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Fossil Monotomidae (Coleoptera: Polyphaga) from Laurasian Cretaceous amber

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Abstract Three new species of root-eating beetle (Coleoptera: Monotomidae) in Cretaceous amber from Spain (Albian) and Myanmar (Cenomanian) are described. *Rhizophtoma longus* sp. nov. is a Spanish monotomid of the tribe Rhizophtomini, previously only known from Lebanese amber (Aptian). The Cretakarenniini tribe nov. is created to include the new species *Cretakarenni birmanicus* gen. et sp. nov., from Myanmar, and *Cretakarenni hispanicus* gen. et sp. nov., from Spain. These three new species, together with the previous fossil species known in this family, have a controversial set of characters that makes it extremely difficult to place them in any other extant group of Monotomidae. Fossil monotomids are not numerous, despite their early diverging placement among the cucujoid clade. An updated list of monotomid fossils is provided. The need to classify the new taxa and compare them with extant and extinct groups of Monotomidae is solved using a key for the subfamilies and tribes.

Keywords Monotominae · Rhizophtomini · New tribe · New species · Spanish amber · Burmese amber

Introduction

Monotomidae (commonly named “root-eating beetles”) are a small family of Coleoptera with 240 species belonging to 33 genera and are found in all zoogeographical regions of the world (Bousquet 2010). The family was known under the name Rhizophagidae until Pakaluk et al. (1994) found that Monotomidae took priority.

Historically, the two subfamilies (i.e. Rhizophaginae and Monotominae) that currently constitute the Monotomidae belonged to the Nitidulidae and Cucujidae, respectively. Crowson (1952) first established the Monotomidae, with a different classification of subfamilies that continued to change until a review by Sengupta (1988). He reviewed all genera and placed them into the present subfamilies Rhizophaginae for the genus *Rhizophagus* Herbst, 1793 and Monotominae for the remaining genera. After the exclusion of some genera from the family, Sengupta (1988) divided Monotominae into four tribes: Monotomini (*Monotoma* Herbst, 1793), Thionini (*Thione* Sharp, 1899 and *Shoguna* Lewis, 1884), Lenacini (*Lenax* Sharp, 1877) and Europini (remaining genera). This classification was followed during different reviews of the family (Lawrence and Newton 1995; Bousquet 2002) until Kirejtshuk et al. (2009) created the fossil subfamily Rhizophtominae for the fossil genus *Rhizophtoma* Kirejtshuk and Azar, 2009. This subfamily, however, was ranked as a tribe within the Monotominae by Bouchard et al. (2011).

Some authors have attempted to define Monotomidae (Sengupta 1988; Lawrence and Newton 1995; Bousquet 2002, 2010; McElrath et al. 2012). Recent cladistic analyses resulted in a basal placement among the cucujoid clade (Robertson et al. 2008; Lawrence et al. 2011), and in the latest phylogenetic analysis, a basal placement is also obtained, but establishing it as base of the Erotylid series in Cucujoidea (Bocak et al. 2014). Nevertheless, the sister taxon to Monotomidae remains currently unclear.

Despite their ancient origin (previous to Early Cretaceous), fossil monotomids are not numerous (Table 1). Their general small size may make them difficult to be found as compression fossils (Martínez-Delclòs et al. 2004). The ancient record for the family corresponds to *Rhizophtoma elateroides* Kirejtshuk and Azar, 2009, described in Lebanese amber from

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Table 1 Fossil species of Monotomidae. Some other records from Lebanese amber (Cretaceous), Baltic amber (Eocene) and Dominican amber (Miocene) await description. Fossil ages are Eocene (E) and Cretaceous (C). New taxa in bold

Age	Place	Subfamily	Tribe	Species	Reference
(E) Lutetian	Baltic amber	Monotominae	Europini	*Europs insterburgensis*	Alekseev (2014)
(C) Cenomanian	Burmese amber	Monotominae	**Cretakarenniini**	***Cretakarenni birmanicus* sp. nov.**	
(C) Albian	Spanish amber	Monotominae	**Cretakarenniini**	***Cretakarenni hispanicus* sp. nov.**	
(C) Albian	Spanish amber	Monotominae	Rhizophtomini	***Rhizophtoma longus* sp. nov.**	
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizophtoma synchrotronica*	Kirejtshuk and Azar (2013)
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizobactron marinae*	Kirejtshuk and Azar (2013)
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizophtoma elateroides*	Kirejtshuk et al. (2009)

the Early Cretaceous (Aptian). *Rhizophtoma synchrotronica* Kirejtshuk, 2013 and *Rhizobactron marinae* Kirektshuk, 2013 were later also described in Lebanese amber (Kirejtshuk et al. 2009; Kirejtshuk and Azar 2013). Some fossils were named from the Eocene Baltic amber, i.e. *Europs* Wollaston, 1954 and *Rhizophagus* Herbst, 1793, although only *Europs insterburgensis* Alekseev, 2014 has been described until now (Helm 1896; Klebs 1910; Larsson 1978; Alekseev 2014). Additionally, "*Monotoma resinorum* Hope, 1842" was cited in Kirejtshuk et al. (2009) as a monotomid described from copal, although it is in fact *Monomma resinorum* Hope, 1842, in Zopheridae, so this mistake needs to be solved. The family has also been found in Lebanese amber, with three additional specimens tentatively placed in this group while awaiting further description due to their resemblance to Lyctinae (Coleoptera: Bostrichidae), in Baltic amber, and in Dominican amber (Poinar 1992; Weitschat and Wichard 2002; Kirejtshuk and Azar 2013). No more monotomids have been described, but it is hoped that the study of new fossils will add information about the evolution of this group of beetles.

In this work, we describe new fossils of Monotomidae from two different Cretaceous outcrops: two new species from the Early Cretaceous (Albian) Spanish amber and one new species from the Late Cretaceous (Cenomanian) Burmese amber. These new species slightly clarify the position of the fossil Rhizophtominae (sensu Kirejtshuk et al. 2009 and Kirejtshuk and Azar 2013).

