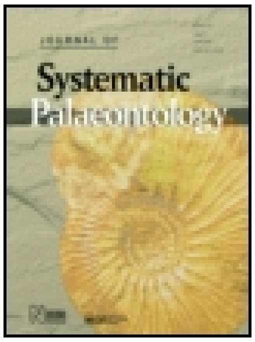

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Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona)

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Springtails (Hexapoda: Entognatha: Collembola) extend into at least the Early Devonian, but have a meagre record as fossils until the latter part of the Mesozoic. Here, we document a diverse fauna of springtails in the order Symphypleona from amber recovered at the Peñacerrada I locality, Moraza, northern Spain, and from the Late Albian Utrillas Group in the Basque-Cantabrian Basin. The fauna includes representatives of all of the principal suborders and infraorders, and most superfamilies, of the Symphypleona. This revision of the fauna includes the discovery and description of five new genera and species scattered across the phylogenetic diversity of the clade: *Pseudosminthurides stoechus* gen. et sp. nov. (Sminthurididae), *Cretokatianna bucculenta* gen. et sp. nov. (Katiannidae), *Sphyrotheciscus senectus* gen. et sp. nov. (Sminthuridae: Sphyrothecinae), *Archeallacma dolichopoda* gen. et sp. nov. (Sminthuridae: Sminthurinae?) and the enigmatic *Katiannasminthurus xenopygus* gen. et sp. nov. (Sminthuridae? *incertae sedis*). This is the earliest amber fauna of springtails yet described, and highlights the remarkably modern character of the group even during the early stages of the Cretaceous.

http://zoobank.org/urn:lsid:zoobank.org:pub:BFF73D0D-31A0-4AE1-9CA4-C62424177C7D

Keywords: Entognatha; springtails; Albian; Peñacerrada I; morphology; taxonomy

Introduction

The springtails (Collembola) are small- (less than 0.3 mm) to medium-sized (over 17 mm) hexapods that comprise one of three lineages of the clade Entognatha, and sister to the insects (class Insecta) (Hennig 1981; Grimaldi & Engel 2005; Engel 2015). In general habitus, species can be segregated into two morphotypes – the elongate forms of the former Arthropleona (today the Poduromorpha, Entomobryomorpha and Tomoceromorpha) and the more globular-bodied Symphypleona and Neelipleona (Neopleona). Springtails derived their 'nom de plume' from the characteristic 'spring' mechanism located on the ventral posterior of the body. This jumping apparatus, or furcula, is formed from the basal fusion of a pair of appendages from the fourth abdominal segment and consists of a single basal manubrium and paired distal dens, with each dens bearing an apical mucro (in some groups the dens and mucro are fused and form a 'mucrodens') (Hopkin 1997; Grimaldi & Engel 2005). The furcula can be brought forward and locked into place by the retinaculum of the preceding abdominal segment. When the furcula is let loose, the force can propel the animal a considerable distance. Some species, particularly those euedaphic groups (Gisin 1943), have the furcula reduced and vestigial or even lacking outright.

As a whole the group is eurytopic, with species occurring in equatorial climates of all manner and extending through the utmost reaches of the Arctic and Antarctic (e.g. Gressitt 1967; Coulson 2007; Coulson *et al.* 2013; Porco *et al.* 2014; Velasco-Castrillón *et al.* 2014). Although principally documented as living in soil and leaf litter, many species live in a variety of vegetation, littoral and neustonic habitats, caves, and on ice fields or glaciers. While most feed on fungal matter, decomposing debris and fecal material, some species prey on micro-organisms, particularly nematodes, and a few others consume fresh plant tissues (Christiansen 1964; Hopkin 1997). There are many species that are commensal, but none is known to be parasitic. Although seemingly insignificant, a few species can become serious agricultural pests (e.g. Wilson & Gerard 2014; Joseph *et al.* 2015), and others are excellent biological indicators of ecosystem health (Hopkin 1997).

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Today there are approximately 8000 described species, organized into no less than 762 genera and 33 families (Janssens & Christiansen 2011), making them the most diverse of the entognathous hexapods and of comparable size to some of the smaller orders of insects such as the Odonata or Neuroptera (Grimaldi & Engel 2005). The group has been treated as either an order (within class Entognatha: e.g. Lubbock 1873; Börner 1901, 1904, 1906, 1913; Paclt 1956; Salmon 1964; Boudreaux 1979; Grimaldi & Engel 2005) or a distinct class, on par with the insects themselves (e.g. Sharov 1966; Manton 1970; Cassagnau 1971; Hopkin 1997; Deharveng 2004; Janssens & Christiansen 2011). Classification as an order, although simply semantic, obviates the need for a proliferation of ranks intercalated between superclass (Hexapoda) and class, permitting Entognatha as a whole to stand in opposition to the insects as well as its subordinate group, the Ellipura (assuming this is a natural grouping at all: see e.g. Bitsch & Bitsch 1998, 2000; Giribet *et al.* 2004). However, the tendency in modern collembolan research has been to accord the group the rank of class, and we have followed that system herein.

Collembola are organized into four traditional orders (Deharveng 2004; Janssens & Christiansen 2011) – Poduromorpha Börner, 1913, Entomobryomorpha Börner, 1913, Neelipleona Massoud, 1971 and Symphypleona Börner, 1901 – although some authors prefer to consider the Neelipleona as subordinate within Symphypleona (e.g. Bretfeld 1986, 1999). A fifth group, Tomoceromorpha, which includes only the superfamily Tomoceroidea, is further distinct and, although generally included among the entomobryomorphs, is more closely related to the Poduromorpha (D'Haese 2002; Xiong *et al.* 2008), but lacking the distinct pronotum of the latter (a likely plesiomorphy owing to its absence also in the Neelipleona and Symphypleona, and given that Isotomidae are so relict). Relationships among these groups have been contentious, but the Neelipleona and Symphypleona are generally considered closely related, as the Neopleona (but see for example Schneider *et al.* 2011 where Neelipleona are allied with the other orders, constituting a clade 'Paradoxopleona'), while Entomobryomorpha are allied to the Tomoceromorpha + Poduromorpha (or Alethoarthropleona), the three constituting the former Arthropleona (e.g. Xiong *et al.* 2008). Both the Neelipleona and Symphypleona are globular in general form, the result of fusion between the thorax and abdominal segments, but in the former the thorax is more developed relative to the abdomen, the species are blind, and the dens is subdivided (Massoud 1971).

The Collembola are of ancient origin, extending back to the Early Devonian by species putatively attributable to the extant family Isotomidae (and perhaps reflective of many entomobryomorphan traits being plesiomorphic for the group) (Greenslade & Whalley 1986). The earliest described Collembola are fragmentary specimens of *Rhyniella praecursor* Hirst & Maulik, 1926, preserved in the chert from near Rhynie, Scotland, a species long famous as the oldest definitive hexapod before insects were also recognized from the same deposit (e.g. Engel & Grimaldi 2004). A second Palaeozoic collembolan was described from a poorly preserved, late Early Permian compression from South Africa as *Permobrya mirabilis* Riek, 1976. Given their soft bodies and generally minute size, only the finest of preservation permits meaningful comparison with extant taxa, and it is therefore from the Cretaceous and later that the record is more developed owing to the occurrence and fidelity of fossiliferous resins. The first Mesozoic springtail discovered was a single individual of *Protentomobrya walkeri* Folsom, 1937, from the Late Cretaceous of Canada, to which was later added seven further species in seven genera (Christiansen & Pike 2002a, b). In the Canadian amber fauna, *P. walkeri* and *Oncobrya decepta* Christiansen & Pike, 2002b were each placed in monotypic, extinct families, although at least *Protentomobrya* Folsom, 1937 is most likely an isotomid (Greenslade & Whalley 1986). The most diverse fauna is that of the mid-Cretaceous of Myanmar, from which have been described 14 species in 13 genera, including one extinct family (Christiansen & Nascimbene 2006). A brief account was provided for a small sampling of specimens preserved in Early Cretaceous Spanish amber (Simón-Benito *et al.* 2002), and while there is mention of Collembola in the Cretaceous ambers of France and Lebanon (Azar 2000; Perrichot 2004; Azar *et al.* 2010; Perrichot *et al.* 2010), none has been thoroughly documented. Although the data are limited to a few deposits, it is apparent that Collembola were diverse by the latter part of the Mesozoic, not surprising for a group of mid-Palaeozoic age. From the Cenozoic, springtails are again documented exclusively in amber, particularly in middle Eocene Baltic and Rovno ambers (e.g. Olfers 1907; Stach 1923; Handschin 1926; Lawrence 1985; Perkovsky *et al.* 2007; Hädicke *et al.* 2013), but also in the early Miocene ambers of Chiapas, Mexico (Christiansen 1971) and the Dominican Republic (Mari Mutt 1983), or in Pleistocene copal from Mizunami, Japan (Yosii 1974).

