

Baltic amber Ibalidae (Hymenoptera: Cynipoidea): a new genus with implications for the phylogeny and historical biogeography of the family

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Abstract. The first definitive ibaliid wasp (Cynipoidea: Ibalidae) is described and illustrated from a female preserved in middle Eocene (Lutetian) Baltic amber. *Archaeibalia succinica* Liu & Engel **gen. et sp.n.** is distinct from all other members of the family, cladistically placed as sister to all other Ibalidae, and classified in its own subfamily, Archaeibaliinae Liu & Engel **subfam.n.** The genus was putatively a parasitoid of wood-boring insects in hardwood trees. Given that the species is exceptionally rare in Baltic amber (a single individual) despite a habitat that would have placed it in immediate proximity with resin flows, the host of *A. succinica* was probably not living in the ‘Baltic amber tree’. The historical biogeography and evolution of ibaliids is reconsidered based on the present paleontological evidence.

Introduction

The Ibalidae is a small family of parasitic wasps comprising 21 extant species, of which most are restricted to the northern hemisphere (Liu & Nordlander, 1994). Three genera, *Eileenella* Fergusson (one species), *Heteribalia* Sakagami (five species), and *Ibalia* Latreille (15 species), are recognized in the family (Ronquist, 1995b; Nordlander *et al.*, 1996; Liu, 1999; Liu & Ronquist, 2006). A series of studies in recent years have covered various aspects of the family, including systematics (Fergusson, 1992; Liu & Nordlander, 1992, 1994; Liu, 1999; Ronquist & Liu, 2006), phylogeny (Ronquist, 1995b, 1999; Nordlander *et al.*, 1996), and historical biogeography (Nordlander *et al.*, 1996). Members of Ibalidae parasitize siricid woodwasps, both in conifers and hardwoods, and some species of *Ibalia* have been used in biological control programmes against harmful siricids (Nordlander *et al.*, 1996 and references therein).

The Ibalidae is of special interest because it is putatively the sister group of all other Cynipoidea except *Austrocynips* (Ronquist, 1995b; Liu *et al.*, 2007a). Ronquist (1999) concluded that the superfamily was perhaps as old as the Late Jurassic [*ca.* 160 million years ago (mya)], basing this

age determination on a phylogenetic analysis, the evolution of characters across the superfamily, and patterns of biogeography inferred from the distribution of modern species, as well as the limited available fossil data, although without explicitly including all of those fossils into his analysis of relationships. The hypothesis was backed by phylogenetic studies of related groups based on extant species (Nordlander *et al.*, 1996; Liu, 1999, 2001, Liu *et al.*, 2007b) as well as additional fossil discoveries, which were coded into analyses with their modern counterparts (Liu *et al.*, 2007a). Nonetheless, the assumed antiquity of Ibalidae has not been critically supported by the fossil record (nor has it been specifically refuted) given that the hitherto only known (unnamed) ibaliid fossil was an isolated compression of a forewing from the Late Miocene (*ca.* 5.5 mya) diatomite volcanic sediments near Cantal, France (Nel, 1996). Although the French fossil is valuable in that it dates the age of *Ibalia* to as early as 5.5 mya, assuming it is properly placed, it is merely a forewing impression and therefore of limited value for phylogenetic inference and cannot be placed among its putative congeners. Thus, the recent identification of a definitive ibaliid in much earlier Baltic amber (middle Eocene, *ca.* 45.1 mya) is of great significance. Herein, we describe this remarkably well-preserved specimen (Fig. 1), which can be placed with confidence in the Ibalidae, although it has several distinct features not found in any extant members of the family. The high quality of amber preservation permitted

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Fig. 1. Photomicrograph of *Archaeibalia succinica* Liu & Engel gen. et sp. n., holotype (AMNH B-JWJ-93).

coding of the new species into an existing character matrix for Cynipoidea (Ronquist, 1996; Liu *et al.*, 2007a), and, despite lacking a putative synapomorphy for the family, the phylogenetic analysis supports inclusion of the fossil within Iballiidae. Accordingly, the fossil was included in a phylogenetic analysis with living species of ibaliids and a revised historical biogeography of the family presented.

Morphological terminology for the taxonomic description largely follows that of Ronquist & Nordlander (1989), Liu & Nordlander (1994), and Liu *et al.* (2007a).

Systematic palaeontology

Family Iballiidae Ashmead

Ronquist (1999) listed several characters as diagnostic for Iballiidae, including: (1) presence of a median notch in the pronotal crest, (2) a pair of posterior scutellar processes, (3) a short metafemur, and (4) an enlarged seventh abdominal tergum in the female metasoma. Apart from character (2), which is not found in the new fossil species, all of the diagnostic characters are shared with *Archaeibalia*. The family comprises three subfamilies: Eileenellinae Kovalev, Iballiinae Ashmead, and the new extinct subfamily Archaeibaliinae **subfam.n.**

Archaeibaliinae Liu & Engel **subfam.n**

Type genus. *Archaeibalia* Liu & Engel **gen.n.**

Diagnosis. As for the genus (*vide infra*).

