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Cretaceous Scolebythidae and Phylogeny of the Family (Hymenoptera: Chrysidoidea)

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ABSTRACT

The genera of Cretaceous Scolebythidae are reviewed, with three new genera and species described from New Jersey (Turonian) and Lebanese (Barremian) amber. The new taxa are *Boreobythus turonius*, new genus and species, in New Jersey amber, and *Zapenesia libanica*, new genus and species, and *Uliobythus terpsichore*, new genus and species, in Lebanese amber. A cladistic analysis of living and fossil species of Scolebythidae is undertaken and a revised classification of the family proposed. *Boreobythus* is the oldest scolebythid in the New World, documenting the presence of the family during the Late Cretaceous in North America. The Eocene genus *Eobythus* is perhaps best considered a junior synonym of *Pristapenesia* but is tentatively retained herein. The historical biogeography of the family is briefly discussed. A key to the living and fossil genera of Scolebythidae is provided.

INTRODUCTION

Wasps of the family Scolebythidae are rarely encountered members of the basal aculeate superfamily Chrysidoidea. Currently only 12 species are known, more than half of which are fossils preserved in amber (table 1). Scant biological data is available for the family, although species are apparently gregarious ectoparasitoids of wood-boring beetles in the families Cerambycidae and

Anobiidae (Brothers, 1981; Melo, 2000), a primitive biological trait among most apocritans. The most extensive biological account has been provided for *Pristapenesia stricta* (Azevedo) in southern Brazil that is also the first description of immature stages for agny scolebythid (Melo, 2000).

The family was proposed by Evans (1963) for two remarkable aculeate wasps, *Clystospenella longiventris* Kieffer (1911) and

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TABLE 1
Hierarchical Classification of Family Scolebythidae

Family SCOLEBYTHIDAE Evans	
Scolebythine Clade	
Genus <i>Scolebythus</i> Evans	
<i>S. madecassus</i> Evans	Madagascar
Genus <i>Clystopsenella</i> Kieffer	
<i>C. longiventris</i> Kieffer	Belize, Brazil, Colombia, Costa Rica, Panamá
Pristapenesiine Clade	
Ycaplocine subclade	
Genus <i>Ycaploca</i> Nagy	
<i>Y. evansi</i> Nagy	South Africa, Australia
<i>Y. fijianus</i> Beaver ^a	Fiji
Pristapenesiine subclade	
Genus † <i>Boreobythus</i> , new genus	
† <i>B. turonius</i> , new species	New Jersey (Cretaceous)
Genus † <i>Libanobythus</i> Prentice and Poinar	
† <i>L. milkii</i> Prentice and Poinar	Lebanon (Cretaceous)
“Pristapenesia group”	
Genus † <i>Zapenesia</i> , new genus	
† <i>Z. libanica</i> , new species	Lebanon (Cretaceous)
Genus † <i>Uliobythus</i> , new genus	
† <i>U. terpsichore</i> , new species	Lebanon (Cretaceous)
Genus † <i>Eobythus</i> Lacau et al. ^b	
† <i>E. patriciae</i> Lacau et al.	France (Eocene)
Genus <i>Pristapenesia</i> Brues [= <i>Dominibythus</i>]	
† <i>P. inopinata</i> (Prentice and Poinar)	Dominican Republic (Miocene)
† <i>P. primaeva</i> Brues	Baltic region (Eocene)
<i>P. stricta</i> (Azevedo)	Brazil

[†]Extinct.
^aThis species differs minutely so from *Y. evansi* except in the presence of the facial depressions (see Beaver, 2002). The material from Africa, Australia, and Fiji should be carefully compared to confirm these differences as the Australian populations have been suspected to be introductions from South Africa (e.g., Naumann, 1990). If conspecificity is confirmed, then introduction into Fiji would not be implausible. However, it may be that the Australian populations are distinct and should be more thoroughly studied (it is difficult to envision these wasps maintaining specific integrity between South Africa and Australia).
^bPerhaps best considered a junior synonym of *Pristapenesia* (see Cladistics and Discussion).

Scolebythus madecassus Evans (1963), from Brazil and Madagascar, respectively. Based just on the anatomy of the species, Evans (1963) hypothesized that scolebythids would have a primitive parasitoid biology, potentially victimizing wood-boring beetles—an insightful prediction as Brothers (1981) and Melo (2000) would later demonstrate. A little over a decade later a third genus was proposed by Nagy (1975) for a species occurring in South Africa and Australia, *Ycaploca evansi* Nagy, although the Australian records have at times been challenged as human introductions from southern Africa (e.g., Naumann, 1990). These three monotypic genera occupied an intriguing austral distribution, occurring

across the great southern continental land-masses. The modern scolebythid fauna has grown only slightly in recent years, with the discovery of a second South American species in 1999 (Azevedo, 1999) and a species on Fiji in 2002 (Beaver, 2002), both well below the equator, a geography supporting the notion that the family had a distribution that was entirely austral. Lately, however, numerous records of scolebythids, all of *C. longiventris*³, north of the equator have been made,

³Some authors alluded to an as-yet undocumented diversity of scolebythids in *Clystopsenella* from the New World tropics (e.g., Gauld, 1995; Lacau et al., 2000). Examination of these “species” has shown them to be *C. longiventris* (Cembra and Azevedo, 2003).

challenging the notion that this is an “austral” family (e.g., Gauld, 1995; Fernandez et al., 2002; Cambra and Azevedo, 2003; Engel, 2005). Indeed, the fossil record of the family, albeit scant, indicates this to be so, such as the occurrence of scolebythids in middle Eocene Baltic amber (Brues, 1933; Brothers and Janzen, 1999).

The first fossil scolebythid was described by Brues (1933) in mid-Eocene Baltic amber as *P. primaeva* and as a species of Bethyridae, a familial placement that went unchallenged until 1999. In 1996 two additional genera were recognized in Early Miocene amber of the Dominican Republic [*Pristapenesia inopinata* (Prentice and Poinar), originally proposed in *Dominibythus*] and Early Cretaceous amber from Lebanon (*Libanobythus milkii* Prentice and Poinar), respectively (Prentice et al., 1996). Brothers and Janzen (1999) subsequently discovered that *P. primaeva* in Baltic amber was actually congeneric with the species in Dominican amber and formally united the two groups. Lacau et al. (2000) proposed another Eocene genus and species, *Eobythus patriciae*, in amber from the Paris Basin. One additional fossil, *Cretabythus sibiricus* Evans (1973), was tentatively placed in Scolebythidae but was later excluded from the family by Carpenter (1986) and Rasnitsyn (1988). Table 1 summarizes the classification of Scolebythidae to the species level, incorporating changes resulting from the cladistic analysis presented herein (see below).

Herein we provide a review of the known Cretaceous genera of Scolebythidae, including the description of a new genus in Turonian amber from New Jersey (fig. 1) and two new genera in Barremian amber from Lebanon (figs. 2, 3). To this account we have provided a revised key to the Recent and fossil genera of Scolebythidae. In addition, we have undertaken a cladistic analysis of living and fossil scolebythids and explored the implications of this phylogeny for understanding the evolution of the family. In all of the fossils considered herein, three of the hallmark synapomorphies of the family are easily visible: the large, exposed, diamond-shaped prosternum, the laterally inserted protrochanters, and the dorsally exposed propleura (i.e., the absence of an anterior flange to the pronotum).

