



ELSEVIER

Contents lists available at ScienceDirect

## Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

### The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber



#### *Le plus ancien Coléoptère Elmidae dans l'ambre du Crétacé inférieur d'Espagne*

David Peris<sup>a,\*</sup>, Crystal A. Maier<sup>b</sup>, Alba Sánchez-García<sup>a</sup>, Xavier Delclòs<sup>a</sup>

<sup>a</sup> Departament d'Estratigrafia, Paleontologia i Geociències Marines, Institut de Recerca de la Biodiversitat (IRBio), Facultat de Geologia, Universitat de Barcelona, Martí i Franquès s/n, 08028 Barcelona, Spain

<sup>b</sup> Division of Entomology, Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

#### ARTICLE INFO

##### Article history:

Received 1<sup>st</sup> August 2014

Accepted after revision 22 November 2014

Available online 6 May 2015

Handled by Annalisa Ferretti

##### Keywords:

Polyphaga

Aquatic beetle

Fossil

El Soplao

Spain

Albian

##### Mots clés :

Polyphaga

Coléoptère aquatique

Fossile

El Soplao

Espagne

Albien

#### ABSTRACT

*Elmadulescens rugosus* Peris, Maier et Sánchez-García n. gen. n. sp. is described based on a single specimen from Spanish amber (El Soplao outcrop, Early Albian, Early Cretaceous). The discovery of this specimen in amber is very interesting, since aquatic beetles are not common in fossil tree resin. This fossil pushes back the oldest known specimen of Elmidae from the Eocene (~40 Ma) to at least the Early Cretaceous (~110 Ma).

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

#### R É S U M É

*Elmadulescens rugosus* Peris, Maier et Sánchez-García n. gen. n. sp. est décrit d'après un spécimen unique d'ambre d'Espagne (gisement d'El Soplao, Albien inférieur, Crétacé inférieur). La découverte de ce spécimen dans l'ambre est notable, puisque les coléoptères aquatiques sont rares dans la résine végétale fossile. Le registre fossile des Elmidae est ainsi repoussé de l'Éocène (~40 Ma) jusqu'au Crétacé inférieur (~110 Ma).

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

\* Corresponding author.

E-mail addresses: [daperce@gmail.com](mailto:daperce@gmail.com), [david.peris@ub.edu](mailto:david.peris@ub.edu) (D. Peris), [cmaier@ku.edu](mailto:cmaier@ku.edu) (C.A. Maier), [alba.sanchez@ub.edu](mailto:alba.sanchez@ub.edu) (A. Sánchez-García), [xdelclos@ub.edu](mailto:xdelclos@ub.edu) (X. Delclòs).

## 1. Introduction

Coleoptera comprises roughly a quarter of all recently described animal and plant species, making them the primary contributor to Earth's biodiversity and the most prolific order of insects (Beutel and Haas, 2000; Hunt et al., 2007). Among the beetles, the transition to a life in water has occurred several times. Thirty beetle families have aquatic representatives and in at least 25, the majority of species are considered aquatic (Jäch and Balke, 2008). Major radiations have evolved in the Noteridae Thomson and Dytiscidae Leach in Adephaga and the Hydrophiloidea and Byrrhoidea in Polyphaga (Kodada and Jäch, 2005a; Ribera et al., 2002).

The Elmidae Curtis (suborder Polyphaga), commonly known as the “riffle beetles”, are one of the important radiations of aquatic Byrrhoidea, found in a variety of running water habitats throughout the world. The family includes more than 1300 species, but the phylogeny for the family and for the Byrrhoidea is still lacking (Čiampor and Čiamporová-Zat'ovičová, 2008; Jäch and Balke, 2008). The Elmidae is divided into subfamilies Larinae LeConte and Elminae Curtis (Kodada and Jäch, 2005a). Although elmids are considered aquatic beetles, only species of the subfamily Elminae can be regarded as “true water beetles” since they complete nearly their entire life cycle in water (Jäch, 1998). Adults of the subfamily Elminae live and feed underwater while the Larinae are considered strictly aquatic only as larvae (Brown, 1987). Adult elmids emerge following pupal eclosion and take their only dispersal flight; this flight can take several days out of the water (Seagle, 1980).

