

A New Bethylid Wasp in Lebanese Early Cretaceous Amber (Hymenoptera: Chrysidoidea), with Comments on other Mesozoic Taxa

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ABSTRACT

A new genus and species of bethylid wasps is described and figured from a female preserved in Early Cretaceous (Barremian) amber from Lebanon. *Holopsenella primotica*, new genus and species, is distinguished from other bethylids and segregated into a new subfamily, Holopsenellinae, along with *Cretabythus sibiricus* Evans in Late Cretaceous (Santonian) Taimyrian amber. Holopsenellines are perhaps basal within the family, representing a stem group to other Bethylidae, and, if so, those features shared with the coeval Lancepyrinae suggest a basal position for that lineage as well. In addition, *Lancepyris alavaensis* Ortega-Blanco and Engel in Early Cretaceous (Albian) amber from northern Spain is considered generically distinct from the type species of the genus, *L. opertus* Azevedo and Azar in Lebanese amber, and is transferred to the new genus, *Zophepyris*, resulting in the new combination, *Zophepyris alavaensis* (Ortega-Blanco and Engel). The genus *Archaeopyris* Evans, currently considered as incertae sedis within the family, is transferred to Lancepyrinae mostly because it shares the same groundplan traits with *Lancepyris*.

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INTRODUCTION

The chrysidoid wasp family Bethyridae is the most diverse lineage of the basal aculeate superfamily, with more than 2200 species (Gauld and Bolton, 1988; Grimaldi and Engel, 2005; Azevedo, 2006; Aguiar et al., 2013). The group is widespread but with its highest diversity pantropically, and members primarily prey on the larvae of Lepidoptera and Coleoptera, although at times victimizing Hymenoptera (Azevedo, 2006). The classification of the family has undergone significant revision during recent years and based on extensive cladistic analyses of the living diversity (e.g., Lanes and Azevedo, 2008; Alencar and Azevedo, 2013). The result of these investigations have been the elimination of past tribal classifications and the reduction of the number of subfamilies to Bethylinae, Scleroderminae, Pristocerinae, Mesitiinae, and Epyrinae. Azevedo and Azar (2012) added to this system a fifth subfamily, Lancepyrinae, based on an extinct genus in Lebanese amber. Interestingly, the Lancepyrinae were not basal in the preliminary phylogenetic analysis, suggesting that bethyrids were already well established by the Barremian (Azevedo and Azar, 2012).

While numerous bethyrid species are known from Paleogene and Neogene deposits (e.g., Azevedo and Azar, 2012; Barbosa et al., 2013), there are comparatively few published species from the Mesozoic although abundant unpublished material is known from New Jersey (Engel, unpublished data) and French ambers (Perrichot and Nel, 2008). Eleven species assigned to Bethyridae have been described from the Cretaceous, and in fossiliferous resins from the Barremian of Lebanon (Azevedo and Azar, 2012), Albian of Spain (Ortega-Blanco and Engel, 2013), Albian-Cenomanian of Myanmar (Cockerell, 1917a, 1917b, 1920), Santonian of Taimyria (Evans, 1973), and Campanian of Canada (McKellar and Engel, 2012, 2014). A 12th species, *Cretabythus sibiricus* Evans in Taimyrian amber, was assigned with hesitation to Scolebythidae (Evans, 1973: refer to Engel and Grimaldi, 2007, and Engel et al., 2013a, for discussion of Cretaceous scolebythids), but Carpenter (1986) considered the placement suspect and Rasnitsyn (1988) emphasized further details that indicate it to be a primitive bethyrid, and we tend to concur with this conclusion (see below). All but three of the Cretaceous species are classified in extinct genera, the exceptions being three in Burmese amber and assigned by Cockerell (1917b, 1920) to *Epyris* Westwood, *Sclerodermus* Latreille, and *Apeneisia* Westwood. It is likely that Cockerell's species are misplaced with respect to modern concepts of these genera and the types should be restudied before the records are considered definitive for the antiquity of their respective genera.