Herein we consider the fauna of Symphypleona as preserved in Early Cretaceous amber from Spain, complementing the earlier overview of Collembola from these deposits by Simón-Benito *et al.* (2002). In the modern fauna, the Symphypleona are represented by 1188 currently recognized species in about 207 genera (Janssens & Christiansen 2011), and are characterized by the formation of their distinct globular shape from the enlargement and fusion of the abdominal segments, as well as the presence of eyes, antennae longer than the head, undivided dens and setose retinaculum (Bretfeld 1999: as Eusymphypleona). Most species are exceptional jumpers and some have a prominent and conspicuous collophore ('ventral tube'), a structure presumably formed of fused eversible vesicles and used in water absorption. They are widely represented in leaf litter, on low vegetation, on the surface of still fresh water or in the tropical intertidal zone, and are abundant on trees, particularly in the canopies of tropical humid forests (Hopkin 1997). In the earlier account of Spanish amber Collembola, four specimens were attributable to Symphypleona, but the available material has now grown to a total of nine. In addition, further preparation of the material has allowed us to refine previous misconceptions regarding the Symphypleona present in the Spanish amber fauna.

Material and methods

Preparation and descriptive methods

The specimen preparation, photography and imaging procedure followed the following steps. Amber initially was screened for inclusions, then embedded in a stable epoxy resin (Epo-tek 301) under vacuum, and finally ground and polished with a water-fed flat lap (Nascimbene & Silverstein 2000). Embedding stabilizes the amber, preventing oxidation and permitting an accurate viewing of the biotic inclusion since it obscures fine surface scratches. Because structures critical for study are principally minute (e.g. setae, details of furcula), it was necessary to meticulously glue some specimens between a glass microscope slide and a cover glass using a drop of the synthetic resin, thereby allowing observation with finer resolution. Preparations were typically between 1.0 and 3.0 mm in thickness, and critical structures were often just microns beneath the surface. Fossils were examined with Motic BA310 and Olympus BX41 compound microscopes, and measurements were taken with Image J software. All measurements were recorded in micrometres because of the small size of the specimens. Subsequently, photomicrography was performed with a Moticam 2500 digital camera attached to a Motic BA310 compound microscope with Motic Images Plus 2.0 software, at the Universitat de Barcelona (Barcelona, Spain). Helicon Focus software was used to combine photos of an inclusion at different foci, which facilitated more accurate illustration. Drawings were prepared using a drawing tube Olympus U-DA 0G06204 attached to the Olympus BX41 compound microscope at the University of Kansas (Lawrence, Kansas). Length measurements were taken along the midline. Morphological terminology used throughout is generally that widely employed in the systematics of Collembola (e.g. Richards 1968; Betsch 1980; Bretfeld 1999; Fjellberg 2007), except for the use of 'opisthosoma' for the combined structure of the thorax and abdomen (opisthosoma = body posterior to prosoma), and the descriptions provided here are aimed at elucidating broader evolutionary patterns (e.g. Grimaldi & Engel 2007). The material is deposited in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain).

Geological setting

The Basque-Cantabrian Basin, northern Spain, along with other Mesozoic basins of the Iberian Plate, is associated with the opening of the northern part of the Atlantic. During the Early Cretaceous, sedimentation in the basin was dominated by sandstones, limestones and marls. Spanning the Albian, at the end of the rift stage, deltaic and estuarine systems developed and evolved vertically into a deltaic system dominated by a fluvial-deltaic environment with siliciclastic input. In general, the amber localities of the Basque-Cantabrian Basin are related to paralic-swamp environments in the eastern region (Utrillas Group *sensu* Barrón *et al.* 2015), or paralic-marine environments in the west (Las Peñosas Fm.) (Peñalver & Delclòs 2010). Spanish Cretaceous amber is principally found in localities distributed in a curvilinear arc from the east to the northwest along the Iberian Peninsula, which corresponds approximately to the seashore during the Early Cretaceous (Delclòs *et al.* 2007). Two main amber-bearing outcrops are found in the eastern area of the Basque-Cantabrian Basin: Moraza, also named Peñacerrada I, in Burgos Province; and Peñacerrada II in Álava Province. The amber from both outcrops belongs to the so-called 'Álava amber', recently dated as Late Albian in age (Barrón *et al.* 2015). In this area continental-transitional deposits can be differentiated into three subunits that are represented by a deltaic succession, with a vertical tendency towards a regression of the deltaic system in the lower−middle subunits and a vertical transgression in the upper subunit. Amber is always associated with coal and lignitic beds or organically rich marl levels from the middle subunit, coinciding with the boundary between the maximum regression and the beginning of the transgression, and it is mainly present at the top of filling sequences of interconnected channels within deltaic bays. One of these amber deposits occurs in Peñacerrada I locality, which has yielded the present specimens of Collembola, and thousands of other arthropod inclusions (e.g. Alonso *et al.* 2000; Engel & Delclòs 2010; Peñalver & Delclòs 2010; Perrichot *et al.* 2011; Peñalver *et al.* 2012; Pérez-de la Fuente *et al.* 2012, 2013; Engel *et al.* 2013a, b, 2015; Ortega-Blanco & Engel 2013; Ortega-Blanco *et al.* 2011a, b, c, d, e, 2014; Sánchez-García *et al.* 2015, 2016; Peris *et al.* in press).

Institutional abbreviation

MCNA: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Systematic palaeontology

Class **Collembola** Lubbock, 1870
Order **Symphypleona** Börner, 1901

Remarks. Following Fjellberg (2007), the nine fossil collembolans studied herein are assignable to Symphypleona *s. str.* based on the presence of: (1) a more or less globular body divided into two parts – the head and a large mass consisting of the greater abdomen (abdominal segments 1–4), the lesser abdomen (abdominal segments 5 and 6), and the more or less fused thorax; (2) antennae as long as or longer than the head; (3) developed eyes; (4) a dens with numerous setae that is not divided; and (5) a channeled mucro (i.e. gutter-like rather than hook-like), and often with serrate edges. Following Lubbock (1862a, b, 1868, 1870) and Salmon (1941) for the old 'Sminthuridae *s. l.*', they also share: (1) a globular body with the thorax smaller than the abdomen; (2) antennae inserted behind the middle of the head, with four antennomeres that are sometimes subdivided and generally much longer than the head; (3) a head with a distinctly elevated vertex; (4) coxae that are not elongate, and are on the outer surface much shorter than the trochanter (elongate in Neelipleona); and (5) the presence of bothriotrichia. Table 1 summarizes our preferred, simplified classification of families of Symphypleona.

Table 1. A simplified, hierarchical classification of Symphypleona (modified from that of Bretfeld 1986, 1994, 1999, and excluding Neelipleona).

Order Symphypleona Börner, 1901
Suborder Sminthuridida Bretfeld, 1986
Superfamily Sminthuridoidea Börner, 1906
Family Sminthurididae Börner, 1906
Family Mackenziellidae Yosii, 1961
Suborder Appendiciphora Bretfeld, 1986
Infraorder Katianniformia Bretfeld, 1986
Superfamily Katiannoidea Börner, 1913
Family Katiannidae Börner, 1913
Family Spinothecidae Delamare-Deboutteville, 1961
Family Arrhopalitidae Stach, 1956
Family Collophoridae Bretfeld, 1999
Superfamily Sturmioidea Bretfeld, 1994
Family Sturmiidae Bretfeld, 1994
Infraorder Sminthuriformia Bretfeld, 1986
Superfamily Sminthuroidea Lubbock, 1862a
Family Bourletiellidae Börner, 1913
Family Sminthuridae Lubbock, 1862a
Subfamily Sminthurinae Lubbock, 1862a
Subfamily Songhaicinae, subfam. nov.
Subfamily Sphyrothecinae Betsch, 1980
Superfamily Dicyrtomoidea Börner, 1906
Family Dicyrtomidae Börner, 1906
Subfamily Dicyrtominae Börner, 1906
Subfamily Ptenothricinae Richards, 1968

Superfamily **Sminthuridoidea** Börner, 1906
Family **Sminthurididae** Börner, 1906
Genus ***Pseudosminthurides*** gen. nov.

Type species. *Pseudosminthurides stoechus* sp. nov.

Diagnosis. Male. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head lacking spines, with a pair of large interocular vesicles; eyes with at least 4+4 ommatidia; antenna short and stout, fourth antennomere not subdivided, third and second antennomeres modified into a clasping organ. Tibiotarsus distinctly tuberculate. Abdomen without cuticular spines and broadened setae; greater abdomen with bothriotrichia ABC distributed in an oblique line (AB equidistant with BC). Dens about 4.4× mucro length, with a row of straight, spine-like setae along outer margin; mucro length distinctly less than twice as long as wide; mucro with broad, membranous, outer striated mucronal lamella much wider than inner striated, membranous lamella; a simple, narrow mid-ventral, keel-like lamella present along mucronal rachis; mucronal seta absent.

Female. *Latet*.

Derivation of name. The genus-group name is a combination of the Greek, ψευδος (meaning 'false'), and *Sminthurides* Börner, 1900, type genus of the family. The gender of the name is masculine.

Pseudosminthurides stoechus sp. nov.
(Figs 1, 2)

Diagnosis. As for the genus (*vide supra*).

Derivation of name. The specific epithet is considered an adjective and is taken from the Greek στοῖχος, meaning 'line', and in reference to the linear arrangement of bothriotrichia ABC on the greater abdomen.

