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The wasp genus *Clystopsenella* in Early Miocene amber from the Dominican Republic (Hymenoptera: Scolebythidae)

Michael S. Engel1,2

1 Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045-4415, USA (msengel@ku.edu).

2 Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA.

**Abstract.** A new species of scolebythine wasp (Chrysidoidea: Scolebythidae) is described and figured from a female beautifully preserved in Early Miocene amber from the Dominican Republic. The specimen is the first fossil record of the extant genus *Clystopsenella* Kieffer, and is quite similar to the extant *Clystopsenella longiventris* Kieffer, a species that occurs widely from Brazil to Belize. ***Clystopsenella mirabilis*** Engel, new species, is distinguished from *C*. *longiventris* on the basis of size; head, pronotal, and pterostigmal shape; and putative color differences. The living and fossil diversity of the family is summarized and evolutionary patterns within the clade are discussed.

INTRODUCTION

The wasp family Scolebythidae is one of the smaller and lesser understood lineages of the Chrysidoidea. The six living species are scattered across the globe, with two species in the New World tropics (Kieffer, 1911; Day, 1977; Gauld, 1995; Azevedo, 1999; Fernandez *et al*., 2002; Cambra & Azevedo, 2003; Engel, 2005), two species in the Afrotropical region (Evans, 1963; Nagy, 1975; Day, 1977; Evans *et al*., 1979), and a further two in southern Asia and Melanesia (Beaver, 2002; Azevedo *et al*., 2011). One of the African species has also been discovered in Australia, although this is suspected to be an inadvertent introduction (Naumann, 1990). To this day there remains but a single study of the biology of any scolebythid (Melo, 2000), although various anecdotal evidence regarding possible host associations or behaviors have been published (*e.g*., Day, 1977; Evans *et al*., 1979; Brothers, 1981). Melo (2000) reported that *Pristapenesia stricta* (Azevedo) developed gregariously as idiobiont parasitoids of anobiid larvae (Bostrichoidea: Anobiidae). In this species, the adult female digs her way into the beetle’s tunnels and upon discovering the larva proceeds to sting it and deposit several eggs along the immobilized larva. Once the wasp’s larvae eclose, they feed gregariously on the beetle until eventually spinning their pupal cocoons. During the same study, Melo (2000) was able to document sibling mating and noted that this, along with their association with wood-boring beetle hosts, likely confers upon scolebythids an ease for becoming adventive. Indeed, accidental introduction had already been suggested as a possible explanation for the widely disjunct occurrences of *Ycaploca evansi* Nagy (Naumann, 1990). *Ycaploca evansi* has been assumed to develop on larvae of Cerambycidae (Day, 1977; Brothers, 1981), while *Scolebythus madecassus* Evans was found in presumed beetle burrows in rotting wood (Evans *et al*., 1979).

Fossil scolebythids significantly outnumber the presently known extant species (Aguiar *et al*., 2013; Table 1). The first fossil scolebythid, *Pristapenesia primaeva* Brues, was described as a bethylid (as the family Scolebythidae was not established until several decades later) in middle Eocene Baltic amber (Brues, 1933). Brues (1933) did not recognize the similarity between *Pristapenesia* Brues and *Clystopsenella* Kieffer, the only two scolebythids then known and both placed in Bethylidae. It was not until three decades later that Evans (1963) realized, when describing *Scolebythus* Evans, the distinctiveness of the group from bethylids, although he did not at that time realize that *P*. *primaeva* belonged to the same lineage. Prentice *et al*. (1996) also did not realize the proper placement of *P*. *primaeva* when they described two fossil scolebythids from Lebanese and Dominican amber. Indeed, it was not until Brothers & Janzen (1999) studied a new series of male and female *P*. *primaeva* that the proper placement for this genus was discovered, and that the Dominican amber fossil described by Prentice *et al*. (1996) was congeneric. In fact, it is now understood that *Pristapenesia* also includes two of the modern species (Azevedo *et al*., 2011). Subsequently, scolebythids have been discovered in numerous deposits, virtually all being represented by inclusions in amber with the sole exception of two species from Liaoning, China (Cai *et al*., 2012). Cretaceous scolebythids have been discussed and described from Neocomian and Aptian Lebanese amber (Prentice *et al*., 1996; Engel & Grimaldi, 2007a), Aptian Jordanian amber (Kaddumi, 2005: appears to be an individual of *Zapenesia* Engel & Grimaldi), Albian Spanish amber (Engel *et al*., 2013), Turonian New Jersey amber (Engel & Grimaldi, 2007a), and Campanian Canadian amber (McKellar & Engel, 2012; Engel *et al*., 2013) (Table 1). The genus *Cretabythus* Evans in Late Cretaceous Taimyrian amber, at times suspected of being a scolebythid (Evans, 1973), is almost assuredly a primitive bethylid (Carpenter, 1986; Rasnitsyn, 1988; Engel *et al*., in prep.). The Paleogene and Neogene diversity has included until now only three species — *P*. *primaeva* in the middle Eocene amber of the Baltic and Rovno regions (Brues, 1933; Brothers & Janzen, 1999; Perkovsky & Rasnitsyn, 2013), *Eobythus patriciae* Lacau *et al*. in Early Eocene amber of the Paris Basin (Lacau *et al*., 2000), and *P*. *inopinata* (Prentice *et al*.) in Early Miocene amber from the Dominican Republic (Prentice *et al*., 1996). It should be noted that the genus *Eobythus* Lacau *et al*. (2000) is almost assuredly a synonym of *Pristapenesia* and its sole species should be transferred to the latter genus (*vide etiam* Engel & Grimaldi, 2007a; Engel *et al*., 2013).

