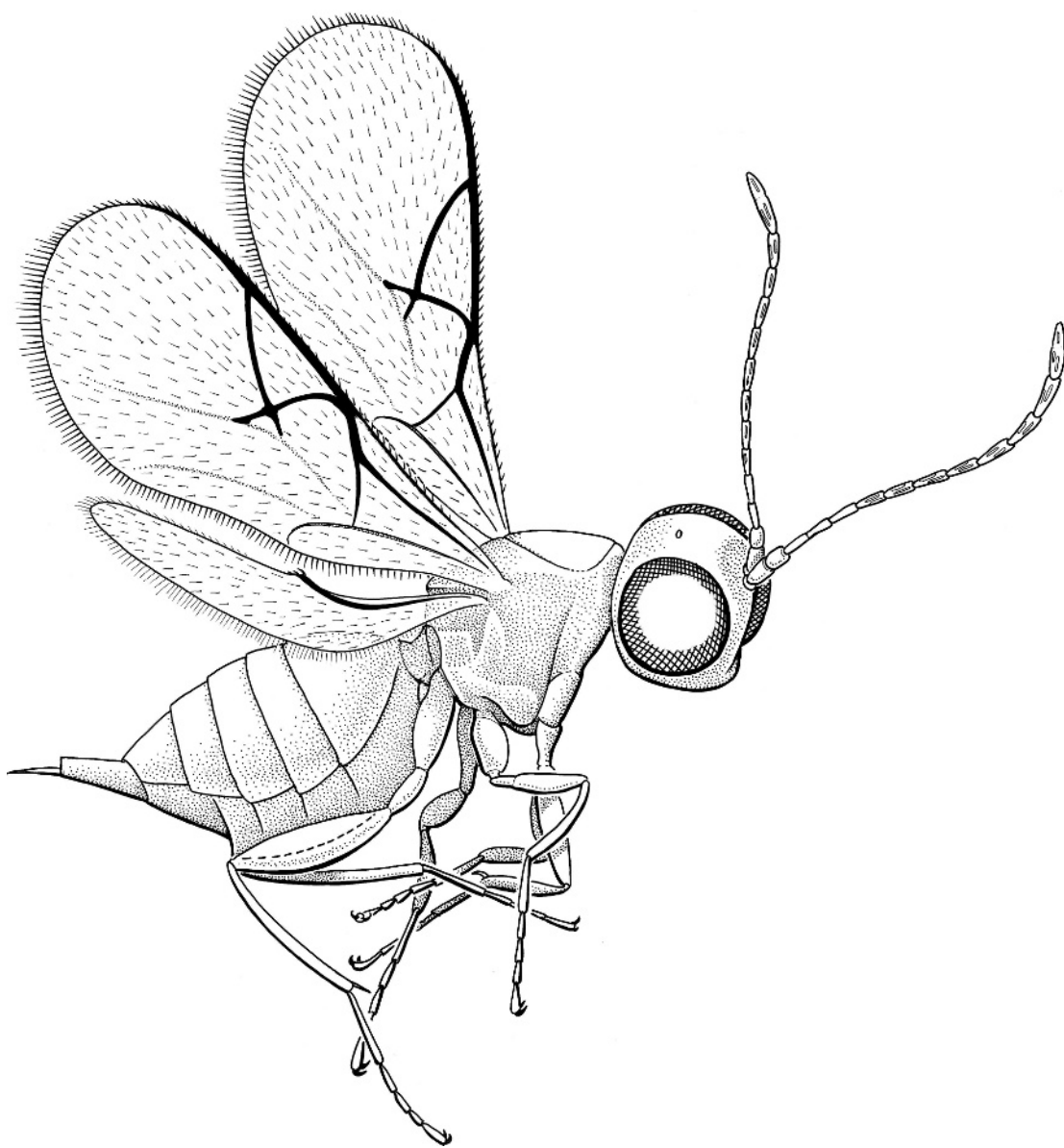
Fig. 14. Holotype female of *Jerseucoila plesiosoma* Liu and Engel, new genus and species (NJ-1006).

pound eye much longer than malar space, nearly five times longer than malar length. Lateral surface of pronotum apparently glabrous. Mesoscutum weakly curved dorsally in lateral view; mesoscutellum slightly sloped posteriorly and with weakly defined central plate; mesopleuron apparently glabrous; mesocoxa directed vertically and not inserted on separate, oblique posterior area.

Propodeum devoid of processes. Wings hyaline, with scattered pubescence; all wing margins, especially posterior margins, ciliate. Forewing with marginal cell closed, about three times as long as wide; bulla in $Sc+R_1$ absent; 2r-rs oblique, sloping outward posteriorly; areolet absent; Rs+M reduced, scarcely traceable, apparently arising from posterior end of first free abscissa of M (=

basal vein). Metabasitarsus nearly as long as combined lengths of second to fifth metatarsomeres; pretarsal claws simple, without basal lobe. Postpetiolar metasomal terga not fused, all subequal in length along middorsal line except metasomal T2 more elongate; hypopygium of female long and slender. **Male.** Unknown.

HOLOTYPE: Female, AMNH NJ-1006, Late Cretaceous (Turonian), White Oak Pit, Sayreville, Middlesex County, New Jersey; deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, AMNH.

ETYMOLOGY: The specific epithet is a combination of the Greek words *plesios* (meaning "near") and *soma* (meaning "body").

Syneucoila Liu and Engel, new genus

TYPE SPECIES: *Syneucoila magnifica* Liu and Engel, new species.

DIAGNOSIS: Typical eucoiline with postpetiolar metasomal terga fused but exhibiting a relatively shortened head (not elongate), possessing an anterior metepimeral impression, and with a well-developed subalar pit and subalar area. Additional features defining the genus include: broad metasubpleural depression anterior to metacoxal foramen present; metacoxa without setal patches; forewing with marginal cell closed; R1 complete and elongate, surpassing marginal cell apex; marginal ciliae of wing distinctly elongate along posterior margin of forewing.

ETYMOLOGY: The new genus-group name is a combination of *syn-* (Greek, meaning "together"; a reference to the fused metasomal terga relative to other Cretaceous eucoilines) and *Eucoila*, type genus of the subfamily. The name is feminine.

Syneucoila magnifica Liu and Engel, new species
figures 15, 16

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body length 0.73 mm; forewing length 0.65 mm. Body mostly dark brown; wings hyaline, without macula or band. Antenna cylindrical; pedicel almost spherical; F1 distinctly longer than F2; elongate placodeal sensilla distinct on at least distal flagellomeres. Frons, vertex, gena, and malar space glabrous; malar space with distinct sulcus; lower face somewhat elevated in upper part; gena not expanded behind compound eye; compound eye nearly three times longer than malar space. Lateral surface of pronotum glabrous. Mesoscutum curved dorsally in lateral view; mesoscutellum posteriorly sloped and dorsally with a central plate; mesopleuron glabrous, subalar pit well developed; mesopectus not protruding ventrally, mesocoxa directed vertically and not inserted on separate, oblique posterior area. Propodeum devoid of processes; lateral propodeal carina distinct. Wings hyaline, with sparse pubescence; all wing margins ciliate, ciliae particularly elongate along apical posterior margin of forewing. Forewing with marginal cell, triangular closed, about 2.5 times as long as wide; bulla in Sc+R_1 present; 2r-rs short, projecting straight posteriorly; areolet absent; Rs+M reduced, hardly traceable, apparently arising from posterior end of first free abscissa of M (= basal vein). Metabasitarsus slightly more than one-half as long as combined lengths of second to fifth metatarsomeres; pretarsal claws simple, without basal lobe. Postpetiolar metasomal T2–4 fused. **Male.** Unknown.

TYPE MATERIAL: Female, AMNH NJ-1075, Late Cretaceous (Turonian), White Oak Pit, Sayreville, Middlesex County, New Jersey; deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, AMNH.

ETYMOLOGY: The specific epithet is taken from the Latin word *magnificus* (meaning "splendid") and is a reference to the esthetic beauty of the holotype.

FAMILY CYNIPIDAE LATREILLE

COMMENTS: Although the family Cynipidae is universally accepted as monophyletic, satisfactory character evidence readily defining the family is lacking except for its phytophagous habit. Numerous characters have been put forward as putative synapomorphies for the family, including the lack of the lateral pronotal carina and an open marginal cell in forewing (Liljeblad and Ronquist, 1998), as well as a medially narrowed dorsellum (Ronquist, 1999). However, all of these putative synapomorphies have exceptions both within Cynipidae (as rever-

Fig. 15. Photomicrograph of holotype female of *Syneucoila magnifica* Liu and Engel, new genus and species (NJ-1075).

sals) and in Figitidae (as parallelisms) (e.g., Ronquist, 1999). Nonetheless, the family can still be reasonably defined based on a combination of morphological attributes. In addition to the aforementioned characters, the following traits can be useful in the diagnosis of cynipids: (1) dorsal pronotal area absent; (2) metasoma of female strongly compressed; (3) Rs+M arising from middle of the first free abscissa of M (= basal vein); (4) 2r-rs about 0.5–0.65 times as long as $Sc+R_1$; (5) R_1 lateral of 2r-rs directed distinctly obliquely laterally rather than more or less perpendicular to anterior wing margin; and (6) R+Rs and $Sc+R_1$ smoothly continuous, not forming a distinct angle (see Liljeblad and Ronquist, 1998).

SUBFAMILY INCERTAE SEDIS

Tanaoknemus Liu and Engel, new genus

TYPE SPECIES: *Tanaoknemus ecarinatus* Liu and Engel, new species.

DIAGNOSIS: Male antenna 14-segmented, with F1 distinctly excavated laterally. Compound eye prominent; gena not expanded behind compound eye; vertex, gena, malar space, and face glabrous; lower face with a simple, more or less complete median carina. Pronotum dorsomedially strongly extended anteriorly; anterior pronotal flange short; lateral pronotal carina present; lateral pronotal surface transversely costate on upper half, and without foveate sculpture. Mesoscutum glabrous; lateral notauli distinct; mesoscutellum posteriorly truncate, without process; mesopleural impression anteriorly present, convergent to a longitudinal impression along ventral margin of lower mesopleuron toward posterior two-thirds and divided into several foveae by vertical carinae; lateroventral carina of mesopectus present and complete; lower mesopleuron ventrally not expanded. Forewing with bulla in $Sc+R_1$ present; Rs+M issuing from middle of the first free abscissa of M (= basal vein). Mesocoxa inserted vertically and not obliquely at separate posterior area; metacoxa dorsally distinctly depressed and with a rounded, anterolateral triangular crest; metatibia longer than metafemur by one-third. Petiolar annulus low,
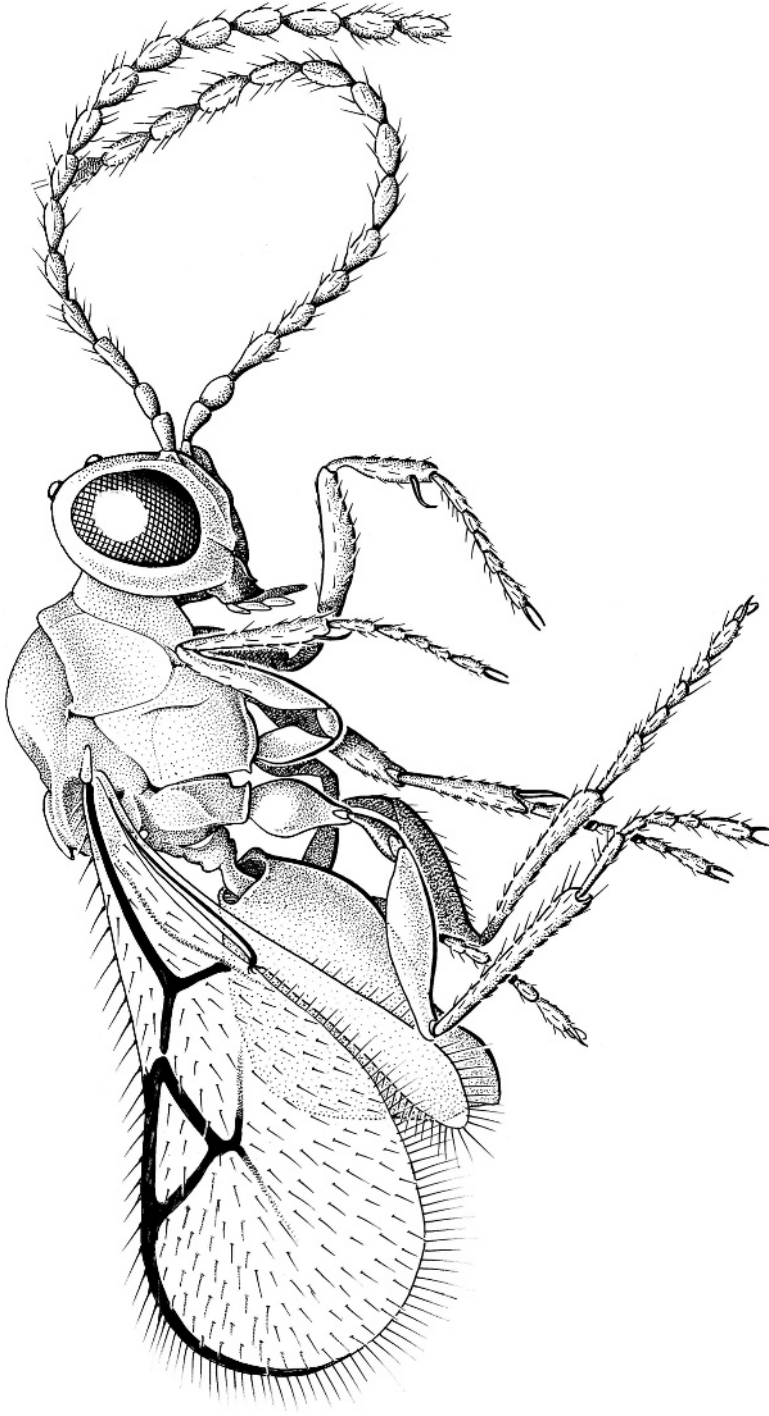
Fig. 16. Holotype female of *Syneucoila magnifica* Liu and Engel, new genus and species (NJ-1075).