Geological and palaeontological context

The Spanish specimens were found in the Peñacerrada I outcrop (northern Spain) located in the Eastern area of the Basque Cantabrian Basin (see location in Alonso et al. 2000; Peñalver and Delclòs 2010). Amber was provided from the middle subunit of the Escucha Formation, characterized by organic-rich limestones, sandstones and siliceous microconglomerates originating during the period of maximum regression and deltaic progradation (Martínez-Torres et al. 2003). The Escucha Fm. is considered to have formed in the Early Cretaceous (Albian), based on geological and palaeobiological features (Barrón et al. 2001; Delclòs et al. 2007; Peñalver and Delclòs 2010).

To date, 3,014 bioinclusions have been reported from Peñacerrada I. Together with fungi and cryptogram remains, the majority of the inclusions belong to Arthropoda, i.e. some Crustacea, Chelicerata and mainly Hexapoda. Representatives of 17 hexapod orders are embedded in amber from Peñacerrada I (Alonso et al. 2000; Delclòs et al. 2007; Peñalver and Delclòs 2010; Engel et al. 2014; Sánchez-García et al. 2014). Coleoptera, accounting 83 specimens, is the third most represented order.

The Burmese specimen was found in the Noije Bum hill mines, in Kachin state, 18 km south-west of the town of Tanai (northern Myanmar) (see location in Grimaldi et al. 2002; Cruickshank and Ko 2003). Amber is located in the finer facies of sedimentary rocks, which consist of sub-millimetre black, yellow, grey and light green clasts buried in a nearshore marine, estuarine or lagoonal environment dominated by volcanic ejecta and ash (Grimaldi et al. 2002; Cruickshank and Ko 2003; Shi et al. 2012). Burmese amber is considered to originate from the Late Cretaceous (early Cenomanian) according to Shi et al. (2012), based on radiometric methods.

Burmese amber at the American Museum of Natural History (AMNH, New York) comprises 3,100 specimens, including several plants, Nematoda, Onychophora and mainly Arthropoda. The two major published collections of Burmese amber (at AMNH and at the Natural History Museum, London) together contain approximately 228 families of organisms (Zherikhin and Ross 2000; Grimaldi et al. 2002). Among them, approximately 40 families are described as Coleoptera (16 % of all studied inclusions) (Shi et al. 2012).

Material and methods

The bioinclusions described are from Spanish and Burmese amber. They originate from two different institutions: the Spanish specimens from the Museo Ciencias Naturales de Álava Vitoria-Gasteiz, Álava, Spain (MCNA), and the Burmese specimens from the American Museum of Natural

History (AMNH). Samples from the AMNH have the abbreviation "JZC Bu–" referring to the personal Burmese amber collection of Mr. James Zigras, which was generously donated to the museum for study.

The Spanish samples mentioned in this paper are named as follows: MCNA–8655, MCNA–9158, MCNA–9184, MCNA–9317 and MCNA–9552; the Burmese sample is named as follows: JZC Bu–33C. All pieces were cut and polished, and MCNA pieces were also embedded in a transparent epoxy resin according to Nascimbene and Silverstein (2000). Specimens were 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 an Olympus BX41 stereomicroscope. Drawings were then inked and scanned into CorelDraw X6. General photomicrographs were created with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens, or in cases of insufficient clarity, the photographic equipment comprised an Olympus Camedia C-5050 digital camera attached to an Olympus SZX9 stereomicroscope. Photographs were merged using the software Combine ZP edited with Photoshop Elements 10 and CorelDraw X6.

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

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Cucujoidea Latreille, 1802
Family Monotomidae Laporte, 1840
Subfamily Monotominae Laporte, 1840
Tribe Cretakarenniini tribe nov.

Type genus Cretakarenni gen. nov.

Diagnosis Antennae short, ten-segmented, with one-segmented club; neck constriction present; pronotum as long as maximum width, widest at the anterior half; scutellum as long as wide; expressed absutural lines along the elytra; procoxal cavities transverse with exposed trochantins.

Genus *Cretakarenni* gen. nov. (Figs. 1 and 2)

Etymology The new genus-group is a combination of the Greek word *Cretaceous* and the Burmese word *karenni*, a Tibetan-Burmese ethnic minority of Myanmar whose women decorate their necks with rings, making them look long.

Type species Cretakarenni birmanicus sp. nov.

Diagnosis Vertex of head punctured; metacoxae widely separated; postcoxal lines present, diverging posteriorly; subtriangular tibiae; tarsal formula 5–5–5; tarsomere 1 small, some tarsomeres ventrally lobed.

Description Body flattened, lateral margins subparallel; dorsal surface conspicuously setose (Figs. 1a and 2a).

Head narrower than prothoracic width, slightly declined. Head with elongated rostrum, constricted posteriorly to form a neck; vertex of head punctured. Compound eyes protuberant, entire, coarsely faceted. Antennal insertion concealed from above; antennae ten-segmented, capitate, with one-segmented club, not reaching middle of prothorax.

Prothorax subquadrate, anterior half slightly wider than posterior half, widest in the middle; lateral margins slightly sinuate, carinate, finely crenulated, and setiferous (Figs. 1a and 2a). Anterior angles of pronotum rounded; pronotal disk punctured; base of prothorax distinctly narrower than elytral bases. Prosternum anteriorly longer than prosternal process,

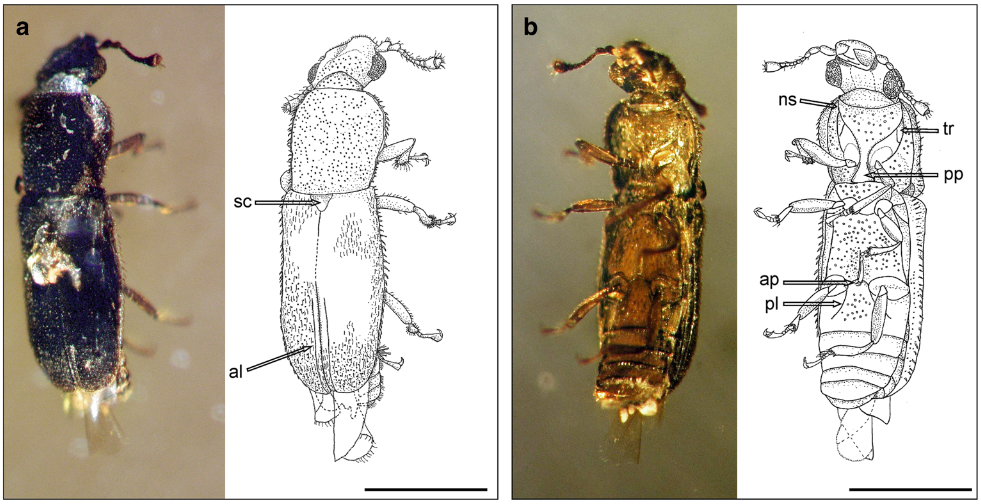

Fig. 1 *C. birmanicus* sp. nov., JZC Bu–33C, holotype, from Myanmar; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus. *Scale bars*=0.5 mm. Abbreviations: absutural lines, *al*; scutellum, *sc*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*; postcoxal lines, *pl*