Here is described a new species of *Clystopsenella* recently identified from a single female preserved in Early Miocene amber of the Dominican Republic. This is the first fossil record of the genus as well as for the subfamily Scolebythinae, and although *Clystopsenella* are well known from Central America today (*e.g*., Cambra & Azevedo, 2003; Engel, 2005), they have not been encountered throughout the Caribbean. It would therefore appear that *Clystopsenella*, like *Pristapenesia*, was once a component of the ancient forests of Hispaniola, but disappeared during the intervening geological stages.

MATERIAL AND METHODS

The fossil described herein was located in an average-sized, irregular piece of light yellowish orange amber, representing a small runnel with various flows. The wasp is positioned in the direction of the flows and situated near the border between different runnel sections and with its metasomal apex near a natural break in the piece. In order to obtain a clear view of the wasp, the piece was trimmed and polished to a size of approximately 13 mm in length and 13 mm in maximum height. The final piece has a roughly trapezoidal cross-section, with a maximum depth of 8.5 mm, and a depth of approximately 7 mm at the level of the wasp. A polished plane was prepared along the left side of the wasp, and another parallel with its dorsal surface (Figs. 1, 2). A ventral view was not possible owing to the position of the wasp within the flows of the piece and at the border between runnel sections, nor was it possible to polish the surface to its posterior as the apex of the metasoma and ovipositor are at that surface. The opposing end was polished to provide a clear view of the face directly onward. The right side of the wasp is also situated along an internal flow and fracture and therefore no preparation was possible to allow a view from that direction. Fortunately, the piece is remarkably clear of debris and there is little that hinders a suitable view of the fossil. As noted, the wasp is preserved in line with the runnel flow, and has its wings reclined over the body (Figs. 1, 2). The legs are tucked under the body and extend slightly ventrally from the wasp’s long axis. The antennae are curled outward and around the sides of the head, and the metasoma is gradually bent upward beginning at about metasomal segments III and IV, such that the terminus is nearly orthogonal to the longitudinal axis of the body (Fig. 1). There is a single syninclusion, that being a small barklouse (Psocoptera) to the right of the metasomal apex and away from the wasp at the internal flow’s surface.

The origin and age of Dominican amber has been covered by Iturralde-Vinent & MacPhee (1996, 1999), Grimaldi (1995), and Grimaldi & Engel (2005), and this deposit is one of the most prolific of Neogene ambers. A Canon 7D digital camera and an Infinity K-2 long-distance microscope lens were used to capture the images presented here. The specimen was measured by means of an ocular micrometer through an Olympus SZX-12 stereomicroscope. Morphological terminology follows that used in earlier studies of fossil Scolebythidae (Engel & Grimaldi, 2007a; Engel *et al*., 2013). The descriptions are presented here in the context of establishing a more robust pattern of character distributions and taxonomic diversity (both temporal and spatial) for scolebythids (*e.g*., Grimaldi & Engel, 2007), and as a framework for discussing the evolutionary history of the group.

