

New species of fossil oribatid mites (Acariformes, Oribatida), from the Lower Cretaceous amber of Spain



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ABSTRACT

Mites are relatively common and diverse in fossiliferous ambers, but remain essentially unstudied. Here, we report on five new oribatid fossil species from Lower Cretaceous Spanish amber, including representatives of three superfamilies, and five families of the Oribatida. *Hypovortex hispanicus* sp. nov. and *Tenuelamellarea estefaniae* sp. nov. are described from amber pieces discovered in the San Just outcrop (Teruel Province). This is the first time fossil oribatid mites have been discovered in the El Soplao outcrop (Cantabria Province) and, here, we describe the following new species: *Afronothrus ornosae* sp. nov., *Nothrus vazquezae* sp. nov., and *Platylidodes sellnicki* sp. nov. The taxa are discussed in relation to other fossil lineages of Oribatida as well as in relation to their modern counterparts. Some of the inclusions were imaged using confocal laser scanning microscopy, demonstrating the potential of this technique for studying fossil mites in amber. A table, including all the known Mesozoic oribatid mites preserved in amber, is included.

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1. Introduction

Oribatid mites are common in almost all terrestrial ecosystems, with approximately 10,000 species known (Subías, 2004, updated online version 2015). However, as fossils they are rare, especially in pre-Cenozoic strata, where they are often overlooked due to their minute size. Oribatid mites have a long evolutionary history, with the oldest fossils coming from Paleozoic outcrops (Norton et al., 1988; Subías and Arillo, 2002). The oldest described oribatid mites preserved in fossil resins come from the Albian Spanish amber outcrops, with six species having been described (Arillo and Subías, 2000, 2002; Arillo et al., 2008, 2009, 2010, 2012). All known pre-Cenozoic fossil oribatid mites are summarized in Arillo et al. (2012). At least five undescribed fossil oribatid mites are recorded in older Lebanese amber and a huge collection of undescribed specimens is known in slightly younger Myanmar amber (Dany Azar pers. comm.). Here, we describe five new species belonging to the superfamilies Crotonioidea (families Nothridae and

Trhypochthoniidae), Neolioidoidea (family Neolioididae), and Licneremaeoidea (families Lamellareidae and Scutoverticidae) Table 1.

The superfamily Crotonioidea has a cosmopolitan distribution and comprises seven families (Norton and Behan-Pelletier, 2009): Camisiidae, Crotoniidae, Hermaniidae, Malaconothridae, Nanhermanniidae, Nothridae, and Trhypochthoniidae. However, note that Subías et al. (2012) consider Hermaniidae and Nanhermanniidae to be members of the superfamily Nanhermannioidea, as part of the Brachypyliina. Crotonioidea is one of the best known superfamilies in Mesozoic strata; *Palaeochthonius krasilovi* Krivolutsky, 1977 (Trhypochthoniidae) and *Juracarus serratus* Krivolutsky, 1977 (Trhypochthoniidae) were described from the Jurassic (Tithonian) of Burea River Bank, Far East of Russia (Krivolutsky and Krassilov, 1977), *Thrypochthonius lopezvallei* Arillo, Subías and Shtanchaeva, 2012 (Thrypochthoniidae) was described from Spanish Albian amber, and *Eocamisia sukatshevae* Bulanova-Zachvatkina, 1974 (Camisiidae) was described from the Upper Cretaceous Siberian amber. The family Nothridae has not previously been recorded in Mesozoic strata but was known from Eocene Baltic amber (Sellnick, 1918).

The superfamily Neolioidoidea only includes the family Neolioididae, which is found worldwide in temperate to tropical regions

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Table 1

Known fossil oribatid mites from Cretaceous ambers.

HOLOSOMATA**(Supercohort Desmonomatides, Cohort Nothrina)****Superfamily Crotonioidea Thorell, 1876**

Family Trhypochthoniidae Willmann, 1931

Genus *Afronothrus* Wallwork, 1961*Afronothrus ornosae* Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)Genus *Trhypochthonius* Berlese, 1904*Trhypochthonius lopezvallei* Arillo, Subías and Shtanchaeva, 2012 (San Just amber, Spain) (Albian)

Family Camisiidae Oudemans, 1900

Genus *Eocamisia* Bulanova-Zachvatkina, 1974*Eocamisia sukatshevae* Bulanova-Zachvatkina, 1974 (Siberian amber, Taimyr, Federation of Russia) (Santonian)

Family Nothridae Berlese, 1896

Genus *Nothrus* Koch, 1836*Nothrus vazquezae* Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)**BRACHYPYLINA****(Supercohort Desmonomatides, Cohort Brachypylina)****Superfamily Neoliodoidea Sellnick, 1928**

Family Neoliodidae Sellnick, 1928

Genus *Platylodes* Berlese, 1916*Platylodes sellnicki* Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)**Superfamily Plateremaeoidea Trägårdh, 1926**

Family Plateremaeidae Trägårdh, 1926

Genus *Rasnitsynella* Krivolutsky, 1976*Rasnitsynella punctulata* Krivolutsky, 1976 (Siberian amber, Taimyr, Federation of Russia) (Santonian)**Superfamily Cepheoidea Berlese, 1896**

Family Cepheidae Berlese, 1896

Genus *Eupterotegeus* Berlese, 1916*Eupterotegeus bitranslamellatus* Arillo and Subías, 2002 (Peñacerrada I amber, Spain) (Albian)Genus *Ommatocephus* Berlese, 1913*Ommatocephus nortoni* Arillo, Subías and Shtanchaeva, 2008 (Salinillas de Buradón amber, Spain) (Albian)**Superfamily Zetorchestoidea Michael, 1898**

Family Archaeorchestidae Arillo and Subías, 2000

Genus *Strieremaeus* Sellnick, 1919(= *Archaeorchestes* Arillo and Subías, 2000)*Strieremaeus minguetzeae* (Arillo and Subías, 2000) (Peñacerrada I amber, Spain) (Albian)**Superfamily Carabodoidea Koch, 1837**

