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Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber

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ABSTRACT

Twenty specimens of Staphylinidae (Coleoptera: Polyphaga) were found in the Early Cretaceous Spanish amber. Two new genera and four new species are reported in these samples: *Cretasonoma corinformibus* in the supertribe Faronitae, and *Penarhytus tenebris* in the supertribe Pselaphitae, both in the subfamily Pselaphinae; *Prosolierius parvus* in the subfamily Solieriinae; and *Kachinus magnificus* in the subfamily Scydmaeninae. Both *Prosolierius* and *Kachinus* exemplify the similarity between Cretaceous Spanish amber and Cretaceous Lebanese and Burmese amber, despite their different ages. Pselaphinae is the most common rove beetle subfamily in amber inclusions worldwide, their small size and cryptic litter-dwelling perhaps make them susceptible to being trapped by resin and conserved. *Kachinus magnificus*, reported in six of the Scydmaeninae specimens from Spanish amber, is the oldest species formally described for the subfamily. *Penarhytus tenebris* and *Prosolierus parvus* come from the Peñacerrada I amber deposit, *Kachinus magnificus* from the El Soplao amber deposit, and *Cretasonoma corinformibus* is found at both locations, in the Basque-Cantabrian Basin, on the northern Iberian Plate (today the Iberian Peninsula).

1. Introduction

The beetle family Staphylinidae Latreille, 1802, also commonly known as rove beetles, currently include more than 57,000 described species (extant and extinct) (Newton, unpublished database). The Staphylinidae, as redefined with the addition of Scydmaeninae, are the largest family of Coleoptera (Grebennikov and Newton, 2009) and the largest family of any animal phylum (Thayer et al., 2012). The oldest known fossils of a rove beetle were reported by Gore (1988) and Fraser et al. (1996) from some Late Triassic compression deposit in northern Virginia (USA, late Carnian–early Norian, 220–230 Ma). They were examined by D. Grimaldi but the coarse grain of the matrix precludes the observation of any details (Chatzimanolis et al., 2012). As far as a second record of the same deposit is concerned, *Leehermania prorova* Chatzimanolis, Grimaldi, and Engel, 2012 was erected as the earliest staphylinid (Chatzimanolis et al., 2012).

Up to now, several papers describe new Mesozoic staphylinid taxa; before description of *Leehermania prorova*, 30 new species were described from Jurassic deposits, six species from Jurassic–Cretaceous deposits, and 30 species from Cretaceous deposits (Thayer et al., 2012). A review of the Mesozoic fossil staphylinids was provided by Chatzimanolis et al. (2012), however, several new species have recently been described (see Table 1).

The objective of the present study is to examine and describe a total of 20 staphylinid beetle specimens found in Early Cretaceous Spanish amber. We also provide updated data on the Staphylinidae in the fossil record, and propose the possibility of there being similar palaeoenvironmental conditions in Lebanese, Spanish, and Burmese Cretaceous resinous forests.

2. Geographic and geological context

All specimens were derived from the amber deposits of Peñacerrada I and El Soplao (northern Spain, Fig. 1). The samples are dated from the Early Cretaceous; as early Albian in age (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010). Both

Abbreviations: CES, El Soplao collection in Cueva El Soplao, Celis, Cantabria, Spain; Fm, Formation; Ma, Millions of years before present; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

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Table 1
New Mesozoic fossil taxa described in Staphylinidae since last review by Chatzimanolis et al. (2012).

Age	Taxon	Origin	Reference
Middle Jurassic	*Juroglypholoma antiquum* Cai, Huang, Thayer and Newton, 2012	Jiulongshan Formation, China	Cai et al., 2012
	Sinanthobium daohugouense Cai and Huang, 2013		Cai and Huang, 2013a
Late Jurassic	*Juroglypholoma talbragarense* Cai, Yan, Beattie, Wang and Huang, 2013	Talbragar Fish Bed, Australia	Cai et al., 2013a
	Protachinus minor Cai, Yan, Beattie, Wang and Huang, 2013		
Early Cretaceous	*Cretoprosopus problematicus* Solodovnikov and Yue, 2012	Yixian Formation, China	Solodovnikov et al., 2012
	Cretoquedius distinctus Solodovnikov and Yue, 2012		
	Cretoquedius dorsalis Solodovnikov and Yue, 2012		
	Cretoquedius infractus Solodovnikov and Yue, 2012		
	Durothorax creticus Solodovnikov and Yue, 2012		
	Megolisthaerus minor Cai and Huang, 2013		Cai and Huang, 2013b
	Mesocoprophilus clavatus Cai and Huang, 2013		Cai and Huang, 2013c
	Mesostaphylinus antiquus Solodovnikov and Yue, 2012		Solodovnikov et al., 2012
	Mesostaphylinus elongates Solodovnikov and Yue, 2012		
	Mesostaphylinus yixianus Solodovnikov and Yue, 2012		
	Paleothius gracilis Solodovnikov and Yue, 2012		
	Paleowinus ambiguus Solodovnikov and Yue, 2012		
	Paleowinus chinensis Solodovnikov and Yue, 2012		
	Paleowinus fossilis Solodovnikov and Yue, 2012		
	Paleowinus mirabilis Solodovnikov and Yue, 2012		
	Paleowinus rex Solodovnikov and Yue, 2012		
	Protodeleaster glaber Cai, Thayer, Huang, Wang and Newton, 2013		Cai et al., 2013b
	Pseudanotylus archaicus (Yue, Makranczy and Ren, 2012)		Cai and Huang, 2013d
	Quedius cretaceous Cai and Huang, 2013		Cai and Huang, 2013e
	Sinoxytelus transbaicalicus Cai, Yan and Vasilenko, 2013	Urey beds, Russia	Cai et al., 2013c
	Thayeralinus fieldi Solodovnikov and Yue, 2012	Yixian Formation, China	Solodovnikov et al., 2012
	Thayeralinus fraternus (Zhang, Wang and Xu, 1992)		
	Thayeralinus giganteus Solodovnikov and Yue, 2012		
	Thayeralinus glandulifer Solodovnikov and Yue, 2012		
	Thayeralinus longelytratus Solodovnikov and Yue, 2012		
Late Cretaceous	*Phloeocharis agerata* Chatzimanolis, Newton, and Engel, 2013	Raritan Formation, New Jersey	Chatzimanolis et al., 2013

outcrops are located in the Basque-Cantabrian Basin, El Soplao outcrop is located in the western area, whereas Peñacerrada I is located in the eastern area of the Basin (see locations in Peñalver and Delclòs, 2010).