SYSTEMATIC PALEONTOLOGY

Genus *Clystopsenella* Kieffer

***Clystopsenella mirabilis*** Engel, new species

(Figs. 1–4)

Diagnosis: The new fossil species is slightly smaller than its congener (length of body and forewing 5.9 mm and 3.1 mm, respectively, in the fossil versus 7–10 mm and 4–6 mm, respectively, for *Clystopsenella longiventris* Kieffer), has the legs concolorous with the mesosoma [the legs are distinctly lighter than the mesosoma in *C*. *longiventris* (Fig. 5)], has a head that is slightly longer than wide (Fig. 3) (slightly wider than long in *C*. *longiventris*), head largely yellow brown except black on vertex and above level of ocellar triangle (Fig. 3) (dark brown to black throughout, sometimes with three streaks of lighter coloration on vertex in *C*. *longiventris*); has a much shorter pronotal disc (disc is about 0.21x mesoscutal length, versus 0.51x in *C*. *longiventris*); and the margin of the pterostigma inside the marginal cell is straight [convex in *C*. *longiventris* (Fig. 5)].

Description: ♀: Total body length, excluding ovipositor, *ca*. 5.9 mm; forewing length 3.1 mm. Head broad apically (Fig. 3), slightly longer than wide, length 0.94 mm, width (across compound eyes) 0.88 mm; frons width 0.59 mm; mandible with four sharp teeth in an oblique series, apical tooth largest. Clypeus short, strongly transverse, much shorter than diameter of antennal torulus (Fig. 3), apical margin without median lobe but with faint, narrow apicolateral convexities (weaker than those in *C*. *longiventris*). Malar space distinctly long, more than three-quarters basal mandibular width, basal mandibular width 0.19 mm, malar space 0.16 mm. Frontal line weakly carinate from median ocellus to near clypeal apex; frontal prominence between antennal toruli absent; face lateral to antennal toruli gently depressed for reception of scape; antennal toruli separated by about torular diameter. Antennal scape slightly curved, thicker than other antennal articles; pedicel conical, length slightly more than twice apical width; 11 flagellomeres; flagellomeres each slightly longer than wide. Inner margins of compound eyes straight, parallel (Fig. 3); compound eye length 0.55 mm (distance between compound eyes approximately 1.1x compound eye length); compound eye bare; ocellar triangle positioned below upper tangent of compound eyes (Fig. 3), ocellar triangle obtuse (width 0.20 mm, length 0.14 mm), distance between ocellar triangle and peak of vertex in frontal view 0.24 mm (distance 1.2x ocellar triangle width or 4x diameter of median ocellus); ocellocular distance 0.22 mm; diameter of median ocellus 0.06 mm. Vertex arched in frontal view (Fig. 3); occipital carina absent; gena slightly broader than compound eye. Pronotum short (Fig. 2), with anterior border declivitous (Fig. 1); pronotal disc short, medial length of disc 0.11 mm (pronotal disc about 0.21x medial length of mesoscutum); pronotal collar absent such that elongate propleura exposed dorsally; mesoscutum wider than long, medial length 0.53 mm, intertegular distance 0.69 mm; notauli distinctly impressed, complete and parallel throughout length; parapsidal lines more weakly impressed (most easily visible under lateral lighting), complete and parallel throughout length, extending posteriorly to anterolateral angle of axilla; notauli divide mesoscutum into roughly equal thirds; parapsidal lines divide portion of mesoscutum outside of notaulus into outer third and inner two-thirds; mesoscutellum separated from mesoscutum by transverse furrow composed of two widely separated pits, wider than long, about two-thirds length of mesoscutum; metanotum exceedingly short; metapostnotum partially obliterated, short, subtriangular, and slightly concave centrally, about 0.4x as long as wide. Legs with procoxae flattened, protrochanters inserted laterally; femora slightly swollen (profemur not as pronouncedly swollen as in *C*. *longiventris*) and metafemur laterally flattened; tibial spur formula 1-2-2; pretarsal claws simple, arolium absent. Forewing with R1 present; marginal cell closed (Fig. 4), with acutely rounded apex, apex curving away from anterior margin of wing by a little more than a vein width, weakly appendiculate; Rs tubular throughout; prestigma slightly thickened; pterostigma slightly longer than broad, subtriangular and broader apically, posterior border weakly convex, border inside marginal cell straight and slightly oblique, r-rs arising at widest point near apical third (Fig. 4); basal vein distad 1cu-a by vein width, straight, longer than first abscissa Rs, forming angle with first abscissa Rs; Rs+M tubular, first abscissa distinctly shorter than that beyond 1m-cu; second abscissa Rs slightly longer than first abscissa Rs and about as long as r-rs; transverse tangent from second abscissa Rs slightly apicad of ptersotigmal apex; apicalmost abscissa Rs (that forms posterior border of marginal cell) almost three times length of r-rs; submarginal cell comparatively short, about as long as marginal cell (not greatly longer than marginal cell); discoidal cell (medial cell) closed (Fig. 4), with 1m-cu tubular, cell longer than wide; subdiscoidal cell narrowly open in posterior apical corner; Cu basad 1m-cu tubular but nebulous distad 1m-cu. Hind wing with 4 distal hamuli. Metasoma slender and long (Figs. 1, 2); sternum V with medioapical, raised, subtriangular area anterior to marginal zone.