Family Otocephidae Balogh, 1961

Genus *Cretaceobodes* Arillo, Subías and Shtanchaeva, 2010*Cretaceobodes martinezae* Arillo, Subías and Shtanchaeva, 2010 (San Just amber, Spain) (Albian)**Superfamily Cymbaeremaeoidea Sellnick, 1928**

Family Ametroproctidae Subías, 2004

Genus *Ametroproctus* Higgins and Woolley, 1968*Ametroproctus valeriae* Arillo, Subías and Shtanchaeva, 2009 (San Just amber, Spain) (Albian)**Superfamily Licneremaeoidea Grandjean, 1931**

Family Lamellareidae Balogh, 1972

Genus *Tenuelamellarea* Subías and Iturrondobeitia, 1978*Tenuelamellarea estefaniae* Arillo and Subías sp. nov. (San Just amber, Spain) (Albian)

Family Scutoverticidae Grandjean, 1954

Genus *Hypovortex* Krivolutsky, 1969*Hypovortex hispanicus* Arillo and Subías sp. nov. (San Just amber, Spain) (Albian)

(Subías et al., 2012). Several fossil species are known from Cenozoic (Baltic, Mexican and Dominican) ambers (Dunlop et al., 2015).

The superfamily Licneremaeoidea *sensu* Norton and Behan-Pelletier (2009) comprises nine families: Adhaesozetidae, Charassobatidae, Dendroeremaeidae, Eremellidae, Lamellareidae, Licneremaeidae, Micreremidae, Passalozetidae, and Scutoverticidae. However, the limits of this superfamily are unclear after Subías et al. (2012) excluded Adhaesozetidae, Charassobatidae and Eremellidae. Some fossil species belonging to the families Micreremidae and Licneremaeidae are known in Baltic amber while the family Scutoverticidae was recorded in Mexican and Dominican ambers (Dunlop et al., 2015).

2. Material and methods

The amber discussed here originates from two different Spanish amber localities (Fig. 1). Specimens CPT-4068 and CPT-4165 were found in the San Just outcrop, in amber from grey-black claystones with abundant plant remains in the upper part of the Regachuelo Member (Escucha Fm., Lower Cretaceous, Albian, *sensu* Villanueva-Amadoz et al., 2010), which correspond to a deposit of a fluvial deltaic swamp. The San Just outcrop (Peñalver et al., 2007; Peñalver and Delclòs, 2010) is located in the municipality of Utrillas (Teruel Province, Aragón Autonomous Community, eastern Spain). Lastly, three specimens (CES-412, CES-505, CES-582) were found in the El Soplao outcrop which is near the village of Rábago (Cantabria Province, northern Spain). This outcrop occurs in Las Peñas Fm., dated as Albian, and is associated with broadly deltaic-estuarine environments. The age, composition and fauna of Spanish amber have been reviewed by Delclòs et al. (2007), Najarro et al. (2009, 2010), Peñalver and Delclòs (2010) and Barrón et al. (2015).

Specimens were prepared for optimal microscopic study following the procedure outlined by Corral et al. (1999). Camera lucida drawings were made using an Olympus U-DA drawing tube attached to an Olympus BX50 compound microscope. Photomicrographs were executed using an OPTIKA Pro 5 digital camera attached to an Olympus BX50 compound microscope.

Confocal laser scanning microscopy (CLSM) of specimens CPT-4068 and CPT-4165 was performed at the Museo Nacional de Ciencias Naturales (Madrid, Spain). All slides were obtained with a Leica TCS SPE-DM 5500 CS Q V-Vis confocal microscope (Manheim,



Fig. 1. Map of the Iberian Peninsula showing the amber outcrops studied.

D-68165, Germany) with an HC PL APO CS 20x NA 0.70 dry objective, and the Leica Application Suite Advanced Fluorescence software. Both samples were excited with a 488 nm laser and the fluorescence emission was collected from approximately 10 nm above the excitation wavelength up to 800 nm. Laser power for acquisition was set by viewing the fluorescence emission and increasing the power until the rate of increase in fluorescence slowed. The intensity setting of the slider was realized steplessly via an acousto-optic tunable filter (AOTF). Then, the photomultiplier gain for acquisition was set by viewing the image and increasing the gain until signal overload was detected, at which point the gain was backed off slightly. Pixel matrices of 2048 × 2048 or 2048 × 1024, speed 400 Hz, frame average 4, and zoom setting from 1.7–2, were elected in the single capture. An Airy unit setting of 1 was routinely used for the observation pinhole. Image processing was assessed using the Leica Metamorph[®] v7.7.1 software (Universal Imaging, Downingtown, PA, USA). The Metamorph[®] software package contains routines to enhance images, both to change image brightness and contrast as background and smoothing images. We chose image-processing filters commonly used to improve image quality in mites fossilized in amber. The best focus was created starting from a new image by performing a selected arithmetic or Boolean logic operation on the planes in a stack. After creation, the different viewing angles of the 3D model were examined using the movie commands.

3. Systematic palaeontology

Family: Nothridae Berlese, 1896

Genus *Nothrus* Koch, 1836

Type species: *Nothrus palustris* Koch, 1839

Nothrus vazquezae Arillo and Subías sp. nov.

Figs. 2, 3A

Derivation of name. The specific epithet is matronymic in honour of our colleague, the hemipterologist, Dr. Ángeles Vázquez.

Type material. Holotype, CES-505, housed in the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, only lacking part of the prodorsal and notogastral cuticle. Preserved in a piece of amber trimmed to 1 × 1 mm (in an epoxy resin trapezoid 21 × 14 × 1 mm), which is clear in the dorsal view of the animal but quite turbid on its ventral side. The sample was part of a single piece, which was subsequently divided into 20 fragments (CES-487–CES-506) for optimal study. Syninclusions comprised four Coleoptera (families Staphylinidae, Latridiidae, Dermestidae and Latridiidae; David Peris pers. comm.), four Thysanoptera, 10 Hymenoptera, one Homoptera, one Diptera, one Psocoptera, and a further Acari (of the Actinedidae).

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñas Fm., Lower Cretaceous (Albian).

Description. Measurements: 551 μm long and 156 μm wide.