Brown (1987) hypothesized the antiquity of the elmids based on the geographical distribution of extant forms. Under the present understanding of continental drift, he predicted the probable origin of the family before Cretaceous. Despite their theoretical antiquity and their common aquatic habitat, the fossil record of this family is very scarce. Kodada and Jäch (2005a) and Kirejshuk and Ponomarenko (2014) summarized the fossil record, which consists of some fossils from glacial and post-glacial deposits very similar to extant species (Brown, 1987) and *Palaeorihelmis samlandica* Bollow from the Eocene Baltic amber. *P. samlandica* bears similarity to the extant genera *Riolus* Mulsant et Rey and *Limnius* Illiger, and was the oldest elmid fossil known (approximately 40 Ma) (Bollow, 1940; Wichard et al., 2009).

The aim of this work is to provide evidence for the oldest known fossil riffle beetle, collected from Early Cretaceous amber from Spain. With this evidence, the origin of elmids at least before 110 Ma is confirmed.

*Institutional abbreviations.* CES—El Soplao collection in El Soplao cave, Celis, Cantabria, Spain.

*Other abbreviations.* Ma—millions of years ago.

## 2. Outcrop and geological setting

The El Soplao site is one of the most important Cretaceous amber deposits from Spain. Together with the Peñacerrada I and the San Just sites (the three most intensively studied amber deposits), and some other less

studied localities, the Spanish Cretaceous amber is found in outcrops distributed in a narrow arc from eastern to northern Iberian Peninsula (Peñalver and Delclòs, 2010). This capricious distribution is coincident with the north marine coastline of the Iberian plate during the Early Cretaceous (fig. 2 in Peñalver and Delclòs, 2010).

The El Soplao site is Early Albian from the western part of the Basque-Cantabrian Basin (northern Spain). The amber-bearing deposit occurs in a non-marine to transitional marine siliciclastic unit (Las Peñas Formation), in a deltaic-estuarine environment developed in the regressive stage of a regressive-transgressive cycle (Najarro et al., 2009, 2010).

The amber pieces were found in a level of organic-rich clays 0.7–2.5 m thick, along with dinoflagellates, spores of vascular cryptogams, pollen grains of gymnosperms and angiosperms, abundant gymnosperm plant cuticle remains, charcoal, and marine or brackish-water invertebrates, such as gastropods and bivalves. The presence of serpulids and bryozoans as epibionts, on the surface of some amber pieces (originally epibionts of the resin masses), indicates both a littoral to coastal marsh palaeoenvironment and a mixed assemblage of resin deposit (Najarro et al., 2010; Peñalver and Delclòs, 2010).

To date, this amber deposit has yielded 649 arthropod bio-inclusions belonging to Arachnida (Acari and Araneae), Crustacea (Order Tanaidacea) and Hexapoda in 14 recognized orders: Collembola, Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, Mecoptera, and Diptera (Pérez-de la Fuente, 2012).

## 3. Materials and methods

The sample described in this paper is CES-567; no other syninclusion is found with it. This fragile piece of amber was cut and embedded in a transparent epoxy resin, following the process described in Nascimbene and Silverstein (2000).

The specimen reported in this paper was examined under three different lenses, i.e., a Leica MS5 stereomicroscope, and a Motic BA310 and an Olympus BX41 compound microscopes with reflected and transmitted light. Photomicrographs were made with a Canon EOS 7D digital camera attached to an Infinity K-2 long distance microscope lens for general habitus, and a MOTICAM 2500 camera attached to the Motic BA310 compound microscope for lateral habitus and details. All of them were arranged and sharpened with CombineZP (Hadley, 2010) and edited with Photoshop Elements 10 and CorelDraw X6. Illustrations were prepared with the aid of a camera lucida attached to an Olympus BX41 compound microscope.

Terminology in the description follows that used in Lawrence et al. (2000) and characters used for the placement of the genus follow Shepard (2002) and Kodada and Jäch (2005a). The family classification is from Bouchard et al. (2011).