Archaeibalia Liu & Engel **gen.n**

Type species. *Archaeibalia succinica* Liu & Engel **sp.n.**

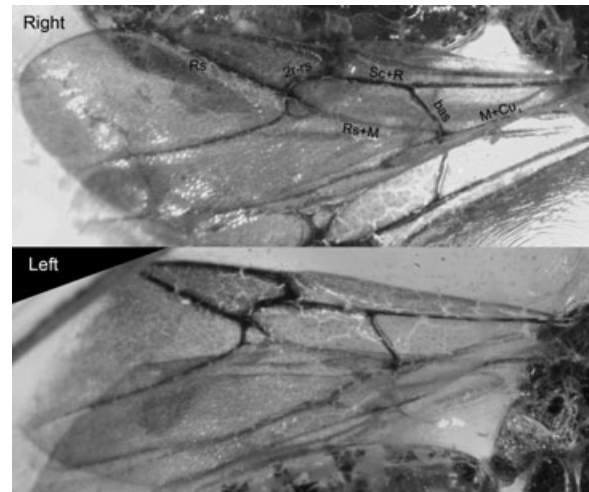


Fig. 2. Forewings of *Archaeibalia succinica* Liu & Engel gen. et sp. n. (AMNH B-JWJ-93). The right forewing (above) overlaps the hindwing, giving the impression that there is a vein anterior to Sc+R. The left forewing (below) is also included for comparison. The abbreviation “bas” is used for “basalis” (= first free abscissa of M).

Diagnosis. The new genus can be easily distinguished from all other ibaliid genera by the combination of the following characters: (1) head and mesosoma lacking strong integumental sculpture, especially the strong transverse striation of mesosoma, and distinct pubescence; (2) antenna with 23 flagellomeres; (3) lacking a broad dorsal pronotal area behind the transverse pronotal crest; (4) forewing (Fig. 2) with 2r-rs almost parallel to distal part of vein M, Rs + M originating from posterior end of ‘basalis’ (= basal vein or first free abscissa of M), marginal cell three times as long as wide; (5) lateral pronotal carina dorsally raised, but not raised into a triangular process; (6) metacoxa with a deep groove, laterally lobe-shaped; metafemur short and slightly longer than two-thirds metatibia; metatibia distinctly curved; first metatarsomere (metabasitarsus) slightly shorter than combined length of metatarsomeres II–V; (7) post-petiolar metasoma strongly compressed laterally, but not blade-shaped as in *Ibalia*; arrangement of post-petiolar metasoma very similar to modern *Ibalia*, with abdominal tergum VII dorsally enlarged and posteriorly broadly emarginate; and (8) metasoma generally glabrous, except abdominal tergum VIII covered with moderately dense, long setae.

Etymology. The genus group name is a combination of *archaios* (Greek, meaning ‘old’, ‘ancient’) and *Ibalia*, type genus of the family. The name is feminine.

Archaeibalia succinica Liu & Engel **sp.n**

(Figs 1, 2)

Description. *Female.* Body length 6.0 mm. Body entirely dark brown to black, with antennae, compound eyes, and legs

mostly brown. Fore- and hindwings subhyaline and evenly lightly ferruginous. Vertex flat and glabrate; upper face completely rugulose; antennal scrobes distinctly depressed deep grooves clearly delimited laterally by carinae. Gena distinctly expanded behind compound eye [but not to the same degree as in *Ibalia* (*Tremibalia*)] and largely glabrate, obliquely carinate behind compound eye. Compound eye length about 4.5 times that of malar space. Antenna with 23 flagellomeres, second flagellomere distinctly shorter than first flagellomere ($F2/F1 = 0.85$). Pronotum dorsomedially raised, transverse crest indistinct with a slight median emargination; lateral surface of pronotum mostly rugulose-reticulate, posteroventrally with longitudinal striation; propleuron protruding ventrally into an inverted trapezoid. Mesoscutum finely transversely striate, not developed as strong transverse costae found in extant members of the family; median mesoscutal impression absent, notauli percurrent; longitudinal impression present along lateral margin; mesoscutellum with well-defined scutellar foveae, slanting posteriorly. Femoral groove of mesopleuron not as prominent as in *Ibalia*, glabrous, without longitudinal striation; speculum glabrous. Fore- and hindwings subhyaline, evenly ferruginous, and covered with dense short bristles; forewing 2r-rs almost parallel to distal part of vein M, Rs + M originating from posterior end of 'basalis' (= first free abscissa of M), marginal cell three times as long as wide. Anterior lateral crest of metacoxa rounded and low; anterior mesotibial spur present and straight; metafemur short and slightly longer than two-thirds metatibia; metatibia distinctly curved; first metatarsomere (= metabasitarsus) slightly shorter than combined length of metatarsomeres II–V, anterior apical process of metatarsomere II absent. Anterolateral propodeal process distinct; posterior propodeal process low; lateral propodeal carina not elevated medially. Metasoma as long as head and mesosoma combined; abdominal tergum VIII with dense setae, but not obscuring integument.