Here we describe a new Early Cretaceous bethyrid in Barremian amber from Lebanon (fig. 1). The new species exhibits a number of features similar to the previously described *Lancepyris* Azevedo and Azar, such as the closed marginal cell that tapers apically to an acute point, owing to an apically straight Rs; Rs+M and Cu parallel to each other as well as the posterior wing margin; the straight 1Rs/1M; presence of C; evenly narrow costal cell; straight anterior wing margin; distinct notauli; gently and evenly concave pronotal posterior margin; metasoma longer than the mesosoma; absence of dorsal posterolateral spines or tubercles on propodeum; and presence of ocelli; most of which are assuredly plesiomorphic for the family. The genus, however, possesses some prominent and important features, such as the more complete wing

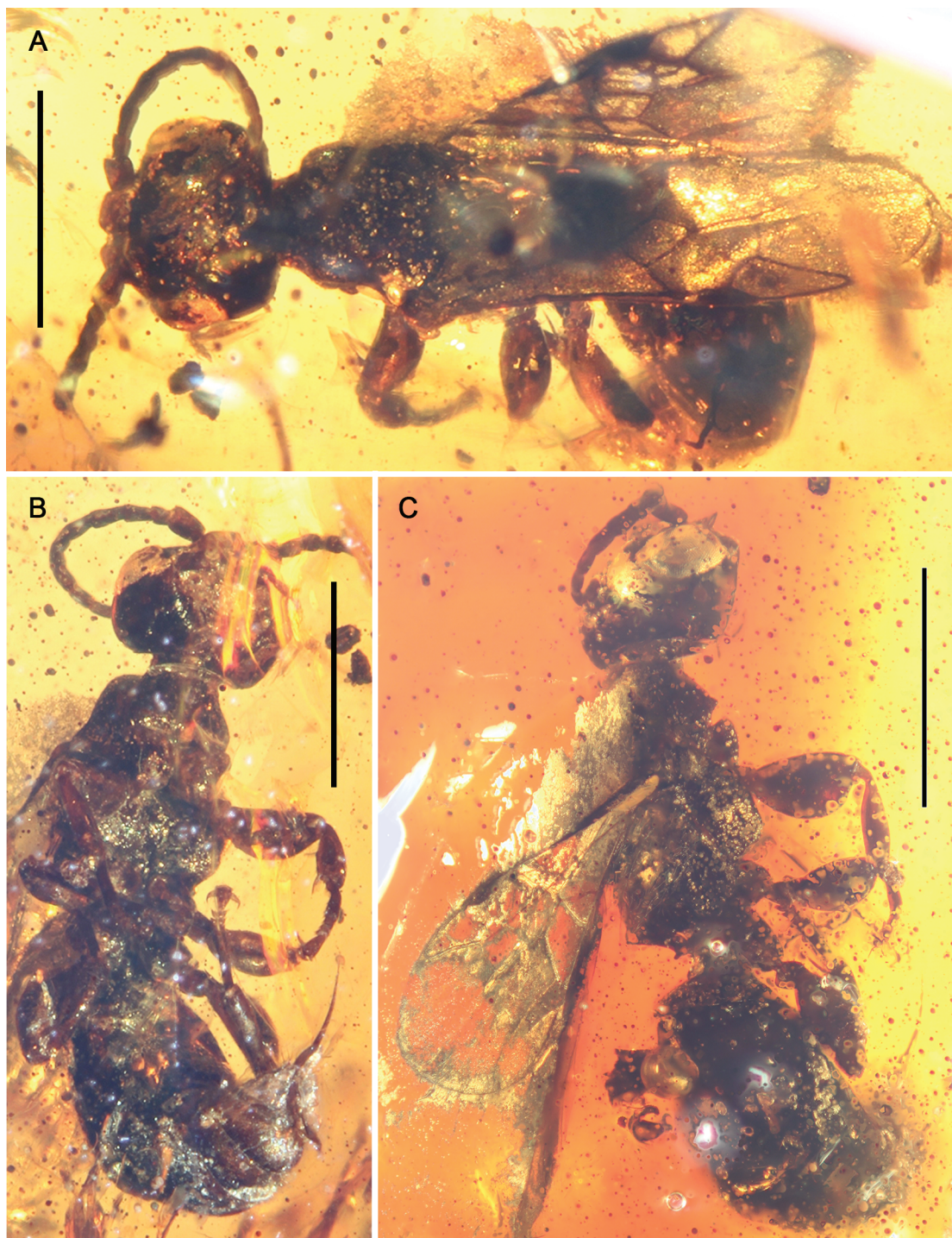


FIGURE 1. Microphotographs of the holotype female of *Holopsenella primotica*, new genus and species (AMNH L-924), in Lebanese Early Cretaceous amber (scale bars = 1 mm). **A.** Dorsal view. **B.** Ventral view. **C.** Lateral view.

venation with closed submarginal, discoidal, and subdiscoidal cells (likely plesiomorphies), the presence of only 12 antennal articles (an apomorphy), transverse pronotal disc (a plesiomorphy), and more prominently swollen femora (a plesiomorphy), which permit us to segregate it into a separate subfamily. In addition, we provide comments on two other Cretaceous bethylids, refining their placements.