Type material. Holotype ♂, MCNA 12788.1, virtually complete, dorsoventrally exposed. Preserved in a clear yellow turbid piece of amber trimmed to 1.0 × 0.9 × 0.1 cm (in an epoxy resin trapezoid 2.2 × 1.5 × 0.2 cm), and accompanied by much debris and arthropod remains (e.g. scales). An internal fracture in the amber runs along the specimen, obscuring some details of the head and body, and the right antenna is lost. The hind legs are obscured by the opaque body mass. Syninclusions include three acari and a further springtail (of the Entomobryomorpha and to be treated in a subsequent work focusing on that order: Sánchez-García & Engel in press).

Figure 1. Photomicrographs of the holotype male of *Pseudosminthurides stoechus* gen. et sp. nov., MCNA 12788.1. **A,** dorsal habitus; **B,** detail of left antenna in ventral view; **C,** detail of furcula in ventral view. Figures made from consecutive pictures taken at successive focal planes.

Inclusions in piece MCNA 12788 and another entomobryomorphan collembolan plus three acari in piece MCNA 12787 were originally part of a single piece of amber that was divided into two fragments for optimal study.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Male. Total length as preserved (from the tip of the head to the tip of the opisthosoma) 631 μm.

Head. Dorsoventrally exposed preventing cephalic diagonal measurement, length 160 μm as preserved; vertex of head with numerous small, slender acuminate setae, and one pair of large interocular vesicles. Eyes poorly visible, with at least four ommatidia apparently visible in right eyepatch.

Antenna. Fairly stout, short, length 221 μm, about 1.38× as long as cephalic length; fourth antennomere not subdivided; third and second antennomeres modified into a clasping organ as figured (Figs 1B, 2), with different elements sitting on distinct papillae.

Legs. Mostly obscured; coxa and trochanter not visible; lengths of profemur and protibiotarsus: 77 μm (measured on left fore leg) and 118 μm (measured on right fore leg); mesotibiotarsus: 112 μm (measured on right mid leg); tibiotarsus with distinct tubercles accompanied

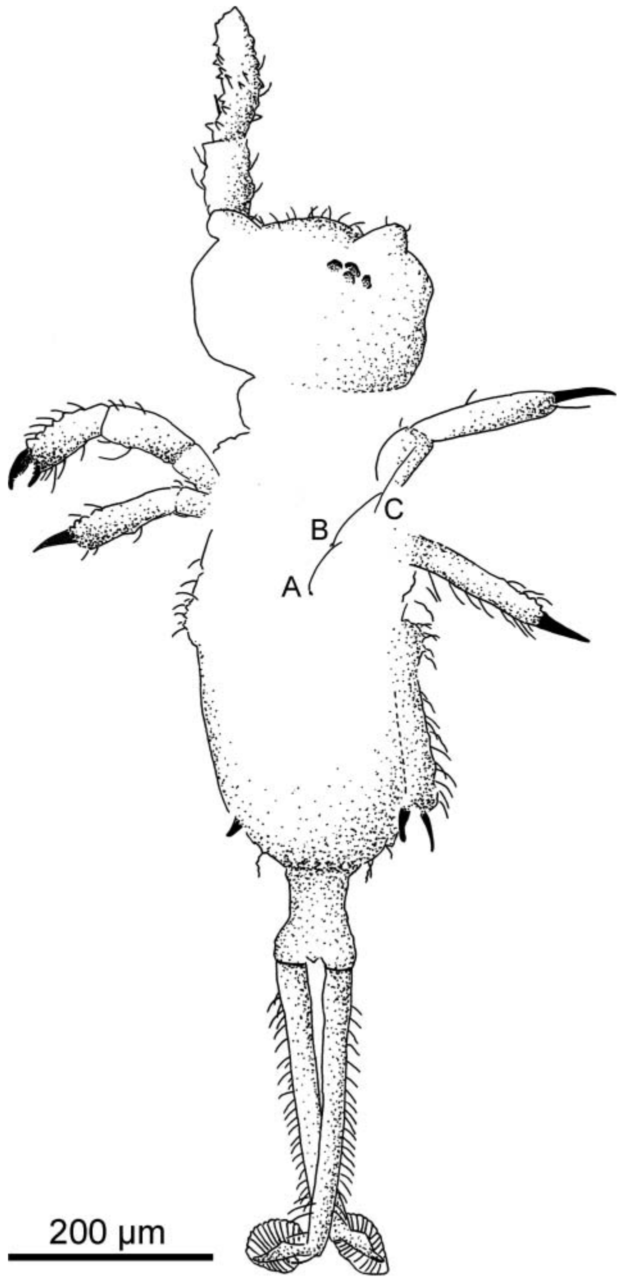

Figure 2. Camera lucida drawing of the holotype male of *Pseudosminthurides stoechus* gen. et sp. nov., MCNA 12788.1. Abbreviations: A, B, C, bothriotrichia A, B, C.

by numerous small, slender acuminate setae; tibiotarsal organ not visible; fore and mid legs with narrow unguiculus bearing a simple, setaceous apical filament about as long as unguis; unguis elongate, length 67 μm, about 0.54× length of tibiotarsus, nearly straight and sharp apically; hind legs with unguis more curved and shorter than on fore and mid legs; unguiculus about as long as unguis.

Collophore. Not visible.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma with traces of thoracic segmentation present, length 471 μm as preserved; greater abdomen and thorax clothed largely with sparse, short slender setae; greater abdomen with three pairs of setaceous bothriotrichia (ABC) distributed in an oblique line ('linear pattern'; AB equidistant with BC); lesser abdomen not distinguishable, with two pairs of slender setaceous trichobothria.

Furcula. Long and slender; manubrium length 87 μm; dens length 282 μm, with a row of straight, spine-like setae along outer margin, ventral margin smooth; mucro length 64 μm, broad, width 49 μm, from above about 1.29× as long as broad, pointed in lateral view; mucronal lamellae large, broad, membranous, and unequal; outer lamella transversely striate, much wider than inner striated lamella, with a simple, very narrow, smooth, mid-ventral, keel-like lamella along mucronal rachis; mucronal seta absent. Ratio of mucro, dens, manubrium: 1.00:4.42:1.37.

Female. *Latet*.

Remarks. Members of the family Sminthurididae are all small, less than 1 mm, and differ from other families by males having antennomeres II and III modified into clasping organs which they interlock with the female antennae during courtship. In addition, the fifth abdominal segment bears two pairs of bothriotrichia, and anal appendages are lacking in females (Fjellberg 2007). Sminthurididae comprise 11 extant genera, those of *Sminthurides* and *Sphaeridia* Linnaniemi, 1912 being the most diverse.

The new species bears a remarkable superficial similarity to extant males of the genus *Sminthurides*. Extant species of this genus are dimorphic, with females much larger than males, and the fourth antennomere is often subdivided. Males have modified antennomeres II and III forming a clasping organ, and the second antennomere bears a single bothriothrix on the outer surface (except two in *Sminthurides penicillifer* (Schäffer, 1896)). *Sminthurides* also have 6−8 ommatidia (two of them usually much smaller than the others); pro- and mesopretarsal claws long and narrow, with a slender unguiculus; metapretarsal claws short, with a broad basal lamella on the unguiculus; an unguiculus with a setaceous apical filament which reaches beyond the apex of the unguis; and a mucro with a single mid-ventral, keel-like lamella and two dorsal (inner, outer) lamellae of which the inner one is typically serrated and the outer has an undulating margin (Fjellberg 2007). *Pseudosminthurides stoechus* gen. et sp. nov. largely agrees with *Sminthurides* in general habitus, its modified antennae, complex pretarsal morphology, and shape of the mucrones. However, the sockets of the three bothriotrichia (ABC) on the right side of the greater abdomen are distributed in an oblique line in *P. stoechus* instead of the form of an obtuse angle that opens anteriorly as is present in *Sminthurides*, or posteriorly in *Sphaeridia*. One lateral seta is usually present at the base of the mucro in *Sminthurides*, while some species as well as *P. stoechus* lack this. Although eyes are difficult to discern in *P. stoechus* owing to the nature of its preservation, at least four ommatidia can be seen; but no details of the mouthparts, collophore, and retinaculum are visible in the holotype of *P. stoechus*, preventing comparison with extant sminthuridids.

Superfamily **Katiannoidea** Börner, 1913
Family **Katiannidae** Börner, 1913
Genus ***Cretokatianna*** gen. nov.

Type species. *Cretokatianna bucculenta* sp. nov.

Diagnosis. Female. The genus is distinguished from all other genera by its unique combination of the following characters: body small-sized (<0.5 mm); head with two lateral, cheek-like bulging pouches, separated by a broad median ridge; up to four heavy spines on head; eyes with at least 6+6 ommatidia; antenna about 1.5× head length; fourth antennomere longer than third antennomere, with 14 subsegments. Abdomen without cuticular spines and broadened setae; greater abdomen with bothriotrichia ABC forming an obtuse angle opening anteriorly (AB equidistant with BC); subanal appendage present, anteriorly recurved and downwardly directed towards genital orifice, apically split into several branches. Dens without spines, about 4.3× mucro length; mucro comparatively simple, with narrow, smooth inner and outer lamellae; mucronal seta absent.

Male. *Latet*.

Derivation of name. The generic name is a combination of the prefix for Cretaceous, and *Katianna* Börner, 1906, type genus of the family. The gender of the name is feminine.

Cretokatianna bucculenta sp. nov.
(Figs 3, 4)

2002 *Fasciosminthurus*? sp. Simón-Benito, Ortuño & Espantaleón: 87, fig. 3a.