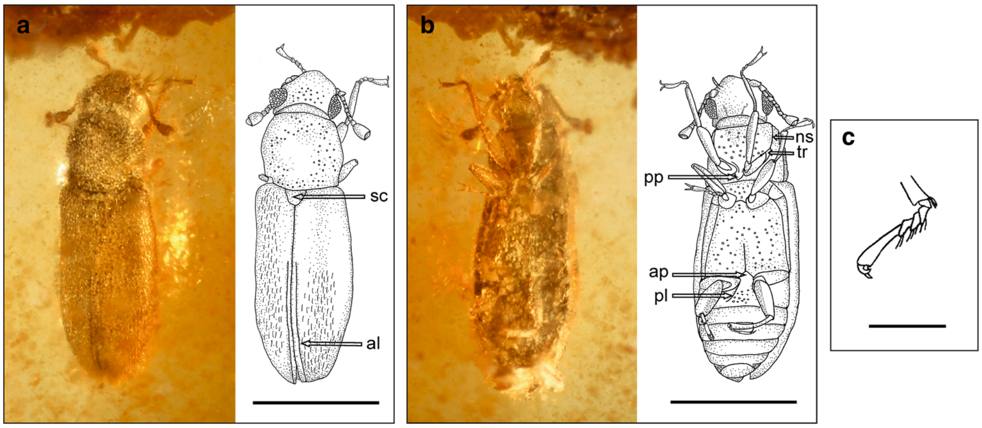

Fig. 2 *C. hispanicus* sp. nov., MCNA–8655, holotype, from Spain; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus; **c** camera lucida illustration of protarsi. *Scale bars* in **a**, **b**= 0.5 mm, **c**=0.1 mm. Abbreviations: absutural lines, *al*; scutellum, *sc*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*; postcoxal lines, *pl*

coarsely punctured; prothoracic episternum clearly delimited by complete notosternal suture (Figs. 1b and 2b).

Scutellum as long as wide, narrowed posteriorly and rounded apically. Elytral absutural lines distinctly expressed along the apical half of the elytra.

Procoxal cavities markedly transverse, externally separate; procoxal trochantins exposed (Figs. 1b and 2b); mesocoxal cavities widely separated. Metasternum coarsely punctured; metaventral medial line long; metacoxal cavities widely separated; metacoxae not extending laterally to meet elytra. Trochanters prominent; femora with inner depression to receive the tibiae; subtriangular tibiae; outer apical angle of tibiae with two spines. Tarsal formula 5–5–5, first tarsomere small and some tarsomeres slightly lobed ventrally (Fig. 2c).

Abdomen with five ventrites. Postcoxal lines on ventrite 1 slightly curved, divergent (Figs. 1b and 2b). Ventrite 1 longest, as long as ventrites 2 and 3 combined, coarsely punctured between the postcoxal lines; ventrites 2–4 subequal in length; ventrite 5 one-and-a-half times length of ventrite 2.

Cretakarenni birmanicus sp. nov. (Fig. 1)

Holotype JZC Bu–33C, a complete specimen, sex unknown, preserved in a piece of fully transparent amber in syninclusion with three other Coleoptera (i.e. two Staphylinidae and one Leiodidae), two Diptera (Cecidomyiidae) and one Hymenoptera, all housed in the amber collection of the AMNH (New York, USA).

Type locality Myanmar: Kachin State, near Tanai; Late Cretaceous (early Cenomanian) in age (Shi et al. 2012).

Etymology The specific epithet *birmanicus* comes from the traditional Latin name of the country in which the holotype was found (Burma, Myanmar since 2010).

Diagnosis Well-developed antennal cavities on ventral side; prosternal process gradually narrows and then expands; intercoxal process of ventrite 1 broad and rounded at apex; tarsomeres 1–3 short; tarsomere 4 narrowly lobed ventrally.

Description Length 1.45 mm; maximum body width 0.39 mm; ratio of body length to greatest body width 3.7.

Head with well-developed antennal cavities on ventral side. Scape robust, widest apically, pedicel smaller than scape, with a similar shape; antennomere 3 narrower than pedicel and elongated; antennomeres 4–9 short, quadrate, of same length, slightly wider from 7 to 9; antennomere 10 forming a single compact club, oval and truncate apically (Fig. 1a).

Ratio of pronotal length to the greatest pronotal width 1.1; anterior margin of pronotum straight; lateral pronotal margins not raised; pronotal disk finely punctured; posterior angles of pronotum slightly obtuse, nor produced and acute (Fig. 1a). Prosternal process gradually narrows and then expands, not overlapping mesoventrite, apex truncate (Fig. 1b).

Ratio of elytral length to greatest width 2; ratio of elytral length to pronotal length 1.9. Elytra finely punctured, diffuse (not in longitudinal rows); margins finely crenulated and setiferous (Fig. 1). Elytra exposing last abdominal segment and the pygidium, only discernible in oblique habitus.

Legs with tarsomere 1 reduced and partly concealed; tarsomeres 2–3 short, with the same shape as tarsomere 1, all three stouter; tarsomere 4 short, narrowly ventrally lobed, tarsomere 5 longer than the rest combined; tarsal claws of equal length, simple.

Abdomen with intercoxal process of ventrite 1 broad and rounded at apex.

Cretakarenni hispanicus sp. nov. (Fig. 2)

Coleoptera, fam. indet. in dorso-lateral view, MCNA–8655, body length 1.2 mm, in Alonso et al. (2000: Fig. 12–7)

Holotype MCNA–8655, a complete specimen, sex unknown, preserved in a piece of fully transparent amber, deposited in the amber collection of the MCNA (Vitoria-Gasteiz, Spain).

