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Short communication

Molliberus albae gen. et sp. nov., the oldest Laurasian soldier beetle (Coleoptera: Cantharidae) from the Lower Cretaceous Spanish amber

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A B S T R A C T

A new soldier beetle (Coleoptera: Cantharidae), *Molliberus albae* gen. et sp. nov., is described and illustrated from the El Soplao Lower Cretaceous (lower Albian) amber deposit in northern Spain. This is the first fossil species in the family to be described from the Spanish amber and the oldest representative in Europe. The new species shows affinities with the Late Cretaceous (early Cenomanian) species from Myanmar, and the fossil is compared with the other Cretaceous fossil species. The elongate prognathous head is a diagnostic character of *Molliberus albae* gen. et sp. nov., from which it may be inferred that this species fed on pollen or nectar.

1. Introduction

The family Cantharidae is made up of approximately 5000 species present on all inhabited continents of the world (Ramsdale, 2010). They are more abundant in forested areas but can also be found on riverbanks and in more xeric habitats. Members of this family spend most of their life in the larval stage, preferably in humid soil, litter, or other plant waste, feeding on fluids or plant material (Ramsdale, 2010). Adults only live for a few weeks, are very active and inhabit a wide variety of plants. They can feed on other invertebrates that inhabit the foliage but also on nectar and pollen.

Although all recent molecular phylogenetic studies support the monophyly of Cantharidae (Bocáková et al., 2007; Kundrata and Bocák, 2010; Kundrata et al., 2014; McKenna et al., 2015; Zhang et al., 2018), Hsiao et al. (2017) considered such results inconclusive because of the insufficient number of Cantharidae included in studies focussing on other elateroid groups. A brief review of the relationship between Cantharidae and related families is given in Hsiao et al. (2017), indicating different results depending on the authors.

This family is very common in Cenozoic amber (Kazantsev, 2013; Alekseev, 2017; Fanti, 2017). However, only six species have been described from the Cretaceous, all from the Myanmar amber, early Cenomanian in age, in the Hukawng Valley (Kachin State, Myanmar) (Table 1). Undescribed cantharids, at indeterminate level, has been reported in compression deposits from the upper Aptian Koonwarra fossil bed (Australia) (Jell and Duncan, 1986; Jell, 2004; Nicholson, 2012), in amber inclusions from the Lebanese amber, Barremian in age (Kirejtshuk and Azar, 2013), and from the Myanmar amber (Rasnitsyn and Ross, 2000; Poinar et al., 2007; Binder, 2008; Boucot and Poinar, 2010; Ross et al., 2010; Poinar and Fanti, 2016).

Here, we describe a new genus and species of Cantharidae based on a specimen preserved in the Lower Cretaceous Spanish amber. *Molliberus albae* gen. et sp. nov. is the oldest known confirmed record of the family on the European continent.

2. Geological setting

Spanish Cretaceous amber is composed of numerous amber-bearing deposits, most of which are distributed in the eastern to the

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Table 1
Checklist of fossil cantharids known from the Cretaceous, modified after Peris (2016).

Origin	Age	Species	References
Myanmar amber	99 Mya	*Ornatomalthinus elvirae* Poinar et Fanti, 2016	Poinar and Fanti, 2016
Myanmar amber	99 Mya	*Archaeomalthodes rosetta* Hsiao, Ślipiński et Pang, 2017	Hsiao et al., 2017
Myanmar amber	99 Mya	*Myamalycocerus vitalii* Fanti et Ellenberger, 2017	Fanti and Ellenberger, 2017
Myanmar amber	99 Mya	*Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger, 2018	Fanti et al., 2018
Myanmar amber	99 Mya	*Sanaungulus curtipennis* Fanti, Damgaard et Ellenberger, 2018	Fanti et al., 2018
Myanmar amber	99 Mya	*Sanaungulus ghitaenoerbyae* Fanti, Damgaard et Ellenberger, 2018	Fanti et al., 2018
Spanish amber	110 Mya	*Molliberus albae* sp. nov.	This work

northern part of the Iberian Peninsula, describing a narrow arc. Of these, three deposits stand out because of the numerous bioinclusions that have been described embedded in their amber (Peñalver and Delclòs, 2010). The El Soplao deposit is near the village of Rábago, in the autonomous region of Cantabria, northern Spain (Fig. 1). This amber is early Albian in age and is found in a heterolithic sandstone-siltstone and carbonaceous mudstone unit related to broadly coastal delta-estuarine environments from the Las Peñosas Formation, in the western Basque-Cantabrian Basin (Najarro et al., 2009). Besides abundant amber pieces, gymnosperm plant cuticles, fusainised wood and diverse palynomorphs, some marine or brackish-water invertebrates, such as serpulids, bryozoans, gastropods and bivalves, have also been found in the sediment, indicating a slight marine influence on the depositional environment (Najarro et al., 2010). Illustrations and more detailed information about the location, geology and stratigraphic profile of the El Soplao amber deposit can be found in Najarro et al. (2009) and Pérez-de la Fuente (2012).