SYSTEMATIC PALEONTOLOGY

FAMILY SCOLEBYTHIDAE EVANS

Scolebythidae Evans, 1963: 7. Type genus: *Scolebythus* Evans, 1963.

DIAGNOSIS: Typically slender wasps without heavy sculpturing, ranging in size from ca. 2–12 mm in total length. Head hypognathous; pronotum lacking anterior flange such that propleura visible in dorsal aspect; pronotal posterior dorsal-facing surface (i.e., pronotal collar sensu Goulet and Huber, 1993) frequently greatly reduced; propleura widely separated posteriorly, with large, exposed, diamond-shaped prosternum; protrochanter inserted laterally near base of procoxa; meso- and metatibiae with long slender setae only; macropterous; hind wing lacking closed cells, with C long and Sc+Rs absent.

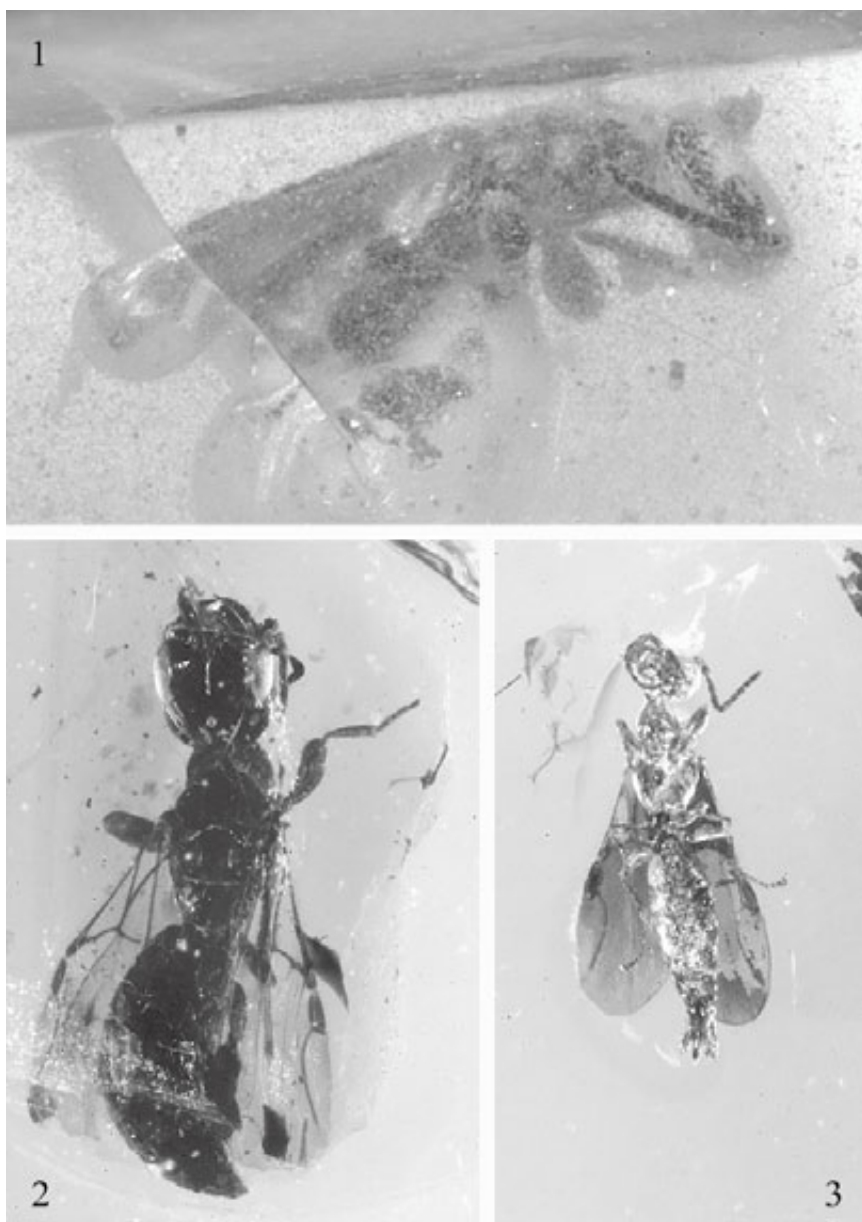
Genus *Libanobythus* Prentice and Poinar

Libanobythus Prentice and Poinar In Prentice et al., 1996: 807. Type species: *Libanobythus milkii* Prentice and Poinar In Prentice et al., 1996, monobasic and original designation.

Lybanobythus Azevedo, 1999: 2. *Lapsus calami*.

DIAGNOSIS: Head broad; frontal prominence absent; clypeus transverse, clypeal apex short; face lateral to antennal torulus flat; ocelli forming equilateral triangle, near upper tangent of compound eyes; occipital carina present; pronotal collar present, dorsal surface of pronotum nearly 1.5 times as long as mesoscutum; propleura well developed, anteriorly forming a long neck; notauli absent; prosternum large, exposed, diamond-shaped; parapsidal lines absent; forewing with open marginal cell; Rs long, much longer than pterostigma, terminating near anterior wing margin, tubular over entire length; R₁ absent; margin of pterostigma within marginal cell convex; 1m-cu present, tubular; Rs+M tubular; Cu basad 1m-cu tubular, distad 1m-cu nebulous; first submarginal cell short; metafemur not flattened; tibial spur formula 1-1-1; pretarsal claws simple. Refer also to Prentice et al. (1996) for additional characters.

COMMENTS: Prentice et al. (1996) considered *Libanobythus* to be sister to all other



Figs. 1–3. Photomicrographs of Cretaceous Scolebythidae. 1. Female holotype of *Boreobythus turonius*, new genus and species (AMNH). 2. Female holotype of *Zapenesia libanica*, new genus and species (Azar 146-A). 3. Male holotype of *Uliobythus terpsichore*, new genus and species (Azar 157-A).

scolebythid genera based on the presence of a pronotal collar. A cladistic analysis of the family (Carpenter, 1999; Lacau et al., 2000; see below), however, places *Libanobythus*

in a clade with other, principally fossil genera and not as sister to the remaining scolebythid taxa. The pronotal collar of *Libanobythus* would thus appear to be

a secondary reversal and not plesiomorphic. Further details of the cladistic analysis are presented below.

Boreobythus, new genus

TYPE SPECIES: *Boreobythus turonius*, new species.