The El Soplao amber-bearing deposit is included in the Las Peñosas Formation, in a unit of heterolithic sandstones–siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (Najarro et al., 2009). The Peñacerrada I amber-bearing deposit lies within the Escucha Formation, in the middle subunit, which contains abundant grey lutitic and silty levels that are rich in coal at the top of the filling sequences of the interdistributary deltaic bays (Martínez-Torres et al., 2003). It is characterized by sandstones and siliceous microconglomerates, which originated during the period of maximum regression and deltaic progradation (Martínez-Torres et al., 2003). Las Peñosas Fm. and Escucha Fm. are considered contemporary in age, based on geological features and biological palaeobiological content (Barrón et al., 2001; Najarro et al., 2009, 2010; Peñalver and Delclòs, 2010; Pérez-de la Fuente et al., 2012).

A total of 2843 bioinclusions were reported from Peñacerrada I (Peris et al., 2013). The majority of the inclusions belong to Arthropoda, there are some Crustacea, Chelicerata and several Hexapoda; among this last subphylum, representatives of the orders Collembola, Archaeognatha, Blattaria, Isoptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, Neuroptera, Hemiptera, Raphidioptera, Coleoptera, Trichoptera, Hymenoptera, Lepidoptera, and Diptera were found (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010).

From the El Soplao deposit, 546 bioinclusions were reported (Pérez-de la Fuente, 2012; Peris et al., 2013), including fungi, plants, and diverse arthropods. The Hexapoda orders found are Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Hymenoptera, and Diptera; the last two orders are the most abundant (Najarro et al., 2010).

Coleoptera is one of the most common insect orders found in Spanish amber, with 68 specimens from the Peñacerrada I deposit and 51 from the El Soplao. Note the different proportions in the total number of beetles between the two deposits, *i.e.*, 68 beetles from 2843 bioinclusions in Peñacerrada I; and 51 from 546 bioinclusions in El Soplao. Coleoptera was more abundant in El Soplao than in Peñacerrada I, maybe due to different local palaeoenvironmental conditions at the two deposits.

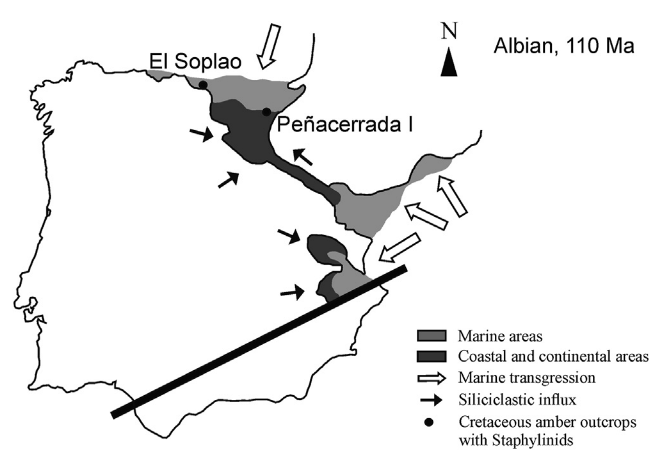

Fig. 1. Palaeogeographic map of the Iberian Peninsula during the Albian with the locations of the Peñacerrada I and the El Soplao amber deposits (Early Cretaceous). Modified from Mas et al. (2004).