In addition to Arachnida (Acari and Araneae) and Crustacea (Order Tanaidaceae), 14 recognised Hexapoda orders have been found, with 649 arthropod bioinclusions (Pérez-de la Fuente, 2012). Coleoptera is represented by 51 bioinclusions (Peris et al., 2016), of which five different families have already been studied: Staphylinidae Latreille, 1802, Nemonychidae Bedel, 1882, Caridae Thompson, 1863, Elmidae Curtis, 1830, and Cryptophagidae Kirby, 1826 (Peris, 2016). Previously only cited at family level or illustrated (Peris et al., 2013, 2016; Peris, 2015; Rasnitsyn et al., 2016; Fanti, 2017), the Cantharidae is the sixth different family of Coleoptera to be described from this amber deposit.

3. Material and methods

The amber with the soldier beetle inclusion was loaned by the Institutional Collection of the El Soplao amber deposit, housed in the laboratory of the El Soplao Cave (Celis-Rábago, Cantabria, Spain) under accession number CES-522. The piece of amber was cut and polished before being embedded in a transparent epoxy resin, following the procedure described in Nascimbene and Silverstein (2000).

The specimen was examined under a Leica MS5 stereomicroscope and an Olympus BX41 compound microscope. Drawings were made under incident and transmitted light with the aid of a camera lucida attached to the Leica MS5 stereomicroscope. Drawings were then inked and scanned into CorelDraw X8. Photographs were merged using the software Combine ZP and edited with Photoshop Elements 10 and CorelDraw X8.

We followed the family-group classification of Bouchard et al. (2011). The specific terminology for characters follows that of Lawrence et al. (1999, 2010).

This work is registered in Zoobank under urn:lsid:zoobank.org:pub:3F024B92-AF57-4870-82AD-19EF76D0EA8A.

4. Systematic palaeontology

Family Cantharidae Imhoff, 1856 (1815)

Subfamily Cantharinae Imhoff, 1856 (1815)
Tribe Cantharini Imhoff, 1856 (1815)

Molliberus gen. nov.
Type species: *Molliberus albae* sp. nov. The genus is at present monotypic.

Derivation of the name. The generic name *Molliberus* is a combination of the Latin *mollis* = soft (in reference to the less sclerified integuments that characterize the family) and *iberus* (Iberia) = Iberian Peninsula (in reference to the geographic location of the amber deposit). The gender is masculine.
Diagnosis. Head elongated anteriorly in a rostrum, not constricted behind the eyes; antennae filiform, sparsely covered by short setae, antennae reaching the second half of the elytra; anterior edge of pronotum expanded, covering part of the head; elytra elongated covering the last abdominal segments; elytral surface striate with rows of reticulate punctures; legs long; two spines in pro- and mesotibiae, apical margin of metatibia hidden; third tarsomeres apically straight, not bilobed as fourth tarsomeres, claws simple, without denticle at base.

Molliberus albae sp. nov.
(Fig. 2)

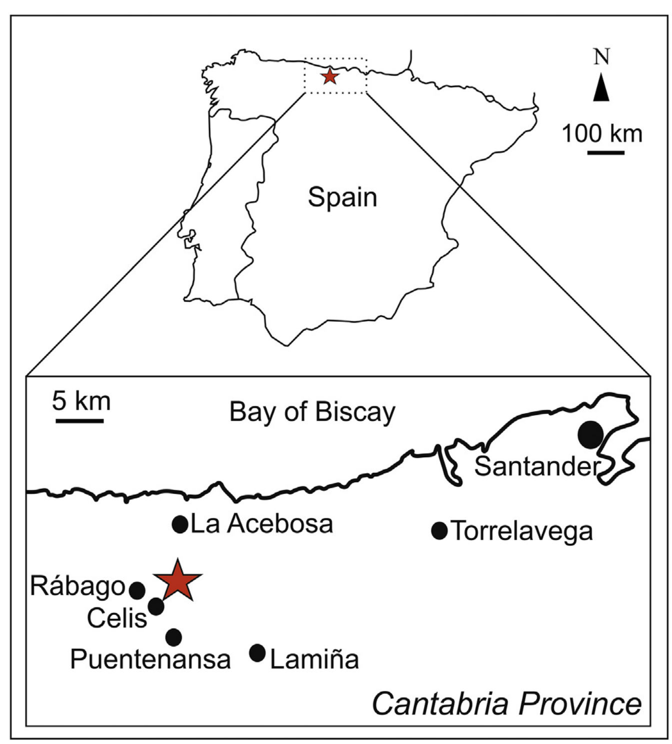

Fig. 1. Location of the El Soplao amber deposit (Celis-Rábago, Cantabria Province, Spain) marked with a star.