Male. Unknown.

Type material. Holotype, AMNH B-JWJ-93, ♀, Baltic Amber: Eocene: Lutetian. Deposited in the Amber Collection, Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York.

Etymology. The specific epithet is taken from the Latin term *succinum*, meaning 'amber'. A general name for Baltic amber is succinite, referring to the presence of succinic acid within the resin.

Phylogenetic analyses

The original character matrix of Cynipoidea by Ronquist (1995b) was expanded by Liu *et al.* (2007a) with additional characters and data for six well-preserved fossil genera from the Cretaceous; i.e. *Protimaspis* Kinsey, *Stolamissus* Liu & Engel, *Micropresbyteria* Liu & Engel, *Tanaoknemus* Liu & Engel, *Proliopteron* Liu & Engel, and *Anteucoila* Liu & Engel. Given that the genera *Micropresbyteria* and

Tanaoknemus are known from males only and that cladistic reconstruction of cynipoid phylogeny depends disproportionately on attributes of female morphology, these two genera were excluded from our present analyses. Coding these genera for the matrix gives an excessive amount of missing data, which potentially can cause negative perturbation to the analysis (Schuh, 2000). Ronquist (1995b) coded 110 external morphological characters for a cladistic analysis of higher-level relationships among Cynipoidea, whereas Liu *et al.* (2007a) expanded this to 112 characters and incorporated new Cretaceous fossils. We used Liu *et al.*'s (2007a) 112 characters, with one modification to Ronquist's (1995a) original character description—an additional code was inserted before the ordered series in character number 7. The modified description for character number 7 is 'Number of flagellomeres (females): (0) 23; (1) 13; (2) 12; (3) 11; (4) 10. Ordered 01234'. The coding for this character in the original matrix was modified accordingly to retain the ordered sequence used by Ronquist (1995a). Otherwise the original character descriptions and character matrix of Ronquist (1995a) and the updates by Liu *et al.* (2007a) should be consulted. The coding of the new species is given in Table 1, and the final character matrix consisted of 24 Operational Taxonomic Units (OTUs) and 112 characters, including 13 ordered and 99 unordered. For the full character matrix, the senior author should be contacted.

For cladistic analyses we used parsimony as implemented in PAUP*4.0 beta 10 (Swofford, 2003) using the branch-and-bound search algorithm. Bootstrap values were calculated using the parsimony heuristic search method (10 000 replicates, character number resampled at each replicate = 101). According to Liu *et al.* (2007a), *Anteucoila* can be placed definitely in Eucoilinae (Figitidae) because it possesses a mesoscutellar cup or plate, a putative synapomorphy for the subfamily. Similarly, according to Ronquist (1995b, 1999), the monophyly of the Figitidae including Eucoilinae is well established and so is the sister relationship between Figitidae and Cynipidae. The character matrix of Ronquist (1995b) was intended for analysis of cynipoid phylogeny at the family level and thus did

Table 1. Character states for *Archaeibalia succinica* Liu & Engel **gen. et sp.n.** for incorporation of a matrix of representatives of extant and extinct Cynipoidea. Characters and character states are coded as in Ronquist (1995b) with updates from Liu *et al.* (2007a), except for character 17 modified to 'Number of flagellomeres (female): (0) 23; (1) 13; (2) 12; (3) 11; (4) 10. Ordered 01234', all other taxa in the matrix were re-coded for this character accordingly (for the full character matrix, the senior author should be contacted).

Character								
Taxon	1	6	11	16	21	26	31	36
<i>A. succinica</i>	0?00?	20?0?	?21??	?111?	?0001	10111	00?00	21111
Taxon	41	46	51	56	61	66	71	76
<i>A. succinica</i>	00001	10010	00011	001?0	00000	00?00	0?0?0	00???
Taxon	81	86	91	96	101	106	111	
<i>A. succinica</i>	000?0	00000	000?0	00001	000?0	?0000	01	

Table 2. Character states for *Archaeibalia succinica* Liu & Engel gen. et sp.n. for incorporation in a matrix of Ibalidae. Characters and character states are coded as in Nordlander *et al.* (1996) and Liu *et al.* (2007a) (for the full character matrix, the senior author should be contacted).