Type locality Spain: Peñacerrada I, Moraza, Burgos Province; Early Cretaceous (Albian) in age (Delclòs et al. 2007).

Etymology The specific epithet *hispanicus* is the Latin name of the country in which the holotype was found (Spain).

Diagnosis Antennal cavities on ventral side absent; prosternal process parallel-sided; intercoxal process of ventrite 1 slender and pointed at apex; tarsomeres 2–4 lobed ventrally.

Description Length 1.22 mm; maximum body width 0.38 mm, on the elytra; ratio of body length to greatest body width 3.2.

Head with antennal cavities absent on ventral side. Scape robust and globular, widest medially, as long as wide, pedicel smaller than scape, globular; antennomere 3 narrower than pedicel and elongated; antennomeres 4–6 short, quadrate; antennomeres 7–9 slightly transverse, increasing slightly in length from 7 to 9; antennomere 10 forming a single compact club, oval and truncate apically (Fig. 2a).

Ratio of pronotal length to the greatest pronotal width 0.9; anterior margin of pronotum rounded; lateral pronotal margins with a raised margin; pronotal disk coarsely punctured; posterior angles of pronotum right, nor produced and acute (Fig. 2a). Prosternal process parallel-sided, not overlapping mesoventrite, apex acute (Fig. 2b).

Ratio of elytral length to greatest width 1.9; ratio of elytral length to pronotal length 2.4. Elytral punctures not discernible. Elytra exposing last abdominal segment.

Legs with outer edge of tibiae crenulate. Tarsomere 1 reduced and partly concealed; tarsomeres 2–3 narrowly ventrally lobed; tarsomere 4 short, ventrally lobed; tarsomere 5 as long as the other tarsomeres combined; tarsal claws of equal length, simple (Fig. 2c).

Abdomen with intercoxal process of ventrite 1 slender and pointed at apex.

Tribe Rhizophtomini Kirejtshuk and Azar 2009
Genus *Rhizophtoma* Kirejtshuk and Azar 2009

Type species Rhizophtoma elateroides Kirejtshuk and Azar 2009

Rhizophtoma longus sp. nov. (Fig. 3)

Holotype MCNA–9184, a complete specimen, sex unknown, preserved in a piece of fully transparent amber, deposited in the amber collection of the MCNA (Vitoria-Gasteiz, Spain). The specimen has a clear and fully accessible dorsal habitus; by contrast, the ventral habitus has a more restricted view, with some characters not clearly visible.

Type locality Spain: Peñacerrada I, Moraza, Burgos Province; Early Cretaceous (Albian) in age (Delclòs et al. 2007).

Etymology Specific epithet *longus* is Latin, after the length of the holotype, the largest in the genus.

Diagnosis Pronotum with sides parallel, not crenulated; pronotal apical angles acutely projecting; elytral punctures seriate.

Description Body flattened, lateral margins parallel; dorsal surface with moderately conspicuous and sub-recumbent fine and short hairs. Length 1.42 mm measured in dorsal view, but part of the head is declined; maximum body width 0.46 mm; ratio of body length to greatest body width 3.1.

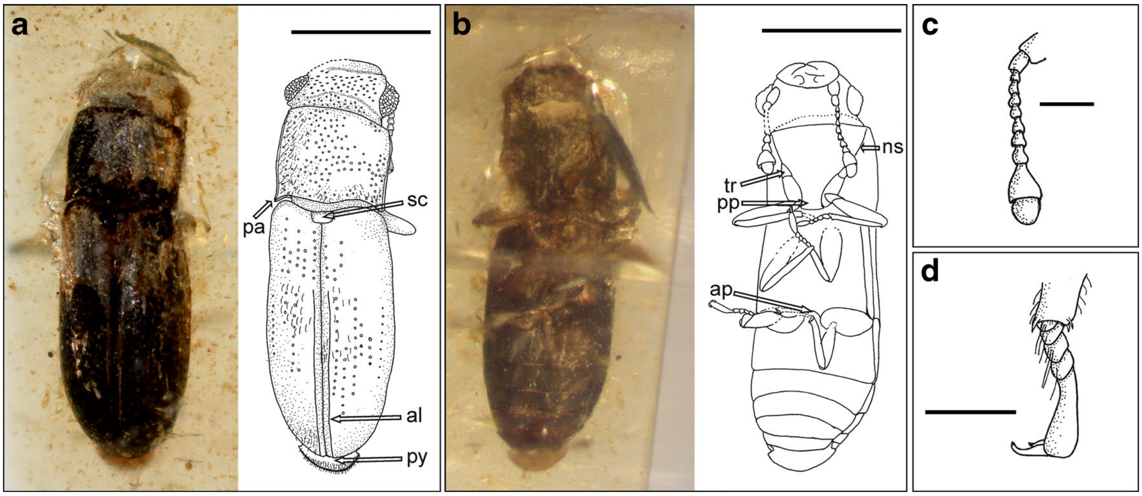

Fig. 3 *R. longus* sp. nov., MCNA–9184, holotype, from Spain; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus; **c** camera lucida illustration of antenna; **d** camera lucida illustration of metatarsi. *Scale bars* **a**, **b**= 0.5 mm; **c**, **d**=0.1 mm. Abbreviations: pronotal apical angles, *pa*; absutural lines, *al*; scutellum, *sc*; pygidium, *py*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*

Head narrower than prothoracic width, triangular, with elongate rostrum; strongly declined, without constriction posteriorly; vertex of head sparsely and coarsely punctured (Fig. 3a). Compound eyes small, entire, coarsely faceted. Antennal insertion apparently concealed from above; antennal cavities absent on ventral side; antennae 11-segmented, capitate, with two-segmented club; extending posteriorly to middle of prothorax. Scape oval, longer than wide; pedicel smaller than scape, suboval; antennomeres 3–9 subconical, narrower than pedicel, wider apically; antennomere 10 and 11 forming a club; antennomere 10 widest, cup-shaped, receiving antennomere 11; antennomere 11 subconical and rounded apically (Fig. 3c).