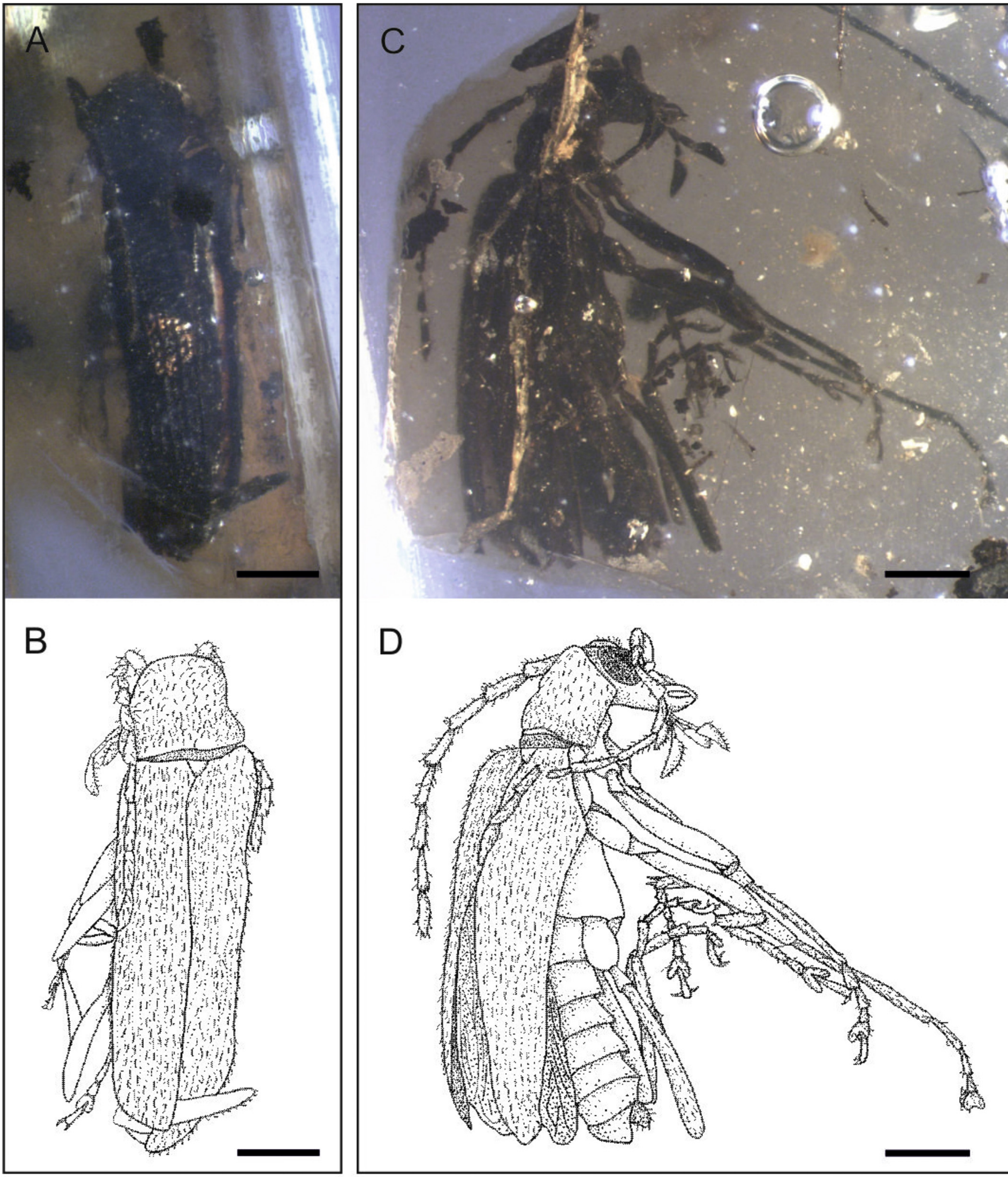

Fig. 2. *Molliberus albae* Peris et Fanti gen. et sp. nov. in Spanish amber. Holotype CES-522 (Bars = 500 μm). A. Photograph of general habitus, dorsal; B. Illustration of general habitus, dorsal; C. Photograph of general habitus, lateroventral; D. Illustration of general habitus, lateroventral.