Fig. 17. Photomicrograph of holotype male of *Tanaoknemus ecarinatus* Liu and Engel, new genus and species (CAS-78).

postsubpleuron short; petiole slightly longer than wide and longitudinally carinate.

COMMENTS: The presence of a unique mesopleural impression and unusually long tibia separate the genus from all other cynipoids. The lack of the lateral pronotal carina, presence of a bulla in Sc+R$_1$, and Rs+M issuing from the middle of the first free abscissa of M (i.e., basal vein) suggest affinity with the family Cynipidae. Although the relatively long petiole is a feature often found in Figitidae and is not known in extant Cynipidae, the trait has evolved independently in many Hymenopteran lineages, including several times within Cynipoidea. We therefore interpret its presence in *Tanaoknemus* as an autapomorphy, and the genus is provisionally placed as a basal clade of Cynipidae.

ETYMOLOGY: The new genus-group name is a combination of the Greek words *tanao-* (meaning "long" or "outstretched") and *knem-* (meaning "the leg between the knee and ankle"). The name is a reference to the unusually long tibia of the new genus relative to other cynipoids. The name is masculine.

Tanaoknemus ecarinatus Liu and Engel,
new species
figures 17, 18

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Male.** Body length 1.20 mm; length of forewing about 1.00 mm (tip of wing not well preserved). Body mostly black; wings hyaline, without any macula or band. Antenna cylindrical, 14-segmented (10-segmented on the other side, but that is apparently an abnormality); F1 laterally excavated; elongate placodeal sensilla present on all flagellomeres. Head compressed longitudinally, attached high to mesosoma; frons, vertex, gena, and malar space glabrous; compound eye prominent, vertically more than twice as high as malar space; gena not expanded behind compound eye. Lateral surface of pronotum transversely weakly costate in upper half; mesoscutum dorsally slightly curved in lateral view, glabrous with sparse pubescence, without transverse costa; median impression and lateral notauli percurrent; mesoscutellum dorsally flat and irregularly sculptured, without posterior processes; mesoscutellar sulcus me-
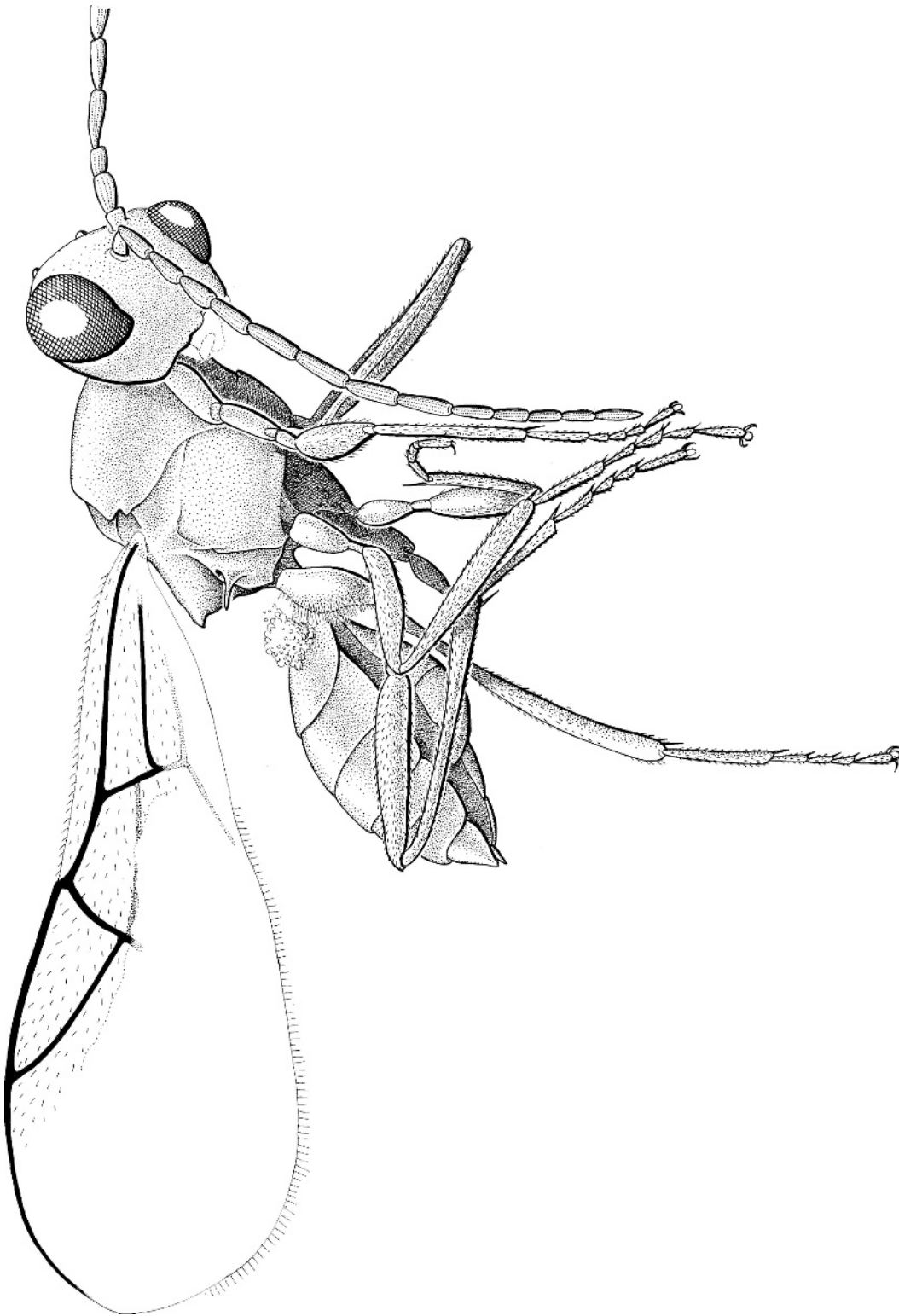
Fig. 18. Holotype male of *Tanaoknemus ecarinatus* Liu and Engel, new genus and species (CAS-78).

dially divided into two large foveae by a longitudinal carina; mesopleuron glabrous. Mesocoxa inserted vertically beneath mesopleuron. Propodeum with no processes; nucha short; lateral propodeal carina percurrent and dorsally not curved in lateral view. Wings entirely hyaline and pubescent; wing margins ciliate. Forewing with marginal cell closed, about three times as long as wide; bulla in $Sc+R_1$ present; 2r-rs oblique, sloping outward posteriorly; areolet large; Rs+M nebulous, arising from the middle of the first free abscissa of M (= basal vein). First metatarsomere slightly shorter than combined length of second through fifth metatarsomeres; metacoxa dorsally distinctly depressed, anterolaterally with a rounded triangular crest; metatibia dorsolaterally with a distinct longitudinal carina; all pretarsal claws simple, without basal lobe. Petiolar annulus slightly longer than wide and longitudinally carinate, attached low to propodeum; all metasomal terga subequal along middorsal line in lateral view, each with posterior margin oblique and almost straight. **Female.** Unknown.

HOLOTYPE: Male, CNC CAS-78, Late Cretaceous (Campanian), Medicine Hat, Alberta, Canada; deposited in CNC.

ETYMOLOGY: The specific epithet is derived from Latin and is a combination of *e-* (meaning "without") and *carinatus* (meaning "keeled"). The name describes the lack of a lateral pronotal carina in the new species.

SUBFAMILY CYNIPINAE LATREILLE
TRIBE AYALCINI ASHMEAD

Kinseycynips Liu and Engel, new genus

TYPE SPECIES: *Aulacidea succinea* Kinsey, 1919.

DIAGNOSIS: Antenna of female long and slender, reaching beyond posterior end of mesosoma when in repose and 14-segmented; F1 slightly curved and slightly shorter than F2 (50:55); placodeal sensilla present on all flagellomeres. Compound eyes prominent and long, about twice as long as malar space; gena and vertex glabrous; clypeus ventrally projecting over mandibles, anterior margin trapezoidal; epistomal sulcus absent; facial strigae radiating from clypeus and reaching compound eye; lower face laterally with radiating strigae reaching lower margin of compound eye and medially glabrous. Pronotum long medially, ratio of median to posterior distance between dorsal and ventral margins about 0.56; lateral pronotal carina absent; pronotal surface longitudinally strigate; mesoscutum strongly convex and glabrous, with percurrent notauli; mesopleuron including mesopleural triangle glabrous; mesoscutellum convex, dorsally with broadly spaced costae, posteriorly sloped gradually; mesoscutellar sulcus medially subdivided into two foveae by a longitudinal carina; mesopectus ventrally not projected; mesocoxa directed vertically downward; metapleural sulcus anteriorly ends high, distance between upper metapectal margin and its anterior end about half the distance between its anterior end and anteroventral margin of episternum; metacoxal foramen close to anterior margin of metepisternum. Forewing with marginal cell closed anteriorly; R_1 laterad of 2r-rs directed strongly obliquely laterally; Rs+M arising from just posterior of middle of first free abscissa of M; areolet present. (Note that we were unable to observe the venation clearly in the holotype. This may be due to deterioration of the specimen in a relatively exposed area through time. Thus, the above description is largely based on Kinsey's original illustration, assuming that his observations and interpretations of the wing were correct.) Pretarsal claws of all legs simple, without tooth. Nucha low and short, about one-eighth length of metacoxa, dorsally glabrous. Petiole short and inconspicuous, dorsal part crescent-shaped, and glabrous; metasoma laterally strongly compressed, as long as head and mesosoma combined; metasomal T2–3 not fused, about half as long as postpetiolar metasoma; ventral spine of metasomal S6 short, slightly separated from and extending beyond apex of lateral flap.

ETYMOLOGY: The new genus is named after Dr. Alfred C. Kinsey (1894–1956) for his significant contributions to the study of gall wasps. His collection of gall wasps is estimated to amount to five million specimens and two million galls, and is now deposited in the AMNH. In addition to the description of about 400 new species of gall wasps, he pioneered the search for gall wasp phylogeny. Dr. Kinsey studied gall wasps for more than

20 years, but later turned his interest to, and became more widely known for, studies of human sexual behavior.

COMMENTS: *Aulacidea succinea* is considered here to belong to the gall wasp family Cynipidae owing to the absence of the lateral pronotal carina, a synapomorphy for the cynipids, and to the complete absence of synapomorphies defining the sister family Figitidae (e.g., Rs+M arising from distinctly after middle of the first free abscissa of M, metasomal T2 with distinctly oblique posterior margin). Ronquist (1999) suggested that *A. succinea* belonged to the inquiline complex of *Synergus* (Synergini). However, the following characters clearly separate the species from the latter: lower face not covered with radiating strigae, but with a medial glabrous area; dorsal part of petiole small, glabrous, and crescent-shaped; and metasomal T2–3 not fused to form a large tergite covering more than half of the postpetiolar metasoma. Furthermore, the glabrous and asetose mesoscutum of *A. succinea* differs from all inquilines except *Synophromorpha*. Indeed, the fossil is further separated from all inquilines by several features, including toothless pretarsal claws; a clypeus projecting over the mandibles, with its anterior margin trapezoidal; and absence of the epistomal sulcus. Indeed, the fossil can be easily identified as Aylacini using the key to tribes of Neotropical Cynipidae provided by Buffington et al. (2005).

Within Aylacini, the new genus more closely resembles those genera that produce galls on *Rubus* spp. and *Potentilla* spp. (i.e., *Xestophanes* and *Diastrophus*) in that all share glabrous integument on the vertex, mesoscutum, and mesopleuron. However, *Kinseycynips* can be easily distinguished from these by its toothless claws, closed marginal cell, and 14-segmented antenna in the female. *Kinseycynips* is also similar to *Aulacidea*, the genus where Kinsey (1919) originally placed his species, but *Aulacidea* females have only 13-segmented antennae, the vertex and mesoscutum coriaceous or otherwise sculptured (but never glabrous), and the mesopleuron longitudinally striate. Because the new genus shares more similarities with those aylacine genera galling on rosaceous, mostly woody hosts, we think that it was associated with a woody host of the

rose family. However, in the absence of a cladistic analysis we cannot exclude the possibility that *Kinseycynips* was a galler of herbaceous species of the rose family.