Integument of head glabrous and somewhat shining, impunctate except for minute, shallow depressions around some setal bases; mesosoma and legs largely glabrous and somewhat shining except metanotum with space transverse striae, metapostnotum with weak striae, propodeum weakly and finely imbricate and laterally with short, transverse striae in depressions corresponding to placement of fused metathoracic-propodeal suture. Metasoma weakly imbricate except sternum V with more polished surface on medioapical, raised, subtriangular patch.

Pubescence generally sparse and short, particularly sparse on head except along ventral margin of mandible. Mesosoma with setae short and sparse except those on pleura longer. Metasoma with generally sparse and short setae, those setae laterally a bit more numerous and longer, particularly and progressively so on more apical segments such that apicolateral setae on terga V and VI and setae in apical half of tergum VI are numerous, long, and largely erect; sterna with sparse short, erect setae progressively longer on more apical sterna, apicolateral setae on sterna V and VI long and distinctly more numerous, sternum V with patches of dense, short, fine, and appressed setae lateral to medial subtriangular elevation.

Coloration poorly preserved owing to clearing of integument in areas (note that the metasomal coloration is likely largely augmented by taphonomic factors and so has not been used in the diagnosis of the species); head and mouthparts generally yellow brown except face above ocellar triangle and vertex from above black (Figs. 1–3); antenna light yellow brown. Mesosoma and legs largely yellow brown except with areas of brown medially on meso- and metafemora. Tegula and humeral plate dark brown; axillary sclerites yellow brown; veins largely brown to dark brown except apicalmost abscissa of Rs+M, 1m-cu, apex of prestigma, and base of pterostigma lighter (Figs. 2, 4); wing membranes hyaline and slightly tinged brown, with darker streak in membrane extending as a transverse band from about base of prestigma and origin of Rs to posterior margin around level of 1cu-a and in basal halves of discoidal (medial) and subdiscoidal (cubital) cells (Figs. 2, 4), also slightly more infumate along anterior margin at apex of marginal cell (Fig. 4). Metasoma generally light yellow brown except basal half of first tergum brown, and apical thirds brown except interrupted medially.

♂: *Latet*.

Holotype: ♀, AMNH DR-924-H-211; Dominican Republic, Early Miocene amber, specific mine unknown; deposited in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York.

Etymology: The specific epithet is the Latin word *mirabilis*, meaning, “wonderful”.