Derivation of the name. The specific epithet *albae* is derived from the name of the first author's daughter, Alba Peris Ramírez. The name of this species is registered in ZooBank under urn:lsid:zoobank.org:act:A4450937-DF2C-452B-8B5D-172052829E64.
Holotype. CES-522; El Soplao deposit, lower Albian (Najarro et al., 2009, 2010), in the municipality of Celis (Cantabria, Spain). The specimen is an adult female, found in syninclusion with botanical fragments, wood remains and air bubbles. The piece is housed in the Institutional Collection of specimens from the El Soplao amber outcrop, located in the laboratory of the El Soplao Cave (Celis-Rábago, Cantabria, Spain).
Diagnosis. See generic diagnosis.
Description. Adult female, winged, entirely dark brown, body surface covered with inconspicuous, dense, short, depressed pubescence (Fig. 2A–B). Body length 2.95 mm measured in dorsal view although the head is declined; maximum body width 0.85 mm; ratio of body length to greatest body width 3.47. Head roundish, slightly narrower than the pronotum, anterior part elongated in a rostrum visible from above (Fig. 2C–D), not constricted behind the eyes. Eyes entire, large and covering a substantial part of the head. Mandibles without teeth. Maxillary palps 4-segmented with the first two segments being of similar width but the second segment 1.4 times longer, the third segment is equal in length to the first one but slightly wider apically, last segment securiform, as long as the three previous segments (Fig. 2C–D). Labium with ligula deeply bilobed; palps 3-segmented with the first two thin and elongated, similar in size, and the third segment securiform, 2.1 times longer than the previous segment. Mandibles elongate, curved, simple. Antennae 11-segmented, filiform, sparsely covered by short setae; antennal insertion exposed from above, widely separated; antennae reaching the second half of the elytra (Fig. 2C–D). Scape long and robust, pedicel 0.4 times the length of scape, globular in shape; third antennomere slightly thinner than scape and similar in width to the rest of antennomeres, 1.4 times longer than pedicel; fourth antennomere 3 times longer than previous one; fifth antennomere 0.8 times the length of previous antennomere, the rest of antennomeres equal in length; all antennomeres with tuft of setae at the apex.

Pronotum longer than wide, sub-rectangular, ratio of pronotal length to greatest pronotal width 0.88, anterior edge expanded, covering part of the head; sides straight up to mid length and slightly divergent posteriorly; posterior edge slightly sinuous (Fig. 2A–B). Scutellum small, triangular with roundish apex. Elytra long, complete, ratio of elytral length to greatest elytral width 2.62. Elytral base slightly wider than pronotum, parallel-sided, slightly narrowed after mid length, roundish at apex; surface striate with rows of reticulate punctures (Fig. 2A–B).

Procoxae conical, prominent, projecting well below prosternum; mesocoxae prominent. Legs long and slender; trochanters elongate oblique; femora and tibiae cylindrical; tibiae cylindrical, slender, equipped with numerous setae; two spines in pro- and mesotibiae, tarsi pentamerous, first tarsomere 1.5 times longer than the second, third tarsomere slightly shorter than second, fourth tarsomere ventrally bilobed, fifth tarsomere as long as the first one; claws simple without tooth at base (Fig. 2C–D). Abdomen with seven symmetrical ventrites and a setose pygidium.

Remarks. Five species of the subfamily Cantharinae and one of Malthininae Kiesenwetter, 1852, are known from the Mesozoic Myanmar amber deposits (Table 1); all the specimens have reticulate punctures on the elytra and a striate disk. *Molliberus albae* gen. et sp. nov. is similar to *Ornatomalthinus elvirae* Poinar et Fanti, 2016, but differs in having long elytra covering the last abdominal segments, an anteriorly expanded pronotum and different elytral punctuation (punctures are larger in *Ornatomalthinus*). It also differs from *Myamalycocerus vitalii* Fanti et Ellenberger, 2017, because this latter has a subquadrate pronotum with a deep central depression and two rounded thickenings close to the anterior edge. *Molliberus albae* gen. et sp. nov. has filiform antennae with many setae, thus differing from *Burmomiles* Fanti, Damgaard et Ellenberger, 2018, and *Sanaungulus* Fanti, Damgaard et Ellenberger, 2018, which have pectinate antennae. Finally, it differs from *Archaeomalthodes rosetta* Hsiao, Ślipiński et Pang, 2017 (in Malthininae), because the latter has fusiform terminal maxillary palpomere and a trapezoidal pronotum.