DIAGNOSIS: Head elongate (fig. 2); frontal prominence absent; clypeal apex weakly produced; malar space apparently more than one-half basal mandibular width; face lateral to antennal torulus flat; compound eyes relatively small, length only slightly more than distance from upper tangent of compound eyes to preoccipital ridge; inner margins of compound eyes very minutely converging below; ocelli almost entirely obscured by fine layer of microscopic bubbles but apparently near upper tangent of compound eyes; occipital carina absent; pronotal collar present, dorsal surface of pronotum nearly 1.5 times as long as mesoscutum; propleura well developed, anteriorly forming a short neck; notauli absent; prosternum large, exposed, broadly triangular posteriorly (fig. 2); parapsidal lines absent; forewing with open marginal cell; Rs long, much longer than pterostigma, terminating near anterior wing margin (fig. 2), tubular over entire length; R_1 present on wing margin; pterostigma relatively small, margin within marginal cell convex; 1m-cu present, tubular; Rs + M tubular; Cu distad separation from M nebulous (i.e., abscissae basad and distad 1m-cu nebulous); first submarginal cell short; metafemur not flattened; tibial spur formula indeterminate from fossil; pretarsal claws simple.

ETYMOLOGY: The genus-group name is a combination of *boreas* (Greek, meaning "north wind") and *-bythus* (root of the type genus for the family, *Scolebythus*). The name refers to the fact that this fossil comes from the furthest north paleolatitude among Cretaceous scolebythids. The name is masculine.

COMMENTS: *Boreobythus* has, perhaps, the most plesiomorphic habitus of any scolebythid, overall resembling a primitive bethyid, particularly in the shape of the head. However, despite the superficial shape of the head, the greatly enlarged and exposed prosternum, the laterally articulated protrochan-

ters, and the enlarged propleura that form a short neck attest to its placement in Scolebythidae.

Boreobythus turonius, new species
figures 1, 4

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: As described for the genus, with the following additions: Total body length ca. 2.0 mm; forewing length ca. 1.3 mm. **Head.** Head longer than broad, upper tangent of compound eyes to vertex approximately equal to length of compound eye; inner margin of compound eyes straight, parallel; gena narrower than compound eye in lateral view. Scape short, approximately equal to combined lengths of F1 and F2; length of F1 equal to that of F2, both shorter than F3. Integument black except antenna dark brown. **Mesosoma.** Surface sculpturing unobservable, integument apparently black; legs dark brown. Forewing with basal vein confluent with 1cu-a; basal vein approximately straight with Rs and of equal length; hind wing unobservable; wing veins dark brown, membrane lightly infumate. **Metasoma.** Terga and sterna dark brown, apparently imbricate.

HOLOTYPE: Female, NEW JERSEY: Sayreville, White Oaks pit, coll. Paul Nascombene. Specimen deposited in the Amber Collection, Division of Invertebrate Zoology, American Museum of Natural History. The amber enclosing the holotype is turbid (fig. 1) obscuring many features of the wasp.

ETYMOLOGY: The specific epithet is a reference to Turonian, the age of the amber in which the fossil was discovered.

Zapenesia, new genus

TYPE SPECIES: *Zapenesia libanica*, new species.

DIAGNOSIS: Small wasps (between 2 and 3 mm in total body length). Head elongate; frontal prominence absent; clypeal apex straight; malar space more than one-half basal mandibular width; face lateral to antennal torulus gently depressed; compound eyes relatively small, length only slightly more than distance from upper tangent of compound

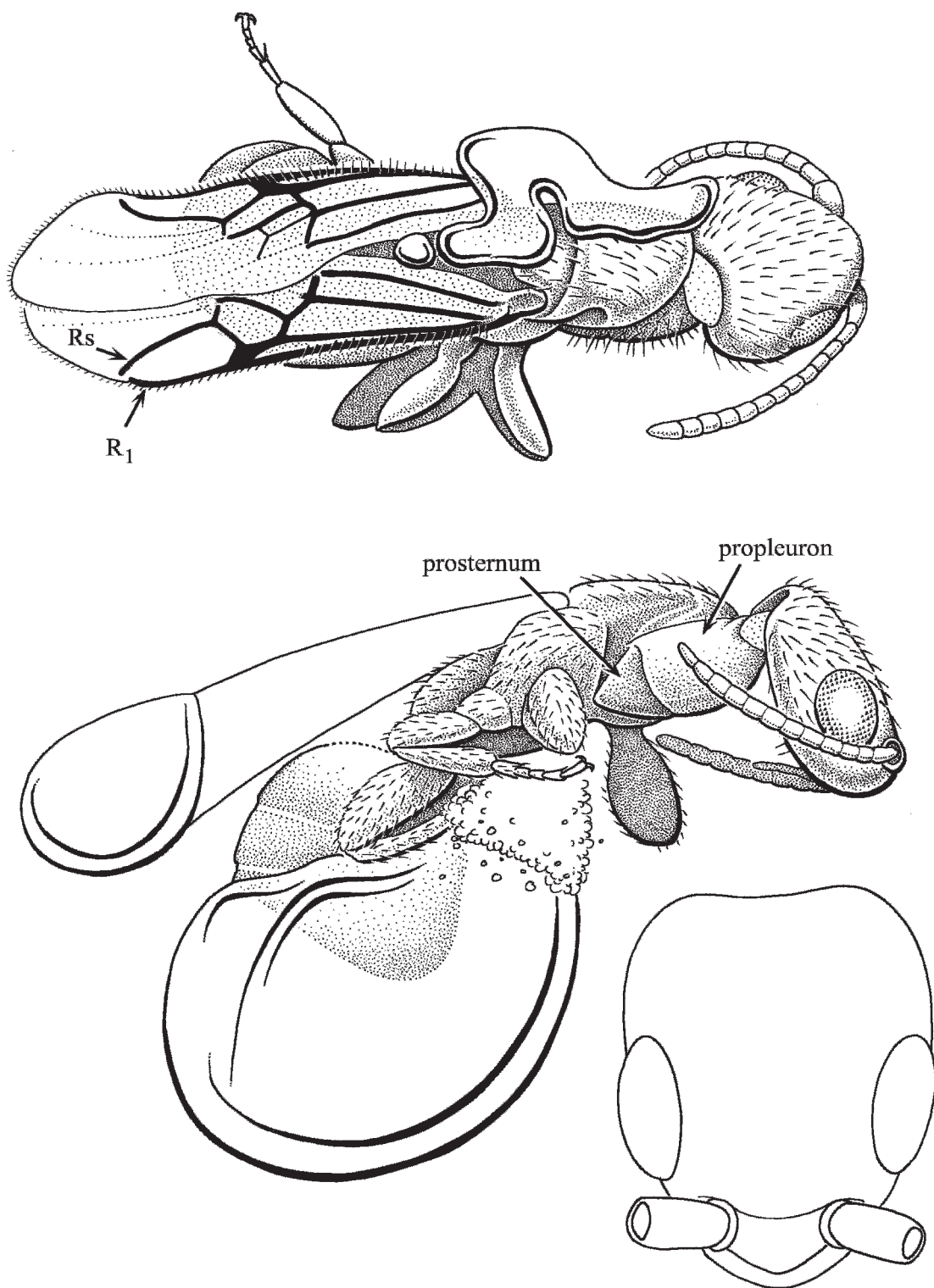


Fig. 4. Dorsal and lateral views of *Boreobythus turonius*, new genus and species, in New Jersey amber (AMNH). Ocelli are likely present but are obscured by layer of Schimmel over face (position of setae, however, can be ascertained as they stick through and above this layer).