#### 4. Systematic palaeontology

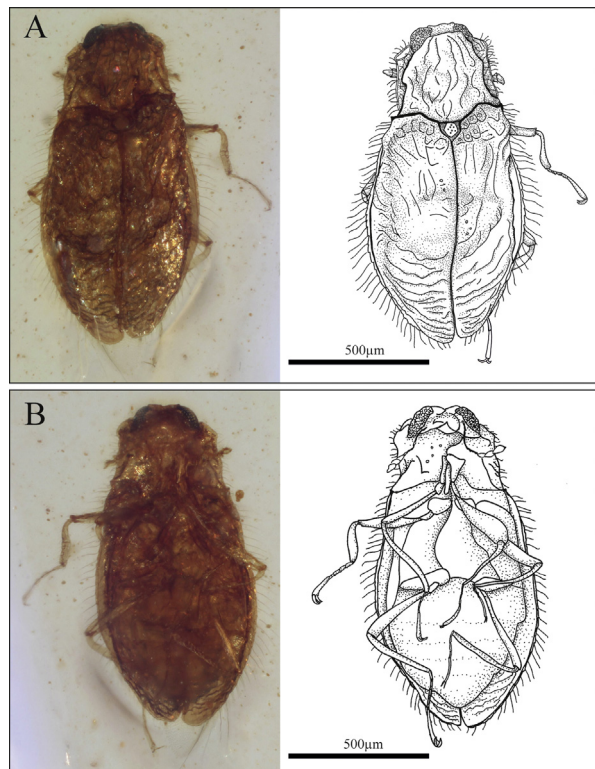
Order COLEOPTERA Linnaeus, 1758  
 Suborder POLYPHAGA Emery, 1886  
 Superfamily BYRRHOIDEA Latreille, 1804  
 Family ELMIDAE Curtis, 1830  
 Subfamily incertae sedis  
 Genus *Elmadulescens* Peris, Maier et Sánchez-García n. gen.

Figs. 1 and 2

**Derivation of name.** The generic name is the combination of *Elm* – from Elmidae and – *adulescens* from the Latin of “young”. The suffix was chosen because it is the oldest fossil Elmidae, so the youngest in classification.

**Type species.** *Elmadulescens rugosus* Peris, Maier et Sánchez-García n. sp.

**Diagnosis.** Dorsal body surface covered with long, and evenly dispersed setae; antennae with last three antennomeres slightly wider than the preceding antennomeres; pronotum with strong sublateral carinae, without transverse or longitudinal depressions or grooves; dorsal surface strongly punctuate and wrinkled, elytral punctures



**Fig. 1.** (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES–567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). A. Photo and camera lucida drawing of the dorsal habitus. B. Photo and camera lucida drawing of the ventral habitus. Both drawings are not from the same angle than the photos.

**Fig. 1.** (Couleur en ligne.) *Elmadulescens rugosus* n. gen. n. sp., holotype (CES–567), déposé dans la collection d’ambre du laboratoire de la grotte d’El Soplao (Celis, Cantabrie, Espagne). A. Photo et dessin de l’habitus en vue dorsale. B. Photo et dessin de l’habitus en vue ventrale. Les deux dessins n’ont pas été réalisés sous le même angle que les photographies.

organized in longitudinal rows, intervals very sclerotized and slightly convex near base; edge of the pronotum and elytron thickened, bearing a row of erect, long setae.

**Description.** Body elongate, subparallel, moderately convex (Figs. 1A, 2A). Dorsal surface covered with long and disperse erect setae; setae narrowed and acute apically, hair-like.

Head deflexed, slightly retracted into prothorax (Fig. 2A). Eyes strongly protuberant and coarsely faceted, separated by a distance equal to the width of eye (Fig. 1A). Antennae long, filiform, with more than nine antennomeres (only nine are visible in the specimen, there are likely eleven antennomeres) (Fig. 2D); antennal insertions widely separated, inserted at the level of the eyes; scape slightly longer than pedicel.

Pronotum quadrate, 1.5 times wider than head; surface deeply punctured; disc of pronotum with two longitudinal sublateral carinae, lacking obvious depressions or grooves; surface strongly wrinkled; lateral borders of pronotum subparallel, slightly convergent near apex (Fig. 1A). Prosternum moderately long in front of procoxae, about as long as procoxae; prosternal process long, moderately narrow, subparallel, with rounded apex. Scutellum pentagonal, about as wide as long. Metaventrite long, approximately twice the length of the first abdominal ventrite (Fig. 1B).

Elytra deeply punctuate; without sublateral carinae; elytral surface apparently without grooves or depressions, but strongly wrinkled (Fig. 1A). Elytral humeri with strong and distinctly protuberant carinae.