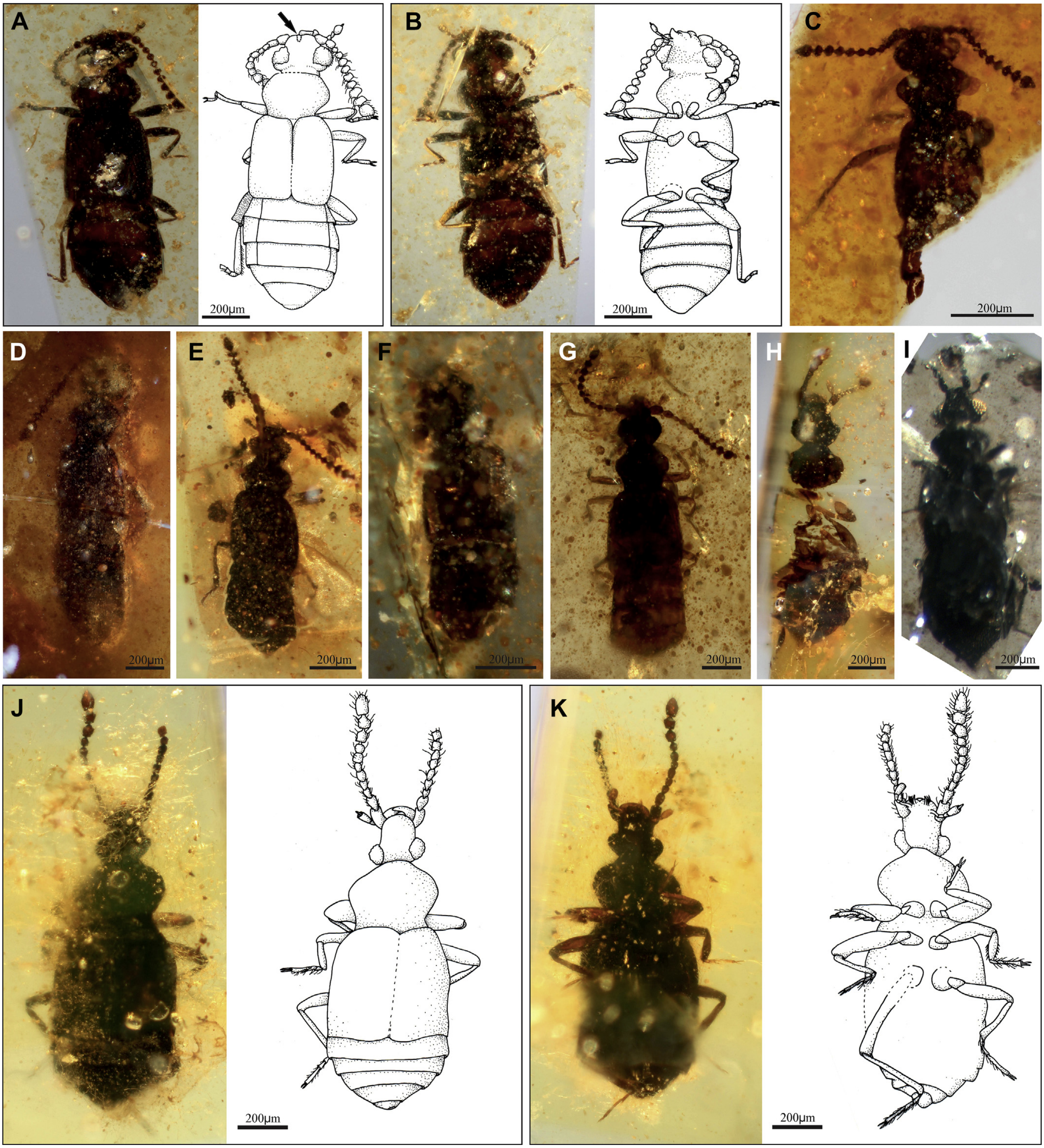

Fig. 2. *Cretasonoma corinformibus* gen. et sp. nov. (A–I) and *Penarhytus tenebris* gen. et sp. nov. (J–K). **A**. Photo and camera lucida drawing of MCNA–8654, holotype, from Peñacerrada I amber; dorsal habitus; the arrow indicates the sulcus between the antennal tubercles. **B**. Photo and camera lucida drawing of MCNA–8654, holotype; ventral habitus. **C**. Photo of MCNA–9990, paratype, from Peñacerrada I amber; dorsal habitus. **D**. Photo of MCNA–12663, paratype, from Peñacerrada I amber; dorsal habitus. **E**. Photo of MCNA–13254, paratype, from Peñacerrada I amber; dorsal habitus. **F**. Photo of MCNA–14251, paratype, from Peñacerrada I amber; dorsal habitus. **G**. Photo of CES–433.1, paratype, from El Soplao amber; dorsal habitus. **H**. Photo of MCNA–14247, other material studied from Peñacerrada I amber, tentatively placed in this species; dorsal habitus. **I**. Photo of MCNA–14265, other material studied from Peñacerrada I amber, tentatively placed in this species; dorsal habitus. **J**. Photo and camera lucida drawing of MCNA–12683, holotype, from Peñacerrada I amber; dorsal habitus. **K**. Photo and camera lucida drawing of MCNA–12683, holotype; ventral habitus. Scale bars: 200 μm.

3. Material and methods

The samples described in this paper are named as follows. Pieces from the Peñacerrada I deposit: MCNA–8654, MCNA–8912, MCNA–9990, MCNA–12663, MCNA–12683, MCNA–12752, MCNA–13254, MCNA–13611, MCNA–14190, MCNA–14247, MCNA–14251, and MCNA–14265, all of them housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). Pieces from the El Soplao deposit: CES–059.3, CES–433.1, CES–433.2, CES–463, CES–487, CES–566, CES–572, and CES–601, all of them housed at the Institutional Collection from the El Soplao amber deposit, located in the laboratory of the Cueva El Soplao (Celis, Cantabria, Spain). The amber pieces were cut and embedded in a transparent epoxy resin; the preparations were polished once the polymer had hardened (see Corral et al., 1999). All 20 specimens reported in this paper were examined under three different lenses, *i.e.*, a Leica MS5 binocular lens, a Motic BA310 microscope, and an Olympus BX–41 compound microscope with reflected and transmitted light. Photomicrographs were acquired with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens, arranged and optimized with CombineZ and edited with Photoshop Elements 10 and CorelDraw X6. Illustrations were prepared with the aid of a camera lucida attached to the Olympus BX–41 compound microscope.

The total length of the specimens was measured from the anterior margin of the heads to the posterior margin of the body.

4. Systematic palaeontology

Suborder: Polyphaga Emery, 1886
Superfamily: Staphylinoidea Latreille, 1802
Family: Staphylinidae Latreille, 1802
Subfamily: Pselaphinae Latreille, 1802
Supertribe: Faronitae Reitter, 1882
Genus *Cretasonoma* Peris, Chatzimanolis and Delclòs gen. nov.

Derivation of name. The name of the genus is based on the prefix *creta* – from the Cretaceous age of the sample, plus – *sonoma* from the genus *Sonoma* Casey, 1886; a similar extant genus in the tribe.

Type species. Cretasonoma corinformibus sp. nov.

Diagnosis. Antennal tubercles well separated by sulcus extending anteriorly; scape twice as long as pedicel; antennae not reaching beyond one half of the body; large eyes; elytra more than twice as long as pronotum; metasternum longer than mesocoxae.

Description. Minute; body subparallel-sided, dorso-ventrally flattened. Head small, transverse, constricted laterally immediately behind compound eyes to form broad neck; head with large compound eyes. Maxillary palpus 4-segmented with extra small 'pseudosegment'. Antennae with 11 antennomeres; antennal insertions separated. Pronotum transverse, with rounded lateral margins. Elytra as wide as, but longer than pronotum. Tarsal formula 3–3–3; femora robust. Abdomen with six visible sterna.

Cretasonoma corinformibus Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 2A–I
2000 Coleoptera, Staphylinidae in dorsal view, Alonso et al., Fig. 12.6.

Derivation of name. The specific name *corinformibus* is derived from the addition of the Latin *cor* and *informibus*, meaning 'heart shape' and it refers to the pronotum appearance.

Holotype. MCNA–8654 (Fig. 2A–B). The specimen is well preserved within a relative transparent sample of amber.

Paratypes. MCNA–9990 (Fig. 2C), MCNA–12663 (Fig. 2D), MCNA–13254 (Fig. 2E), MCNA–14251 (Fig. 2F), and CES–433.1 (Fig. 2G). MCNA–9990 is an incomplete specimen, lacking almost all the abdomen. Ventral habitus is impossible to observe due the debris in the piece. MCNA–12663 is poorly preserved, lacking the right part of the head under an opaque resin cast. The specimen features seem generally charred. MCNA–13254 is complete, but only the dorsal habitus is available. The amber piece is poorly translucent, which makes observation of the beetle characters difficult. CES–433.1 is complete and well preserved, accessible from both dorsal and ventral habitus, embedded in a relative transparent sample of amber in syninclusion with CES–433.2 (*Kachinus magnificus* gen. et sp. nov.).

Other materials examined. MCNA–14247 (Fig. 2H) and MCNA–14265 (Fig. 2I). Specimen MCNA–14247 missing elytra and large part of the abdomen. Specimen MCNA–14265 is slightly larger (total length 1.6 mm) than the rest of the specimens but the morphology of the head and prothorax is identical. Unfortunately, the specimen is blackened, and it is difficult to observe the characters over the body surface, which precludes us from describing it as a different species.

Type locality. All specimens with MCNA – come from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain). The amber was found at the middle subunit of the Escucha Fm., and is early Albian in age (Delclòs et al., 2007, and references therein). CES–433.1 is from the El Soplao deposit, in the municipality of Celis (Cantabria, Spain). The amber was found at the Las Peñosas Fm., and is early Albian in age (Najarro et al., 2009).