Character										
Taxon	1	6	11	16	21	26	31	36		
<i>A. succinica</i>	10???	10000	10?00	0--0	0--00-	-0-10	2012?	00001		
Taxon	41	46	51	56	61	66	71	76	81	
<i>A. succinica</i>	0-000	--10?	?2??0	0-0??	0-000	0000-	?000?	----	--	

not include any eucoilines. Therefore, the data matrix updated herein was analysed with the relationship between *Anteucoila*, the other taxa of Figitidae, and Cynipidae constrained as ((*Isocolus*, *Diastrophus*), (*Euceroptres*, *Melanips*, *Anteucoila*)), and unconstrained. MACCLADE 4.08 (Maddison & Maddison, 2005) was used to identify the number of unambiguous character-state changes on each topology.

Because the results of the aforementioned cladistic analyses supported *A. succinica* as a member of Ibalidae (*vide infra*), we also coded the species into a previously published character matrix for species of the family (Nordlander *et al.*, 1996; Liu, 1999) in order to test the relationship of the species with extant ibaliids. In addition, we wanted to test whether the addition of the fossil would change the polarization of some characters and thus alter phylogenetic relationships among the diverse extant clade consisting of *Ibalia* and *Heteribalia*. Characters and character states were coded as in Nordlander *et al.* (1996), with updates from Liu (1999). Codes of all characters for the new species are provided in Table 2. The final character matrix consisted of 22 taxa and 82 characters, of which 11 were ordered (as in the earlier analyses). For the full character matrix, the senior author should be contacted. A phylogenetic analysis using PAUP was run with the same settings as in the aforementioned analyses, except that multiple outgroups were used, with *Eileenella*, *Archaeibalia*, and Liopteridae as successively more distant outgroups following the higher-level relationships of Cynipoidea derived from the first two analyses. Bootstrap support value calculation and character optimization were the same as in the aforementioned analyses.

The results of the species-level phylogenetic analysis were used for reconstruction of biological and biogeographical patterns. The biogeographical analysis utilized DIVA 1.2, a computer program that uses dispersal-vicariance analysis to infer ancestral distributions based on a three-dimensional cost matrix derived from a simple biogeographical model. Unlike other historical biogeographical methods, the dispersal-vicariance model does not make a priori assumptions about the shape or existence of general biogeographical patterns and is considered particularly useful in reconstructing the distributional history of a group in the absence of a general hypothesis of area relationships ('taxon biogeography') (Ronquist, 1996, 1997). This method has been employed for the reconstruction of the ancestral distribution of Ibalidae (Nordlander *et al.*, 1996; Liu, 1999). As in Nordlander *et al.* (1996) and Liu (1999), the historical biogeography of Ibalidae was analysed in terms of five main distributional areas: (i) New Guinea, (ii) Western

Nearctic, (iii) Eastern Nearctic, (iv) Western Palearctic, and (v) Eastern Palearctic + North-eastern Oriental.

Results and discussion

Phylogenetic analyses

The phylogenetic analysis of higher-level relationships within Cynipoidea resulted in five equally parsimonious topologies (length = 234 steps; consistency index = 0.55; retention index = 0.79). A monophyletic Ibalidae including *Archaeibalia* was retrieved in all five trees, with nine synapomorphies identified, including five unambiguous character changes. The five unambiguous character-state transitions that support a monophyletic Ibalidae are: (1) median dorsal length of pronotum behind anterior, vertical surface long (character 18: 1), (2) pronotal crest with a small incision medially (character 19: 1); (3) posterolateral propodeal process present (character 37: 1); (4) sternal part of petiolar annulus absent (character 54: 1); and (5) abdominal tergum VII conspicuously enlarged (character 58: 1). The clade was also supported by a bootstrap value of 72% (Fig. 3). With regard to the other relationships within Cynipoidea, the addition of *Archaeibalia* resulted in higher resolution in two deep relationships as compared with Liu *et al.* (2007a). First, *Protimaspis*, a fossil genus described from Manitoba, Canada (*ca.* 80–75 Ma) was supported as sister to the clade consisting of Liopteridae, the 'microcynipids' (comprising Cynipidae and Figitidae), and three other fossil taxa, *Stolamissus* (New Jersey, U.S.A., 90 Ma), *Proliopteron* (Alberta, Canada, *ca.* 80–75 Ma), and *Anteucoila* (Alberta, Canada, *ca.* 80–75 Ma). Second, *Proliopteron* was supported as sister to extant Liopteridae (Fig. 3). Constrained analysis of the same character matrix, as mentioned above, resulted in a single topology (length = 236 steps; consistency index = 0.55; retention index = 0.79) (Fig. 4). This analysis placed *Archaeibalia* in Ibalidae, as in the unconstrained analysis, and was otherwise identical to the single tree found by the comparable analysis in Liu *et al.* (2007a). The set of unambiguous character changes in the unconstrained analysis remained the same. Except for the addition of *Archaeibalia*, the results of both phylogenetic analyses showed little or no difference compared with those of Liu *et al.* (2007a). In fact, the addition of *Archaeibalia* resulted in greater resolution in the unconstrained analysis. In both analyses, constrained or unconstrained, *Archaeibalia* was sister to the rest of Ibalidae.