Kinseycynips succinea (Kinsey), new combination
figure 19

Aulacidea succinea Kinsey, 1919: 48.

DIAGNOSIS: As for the genus (see above).
HOLOTYPE: Female, Eocene (Lutetian), Baltic amber; deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, AMNH. Kinsey (1919) stated, "Type: a single specimen from collection of the Königsberg Museum, and temporarily at the Bussey Institution, of Harvard University." Once thought to be lost, the specimen was recently rediscovered in the Kinsey Collection at the AMNH.

CYNIPOIDEA INCERTAE SEDIS

Two additional specimens of cynipoid wasps were recognized, but owing to poor preservation and obscured views through the amber they were not identifiable beyond the level of superfamily. There was one specimen each in Canadian and New Jersey ambers. We provide here their accession numbers so that future workers, with new questions and techniques for old material, might know of their existence and perhaps seek them for study: NJ-1069 in the AMNH and CAS-282 in the CNC.

CLADISTICS
METHODS

The character matrix from a recent cladistic analysis of the higher-level phylogeny of Cynipoidea (Ronquist, 1995b) was supplemented with data on six of the more plesiomorphic, fossil taxa described in this monograph; i.e., *Protimaspis, Stolamissus, Micropresbyteria, Tanaoknemus, Proliopteron,* and *Anteucoila* (for the purposes of the higher-level analysis, *Anteucoila* and *Jerseucoila* are identical and so only one has been coded for study). The six genera were included because each is well preserved and allows detailed

Fig. 19. Photomicrograph of holotype female of *Kinseycynips succinea* (Kinsey).

morphological study and thereby meaningful comparison to modern taxa. Furthermore, each of these genera possesses a unique combination of plesiomorphic features making their assignment to higher groups in the absence of a cladistic analysis more subjective (in contrast to taxa like, *Syneucoila* and *Kinseycynips*, which are distinctly more modern and exhibit a number of synapomorphies for their respective families and subfamilies). Ronquist (1995b) coded 110 external morphological characters for his cladistic analysis of higher-level relationships in the Cynipoidea. For descriptions of characters and the complete character matrix for modern taxa refer to Ronquist (1995b). Two new characters are supplemented in our present re-analysis (codings for the extant taxa for these two characters are provided in table 2):

111. Shape of remnant of pterostigma: 0, short and thick; 1, long and thin.

112. Shape of metacoxa: 0, dorsally depressed or not, but never with anterolateral crest; 1, strongly depressed dorsally to form a longitudinal furrow with a more or less triangular, anterolateral crest.

Although the six fossil genera that are included in the matrix are relatively well preserved and we were able to code them for most of the 112 characters (table 3), two of the genera (i.e., *Tanaoknemus* and *Micropresbyteria*) are only known from males. Because cladistic reconstruction of cynipoid phylogeny depends disproportionately on attributes of female morphology, the two genera were initially excluded to avoid negative perturbation to the analysis by an excessive amount of missing data (Schuh, 2000). Nonetheless, we included the two genera in further analyses to explore, albeit in a limited fashion, whether the absence of data indeed had an overall effect.

TABLE 2
Partial Data Matrix for Cynipoidea
(New characters 111 and 112 for Recent and fossil genera)

	1 1 1 1 1 2
Outgroup	00
Austrocynips	00
Eileenella	00
Ibalia	01
Heteribalia	00
Kiefferiella	00
Paramblynotus	00
Mesocynips	00
Dallatorrella	00
Xenocynips	00
Tessmannella	00
Oberthuerella	00
Liopteron	00
Peras	00
Pseudibalia	00
Isocolus	10
Diastrophus	10
Euceroptres	10
Melanips	10
Stolamissus	00
Protimaspis	01
Proliopteron	10
Anteucoila	00
Presbyfigites	00
Micropresbyteria	01

Among the fossil genera considered herein, *Anteucoila*, *Jerseucoila*, and *Syneucoila* possess a mesoscutellar cup or plate, a feature unique to the subfamily Eucoilinae (Figitidae). Therefore, the presence of this feature in these taxa solidly places them in Eucoilinae. According to Ronquist (1995b, 1999), the monophyly of the Figitidae including Eucoilinae is well established. The character matrix he constructed (Ronquist, 1995b) is intended for analysis of cynipoid phylogeny at the familial level and did not include any eucoilines. Thus, the data matrix updated herein was analyzed with the position of *Anteucoila* within Figitidae constrained as well as unconstrained. *Anteucoila* was selected to represent these fossils as it is the more plesiomorphic and complete of the three.

Cladistic analyses were conducted using parsimony as implemented in NONA (Goloboff,

1997) with the options "hold 10,000; mult 5,000", and character optimization and tree visualization were performed using WinClada (Nixon, 2002). Statistics from individual analyses are provided in the corresponding figure captions.

RESULTS

Parsimony analysis of the data, with *Tanaoknemus* and *Micropresbyteria* excluded, and with no constraints resulted in 11 equally parsimonious topologies (fig. 20). According to the analysis, *Protimaspis* is one of the basalmost clades among cynipoids except *Austrocynips*, but its position relative to Ibaliidae and the stem taxa of microcynipoids and liopterids is unresolved. The genera *Stolamissus*, *Proliopteron*, and *Anteucoila* form an unresolved cluster with the stem species of the microcynipoids and the liopterids (fig. 20). When the same matrix was analyzed with the position of *Anteucoila* with Figitidae constrained (once again, reflecting the placement of Eucoilinae within this family), a single topology was recovered that was only one step longer than the first analysis, but also with slightly better tree statistics (fig. 21) (since two nodes were actually constrained, their support is low). Interestingly, the overall topology from this analysis matches Ronquist's original tree, with the obvious difference of the addition of the fossil taxa. The single tree from the constrained analysis is therefore preferred as the most plausible phylogeny for the Cynipoidea over the suite of trees resulting from the unconstrained analysis. Given that eucoilines were not originally included, we think this to be a safe assertion. According to this analysis (fig. 21), Austrocynipidae, Ibaliidae, *Protimaspis*, and *Stolamissus* form a basal grade, each being progressively more related to Liopteridae + microcynipoids. *Proliopteron* is supported as sister to the remainder of the Liopteridae (fig. 21).

Both unconstrained (fig. 22) and constrained, with respect to *Anteucoila* (fig. 23), analyses of the data matrix with the addition of *Tanaoknemus* and *Micropresbyteria* resulted in two equally parsimonious topologies each. The two trees resulting from the un-

TABLE 3
Partial Data Matrix for Cynipoidea
(Codings for new fossil genera only; refer to Ronquist, 1995b, for complete explanation of characters 1–110 and codings for extant groups; codings for the new characters, 111 and 112, are presented in table 2 for all Recent and fossil genera.)

```
                  1111111111222222222233333333334444444444555555555566666666667777777778
         1234567890123456789012345678901234567890123456789012345678901234567890123456789 0

Stolamissus       0?00??1?0??20??0001-0001?0?101?1??11000101?100?1110?00001000000-0?000???
Protimaspis       ??00??0?0??20??00000001?0200??110?00101101?1?2011?0?00000000?00-0?000???
Proliopteron      110??0?0??1101000?011??010??101??120?2100011010007110?00?0?00-0?001???
Anteucoila        0-10??0?0??21??0001-0020101101101?11201110000011007000000000000-00000???
Micropresbyteria  1110??0?1?210??0001-0020107110101?11?011000001117?2?1000000??????2?0-0?001???
Tanaoknemus       ??10??0?0?0?12??0021-0120?0?1101?1112011100007101007100007?0?2?20000020-0?011???
```

```
                  1111111111
         888888888899999999990000000001
         123456789012345678901234567890

Stolamissus       100??000000?00?00?000?0?0?0000
Protimaspis       000??000000?0?000000?000?0?0000
Proliopteron      ?00?0100?0000-0000000000?0?0000
Anteucoila        000?000000000??000000000?0?0000
Micropresbyteria  ?00?000000000-0??00??0??0??0???
Tanaoknemus       100?000000?0?0??00??00??00?0???
```
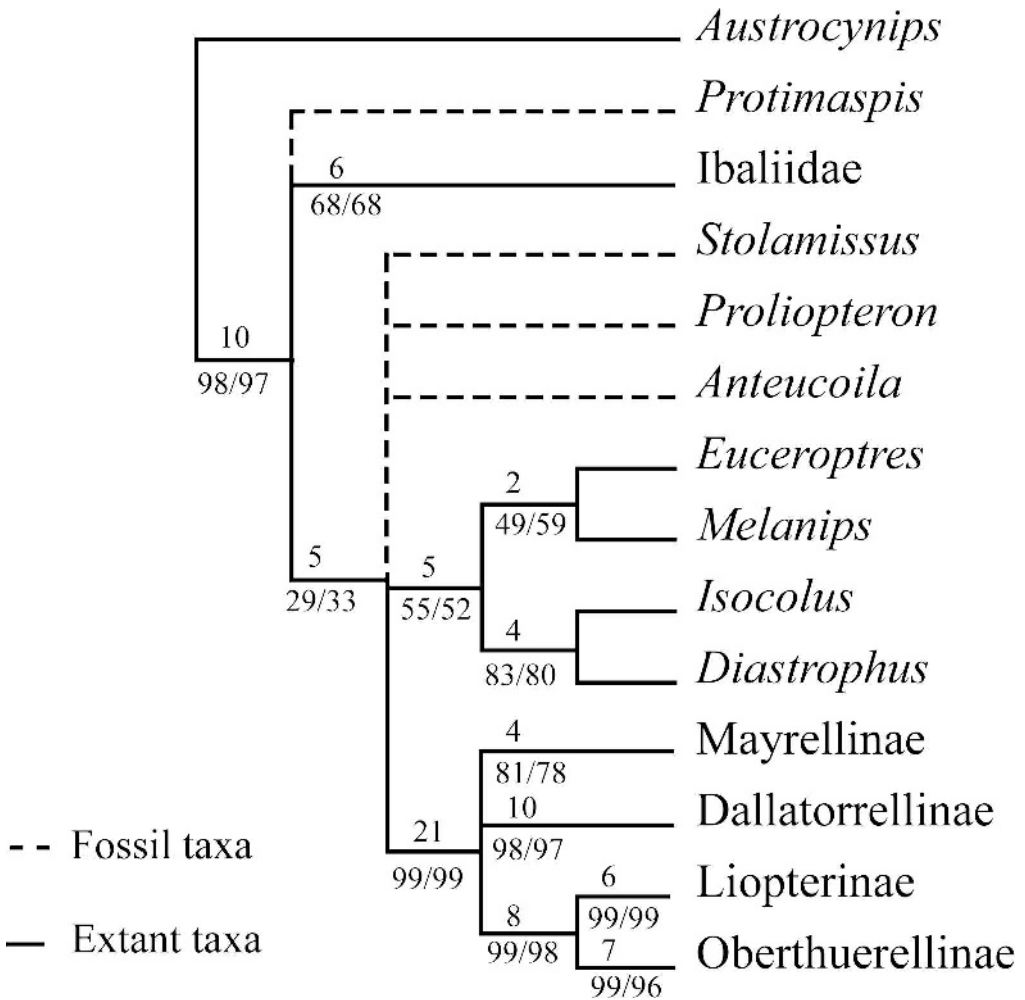
Fig. 20. Strict consensus of 11 shortest trees (L = 227, CI = 56, RI = 79) resulting from parsimony analysis of Ronquist's (1995b) data matrix, supplemented with paleontological data for several Late Cretaceous amber fossils described herein. We have added to the original matrix two additional characters (refer to section on Cladistics) and four fossil taxa (i.e., *Protimaspis*, *Stolamissus*, *Anteucoila*, and *Proliopteron*). No constraints were applied to the search which consisted of: hold 10,000; mult 5,000; wh*; max* in NONA (Goloboff, 1997). Values above branches are the number of unambiguous character changes supporting particular nodes, while those below are Jackknife and Bootstrap values.

constrained analysis were 235 steps (fig. 22), whereas the two resulting from the constrained analysis were 239 steps (fig. 23). The cladograms of the two analyses are essentially identical except for the position of *Anteucoila*, and they are the same as the constrained analysis without the inclusion of *Tanaoknemus* and *Micropresbyteria*. *Tanaoknemus* and *Micropresbyteria* are basal, from the base upward, to *Proliopteron* and extant liopterids.