Description. Total length (as preserved) approximately 1.16 mm; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head small, narrower than pronotum, width (including compound eyes) 0.26 mm, upper interocular distance 0.13 mm; compound eyes large sized. Maxillae not visible except maxillary palp, maxillary palps with four palpomeres plus small apical 'pseudosegment', base of maxillary palpomere I not visible, palpomere I thinner and longer than palpomere II; palpomere II expanded apically; palpomere III spherical, shorter and wider than II, palpomere IV expanded, wide, with rounded apex, nearly as long as palpomere II but much wider than rest of palpomeres. Antennae less than 0.5 times as long as the body; scape and pedicel robust, scape longer than wide, twice as long as pedicel; pedicel almost spherical; antennomere III small, half the width of antennomere II and approximately 0.3 times its length; antennomeres III–VIII subquadrate, gradually increasing in size; antennomeres IX and X transverse, antennomere X wider than IX; antennomere XI has width similar to antennomere X, but 1.5 times longer than antennomere IX, apically compressed. Pronotum length 0.15 mm; pronotum wider than head, transverse, maximum width at middle, maximum width of pronotum 0.28 mm, lateral margins at middle gently convex, but becoming concave posteriorly; posterior margin relatively straight in dorsal view. Elytra truncate exposing five tergites, about as wide as pronotum, at suture clearly longer than pronotum; elytra twice as long as pronotum; combined width of elytra 0.34 mm, length of elytron 0.37 mm, posterior margin straight, gradually becoming wider; fovea not clearly visible. Metasternum three times longer than mesocoxae. Legs relatively short; procoxae and mesocoxae narrowly separated; metacoxae contiguous; metatrochantin exposed; femora robust; tibiae with spines apically; tarsi with basal two tarsomeres short, similar in length, third tarsomeres longer than preceding two; two apical tarsal claws. Abdomen nearly as wide as posterior width of elytra and longer than it, maximum width of abdomen 0.38 mm, near middle; individual abdominal segments largely transverse except sternum VIII, enlarged and more narrow apically.

Discussion. Cretasonoma corinformibus gen. et sp. nov. is described as belonging to the subfamily Pselaphinae based on the characters: 1) antennae inserted anterior to a line drawn between anterior margins of eyes; 2) elytra exposing some abdominal segments; 3) body robust; 4) maxillary palps with an apical 'pseudosegment'; and 5) tarsi 3–3–3 (Newton et al., 2001). *Cretasonoma* gen. nov. believed to belong to the supertribe Faronitae due to the presence of the following defining visible characters: 1) filiform or clavate antennae, without final club; 2) double clawed tarsi; 3) first two tarsomeres short and with similar length; 4) third tarsomeres much longer; 5) metacoxae contiguous, each projected to the trochanter union (Newton et al., 2001). *Cretasonoma* gen. nov. might be confused with several Recent genera in the supertribe because of the similarity between many of them. *Cretasonoma* gen. nov. shares with *Sonoma* the rounded lateral borders of the pronotum, elytra much longer than pronotum and long metasternum, and with *Megarafonus* Casey, 1987 the antennal tubercles separated by sulcus. However, *Cretasonoma* gen. nov. can be distinguished from *Sonoma* since in *Sonoma* the pronotum is clearly narrower than the elytra, the antennal tubercles are connected by a concave frontal bridge, and by smaller-sized eyes. *Cretasonoma* gen. nov. can be distinguished from *Megarafonus* since in *Megarafonus* the elytra are short, similar in length to the pronotum, and by a short metasternum, about as long as mesocoxae. *Cretasonoma* gen. nov. might also be confused with *Faronidius* Casey, 1887 since both genera have a transverse head with big eyes, a groove between antennal tubercles, and elytra that are twice as long as pronotum (Casey, 1887), but in *Faronidius* the pronotum sides are curved more acutely than in *Cretasonoma* gen. nov. and the abdomen is distinctly shorten than the elytra. *Golasa* Raffray, 1994 or *Galosites* Jeannel, 1962 are also genera somewhat similar to *Cretasonoma* gen. nov. which can be distinguished by their longer antenna and the third abdominal tergite which is much longer than the rest. Another similar genus is *Sagola* Sharp, 1874, which has smaller eyes, a longer scape and a more robust body than *Cretasonoma* gen. nov.

Supertribe: Pselaphitae Latreille, 1802
Tribe: Arhytodini Raffray, 1890
Genus *Penarhytus* Peris, Chatzimanolis and Delclòs gen. nov.
Derivation of name. The generic name is derived from the combination of *pen*, from the deposit name Peñacerrada, plus *arhytus*, a derivation of the tribe's name Arhytodini.
Type species. *Penarhytus tenebris* sp. nov.
Diagnosis. Large eyes, highlighting laterally; antennae as long as head and pronotum together, with a conspicuous club of three antennomeres, last antennomere 1.5 times as long as the preapical antennomere; pronotum transverse, much wider and longer than the head; tarsi with basal two tarsomeres short, similar in length, third tarsomere longer than preceding two; two apical tarsal claws; abdomen dorsally shorter than elytra length.
Description. Minute, body constricted between pronotum and elytra. Head transverse, with large eyes. Maxillary palpi 4-segemented with extra 'pseudosegment'. Antennae 11-segmented, with 3-segmented club. Pronotum transverse, much wider and longer than head, rounded antero-medially. Elytra longer and wider than pronotum. Tarsal formula 3–3–3. Abdomen as wide as maximum elytra, compact.
Penarhytus tenebris Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 2J–K
Derivation of name. The specific name is the Latin *tenebris*, which means 'dark', and refers to its coloration.
Holotype. MCNA–12683. The specimen is complete and well preserved in a transparent amber piece. A sparse fungal web overlies the specimen within the resin.
Type locality. The specimen comes from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain).
Description. Length 1.4 mm; colour reddish brown to black. Head elongate anteriorly, narrower than pronotum, width (including compound eyes) 0.30 mm; with frons 1.5 times longer than the rest of the head; eyes prominent. Maxillae not visible except maxillary palp; palpomere III triangular, IV narrowed at base, gradually expanding, truncate apically. Antennae as long as head and pronotum together; scape and pedicel robust, both antennomeres 1.4 times longer than wide; pedicel 1.4 times longer than antennomere III; antennomeres III–VI slightly longer than wide, similar in shape; antennomere VII quadrate, shorter than VIII and IX; antennomeres IX and X quadrate, similar in length, but 1.5 times wider than antennomere VIII; antennomere XI as wide as antennomere X, but 1.5 times as long as antennomere IX, apically compressed and rounded. Pronotum transverse, maximum width at middle 0.47 mm, lateral margins medially gently convex but constricted posteriorly; anterior margins rounded; posterior margins relatively straight in dorsal view. Elytra truncate exposing five tergites, wider than pronotum, and wider than long at maximum width; combined width of elytra 0.63 mm, length of elytron 0.49 mm; posterior margin straight. Procoxae, mesocoxae, and metacoxae narrowly separated; tarsi with basal two tarsomeres short, similar in length, third tarsomere longer than preceding two; two apical tarsal claws. Abdomen maximum width 0.63 mm; shorter than elytra length, with six visible sterna; sternum III and IV wider than the rest, both with equal length, 1.5 times longer than V; sternites V–VI equal in length but decreasing in width; individual abdominal segments transverse except sternum VII, enlarged and more narrow apically.
Discussion. Penarhytus tenebris gen. et sp. nov. is described as belonging within Pselaphinae based on the combination set of characters that define the family (see Remarks for *Cretasonoma corinformibus* gen. et sp. nov.). The new genus may be mistaken for a Faronitae due to its two basal tarsomeres being short and the last tarsomere much longer, but faronites also have short mesotrochanters and antennae without a club (Chandler, 1975; Newton et al., 2001). In contrast, members of the supertribe Pselaphitae are characterized by: 1) mesotrochanter comparatively long; 2) dorsal margin of the mesofemur distant from coxal articulation; 3) metacoxae at least narrowly separated; 4) at least the fourth maxillary palpomere enlarged or modified; and 5) with second and third tarsomere longer than basal tarsomere (list of characters from Newton et al., 2001). All the defining characters of Pselaphitae are present in *Penarhytus* gen. nov. except that the first and the second tarsomeres are subequal in length. We place *Penarhytus* gen. nov. in the tribe Arhytodini based on the following characters: 1) first and second tarsomeres subequal in length; 2) maxillary palp not evident (presumably reduced); and 3) first two visible abdominal tergites subequal in length (Newton et al., 2001). However, Arhytodini is characterized by having a single tarsal claw on each tarsus, and *Penarhytus* gen. nov. has two tarsal claws in each tarsus. We take the conservative approach and place *Penarhytus* gen. nov. in Arhytodini rather than describe of a new tribe based on the different number of tarsal claws.