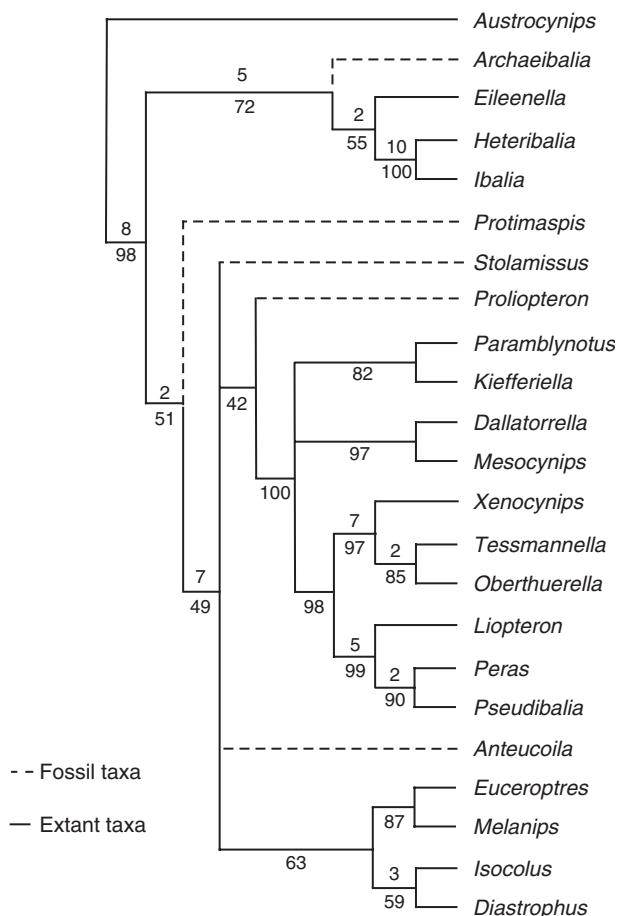


Fig. 3. Strict consensus of five shortest trees ($L = 234$, $CI = 0.55$; $RI = 0.79$) resulting from parsimony analysis of Ronquist's (1995b) data matrix, updated by Liu *et al.* (2007a) with data for several Late Cretaceous amber fossils and *Archaeibalia succinica*. No constraints were applied to the search using the branch-and-bound algorithm (Swofford, 2003). Values above branches are the number of unambiguous character changes supporting particular nodes and those below are Bootstrap values.

Because of *Archaeibalia*'s position within Ibaliiidae (and concomitant exclusion from the modern subfamilies), its great antiquity, its unique morphological features (and presumed biology), and that it is now extinct, establishment of a separate subfamily for the genus is warranted (*vide supra*).

Between the constrained and unconstrained phylogenetic reconstructions, the constrained reconstruction was preferred as the most plausible phylogeny for Cynipoidea for the same reason as argued by Liu *et al.* (2007a), i.e. *Anteucoila* shares the most prominent synapomorphy of extant Eucoilini and therefore can be placed reliably in the tribe, which convincingly has been shown to be a clade deeply nested within Figitidae (Ronquist, 1999). Because no eucoiline species was included in the original analysis of Ronquist (1995b), it is possible that certain synapomorphic features for all figitids, including eucoilines, were not included, which is obviously