Prothorax subquadrate, 1.1 times wider than long, parallel-sided; anterior margin of pronotum straight, anterior angles rounded; lateral margins carinate but not crenulated; posterior angles of pronotum acutely projecting; posterior margin of pronotum slightly sinuate with a rounded projection in the middle (Fig. 3a). Pronotal disk coarsely punctured. Base of prothorax distinctly narrower than elytral bases. Prosternum anteriorly very long, 3.2 times the distance between procoxae. Prothoracic episternum clearly delimited by complete notosternal suture (Fig. 3b). Prosternal process gradually narrows and then expands, not overlapping mesoventrite.

Scutellum strongly transverse. Ratio of elytral length to greatest width 1.9; ratio of elytral length to pronotal length 2.7. Elytral margins carinate; elytral disk with seriate punctures; absutural lines distinctly expressed along the apical two thirds of the elytra (Fig. 3a). Elytra entire, exposing pygidium.

Procoxal cavities strongly transverse, externally separated by less than one procoxal length; procoxal trochantins exposed. Mesocoxae hidden under the legs. Metacoxal cavities widely separated. Trochanters prominent; subtriangular tibiae. Tarsal formula 5–5–5, first tarsomere reduced, partially concealed by the tibia; tarsomeres 2–4 short, narrowly lobed ventrally; tarsomere 5 longer than the rest combined; tarsal claws of equal length, simple (Fig. 3d).

Five abdominal ventrites. Abdomen with intercoxal process of ventrite 1 slender and rounded at apex (Fig. 3b). Postcoxal lines on ventrite 1 absent; ventrite 1 the longest, similar length to ventrites 2 and 3 together; ventrites 2–4 slightly decreasing in length; ventrite 5 increasing in length compared with the previous ventrite, 1.5 times the length of ventrite 2.

Remarks Although the resemblance of *Rhizophtoma longus* sp. nov. to *R. elateroides* and *R. synchrotronica* is evidenced by an uncommon set of characters, they are not completely identical. *R. longus* sp. nov. is slightly longer than the other two and has a subquadrate pronotum with the margins not crenulated, similar to *R. synchrotronica* but differing from the latter by the posterior angles of the pronotum, which are acutely projecting, and by the seriate punctures along the elytral disk; in *R. synchrotronica*, the posterior angles of the pronotum are straight and the punctures on the elytral disk are diffuse. In contrast, *R. elateroides* has a bell-shaped pronotum with crenulated lateral margins; although the posterior angles of the pronotum are acutely projecting and it has a sinuate posterior margin, like the new species *R. longus* sp. nov., it can be easily differentiated by the general shape of the anterior portion of the pronotum.

Additional material The specimens MCNA–9317 and MCNA–9552 were also collected in Peñacerrada I, like the holotype of *R. longus* sp. nov. This material is included in two amber pieces with high transparency, but their conservation precludes any certain placement beyond their resemblance with the new species *R. longus* sp. nov. described above.

Specimen MCNA–9317 (Fig. 4a) shares with *R. longus* sp. nov. in its shape and size, antennal morphology and general

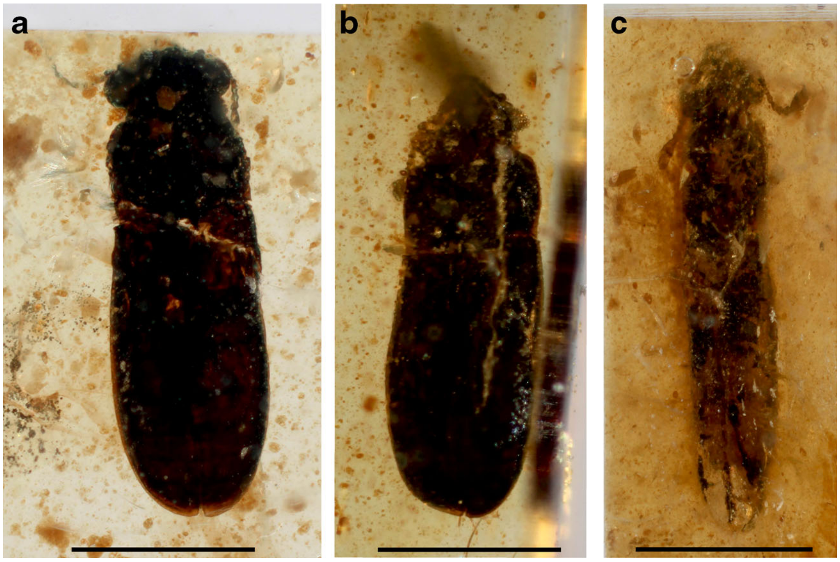

Fig. 4 Photos of additional specimens, from Spain; **a** specimen MCNA–9317; **b** specimen MCNA–9552; both specimens (**a**) and (**b**) associated with *R. longus* sp. nov.; **c** specimen MCNA–9158, unknown emplacement beyond Monotomidae. *Scale bars*=0.5 mm

appearance. However, some differences are evident in the pronotal lateral margins, which are slightly sinuate and confer to the pronotum, a bell-shaped appearance only on the right side, more similar to *R. elateroides*; however, this visual effect may also be attributed to its preservation state because the left side seems to have a parallel margin, as occurs in *R. longus* sp. nov.

Specimen MCNA–9552 (Fig. 4b) is slightly smaller than *R. longus* sp. nov. but shares all the diagnostic characters of the new species. The preservation of this sample precludes a more complete analysis: it has a longitudinal fracture along the entire body length and the left side of the head and pronotum is degraded to some extent.

Unplaced specimens One additional piece of amber from Peñacerrada I, MCNA–9158 (Fig. 4c), contains one specimen with general features that resemble those of species in the Monotomidae (see "Discussion"). Some general characters suggest its placement in Rhizophtomini: head triangular; absence of neck constriction; antennae 11-segmented, with two-segmented club, antennomere 10 the widest, cup-shaped, receiving antennomere 11, rounded apically; pronotum parallel and elytra subparallel-sided. However, no more details are available as the body of this specimen has been degraded by fungal growth, covering most of the ventral habitus; additionally, part of the head and apical part of the body are completely degraded. As a result, it is impossible to observe all the diagnostic characters needed to firmly place this specimen in any tribe or genera, and thus its classification remains unclear.