5. Discussion

The maxillary palpomeres different in length to the last securiform segment, the long elytra, the symmetrical last abdominal segments, the prothorax without lateral processes, the presence of tibial spurs and the fourth tarsomere undivided by a transverse split at basal part, clearly distinguish this new genus as belonging to the subfamily Cantharinae. In the new fossil species, the head is also slightly prolonged in a kind of rostrum, as can currently be found only in some Chauliognathinae LeConte, 1861, such as *Psilorrhynchus* Gemminger and Harold, 1869, and some species of *Chauliognathus* Hentz, 1830 and *Daiphron* Gorham, 1881 (Biffi, 2017), while it is circular and very rarely lengthened in Cantharinae (Brancucci, 1980). The third apically straight and not bilobed tarsomere is very rare in representatives of the tribe Cantharini and present in the extant genus *Rhagonycha* Eschscholtz, 1830, which differs from *Molliberus* gen. nov. in its bifid claws at apex rather than simple as in the latter. This peculiarity of the tarsomere is more frequent in the tribe Podabrini Gistel, 1856, whose genera are however characterised by the head being distinctly constricted behind the eyes and by the anteriorly truncated pronotum.

Many adult Cantharini are opportunistic predators of foliage-frequenting invertebrates but also feed on nectar; however, nothing is known about the feeding habits of many groups (Ramsdale, 2010). The elongate prognathous form of the head in a rostrum, a diagnostic character of *Molliberus albae* gen. et sp. nov., may be an adaptation to the adult diet, as in representatives of the genus *Chauliognathus*, which are purely phytophagous and feed on pollen and nectar (Miskimen, 1961; Rausher and Fowler, 1979; Ramsdale, 2010). Despite the importance of potential pollinators in the mid-Cretaceous, when angiosperms diversified from several nondiverse lineages to gain their current global domination (Benton, 2010), direct evidence of pollination is still scarce from the Cretaceous. The only three examples to have been described are from the Spanish amber, and in all cases the insects were gymnosperm pollinators (Peris et al., 2017). Although indirect evidence, morphological adaptations and behavioural inferences for pollen and nectar feeding are numerous in the Cretaceous fossil record (e.g. Ren et al., 2009; Myskowiak et al., 2016; Hsiao et al., 2017; Fanti and Ellenberger, 2017; Makarkin, 2017; the present study), the description of a reliable ecological relationship between insects and the first flowers is still lacking. The difficulty lies in the absence of angiosperm pollen grains together with the fossil insects that would make it possible to infer a direct association.

The new species shows similar characters to soldier beetles from the Myanmar amber deposit and confirms the affinities between these deposits previously found for other groups of Coleoptera, Diptera and Hymenoptera (Peris et al., 2014; Peris and Delclòs, 2015). Thus, the soldier beetle species known from Cretaceous deposits appear to have many characters that are not present or are rare in living species, such as the evident lycid mimic in *Ornatomalthinus*, the remarkable diversity of the antennae in *Burmomiles* and *Sanaungulus*, or the rostrum in *Molliberus* gen. nov. None of these peculiarities are commonly found, perhaps due to paleobiological or climatic and environmental affinities around 100 million years ago, which changed with the success of the angiosperms, displacing the previous vegetation as well as its associated fauna.

6. Conclusions

Molliberus albae gen. et sp. nov. is currently the oldest described species in the family after six different species were previously described from the lower Cenomanian amber of Myanmar. At present, cantharid origin and evolution have only been traced back to the Early Cretaceous (McKenna et al., 2015); nonetheless, it is conceivable that this date could be moved back, as has already been suggested in Fanti (2017), at least to the Jurassic. Extant members of this family are mainly predators, but some species are flower visitors, acting as pollinators. Consequently, their diversity around the mid-Cretaceous is of special interest for the study of plant-insect evolution. The rostrum observed in *Molliberus albae* gen. et sp. nov., a character not commonly found in the family, resembles the rostrum of the nectivory and pollinivory genus *Chauliognathus*. Such a long rostrum may be indicating a nectivory or pollinivory habit of the new species. The absence of pollen grains in the piece studied precludes a definitive conclusion for now, but we hope that future research on other fossil specimens in the family will provide more details about the implications of this family in the early evolution of the flowering plants.

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