However, the clade consisting of (*Tanaoknemus* (*Micropresbyteria* (*Proliopterion* + extant liopterids))) is "supported" by merely a single female character (i.e., character 56: petiole is at least partially longitudinally carinate) (fig. 24). This is obviously a tenuous position given that the *Tanaoknemus* and *Micropresbyteria* are known only from males! We therefore think that this is not an entirely reliable homology statement and consider the
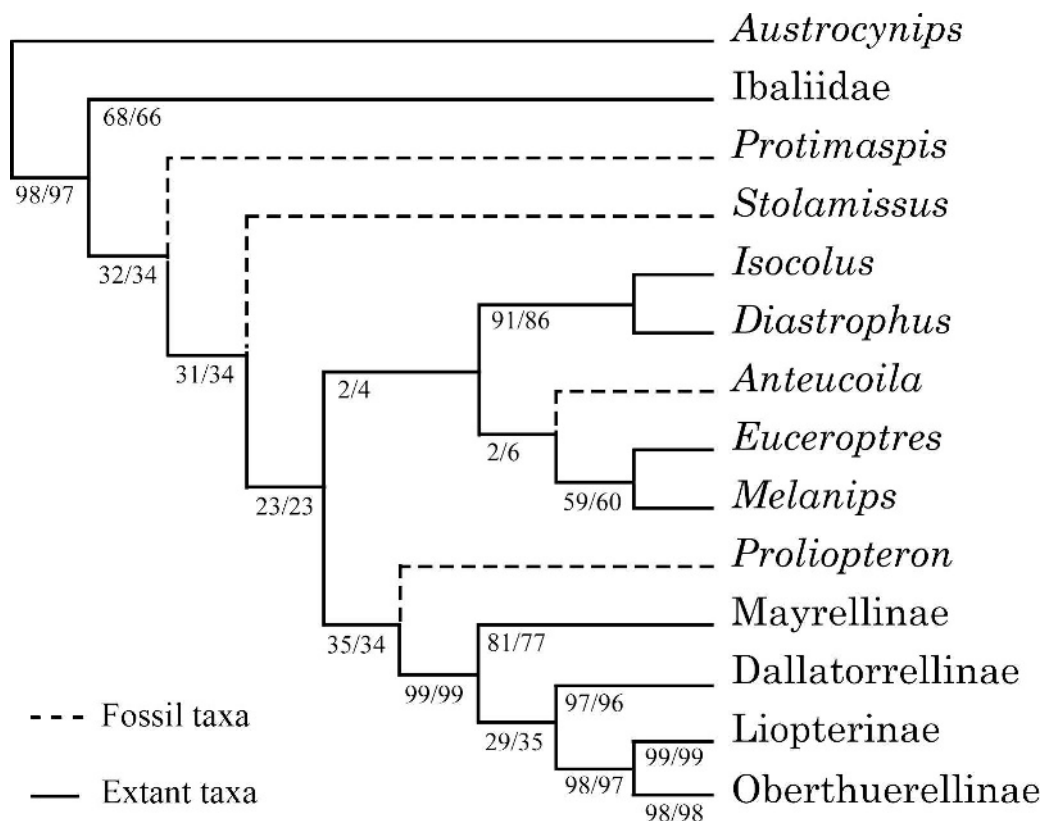
Fig. 21. Preferred set of cladistic relationships among Cynipoidea; strict consensus of the two shortest tree (L = 228, CI = 57, RI = 80) resulting from analysis of the data matrix (as described in the text and in fig. 20), with the phylogenetic position of *Anteucoila* with the two representative figitids constrained.

cladograms with respect to placing these taxa dubious at best (at least until such time as females are discovered for both and a new analysis can be undertaken). Accordingly, we have chosen to concentrate our attention on the few preserved features (i.e., actual, observable characters rather than unknown female attributes) of the two genera, in particular those traits that have been previously identified as being synapomorphies of individual groups. We have used such characters for tentative placements of the two genera within the overall phylogenetic hierarchy of Cynipoidea.

Protimaspis costalis was considered by Kinsey (1937) to be closely related to the tribe Aylacini of the Cynipidae. Kovalev (1994) included it with another fossil species of slightly younger age (i.e., *Protocharips evenhuisi* Kovalev: appendix 1) in his new sub-

family Protocharipinae (Charipidae sensu Kovalev, 1994). Ronquist (1999) transferred *P. costalis* to Rasnicynipidae and kept *P. evenhuisi* as a tribe of Charipinae (then in Figitidae), pointing out that the actions were only tentative in the absence of supporting synapomorphies. However, *Protimaspis* possesses several plesiomorphies that are found only in Austrocynipidae and Ibaliidae, including the venation and the manner by which the mesocoxa is inserted into the mesopectus. The cladistic analysis presented herein suggests that *Protimaspis* represents a clade basal to all cynipoids except Austrocynipidae and Ibaliidae (figs. 21, 25), and it is therefore accorded familial status as the Protimaspidae. As discussed above, the family was probably a parasitoid of wood-boring insect larvae, as is the case for modern macrocynipoids.
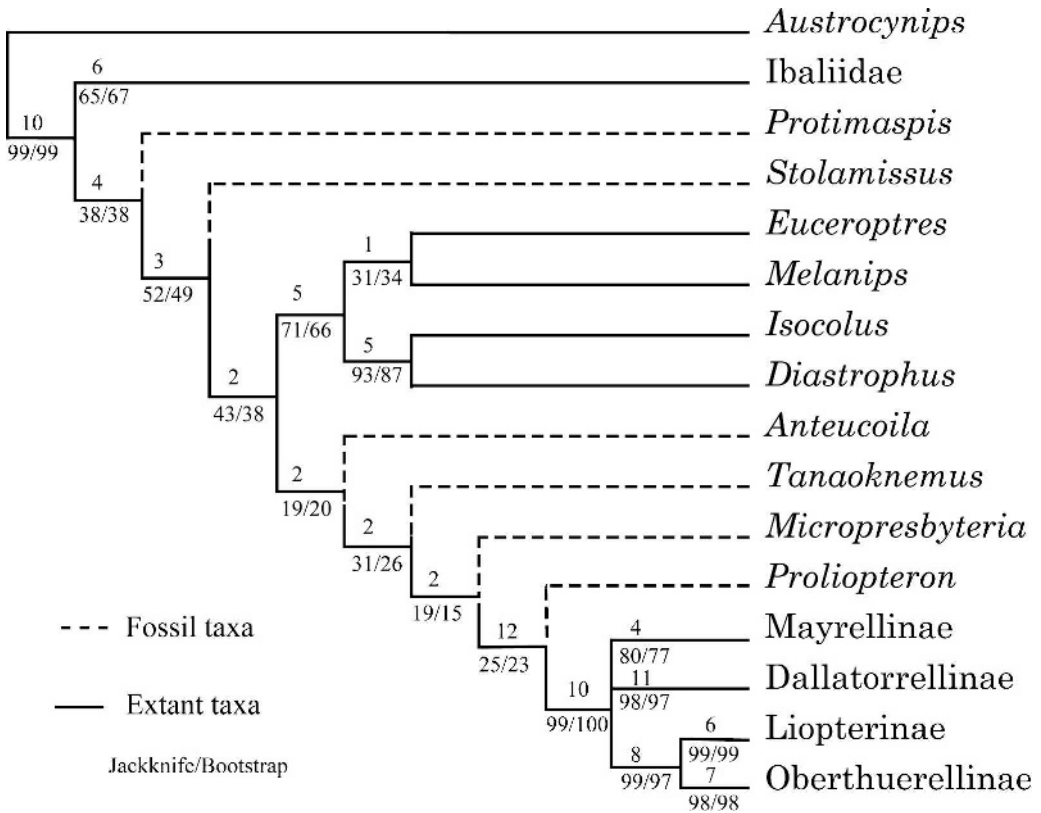
Fig. 22. Strict consensus tree of the two shortest trees (L = 235, CI = 54, RI = 79) resulting from analyses of the data matrix (as described in the text and in fig. 20), with the inclusion of two additional Cretaceous amber taxa known only from males (i.e., *Tanaoknemus* and *Micropresbyteria*) and no constraints.

Above Protimaspidae on the tree is *Stolamissus*, representing the sister group of liopterids and microcynipoids. As already mentioned, the family has several symplesiomorphies shared with the macrocynipoids as well as the derived feature of the mesocoxa inserted downward on the mesopectus (fig. 25). The family is accordingly treated herein as the sole member of a new family, the Stolamissidae.

Two groups are allied to, or fall within, the Liopteridae. *Proliopteron* represents the sister clade to Liopteridae, with the relationship being particularly supported by two synapomorphies: nucha long and metasosoma inserted high on propodeum (fig. 25). In addition, the enlarged fifth metasomal tergum (= sixth abdominal) further suggests liopterid affinity. The concept of the family is here expanded to include the genus, which is placed

in a basal subfamily. The genus *Goerania* can be placed well within Liopteridae with certainty, even though it was not included in the analyses. As already noted, the genus was excluded from the analyses since few of the characters in the matrix could be readily observed on the fossil, resulting in a disturbingly large number of missing data points. Nonetheless, a few of the preserved features permit us to identify it as belonging to the clade consisting of the Gondwanan subfamilies Liopterinae and Oberthuerellinae. As noted, these synapomorphies include: lateral margin of axilla conspicuously raised anteriorly; petiolar annulus long, median dorsal length at least twice as long as minimum dorsal width; and posterior margin of petiole and anterior margin of metasomal T2 abutting, with dorsal margins of the two more or less continuous. We can also positively ex-
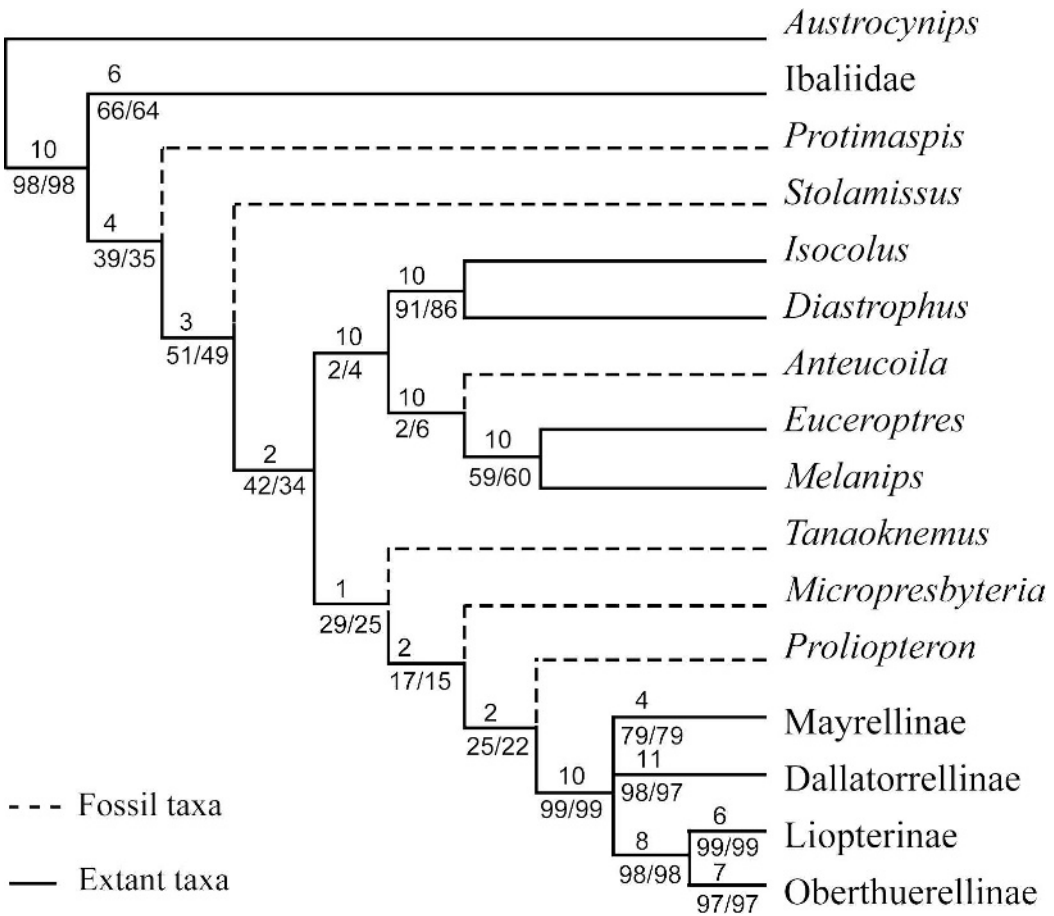
Fig. 23.   Strict consensus tree of the two shortest trees (L = 239, CI = 55, RI = 79) resulting from analysis of the data matrix from figure 22 (i.e., with *Tanaoknemus* and *Micropresbyteria* included), with the phylogenetic relationship of *Anteucoila* with the two representative figitids constrained.

clude *Goerania* from crown-group Oberthuerellinae as well as from crown-group Liopterinae by the absence of foveate sculpture on the lateral surface of the pronotum and by the postpetiolar terga of the metasoma being subequal in length. However, we are uncertain whether these characters unite Liopterinae and Oberthuerellinae relative to Goeraniinae, and we prefer to consider the subfamily in a trichotomy with the modern lineages.