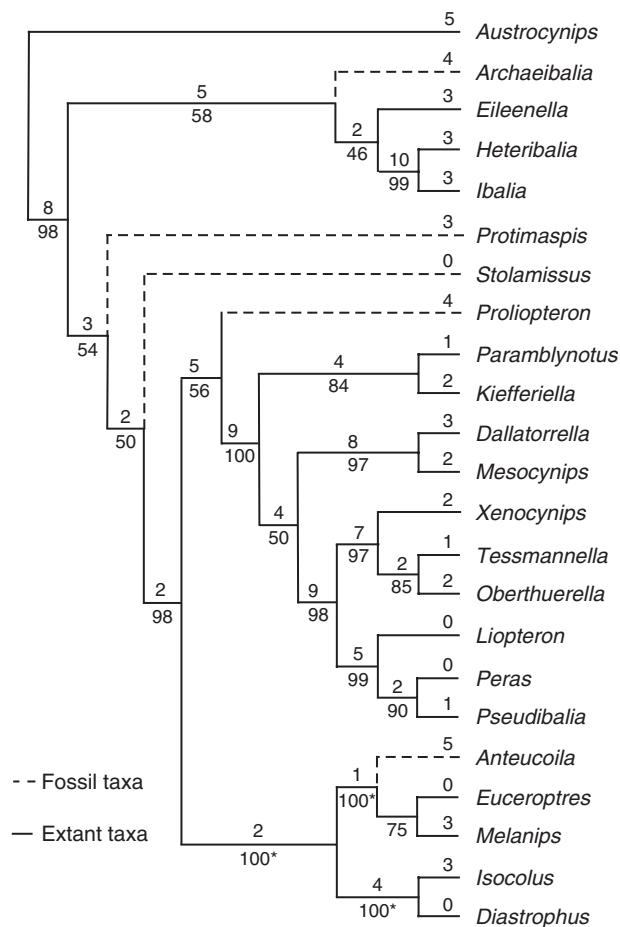


Fig. 4. Single shortest tree ($L = 236$, $CI = 0.55$; $RI = 0.79$) resulting from parsimony analysis of the same dataset using the same search method as in figure 3, but with the figitid membership of *Anteucoila* constrained. Values above branches are the number of unambiguous character changes supporting particular nodes and those below are Bootstrap values.

supported by the fact that the constrained analysis resulted in overall better resolution (cf. Figs 3, 4).

The phylogenetic analysis of species relationships within Ibaliiidae resulted in a single shortest tree (length = 317 steps; consistency index = 0.62, retention index = 0.82) (Fig. 5). The topology of the crown group, consisting of *Ibalia* and *Heteribalia*, is identical to that of Liu (1999), which was itself only slightly different from that of Nordlander *et al.* (1996), again suggesting that the addition of *Archaeibalia* does not dramatically change the polarization of characters and thus affect the resolved phylogeny of this particular clade. As in the analyses of higher-level phylogeny of Cynipoidea, the analysis of ibaliid phylogeny including *Archaeibalia* further demonstrates how discovery and analysis of an ancient 'missing link' can fit well and lend greater support to a robust phylogenetic reconstruction.

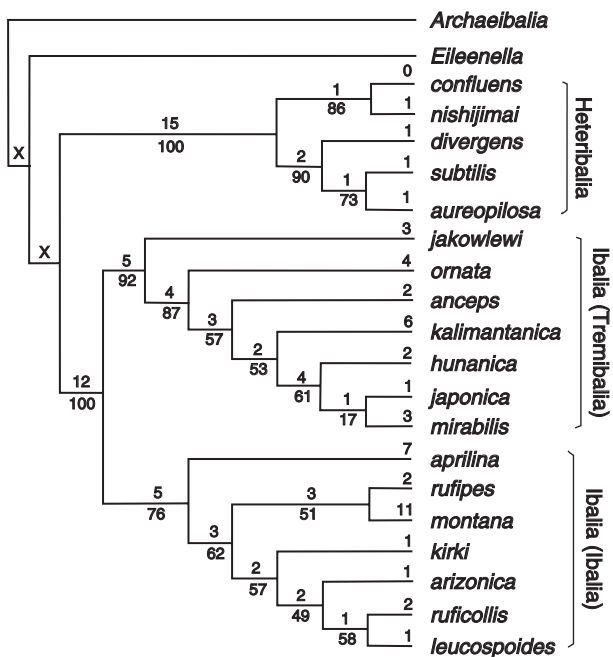


Fig. 5. Single shortest tree ($L = 237$, $CI = 0.62$, $RI = 0.82$) resulting from parsimony analysis of Nordlander *et al.*'s (1996) data matrix, updated with data for *I. kalimantonica* (Liu, 1999) and *Archaeibalia succinica*, using *Eileenella*, *Archaeibalia*, and *Liopteridae* as successively more distant outgroups. The branch-and-bound algorithm was used using PAUP* (Swofford, 2003). Values above branches are the number of unambiguous character changes supporting particular nodes and those below are Bootstrap values.