Diagnosis. As for the genus (*vide supra*).

Derivation of name. The specific epithet is considered an adjective and is taken from the Latin term *bucculentus*, meaning 'with full cheeks', and is a reference to the bulging cheek-like pouches on the head capsule.

Type material. Holotype ♀, MCNA 10047, virtually complete. Preserved in a dark yellow turbid piece of amber trimmed to 0.4 × 0.2 × 0.1 cm (in an epoxy resin trapezoid of 1.2 × 1.0 × 0.1 cm), and accompanied by particles of detritus and bubbles; the amber is also darkened near the inclusion. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Female. Total length as preserved 409 μm.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 226 μm; vertex of head with four stout, rather curved spines; anterior surface with numerous short, slender acuminate setae; head with two lateral, cheek-like bulging pouches which bear short, slender acuminate setae and are separated by a broad median ridge

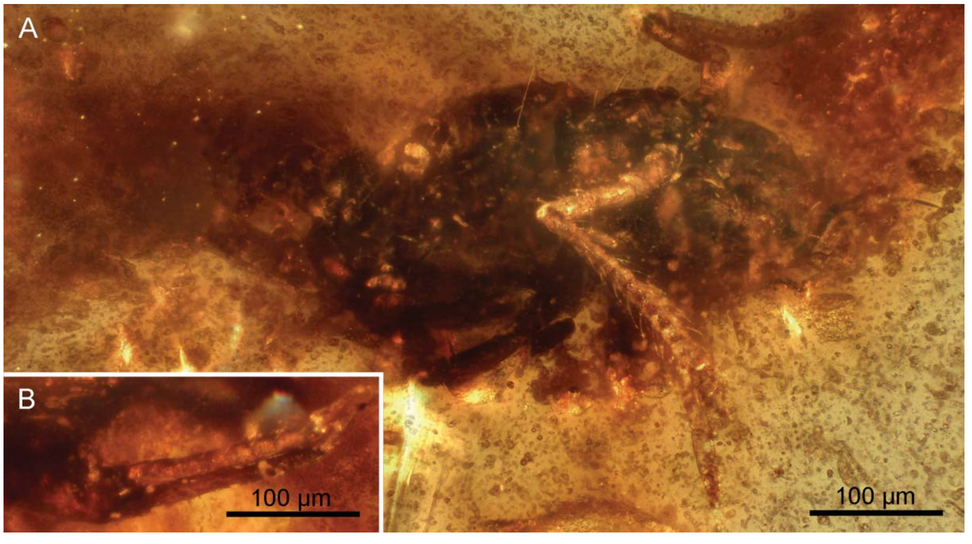

Figure 3. Photomicrographs of the holotype female of *Cretokatianna bucculenta* gen. et sp. nov., MCNA 10047. **A,** dorso-lateral habitus; **B,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

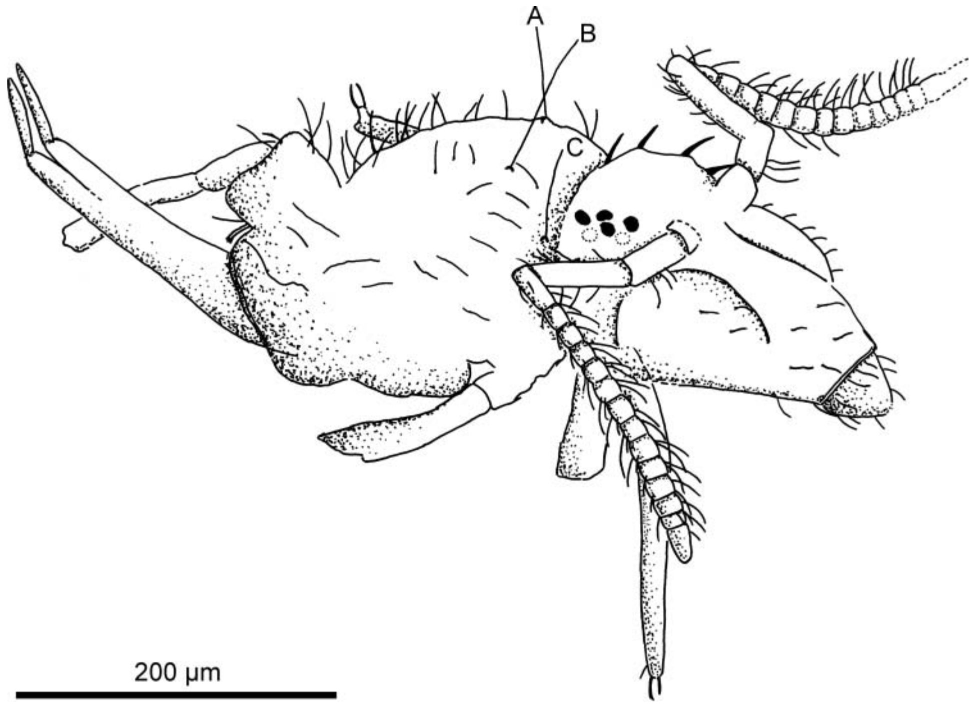

Figure 4. Camera lucida drawing of the holotype female of *Cretokatianna bucculenta* gen. et sp. nov., MCNA 10047. Abbreviations: A, B, C, bothriotrichia A, B, C.

(width 29 μm). Eyes poorly visible, with at least six ommatidia visible in right eyepatch.

Antennae. Relatively long and slender, clearly elbowed between antennomeres III and IV; length about 1.51× as long as cephalic diagonal; antennomere lengths in μm approximately: IV, 210; III, 75; II, 36; I, 18; fourth antennomere with 14 subsegments, basal and apical subsegments slightly longer than intermediate subsegments, each subsegment bearing one whorl of long, slender, curved, acuminate setae (which are approximately as long as the maximum width of the subsegments or slightly longer); third antennomere with a simple, subapical papilla accompanied by long, scattered setae; second antennomere with three large outer setae; first antennomere with no visible setae.

Legs. Mostly obscured by adjacent body mass (only the distal end of an anterior tibiotarsus and its pretarsal complex are visible) preventing measurements; unguis small and thin, poorly visible, tunica apparently absent; unguiculus apparently not reaching apex of unguis; at least one pretarsal seta visible.

Collophore. Not visible.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 217 μm as preserved; greater abdomen and thorax clothed largely with slender, somewhat curved and distinctly not spine-like dorsal setae, such setae becoming longer and more numerous posteriorly; greater abdomen with three setaceous bothriotrichia (ABC) forming an obtuse angle opening anteriorly ('triangular pattern'; AB equidistant with BC); lesser abdomen (fifth and sixth abdominal segments) sharply demarcated from greater abdomen and projected upward, with an anterior, slender setaceous bothriothrix (D), bothriothrix D not thicker than surrounding circumanal setae. Female subanal appendage anteriorly recurved and downwardly directed towards genital orifice, apically split into several branches. Sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 86 μm; dens length 182 μm, with numerous setae at least on outer margin; mucro simple, length 42 μm, slender, pointed in lateral view; mucronal lamellae narrow and unequal; outer mucronal lamella with smooth or at most weakly crenulate dorsal edge; inner lamella smooth; mucronal seta absent; ventral axis of rachis smooth. Ratio of mucro, dens, manubrium: 1.00:4.30:2.00.

Male. *Latet*.

Remarks. Simón-Benito *et al.* (2002) described specimen MCNA 10047 as closely related to some species in the extant genus *Fasciosminthurus* Gisin, 1960 (family Bourletiellidae: Table 1) mainly based on the putatively preserved pattern of colouration. Furthermore, they originally described the specimen as having 8+8 ommatidia, the fourth antennomere with 12−14 subsegments, and the antennae as elbowed between antennomeres III and IV. However, our re-examination of the specimen confirms that other critical features were not shown or described in the original description (e.g. details of the head, bothriotrichial pattern and furcula), or were misinterpreted. Most importantly, the colour pattern described by Simón-Benito *et al.* (2002) is an artifact of preservation and not actually characteristic of the species described, and the putative similarities with *Fasciosminthurus* are illusory.

The placement of *Cretokatianna bucculenta* gen. et sp. nov. in the family Bourletiellidae clearly is unsupported based on numerous traits, most notably: (1) the triangular bothriotrichial pattern (i.e. bothriotrichia ABC form an oblique line ('linear pattern') in Bourletiellidae instead of an obtuse, anteriorly-opening angle ('triangular pattern') as is present in *C. bucculenta*); (2) the length of the annulated fourth antennomere (long in bourletiellids but much shorter in *C. bucculenta*); (3) the overall shape (simple in bourletiellids rather than the modified and generally complex form present in *C. bucculenta*) and position (directed caudal towards the anal orifice versus recurved downward and towards the genital orifice in *C. bucculenta*) of the subanal appendage; and (4) the number of pairs of bothriotrichia on the fifth abdominal segment (two in Bourletiellidae versus the single pair present in *C. bucculenta*).