Subfamily: Solieriinae Newton and Thayer, 1992
Genus *Prosolierius* Thayer, Newton and Chatzimanolis, 2012
Type species. Prosolierius crassicornis Thayer, Newton and Chatzimanolis, 2012, from Cenomanian Burmese amber.
Prosolierius parvus Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 3A–D
Derivation of name. The specific name is derived from the Latin *parvus*, meaning 'tiny'.
Holotype. MCNA–14190 (Fig. 3A–B). The specimen is complete and well preserved within a semi-transparent amber piece.
Paratypes. MCNA–12752 (Fig. 3C) and MCNA–13611 (Fig. 3D). MCNA–12752 is a well preserved specimen in dorsal habitus, within a relatively transparent piece of amber, but the head is hidden both in dorsal and ventral habitus. MCNA–13611 is poorly preserved, with a dark surface only available from lateral habitus. The piece of amber is barely translucent.

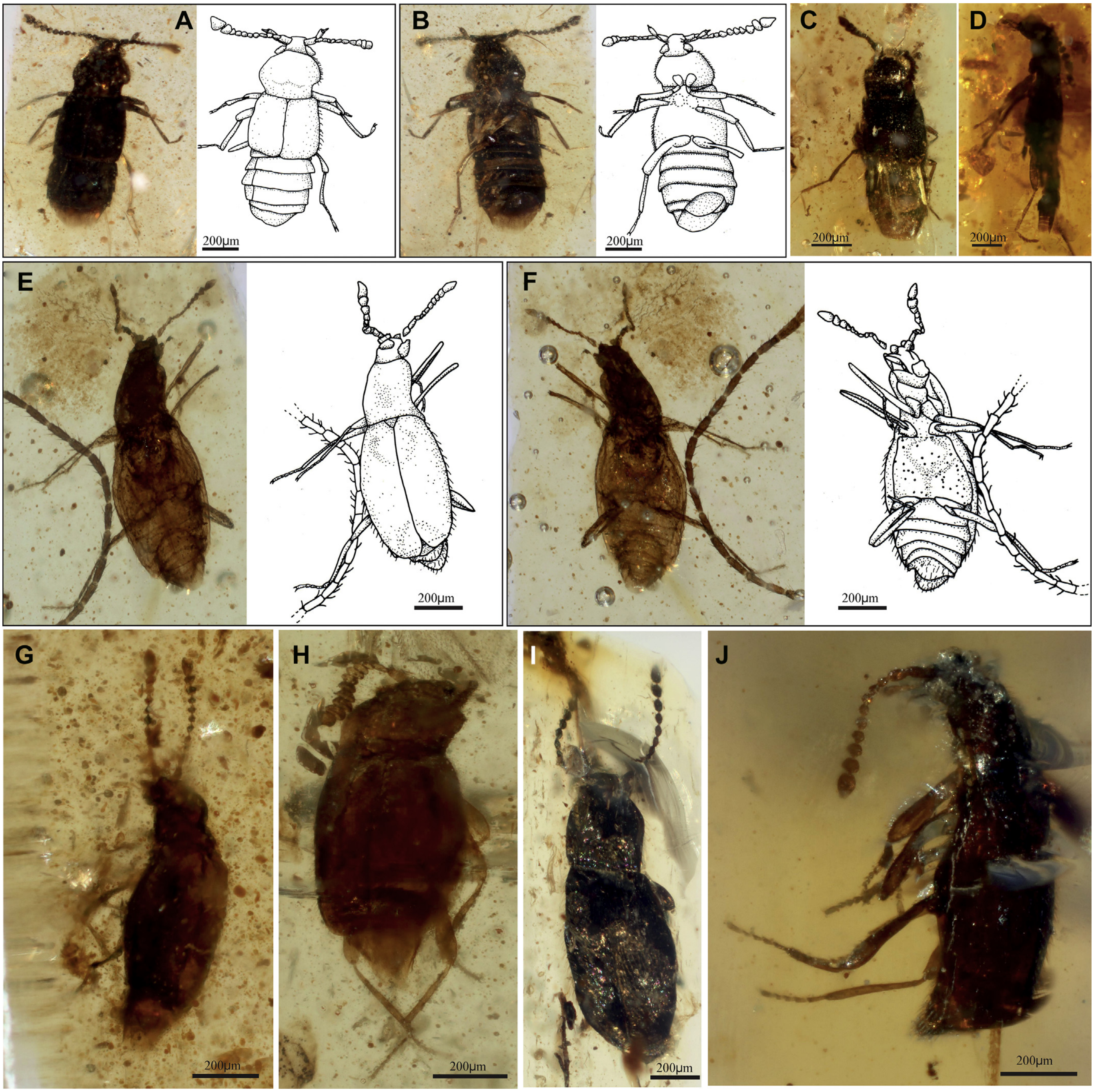

Fig. 3. *Prosolierius parvus* sp. nov. (A–D) and *Kachinus magnificus* sp. nov. (E–J). **A**. Photo and camera lucida drawing of MCNA–14190, holotype, from Peñacerrada I amber; dorsal habitus. **B**. Photo and camera lucida drawing of MCNA–14190, holotype; ventral habitus. **C**. Photo of MCNA–12752, paratype, from Peñacerrada I amber; dorsal habitus. **D**. Photo of MCNA–13611, paratype, from Peñacerrada I amber; lateral habitus. **E**. Photo and camera lucida drawing of CES–463, holotype, from El Soplao amber; dorsal habitus. **F**. Photo and camera lucida drawing of CES–463, holotype; ventral habitus. **G**. Photo of CES–433.2, paratype, from El Soplao amber; oblique habitus. **H**. Photo of CES–566.2, paratype, from El Soplao amber; dorsal habitus. **I**. Photo of CES–601, paratype, from El Soplao amber; dorsal habitus. **J**. Photo of CES–572, other material studied from El Soplao amber, tentatively placed in *Kachinus magnificus* sp. nov.; lateral habitus. Scale bars: 200 µm.