MATERIAL AND METHODS

The new Lebanese specimen is preserved in a small, triangular piece of largely transparent yellow to yellowish-orange amber. The piece was trimmed and polished, then embedded in clear epoxy for stability and further preparation (following the method of Nascimbene and Silverstein, 2000). The wasp inclusion is situated near the narrower end of the piece and to one of the polished sides, with comparatively clear dorsal, right lateral, and ventral views. The left side of the wasp cannot be viewed owing to the fractured and irregular surface of the amber piece (this side could not be polished further without damage), and posteriorly by abundant internal fractures within the piece. There is some particulate debris in the piece and on the wings, as well as some internal fractures that reflect light in such a way as to obscure some structures, but otherwise most characters can be observed without difficulty. The specimen is situated with its legs and metasoma beneath and somewhat curled in, but not such that they are obscured or the venter blocked. Given the prognathy of the head, the mouthparts can be observed relatively well in ventral view, although some reflective areas make particular angles challenging to discern.

The specimen was studied with an Olympus SZX-12 stereomicroscope and a BX-41 compound microscope using both transmitted and reflected light. Photomicrographs were taken with a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, while line illustrations were prepared with the aid of a camera lucida attached to the aforementioned stereomicroscope. Morphological terminology and descriptions follow those generally used elsewhere in bethylid studies (e.g., Azevedo and Azar, 2012; Alencar and Azevedo, 2013; Ortega-Blanco and Engel, 2013; McKellar and Engel, 2014). The descriptions are provided in the context of providing fundamental character data for understanding biodiversity patterns and ultimately permitting the development and testing of evolutionary hypotheses (e.g., Grimaldi and Engel, 2007).

SYSTEMATIC PALEONTOLOGY

Family Bethylidae Haliday

Holopsenellinae, new subfamily

TYPE GENUS: *Holopsenella*, new genus.

DIAGNOSIS: Small wasps, less than 5 mm in length (ca. 3.87 mm in *Holopsenella*, ca. 2.5 mm in *Cretabythus* Evans). Head prognathous; frons without longitudinal carina or polished line; antenna with 12 (female) or 13 (male) articles (*Holopsenella* known from a female with 12, *Cretabythus* known from a male with 13—whether antennae are sexually dimorphic in the