Cretokatianna bucculenta may be placed clearly within the family Katiannidae on the basis of (Betsch 1980; Fjellberg 2007): (1) female subanal appendage recurved and downwardly directed towards the genital orifice, along with its generally complex shape; (2) three pairs of abdominal bothriotrichia with a normal triangular pattern; (3) fourth antennomere longer than third antennomere; (4) antenna elbowed between antennomeres III and IV; (5) 8+8 ommatidia; (6) no spines or dental papilla on adult furcula; and (7) lack of mucronal silk. The presence of forwardly and downwardly directed subanal appendages in females of Katiannidae, and the described bothriotrichial pattern, are characters shared only with Arrhopalitidae (Spinothecidae have pronounced neck organs that are lacking in the fossil). However, the family Arrhopalitidae differs by having only 1+1 ommatidia while Katiannidae have full eyes (8+8 ommatidia) of which only one or two ommatidia may be reduced in size (Collophoridae also have reduced eyes). Species of Katiannidae also share two extra apical, clavate setae just above base of the pretarsal claw. The legs in *C. bucculenta* are too obscured by the body to determine whether or not tibiotarsal or pretarsal setae are present; however, under the highest magnification and with reflected light, a slender seta vaguely can be seen in the distal part. While no details of the ventral tube or retinaculum are visible, the third antennomere possesses a protuberance (only visible on the left antenna) similar to the sensorial papilla typically found in Katiannidae. The thickened cephalic spines in *C. bucculenta* resemble those of the extant genera *Katianna* and *Neokatianna* Snider, 1989; however, the distribution of the spines and the peculiar cheek pouches of the former distinguish it from both extant genera.

Superfamily **Sminthuroidea** Lubbock, 1862a
Family **Sminthuridae** Lubbock, 1862a
Subfamily **Sphyrothecinae** Betsch, 1980
Genus ***Sphyrotheciscus*** gen. nov.

Type species. *Sphyrotheciscus senectus* sp. nov.

Diagnosis. Sex unknown. The genus is distinguished from all other genera by its unique combination of the following characters: Body small-sized (<0.5 mm); head without spines; eyes with 8+8 ommatidia; antenna about 2.0× head length; fourth antennomere longer than third antennomere, with about 14 subsegments. Abdomen without cuticular spines and broadened setae; collophore with sacs very elongate, reaching apices of legs and apically spherically papillate ('warty'). Dens without spines, about 3.5× mucro length; mucronal lamellae narrow and unequal; outer mucronal lamella with edge finely serrate (with at least 13 small teeth), inner lamella smooth; mucronal seta absent; ventral axis of rachis smooth.

Derivation of name. The new genus-group name is a combination of *Sphyrotheca* Börner, 1906, type genus of the subfamily, and the masculine diminutive Greek suffix, *ίσκος*. The gender of the name is masculine.

Sphyrotheciscus senectus sp. nov.
(Figs 5, 6)

2002 *Arrhopalites* sp. Simón-Benito, Ortuño & Espantaleón: 87, fig. 3b.

Diagnosis. As for the genus (*vide supra*).

Derivation of name. The specific epithet is considered an adjective and is taken from the Latin *senectus*, meaning 'aged' or 'very old'.

Type material. Holotype, MCNA 9311, sex unknown, virtually complete. Preserved in a clear yellow turbid piece of amber trimmed to 0.2 × 0.2 × 0.1 cm (in an epoxy resin trapezoid 2.2 × 1.3 × 0.1 cm), and accompanied by particles of detritus and bubbles. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Sex unknown. Total length as preserved 385 μm; habitus sminthuroid.

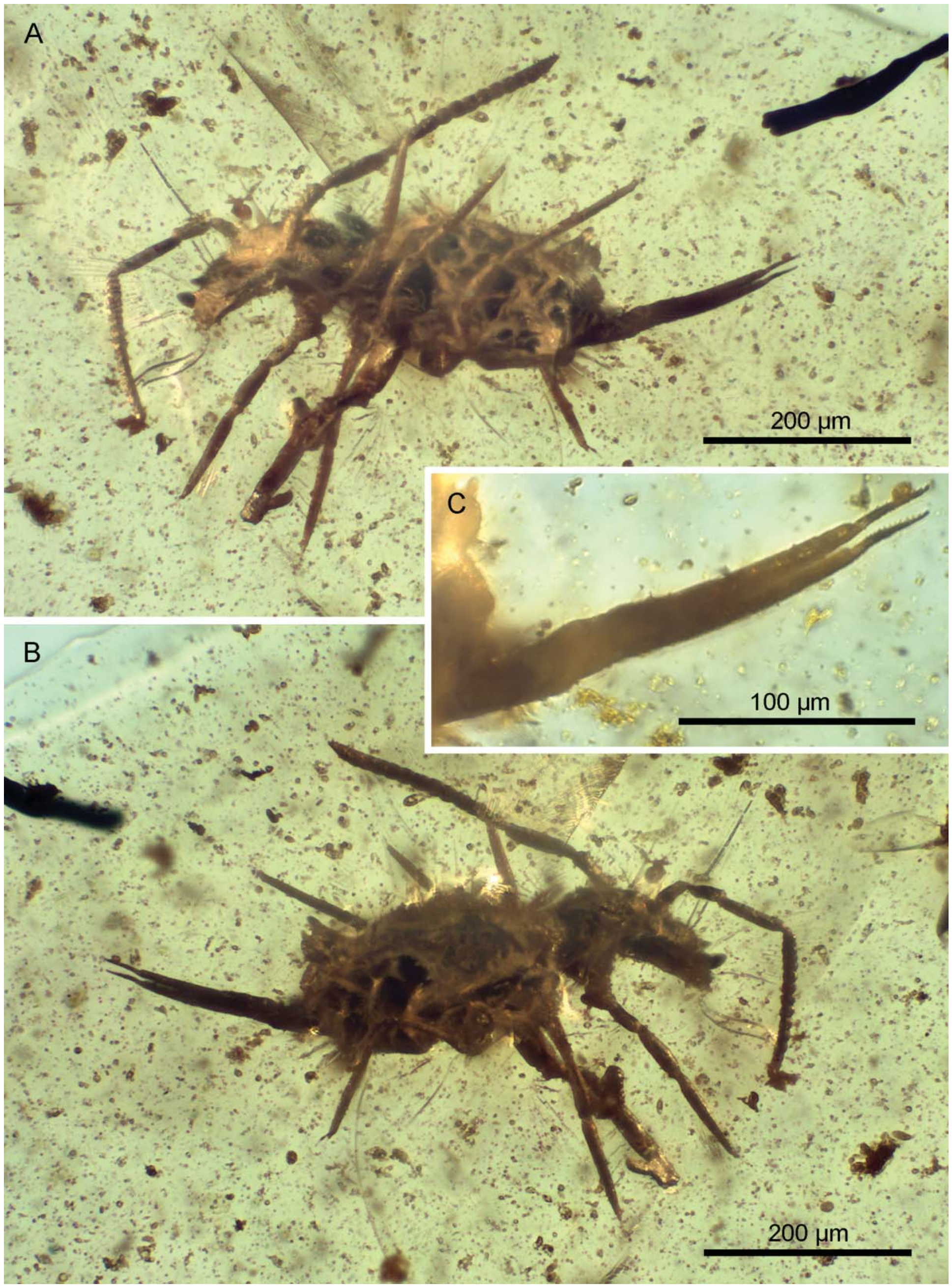

Figure 5. Photomicrographs of the holotype of *Sphyrotheciscus senectus* gen. et sp. nov., MCNA 9311, sex unknown. **A,** ventro-lateral habitus; **B,** dorso-lateral habitus; **C,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 162 µm; labral setae apically expanded and flattened, spear-shaped; eyes with 8+8 ommatidia.

Antennae. Relatively long and slender, clearly elbowed between antennomeres II and IV; length about 2.02× as long as cephalic diagonal; antennomere lengths in µm approximately: IV, 189; III, 72; II, 32; I, 35; fourth antennomere with about 14 subsegments, basal and apical subsegments slightly longer than intermediate subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (setae approximately as long as maximum width of subsegments, or slightly longer); third antennomere with up to four long setae; second and first antennomeres without visible setae.

Legs. Legs with coxae relatively small; lengths of protrochanter, profemur and protibiotarsus: 38, 56 and 100 µm; lengths of mesotrochanter, mesofemur and