Discussion

Taxonomy

Extant Monotomidae share a set of characters that differentiate them from related families: (1) generally narrow-elongate body; (2) head prognathous, with lateral faceted eyes; (3) antennal insertions lateral and partly hidden by projections of frons; (4) antennae short, appearing ten-segmented (antennomere 10 and 11 fused) with a distinct one- or two-segmented club; (5) fronto-clypeal suture absent; (6) tarsal formula 4–4–4, 5–5–5, or a combination of those; (7) abdomen with five ventrites: ventrites 1 and 5, elongated; ventrites 2–4, comparatively short, subequal; (8) procoxae rounded with hidden trochantins in most genera, transverse with partly exposed trochantins in *Rhizophagus*, *Aneurops* Sharp, 1900 and *Malinica* Sengupta, 1988; and (9) procoxal cavities broadly closed externally (Sengupta 1988; Bousquet 2010; McElrath et al. 2012).

Kirejtshuk et al. (2009) and Kirejtshuk and Azar (2013) described the fossil genera *Rhizophtoma* and *Rhizobactron* Kirejtshuk, 2013 from Lebanese amber, and included them in the new subfamily Rhizophtominae within Monotomidae. Although not all the diagnostic characters of Monotomidae were present in the fossils described (in the genus *Rhizophtoma*, antennomere 10 is not fused with 11, and the genus *Rhizobactron* has a three-segmented club and ventrite 1 is as long as ventrites 2–4), they were classified in family Monotomidae based on their general resemblance to extant monotomid genera (Kirejtshuk et al. 2009; Kirejtshuk and Azar 2013). Bouchard et al. (2011) reduced the fossil subfamily to tribal rank within the Monotominae, but Kirejtshuk and Azar (2013) retained its rank of subfamily when describing the fossil genus *Rhizobactron.* The new tribe Cretakarenniini shows intermediate character states between the previously described monotomid fossils and the extant genera of Monotominae. Based on this, we believe that the position of Bouchard et al. (2011), who ranked the taxon as a tribe of Monotominae, is more appropriate until a more exhaustive analysis is performed. Indeed, Monotominae include genera with ambiguous characters such as *Aneurops* and *Malinica*, with transverse procoxae and partly exposed trochantins, as in *Rhizophagus*, the only genus of Rhizophaginae.

Species in Rhizophtomini may be easily distinguished from the remaining groups by the following combination of characters: (1) 11-segmented antennae, with a two- or three-segmented club; (2) absence of neck constriction; (3) pronotum subquadrangular, about as long as wide or, failing that, with strongly projecting posterior angles; (4) setose and coarsely microreticulated integument of dorsum; (5) diffusely punctured elytra; (6) expressed absutural lines (although not described in *Rhizobactron elateroides*, these are clearly visible in the holotype); (7) procoxal cavities transverse, with exposed trochantins (unknown in *Rhizobactron*); (8) laterally closed mesocoxal cavities; (9) lack of submetacoxal lines; (10) elongate trochanters; and (11) narrowly lobed tarsi. Tribe Rhizophtomini comprises fossil species *Rhizophtoma elateroides*, *R. synchrotronica* and *Rhizobactron marinae* from Lebanese amber and *Rhizophtoma longus* sp. nov. from Spanish amber (Table 1).

Species in Cretakarenniini, the new tribe described herein, may be distinguished from the remaining groups by the following combination of characters: (1) antennae short, ten- segmented, with one-segmented club; (2) vertex of head punctured; (3) neck constriction present; (4) pronotum as long as the widest length; (5) pronotal lateral margin finely crenulated, and setiferous; (6) escutellum as long as wide, with rounded margins; (7) procoxal cavities transverse with exposed trochantins; (8) expressed absutural lines; (9) metacoxae widely separated; (10) subtriangular tibiae; and (11) tarsal formula 5–5–5, with some tarsomeres narrowly ventrally lobed. Tribe Cretakarenniini comprises two fossil species described herein: *Cretakarenni birmanicus* sp. nov. and *C. hispanicus* sp. nov. (Table 1).

As such, a new key for the subfamilies and tribes in Monotomidae is required and should also include a key to differentiate fossil species from tribes Rhizophtomini and the new tribe Cretakarenniini. Modified from Sengupta (1988), the new taxa described in this work are shown in bold:

1. Antennae ten-segmented; antennal cavities well-developed and strongly converging; procoxal cavities distinctly transverse with exposed trochantins; and neck constriction absent ....Subfamily Rhizophaginae

   Antennae 11-segmented, neck constriction absent or antennae ten-segmented, neck constriction present, usually prominent; procoxal cavities either round with hidden trochantins or distinctly to somewhat transverse with exposed (at least partially) trochantins (Subfamily Monotominae) 2
2. Procoxal cavities distinctly transverse with exposed trochantins; trochanters elongate; expressed absutural lines along elytra (fossil taxa) 3

   Procoxal cavities only somewhat transverse with partially exposed trochantins or round with hidden trochantins; trochanters short; absutural lines not expressed along elytra (Recent taxa) 8
3. Antennae 11-segmented, with two- or three-segmented club; neck constriction absent; pronotum subquadrangular, about as long as wide or with strongly projecting posterior angles; scutellum transverse (Tribe Rhizophtomini) 4

   Antennae ten-segmented, with one-segmented club; neck constriction present; pronotum as long as wide, widest on anterior half; scutellum as long as wide (**Tribe Cretakarenniini tribe nov.**) 7
4. Antennae with three-segmented club ....*Rhizobactron marinae*

   Antennae with two-segmented club (*Rhizophtoma*) 5
5. Pronotum bell-shaped with crenulated lateral margins ....*Rhizophtoma elateroides*

   Pronotum subquadrate with margins not crenulated 6
6. Posterior angles of pronotum straight; punctures on the elytral disk diffuse ....*Rhizophtoma synchrotronica*

   Posterior angles of pronotum acutely projecting; punctures seriate along elytral disk ....***Rhizophtoma longus* sp. nov.**
7. Antennal cavities present on ventral side; intercoxal process of ventrite 1 broad and rounded at apex; tarsomeres 1–3 short; tarsomere 4 narrowly lobed ventrally ....***Cretakarenni birmanicus* sp. nov.**