Biology

According to Ronquist (1995b), early Cynipoidea probably evolved as parasitoids of woodborers in trees and bushes. *Archaeibalia succinica* has a number of attributes considered characteristic of such a lifestyle: longitudinal depressions along the lower part of the mesopleuron, a shallow femoral groove on the mesopleuron, and a deep longitudinal depression on the metacoxa. Similar depressions and grooves are found in other members of the family and apparently allow the wasps to accommodate appendages in the limited space of the host tunnel (Fergusson, 1992; Ronquist, 1995b). These features, along with its phylogenetic placement in Ibaliiidae, support the conclusion that the new species was a parasitoid of wood-boring insects, like the extant members of the family. On the other hand, *A. succinica* lacks other prominent external structures, such as the strong transverse costae of the pronotum and mesoscutum, the stout processes laterally and posteriorly on the mesoscutellum, and the stout processes of the propodeum characteristic of many other Ibaliiidae. These devices have been considered to facilitate the wriggling motions of adults emerging from the host tunnel (Ronquist, 1999). If this is correct, then it is interesting to speculate on how *A. succinica* escaped from the host tunnel, whether it had a less efficient system

compared with crown-group Ibaliiidae or whether it possessed unique methods for emergence.

The plant host of *A. succinica* probably was a broadleaved woody species based on optimization of life history data on the phylogeny of Cynipoidea using MACCLADE 4.08 (Maddison & Maddison, 2005) (Fig. 6). Given that the species is exceptionally rare in Baltic amber (a single individual from what is otherwise the most abundant and prolific source of amber inclusions in the world) despite a habitat that would have placed it in immediate proximity with resin flows, the insect host of *A. succinica* probably was not living in the 'Baltic amber tree' (a putative conifer, *Pinites succinifera* Göppert, possibly related to modern *Pseudolarix Gordon* species). All extant species of Ibaliiidae parasitize wood-boring hosts living in hardwood trees, except for the subgenus *Ibalia* (*Ibalia*), members of which are associated with coniferous hosts (Fig. 6). In addition, species of *Liopteridae*, the putative sister group of the majority of Cynipoidea (microcynipoids) are also known to use wood-boring hosts living in hardwood trees, where biological data are available (Ronquist, 1995b; Liu *et al.*, 2007b). In fact, within the lineage comprising all cynipoids except *Autrocynips* Riek, *Ibalia* s.str. are quite unusual in that they maintain a tight host-plant association and are associated with coniferous-feeding hosts. This suggests that the evolution and diversification of Cynipoidea may have been principally in association with flowering plants, indicating a mid-Cretaceous diversification for the superfamily and an origin in the latest Jurassic or earliest Cretaceous. Previous historical biogeographical reconstructions for Cynipoidea based on the geographical distribution of living species and their phylogeny reached a similar conclusion about the age of the superfamily (Ronquist, 1995a; Liu *et al.*, 2007b). Nonetheless, this hypothesis must be critically tested by further paleontological discoveries from suitable deposits ranging from the middle Jurassic through mid-Cretaceous.

Historical biogeography of Ibaliiidae

Analysis of historical biogeographical patterns for Ibaliiidae using DIVA 1.2 (Ronquist, 1996) resulted in a single optimal reconstruction that required nine dispersal events (Fig. 7). Nordlander *et al.* (1996) conducted a historical biogeographical reconstruction for Ibaliiidae, concluding that the ancestral distribution of Ibaliiidae included the East Palaearctic and Oriental regions. Under this model, a vicariant event separated *Eileenella*, currently inhabiting New Guinea, and the other two extant genera. Because New Guinea and the Oriental terrain had been widely disjunct during the Mesozoic and Cenozoic until the mid-Tertiary when island arcs started to move southward from continental Asia to collide with New Guinea and Australia (Barron *et al.*, 1981; Hamilton, 1983), the earliest splits in the phylogeny of extant ibaliids probably occurred when one of the islands in these south migrating arcs became separated from Asia (Nordlander *et al.*, 1996). Alternatively, these authors also thought it possible that *Eileenella* might have dispersed recently from South-east Asia, or was an isolated survivor representing a widespread extinction of

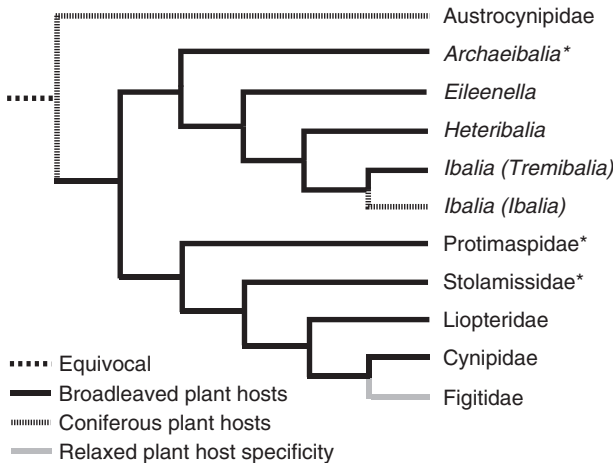


Fig. 6. Evolution of host associations in Cynipoidea: phylogenetic relationships among the major lineages of Cynipoidea summarized from Ronquist (1995b, 1999), Nordlander *et al.* (1996), Liu (1999), and Liu *et al.* (2007a), with *Archaeibalia* included. Optimization of life history data across the phylogeny was undertaken in *MacClade 4.08* (Maddison & Maddison, 2005). Optimizations using different resolving criteria did not change the result (*indicates fossil taxon whose plant host is not known).