Type locality. Specimen comes from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain).

Diagnosis. Length between 1.04 and 1.45 mm; head shorter than pronotum; antenna robust, shorter than combined head through elytra; subquadrate antennomeres III–VIII.

Description. Total length (as preserved) 1.04–1.45 mm (abdomen contracted in holotype); small species, body subparallel-sided, dorso-ventrally flattened; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head small, shorter and narrower than pronotum, width (including compound eyes) 0.20 mm, upper interocular distance 0.13 mm; compound eyes medium sized; frontoclypeal groove indistinct. Maxillae not visible except palpomere; palpomere I small, robust, curved; palpomere II elongate, clavate; palpomere III enlarged, three times as wide as palpomere II, conical; palpomere IV setose, acuminate. Antennal insertions not contiguous, inserted in space below elevated frontal shelf. Eleven antennomeres; scape slightly longer than pedicel; pedicel longer and wider than antennomere III;

antennomeres III–VIII subquadrate, gradually increasing in size; antennomeres IX and X transverse; antennomere X larger than IX; antennomere XI as wide as antennomere X but twice as long, apically compressed. Pronotum wider than long, maximum width at middle, maximum width of pronotum 0.28 mm, lateral margins sinuated, at middle gently convex but concave posteriorly; posterior margin straight in dorsal view. Elytra truncate, exposing abdominal segments III–VII, slightly wider than pronotum, combined width of elytra 0.32 mm, length of elytron 0.34 mm, posterior margin straight; elytra twice as long as pronotum. Legs relatively short; femora slightly clavate; tibia slender; tarsal formula 5–5–5; tarsi elongate; tarsomeres I–IV ventro-apically lobed; apical tarsomere similar in length to basal tarsomere. Abdomen elongate, maximum width of abdomen 0.36 mm, near middle; segments largely transverse except segment VII and VIII. Aedeagus (visible inside abdomen of MCNA–13611) with two slender setose parameres.

Discussion. *Prosolierius parvus* sp. nov. can be distinguished from the other Burmese amber species, *P. tenuicornis* Thayer, Newton and Chatzimanolis, 2012 and *P. mixticornis* Thayer, Newton and Chatzimanolis, 2012 by its length (much shorter than the other two species) and from *P. crassicornis* Thayer, Newton and Chatzimanolis 2012 by a shorter head than pronotum and subquadrate antennomeres III–VIII in *P. parvus* sp. nov., while in *P. crassicornis* the head is subequal in length to the pronotum and antennomeres III–VIII are trapezoidal (wider apically than basally).

Subfamily: Scydmaeninae Leach, 1815
Supertribe: Scydmaenitae Leach, 1815
Tribe: Incertae sedis
Genus *Kachinus* Chatzimanolis, Engel and Newton, 2010

Type species. *Kachinus antennatus* Chatzimanolis, Engel and Newton, 2010, from Burmese amber. *Kachinus magnificus* Peris, Chatzimanolis and Delclòs sp. nov.

Fig. 3E–J

Derivation of name. The specific name *magnificus* is the Latin for ‘magnificent’, due to the great preservation of the specimen.

Holotype. CES–463 (Fig. 3E–F). The holotype is a well preserved sample in a transparent amber piece, in syninclusion with a fragmented antennae proceeding from a larger arthropod, probably a cockroach.

Paratypes. CES–433.2 (Fig. 3G), CES–566.2 (Fig. 3H), and CES–601 (Fig. 3I). CES–433.2 is well preserved in a relatively transparent sample of amber in syninclusion with CES–433.1 (*Cretasonoma corinformibus* gen. et sp. nov.), but only oblique habitus is visible in dorsal or ventral view. CES–566.2 is a broken specimen embedded in a transparent piece of amber, in syninclusion with the Hymenoptera *Microserphites soplaensis* Ortega-Blanco, Delclòs, Peñalver and Engel, 2011(Ortega-Blanco et al., 2011a). CES–601 is a specimen with a dark surface but embedded in a translucent piece of amber.

Other materials examined. CES–572 (Fig. 3J). This specimen is very closely related to the rest of the material. Unfortunately, it is included in a transparent piece of amber but the dorsal and ventral habitus are unclear, and only the lateral habitus is well defined, so for precaution, we do not include it in the type series.

Type locality. The El Soplao deposit, 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. Length 0.80–1.20 mm, antennomere XI twice as long as X, and body sparsely setose.

Description. Total length (as preserved) 0.80–1.20 mm; minute, body slender, elongate and sparsely setose; body light brown. Head subquadrate (excluding compound eyes), narrower than pronotum, not constricted between vertex to occiput; anterior margin of frons emarginated, width (including compound eyes) 0.14 mm, upper interocular distance 0.06 mm. Compound eyes large, positioned medially and coarsely faceted. Maxillary palps with three palpomeres; palpomere I shorter than II; palpomere II slender, elongate; palpomere III strongly clavate, apex not acute, longer and three times as wide as palpomere II. Palpomere IV not visible (as in *K. antennatus*, either absent or indistinguishable from apex of palpomere III). Antennae with eleven antennomeres, setose; antennal insertions not contiguous but separated by length subequal to length of first antennomere; antennomeres IX–XI forming weak club. Antennomeres I–III longer than wide; scape longer and slightly wider than pedicel; pedicel longer than III; antennomeres IV–VIII subequal in size, subquadrate; antennomeres IX and X slightly transverse; antennomere XI acuminate, approximately twice as long as wide, 1.5 times longer than antennomere X. Pronotum wider than head, slightly longer than wide; widest at anterior third; maximum width of pronotum 0.34 mm (CES–601); lateral margins converging posteriorly; anterolateral sides of

Key to the species of *Prosolierius* (modified from Thayer et al., 2012):

1. Antenna very long and slender, longer than combined head through elytra, all antennomeres distinctly elongate; frontoclypeal groove deeply impressed; length ca. 2.6 mm .... *P. tenuicornis*

- Antenna more robust, shorter than combined head through elytra, at least antennomere X transverse; frontoclypeal groove shallowly impressed or indistinct; length ca. 1.2-2.6 mm. 2

2. Head as long as pronotum .... *P. crassicornis*

- Head shorter than pronotum 3

3. Length ca. 2.3–2.6 mm; scape twice as long as pedicel; antennomeres III–VIII longer than wide .... *P. mixticornis*

- Length ca. 1.04–1.4 mm; scape slightly longer than pedicel; antennomeres III–VIII subquadrate .... *P. parvus* sp. nov.