As discussed earlier, we think that *Micropresbyteria* and *Tanaoknemus* can be provisionally placed in Figitidae and Cynipidae, respectively, although we were unable

to resolve the cladistic position of these genera with other cynipoids owing to the unavailability of females. The longitudinally distinctly compressed head and the lack of distinct sculpture on head and mesosoma, short anterior pronotal flange, and the downward insertion of the meso- and metacoxae indicate that *Micropresbyteria* is a microcynipoid. The presence of an obvious dorsal pronotal area, the position of the proximal end of Rs+M close to the posterior end of the first free abscissa of M (i.e., the basal vein), and the presence of the longitudinal carina dorsolaterally on the metatibia strongly suggest that the genus belongs to the Figitidae. Conversely,
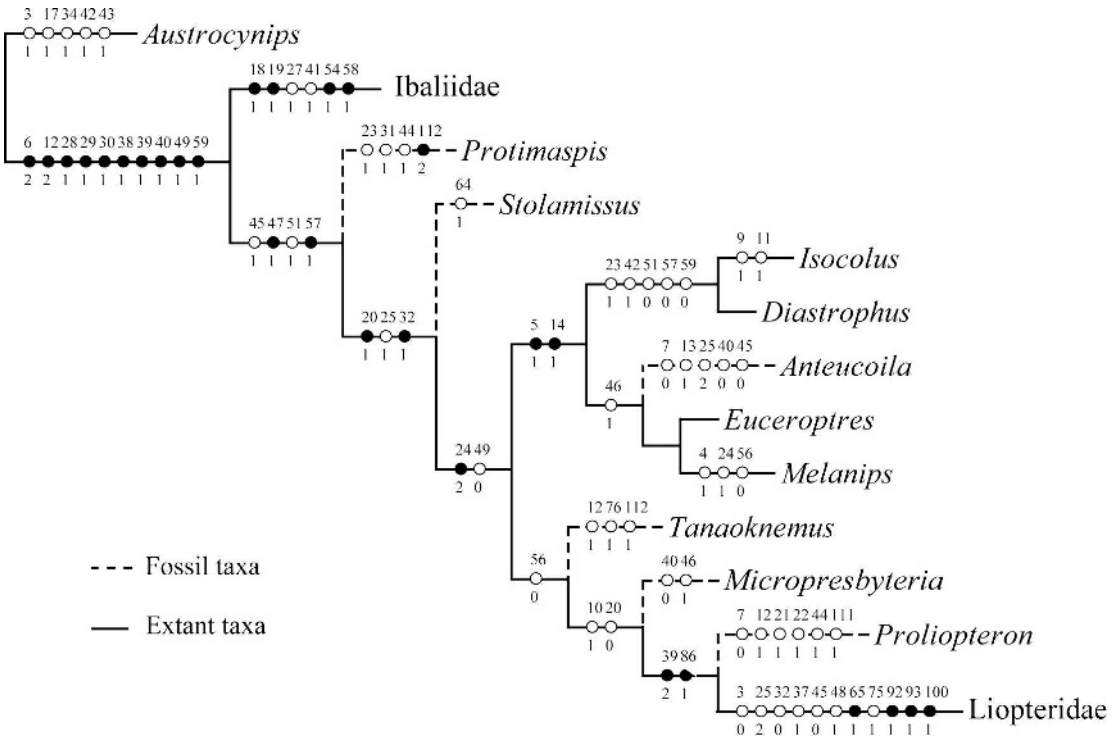
Fig. 24. Character optimization showing unambiguous character changes on internodes of one of the single shortest trees from figure 23 (the two minimal length topologies differ only in relationships within Liopteridae, and thus the subfamilies of this group are collapsed into a single terminal for the purposes of the figure, with those unambiguous character optimizations for the modern liopterid clade being noted). Solid circles indicate unambiguous character transformations; open circles show homoplastic character transformations.

the lack of the lateral pronotal carina, presence of a bulla in $Sc+R_1$, and Rs+M issuing from the middle of the first free abscissa of M (i.e., the basal vein) in *Tanaoknemus* suggest affinity with the Cynipidae. The relatively long petiole of *Tanaoknemus*, a feature often found in Figitidae, is not found in the extant members of Cynipidae. We prefer to tentatively include the genus in Cynipidae based on the afore-mentioned three characters.

DISCUSSION

The Cynipoidea has been widely regarded as being an ancient lineage within Hymenoptera (e.g., Rasnitsyn, 1988; Ronquist et al., 1999). Biogeographic patterns in the basal lineages of Cynipoidea support the notion of an origin and initial divergence of the superfamily in the Jurassic (Ronquist, 1995a, 1995b; Nordlander et al., 1996; Liu, 1998a, 1998b, 2001). Rasnitsyn (1988, 2002) placed the origin of the Cynipoidea in the Late Jurassic based mainly on the existence of Early Cretaceous fossils of the extinct family Archaeocynipidae, which he thought to be stem-group cynipoids (Rasnitsyn and Kovalev, 1988; Rasnitsyn, 1988; Kovalev, 1994, 1995). Kovalev (1994) also placed great emphasis on the characters embodied in Archaeocynipidae for under-standing the early evolution of the Cyni-poidea. Indeed, this author placed the Cyni-poidea into its own infraorder, Cynipomor-pha, and created a second superfamily, Archaeocynipoidea, to include, aside from
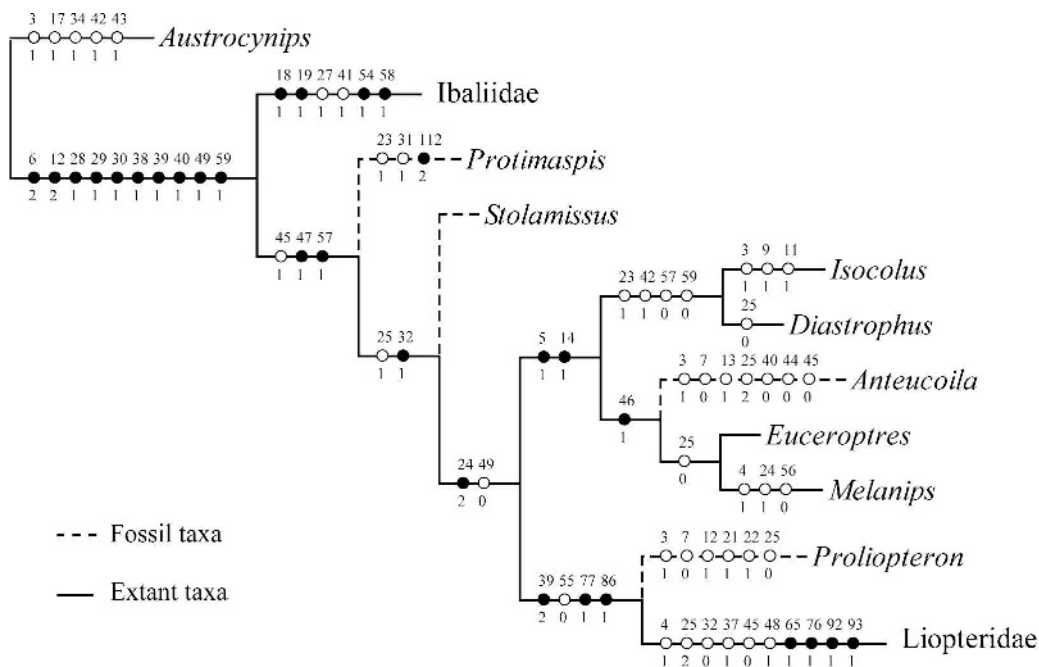
Fig. 25.   Preferred cladogram of cynipoid relationships; character optimization showing unambiguous character changes on internodes of the single shortest tree from figure 21 (the two minimal length topologies differ only in relationships within Liopteridae, and thus the subfamilies of this group are collapsed into a single terminal for the purposes of the figure, with those unambiguous character optimizations for the modern liopterid clade being noted). Solid circles indicate unambiguous character transformations; open circles show homoplastic character transformations.

[4]The name Gerocynipidae as established by Kovalev (1994) has, quite unfortunately, some serious nomenclatural problems and is in fact unavailable. The trouble stems from the fact that the species *Gerocynips zherichini* Kovalev is a nomen nudum. Kovalev (1994), when describing the family, refers to an earlier article establishing the genus *Gerocynips* and its type species, *G. zherichini*. The article is cited as appearing as a chapter in Price et al. (1994), which represents the results of a meeting in Krasnoyarsk, Siberia (August 9–13, 1993) under the auspices of the International Union of Forestry Research Organizations (IUFRO) and the Institute of Forest and Wood, Siberian Branch of the Russian Academy of Sciences. In examining a copy of this publication, however, no article by Kovalev could be found. It therefore appears as if *Gerocynips* were first established in Kovalev (1994). Unfortunately, the ICZN (1999: art. 13) dictates that all new taxa must have an available species explicitly designated as type species. Although Kovalev (1994) does indeed designate *G. zherichini* as the type species, this species is not described therein (again referring back to the elusive article in Price et al., 1994). Thus, *Gerocynips* Kovalev, 1994 is an unavailable name and *G. zherichini* a nomen nudum. Similarly, the family-group name Gerocynipidae Kovalev, 1994 is rendered unavailable since it is based on an unavailable type genus (it is not subsequently made available by Kovalev, 1995). We herein correct this

Archaeocynipidae, the extinct families Gerocynipidae,[4] Rasnicynipidae,[5] and Palaeocynipidae. Under this scheme the archaeocynipoids were a grade from which Cynipoidea

nomenclatural difficulty by newly validating Gerocynipidae and *Gerocynips*, but leaving *G. zherichini* as a nomen nudum and instead designating one of the two actually described species as the type. The nomenclatural details are as follows: **Gerocynipidae** Liu and Engel, new family (type genus: *Gerocynips* Liu and Engel, new genus), diagnosis as that provided by Kovalev (1994); ***Gerocynips*** Liu and Engel, new genus (type species: *G. siberica* Kovalev, 1994), diagnosis as that provided by Kovalev (1994).