Procoxae globular, enlarged, and separated by at least half the width of coxa. Mesocoxae globular and separated by width of coxa; metacoxae transverse, not reaching edge of metasternum; metacoxae narrowly separated; metacoxae with distinct posterior face, excavate posteriorly for reception of metafemora in repose; metatrochanter triangular.

Legs long, femora and tibiae slender; tibiae covered with short setae laterally. Tarsal formula 5–5–5. Tarsi loose, simple, roughly same length as tibiae; apical tarsomeres nearly as long as preceding four tarsomeres combined (Fig. 2C). Tarsal claws long, robust, apparently lacking teeth.

Abdomen with five ventrites. Ventrite I slightly longer than remaining four ventrites.

***Elmadulescens rugosus*** Peris, Maier et Sánchez-García n. sp.

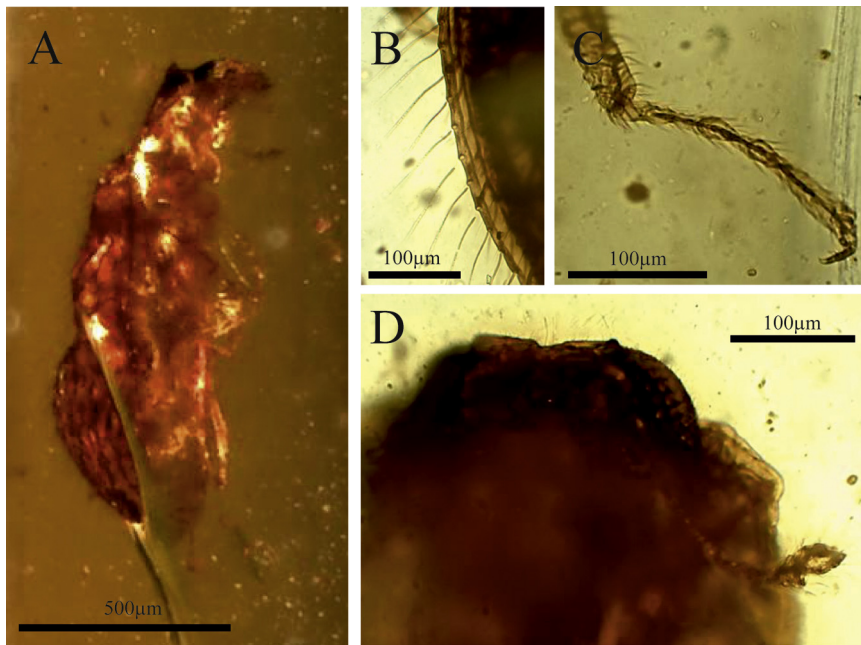
Figs. 1 and 2

**Derivation of name.** The specific epithet *rugosus* is from the Latin of “wrinkled”, referring to the dorsal appearance.

**Holotype.** CES–567, housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). The holotype is a well-preserved specimen in a transparent amber piece, but the dorsal-ventral compression has deformed the natural disposition of some parts and made difficult the observation for some characters.

**Type locality.** The El Soplao site, in the municipality of Celis (Cantabria, Spain). The piece was found at the Las Peñosas Formation, Early Albian in age (Najarro et al., 2009).

**Diagnosis.** See generic description.



**Fig. 2.** (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES-567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). Photos and details of selected characters. A. Lateral habitus. B. Elytral border thickened, with a fringe of long, erect setae. C. Tarsi loose, simple. D. Antenna long, filiform, with a very weak apical club.

**Fig. 2.** (Couleur en ligne.) *Elmadulescens rugosus* n. gen. n. sp., holotype (CES-567), déposé dans la collection d'ambre du laboratoire de la grotte d'El Soplao (Celis, Cantabrie, Espagne). A. Habitus latéral. B. Bord de l'élytre épaissi, avec une frange de soies longues et dressées. C. Tarses mous, simples. D. Antenne longue, filiforme, avec un club apical très délicat.

**Description.** Body elongate, subparallel; length 1.17 mm (as preserved); maximum body width 0.60 mm.

Antennae long, nearly reaching base of the elytron; the last three antennomeres slightly larger than the preceding ones in a very weak apical club (Fig. 2D). Antennomeres IX and X 1.2 times wider than the preceding antennomeres; antennomere XI 1.3 times longer than the antennomere X and subequal in length. Head with slight depression between eyes.