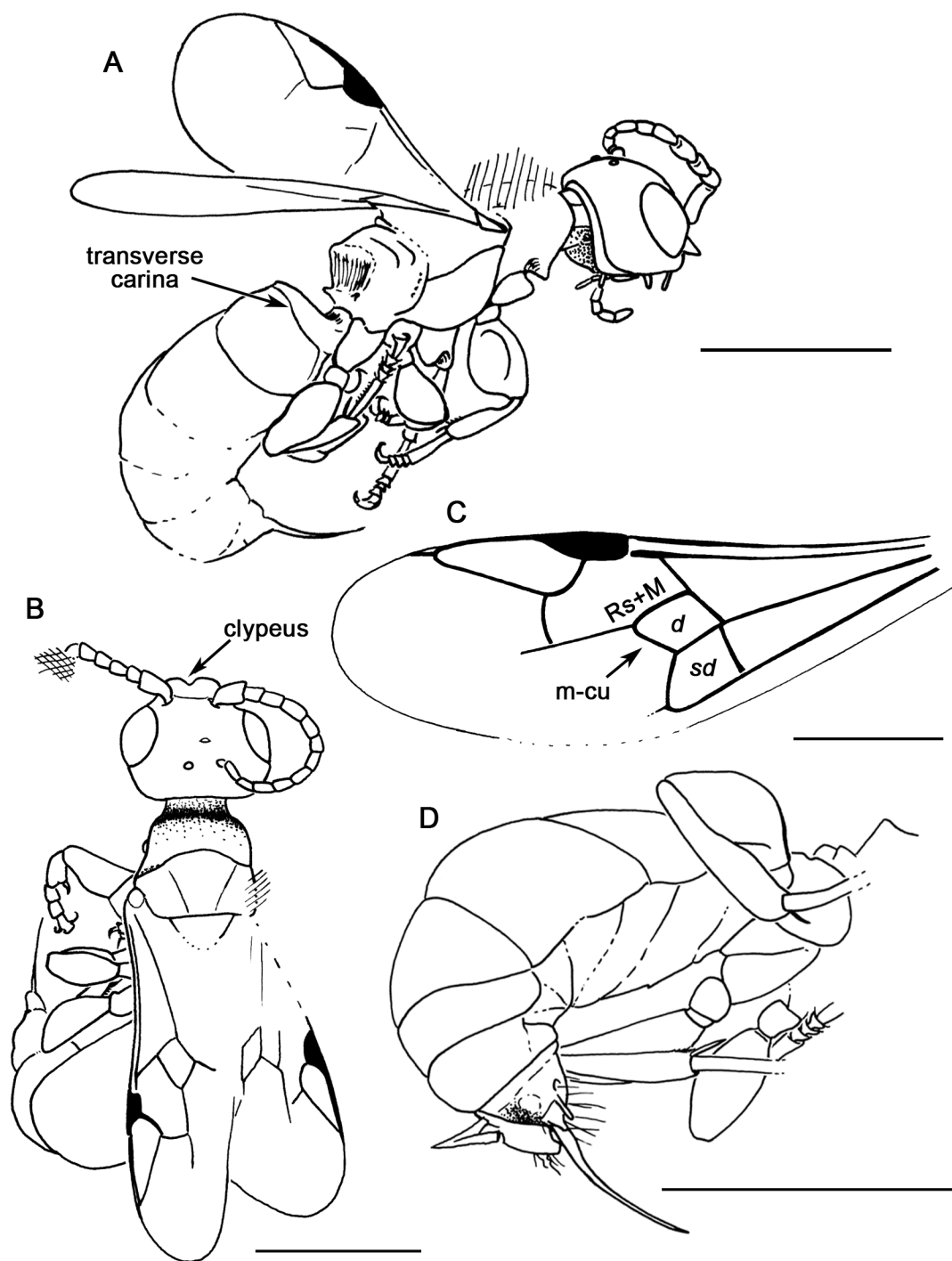


FIGURE 2. Holotype female of *Holopsenella primitica*, new genus and species (AMNH L-924), in Lebanese Early Cretaceous amber (scale bars A, B, D = 1 mm; C = 0.5 mm). A. Lateral view. B. Dorsal view. C. Forewing (*d* = discoidal cell; *sd* = subdiscoidal cell). D. Lateral, ventral-oblique view of metasoma.

group remains to be discovered); compound eyes well developed; ocelli present; mandibles short and thick; maxillary palpus with six palpomeres; labial palpus with four palpomeres (known only in *Holopsenella*). Pronotal disc transverse, not elongate, with lateral borders slightly converging anteriorly, posterior margin of pronotal disc gently and evenly concave; prosternum small, largely obscured by tightly adjoined propleura and procoxae, propleura not visible in dorsal aspect; mesoscutum with notauli distinctly impressed, converging posteriorly but not meeting medially; tegula present; mesoscutellum prominent, surface flat, and narrowly rounded posteriorly, with mesoscutellar groove present across anterior two-thirds of width; metanotum distinctly separating mesoscutellar posterior border from base of propodeum; propodeum not constricted anteriorly; propodeal disc with dorsal posterolateral corners prominent and strongly angulate, but without spines or tubercles. Macropterous; forewing with comparatively complete venation, with tubular and pigmented veins defining seven closed cells (costal, medial, cubital, marginal, submarginal, discoidal, and subdiscoidal), with anterior wing margin straight (not concave/discontinuous as in some other lineages); C present with costal cell narrow and of even width across its length; 1Rs/1M (i.e., vein formed by meeting of individual first abscissae of Rs and M, and generally orthogonal to long axis of wing, rather than Rs+M which is longitudinal vein formed by merger of 1Rs and 1M) straight (not obtusely angled as in Bethylinae); Rs+M tubular, pigmented, straight, parallel to Cu and posterior wing margin (in most other bethylids Rs+M is often absent or if present, then is often not tubular and/or short and frequently obliquely angled relative to posterior wing margin); apical portion of Rs straight, apically closing marginal cell (as in Lancepyrinae; not with Rs arched and forming apically broadened, short to long marginal cell as in some Bethylinae where closed marginal cell is present); marginal cell with acutely rounded apex at anterior wing margin (as in Lancepyrinae), tapering evenly over its length from broadest point near Rs/r-rs juncture; discoidal cell somewhat quadrate; subdiscoidal cell slightly wider than discoidal cell; cu-a straight, about as long as 1M. Hind wing without closed cells. Femora incrassate; pretarsal claws gently arched (not strongly angled basally as in Bethylinae), with minute tooth. Metasoma longer than mesosoma, without constriction between first and second segments; second metasomal tergum slightly larger than third tergum.