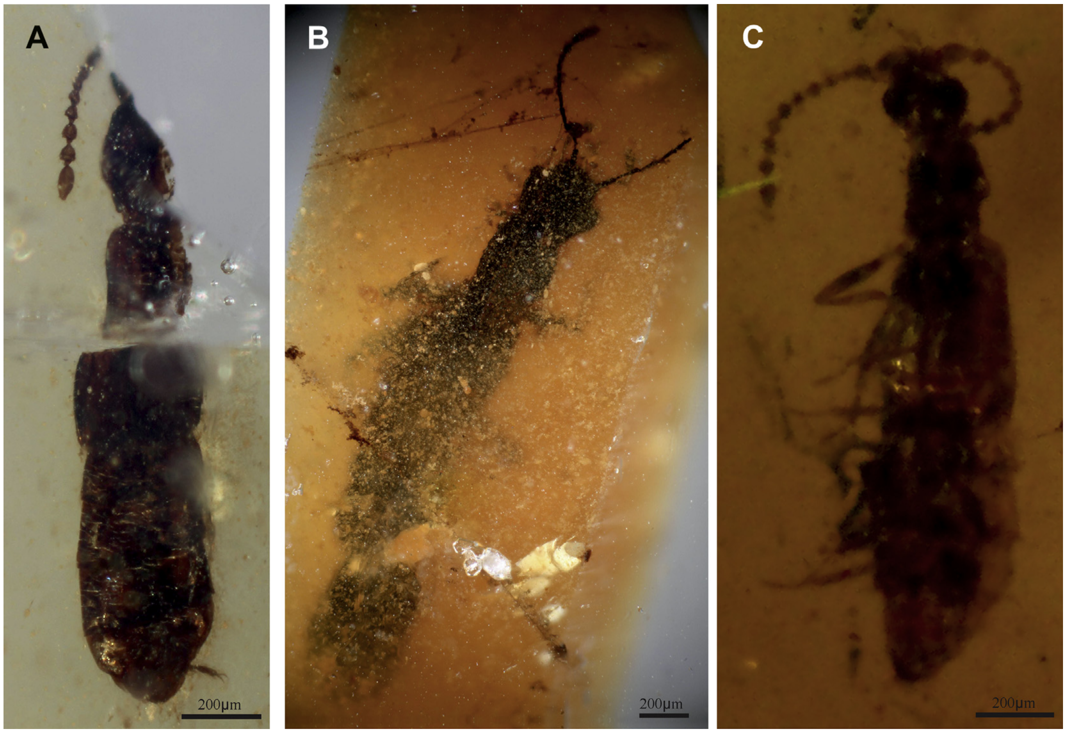

Fig. 4. Unplaced species of Staphylinidae in Spanish amber. **A**. Photo of CES–487, from El Soplao amber; dorsal habitus. **B**. Photo of MCNA–8912, from Peñacerrada I amber; dorsal habitus. **C**. Photo of CES–059.3, from El Soplao amber; dorsal habitus. Scale bars: 200 µm.

pronotum strongly deflexed ventrally. Mesoscutellum small and triangular. Elytra long and slender, truncate, exposing three tergites; approximately twice as long as wide, wider medially, converge slightly anteriorly and posteriorly, sparingly setose with uniform punctuation; hind wings present. Legs long; procoxae contiguous, mesocoxae and metacoxae separated by distance similar to mesocoxal diameter; trochanters small and rounded; femora weakly clavate, slender; tibiae thin and elongate with two spurs apically; tarsal formula 5–5–5; tarsomeres I–IV gradually decreasing in length, tarsomere V slightly longer than I; with two apical claws. Abdomen widest anteriorly, maximum width of abdomen 0.33 mm, as long as metasternum; six visible sterna with exposed pygidium (visible segment VI); visible sternum I as long as visible sterna II and III together, sternum II–V decreasing in length, pygidium as long as sterna IV and V together; posterior margins of sterna I and II straight, posterior margins of sterna III–V arcuate, and pygidium convex.

Discussion. None of the scydmaenines from Cretaceous Spanish amber share the defining character of Hapsomelitae (Poinar and Brown, 2004; Chatzimanolis et al., 2010). In contrast, they resemble more closely the species *Kachinus antennatus*, but *K. antennatus* is approximately 0.6 mm long, the antennae form a weak club with antennomere XI four times as long as antennomere X, and the body is heavily setose. *Kachinus antennatus* was treated by Chatzimanolis and colleagues as belonging to Incertae sedis tribe within Scydmaenitae, but with possible affinities to the tribes Eutheiini or Cephenniini (Chatzimanolis et al., 2010). As occurs with *Kachinus* from Burmese amber, all the specimens described herein as *Kachinus magnificus* sp. nov. do have most of the general characteristics of Eutheiini (*e.g.*, truncate elytra, slender, more or less flat body, general habitus), but again they cannot be assigned to any extant tribes because the head is apparently not constricted between the vertex and the occiput (see Chatzimanolis et al., 2010 and references therein).

5. Unplaced specimens

After the review, it was not possible to assign some of the staphylinid specimens studied in any previously established taxonomic status.

CES–487 (Fig. 4A). The specimen has a separated pronotum and elytra. The specimen is lacking almost all the head except part of an antenna, right side of the pronotum, and part of the elytra; legs are well preserved.

MCNA–8912 (Fig. 4B). The overall habitus of this rove beetle is indicative of the subfamily Paederinae. It is poorly preserved, with a dark surface, and cracked piece of translucent but not transparent amber. It was found in the same stratigraphic horizon as MCNA–8654. Even though we do not formally describe this specimen as a new species due to its poor state of preservation, we provide a preliminary description below.

Description. Total length (as preserved) approximately 2.69 mm; body parallel-sided, dorso-ventrally flattened; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head wider than pronotum, width (including compound eyes) 0.40 mm, upper interocular distance 0.23 mm; head constricted laterally immediately behind compound eyes to form broad neck; compound eyes small, protruding laterally. Maxillae not visible except maxillary palp, maxillary palps with four palpomeres with a length similar to the head, base of maxillary palpomere I not visible, palpomere I–III slenderer (probably collapsed), palpomere IV expanded laterally, wider and longer than palpomere III, fusiform. Antennal insertions exposed, not contiguous by more than the scape length. Antennae with scape robust, pedicel–antennomere VIII thin and elongate, antennomere III longer than the rest; antennomeres IX–XI wider than preceding antennomeres, last antennomere wider that the rest. Pronotum narrower than head, longer than wider, maximum width at middle, maximum width of pronotum 0.36 mm;

posterior margin not marked. Elytra truncate exposing six tergites, slightly wider than pronotum, combined width of elytra 0.48 mm, length of elytron 0.40 mm, posterior margin straight. Legs relatively long, end margin of tibiae with a row of spines; tarsal formula 5–5–? Abdomen as wide as combined width of elytra at base; individual abdominal segments largely transverse.

CES–059.3 (Fig. 4C). This is a Pselaphinae, probably a different species from those we describe above. However, the specimen is on permanent exhibition at Cueva El Soplao (Cantabria, Spain) and we were unable to study it.