Pronotum convex, broader than long, widest at base; maximum length 0.32 mm; maximum width 0.39 mm. Anterior border of pronotum medially produced forward and rounded; width of process 0.20 mm; anterior angles obtuse. Lateral borders of pronotum subparallel, slightly thickened, with fringe of long, erect setae (Fig. 1A). Posterolateral angles of the pronotum acute, closely interlocking with base of elytron; posterior border of pronotum bisinuate. Discal area of pronotum free from obvious depressions or grooves, with sparse, erect setae.

Elytral length 0.85 mm, elytral width 0.60 mm; elytra 2.6 times longer and 1.5 times wider than pronotum. Elytra convex covered with sparse, long, erect setae; lateral elytral border thickened, with a fringe of long, erect setae, as on pronotum (Fig. 2B); elytral apices rounded; elytral borders weakly serrate near apex. Strial punctures on disk deep and rounded, one third as broad as intervals. Elytral intervals highly sclerotized and slightly convex near base.

**Remarks and comparative notes.** A suite of shared characters allows us to confidently place this specimen in the beetle family Elmidae. The combination of long,

slender antennae widely inserted, large, protuberant eyes, a pentagonal scutellum that is abruptly elevated anteriorly, long legs with long, simple tarsi, a 5–5–5 tarsal formula, metacoxae with a posterior face, pronotum with complete lateral carinae, the last tarsomere longer than the other four combined, large tarsal claws, and five abdominal ventrites place this species within Elmidae. The family is divided in two subfamilies, and due to the very small size (1.17 mm in length), the head slightly retracted into the prothorax (the “turtle-neck”), the filiform antennae, long tarsi and tibiae, globose procoxae, long prosternum, and the general habitus of pronotum, *E. rugosus* n. gen. n. sp. may fit correctly into Elminae. However, some inconsistent characters are found and the subfamily remains *incertae sedis* (see below).

This specimen lacks a visible plastron of modified setae, a character shared by all extant Elminae. The lack of a visible plastron does not exclude this specimen from Elminae, though, as even on recently collected specimens the plastron is often nearly impossible to discern if the specimen is submerged in liquid, and the preservation in amber looks remote from dry conditions. Additionally, *E. rugosus* n. gen. n. sp. possesses a unique character: a thickened edge of the pronotum and elytra, where a series of long, erect setae are inserted (Figs. 1A, 2B). No specimens, extant or extinct, with this diagnostic character have ever been described within the family. Only a few genera of Elminae have elytral setae, e.g., *Macronevia* Jäch et Boukal or *Zaitzeviaria* Nomura, but none are as long and conspicuous as the dorsal setae of *E. rugosus* n. gen. n. sp. Long dorsal setae are found in some members of the subfamily Larinae, but all Larinae have

transverse procoxae and most of them have clearly loosely clubbed antennae (Kodada and Jäch, 2005a). By contrast, *Elmadulescens* n. gen. possesses globular procoxae (though very deteriorated and compressed against each other) and filiform antennae. The basal position of this fossil in the family and its ancient age could be the cause of such an ambiguous set of characters.

Several closely related aquatic byrrhoid groups have long dorsal setae. Dryopidae Bilberg, Limmichidae Erichson, and Lutrochidae Kasap et Crowson, also have long elytral setae (Hernando and Ribera, 2005; Ide et al., 2005; Kodada and Jäch, 2005b). Dryopidae adults can be recognized by the short antennae, with most segments broader than long, and antennomeres from IV to the end forming a more or less loose club (Ide et al., 2005). *Elmadulescens* n. gen. is not Limmichidae because the head is not capable of being retracted fully into the pronotum and the dorsal surface of the body is not clearly convex (Fig. 2A) (Lawrence et al., 2000).

*E. rugosus* n. gen. n. sp. does not resemble any extant palaeartic genera of Elmidae. It is similar in size to and possesses sublateral pronotal carinae like *Oulimnius* Gozis, but the long elytral setae distinguish it from this genus. Among other non-Palaeartic genera, it seems most closely allied to an informal group of Neotropical Elmidae composed of *Hintonelmis* Spangler, *Hexacylloepus* Hinton, *Neolimnius* Hinton, *Pilielmis* Hinton, and *Tyletelmis* Hinton, based on the prominent eyes, which have a strong depression between them. It does, however, differ significantly from either of these genera in body form, size, and degree of carination and reticulation on the pronotum.