[5]Originally proposed as Rasnitsyniidae (Kovalev, 1994), the family was subsequently renamed Rasnicynipidae (Kovalev, 1996) owing to homonymy of the type genus, *Rasnitsynia*, with a generic name established in Braconidae (Pagliano and Scaramozzino, 1989). Interestingly, Kovalev (1995), in a key referring to the same material of 1994, used the replacement name as "Rasnicynipidae fam. nov." Although a description was provided (in the key couplet), it was not based on an available genus-group name at that time (the replacement name *Rasnicynips* was not proposed until the 1996 paper) and thus Rasnicynipidae was not validated until later in Kovalev (1996).
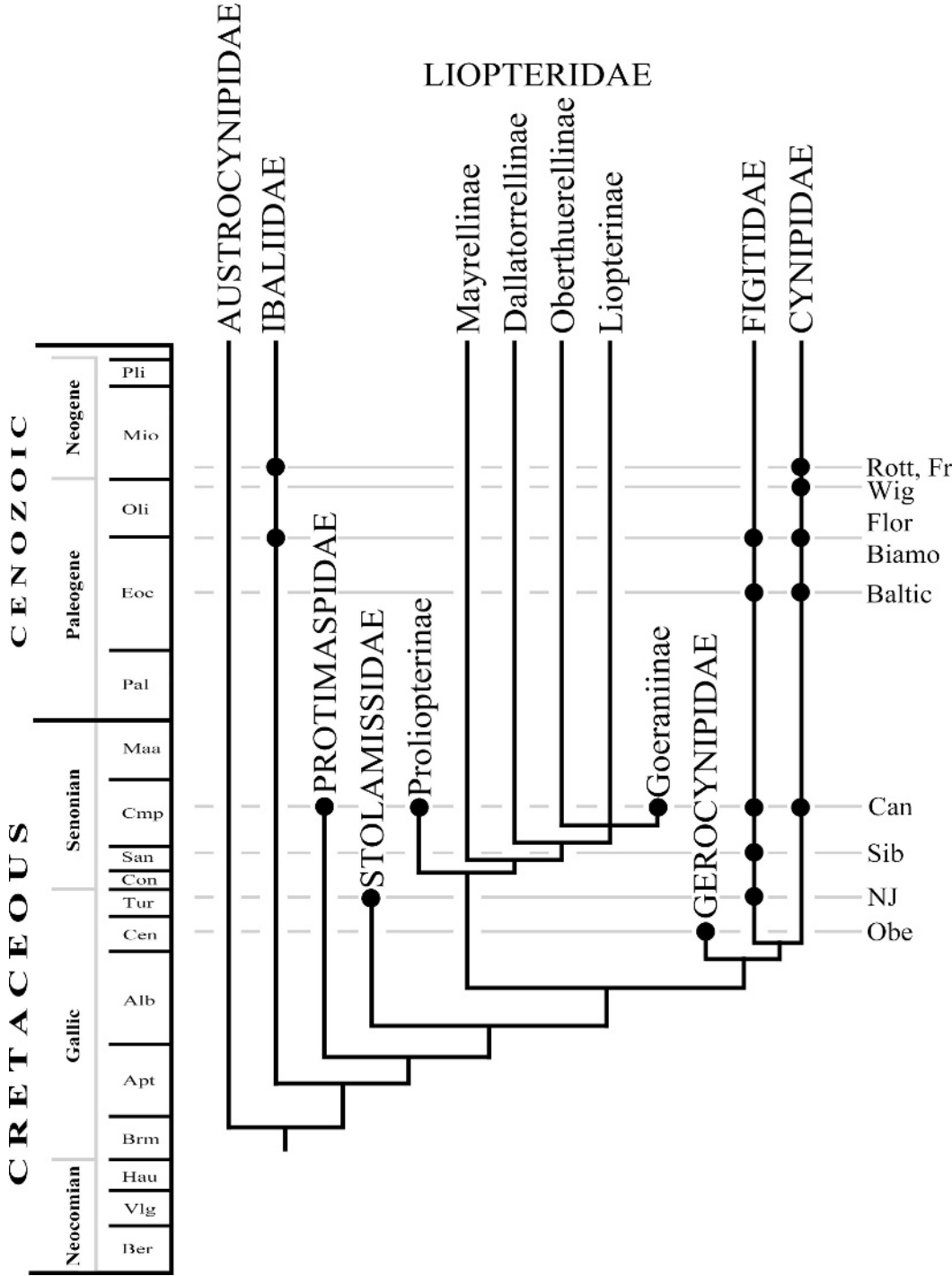
Fig. 26. Phylogeny of the Cynipoidea summarizing relationships among major lineages. Fossil records are tabulated in appendix 1. Abbreviations for particular deposits are: Rott (Rott, Germany), Fr (Cantal, France), Wig (Isle of Wight, England), Flor (Florissant, Colorado), Biamo (Biamo, today Bol'shaya Svetlovodnaya), Baltic (Baltic amber), Can (Canadian amber), Sib (Siberian amber of the Taimyr Peninsula), NJ (New Jersey amber), and Obe (Obeshchayushchiy Creek).
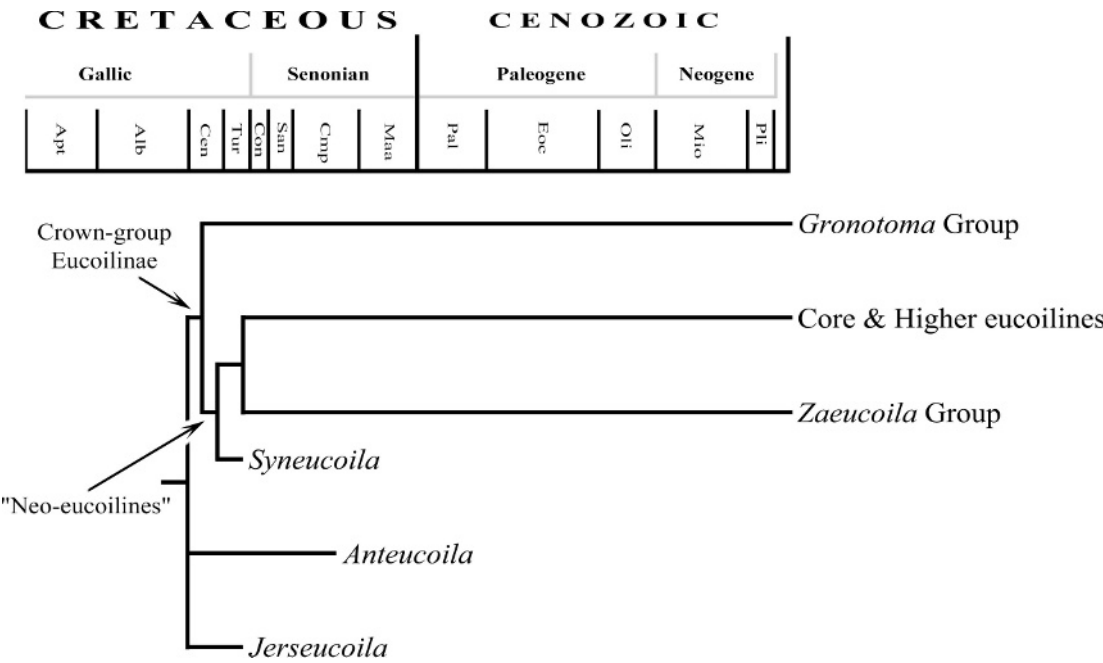
Fig. 27. Phylogeny of Eucoilinae after Fontal-Cazalla et al. (2002) with the putative positions of the three Cretaceous amber taxa (*Anteucoila*, *Jerseucoila*, and *Syneucoila*) being noted (support for clades is outlined in table 4).

arose. Unfortunately, although Gerocynipidae, Rasnicynipidae, and Palaeocynipidae are indeed cynipoids (table 1), the Archaeocynipidae do not belong to the Cynipoidea and are instead more closely allied to the Diapriidae (Ronquist, 1999). As such, to date there are no cynipoid fossils from the Jurassic or Early Cretaceous, and we therefore cannot directly substantiate a Jurassic origin of the superfamily. However, the presence in early stages of the Late Cretaceous of various macrocynipoids and, more significantly, a relatively derived liopterid (*Goerania*) along with definitive eucoilines (Figitidae) indicate that the more basal divergences within Liopteridae and across basal Cynipoidea must have predated the middle Cretaceous. The phylogenetic placement of these fossils therefore suggests an origin of the Cynipoidea sometime in at least the Early Cretaceous (fig. 26). As noted, however, a Late Jurassic origin, as suggested by biogeographic patterns (Nordlander et al., 1996; Ronquist, 1995b; Liu, 1998a, 1998b, 2001), cannot be excluded, and exploration of Early Cretaceous deposits might significantly extend the ages of various cynipoid families. A

cynipoid in the Early Cretaceous amber of Lebanon would be particularly revealing.

While the position of archaeocynipids in Cynipoidea has eroded, the Gerocynipidae, Rasnicynipidae, and Palaeocynipidae were indeed correctly assigned to the superfamily. Ronquist (1999) considered Rasnicynipidae to be the most basal among the microcynipoids, and Gerocynipidae as the next most basal branch of the stem lineage leading to the extant microcynipoid families Cynipidae and Figitidae. Ronquist arrived at this conclusion mainly because both Rasnicynipidae and Gerocynipidae, among several features, have meso- and metacoxae that are directed downward (Kovalev, 1994; Ronquist, 1999), which is the putatively derived state by contrast to that seen in Austrocynipidae and Ibaliidae (also in *Protimaspis*: see above) where the meso- and metacoxae are directed obliquely backward (Ronquist, 1995a). The illustration of the forewing of *Rasnicynip*s, the sole genus of Rasnicynipidae, as presented by Kovalev (1994: fig. 19 and under the name *Rasnitsynia*) shows the proximal end of Rs+M directed toward the posterior end of the first free

TABLE 4
Clade Support for Phylogeny of Eucoilinae
(Briefly summarized from Fontal-Cazalla et al.,
2002, with fossil eucoilines added)

Subfamily Eucoilinae
  1. Mesoscutellar cup present
  2. Mesopleuron with longitudinal carina present
  3. Malar sulcus present (difficult to see in *Jerseucoila* and *Anteucoila*)

Crown-group eucoilines
  4. Metasomal T2–4 fused

"Neo-eucoilines"
  5. Broad metasubpleural depression present

Zaeucoila group + core eucoilines
  6. Subalar pit reduced
  7. Subalar area of mesopleuron reduced
  8. Short vertical carina issuing from ventral margin of antennal torulus

abscissa of M (i.e., the basal vein), a derived character of the Figitidae not found in any other cynipoids. We therefore transfer *Rasnicynips* to Figitidae, tentatively classified therein as a basal subfamily, although more work is required for a more definitive placement (table 1 and appendix 1). Gerocynipidae has been more difficult to place, largely owing to the less perfect preservation as the family is known only as compressions from the Late Cretaceous of the Russian Far East (Kovalev, 1994). Kovalev (1994) concluded that the gerocynipids were gall inducers because only females were discovered and their large and round metasomas resembled several archaic lineages of modern gall-inducing cynipids. As correctly noted by Ronquist (1999), such features would indicate that the gerocynipids belong to Cynipidae. However, he also rightly noted the lack of any observable cynipid synapomorphies in Gerocynipidae and accordingly placed them at the base of micro-cynipids. Pending the discovery of new material permitting a more definitive assignment, we follow Ronquist's placement of the family.

It is particularly remarkable that the Late Cretaceous amber fauna of North America should possess species of the subfamily Eucoilinae. Eucoilines are perhaps related to the Pycnostigminae, and together are perhaps not basal within Figitidae, suggesting that the radiation of this family took place well within the Cretaceous. Perhaps not surprisingly, the Cretaceous fauna includes two genera that are clearly stem groups of modern Eucoilinae. While possessing the distinctive and unique mesoscutellar plate of the subfamily, *Anteucoila* and *Jerseucoila* have the metasomal segments primitively separated (figs. 12, 14), the fusion of the second through fourth metasomal terga representing another feature of modern eucoilines (fig. 27, table 4). The genus *Syneucoila* (fig. 16), on the other hand, is more intriguing in that it is not only a typical crown-group eucoiline but it is apparently intermediate between the basal "*Gronotoma* group" (or tribe Diglyphosemini) and a clade consisting of the "*Zaeucoila* group" and core eucoilines (sensu Fontal-Cazalla et al., 2002) (fig. 27). The appearance of a "neo-eucoiline" as long ago as the Late Cretaceous further attests to the antiquity of the subfamily and thereby the figitids as a whole.

Naturally, the cynipoids are most widely known by the gall wasps (Cynipidae). Although the secondary derivation of phytophagy in the ancestor of cynipids from the grade of parasitoids comprising the remainder of the superfamily is clear (e.g., Malyshev, 1968; Roskam, 1992; Ronquist, 1995b, 1999; and analyses herein), the age and means of this significant evolutionary transition remain unknown. All Cretaceous cynipoid fossils discovered to date belong to parasitoid families. Although the Gerocynipidae could be gall-makers as supposed by Kovalev (1994), this assertion is entirely speculative. The extinct cynipid subfamily Hodiernocynipinae, represented solely by compressions (appendix 1), was included in Cynipidae by Kovalev (1994), but again, no synapomorphy of the family has been identified in these specimens (Ronquist, 1999) and they are perhaps stem-group cynipids at best. If such a placement of hodiernocynipines is correct, it still leaves unresolved whether these taxa were gall-inducers, as the origin of phytophagy could have taken place in the common ancestor of crown-group Cynipidae. However, phytophagy in Cynipidae is assuredly much older than the hodiernocynipines, regardless of their dubious phylogenetic position. *Tanaoknemus*, described herein, is very likely a true cynipid. If this is so, then phytophagy may have

originated in the Late Cretaceous and around the time of angiosperm diversification (Crane and Lidgard, 1989, 1990; Crane et. al, 1995), unless, of course, *Tanaoknemus* is subsequently demonstrated to be basal among true cynipids, in which case the same difficulty ascribed to Hodiernocynipinae applies. The oldest fossil that can be definitively placed in Cynipidae is *K. succinea* (see above). *Kinseycynips* is therefore the oldest, definitive gall wasp, and it probably induced galls on herbaceous host plants belonging to the family Rosaceae (refer to comments in generic description; see above). Considering that definitive species of the Cynipidae have existed since at least the middle Eocene (as evidenced by *Kinseycynips*), we think it reasonable to hypothesize that the gall wasps likely originated much earlier than the age of the known body and trace fossils and that the discovery of more wasp fossils will eventually fill the gap, likely extending definitive cynipids into the Cretaceous (as we suspect from the putative position of *Tanaoknemus* as well as cynipid-like galls from the Late Cretaceous; Scott et al., 1994).

Liljeblad and Ronquist (1998) mapped cynipid hosts on a phylogeny of the family, noting that the inquilines formed a monophyletic group (tribe Synergini). The synergines, consisting of about 200 species, do not induce galls themselves but instead live in galls started and maintained by other species. The Synergini, nested among the gall-inducing cynipids, are likely a relatively recent lineage although there is no direct evidence of their age. Putatively basal lineages of Cynipidae form galls on herbaceous plants, especially species of Papaveraceae and Lamiaceae (Ronquist and Liljeblad, 2001). Presumably the ancestral habit of Cynipidae was gall-inducing behavior on such herbaceous plants, although recent molecular data suggest the opposite, with woody rosid gallers being more primitive (Nylander et al., 2004). Cockerell (1921) described two fossils from the Oligocene (appendix 1) as *Rhodites vetus* and *Andricus vectensis*. Ronquist (1999) suggested that the former might well have been correctly placed in the tribe Diplolepidini, the wasps that induce galls on *Rosa*, but he was not certain about the placement of the other species in Cynipini, the tribe that induces galls on hosts of the plant family Fagaceae. It is interesting that all these fossils are representative of the derived "woody gallers", with the questionable position of *A. vectensis* being pushed momentarily aside. The slightly older *K. succinea*, as we discussed above, was almost assuredly a woody rosaceous galler. Regardless, the earliest gallers were significantly older (by perhaps as much as 45 Ma) than *K. succinea*.