   Antennal cavities on ventral side absent; intercoxal process of ventrite 1 slender and pointed at apex; tarsomeres 2–4 lobed ventrally ....***Cretakarenni hispanicus* sp. nov.**
8. Tarsal formula 5–5–5 or 4–4–4, in both sexes; species narrow or cylindrical; coxae almost contiguous 9

   Tarsal formula 5–5–4 in male and 5–5–5 in female; species different in shape; coxae well separated 10
9. Tarsal formula 4–4–4 in both sexes; head with distinct tempora; front margin of clypeus evenly rounded, with a transverse line on the vertex and the latter characteristically excavated; elytra characteristically sinuate near middle; prothorax somewhat pear-shaped ....Tribe Lenacini

   Tarsal formula 5–5–5 in both sexes; head markedly long, front margin of clypeus notched, without transverse line and excavation on vertex; elytra parallel-sided ....Tribe Thionini
10. Maxillary and labial palpi with segment 2 markedly enlarged ....Tribe Monotomini

    Maxillary and labial palpi with segment 2 normal ....Tribe Europini

Palaeoecology

Biological and ecological diversification was not treated in previous works describing fossil monotomids since such information is usually speculative. Additionally, Monotomidae are found in very diverse environments. While most *Rhizophagus* species are considered saproxylic and inhabit subcortical environments and prey on bark beetles and/or feed on fungal mycelia or spores, *Monotoma* species are primarily found in decomposing plant matter, inhabiting the fruiting bodies of ascomycete fungi (Bousquet 2002; Majka and Bousquet 2010). Although the feeding habits of monotomids are poorly documented, the two genera mentioned previously are mycophagous, feeding on fungi and products of fungal decay under tree bark or in decaying matter (Bousquet 2010, and references therein). Fungi or fungal by-product association seems the most parsimonious ecological niche for fossil monotomids from the Cretaceous, although it is a comparison with the behaviour of the current groups, and other associations may have occurred. Indeed, 78 % of the beetle families found in amber are associated with a saproxylic way of life (Molino-Olmedo 1999). These groups, which are associated with fungal subcortical habitats and with leaf and wood litter, are the most common groups of beetles found in the different deposits of Cretaceous amber worldwide; examples can be found in Kirejtshuk and Azar (2013), Peris et al. (2013, 2014, 2015) and Soriano et al. (2014), along with other examples among the literature on Cretaceous beetles in amber.

Peris et al. (2014) updated the list of taxa described from Cretaceous amber deposits of Lebanon, Spain and Myanmar that have any resemblance. With the new monotomid species described herein, the list has increased. These new species, together with other examples awaiting future description, make it possible to assess the relationship between the ancient environments in which the resin was produced. Despite their different ages, all three ambers share their botanical origin and similar palaeoenvironmental conditions, suggesting that similar ancient life will be found at these sites, as already demonstrated by various examples (see Peris et al. 2014).

Conclusions

Bioinclusions embedded in Cretaceous amber often provide the ancient record for a family or even new extinct groups. The problem is how to relate new taxa to existing ones. Additionally, the relationship among the subfamilies, tribes and genera of Monotomidae has never been analysed in any large-scale molecular or morphological analysis. Bousquet (2010) predicted that several of the genera may be polyphyletic as they currently stand. The result is that the correct relationship between extant monotomid genera/species remains unclear.

The description of the three new monotomid fossil species from Spain (*R. longus* and *C. hispanicus*) and Myanmar (*C. birmanicus*) shows, on one hand, that ancient monotomids had intermediate characters that currently differentiate more recent groups, and that those characters were also diverse in the past. With the new variability described from fossils, analyses aimed at clarifying the position of the monotomid species will be more accurate. On the other hand, despite the different ages of the amber outcrops from Lebanon, Spain and Myanmar, all three sites are revealing an increasing number of shared fauna. This suggests a common denominator between sites, such as the association of some insect groups with the vegetation responsible for high resin production or similar environmental conditions in Cretaceous forests.

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References

Alekseev, V. I. (2014). *Europs insterburgensis* sp. nov., a new root-eating beetle from Baltic amber (Coleoptera: Monotomidae). *Genus, 25*, 415–420.

Alonso, J., Arillo, A., Barrón, E., Corral, J. C., Grimalt, J., López, J. F., López, R., Martínez-Delclòs, X., Ortuño, V., Peñalver, E., & Trincão, P. R. (2000). A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (northern Spain, Basque-Cantabrian basin). *Journal of Paleontology, 74*, 158–178.

Barrón, E., Comas-Rengifo, J., & Elorza, L. (2001). Contribuciones al estudio palinológico del Cretácico Inferior de la Cuenca Vasco-Cantábrica: los afloramientos ambarígenos de Peñacerrada (España). *Coloquios de Paleontologia, 52*, 135–156.

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D., & Vogler, A. P. (2014). Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology, 39*, 97–110.

Bouchard, P., Bousquet, Y., Davies, A. E., Alonso-Zarazaga, M. A., Lawrence, J. F., Lyal, C. H., Newton, 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.

Bousquet, Y. (2002). Monotomidae Laporte 1840. In R. H. Arnett Jr., M. C. Thomas, P. E. Skelley, & J. H. Frank (Eds.), *American beetles volume 2. Polyphaga: Scarabaeoidea through Curculionoidea* (pp. 319–321). Boca Raton: CRC Press.

Bousquet, Y. (2010). 10.8. Monotomidae Laporte 1840. In R. A. B. Leschen & R. G. Beutel (Eds.), *Handbook of zoology. Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Handbook of zoology, Arthropoda: Insecta (Kristensen NP, Beutel RG, eds)* (pp. 319–324). Berlin: Walter de Gruyter.

Crowson, R. A. (1952). The classification of the families of British Coleoptera (cont.). *The Entomologist's Monthly Magazine, 88*, 121–132.

Cruickshank, R. D., & Ko, K. (2003). Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences, 21*, 441–455.

Delclòs, X., Arillo, A., Peñalver, E., Barrón, E., Soriano, C., López del Valle, R., Bernárdez, E., Corral, C., & Ortuño, V. (2007). Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Palevol, 6*, 135–149.