INCLUDED GENERA: Aside from the type genus we tentatively include the Late Cretaceous genus *Cretabythus* Evans. The latter genus had been considered a possible scolebythid by Evans (1973), but as discussed above, this placement was subsequently questioned. Carpenter (1986) and Rasnitsyn (1988) discussed further characters that they considered clearly indicative of a bethylid. *Cretabythus sibiricus* is in need of further revision, but we believe for the moment its similarities with *Holopsenella* are sufficient to place it here until such time as new information is available.

COMMENTS: The subfamily shares with Lancepyrinae the form of the closed marginal cell, with the distal part of Rs almost straight, and Rs+M, Cu, and the posterior wing margin parallel to one another. However, in Holopsenellinae the discoidal and subdiscoidal cells are closed as well as the submarginal cell, and collectively more reminiscent of the wings in Bethylinae, although without the prominently angled 1Rs/1M, posteriorly directed Rs+M, and apically arched Rs. The more complete venation is assuredly a plesiomorphic feature relative to Lancepyrinae, Bethylinae, and all other Bethylidae.

Holopsenella, new genus

TYPE SPECIES: *Holopsenella primotica*, new species.

DIAGNOSIS: **Female.** Head broad, posterior margin in dorsal view straight, with rounded posterolateral corners (figs. 1, 2); vertex flat; occipital carina present (fig. 2A), weak; space between and anterior to antennal toruli depressed; antennal flagellum with 10 flagellomeres; scape distinctly thickened compared to pedicel and flagellum; compound eye circular, separated from posterior head margin in dorsal view by half of eye length; ocelli present (fig. 2B); clypeus projecting anteriorly (fig. 2B), surface comparatively flat except weak longitudinal medial ridge, apical margin with prominent but shallow medial emargination (fig. 2B); mandible short and thick, with at least two sharp apical teeth (likely three, as edge of a third seems partially apparent on left mandible), mandibles overlapping in slightly less than their apical halves, mandibles obscured by projection of clypeus in dorsal view; maxillary palpus elongate; labial palpus short. Forewing with marginal cell closed (fig. 2C), distal part of Rs almost straight resulting in evenly tapering marginal cell across its length, apex of cell acutely rounded; discoidal cell somewhat quadrate; cu-a straight; pterostigma longer than wide, with r-rs arising near pterostigmal midlength, r-rs long and arching apically to meet Rs; m-cu straight, nearly parallel with 1M (fig. 2C), and about as long as 1Cu; subdiscoidal cell slightly wider than discoidal cell, broader posteriorly than anteriorly. Tibial spur formula 1-2-2; basitarsi longest tarsomeres, tarsomeres II–IV distinctly shorter than basitarsi and tarsomeres V. Metasoma not petiolate; first metasomal tergum with weak transverse carina running across angle between anterior-facing and dorsal-facing surfaces (fig. 2A), then curving laterally along lateral disc for short distance.

Male. Unknown.

ETYMOLOGY: The new genus-group name is a combination of the Greek terms *holos*, meaning, “complete,” and the diminutive form of *psen*, meaning “wasp” (the Latinized diminutive *psenella* serves as the stem for two of the most primitive bethyline genera exhibiting the most complete venation found in the family—*Lytopsenella* Kieffer and *Eupsenella* Westwood). The name refers to the comparatively complete wing venation relative to other lineages of Bethyliidae. The gender of the name is feminine.

Holopsenella primotica, new species

Figures 1–2

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: **Female.** Body robust, length (as preserved) 3.87 mm; integument dark brown to black (fig. 1), with sparse, short pubescence. Head broad (figs. 1A, 2B), width across compound eyes 0.88 mm, length (to apex of clypeus) 0.75 mm; integument impunctate and smooth; genae broad; frons slightly convex in profile; depression present between and anterior to antennal toruli and bordering base of projected clypeus; clypeus short, surface smooth, with low mediolongitudinal ridge, otherwise surface flat, sparse, short, erect setae along margin; compound eyes circular, well separated from posterior border of head dorsally and laterally; ocelli present, small; antennal toruli separated by more than one torular diameter, upper portion of torulus slightly bulging; antenna