Prodorsum cuticle irregularly reticulated on its rostral region; with smooth, straight and divergent rostral setae preserved. Lamellar and interlamellar regions not preserved. One lanceolated sensillum preserved, with four fine hairs on one side, ending in a slender tip. *Notogaster* rectangular-shaped, with its surface covered by dark round areolae. Central part of the cuticle lost. Only two pairs of posterior setae preserved: first pair short and smooth, probably representing pair p₁ or h₁; second pair (h₂) plumose, curved and barbed, located on the posterior angles of the notogaster.



Fig. 2. Camera lucida drawing of the holotype of *Nothrus vazquezae* sp. nov. (CES-505) in dorsal habitus. Scale bar 100 μ m.

Ventral side poorly preserved. Adanal and adgenital surfaces covered with areolae similar to those in the notogaster. Anal and genital valves poorly preserved, with setae presumed to be lost.

Gnathosoma with well-preserved palpi and rutelli.

Legs partially preserved, monodactyle. Legs I with a strong projection on the distal part of the femora. Some of the setae short and slightly flattened. At least one seta on the tibia of the leg IV seems to be a solenidium.

Discussion. *Nothrus* is a cosmopolitan and widely distributed genus. First fossil species of *Nothrus* were described by Karsch (1884) from Baltic amber. However, *Nothrus kuehli* Karsch, 1884 was later

considered by Sellnick (1918) as a fossil form of the extant species *Camisia horrida* (Hermann, 1804), and *Nothrus sulcatus* Karsch, 1884 was transferred by Sellnick (1918) to the genus *Platigeocranus* Sellnick, 1918. Sellnick (1918) did not suggest any new placement for *Nothrus punctulum* Karsch, 1884, as the specimens had been lost by the time he reviewed the material, and so the species has *nomen nudum* status. Then, the only valid fossil species from Baltic amber is *Nothrus illautus* Sellnick, 1918, which is easily differentiated from *Nothrus vazquezae* sp. nov. by its larger body size (800 μ m), smooth sensilla, and the flattened h_2 setae.

In Recent fauna, there are around 100 described species of *Nothrus* (Subías, 2004; online version 2015) although their inner relationships are poorly known. *Nothrus vazquezae* sp. nov. shares with the extant species *N. asiaticus* Aoki and Ohnishi, 1974, *N. quadripilus* Ewing, 1909, *N. suramericanus* Hammer, 1958, *N. peruensis* Hammer, 1961, *N. espinarensis* Beck, 1962, *N. becki* Balogh and Mahunka, 1981, *N. senegalensis* Mahunka, 1992, *N. flagellum* Csiszár, 1961, *N. monticola* Hammer, 1961, *N. crassisetus* Mahunka, 1982, and *N. hauseri* Mahunka, 1974, the plumose h_2 setae. However, the h_2 setae are much longer in the extant species, and the sensilla is more setiform (as opposed to lanceolate as in *N. vazquezae*). It is assumed that modern species of *Nothrus* feed on fungi growing on decaying leaf litter.

Family: Trhypochthoniidae Willmann, 1931

Genus *Afronothrus* Wallwork, 1961

Type species: *Afronothrus incisivus* Wallwork, 1961

Afronothrus ornosae Arillo and Subías sp. nov.

Figs. 3B, 4

Derivation of name. The specific epithet is matronymic in honour of our colleague, the apidologist, Dr. Concepción (Paddy) Ornosá.

Type material. Holotype, CES-412, housed at the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, preserved in a piece of amber trimmed to 5 \times 3 \times 1 mm (in an epoxy resin trapezoid 21 \times 15 \times 1 mm), which is clear in the dorsal view of the animal but quite turbid on its ventral side. The sample was part of a single piece, which was subsequently divided into several fragments to allow study of the 48 arthropods in it (including two further Acari, four Araneae, one Psocoptera, two Homoptera, 15 Hymenoptera, seven Neuroptera, 13 Diptera, two Coleoptera, one Lepidoptera and one undetermined arthropod).

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñasas Fm., Lower Cretaceous (Albian).

Description. Measurements: 335 μ m long and 213 μ m wide.

Prodorsum cuticle smooth, with long, smooth, and divergent rostral setae. Lamellar and interlamellar setae extremely long (110 μ m and 158 μ m, respectively). Short sensilla with short stalk gradually widened to elongated smooth head.

Notogaster cuticle covered by well-developed polygonal protuberances. Seven posterior setae preserved, some of them very large (around 190 μ m); probably representing pairs p_2 , h_2 and h_3 ; shortest seta (around 90 μ m) probably representing pair p_1 .

Ventral side not visible due to amber turbidity.

Legs tridactyle. Chaetotaxy partially preserved. Tibia of leg I with well-developed solenidia (85 μ m). The remaining setae, especially those preserved on legs I and II, are medium sized and smooth.

Discussion. *Afronothrus ornosae* sp. nov. represents the first fossil record of the genus *Afronothrus*. Several extant species of the genus have been described from circumtropical/subtropical regions, although Colloff and Halliday (1998) consider all of them to be