Engel, M. S., Peris, D., Chatzimanolis, S., & Delclòs, X. (2014). An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain. *Systematics and Evolution*. doi:10.1163/1876312X-45032121.

Grimaldi, D. A., Engel, M. S., & Nascimbene, P. C. (2002). Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates, 3361*, 1–71.

Helm, O. (1896). Beiträge zur Kenntnis den Insekten des bernstein. *Schriften der Naturforschenden Gesellschaft, Danzig*, (N.F.) 8, 220–231.

Kirejtshuk, A. G., & Azar, D. (2013). Current knowledge of Coleoptera (Insecta) from the Lower Cretaceous Lebanese amber and taxonomical notes for some Mesozoic groups. *Terrestrial Arthropod Reviews, 6*, 103–134.

Kirejtshuk, A. G., Azar, D., Tafforeau, P., Boistel, R., & Fernandez, V. (2009). New beetles of Polyphaga (Coleoptera, Polyphaga) from Lower Cretaceous Lebanese amber. *Denisia, 26*, 119–130.

Klebs, R. (1910). Über Bernsteineinschlüsse im Allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schriften der Physikalisch-ökonomischen Gesellschaft, 51*, 217–242.

Larsson, S. G. (1978). Baltic amber. A palaeobiological study. *Entomonograph, 1*, 1–192.

Lawrence, J. F., & Newton, A. F. (1995). Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In J. Pakaluk & S. A. Ślipiński (Eds.), *Biology, phylogeny, and classification of Coleoptera* (pp. 779–1006). Warszawa: Muzeum i Instytut Zoologii PAN.

Lawrence, J. F., Hastings, A. M., Dallwitz, M. J., Paine, T. A. & Zurcher, E. J. (1999). "*Beetles of the world: a key and information system for families and subfamilies.*" CD-ROM, Version 1.0 for MS-Windows. Melbourne: CSIRO Publishing.

Lawrence, J. F., Beutel, R. G., Leschen, R. A. B., & Slipinski, S. A. (2010). Glossary of morphological terms. In R. A. B. Leschen & R. G. Beutel (Eds.), *Handbook of zoology. Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Handbook of zoology, Arthropoda: Insecta (Kristensen NP & Beutel RG, Eds.)* (pp. 9–20). Berlin: Walter de Gruyter.

Lawrence, J. F., Ślipiński, S. A., Seago, A. E., Thayer, M. K., Newton, A. F., & Marvaldi, A. E. (2011). Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici (Warszawa), 61*, 1–217.

Majka, C. G., & Bousquet, Y. (2010). Monotomidae (Coleoptera) of the Maritime Provinces of Canada. *Journal of the Acadian Entomological Society, 6*, 1–8.

Martínez-Delclòs, X., Briggs, D. E. G., & Peñalver, E. (2004). Taphonomy of insects in carbonates and amber. *Paleogeography, Palaeoclimatology, Palaeoecology, 203*, 19–64.

Martínez-Torres, L. M., Pujalte, V., & Robles, S. (2003). Los yacimientos de ámbar del Cretácico Inferior de Peñacerrada (Álava, Cuenca Vasco-Cantábrica): Estratigrafía, reconstrucción paleogeográfica y estructura tectónica. *Estudios del Museo de Ciencias Naturales de Álava, 18*, 9–32.

McElrath, T., Yves B. & McHugh. J.V. (2012). Monotomidae. Root-eating beetles. Version 06 December 2012 (temporary). http://tolweb.org/Monotomidae/9147/2012.12.06 in The Tree of Life Web Project, http://tolweb.org/. Accessed 23 Sept 2014.

Molino-Olmedo, F. (1999). Importancia del ámbar en el registro fósil de Coleópteros saproxílicos. *Estudios del Museo de Ciencias Naturales de Álava, 14*, 211–215.

Nascimbene, P., & Silverstein, H. (2000). The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In D. Grimaldi (Ed.), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey* (pp. 93–102). Leiden: Backhuys Publishers Leiden.

Pakaluk, J., Ślipiński, S. A., & Lawrence, J. F. (1994). Current classification and family-group names in Cucujoidea (Coleoptera). *Genus (Wroclaw), 5*, 223–268.

Peñalver, E., & Delclòs, X. (2010). Spanish amber. In D. Penney (Ed.), *Biodiversity of fossils in amber from the major world deposits* (pp. 236–270). Manchester: Siri Scientific Press.

Peris, D., Sánchez-García, A., Soriano, C. & Delclòs, X. (2013). Beetle fauna in the Early Cretaceous Spanish amber. In *The 6th International congress on fossil Insect, Arthropods and Amber—Abstract Book* (pp. 74–75). The Lebanese University and the Municipality of Byblos.

Peris, D., Chatzimanolis, S., & Delclòs, X. (2014). Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber. *Cretaceous Research, 48*, 85–95.

Peris, D., Philips, T. K., & Delclòs, X. (2015). Ptinid beetles from the Cretaceous gymnosperm-dominated forests. *Cretaceous Research, 52*, 440–452.

Poinar, G. O., Jr. (1992). *Life in Amber*. Stanford: Stanford University Press.

Robertson, J. A., Whiting, M. F., & McHugh, J. V. (2008). Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea). *Molecular Phylogenetics and Evolution, 46*, 193–205.

Sánchez-García, A., Peñalver, E., Pérez-de la Fuente, R., & Delclòs, X. (2014). A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: palaeobiological implications. *Journal of Systematic Palaeontology*. doi:10.1080/14772019.2014.944946.

Sengupta, T. (1988). Review of the genera of the family Rhizophagidae (Clavicornia: Coleoptera) of the world. *Memoirs of the Zoological Survey of India, 17*, 1–58.

Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., & Li, X. (2012). Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research, 37*, 155–163.

Soriano, C., Pollock, D., Néraudeau, D., Nel, A., & Tafforeau, P. (2014). First fossil record of polypore fungus beetles from Lower Cretaceous amber of France. *Acta Palaeontologica Polonica, 59*, 941–946.

Weitschat, W., & Wichard, W. (2002). *Atlas of the plants and animals in Baltic amber*. Munich: Verlag Dr. Friedrich Pfeil.

Zherikhin, V. V., & Ross, A. J. (2000). A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, London (Geology), 56*, 3–10.