with 12 articles (i.e., 10 flagellomeres); scape short and robust, ventral surface slightly arched, ca. 2 times as long as wide; pedicel slightly longer than wide, shorter than basal flagellomeres; flagellomeres cylindrical, first flagellomere shorter than second flagellomere, remaining flagellomeres slightly and progressively shorter to apicalmost flagellomere, which is longer and slightly tapered apically; vertex flat, with posterior border of head straight in dorsal view, with rounded corners. Pronotum with prominent disc separated from collar (fig. 1A, 2B), discal surface apparently imbricate, lateral surfaces slightly concave; discal surface transverse with lateral borders only slightly converging anteriorly, posterior margin broadly concave; mesoscutum wider than long, integument apparently imbricate and impunctate, notauli well impressed; parapsidal lines not evident; mesoscutellum semioval, wider than long, posterior border narrowly rounded, with weak mesoscutellar groove spanning approximately medial two-thirds of anterior margin; propleuron with lateral margin evenly convex in ventral view, inner borders closely adjoined; prosternum small, largely obscured; metanotum distinct dorsally, separating mesoscutellum and propodeum, sculpture not evident; propodeum about as wide as long, with dorsal posterolateral corners acute, angulate, not projecting as distinct spines or tubercles, posterior border carinate, surface irregularly roughened. Legs with sparse, minute setae; femora distinctly swollen, particularly profemur; tibiae elongate; basitarsi slender, longer than wide, longest tarsomeres; mediotarsomeres short, nearly transverse, around 2 times wider than long; apicalmost tarsomere slightly longer than wide or as wide as long; pretarsal claws long, gently curved apically, with minute ventral tooth in apical third; arolium prominent. Forewing with exceedingly sparse microtrichia; bullae present between pterostigma and C and Sc+R; pterostigma about 3 times longer than wide, faintly convex inside marginal cell, with apex tapering; marginal cell broad basally, with long and apically curved r-rs (fig. 2C); R extending slightly beyond apex of Rs along anterior wing margin; M extending only slightly beyond submarginal cell posterior apex; Cu not reaching wing margin. Metasoma arising low on propodeum, not petiolate, about as long as remainder of body, integument impunctate, smooth to faintly imbricate; first tergum with prominent vertical anterior-facing surface, with weak transverse carina running along ridge with dorsal-facing surface (fig. 2A); last metasomal tergum with prominent, elongate setae; sting exposed, long and slightly curved (fig. 2D).

Male. Unknown.

HOLOTYPE: Female, AMNH L-924 (fig. 1); no. 12, Early Cretaceous (Barremian), northern Lebanon, Bchare Mountain, 2300 m (Antoni Estephan collection); deposited in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet is the New Latin term *primoticus*, meaning, “pertaining to happening early,” and as a reference to both the antiquity and putatively primitive nature of the present species.

Subfamily Lancepyrinae Azevedo and Azar

Zophepyris, new genus

TYPE SPECIES: *Lancepyris alavaensis* Ortega-Blanco and Engel, 2013.

DIAGNOSIS: Female. Head prognathous; frons without longitudinal carina or polished line; space between antennal toruli depressed (similar to *Lancepyris* Azevedo and Azar); antennal flagellum with 11 flagellomeres (similar to *Lancepyris*); scape distinctly thickened compared to

pedicel and flagellum; compound eye well developed, circular, separated from posterior head margin in dorsal view by less than half of compound eye length; ocelli present (similar to *Lancepyris*); clypeus transverse, flat; mandible short and thick, with three apical teeth (similar to *Lancepyris*). Pronotal disc transverse trapezoidal (similar to *Lancepyris*), posterior margin of pronotal disc gently and evenly concave (similar to *Lancepyris*); mesoscutum with notauli distinctly impressed (similar to *Lancepyris*), slightly converging posteriorly, not meeting medially; tegula present (similar to *Lancepyris*); mesoscutellum short, narrowly rounded, mesoscutellar groove not evident (but dorsal view of specimen is darkened and difficult to observe); metanotum distinctly separating mesoscutellar posterior border from base of propodeum (similar to *Lancepyris*); propodeum not constricted anteriorly (similar to *Lancepyris*); propodeal disc with dorsal posterolateral corners rounded, without spines or tubercles (similar to *Lancepyris*). Macropterous; forewing with comparatively tubular and pigmented veins defining four closed cells (costal, medial, cubital, and marginal) (similar to *Lancepyris*), with anterior wing margin straight (similar to *Lancepyris*); C present with costal cell narrow and of even width across length (similar to *Lancepyris*); 1Rs/1M straight; Rs+M absent (or spectral?); marginal cell closed (similar to *Lancepyris*), distal part of Rs almost straight, resulting in evenly tapering marginal cell across its length (similar to *Lancepyris*), apex of cell pointed on wing margin, cell comparatively narrow and elongate, length 4.3 times longer than width; pterostigma longer than wide (similar to *Lancepyris*), with r-rs arising in apical half of pterostigmal length; 1Cu present, tubular, pigmented, parallel with posterior wing margin (similar to *Lancepyris*); cu-a straight. Tibial spur formula 1-2-2 (similar to *Lancepyris*); basitarsi longest tarsomere, as long as remaining tarsomeres combined; pretarsal claws gently arched (similar to *Lancepyris*). Metasoma slightly longer than mesosoma, not petiolate (similar to *Lancepyris*). **Male.** Unknown.