eyes to preoccipital ridge; inner margins of compound eyes parallel; ocelli far behind upper tangent of compound eyes, arranged in an equilateral triangle; occipital carina absent; pronotal collar absent, dorsal surface of pronotum shortened, at most 0.5 times as long as mesoscutum; propleura well developed, anteriorly forming a short neck; notauli faintly impressed but present and complete; prosternum large, exposed, broadly triangular posteriorly; parapsidal lines absent; mesoscutum separated from mesoscutellum by transverse furrow, furrow arching anteriorly medially; metanotum short; metapostnotum evident; forewing with open marginal cell; Rs long, much longer than pterostigma, terminating near anterior wing margin, tubular over entire length; R₁ absent beyond pterostigmal apex; pterostigma of relatively moderate size, margin within marginal cell convex; 1m-cu absent; Rs+M nebulous; Cu distad separation from M nebulous; no submarginal cells (only costal, radial, and first cubital cells closed); metafemur not flattened; tibial spur formula 1-2-2; pretarsal claws simple; sixth metasomal sternum without specialized polished area.

ETYMOLOGY: The genus-group name is a combination of *za* (Greek, "very") and *Apenesia* (the genus of bethylid wasps that the first fossil scolebythid, i.e., *P. primaeva*, was believed to be ancestral to). The name is feminine.

COMMENTS: While the Early Cretaceous genera such as *Libanobythus* and *Uliobythus* are reminiscent in habitus of the Cenozoic *Pristapenesia*, *Zapenesia* and *Boreobythus* have the typical habitus of a generalized chrysidoid. *Zapenesia* is apparently more derived than *Boreobythus* as evidenced by the reduced pronotal dorsal surface and the reduced wing venation.

Zapenesia libanica, new species
figures 2, 5

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: Total body length ca. 2.6 mm; forewing length ca. 1.6 mm. **Head.** Head elongate, distance from upper tangent of compound eyes to preoccipital ridge slightly less than compound eye length, distance between compound eyes approximately equal

to length of compound eye; gena much narrower than compound eye. Scape slightly longer than combined lengths of F1–3. Integument black except antenna dark brown, faintly imbricate and impunctate. **Mesosoma.** Integument black except tegulae and legs dark brown, faintly imbricate and impunctate except for minute punctures at setal bases; setae exceedingly sparse, simple, and minute. Propleura forming a strong, anterior neck, parallel-sided, broadly rounded anteriorly; pronotal dorsal surface much shorter than mesoscutum. Mesoscutal-mesoscutellar sulcus arched anteriorly; posterior border of mesoscutellum weakly and gently convex; metanotum exceedingly short; basal area of propodeum elongate, broadly rounded posteriorly. Wing veins dark brown, membrane hyaline; forewing with basal vein confluent with 1cu-a; venation depicted in figure 5. **Metasoma.** Terga and sterna black, imbricate and impunctate, with exceptionally sparse, minute, simple setae.

HOLOTYPE: Female, LEBANON, Azar-146-A. Specimen deposited in the Muséum National d'Histoire Naturelle, Paris.

ETYMOLOGY: The specific epithet is a reference to Lebanon, the country from which the amber encapsulating this fossil originates.

Uliobythus, new genus

TYPE SPECIES: *Uliobythus terpsichore*, new species.

DIAGNOSIS: Minute wasps (less than 2.0 mm in total length). Head rounded; frontal prominence absent; clypeal apex straight; malar space more than one-half basal mandibular width; face lateral to antennal torulus flat; compound eyes large, encompassing most of lateral surface of head except for malar space; inner margins of compound eyes apparently very minutely converging below (frontal view of face not possible and thus this apparent convergence might be an artifact); ocelli arranged in equilateral triangle near upper tangent of compound eyes; occipital carina absent; pronotal collar absent, dorsal surface of pronotum shortened, at most 0.5 times as long as mesoscutum; propleura well developed, anteriorly forming a distinct neck; notauli present; prosternum

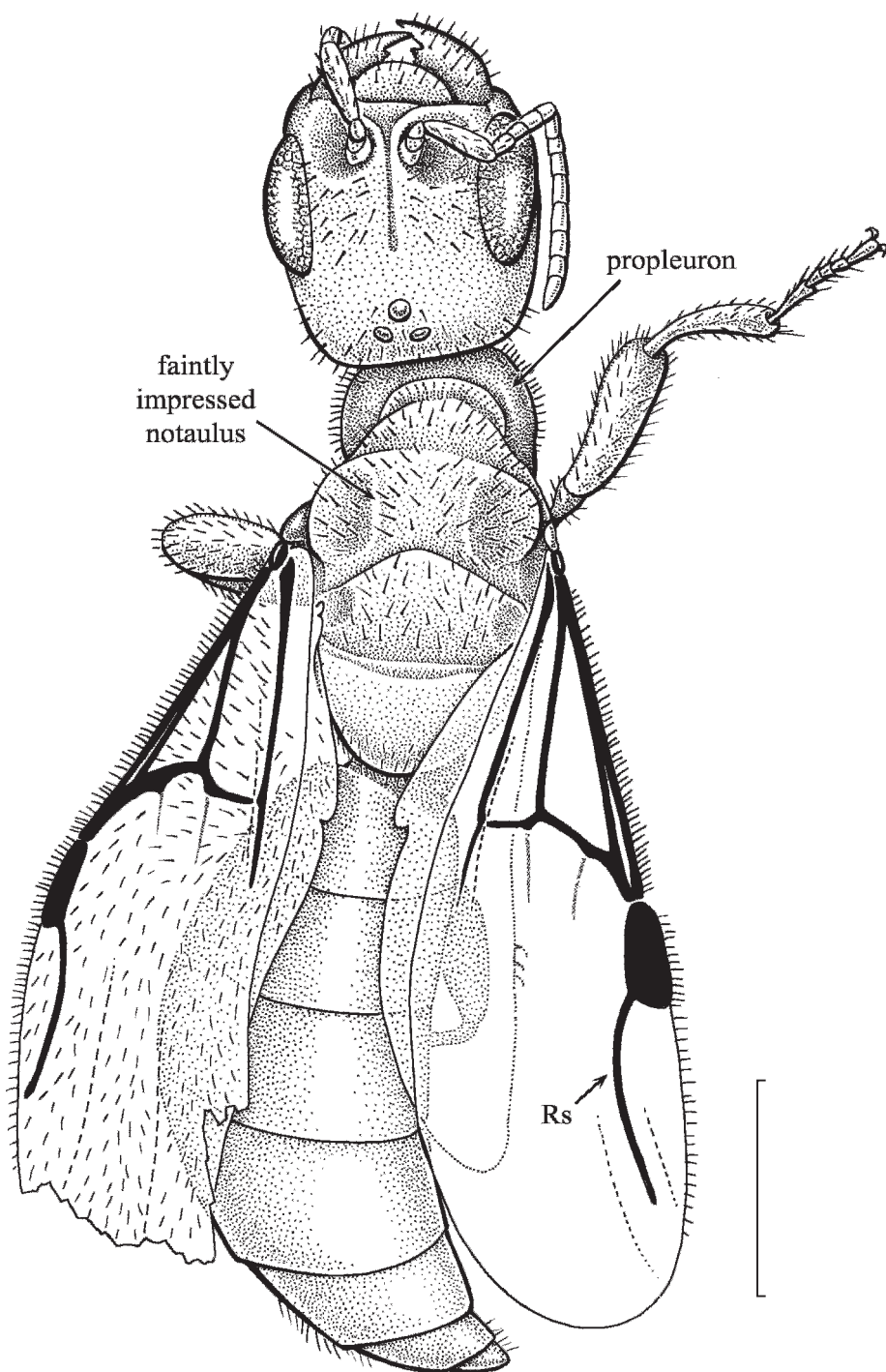


Fig. 5. *Zapenesia libanica*, new genus and species, in Lebanese amber (Azar 146-A); scale bar = 0.5 mm.