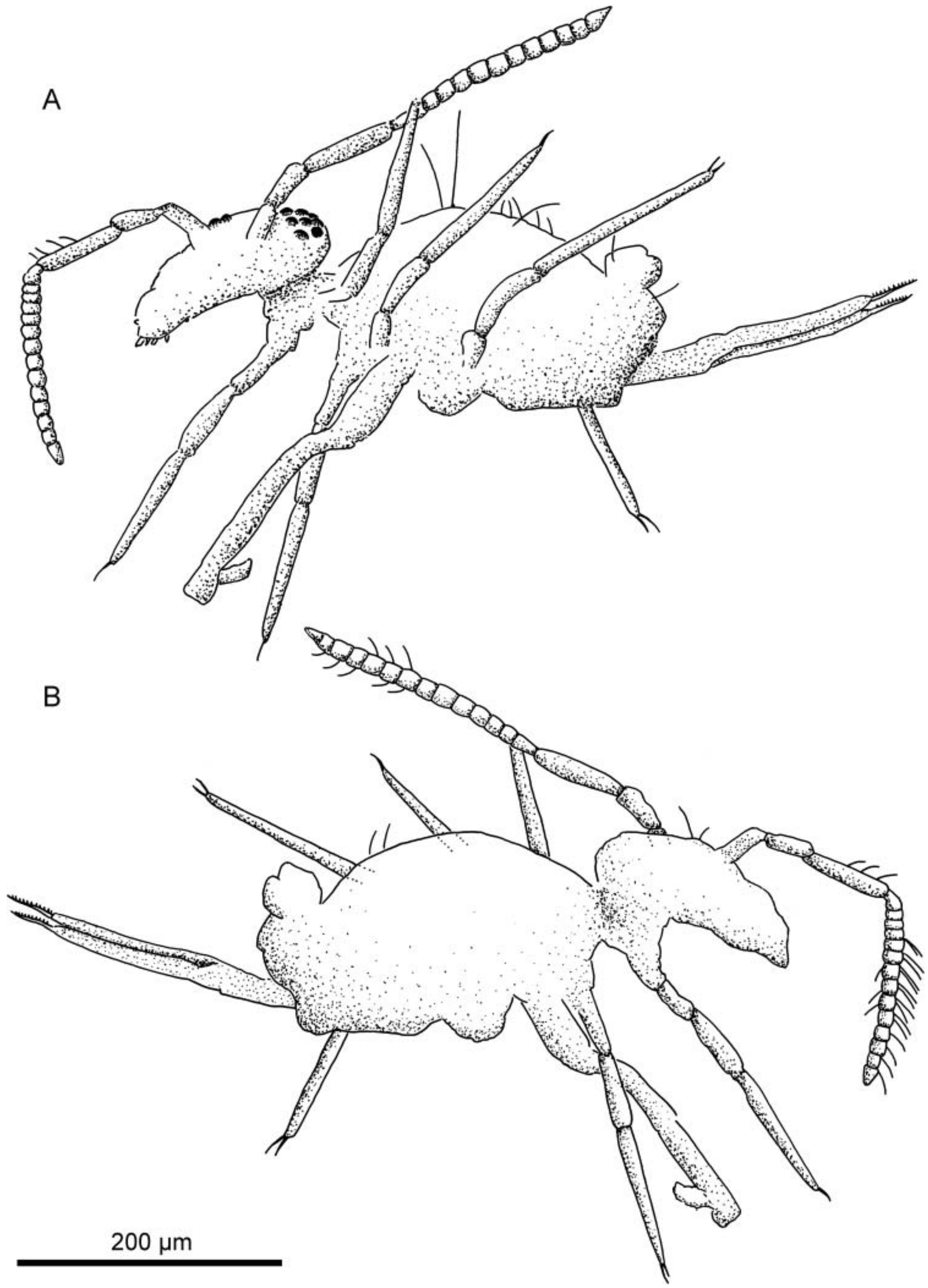

Figure 6. Camera lucida drawings of the holotype of *Sphyrotheciscus senectus* gen. et sp. nov., MCNA 9311, sex unknown. **A,** ventro-lateral habitus; **B,** dorso-lateral habitus.

mesotibiotarsus: 36, 57 and 103 μm; lengths of meta-femur and metatibiotarsus: 61 and 145 μm; unguis small and thin, poorly visible, tunica apparently absent; unguiculus apparently not reaching apex of unguis.

Collophore. Very elongate, base long, protrusible sacs exceedingly elongate and reaching length of legs, apically with surfaces spherically papillate.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 255 μm as preserved; greater abdomen and thorax clothed with very sparse, slender, somewhat curved, and not spine-like setae; only two pairs of setaceous bothriotrichia (AC) present on greater abdomen; lesser abdomen small, sharply demarcated from greater abdomen, with faint indication of basal ring of segment V and projecting upward, with only a few setae visible; subanal appendage not visible; sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 62 μm, without visible setae; dens length 132 μm, without visible setae; mucro length 37 μm, slender, pointed in lateral view; mucronal lamellae narrow and unequal; outer mucronal lamella with edge finely serrate, bearing at least 13 very small, distinctly separated teeth; inner lamella smooth; mucronal seta absent; ventral axis smooth. Ratio of mucro, dens, manubrium: 1.00:3.53:1.66.

Remarks. Contrary to the description and photograph of specimen MCNA 9311 in Simón-Benito *et al.* (2002), the eyes are distinctly present, although faint and nebulous (under some lighting the eyes are challenging to see and this perhaps led Simón-Benito *et al.* (2002) to misinterpret them as absent). These authors also noted the serrated mucro and highly subdivided fourth antennomere, and described a white body colouration, purportedly leading them to classify the specimen within the extant genus *Arrhopalites* Börner, 1906 (Arrhopalitidae). It is true that *Sphyrotheciscus senectus* gen. et sp. nov. shares with *Arrhopalites* a slender mucro with serrated dorsal edges and a sharp, mid-ventral axis (Fjellberg 2007); the presence of well-developed eyes (8+8 ommatidia) is an important feature that is never found in *Arrhopalites* or even Arrhopalitidae, and instead in that family the eyes are distinctly reduced (Betsch 1980). Furthermore, we have determined that characters that were used as diagnostic by Simón-Benito *et al.* (2002) for MCNA 9311 – i.e. the reduced or absent pigmentation putatively shared with members of Arrhopalitidae – are actually artifacts of preservation rather than truly characteristic of the new species. The elongate sacs of the collophore may have also misled an attribution to *Arrhopalites* as such a character is certainly present therein (as well as in the related Collophoridae); however, such a condition is also found among the Sminthuridae, and the structure of the sacs is more like that found in genera of Sphyrothecinae than in Arrhopalitidae. Instead, the species belongs to the Sminthuridae, as evidenced by the combination of the 8+8 eyes, the lesser abdomen incorporating the fifth abdominal segment, and generally sminthuroid habitus. In addition, among the sminthurids bothriotrichial pair B of the greater abdomen are sometimes absent (Bretfeld 1999), and this is the case for *S. senectus*, further highlighting its placement outside of Arrhopalitidae.

The Sminthuridae can be organized into three subfamilies: the largest and nominate subfamily Sminthurinae with 20 genera, the Sphyrothecinae with eight genera, and the monogeneric Songhaicinae, subfam. nov. (type genus: *Songhaica* Lasebikan, Betsch & Dallai, 1980). Songhaicinae comprise a single genus of three Afrotropical (Nigeria, Gambia and Socotra (Yemen): Lasebikan *et al.* 1980; Bretfeld 2005), and one Neotropical, species (Palacios-Vargas *et al.* 1999), diagnosed from the other subfamilies by the combination of: three pairs of sminthuroid setae, a few anterior setae on the dens, and the mucro lacking a subapical incision. The genus *Sphyrotheciscus* can be placed among the Sphyrothecinae owing to the combination of a comparatively short antenna, the absence of setae on the dens, the unequal mucronal lamellae with a subapical incision, the serrate outer mucronal lamella and the absence of bothriotrichial pair B.

Subfamily **Sminthurinae** Lubbock, 1862a
Genus ***Archeallacma*** gen. nov.

Type species. *Archeallacma dolichopoda* sp. nov.

Diagnosis. Sex unknown. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head with spine-like setae; eyes with 8+8 ommatidia; antenna about 2.1× head length; fourth antennomere longer than third antennomere, with about 14–15 subsegments. Metatibiotarsus elongate, more than 1.5× protibiotarsus length. Abdomen without cuticular spines and broadened setae. Dens without spines, about 3.1× mucro length; mucro simple, with narrow smooth outer and inner lamellae; mucronal seta absent.

Derivation of name. The new generic name is a combination of the Greek, ἁρχαιος, meaning 'ancient', and *Allacma* Börner, 1906, a genus of the Sminthurinae. The gender of the name is feminine.

Archeallacma dolichopoda sp. nov.
(Figs 7, 8)

Diagnosis. As for the genus (*vide supra*).

Derivation of name. The specific epithet is considered an adjective and is formed by the Greek words δόλιχος, meaning 'long' and πούς, meaning 'foot', and is a reference to the elongate metatibiotarsus.

Type material. Holotype, MCNA 13850.4, sex unknown, virtually complete, dorsally exposed. The right side of the specimen has the best view of the legs, although they are mainly twisted underneath the body and hidden, and the setation is difficult to discern and can easily be overlooked if care is not taken and the proper lighting used.

Paratype, MCNA 13850.5, partially preserved. The specimen consists of a disembodied head, several legs and the furcula; all except the head are cleared.