ETYMOLOGY: The new genus-group name is a combination of the Greek term *zophos*, meaning, “gloomy” or “dusky” and used to refer to the nether world, and the generic name *Epyris*, commonly used as a stem for many bethylid genera. The gender of the name is masculine.

COMMENTS: *Zophepyris* differ from *Lancepyris* in the more rounded compound eye (subelliptical in *Lancepyris opertus* Azevedo and Azar), the more narrowly elongate marginal cell (broader in *L. opertus*), Rs+M absent (Rs+M present in *L. opertus*), M+Cu not aligned with 1Cu, slightly offset (aligned in *L. opertus*), and cu-a distad 1M (confluent in *L. opertus*). The absence of Rs+M is a noteworthy feature that is more epyrinelike, although it could not be confirmed whether the vein is present spectrally owing to the preservation and darkness of the Spanish amber piece in which the holotype is included.

INCLUDED SPECIES: Presently the genus includes only the type species, *Zophepyris ala-vaensis* (Ortega-Blanco and Engel), new combination.

Genus *Archaeopyris* Evans

Archaeopyris Evans, 1973: 174.

TYPE SPECIES: *Archaeopyris minutus* Evans, 1973, by original designation.

DIAGNOSIS: Male. Antenna with 11 flagellomeres; compound eye large and circular; mandible with four sharp apical teeth; pronotal disc moderately short, depressed anteriorly; meso-

scutum somewhat long, with notauli, and basal mesoscutellar pit or groove not visible; propodeal disc short; propodeal declivity almost vertical; legs not spinose; pretarsal claws weakly dentate; macropterous; forewing with cell 2R1 open and almost lanceolate; prestigma absent; pterostigma rectangular (for a full description see Evans, 1973). **Female.** Unknown.

COMMENTS: According to Evans (1973), *Archaeopyris* could be considered a highly generalized bethylid, and the genus combines features usually recognized in several subfamilies of Bethylinae. The general form is similar to *Epyris*, but the venation is suggestive of some Pristocerinae. However, the pattern of the third section of the forewing Rs suggests a similarity with some Bethylinae, e.g., *Eupsenella* Westwood (see Ramos and Azevedo 2012: 72–76, figs. 93–137). On the other hand, this peculiarity also can be found in Lancepyrinae (Azevedo and Azar, 2012). *Archaeopyris* also exhibit other characters of Lancepyrinae, such as the large compound eyes, the small ocelli, the mandibles with three or more sharp apical teeth, the convex crest of the vertex, the absence of a prestigma, the rectangular pterostigma, the open and almost lanceolate marginal cell, the presence of a long Rs+M, and the sessile metasoma (Azevedo and Azar, 2012: 212, figs. 1–4). Considering these traits, we are convinced that *Archaeopyris* are better placed within Lancepyrinae and we accordingly transfer the genus to this subfamily.

INCLUDED SPECIES: Presently the genus includes only the type species, *Archaeopyris minutus* Evans, 1973, from Santonian-aged Taimyrian amber.

DISCUSSION

The diversity of Mesozoic bethylids has nearly doubled over the last three years, and expanded from described species restricted to two deposits—one from the Early Cretaceous (Albian-Cenomanian) and the other from the Late Cretaceous (Santonian)—to five, with most species from Early Cretaceous ambers. In Lebanese amber there are *L. opertus* and *H. primitica* (Azevedo and Azar, 2012; herein), in Spanish (Peñacerrada) amber there are *Zophepyris alavensis*, *Cretepyris martini* Ortega-Blanco and Engel, and *Liztor pilosus* Ortega-Blanco and Engel (Ortega-Blanco and Engel, 2013; herein), and in Burmese amber *Bethylitella cylindrella* Cockerell, *Apenesia electrophila* Cockerell, *Epyris atavellus* Cockerell, and *Sclerodermus quadridentatus* Cockerell (Cockerell, 1917a, 1917b, 1920: again, it should be noted that his species are in need of revision). From the Late Cretaceous there are *Archaeopyris minutus* Evans, *C. sibiricus*, and *Celonophamia taimyria* Evans in Taimyrian amber (Evans, 1973; Rasnitsyn, 1988), and *C. granama* McKellar and Engel in Canadian amber (McKellar and Engel, 2014). There are numerous specimens in New Jersey amber awaiting description that will expand greatly the Late Cretaceous diversity (M.S.E., unpublished data) and, in fact, the Mesozoic record of Chrysoidea generally has been neglected despite the discovery of many important taxa (e.g., Engel, 2003, 2005; Engel and Grimaldi, 2006; Brothers, 2011; Ortega-Blanco et al., 2011; Azevedo and Azar, 2012; Engel et al., 2013a; McKellar and Engel, 2014). Many of these genera likely represent stem groups to various subsets of bethylid diversity and an extensive cladistic examination of the relationships among the various Mesozoic genera and their extant counterparts would be fruitful once the Turonian New Jersey and Cenomanian French faunas are described. Such taxa have the potential to more fully elaborate our concept of basal bethylid relationships,