DISCUSSION

The specimen described here can easily be placed within *Clystopsenella* owing to the combined presence of an elongate malar space, facial depressions lateral to the antennal toruli, an obtuse ocellar triangle, two pits in the mesoscutal-mesoscutellar furrow, a 1-2-2 tibial spur formula, and a marginal cell apex separated from the anterior margin of the wing, along with the absence of an occipital carina and the partially obliterated metapostnotum. Most importantly, the fossil shares with *C*. *longiventris* the characteristic presence of appressed setal patches on the fifth metasomal sternum and bordering a slightly elevated polished area, a feature unique to *Clystopsenella* among scolebythids. *Clystopsenella longiventris* exhibits variation in size and color across its vast range, and Gauld (1995) suggested that these forms were specifically distinct. Cambra & Azevedo (2003), however, indicated that the color variants intergraded and, most critically, these do not cluster geographically. Whereas *C*. *longiventris* was for a long while believed to only occur in southern and eastern Brazil (Kieffer, 1911; Evans, 1963; Azevedo, 1999), the species has been documented from across Central America (Gauld, 1995; Cambra & Azevedo, 2003; Engel, 2005) and northern South America (Fernandez *et al*., 2002), shattering the notion that scolebythids were a strictly austral group. Moreover, the presence of scolebythids in fossil deposits scattered throughout the Northern Hemisphere and as recently as the Early Miocene further demonstrates that their modern occurrences are not the result of Gondwanan vicariance, much as is the case for several purported insect examples of ‘austral disjunct distributions’ (*e.g*., Grimaldi & Engel, 2005, 2006a). The diversity of and relationships among fossil Scolebythidae (Fig. 6) underscores the reality that the family is today relict. Furthermore, those available fossils also imply that the paleodiversity documented falls far short of adequately reflecting the true diversity, and there was at one time a greater variety of not only species and genera, but of morphological disparity across the clade (Engel *et al*., 2013). The relationships suppose a lengthy ghost lineage for the Scolebythinae (Fig. 6), for which *C*. *mirabilis* at least partially, albeit trivially, narrows the gap. It is peculiar that among the plethora of Cretaceous Scolebythidae, all are of the Pristapenesiinae, leaving one to wonder why the sampling should be skewed away from Scolebythinae. It is possible that stem group scolebythines might be easily confused with primitive pristapenesiines with more completely developed wing venation (*e.g*., *Boreobythus turonius* Engel & Grimaldi), and where subtle features such as the number of tibial spurs or the presence of the facial depressions for receipt of the antennal scape are obscured. Regardless, the phylogenetic, temporal, and geographic distribution of the available fossils emphasizes the need for continued paleontological exploration.

It is fairly common to discover surviving genera in Dominican amber that are either not present across modern Hispaniola, do not occur in the Greater or Lesser Antilles (save for Trinidad and Tobago which are positioned on the South American continental shelf), or, in more extreme examples, are no longer found in the Western Hemisphere. Examples of such localized extinctions include (this list is by no means exhaustive but merely highlights examples across the phylogenetic spectrum of Insecta) bristletails of the genus *Trinemurodes* Silvestri (Sturm & Mendes, 1998); silverfish of the genus *Hemitrinemura* Mendes (Mendes & Poinar, 2004); termites of the genera *Mastotermes* Froggatt, *Dolichorhinotermes* Snyder & Emerson, *Coptotermes* Wasmann, and *Constrictotermes* Holmgren (Krishna & Grimaldi, 1991, 2009); barklice of the genus *Belaphopsocus* Badonnel (Grimaldi & Engel, 2006b); termite bugs of the genus *Termitaradus* Myers (Grimaldi & Engel, 2008; Engel, 2009a); stag beetles of the genus *Syndesus* MacLeay (Woodruff, 2009); the histerid genus *Trypanaeus* Eschscholtz (Chatzimanolis *et al*., 2006); weevils of the genera *Proeces* Schönherr, *Dryophthorus* Germar, and *Stenommatus* Wollaston (Davis & Engel, 2006, 2007); the dustywing genus *Spiloconis* Enderlein (Meinander, 1998; Engel & Grimaldi, 2007b; Grimaldi *et al*., 2013a); valeseguyid and carnid flies (Grimaldi, 1991, 1997); window flies of the genus *Metatrichia* Coquillett (Yeates & Grimaldi, 1993); parasitoid wasps of the genera *Ophrynopus* Konow, *Ceraphron* Jurine, *Masona* van Achterberg, *Leucospis* Fabricius, *Leptofoenus* Smith, *Bocchus* Ashmead, *Ceratochrysis* Cooper, and *Pristapenesia* Brues (Olmi, 1989; Prentice *et al*., 1996; Brothers & Janzen, 1999; van Achterberg, 2001; Engel, 2002, 2006, 2008, 2009b, 2013); fig wasps of the genera *Pegoscapus* Cameron and *Tetrapus* Mayr (Peñalver *et al*., 2006); the ant genera *Leptomyrmex* Mayr, *Azteca* Forel, *Neivamyrmex* Borgmeier, and *Paraponera* Smith (Baroni Urbani, 1980; Wilson, 1985, 1988; Baroni Urbani & Wilson, 1987); apoid wasps of the genera *Lindenius* Lepeletier & Brullé and *Pison* Spinola (Antropov & Pulawski, 1996; Bennett & Engel, 2006, 2008); and bees of the genera *Chilicola* Spinola, *Neocorynura* Schrottky, *Thaumatosoma* Smith, *Anthophorula* Cockerell, and *Euglossa* Latreille (Engel, 1995, 1999a, 1999b, 1999c; Engel *et al*., 2012), among many other arthropod lineages. To this long list of regional extinctions may be added the genus *Clystopsenella*, but given how little we know of the true distribution for *C*. *longiventris* one might wonder if in time it too shall reveal itself somewhere in the Greater Antilles, much as some lineages first known from amber fossils are later found in the modern fauna (e.g., Schuh & Polhemus, 1980; Lawrence, 1995; Grimaldi & Engel, 2006a; Wild & Cuezzo, 2006; Grimaldi *et al*., 2013b).