Both type specimens are preserved in a dark orange turbid piece of amber trimmed to 1.2 × 1.1 × 0.3 cm (in an epoxy trapezoid of dimensions 2.3 × 1.3 × 0.3 cm), and

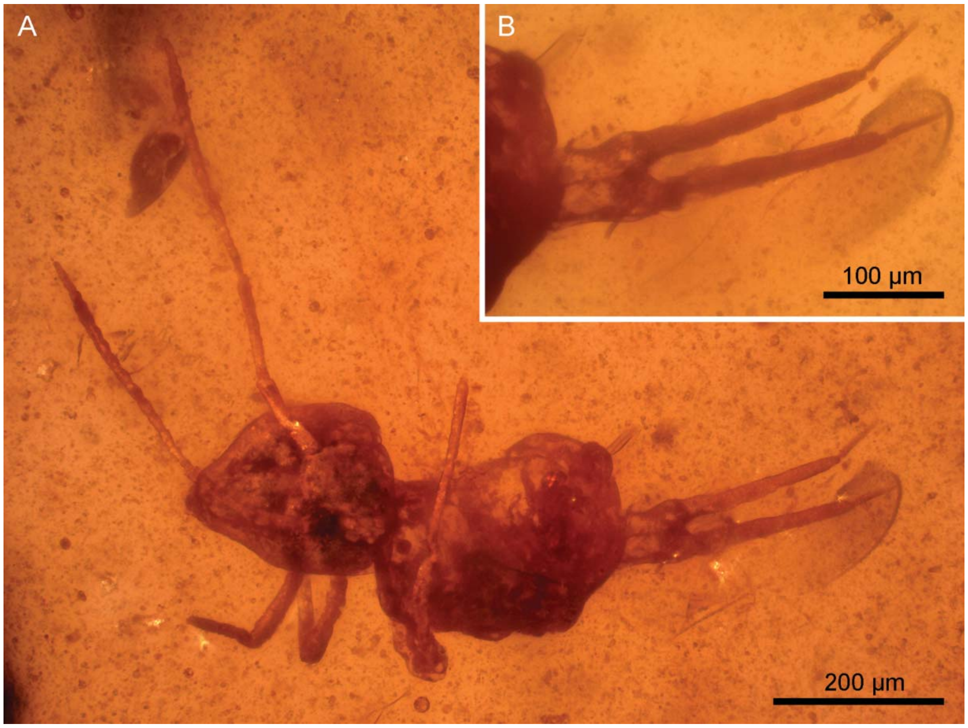

Figure 7. Photomicrographs of the holotype of *Archeallacma dolichopoda* gen. et sp. nov., MCNA 13850.4, sex unknown. **A,** dorsal habitus; **B,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

are together with many arthropod and plant remains (e.g. stellate hairs), fungal hyphae and coprolites.

Other material examined. MCNA 14284.2 (Figs 9, 10), sex unknown, virtually complete, with blackened cuticle somewhat altered due to fossilization, and several structures hidden and poorly visible due to position (mostly antennae and legs). Preserved in a dark orange turbid piece of amber trimmed to 1.1 × 0.8 × 0.1 cm (in an epoxy trapezoid of dimensions 2.1 × 1.3 × 0.2 cm), together with one fly, and accompanied by particles of detritus and bubbles. MCNA 14284.2 matches the diagnosis of *Archeallacma dolichopoda* for some characters, but other features remain unclear and we cannot attribute it to this species with complete confidence (*vide* Remarks, *infra*).

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Sex unknown. Based mainly on the holotype (MCNA 13850.4) except for details of setae which are better preserved in the paratype (MCNA 13850.5): total length as preserved 519 µm; habitus sminthuroid.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 246 µm; vertex of head with up to six spine-like setae; anterior surface with some small, slender acuminate setae; both sides of head separated by a narrow median ridge; eyes with 8+8 ommatidia (only visible in holotype).

Antennae. Very long and slender; length about 2.12× as long as cephalic diagonal; antennomere lengths in µm approximately: IV, 293; III, 122; II, 67; I, 41; fourth antennomere with about 14 (in paratype)−15 (in holotype) subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (which are approximately as long as maximum width of subsegments, except for some that are twice diameter of subsegments); third antennomere with long, scattered setae; second antennomere with up to three very long outer setae and two smaller inner setae; first antennomere without visible setae.

Legs. Legs with coxae relatively small; lengths of protrochanter, profemur and protibiotarsus: 66, 92 and 174 µm; lengths of mesotrochanter, mesofemur and mesotibiotarsus: 75, 105 and 194 µm; lengths of metatrochanter, metafemur and metatibiotarsus: 67, 141 and 273 µm; only protibiotarsus apparently with numerous slender, acuminate, straight to slightly curved setae, longest about as long as widest width of protibiotarsus (visible in paratype); unguis small and thin, with a basal tunica; unguiculus apparently not reaching apex of unguis.

Collophore. Not visible.

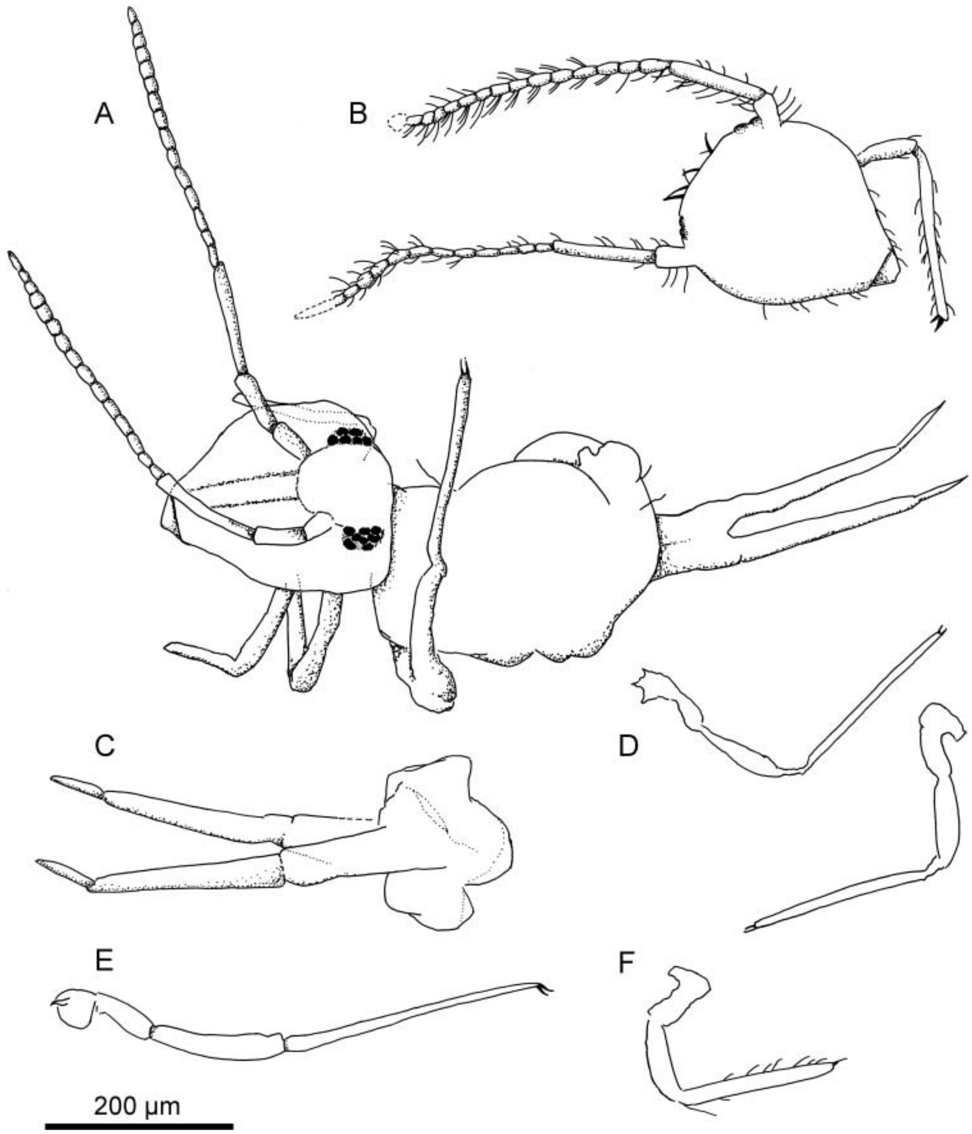

Figure 8. Camera lucida drawings of the holotype (**A**) and paratype (**B**−**F**) of *Archeallacma dolichopoda* gen. et sp. nov., MCNA 13850.4 (holotype), 13850.5 (paratype), sex unknown. **A,** dorsal habitus; **B,** head; **C,** furcula; **D,** hind leg; **E,** mid legs; **F,** fore leg.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 274 μm as preserved; greater abdomen and thorax without visible setae (probably due to preservation); bothriotrichia not visible; lesser abdomen small, sharply demarcated from greater abdomen and projecting upward, with small basal ring of fifth abdominal segment, with only a few setae visible; subanal appendage not visible; sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 75 μm, without visible setae; dens length 195 μm, without visible setae; mucro simple, slender, length 63 μm, pointed in lateral view; mucronal lamellae narrow, unequal, smooth; mucronal seta absent; ventral axis of rachis smooth. Ratio of mucro, dens, manubrium: 1.00: 3.07: 1.18.