6. Staphylinid tribes studied; their presence in amber

Staphylinidae considered one of the most successful groups of extant and fossil insects (Grebennikov and Newton, 2009; Grimaldi and Engel, 2005; Rasnitsyn and Quicke, 2002; Thayer, 2005). Staphylinidae, in terms of the abundance found in amber, ranked the fourth beetle family, after Scirtidae, Elateridae and Anobiidae. Although Staphylinidae and Elateridae were probably more abundant in palaeoecosystems, some families are possibly over represented in the amber record due to their close relationship with resin producing trees (Rasnitsyn and Quicke, 2002). In Recent temperate forests, staphylinids comprise half or more of beetle individuals and one quarter or more of the beetle biomass (Grimaldi and Engel, 2005). In Cretaceous Spanish amber, staphylinids represent approximately one-sixth of the total number of beetles found. Herein, we describe four new species as members of the subfamilies Pselaphinae, Solieriinae, and Scydmaeninae, and include brief mentions of three other taxa awaiting formal descriptions, pending the availability of new specimens, or better techniques that will allow them to be studied more accurately.

The extant species divided into two supertribes, *i.e.*, Scydmaenitae and Mastigitae. The additional fossil supertribe Hapsomelitae was erected by Poinar and Brown (2004) and redefined by Chatzimanolis et al. (2010); but Chatzimanolis et al. (2010) expressed doubts as to the taxonomic value of the diagnostic characters. Indeed, Hapsomelitae seem to be an inadequately defined assemblage of genera that only share greatly elongated abdominal sterna V and VI (Chatzimanolis et al., 2010; Jaloszynski, 2012).

Fossil Scydmaeninae were reviewed by O'Keefe et al. (1997) and Chatzimanolis et al. (2010) and not many records are known in fossil deposits; *Kachinus antennatus* was described from Burmese amber (early Cenomanian, Shi et al., 2012) as the oldest known member of the subfamily (Chatzimanolis et al., 2010). So, *Kachinus magnificus* sp. nov., described herein, is now the oldest species formally described in the subfamily, although Scydmaeninae have also been reported, but not described yet, from Early Cretaceous deposits in Lebanon (Kirejtshuk and Azar, 2013). Since the publication of Chatzimanolis et al. (2010), only *Euroleptochromus sabathi* Jaloszynski, 2012 has been recorded as a new species of the subfamily, from Middle-Eocene Baltic amber (Jaloszynski, 2012).

Pselaphinae common as amber inclusions (Chatzimanolis and Engel, 2013; Weitschat and Wichard, 2002). This is somewhat puzzling because Pselaphinae a relatively rare group of rove beetles in recent collections. Some factors influencing this disparity might involve the environment where the beetles lived and where the resin was produced. Staphylinidae generally most abundant in forest or woodland habitats, but many species do occur in, and may be restricted to, grasslands, shrublands, or areas above the tree-line, which worm their way between the interstices of decaying leaves and humus (Grimaldi and Engel, 2005; O'Keefe, 2001). Most Pselaphinae are found in leaf and wood litter of the forest soil (Newton and Thayer, 1995). Their small size (less than 3 mm) and cryptic habitats in forest litter may make them susceptible to being trapped in sticky resins, and thereby being conserved until today (Martínez-Delclòs et al., 2004).

Both Pselaphinae and Scydmaeninae are known to be associated with ants or termites (Newton et al., 2001; O'Keefe, 2001). Even though most of these associations might be incidental, a few Pselaphinae and Scydmaeninae are truly myrmecophilous. It is therefore puzzling that no ants have been found in the Cretaceous Spanish amber while several were found and described in Cretaceous French amber (Nel et al., 2004; Perrichot et al., 2008) and other amber from around the world (Barden and Grimaldi, 2013, and references therein; Grimaldi and Agosti, 2000; McKellar et al., 2013). As with ants, the record of termites from Spanish amber has been sparse with only an imago and some wings known (Engel and Delclòs, 2010). In contrast, the sediments analyzed in some of the Spanish deposits are full of termite coprolites, which indicates that this group of insects is an essential plant decomposer of the Cretaceous resinous forests.

6.1. Comparative of Cretaceous amber deposits; palaeobiological point of view

The Spanish staphylinids described here demonstrate the similar conditions where some of the most abundant Cretaceous resins were produced. It is not the first time that the biota described from Spanish amber coincides with genera previously found in Cretaceous Lebanese or Burmese ambers. There are, for example, several ceratopogonid genera (Diptera: Ceratopogonidae), particularly *Archiaustroconops* Szadziewski, 1996, with representatives in the three amber deposits (Borkent, 2013, and references therein). There are also some examples within Hymenoptera, *e.g.*, genera *Serphites* Brues, 1937, *Galloromma* Schlüter, 1978, and *Burmaphron* Engel and Grimaldi, 2009, present in Spanish and Burmese ambers; or the genus *Libanophron* Engel and Grimaldi, 2009, found in Spanish and Lebanese amber (Ortega-Blanco et al., 2011a, 2011b, 2011c).

With this study of Staphylinidae beetles from Spanish amber, two more examples will be added to the list of genera shared by Spanish amber, and Burmese and Lebanese amber: *Prosolierius*, from Burmese and Lebanese amber (Thayer et al., 2012) and *Kachinus* from Burmese amber (Chatzimanolis et al., 2010).

Some of the species described from Cretaceous amber deposits in the northern hemisphere are currently only known from restricted areas of the southern hemisphere, mainly Australasian and Neotropical regions (Peris et al., in press, and references therein; Thayer et al., 2012). A different palaeobiogeographical distribution of taxa during the Cretaceous is evident for these species, probably because of the global tropical/subtropical conditions during part of the Cretaceous (Gale, 2000). One of the resemblances between the three areas with Cretaceous amber (*i.e.*, Lebanon, Spain and Burma) may be their botanical origin. Although the three deposits are of different ages — Lebanese amber is Aptian (Ross et al., 2010), Spanish amber is Albian (Peñalver and Delclòs, 2010), and Burmese amber is early Cenomanian (Shi et al., 2012) — all three deposits share the conifer origin for the resin, probably from araucariaceans or cheirolepidiaceans, in forests that developed in a tropical or subtropical climate (Azar et al., 2010; Peñalver and Delclòs, 2010; Ross et al., 2010). It is not surprising that a similar insect community lived under the same palaeobotanical assemblage and palaeoenvironmental conditions, as the fossils from the three deposits confirm.

7. Conclusions

Two new genera and four new species of Staphylinidae are described based on twenty fossil specimens from two Early

Cretaceous amber deposits in Spain, *i.e.*, Peñacerrada I and El Soplao, both in the Basque-Cantabrian Basin. Two of these four new species are included in the Pselaphinae, one in Solieriinae, and the other in Scydmaeninae. The genera *Prosolierius* (Solieriinae) and *Kachinus* (Scydmaeninae) were previously described from finds in Burmese amber (*Prosolierius* was also named from finds in Lebanese amber). This therefore offers new evidence of the similarity between these distant forests, both palaeogeographically and in age. The species described as *Kachinus magnificus* sp. nov. is the oldest species formally described for the Scydmaeninae, which are little known as fossils.

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