groundplan features of the Bethylidae, along with character and diversity changes across the Cretaceous. We have considered *Cretabythus* Evans as allied to *Holopsenella* and this seems likely given the available character information. Nonetheless, a critical revision of *Cretabythus* is warranted. The preservation of historical Taimyrian material is such that new material may be the only way to resolve many character state codings (M.S.E., personal obs.), although the application of techniques such as micro-CT scans may offer a way to circumvent these challenges (as has been done for other small amber inclusions, e.g., Perrichot et al., 2011; Chatzimanolis et al., 2013; Engel et al., 2011, 2013b). In addition to their varied phylogenetic and classificatory implications, it remains to be discovered what these enigmatic Mesozoic taxa can illuminate about the early biology and ecology of the family. While the putatively primitive subfamily Bethylinae principally victimize larval Lepidoptera, most other bethylids attack coleopterous prey and such an association is likely plesiomorphic for the family, with beetles suspected as hosts for the Cretaceous groups. Furthermore, the records of Cretaceous bethylids are our only direct source of information regarding patterns of diversification for the family across the biotic backdrop of the period, which among other things was a time when angiosperms appeared and rose to floristic dominance, ecologically dominant aculeates debuted, termite societies were diversifying, and weevils were poised to take the lead in coleopteran diversity (e.g., Grimaldi and Engel, 2005; Engel and Grimaldi, 2005; Ohl and Engel, 2007; Engel et al., 2009, 2016; Ware et al., 2010; Michez et al., 2012; Barden and Grimaldi, 2014, 2016; McKellar et al., 2013; Krishna et al., 2013; Peris et al., 2014).

We have considered Holopsenellinae as a putatively basal, perhaps even stem, subfamily within Bethylidae, and that their shared distinctive features with Lancepyrinae (e.g., the form of the marginal cell, etc.: see above) are symplesiomorphic for the family (although Lancepyrinae have more features in common with typical bethylids suggesting they would be closer to the crown). This would tend to suggest that future, more expanded analyses might recover lancepyrines in a more basal position relative to Bethylinae than has been recovered previously (Azevedo and Azar, 2012). Naturally, this hypothesis requires testing by future analyses and after the considerable Turonian diversity is documented. Another possibility is that the various and similar vein reductions observed in Falsiformicidae (M.S.E., personal obs.), an extinct relative of bethylids (Perrichot et al., 2014; M.S.E., personal obs.), are not independently derived, in which case Holopsenellinae and perhaps also Lancepyrinae would fall more basal to Falsiformicidae + Bethylidae. If this were the case, then it would be most prudent to reduce falsiformicids to a subfamily of Bethylidae rather than proliferate a number of small, extinct families collectively forming a grade to Bethylidae. That said, if these groups formed a grade to bethylids as well as Chrysididae, then the more practical and nomenclaturally stable solution would be the elevation of holopsenellines, retention of a family Falsiformicidae, and possible elevation of Lancepyrinae. In regard to the aforementioned vein reductions in Falsiformicidae, at least here the reductions are perhaps independent as similar patterns are widespread across Chryridoidea and clearly of independent derivation (e.g., Chrysididae, Dryinidae, Scolebythidae). Lastly, the Cretaceous genera *Liztor* Ortega-Blanco and Engel and *Cretepyris* Ortega-Blanco and Engel are presently difficult to classify and also require deeper consideration in a Hennigian framework. Although none can be confidently placed in Epyrinae (although in older

systems employing a polyphyletic concept of the subfamily they would fall best therein), they do have features reminiscent of lineages such as Epyrinae and Scleroderminae, or at least more derived than Lancepyrinae and Bethylinae. For now we prefer to consider *Liztor* and *Cretepyris* as incertae sedis in regard to subfamilial placement. Clearly any number of exciting avenues are open for future cladistic exploration among Mesozoic bethylids and bethylidlike taxa.

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