an originally Gondwanan lineage. The discovery of *A. succinica* in middle Eocene Baltic amber indicates that ibaliids were widespread at that time (Fig. 6). The long list of autapomorphic features possessed by *A. succinica*, the age and position of *A. succinica* as sister to all other Ibaliiidae, and the long list of synapomorphic features of its sister clade suggest that the split between *Archaeibalia* and the remainder of the family had taken place relatively early. It is possible that a rather early vicariant event separated the two lineages; e.g. the collision of the Indian subcontinent with Asia very late in the Eocene, effectively closing the Tethys Sea (Rögl & Steininger, 1984). However, it is perhaps premature to definitively ascribe any vicariant explanation given that so few fossils are known for this archaic lineage and biogeographical patterns are extremely sensitive to the addition of fossil data (e.g. Grimaldi & Engel, 2005).

It is possible that ibaliids continued to be widespread throughout most of the Palaeartic until the drastic global decline in temperature at the Eocene–Oligocene transition. The distribution we see today among Palaeartic ibaliids was probably established during the Pleistocene glaciations (Wolfe, 1978, 1980, 1985, 1987; Potts & Behrensmeier, 1992). As discussed above, early ibaliids, including *A. succinica*, were probably associated with broadleaved trees (Fig. 6). After the Eocene–Oligocene transition, surviving species were restricted to mid- or low latitudes where broadleaved trees are dominant or at least comprise important elements in the regional vegetation. This would account for the distribution of the species of *Eileenella*, *Heteribalia*, and *Ibalia (Tremibalia)*. Some species later became adapted to the new, cooler climatic conditions at higher latitudes of the northern hemisphere and evolved associations with wood-boring hosts in coniferous trees, such as the

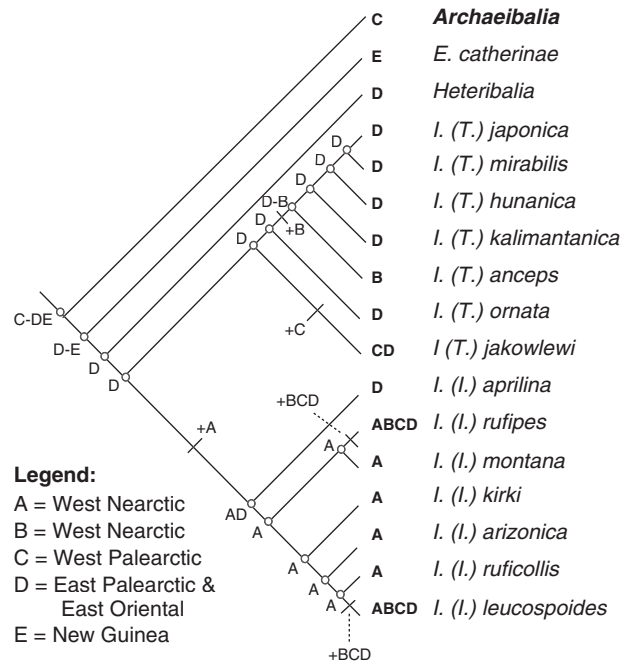


Fig. 7. Updated reconstruction of cladistic historical biogeography for Ibaliiidae based on Liu (1999) and the present study using DIVA 1.2 (Ronquist, 1996) (exact solution, nine dispersal events are required). Dispersal events are indicated on the branches and implied between-area vicariance events are indicated by hyphens in the ancestral distributions. The addition of *Archaeibalia* implies a broader ancestral distribution for Ibaliiidae, but requires no major modifications of Liu’s (1999) reconstruction for the the rest of the family.

species *Ibalia (Ibalia) rufipes* Cresson and *I. (I.) leucospoides* (Hochenwarth) (Liu & Nordlander, 1992, 1994; Nordlander *et al.*, 1996; Liu, 1999). Obviously these two species eventually expanded their distributions along with the coniferous forests, whereas change in coniferous plant communities as a result of local geological and climatological dynamics in the south-western U.S.A. and adjacent areas of Mexico led to the formation of several other species (Nordlander *et al.*, 1996). Earlier, ancient species in those same high latitude habitats of the north were not as fortunate as the younger species of *Ibalia* s.str., failing to adapt to the altered environmental conditions, and succumbed to extinction like *A. succinica*.

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