large, exposed, broadly triangular posteriorly; parapsidal lines present; forewing with open marginal cell; Rs long, much longer than pterostigma, terminating near anterior wing margin, tubular over entire length; R₁ absent beyond pterostigmal apex; pterostigma relatively large, margin within marginal cell strongly convex; 1m-cu absent; Rs+M nebulous and evident only at extreme base; Cu distad separation from M nebulous and evident only at extreme base; no submarginal cells (only costal, radial, and first cubital cells closed); metafemur not flattened; tibial spur formula 1-1-1; pretarsal claws simple.

ETYMOLOGY: The genus-group name is a combination of *oulios* (Greek, "deadly") and *-bythus* (root of the type genus for the family, *Scolebythus*). The name refers to the fact that these wasps are deadly parasitoids of wood-boring beetles. The name is masculine.

Uliobythus terpsichore, new species
figures 3, 6

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: Total body length ca. 1.4 mm (excluding everted male genitalia); forewing length ca. 1.0 mm. **Head.** Head apparently roughly ovoid, moderately broad, distance between compound eyes approximately equal to length of compound eye; gena much narrower than compound eye. Scape apparently short, perhaps only slightly more than combined lengths of F1 and F2 (difficult to determine owing to imperfect view of head in facial view). Integument dark brown and faintly imbricate. **Mesosoma.** Integument dark brown and apparently imbricate and impunctate. Propleura forming a strong, anterior neck, converging anteriorly, with distinct longitudinal striae; pronotal dorsal surface much shorter than mesoscutum. Transverse mesoscutal-mesoscutellar sulcus straight between tegulae; posterior border of mesoscutellum arched posteriorly; metanotum roughly U-shaped in dorsal aspect; basal area of propodeum narrowing posteriorly. Wing veins brown, membrane infumate; forewing with basal vein confluent with 1cu-a; venation depicted in figure 6. **Metasoma.** Terga and sterna dark brown, imbricate and

impunctate, with sparsely scattered, short, simple setae; genitalia as depicted in figure 6.

HOLOTYPE: Male, LEBANON: Hamman / Mdeirij, Azar-157-A. Specimen deposited in the Muséum National d'Histoire Naturelle, Paris.

ETYMOLOGY: The specific epithet is a noun in apposition and is the name of Terpsichore, one of the nine Muses of Greek mythology. Terpsichore was the Muse of Dance and was selected for the epithet since the position of preservation of the holotype gives the appearance of an elegant and pirouetting dancer.

KEY TO GENERA OF SCOLEBYTHIDAE

It should be noted that in the key of Azevedo (1999) the genus *Libanobythus* is treated as having notauli present (an error perpetuated by Lacau et al., 2000) while these are actually absent (see Prentice et al., 1996: 807).

1. Vein R₁ of forewing present, either fusing apically or nearly meeting Rs 2
- Vein R₁ of forewing absent, and thereby not fusing with Rs apically. 5
2. Marginal cell apex closed (i.e., R₁ and Rs fusing apically); pronotal collar absent [Recent] 3
- Marginal cell apex open (i.e., R₁ and Rs not meeting); pronotal collar present [Cretaceous; New Jersey amber].
. *Boreobythus*, n.gen.
3. First submarginal cell not enlarged, shorter in length than marginal cell; frons without median prominence between antennal toruli; malar space evident 4
- First submarginal cell elongate, longer than marginal cell; frons with median prominence between antennal toruli; malar space exceedingly minute, nearly unidentifiable [South Africa and Australia]. *Ycaploca* Nagy
4. Occipital carina present; malar space short, less than one-half basal mandibular width; marginal cell apex situated along anterior wing margin; S5 without special patches of setae [Madagascar] *Scolebythus* Evans
- Occipital carina absent; malar space well over one-half basal mandibular width; marginal cell apex arched away from anterior wing margin; S5 with two patches of appressed, dense setae [widespread Western Hemisphere] *Clystopsenella* Kieffer
5. Apical portion of Rs tubular; forewing with or without closed submarginal cell [Cretaceous; Lebanese amber] 6