Among the Cynipidae, the familiar oak gall wasps (tribe Cynipini) are disproportionately more diverse compared to other lineages, with about 1000 described species (Liljeblad and Ronquist, 1998). As their name suggests, species of the tribe are almost exclusively associated with oaks of the genus *Quercus* (Fagaceae). It would be of particular interest to find evidence on the age of such a diverse lineage and one with such conservatism in host use (hence the interest in the identity of Cockerell's *A. vectensis*). Ronquist (1999) considered the Cynipidae to be from at least 80–85 Ma based on sister-group dating of figitid fossils in Siberian amber (Kovalev, 1994). Herein we consider the Cynipidae to be slightly older, perhaps extending to 90 Ma (fig. 26). Certainly, given the derived position of the oak gall wasps in the family, the Cynipini are undoubtedly much younger, clearly having a Tertiary origin and radiation. The Tertiary age of Cynipini is largely dicatated by the fossil record of its hosts. Although an exceedingly primitive and undescribed flower of Fagaceae has been discovered in New Jersey amber (see Grimaldi and Engel, 2005: fig 14.5), fossils of Fagaceae s. str. (i.e., excluding Nothofagaceae) are basically confined to the Tertiary (Herendeen et al., 1995). Megafossils of the modern genera *Quercus*, *Castanea*, *Castanopsis*, and *Fagus* are documented from as long ago as the middle Eocene, and by the Eocene–Oligocene several of the major lineages of oaks had originated (some represented by archaic forms), and the oak flora had clearly become prominent and diverse by the Miocene (e.g., Nixon, 1989, 1993; Herendeen et al., 1995; Manos et al., 1999, 2001; Manchester and Dillhoff, 2004). Interestingly, the fossil record of cynipines is more thoroughly documented by paleobotanical evidence rather than by fossils of the oak gall wasps themselves (a situation similar to

the leaf-cutter bees, where the earliest records of the group come from the distinctive traces they produced in fossilized leaves; e.g., Engel, 2004; Engel and Perkovsky, 2006). Fossils of galls are quite diverse in the Tertiary (e.g., Larew, 1986, 1992). The earliest, definitive evidence of the association between Cynipini and oaks are some fossil galls described from middle Miocene (ca. 12.5–15 Ma) deposits of the western United States (Waggoner and Poteet, 1996; Waggoner, 1999), as well as in younger deposits. These ichnofossils are well-preserved leaf galls on *Quercus hannibali* Dorf, a fossil species morphologically similar to the extant species *Q. chrysolepis* Liebman. It seems reasonable to assume that cynipines are perhaps as old as the Eocene, with their radiation roughly corresponding with the Late Eocene through Miocene diversification of oaks.

ACKNOWLEDGMENTS

REFERENCES

Ashmead, W.H. 1895. Notes on the genus *Liopteron* Perty. Proceedings of the Entomological Society of Washington 3: 174–178.

Ashmead, W.H. 1896. Description of new parasitic Hymenoptera. Transactions of the American Entomological Society 23: 179–190.

Ashmead, W.H. 1903. Classification of the gall-wasps and the parasitic cynipoids, or the superfamily Cynipoidea, IV. Psyche 10: 210–215.

Brues, C.T. 1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. Bulletin of the Museum of Comparative Zoology 54: 3–125.

Buffington, M., Z. Liu, and F. Ronquist. 2005. Cynipoidea. *In* F. Fernández and M. Sharkey (editors), Introducción a los Hymenoptera de la región Neotropical. Bogotá D.C.: Sociedad Colombiana de Entomología, xx + 870 pp.

Cameron, P. 1905. A new species of Cynipidae from South Africa, representing a new subfamily. Annals of Natural History, series 7, 16: 20–21.

Cockerell, T.D.A. 1921. Fossil arthropods in the British Museum, V. Annals and Magazine of Natural History, series 9, 7: 1–25.

Crane, P.R., E.M. Friis, and K.R. Pedersen. 1995. The origin and early diversification of angiosperms. Nature 374(6517): 27–33.

Crane, P.R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246(4930): 675–678.

Crane, P.R., and S. Lidgard. 1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. *In* P.D. Taylor and G.P. Larwood (editors), Major evolutionary radiations: 377–407. Oxford: Clarendon Press, xi + 437 pp.

Dalla Torre, K.W., and J.J. Kieffer. 1910. Cynipidae. Das Tierreich 24: 1–891.

Engel, M.S. 2004 [2005]. Geological history of the bees (Hymenoptera: Apoidea). Revista de Tecnologia e Ambiente 10(2): 9–33.

Engel, M.S., and E.E. Perkovsky. 2006. An Eocene bee in Rovno amber, Ukraine (Hymenoptera: Megachilidae). American Museum Novitates 3506: 1–12.

Fontal-Cazalla, F.M., M.L. Buffington, G. Nordlander, J. Liljeblad, P. Ros-Farre, J.L. Nieves-Aldrey, J. Pujade-Villar, and F. Ronquist. 2002. Phylogeny of the Eucoilinae (Hymenoptera: Cynipoidea: Figitidae). Cladistics 18(2): 154–199.

Geoffroy, E.-L. 1762. Histoire abrégée des Insectes qui se trouvent aux environs de Paris; dans laquelle ces Animaux sont rangés suivant un ordre méthodique. Paris: Durand, viii + 523 pp. [vol. 1], 690 pp. [vol. 2].

Goloboff, P.A. 1997. NoName (NONA), version 2.0. Program and documentation. Fundación e Instituto Miguel Lillo, Tucumán.

Gradstein, F., J. Ogg, and A. Smith. 2004. A geologic time scale 2004. Cambridge: Cambridge University Press, xix + 589 pp.

Grimaldi, D., and M.S. Engel. 2005. Evolution of the insects. Cambridge: Cambridge University Press, xv + 755 pp.

Grimaldi, D., A. Shedrinsky, and T.P. Wampler. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 1–76. Leiden: Backhuys, viii + 498 pp.

Hartig, T. 1840. Ueber die Familie der Gallwespen, III. Zeitschrift für Entomologie, Germar 2: 176–209.

Hedicke, H. 1922. Beiträge zur Kenntnis der Cynipiden (Hym.). X. Eine neue Unterfamilie der Cynipiden. Deutsche Entomologische Zeitschrift 1922: 190–192.

Hellén, W. 1931. Zur Kenntnis der Cynipiden-Fauna Islands. Göteborgs Kungliga Vetenskaps- och Vitterhetssamhälles Handlingar, Femte Följden 2: 1–8.

Herendeen, P.S., P.R. Crane, and A.N. Drinnan. 1995. Fagaceous flowers, fruits, and cupules from the Campanian (Late Cretaceous) of central Georgia, USA. International Journal of Plant Science 156(1): 93–116.

Hong, Y.-C. 2002. Amber insects of China. Beijing: Science and Technology Press, [iii] + 4 + 653 + 48 pp. [In Chinese]

International Commission on Zoological Nomenclature [ICZN]. 1999. International Code of Zoological Nomenclature [4th ed.]. London: International Trust for Zoological Nomenclature, xxix + 306 pp.

Kieffer, J.J. 1903. Description de trois cynipides exotiques. Marcellia 2: 84–90.

Kieffer, J.J. 1911. Nouveaux cynipides exotiques. Bolletino della Società Entomologica Italiana 41: 244–254.

Kinsey, A.C. 1919. Fossil Cynipidae. Psyche 26: 44–49.

Kinsey, A.C. 1937. Family Cynipidae. University of Toronto Studies, Geological Series 40: 21–27.

Kovalev, O.V. 1994. Palaeontological history, phylogeny and the system of brachycleistogastromorphs and cynipomorphs (Hymenoptera, Brachycleistogastromorpha infraorder n., Cynipomorpha infraorder n.) with description of new fossil and recent families, subfamilies and genera. Entomologicheskoe Obozrenie 73(2): 385–426. [In Russian: English translation in Entomological Review, 1995, 74(4): 105–147]

Kovalev, O.V. 1995. New taxa of fossil cynipoids (Hymenoptera, Cynipoidea) from the Cretaceous and Palaeogene. Amber and Fossils 1(1): 9–16.

Kovalev, O.V. 1996. New higher taxa of cynipoids (Hymenoptera, Cynipoidea): Renaming of a family and description of a new family, new subfamily, and genus. Entomologicheskoe Obozrenie 75(2): 408–416. [In Russian]

Krombein, K.V., P.D. Hurd, Jr., D.R. Smith, and B.D. Burks, editors. 1979. Catalog of Hymenoptera in America north of Mexico. Washington, DC: Smithsonian Institution Press, xvi + 2735 pp.

Larew, H.G. 1986. The fossil gall record: a brief summary. Proceedings of the Entomological Society of Washington 88(2): 385–388.

Larew, H.G. 1992. Fossil galls. *In* J.D. Shorthouse and O. Rohfritsch (editors), Biology of insect-induced galls: 50–59. Oxford: Oxford University Press, x + 285 pp.

Latreille, P.A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusiers sociétés savantes. Tome troisième. Paris: Dufart, xii + 467 pp.

Liljeblad, J., and F. Ronquist. 1998. A phylogenetic analysis of higher-level gall wasp relationships. Systematic Entomology 23(3): 229–252.

Liu, Z. 1998a. Phylogenetic systematics and historical biogeography of macrocynipoids parasitizing woodboring insects. Acta Universitatis Agriculturae Sueciae, Silvestria 62: 1–26.

Liu, Z. 1998b. A new species of *Ibalia* from Borneo, and revised phylogeny and historical biogeography of Ibaliidae (Hymenoptera: Cynipoidea). Journal of Hymenoptera Research 7(2): 149–156.

Liu, Z. 2001. Phylogeny, biogeography, and revision of the subfamily Dallatorrellinae (Hymenoptera: Liopteridae). American Museum Novitates 3353: 1–23.

Liu, Z., and G. Nordlander. 1992. Ibaliid parasitoids of siricid woodwasps in North America: two new *Ibalia* species and a key to species (Hymenoptera: Cynipoidea). Proceedings of the Entomological Society of Washington 94(4): 500–507.

Liu, Z., and G. Nordlander. 1994. Review of the family Ibaliidae (Hymenoptera: Cynipoidea) with keys to genera and species of the world. Entomologica Scandinavica 25(4): 377–392.

Liu, Z., G. Nordlander, and F. Ronquist. 2007. Systematics, phylogeny, and historical biogeography of *Paramblynotus* Cameron, 1908 (Hymenoptera: Cynipoidea: Liopteridae). Bulletin of the American Museum of Natural History 304: 1–151.

Malyshev, S.I. 1968. Genesis of the Hymenoptera and the phases of their evolution. London: Methuen, viii + 319 pp.

Manchester, S.R., and R.M. Dillhoff. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the middle Eocene of Pacific Northwestern North America. Canadian Journal of Botany 8210: 1509–1517.

Manos, P.S., J.J. Doyle, and K.C. Nixon. 1999. Phylogeny, biogeography, and process of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). Molecular Phylogenetics and Evolution 12(3): 333–349.

Manos, P.S., Z.-K. Zhou, and C.H. Cannon. 2001. Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution. International Journal of Plant Science 162(6): 1361–1379.

Nel, A. 1996. The first fossil *Ibalia* from the Upper Miocene of Cantal (France) (Hymenoptera, Cynipoidea). Bulletin de la Société Entomologique de France 101(2): 141–143.

Nieves-Aldrey, J.L. 2001. Cynipidae, Hymenoptera: Fauna Iberica [volume 16]. Madrid: Museo Nacional de Ciencias Naturales, 636 pp.

Nieves-Aldrey, J.L., H. Vårdal, and F. Ronquist. 2004. Comparative morphology of terminal-instar larvae of Cynipoidea: Phylogenetic implications. Zoologica Scripta 34(1): 15–36.

Nixon, K.C. 1989. Origins of Fagaceae. *In* P.R. Crane and S. Blackmore (editors), The evolution, systematics, and fossil history of the Hamamelidae: volume 2, ''Higher'' Hamamelidae: 23–43. Oxford: Oxford University Press, xii + 356 pp.

Nixon, K.C. 1993. The genus *Quercus* in Mexico. *In* T.R. Ramamoorthy (editor), Biological diversity of Mexico: origins and distribution: 447–458. Oxford: Oxford University Press, xxxix + 812 pp.

Nixon, K.C. 2002. WinClada, version 1.00.08. Program and documentation. Cornell University, Ithaca.

Nordlander, G. 1984. Vad vet vi om parasitiska Cynipoidea? Entomologisk Tidskrift 105(1–2): 36–40. [with English summary]

Nordlander, G., Z. Liu, and F. Ronquist. 1996. Phylogeny and historical biogeography of the cynipoid wasp family Ibaliidae (Hymenoptera). Systematic Entomology 21(2): 151–166.