## 5. Discussion

Members of the subfamily Elmidae are typically found in the benthos of streams and rivers, though they can be found in a variety of other aquatic habitats, including seeps and springs, as well as at the margins of lakes and ponds (subfamily Elminae); or above the water line in the splash zone, on downstream surfaces of rocks, logs, and branches, or accumulated in leaf packs (subfamily Larainae) (Jäch and Balke, 2008; Kodada and Jäch, 2005a; Maier, 2012). Despite their close association with aquatic environments, the fossil record for Elmidae, and Byrrhoidea in general, is sparse. Their small size and affinity to fast-flowing water makes them unlikely to be preserved into compression fossils.

*E. rugosus* n. gen. n. sp. is the oldest recorded fossil for the family and the only elm mid fossil recorded since *P. samlandica* was described from Eocene Baltic amber (Bollow, 1940; Kirejshuk and Ponomarenko, 2014), because *Potamophilites* Haupt, recorded as an elm mid by Kirejshuk and Ponomarenko (2014), is actually a dryopid (Haupt, 1956). The family's aquatic habit is probably the main cause for their scarcity in amber fossils; they seem unlikely candidates for preservation in tree resins taking into account the chemical hydrophobic character of the resin and the behaviour of these beetles. It is not impossible, though, that an aquatic beetle could be found in amber as it takes its brief maiden flight after pupation (Seagle, 1980; Wichard et al., 2009). Based on the wrinkled dorsal surface of the fossil, it is possible that *E. rugosus* n. gen.

n. sp. was a general specimen, one not yet firmly sclerotized after pupation. This specimen was probably trapped on a resin flow while it was searching for aquatic habitat, but the finding of the specimen embedded in amber with the wings folded may indicate that this specimen was not trapped in flight or pulled by the wind. The discovery of recent elmids of the subfamily Larainae above the water line increases the possibility that a specimen of this family could be found embedded in fossil resin while associated with a rock or wood surface near water.

The plastron, a very thin layer of air held by a dense coating of water-repellent cuticular structures, acts as a physical gill so that adults do not need to come to the surface for respiration (Hinton, 1976; Spangler and Perkins, 1989). The strategy occurs in diverse aquatic coleopteran lineages and there is evidence suggesting that this structure evolved several times within the order, as it is found in some members of Hydrophilidae Latreille, Dryopidae, Elmidae, and Curculionidae Latreille (Schowalter, 2009). The plastron is often difficult to discern in extant specimens and can be easily overlooked in the descriptions. Nonetheless, *E. rugosus* n. gen. n. sp. shows a thickened edge of the pronotum and elytra with a series of long, erect setae, that may have been related or work together with plastron respiration. In addition, the dorsal surface of the prothorax and elytra are covered with sparse, long, erect setae, which resembles that of some aquatic and riparian genera of Dryopidae and other elmids, may have entrapped air for underwater respiration and for prevention of wetting of the body (Kodada and Jäch, 2005a, 2005b).

On the other hand, *E. rugosus* n. gen. n. sp. exhibits other morphological adaptations to their unusual habitat. The very strongly sclerotized cuticle, and retractable head into the prothorax, are also features to minimize injury if the beetles become dislodged in strong current; the legs are long and tarsal claws are very large and stout, which enables them to cling firmly to substrate (Kodada and Jäch, 2005a). Their small size enables elmids to seek refuge in interstices, although small size may not have evolved as an adaptation directly related to a life in fast-flowing water, but as an adaptation related to plastron respiration (Ward, 1992). Indeed, elmids are smaller than most aquatic coleopterans. This entire suite of characters suggests that *E. rugosus* n. gen. n. sp. was adapted to life in rapids, as with other members of Elminae, although it is speculative.

The absence of the family from other published lists of Coleoptera in amber and from other descriptions of Cretaceous fossil beetles (Grimaldi et al., 2000; Penney, 2010 and references herein; Poinar, 1992; Poinar and Milki, 2001; Skidmore, 1999) makes this specimen both unique and valuable.

## 6. Conclusions

One new genus and species of Elmidae is described based on a single fossil specimen from Early Cretaceous amber of Spain, in the El Soplao deposit. *E. rugosus* n. gen. n. sp. is the oldest member of Elmidae, and suggests the possible pre-Cretaceous origin for the family, indicating that elmids existed already at 110 Ma, and the adaptability of the Byrrhoidea to aquatic environments since the

Cretaceous. Additionally, it is the only aquatic beetle found in any Mesozoic amber locality, probably because fossilization of aquatic specimens in tree resin is rare.