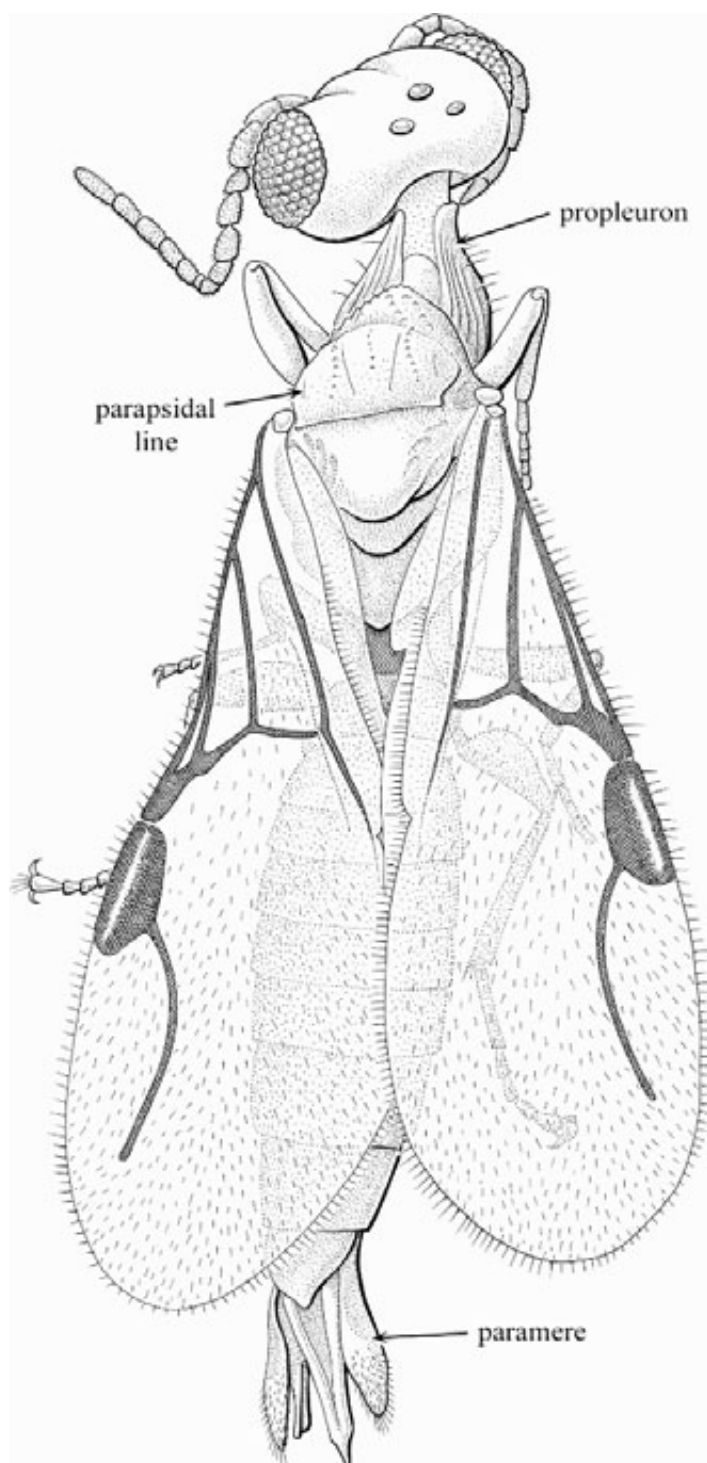


Fig. 6. *Uliobythus terpsichore*, new genus and species, in Lebanese amber (Azar 157-A).

TABLE 2
Character Descriptions
(All characters are considered nonadditive)

1. Forewing marginal cell: apex on margin of wing (0); apex curving away from margin of wing (1); open, Rs present as a short stub (2); open, Rs long, terminating near wing margin (3).
2. First submarginal cell: short (0); elongate (1); open (2).
3. Clypeal apex: short (0); produced (1).
4. Frontal prominence: absent (0); present (1).
5. Facial depression: flat lateral to antennal toruli (0); depressed lateral to antennal toruli (1).
6. Ocellar triangle: equilateral (0); obtuse (1).
7. Occipital carina: present (0); absent (1).
8. Malar space: very short (0); one-third basal mandibular width (1); one-half or more basal mandibular width (2).
9. Pronotal collar: present (0); absent (1).
10. Notauli: present (0); reduced posteriorly (1); not apparent (2).
11. Metapostnotum: distinct (0); partially obliterated (1); not apparent (2).
12. Mesotibial spurs: two (0); one (1); none (2) ^a .
13. Metatibial spurs: two (0); one (1); none (2) ^a .
14. Female sixth sternum: simple (0); with polished area and setae (1).
15. Forewing Rs, apical portion: tubular (0); nebulous (1).
16. Forewing 1m-cu: tubular (0); nebulous or absent (1).
17. Forewing basal part Rs+M: tubular (0); nebulous (1).
18. Forewing Cu distad 1m-cu: tubular (0); nebulous or absent (1).
19. Forewing Cu basad 1m-cu: tubular (0); partly nebulous (1).
20. Median ocellus: aligned or anterior to upper tangent of compound eyes (0); well posterior to upper tangent of compound eyes (1).
21. Parapsidal lines: present (0); absent (1).
22. Metafemur: not flattened (0); flattened (1).
23. Mesoscutellum: separated from mesoscutum by transverse furrow (0); separated from mesoscutum by pair of segregated pits (1).
24. Forewing R ₁ : present (0); absent or vestigial at best (1).

^aThe alleged complete absence of tibial spurs in *Eobythus* is extremely unusual among Hymenoptera, particularly Aculeata, and should be confirmed.

— Apical portion of Rs nebulous; forewing without closed submarginal cell [Tertiary to Recent]	8	behind upper tangent of compound eyes; two metatibial spurs	<i>Zapenesia</i> , n.gen.
6. Forewing without closed submarginal cell; dorsal-facing surface of pronotum greatly reduced, much smaller than mesoscutum . . .	7	8. Frontal prominence present; occipital carina present; metafemur not flattened [Eocene to Recent]	<i>Pristapenesia</i> Brues
— Forewing with closed submarginal cell; dorsal-facing surface of pronotum enlarged, larger than mesoscutum.		— Frontal prominence absent; occipital carina absent; metafemur flattened [Eocene].	<i>Eobythus</i> Lacau et al. ⁴
—			
7. Minute wasps (less than 2 mm in total length), with more typical scolebythid habitus; face without impressed medial line, without depressions lateral to antennal toruli; parapsidal lines faint but present; ocelli positioned just above upper tangent of compound eyes; one metatibial spur			
— Small wasps (ca. 2.6 mm total length), with bethylid-like habitus; face with strong medial line impressed from between antennal toruli to upper tangent of compound eyes, with gentle depressions lateral to antennal toruli; parapsidal lines absent; ocelli positioned far			

CLADISTICS

Recently, Carpenter (1999) and Lacau et al. (2000) have presented cladistic analyses of

⁴This genus should perhaps be synonymized with *Pristapenesia* (vide Cladistics and Discussion). Also, the occipital carina is purportedly absent, yet figure 3 in Lacau et al. (2000), albeit small and faint, shows a minute line on the posterior and undersurfaces of the head which suggests a weak carina may indeed be present. The “flattened” metafemur may be the result of misinterpretation of compression along the specimen’s legs, typical for such fossils.

relationships within Scolebythidae. These data matrices included all known genera, including the fossils *Libanobythus*, *Pristapenesia* (as *Dominibythus* in those papers), and *Eobythus* and 14 and 24 characters of adult external morphology, respectively. For the present analysis of scolebythid relationships we have essentially employed these data with the following minor additions and modifications: **1.** we have coded each species of *Pristapenesia* (*P. inopinata*, *P. stricta*, and *P. primaeva*) and *Ycaploca* (*Y. evansi* and *Y. fijianus* Beaver) owing to variation within the genus of some characters, in this way testing the monophyly of the genera as they are currently conceived; **2.** we have added the new fossil taxa described herein; **3.** we split character state two of Carpenter’s first character concerning the marginal cell, the resulting states being “2: open, Rs present as a short stub” (= *Pristapenesia*) and “3: open, Rs long, terminating near wing margin” (= *Libanobythus* and *Boreobythus*; see table 2); **4.** we have eliminated Lacau et al.’s character 21 (i.e., pronotal length relative to mesoscutum) owing to a lack of discrete states—even in their own matrix this character is meaningless and is perplexingly coded as identical for all taxa including the outgroup (i.e., these authors have identified only one character state for *all* taxa; moreover, the real difference is the development of the pronotal collar, which results in a larger dorsal surface of the pronotum relative to the mesoscutum and is therefore not independent of character 9); **5.** we have added a new character (character 24) concerning the development of R_1 in the forewing (Table 2); and **6.** we have corrected a number of errors concerning the character states found in fossil scolebythids as presented by Lacau et al. (2000). These authors code *Libanobythus* as “parapsidal lines present” (their character 22, our character 21) when the fossil lacks these grooves (see Prentice et al., 1996). *Libanobythus* was also erroneously coded as “1m-cu nebulous” (character 16), “basal part of Rs+M nebulous” (character 17), and “Cu basal of m-cu nebulous” (character 19) when all of these veins are tubular and pigmented in the fossil (see Prentice et al., 1996). Although Lacau et al. (2000) code *E. patriciae* as “1m-cu tubular” (character 16)