Nylander, J.A.A., F. Ronquist, J.P. Huelsenbeck, and J.L. Nieve-Aldrey. 2004. Bayesian phylogenetic analysis of combined data. Systematic Biology 53(1): 47–67.

Pagliano, G., and P. Scaramozzino. 1989 [1990]. Elenco dei generi di Hymenoptera del Mondo. Memorie della Societa Entomologica Italiana 68(1989): 1–210.

Presl, J.S. 1822. Deliciae Pragensis, historiam naturalem spectantes [Additamenta ad faunam protogaeam, sistens descriptiones aliquot animalium in succino inclusorum, p. 191–210]. Prague: Calve, viii + 244 pp.

Price, P.W., W.J. Mattson and Y.N. Baranchikov (editors) XPATH ERROR: unterminated function parameters; missing ')'., The ecology and evolution of gall-forming insects. St. Paul, MN: United States Department of Agriculture [Forest Service, North Central Forest Experiment Station, General Technical Report GTC-NC-174], [vii] + 222 + [1] pp.

Rasnitsyn, A.P. 1988. An outline of evolution of the hymenopterous insects. Oriental Insects 22: 115–145.

Rasnitsyn, A.P. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (= Vespida Laicharting, 1781). *In* A.P. Rasnitsyn and D.L.J. Quicke (editors), History of insects: 242–254. Dordrecht: Kluwer Academic Publishers, xii + 517 pp.

Rasnitsyn, A.P., and O.V. Kovalev. 1988. The oldest Cynipoidea (Hymenoptera: Archaeocynipidae fam. n.) from the Early Cretaceous Transbaikalia. Vestnik Zoologii 1988(1): 18–21. [in Russian].

Riek, E.F. 1971. A new subfamily of cynipoid wasps (Hymenoptera: Cynipoidea) from Australia. *In* S. Asahinas, J.L. Gressitt, Z. Hidaka, T. Nishida and K. Nomura (editors), Entomological essays to commemorate the retirement of Professor K. Yasumatsu: 107–112. Tokyo: Hokuryukan, vi + 389 pp.

Ronquist, F. 1994. Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). Evolution 48(2): 241–266.

Ronquist, F. 1995a. Phylogeny and classification of the Liopteridae, an archaic group of cynipoid wasps (Hymenoptera). Entomologica Scandinavica, supplement 46: 1–74.

Ronquist, F. 1995b. Phylogeny and early evolution of the Cynipoidea (Hymenoptera). Systematic Entomology 20(4): 309–335.

Ronquist, F. 1999. Phylogeny, classification and evolution of the Cynipoidea. Zoologica Scripta 28(1–2): 139–164.

Ronquist, F., and J. Liljeblad. 2001. Evolution of the gall wasp-host plant association. Evolution 55(12): 2503–2522.

Ronquist, F., and J.L. Nieves-Aldrey. 2001. A new subfamily of Figitidae (Hymenoptera, Cynipoidea). Zoological Journal of the Linnean Society 133(4): 483–494.

Ronquist, F., and G. Nordlander. 1989. Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibaliidae). Entomologica Scandinavica, supplement 33: 1–60.

Ronquist, F., A.P. Rasnitsyn, A. Roy, K. Eriksson, and M. Lindgren. 1999. Phylogeny of Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. Zoologica Scripta 28(1–2): 13–50.

Roskam, H.C. 1992. Evolution of the gall-inducing guild. *In* J.D. Shorthouse and O. Rohfritsch (editors), Biology of insect-induced galls. Oxford: Oxford University Press, x + 285 pp.

Schuh, R.T. 2000. Biological systematics: principles and applications. Ithaca: Cornell University Press, ix + 236 pp.

Scott, A.S., J. Stephenson, and M.E. Collinson. 1994. The fossil record of leaves with galls. In M.A.J. Williams (editor), Plant galls: organisms, interactions, populations: 447–470. Oxford: Clarendon Press, xiv + 487 pp.

Statz, G. 1938. Neue funde parasitischer Hymenopteren aus dem Tertiär von Rott am Siebengebirge. Decheniana 98A: 71–144.

Thomson, C.G. 1862. Försök till uppställning och beskrifning af Sveriges Figiter. Öfversigt ag Kongliga Vetenskaps-Akademiens Förhandlingar 18: 395–420.

Vårdal, H., G. Sahlén, and F. Ronquist. 2003. Morphology and evolution of the cynipoid egg (Hymenoptera). Zoological Journal of the Linnean Society 139(2): 247–260.

Waggoner, B.M. 1999. Fossil oak leaf galls from the Stinking Water paleoflora of Oregon (middle Miocene). PaleoBios 19: 8–14.

Waggoner, B.M., and M.F. Poteet. 1996. Unusual oak leaf galls from the middle Miocene of northwestern Nevada. Journal of Paleontology 70(6): 1080–1084.

Weld, L.H. 1952. Cynipoidea (Hym.) 1905–1950, being a supplement to the Dalla Torre and Kieffer monograph, the Cynipidae in Das Tierreich, Lieferung 24, 1910, and bringing the systematic literature of the world up to date, including keys to families and subfamilies and lists of new generic, specific and variety names. Ann Arbor, MI: Privately printed, 351 pp.

APPENDIX 1
Described Fossil Cynipoidea

The following table summarizes those fossil species described within the Cynipoidea. The classificatory structure follows that from table 1 in the text. Geological ages follow those of Gradstein et al. (2004). Various fossils originally described as cynipoids but subsequently removed are not included herein. The family †Archaeocynipidae (Rasnitsyn and Kovalev, 1988) was removed from the Cynipoidea by Ronquist (1999) and suggested to be more closely allied to the Diapriidae (Proctotrupoidea). Similarly, various putative "cynipids" in Eocene amber from China (Hong, 2002) are not included as they appear to be misidentifications. In particular, †*Sinocynipites fushunensis* Hong and †*Hemerocynipites wanghuacunensis* Hong appear to be proctotrupoid wasps (Proctotrupoidea), †*Eocynipites xilutianensis* Hong is a male ant (Aculeata: Formicidae), and †*Eucynipites guchengzensis* Hong and †*Asiacynipites virides* Hong cannot be determined to superfamily (Apocrita incertae sedis). Hong's ability to grossly misidentify specimens and to oversplit taxa such that nearly everything resides in a new genus or higher taxonomic entity is infamous (all of this material needs to be reevaluated and revised). Lastly, the species †*Gerocynips zherichini* Kovalev is excluded as this is a nomen nudum (refer to footnote 4 in the text). Note also that Brues' (1910) *Andricus myrciae* is in fact a synonym of *Cecidomyia pontaniiformis* Cockerell (Kinsey, 1919) and is therefore not included here.

Taxon	Deposit	Age
Family IBALIIDAE Thomson, 1862		
Subfamily Incertae sedis		
Genus †*Protoibalia* Brues, 1910		
†*Protoibalia connexiva* Brues, 1910	Florissant, Colorado	Eocene–Oligocene
Subfamily Ibaliinae Thomson, 1862		
Genus *Ibalia* Latreille, 1802		
†*Ibalia* sp. (Nel, 1996)	Cantal, France	Miocene
Family †PROTIMASPIDAE Liu and Engel, n. fam.		
Subfamily †PROTIMASPINAE Liu and Engel, n. subfam.		
Genus †*Protimaspis* Kinsey, 1937		
†*Protimaspis costalis* Kinsey, 1937	Canadian amber	Campanian
Family †STOLAMISSIDAE Liu and Engel, n. fam.		
Subfamily †STOLAMISSINAE Liu and Engel, n. subfam.		
Genus †*Stolamissus* Liu and Engel, n. gen.		
†*Stolamissus mirabilis* Liu and Engel, n. sp.	New Jersey amber	Turonian
Family LIOPTERIDAE Ashmead, 1895		
Subfamily †Proliopterinae Liu and Engel, n. subfam.		
Genus †*Proliopteron* Liu and Engel, n. gen.		
†*Proliopteron redactus* Liu and Engel, n. sp.	Canadian amber	Campanian
Subfamily †Goeraniinae Liu and Engel, n. subfam.		
Genus †*Goerania* Liu and Engel, n. gen.		
†*Goerania petiolata* Liu and Engel, n. sp.	Canadian amber	Campanian
Family †GEROCYNIPIDAE Liu and Engel, n. fam.		
Subfamily †GEROCYNIPINAE Liu and Engel, n. subfam.		
Genus †*Gerocynips* Liu and Engel, n. gen.		
†*Gerocynips zherichini* Kovalev, 1994	Obeshchayushchiy Creek	Cenomanian
†*Gerocynips sibirica* Kovalev, 1994	Obeshchayushchiy Creek	Cenomanian
†*Gerocynips florenskayae* Kovalev, 1994	Obeshchayushchiy Creek	Cenomanian
Genus †*Antiquecynips* Kovalev, 1994		
†*Antiquecynips orientalis* Kovalev, 1994	Obeshchayushchiy Creek	Cenomanian
Genus †*Arctogerocynips* Kovalev, 1994		
†*Arctogerocynips magadanicus* Kovalev, 1994	Obeshchayushchiy Creek	Cenomanian
Family FIGITIDAE Thomson, 1862		
Subfamily Incertae sedis		
Genus †*Micropresbyteria* Liu and Engel, n. gen.		
†*Micropresbyteria caputipressa* Liu and Engel, n. sp.	Canadian amber	Campanian

APPENDIX 1
(Continued)

Taxon	Deposit	Age
Subfamily †Rasnicynipinae Kovalev, 1996		
Genus †*Rasnicynips* Kovalev, 1996		
†*Rasnicynips eximia* (Kovalev, 1994)	Taimyr amber	Santonian
Subfamily †Palaeocynipinae Kovalev, 1995		
Genus †*Palaeocynips* Kovalev, 1994		
†*Palaeocynips arcticus* Kovalev, 1994	Taimyr amber	Santonian
Genus †*Palaeocynipiana* Kovalev, 1994		
†*Palaeocynipiana santonica* Kovalev, 1994	Taimyr amber	Santonian
Subfamily Charipinae Dalla-Torre and Kieffer, 1910		
Genus †*Protocharips* Kovalev, 1994		
†*Protocharips evenhuisi* Kovalev, 1994	Taimyr amber	Santonian
Subfamily Eucoilinae Thomson, 1862		
Genus †*Anteucoila* Liu and Engel, n. gen.		
†*Anteucoila delicia* Liu and Engel, n. sp.	Canadian amber	Campanian
Genus †*Jerseucoila* Liu & Engel, n. gen.		
†*Jerseucoila plesiosoma* Liu and Engel, n. sp.	New Jersey amber	Turonian
Genus †*Syneucoila* Liu & Engel, n. gen.		
†*Syneucoila magnifica* Liu and Engel, n. sp.	New Jersey amber	Turonian
Subfamily Figitinae Thomson, 1862		
Genus *Figites* Latreille, 1802		
†*Figites solus* Brues, 1910	Florissant, Colorado	Eocene–Oligocene
Genus †*Palaeofigites* Kovalev, 1995		
†*Palaeofigites balticus* Kovalev, 1995	Baltic amber	Eocene (Lutetian)
Subfamily Aspicerinae Dalla Torre and Kieffer, 1910		
Genus †*Palaeoaspicera* Kovalev, 1994		
†*Palaeoaspicera orientalia* Kovalev, 1994	Taimyr amber	Santonian
Family CYNIPIDAE Latreille, 1802		
Subfamily Incertae Sedis		
Genus †*Tanaoknemus* Liu and Engel, n. gen.		
†*Tanaoknemus ecarinatus* Liu and Engel, n. sp.	Canadian amber	Campanian
Subfamily †Hodiernocynipinae Kovalev, 1994		
Genus †*Hodiernocynips* Kovalev, 1994		
†*Hodiernocynips primigenius* Kovalev, 1994	Bol'shaya Svetlovodnaya (Biamo)	Eocene–Oligocene
†*Hodiernocynips planus* (Statz, 1938)	Rott, Germany	Miocene (Aquitanian)
†*Hodiernocynips rotundatus* (Statz, 1938)	Rott, Germany	Miocene (Aquitanian)
†*Hodiernocynips spiniger* (Statz, 1938)	Rott, Germany	Miocene (Aquitanian)
†*Hodiernocynips progenitrix* (Kinsey, 1919)	Florissant, Colorado	Eocene–Oligocene
†*Hodiernocynips ampliforma* (Kinsey, 1919)	Florissant, Colorado	Eocene–Oligocene
Subfamily Cynipinae Latreille, 1802		
Genus †*Kinseycynips* Liu and Engel, n. gen.		
†*Kinscynips succinea* (Kinsey, 1919)	Baltic amber	Eocene (Lutetian)
Genus *Diplolepis* Geoffroy, 1762		
†*Diplolepis vetus* (Cockerell, 1921)	Isle of Wight, England	Oligocene
Genus *Andricus* Hartig, 1840		
†*Andricus vectensis* Cockerell, 1921	Isle of Wight, England	Oligocene
Incertae Sedis		
†*"Cynips" succinea* Presl, 1822	Baltic amber	Eocene (Lutetian)