## Acknowledgements

We thank Rafael López-del Valle (Museo de Ciencias Naturales de Álava, Spain) the preparation of the Spanish sample and to the management team of the El Soplao Cave (Cantabria, Spain) the loan of the specimen. We are also grateful to Michael Engel (Natural History Museum and University of Kansas, Kansas) for providing support to this investigation, hosting DP at the University of Kansas. Thanks also to Ignacio Ribera (Institut de Biologia Evolutiva (CSIC-UPF), Spain) for the ideas about the placement of the specimen, to Matthew Gimmel (University of Kansas, Kansas) for helpful comments and input, to Vincent Perrichot (University of Rennes-1, France) for the French translations along the manuscript, and to anonymous reviewers for their useful criticisms and corrections. This work is part of the Ph.D. dissertations of DP and AS-G, supported by grants from the Spanish Ministry of Education, Culture and Sports and Spanish Ministry of Economy and Competitiveness, respectively. This is a contribution to the project CGL2011–23948, named “The Cretaceous amber of Spain: A multidisciplinary study II”, from the Spanish Ministry of Economy and Competitiveness. This research was also supported by US National Science Foundation grant #DEB–0816904 to Andrew Short and the KU Entomology Endowment Summer Scholarship to CAM.

## References

- Beutel, R.G., Haas, F., 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* 16, 103–141.
- Bollow, H., 1940. Die erste Helminidae [sic] (Col, Dryop.) aus Bernstein. *Mitt. Münch. Entomol. Ges.* 30, 117–119.
- Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H., Newton Jr., A.F., Reid, C.A.M., Schmitt, M., Ślipiński, S.A., Smith, A.B.T., 2011. Family-group names in Coleoptera (Insecta). *Zookeys* 88, 1–972.
- Brown, H.P., 1987. Biology of riffle beetles. *Annu. Rev. Entomol.* 32, 253–273.
- Čiampor, F., Čiamporová-Zat'ovičová, Z., 2008. A new species of *Hedyselmis* Hinton and notes on the phylogeny of the genus (Coleoptera: Elmidae). *Zootaxa* 1781, 55–62.
- Grimaldi, D.A., Shedrinsky, A., Wampler, T., 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. In: Grimaldi, D.A. (Ed.), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys, Leiden, pp. 1–76.
- Hadley, A., 2010. *Combine ZP 1.0 Image Stacking Software*.
- Haupt, H., 1956. Beitrag zur Kenntnis der eozänen Arthropodenfauna des Gieseltales. *Nova Acta Leop. N.S.* 18, 1–90.
- Hernando, C., Ribera, I., 2005. *Limnichidae* Erichson, 1846. In: Beutel, R.G., Leschen, R.A.B. (Eds.), *Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles*. Walter de Gruyter, Berlin, pp. 512–518.
- Hinton, H.E., 1976. Plastron respiration in bugs and beetles. *J. Insect Physiol.* 22, 1529–1550.
- Hunt, T., Bergsten, J., Levkancicova, Z., Papadopoulou, A., John, St., Wild, O., Hammond, R., Ahrens, P.M., Balke, D., Caterino, M., Gómez-Zurita, M.S., Ribera, J., Barraclough, I., Bocakova, T.G., Bocak, M., Vogler, L.A.P., 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* 318, 1913–1916.
- Ide, S., Costa, C., Vanin, S.A., 2005. *Lutrochidae* Kasap et Crowson 1975. In: Beutel, R.G., Leschen, R.A.B. (Eds.), *Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles*. Walter de Gruyter, Berlin, pp. 508–512.
- Jäch, M.A., 1998. Annotated check list of aquatic and riparian/littoral beetle families of the world. In: Jäch, M.A., Ji, L. (Eds.), *Water beetles of China, Vol. II. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein*, Wien, pp. 25–42.
- Jäch, M.A., Balke, M., 2008. Global diversity of water beetles (Coleoptera) in freshwater. *Hydrobiologia* 595, 419–442.