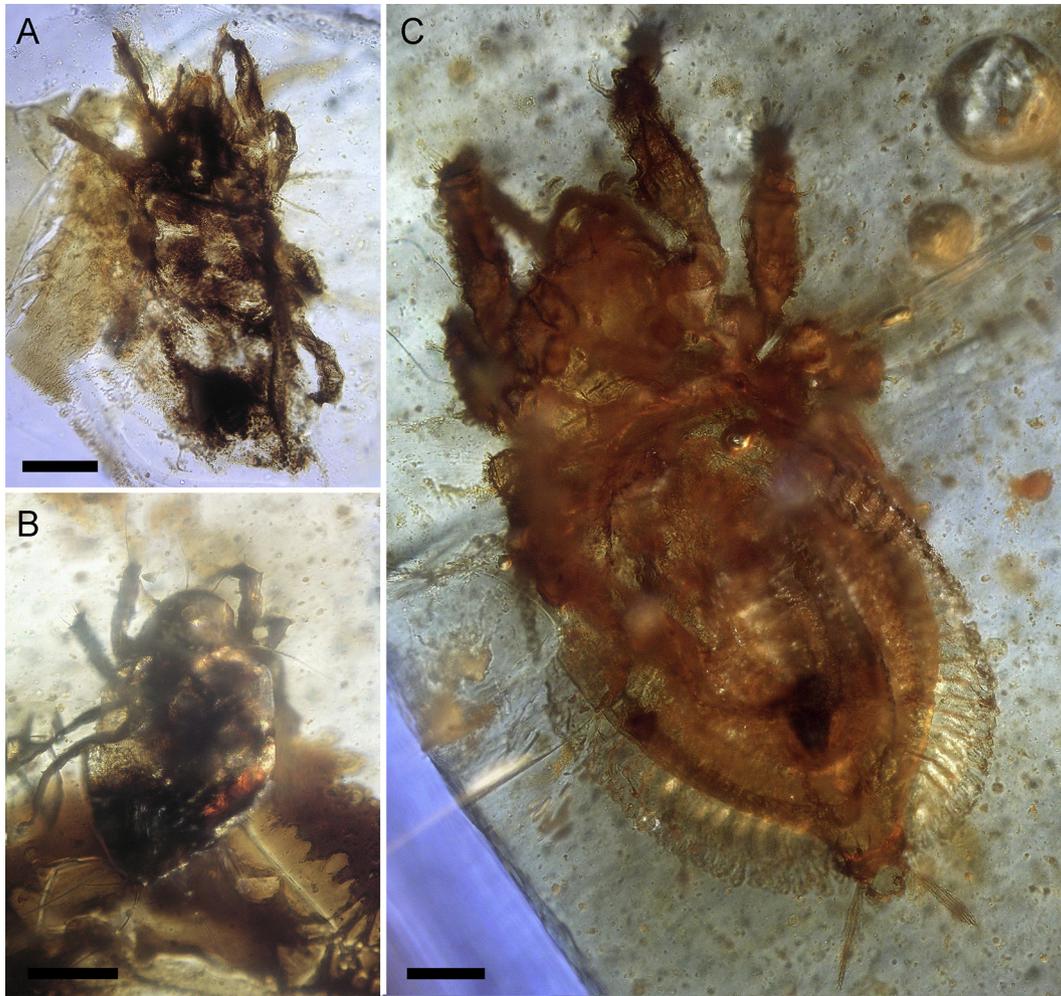


Fig. 3. Microphotographs. A. Holotype of *Nothrus vazquezae* sp. nov. (CES-505) in dorsal habitus. B. Holotype of *Afronothrus ornosae* sp. nov. (CES-412) in dorsal habitus. C. Holotype of *Platylodes sellnicki* sp. nov. (CES-582) in dorsal habitus. Scale bars 100 μ m.

synonyms of the species *Afronothrus incisivus* Wallwork, 1961, a species mainly recorded from organic horizons in forest soils. The only other valid species is *Afronothrus arboreus* Ramani and Haq, 1992 described from India and collected from coconut tree leaf litter. The new species is easily distinguished from *A. incisivus* and *A. arboreus* by its minute size and the extremely elongated interlamellar and posterior notogastral setae. The notogastral sculpture pattern, bearing larger polygons, is also different.

Family: Neolioididae Sellnick, 1928

Genus *Platylodes* Berlese, 1916

Type species: *Nothrus doderleini* Berlese, 1883

Platylodes sellnicki Arillo and Subías sp. nov.

Figs. 3C, 5

Derivation of name. The specific epithet is patronymic in honour of the acarologist Dr. Max Sellnick, who described the other known fossil species belonging to this genus from Baltic amber.

Type material. Holotype, CES-582, housed at the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, preserved in a clear piece of amber trimmed to $11 \times 5 \times 1$ mm (in an epoxy resin trapezoid $20 \times 14 \times 1.5$ mm). The sample was part of a single piece, which was subsequently divided into three fragments (CES-

582–CES-584) for optimal study. Syninclusions comprised one Coleoptera (family Aderidae; David Peris pers. comm.), and one Hymenoptera.

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñasas Fm., Lower Cretaceous (Albian).

Description. Measurements: 988 μ m long and 552 μ m wide.

Prodorsum swollen on each side, with double arches. Rostral setae dilated, with irregular striae. Lamellar, interlamellar and exobothridial setae quite similar to rostral setae but smaller, all inserted on small apophyses. Sensillus short and clavate, strongly roughened.

Anterior margin of the notogaster intruded inside the prodorsum; posterior part narrowed. Cuticle bearing a large number of minute clear light holes between the medial and marginal parts; holes arranged in irregular rows, with darker lines crossing between them. Two pairs of caudal apophyses preserved: inner apophyses bearing a pair of long, plumose and serrated setae (p_1); outer apophyses bearing two minute dilated and striated setae (p_2). Exuviae of larva and nymphae preserved.

Ventral side ano-genital region well-preserved. Seven pairs of genital setae (one short and setose) preserved, five of them situated on the anterior field of the genital plate, and two situated on the

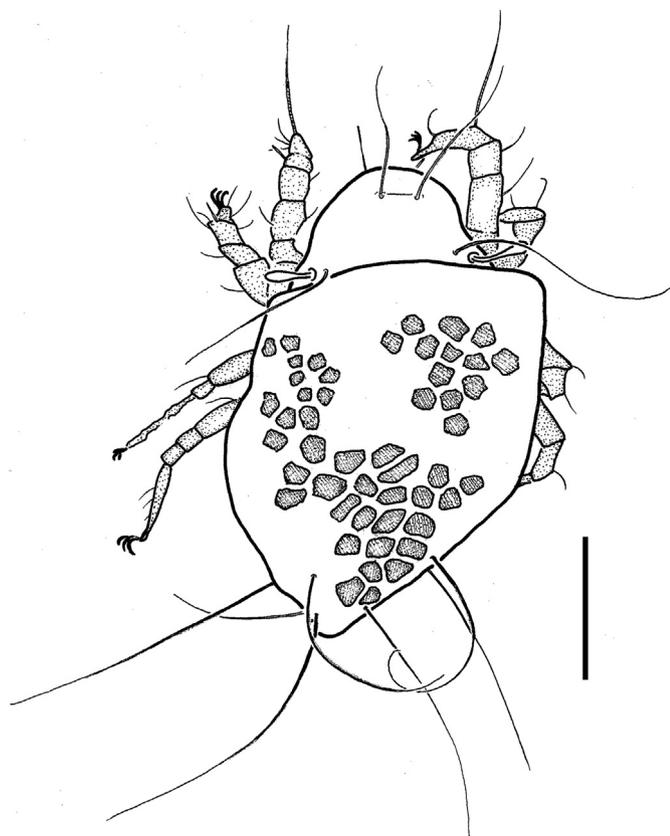


Fig. 4. Camera lucida drawing of the holotype of *Afronthrus ormosae* sp. nov. (CES-412) in dorsal habitus. Scale bar 100 μ m.

posterior field and separated by a narrow furrow. Anal setae not preserved. One aggenital seta preserved, being short and spatulate. Two adanal setae preserved near the left anal valve, similar to the aggenital seta.