TABLE 3
Data Matrix for Relationships within Scolebythidae^a
(Character descriptions in table 2; Plumariidae is the outgroup)

Taxon	Characters and character states
	11111111122222
	123456789012345678901234
Plumariidae	00*0000\$*\$0000000000*000
† <i>Boreobythus turonius</i>	30100?1212???0001101000
<i>Clystopsenella longiventris</i>	100011121010010001010110
† <i>Eobythus patriciae</i>	2200001212222?1?10011101
† <i>Libanobythus milkii</i>	3000000?02?11?0001001001
† <i>Pristapenesia inopinata</i>	2211000211211?1111100001
† <i>Pristapenesia primaeva</i>	2211000212211?1111101001
<i>Pristapenesia stricta</i>	2211000212211?1111101001
<i>Scolebythus madecassus</i>	001011011010000001000010
<i>Ycaploca evansi</i>	111100001001100001000000
<i>Ycaploca fijianus</i>	111110001001100001000000
† <i>Zapenesia libanica</i>	320010121000000111111001
† <i>Uliobythus terpsichore</i>	3200001210?11?0111110001

^aInterrogative marks (?) indicate unknown character states; asterisks (*) indicate complete polymorphisms, and dollar (\$) marks indicate subset polymorphisms as follows: character 8: Plumariidae = 0,1; character 10: Plumariidae = 1,2.

both their illustrations and the photographs of the fossils do not show this vein. Thus, it would appear (despite their description and matrix) that this fossil lacks 1m-cu or it is nebulous at best. Owing to this apparent confusion we have conservatively coded *E. patriciae* as “unknown” for character 16. A complete, corrected matrix for the Scolebythidae appears in table 3 with character descriptions presented in table 2. Analysis of the unordered data in *Nona* (*wh**; *max** commands) resulted in a two equally parsimonious trees (length 55, CI 0.57, RI 0.70), the strict consensus of which appears in figure 7.

DISCUSSION

Our phylogeny does not differ dramatically from those proposed by Carpenter (1999) and Lacau et al. (2000) except in the relative positions of *Libanobythus* and *Ycaploca* in Carpenter’s cladogram, in the position of *Eobythus* in Lacau et al.’s cladogram, and by the addition of three new taxa. Herein we discuss a series of clades but do not formalize

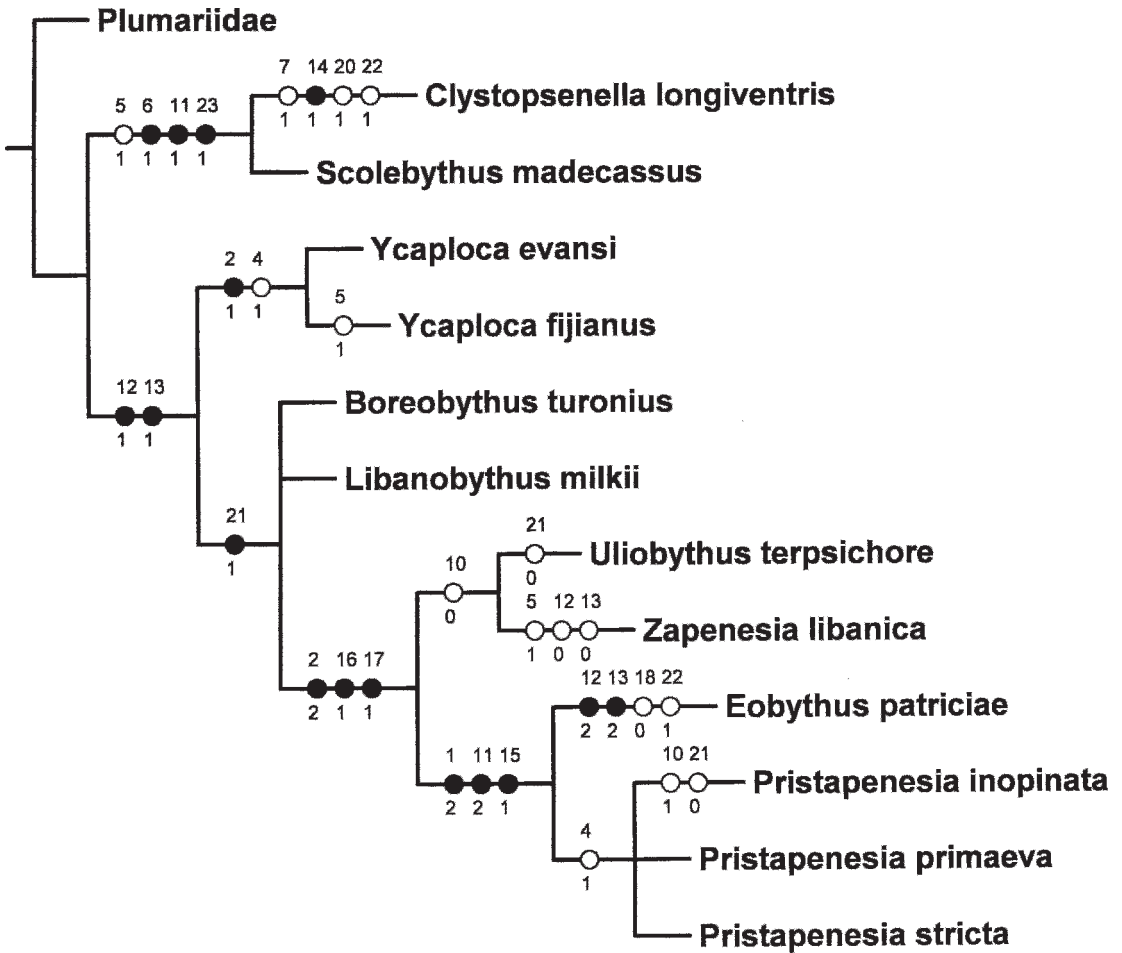


Fig. 7. Cladogram of scolebythid relationships (strict consensus of two equally parsimonious topologies: $L = 55$; $CI = 0.57$; $RI = 0.70$), with only unambiguous character state transformations indicated. Closed circles indicate unique transformations, open circles indicate homoplasious transformations; character numbers are indicated above the branch, character states beneath the branch. Synapomorphies for Scolebythidae were not included.