- Kirejshuk, A.G., Ponomarenko, A.G., 2014. Taxonomic list of fossil beetles of the suborder Scarabaeina (part 2). <http://www.zin.ru/Animalia/Coleoptera/eng/paleosy1.htm> (accessed 24.02.15).
- Kodada, J., Jäch, M.A., 2005a. Elmidae Curtis, 1830. In: Beutel, R.G., Leschen, R.A.B. (Eds.), *Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles*. Walter de Gruyter, Berlin, pp. 471–496.
- Kodada, J., Jäch, M.A., 2005b. Dryopidae Bilberg 1820. In: Beutel, R.G., Leschen, R.A.B. (Eds.), *Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles*. Walter de Gruyter, Berlin, pp. 496–508.
- Lawrence, J.F., Hastings, A.M., Dallwitz, M.J., Paine, T.A., Zurcher, E.J., 2000. Elateriformia (Coleoptera): descriptions, illustrations, identification and information retrieval for families and subfamilies. Version: 9th October 2005, Available from: <http://delta-intkey.com> (July-07-2014).
- Maier, C.A., 2012. *Elachistelmis* gen. n. (Coleoptera: Elmidae: Elminae) from Suriname, with description of two new species. *Zootaxa* 3500, 61–69.
- Najarro, M., Peñalver, E., Rosales, I., Pérez-de la Fuente, R., Daviero-Gomez, V., Gomez, B., Delclòs, X., 2009. Unusual concentration of Early Albian arthropod bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, northern Spain): Palaeoenvironmental and palaeobiological implications. *Geol. Acta* 7, 363–387.
- Najarro, M., Peñalver, E., Pérez-de la Fuente, R., Ortega-Blanco, J., Menor-Salván, C., Barrón, E., Soriano, C., Rosales, I., López del Valle, R., Velasco, F., Tornos, F., Daviero-Gomez, V., Gomez, B., Delclòs, X., 2010. Review of the El Soplao amber outcrop, Early Cretaceous of Cantabria, Spain. *Acta Geol. Sin.* 84, 959–976.
- Nascimbene, P., Silverstein, H., 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi, D. (Ed.), *Studies on Fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, pp. 93–102.
- Peñalver, E., Delclòs, X., 2010. Spanish amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 236–271.
- Penney, D., 2010. Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester.
- Pérez-de la Fuente, R., (Unpublished PhD Thesis) 2012. *Paleobiología de los Artrópodos del ámbar Cretácico de El Soplao (Cantabria, España)*. University of Barcelona.
- Poinar Jr., G.O., 1992. *Life in Amber*. Stanford University Press, California.
- Poinar Jr., G.O., Milki, R.K., 2001. *Lebanese Amber: The Oldest Insect Ecosystem in Fossilized Resin*. Oregon State University Press, Corvallis.
- Ribera, I., Beutel, R.G., Balke, M., Vogler, A.P., 2002. Discovery of Aspidytidae, a new family of aquatic beetles. *Proc. R. Soc. Biol. Sci.* 269, 2351–2356.
- Schowalter, T.D., 2009. *Insect ecology. An Ecosystem Approach*. Elsevier Inc., China.
- Seagle, H.H., 1980. Flight periodicity and emergence patterns in the Elmidae (Coleoptera: Dryopoidea). *Ann. Entomol. Soc. Am.* 73, 300–307.
- Shepard, W.D., 2002. Elmidae Curtis 1830. In: Arnett, R.H., Thomas, M.C., Skelley, P.E., Howard, F.J. (Eds.), *American beetles. Polyphaga: Scarabaeoidea through Curculionoidea*. CRL Press LLC, Florida, pp. 117–120.
- Skidmore, R.E., 1999. Checklist of Canadian amber inclusions in the Canadian National Collection of Insects. Research Branch Agriculture and Agri-Food Canada electronic publication, Canada.
- Spangler, P.J., Perkins, P.D., 1989. A revision of the neotropical aquatic beetle genus *Stenhelmoides* (Coleoptera: Elmidae). *Smithson Contr. Zool.* 479, 1–63.
- Ward, J.V., 1992. *Aquatic insect ecology 1. Biology and habitat*. John Wiley & Sons Inc, United States of America.
- Wichard, W., Gröhn, C., Seredszus, F., 2009. *Aquatic Insects in Baltic Amber: Wasserinsekten im Baltischen Bernstein*. Verlag Kessel, Remagen-Oberwinter, Germany.