Legs tridactyle, covered by cerotegument. Most of the leg setae are short and spatulate, but tibiae I presents one short, smooth seta (perhaps a short solenidia).

Discussion. Although several fossil species of the family Neolioididae have been described from Cenozoic ambers, only one of them is included in the genus *Platyliodes*. *Platyliodes ensigerus* Sellnick, 1918 was originally described within the genus *Neolioides* Berlese, 1888. Overall, *Platyliodes sellnicki* sp. nov. closely resembles *P. ensigerus* but the latter has longer and narrower p_1 setae. Seven extant species of *Platyliodes* have been described from the Holarctic region, of these only two have plumose and serrate p_1 setae: *P. macroprionus* Woolley and Higgins, 1969 (known from the Nearctic region and Japan) and *P. montanus* Fujikawa, 2001 (Japan). However, *P. macroprionus* is easily distinguished from *P. sellnicki* by its fan-shaped rostral setae, and *P. montanus* has quite a different pattern on the notogastral cuticle (with dark-coloured pustules among the light holes as opposed to the dark irregular lines present in *P. sellnicki*). Extant species of *Platyliodes* are mostly sampled on mosses and lichens.

Family: Lamellareidae Balogh, 1972

Genus *Tenuelamellarea* Subías and Iturrondobeitia, 1978

Type species: *Tenuelamellarea hispanica* Subías and Iturrondobeitia, 1978

Tenuelamellarea estefaniae Arillo and Subías sp. nov.

Figs. 6, 7

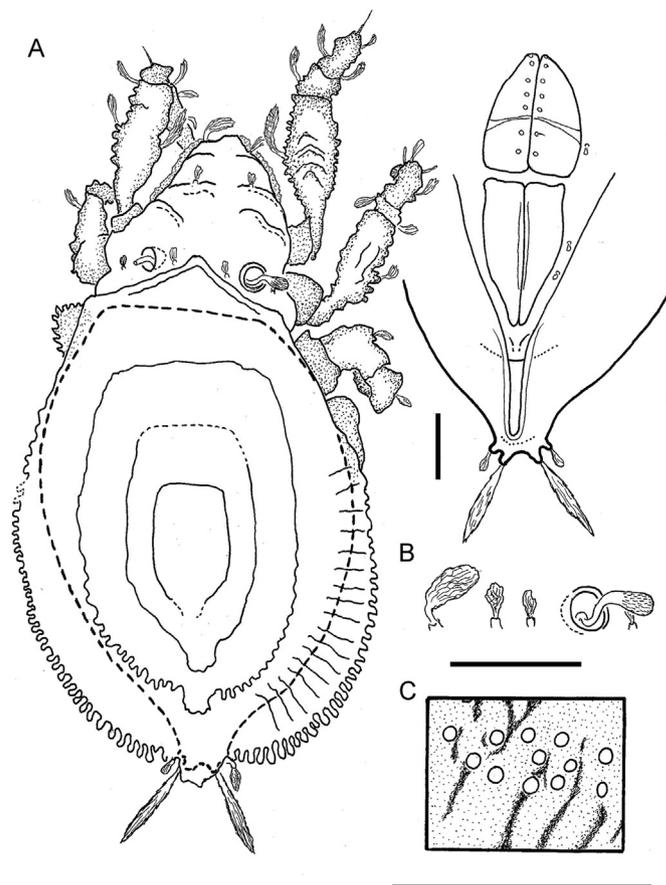


Fig. 5. Camera lucida drawings of the holotype of *Platyliodes sellnicki* sp. nov. (CES-582). A. Dorsal habitus (left), and ventral view of anal and genital region (right). B. Rostral, lamellar and interlamellar setae and sensillum. C. Notogastral sculpture. Scale bars 100 μ m.

Derivation of name. The specific epithet is matronymic in honour of our colleague Estefanía Mas.

Type material. Holotype, CPT-4165, housed at the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel Province, Spain). Incomplete specimen with partially damaged notogaster and lacking legs, preserved in a clear piece of amber trimmed to $2 \times 2 \times 1$ mm (in an epoxy resin trapezoid $21 \times 15 \times 1$ mm). No syninclusions.

Type locality and stratigraphy. Specimen collected from the San Just outcrop, in the municipality of Utrillas (Teruel Province, Spain). Escucha Fm., Lower Cretaceous (Albian).

Description. Measurements: 412 μ m long and 178 μ m wide.

Prodorsum rostrum slightly protruding in the form of a tooth. Rostral setae smooth and arched. Lamellar, interlamellar and exobothridial setae not preserved. Two long, parallel and narrow lamellae originating from the bothridia, ending in two non-protruding cusps, separated from rostral edge. Both cusps connected via a thin translamella (barely a line). Two thin tutorial lines originating close to the bothridia. Right sensillum preserved, bearing a short stalk and a broad head with short pilosity.

Notogaster longer than wide. Dorsosejugal suture slightly arched. Humeral shoulder barely protruding. Notogastral setae and porous areas not preserved, with only some visible alveoli. Two well visible horizontal *im* lyrifissures.