them taxonomically given that the addition of new fossil material and further characters in the future will undoubtedly change the classification. The pristapenesiine clade (table 1) is supported by the reduction to a single meso- and metatibial spurs while *Ycaploca* is placed basal in this group, separated from the principally fossil genera (except for *P. stricta*) by the presence of parapsidal lines (parapsidal lines are apomorphically lost in the other genera; fig. 7). *Ycaploca* is therefore considered as the sole representative ycaplocine subclade, with the remainder of the pristape-

nesiine clade belonging to a nominate subclade (table 1). Within this clade of fossil genera, *Boreobythus* is most primitive by the retention of the tubular and pigmented R_1 vein along the leading edge of the marginal cell. All other genera in the clade have the apomorphic reduction of this vein, although support for their monophyly remains ambiguous enough to prevent them from appearing as a clade in the analysis. The *Pristapenesia* group, consisting of the genera *Uliobythus*, *Zapenesia*, *Eobythus*, and *Pristapenesia* itself, is united by further reduction of the wing

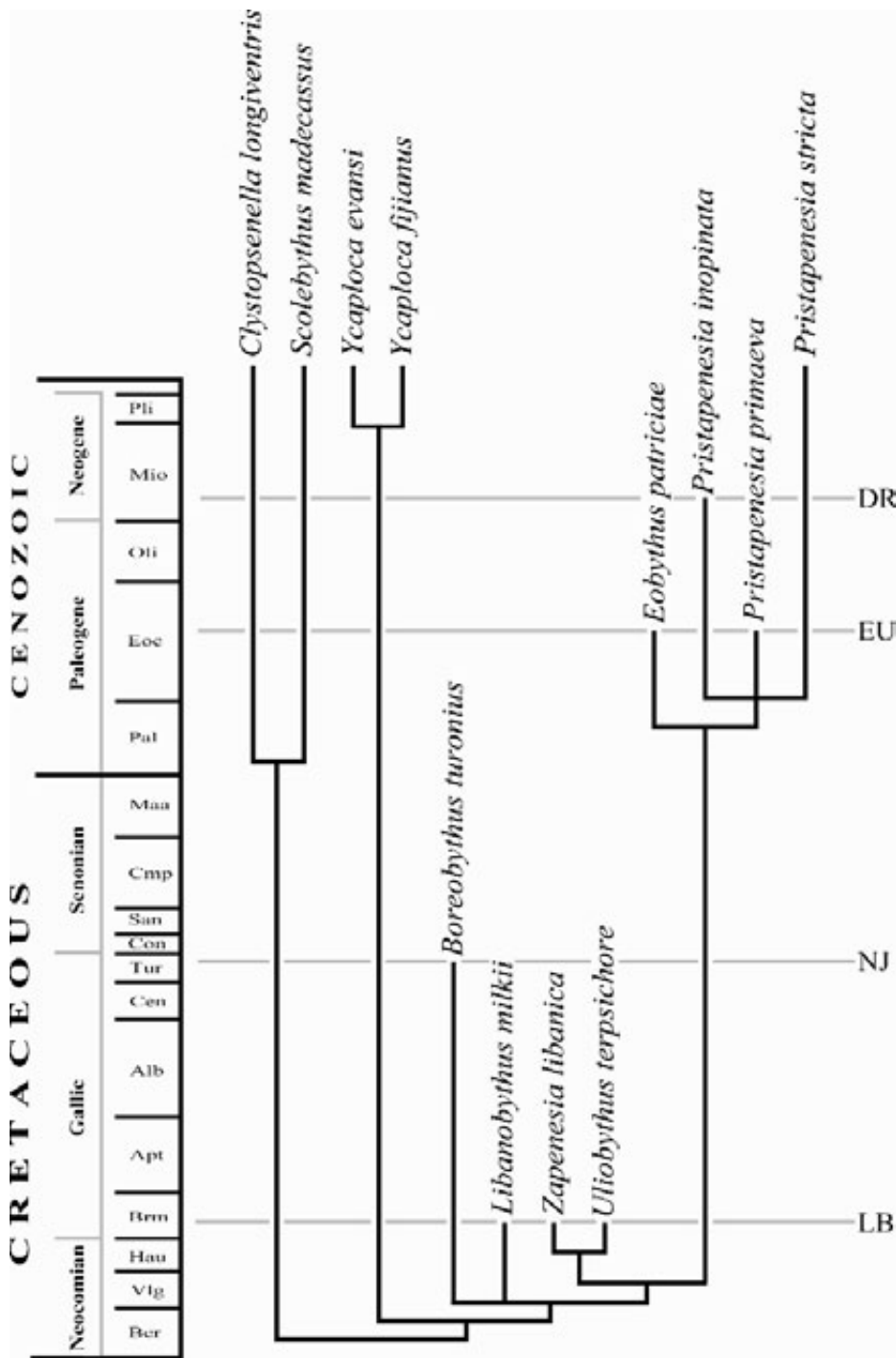


Fig. 8. Phylogeny of Scolebythidae. Abbreviations for amber deposits: DR, Dominican Republic; EU, European ambers (Baltic and Parisian); NJ, New Jersey; LB, Lebanon.

venation, notably the apomorphic presence of an open marginal cell; the nebulous, spectral, or completely absent 1m-cu (linked to the loss of submarginal cells); and the nebulous, spectral, or absent Rs+M (fig. 7). *Scolebythus* and *Clystopsenella* are retained as a monophyletic group at the base of scolebythid phylogeny. The genera are united by the presence of the facial depression lateral to the antennal torulus (although this is apparently independently acquired by *Y. fijianus*), the obtuse ocellar triangle, the partially obliterated metapostnotum, and the presence of pits separating the mesoscutum and mesoscutellum (fig. 7). A cladistic classification of the family to the species level is presented in table 1. The large number of enigmatic traits in *Eobythus* should be more carefully explored owing to the obvious errors reported in the original description. That the specimens strongly resemble those of *P. primaeva* suggests that *Eobythus* should be synonymized with *Pristapenesia* and that *E. patriciae* should be transferred to this genus. We reserve such a formal change until the material of *E. patriciae* is available for re-study and its uncertain character states confirmed or revised.

Even a cursory zoogeographic analysis of Recent and fossil scolebythids indicates extensive extinctions in the family leaving only relict remnants. Based solely on living taxa this family has been considered to have a classic austral disjunct distribution (southern Brazil, South Africa, Madagascar, and Australia; e.g., Brundin, 1966). It is difficult to explain the historical biogeography of the family based on the present analysis by austral vicariance alone. Overall, the placement of the fossil taxa, particularly the Cretaceous taxa, in the phylogeny suggests significant extinction across the entire family (fig. 8). It seems most likely that the family was widely distributed throughout the Cretaceous and early Tertiary, experiencing significant northern extinctions during the climatic changes of the Eocene-Oligocene transition, with a single species holding on in the West Indies until late in the Miocene. If this hypothesis is correct, then it is perhaps possible that *Clystopsenella* was a northern element that progressed southward during the later Tertiary. Alternatively, the scolebythine clade may indeed represent

southern vicariance between *Scolebythus* and *Clystopsenella*, the later progressing northward during the Tertiary in this secondary scenario (although this seems unlikely). However, such austral vicariance cannot account for the divergences in the pristapenesiine clade (fig. 8). Clearly, numerous fossils of scolebythids await discovery and these will undoubtedly provide significant insights into the geological history of this relict family.

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