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**Table 1.** Hierarchical classification and distribution of Scolebythidae (updated from Engel *et al*., 2013).

Family SCOLEBYTHIDAE Evans

Subfamily Scolebythinae Evans

Genus *Scolebythus* Evans

*S*. *madecassus* Evans Madagascar

Genus *Clystopsenella* Kieffer

*C*. *longiventris* Kieffer Belize, Brazil, Colombia, Costa Rica, Panamá

†*C*. *mirabilis*, n. sp. Dominican amber (Miocene)

Subfamily Pristapenesiinae Engel *et al*.

Genus *Ycaploca* Nagy

*Y*. *evansi* Nagy South Africa, Australia

*Y*. *fijianus* Beaver Fiji

Genus †*Boreobythus* Engel & Grimaldi

†*B*. *turonius* Engel & Grimaldi New Jersey amber (Turonian)

Genus †*Libanobythus* Prentice & Poinar

†*L*. *milkii* Prentice & Poinar Lebanese amber (Neocomian)

Genus †*Ectenobythus* Engel *et al*.

†*E*. *iberiensis* Engel *et al*. Spanish amber (Albian)

Genus †*Necrobythus* Engel *et al*.

†*N*. *pulcher* Engel *et al*. Canadian amber (Campanian)

Genus †*Sphakelobythus* Engel *et al*.

†*S. limnopous* Engel *et al*. Canadian amber (Campanian)

Genus †*Zapenesia* Engel & Grimaldi

†*Z*. *libanica* Engel & Grimaldi Lebanese & Jordanian amber (Aptian)

Genus †*Uliobythus* Engel & Grimaldi

†*U*. *terpsichore* Engel & Grimaldi Lebanese amber (Aptian)

Genus †*Mirabythus* Cai *et al*.

†*M*. *lechrius* Cai *et al*. China (Barremian)

†*M*. *liae* Cai *et al*. China (Barremian)

Genus †*Eobythus* Lacau *et al*.

†*E*. *patriciae* Lacau *et al*. Parisian amber (Eocene)

Genus *Pristapenesia* Brues

†*P*. *primaeva* Brues Baltic & Rovno amber (Eocene)

†*P*. *inopinata* (Prentice & Poinar) Dominican amber (Miocene)

*P*. *asiatica* Azevedo *et al*. China, Thailand

*P*. *stricta* (Azevedo) Brazil

FIGURE CAPTIONS

**Figures 1–2.** Photomicrographs of holotype (AMNH DR-924-H-211) female of *Clystopsenella mirabilis*, new species, in Early Miocene amber from the Dominican Republic. **1.** Lateral habitus. **2.** Dorsal habitus.

**Figures 3–4.** Photomicrographs of holotype (AMNH DR-924-H-211) female of *Clystopsenella mirabilis*, new species. **3.** Facial view. **4.** Detail of apical forewing venation.

**Figure 5.** Lateral habitus of female of *Clystopsenella longiventris* Kieffer from the Orange Walk District of northwestern Belize (as reported by Engel, 2005).

**Figure 6.** Phylogeny of Scolebythidae (after Engel *et al*., 2013), with fossil deposits indicated and the distribution of modern species summarized near the terminus of each branch. Abbreviations for deposits are: DR, Dominican Republic amber; BA, Baltic amber (includes also the records from the generally contemporaneous Rovno amber); PA, Parisian amber; CA, Canadian amber; NJ, New Jersey amber; SP, Spanish amber; LB, both Lebanese amber deposits (include also the Aptian Jordanian record of *Zapenesia* Engel & Grimaldi); LN, Liaoning, China.