Ventral side Anal and genital plates well-developed, one close to another. Genital plates with at least five pairs of alveoli; anal plates

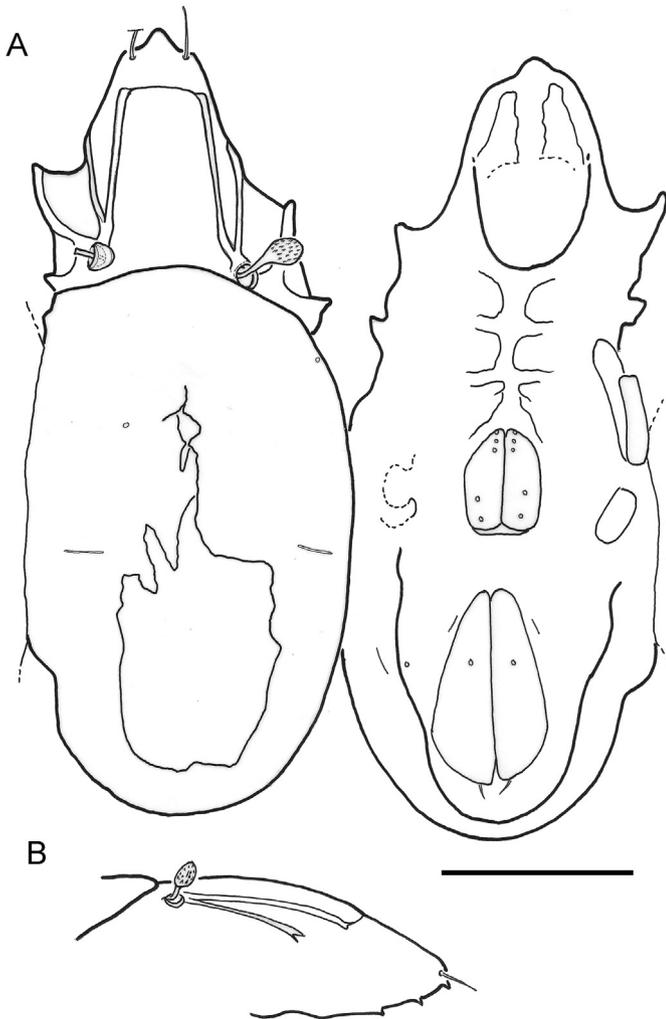


Fig. 6. Camera lucida drawings of the holotype of *Tenuelamellarea estefaniae* sp. nov. (CPT-4165). A. Dorsal (left) and ventral (right) habitus. B. Lateral view of prodorsum. Scale bar 100 μ m.

with only one pair of alveoli preserved. Adanal *iad* lyrifissures in paraanal position. Adanal setae ad_1 short, one alveolus of ad_3 set preserved.

Legs not preserved.

Discussion. Among the genera included in the family Lamellareidae, only *Tenuelamellarea* has narrow lamellae. The Lamellareidae is a small family without any fossil record that includes only three genera: *Lamellarea* Kok, 1968, *Microlamellarea* Coetzee, 1987 and *Tenuelamellarea* Subías and Iturrondobetia, 1978. The genus *Tenuelamellarea* has a very unusual distribution, its four described species being known from Spain, Hawaii Islands, Argentina, Sri Lanka, South Africa and two subantarctic Islands (Saint Paul and Amsterdam). *Tenuelamellarea estefaniae* sp. nov. seems to be closely related to *Tenuelamellarea argentinensis* Martínez, Velis, Eguaras and Fernández, 1995 given its poorly developed lamellar cuspis, distant from the rostral setae. However, *T. argentinensis* has a better developed translamella, the head of the sensilla is elongated and the notogaster is more or less circular. The feeding behaviour of the extant species is still poorly known, but they seem to be related to leaf litter.

Family: Scutoverticidae Grandjean, 1954

Genus *Hypovortex* Krivolutsky, 1969

Type species: *Hypovortex mirabilis* Krivolutsky, 1969

Hypovortex hispanicus Arillo and Subías sp. nov.

Figs. 8, 9

Derivation of name. The specific epithet is taken from the Latin term *Hispania*, meaning 'Spain'.

Type material. Holotype, CPT-4068, housed at the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel Province, Spain). Incomplete specimen with partially damaged notogaster and lacking legs, preserved in a clear piece of amber trimmed to $4 \times 1 \times 1$ mm (in an epoxy resin trapezoid $23 \times 8 \times 1$ mm). Syninclusions comprised one Diptera (Phoridae), one undetermined insect, two coprolites, and some hyphae of sooty moulds (see discussion below).

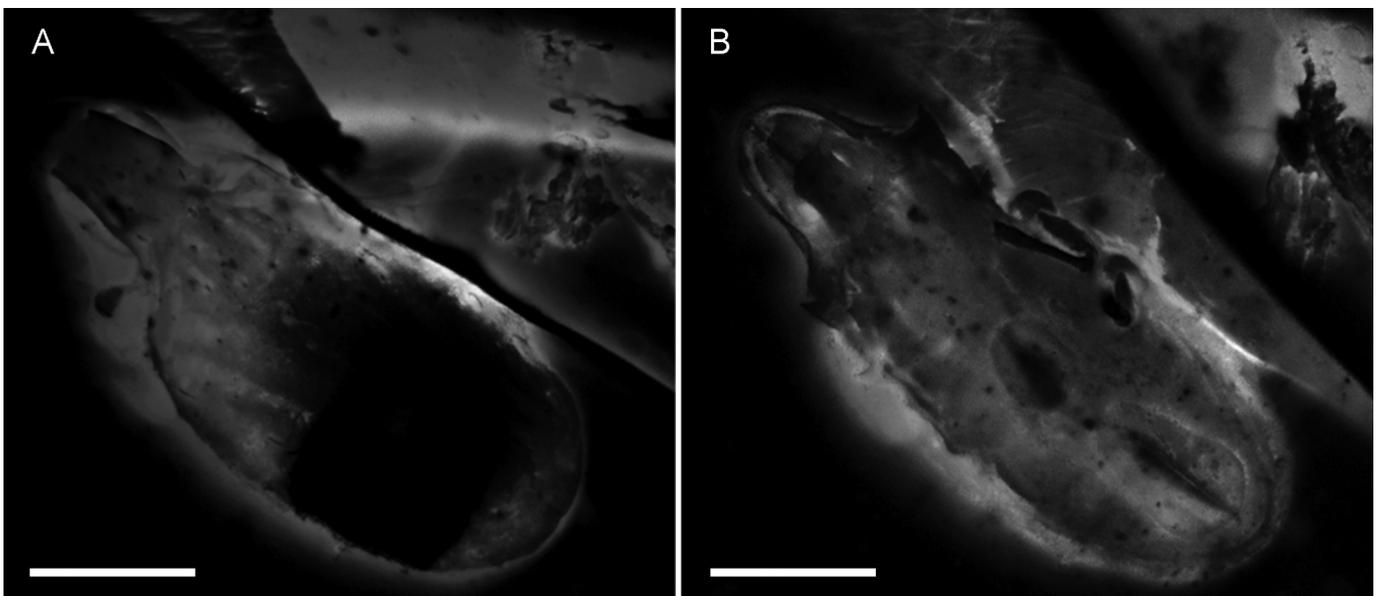


Fig. 7. Confocal microphotographs of the holotype of *Tenuelamellarea estefaniae* sp. nov. (CPT-4165). A. Dorsal habitus. B. Ventral habitus. Scale bars 100 μ m.

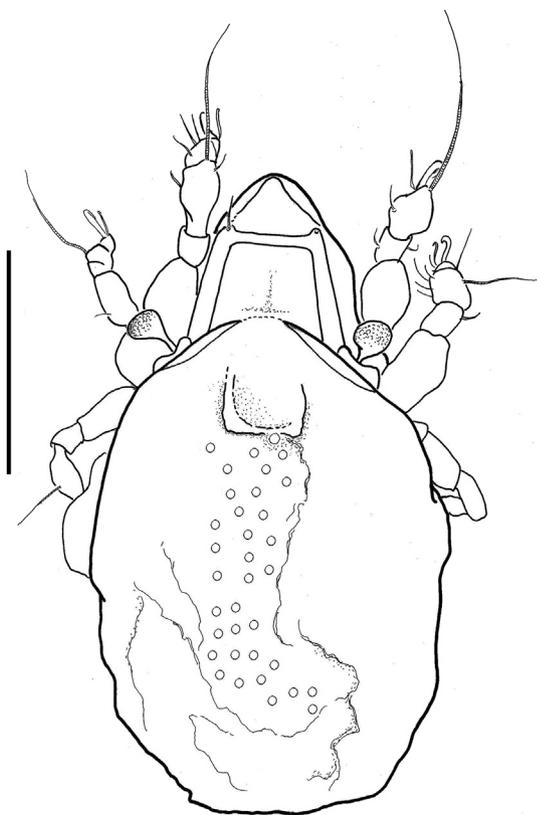


Fig. 8. Camera lucida drawing of the holotype of *Hypovertex hispanicus* sp. nov. (CPT-4068) in dorsal habitus. Scale bar 100 μ m.



Fig. 9. Confocal microphotograph of the holotype of *Hypovertex hispanicus* sp. nov. (CPT-4068) in dorsal habitus. Scale bar 100 μ m.

Type locality and stratigraphy. Specimen collected from the San Just outcrop, in the municipality of Utrillas (Teruel Province, Spain). Escucha Fm., Lower Cretaceous (Albian).

Description. Measurements: 285 μ m long and 151 μ m wide.

Prodorsum rostral edge with a rounded tooth. One lamellar setae preserved, being short and smooth. Rostral, interlamellar and exobothridial setae not preserved. Two parallel lamellae well-developed, with very short cusps, connected through a well-developed translamella. Sensillae short-stalked, with globose head. Prodorsal cuticle apparently smooth.

Notogaster cuticle partially lost. All the cuticle densely foveolated, lacking irregular ridges. Anterior part of the notogaster with a well-defined lenticulus. Notogastral setae not preserved.

Ventral side obscured due to amber turbidity.

Legs tridactyle; lateral claws very thin, looking like simple setae. Legs I and II without lamellate growths. Some leg setae preserved, with long solenidia on tibiae I and II.

Discussion. The genus *Hypovertex* was recently reviewed by Shtanchaeva and Netuzhilin (2003). Seven extant species are known from the Palearctic region, Argentina, India and Tanzania. Among these, only two species have a poorly developed lamellar cuspis: *H. mirabilis* Krivolutsky, 1969, and *H. lenticulatus* Kahwash, Ruiz and Subías, 1990. *Hypovertex hispanicus* sp. nov. is distinguished from *H. mirabilis* by the absence of lamellate outgrowths on legs I and II, and by the well-defined lenticulus of the notogaster. The new species closely resembles *H. lenticulatus* but differs in terms of its shorter lamellar cusps and the notogastral sculpture (foveolated in *H. hispanicus* as opposed to the irregular short ridges in *H. lenticulatus*). Extant *Hypovertex* species are sampled in a great diversity of habitats, from the litter of different plants, from Alpine desert in Kilimanjaro, to sand samples in coastal dunes. The posterior part of the mite presents some fossilized aerial hyphae of sooty moulds of the genus *Metacapnodium* (Metacapnodiaceae, Ascomycetes).

4. Concluding remarks

Based on the species described in Spanish amber, it would seem that the non-euedaphic species are the most frequent. A number of these correspond to typical decayed leaf-litter genera, including *Nothrus*, *Afronothrus*, *Hypovertex* and *Tenuelamellarea*; some would appear to include moss- and lichen-living species, such as *Platylidos* and *Eupterotegeus* (Arillo and Subías, 2002); and others would even seem to present surface behaviour, including *Ommatocephus* and *Ametroproctus*, which probably inhabit tree bark, and *Strieremaeus*, which probably inhabits the ground, rocks or tree trunks (Arillo and Subías, 2000; Arillo et al., 2008, 2009). Most of the species described probably feed on fungi hyphae (see the discussion above of *Hypovertex hispanicus*) or on pollen grains and spores.

Interestingly, a number of significant groups among the Recent fauna have not yet appeared in the pre-Cenozoic record. This is the case for example of Mixonomata (which includes the very common Euptyctima), and Oppioidea, both of which are present in Cenozoic ambers. In addition, most of the superfamilies in the non-monophyletic group Poronoticae are absent in the pre-Cenozoic record.

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References

- Arillo, A., Subías, L.S., 2000. A new fossil oribatid mite, *Archaeorchestes minguezae* gen. nov., sp. nov. from the Spanish Lower Cretaceous amber. Description of a new family, Archaeorchestidae (Acariformes, Oribatida, Zetorchestoidea). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 84, 231–236.
- Arillo, A., Subías, L.S., 2002. Second fossil oribatid mite from the Spanish Lower Cretaceous amber. *Eupterotegeus bitranslamellatus* n. sp. (Acariformes, Oribatida, Cepheidae). *Acarologia* 42, 403–406.
- Arillo, A., Subías, L.S., Shtanchaeva, U., 2008. A new fossil oribatid mite, *Ommatocephus nortoni* sp. nov. (Acariformes, Oribatida, Cepheidae) from a new outcrop of Lower Cretaceous Álava amber (northern Spain). *Systematic & Applied Acarology* 13, 252–255.
- Arillo, A., Subías, L.S., Shtanchaeva, U., 2009. A new fossil species of oribatid mite, *Ametroproctus valeriae* sp. nov. (Acariformes, Oribatida, Ametroproctidae), from the Lower Cretaceous amber of San Just, Teruel Province, Spain. *Cretaceous Research* 30, 322–324.
- Arillo, A., Subías, L.S., Shtanchaeva, U., 2010. A new genus and species of oribatid mite, *Cretaceobodes martinezae* gen. et sp. nov. from the Lower Cretaceous amber of San Just (Teruel Province, Spain) (Acariformes, Oribatida, Otocephidae). *Paleontological Journal* 44, 287–290.
- Arillo, A., Subías, L.S., Shtanchaeva, U., 2012. A new species of fossil oribatid mite (Acariformes, Oribatida, Trhypochthoniidae) from the Lower Cretaceous amber of San Just (Teruel Province, Spain). *Systematic & Applied Acarology* 17, 106–112.
- Barrón, E., Peyrot, D., Rodríguez-López, J.P., Meléndez, N., López del Valle, R., Najarro, M., et al., 2015. Palynology of Aptian and upper Albian (Lower Cretaceous) amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern Spain). *Cretaceous Research* 52, 292–312.
- Colloff, M.J., Halliday, R.B., 1998. *Oribatid Mites: a Catalogue of Australian Genera and Species*. Monographs on Invertebrate Taxonomy. CSIRO Publishing, Melbourne, 224 pp.
- Corral, J.C., López del Valle, R., Alonso, J., 1999. El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava* 14, 7–21.
- Delclòs, X., Arillo, A., Peñalver, E., Barrón, E., Soriano, C., López del Valle, R., et al., 2007. Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Palevol* 6, 135–149.
- Dunlop, J.A., Penney, D., Jekel, D., 2015. A summary list of fossil spiders and their relatives. In: *World Spider Catalog*. Natural History Museum, Bern.
- Karsch, F., 1884. Neue Milben in Bernstein. *Berliner Entomologische Zeitschrift* 28, 175–176.
- Krivolutsky, D.A., Krassilov, V.A., 1977. Oribatid mites from Upper Jurassic, USSR. In: Skarlato, O.A., Balashov, S. (Eds.), *Morphology and Diagnostics of Mites*. Academy of Sciences of the USSR, Leningrad, pp. 16–24.
- Najarro, M., Peñalver, E., Rosales, I., Pérez-de la Fuente, R., Daviero-Gomez, V., Gomez, B., et al., 2009. Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): palaeoenvironmental and palaeobiological implications. *Geologica Acta* 7, 363–387.
- Najarro, M., Peñalver, E., Pérez-de la Fuente, R., Ortega-Blanco, J., Menor-Salván, C., Barrón, E., et al., 2010. Review of the El Soplao amber outcrop, Early Cretaceous of Cantabria (Spain). *Acta Paleontologica Sinica* 84, 959–976.
- Norton, R.A., Behan-Pelletier, V.M., 2009. Suborder Oribatida. In: Krantz, G.W., Walter, D.E. (Eds.), *A Manual of Acarology*. Texas Tech University Press, Texas, pp. 430–564.
- Norton, R.A., Bonamo, P.M., Grierson, J.D., Shear, W.A., 1988. Oribatid mite fossils from a terrestrial deposit near Gilboa, New York. *Journal of Paleontology* 62, 259–269.
- Peñalver, E., Delclòs, X., 2010. Spanish amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 236–270.
- Peñalver, E., Delclòs, X., Soriano, C., 2007. A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretaceous Research* 28, 791–802.
- Sellnick, M., 1918. Die Oribatiden der Bernsteinsammlung der Universität Königsberg i. Pr. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg* 59, 21–42.
- Shtanchaeva, U., Netuzhilin, I., 2003. Review of the world fauna of oribatid mites of the family Scutoverticidae (Acariformes, Oribatida) with description of new species. *Zoologicheskii Zhurnal* 82, 781–803.
- Subías, L.S., 2004. Listado sistemático, sinónimo y biogeográfico de los ácaros oribátidos (Acariformes: Oribatida) del mundo. *Graellsia* 60, 3–305. Updated march 2015. http://escalera.bio.uclm.es/usuarios/bba/cont/docs/RO_1.pdf.
- Subías, L.S., Arillo, A., 2002. Oribatid fossil mites from the Upper Devonian of South Mountain, New York and the Lower Carboniferous of County Antrim, North Ireland (Acariformes, Oribatida). *Estudios del Museo de Ciencias Naturales de Álava* 17, 93–106.
- Subías, L.S., Shtanchaeva, U., Arillo, A., 2012. Listado de los ácaros oribátidos (Acariformes, Oribatida) de las diferentes regiones biogeográficas del mundo. *Monografías electrónicas de la Sociedad Entomológica Aragonesa* 4, 1–815.
- Villanueva-Amadoz, U., Pons, D., Diez, J.B., Ferrer, J., Sender, L.M., 2010. Angiosperm pollen grains of San Just site (Escucha Formation) from the Albian of the Iberian Range (north-eastern Spain). *Review of Palaeobotany and Palynology* 162, 362–381.

Appendix A. Supplementary data

Supplementary video related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2016.02.009>.