Remarks. MCNA 14284.2 closely resembles the holotype of *Archeallacma dolichopoda* gen. et sp. nov., sharing with it the relative head, body and leg ratios, antennal structure, the much elongate metatibiotarsus, a similarly shaped pretarsal complex, the few large abdominal setae (none spine-like), the demarcated lesser abdomen, and the mucronal shape (with smooth mucronal lamellae). Despite the similar dens and mucro ratios, MCNA 14284.2 differs from typical *A. dolichopoda* in having a less elongate furcula when compared with the length of the body. Moreover, MCNA 14284.2 is somewhat larger than the holotype of *A. dolichopoda* (Table 2). The shared features listed all lead us to

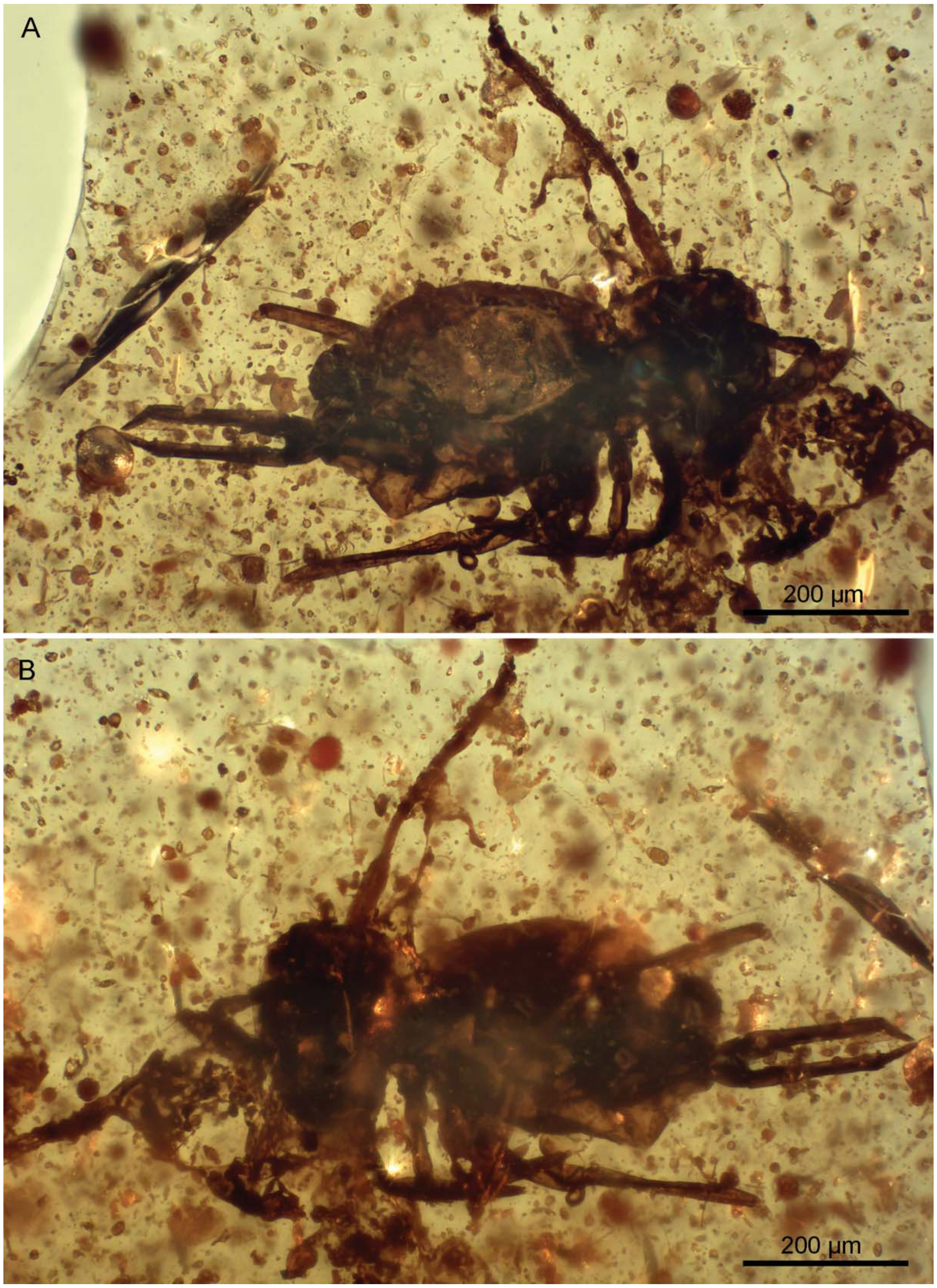

Figure 9. Photomicrographs of specimen MCNA 14284.2, a possible individual of *Archeallacma dolichopoda* gen. et sp. nov. **A,** dorsal habitus; **B,** ventral habitus. Figures made from consecutive pictures taken at successive focal planes.

believe that it is likely another specimen of the same species, but this remains somewhat unresolved and so we have not designated it as a part of the type series. Hopefully more complete material will eventually be recovered to permit a more thorough characterization of the species and a critical test as to whether MCNA 14284.2 is correctly placed within *A. dolichopoda*.

Archeallacma dolichopoda is difficult to place accurately among Sminthuridae, but placement within the subfamily Sminthurinae seems most appropriate owing to the apparent lack of a subapical incision on the mucro, the smooth mucronal lamellae, and the comparatively elongate antennae.

Incertae sedis

Genus ***Katiannasminthurus*** gen. nov.

Type species. *Katiannasminthurus xenopygus* sp. nov.

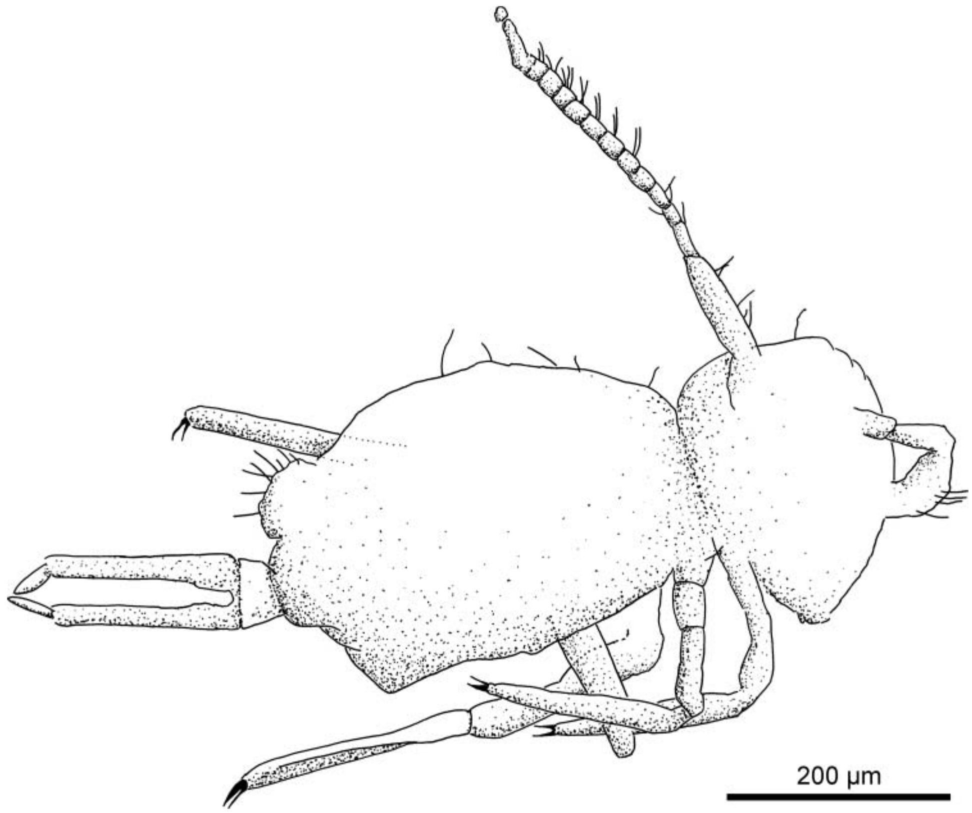

Figure 10. Camera lucida drawing of specimen MCNA 14284.2, a possible individual of *Archeallacma dolichopoda* gen. et sp. nov.

Diagnosis. Female. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head without spines; eyes with at least 5+5 ommatidia; antenna about 3.3× head length; fourth antennomere longer than third antennomere, with 14 subsegments. Abdomen with very long, coarse, spine-like setae; subanal appendage long, anteriorly recurved and downwardly directed towards genital orifice, not branched at apex. Dens without spines, about 2.9× mucro length; mucro simple, with narrow, smooth inner and outer lamellae; mucronal seta absent.

Male. *Latet*.

Derivation of name. The genus-group name combines the generic names *Katianna*, type genus of Katiannidae, and *Sminthurus* Latreille, 1802, type genus of Sminthuridae. The gender of the name is masculine.

Katiannasminthurus xenopygus sp. nov.
(Figs 11, 12)

2002 *Sminthurus*? sp. 2 Simón-Benito, Ortuño, & Espantaleón: 87, fig. 2f.

Diagnosis. As for the genus (*vide supra*).

Table 2. Characters for separation of the different Spanish Early Cretaceous (Late Albian) Symphypleona (measurements in μm).

				Antennomeres							
Specimen Species	Total length	Opisthosoma	Head	IV	III	II	I	Manubrium	Dens	Mucro	Mucro/ dens ratio
MCNA 12788.1 *Pseudosminthurides stoechus*	631	471	160	—	—	—	—	87	282	64	4.42
MCNA 10047 *Cretokatianna bucculenta*	409	217	226	210	75	36	18	86	182	42	4.29
MCNA 9311 *Sphyrotheciscus senectus*	385	255	162	189	72	32	35	62	132	37	3.53
MCNA 13850.4/5 *Archeallacma dolichopoda*	519	274	246	293	122	67	41	75	195	63	3.07
MCNA 14284.2 *A. dolichopoda*?	562	377	252	285	99	—	—	—	169	43	3.90
MCNA 10048 *Katiannasminthurus xenopygus*	744	595	193	399	164	77	—	114	219	76	2.90
MCNA 10016 Indeterminate	590	475	193	296	76	63	27	—	—	—	—
MCNA 11231.1 Indeterminate	321	195	125	—	—	—	—	—	—	—	—

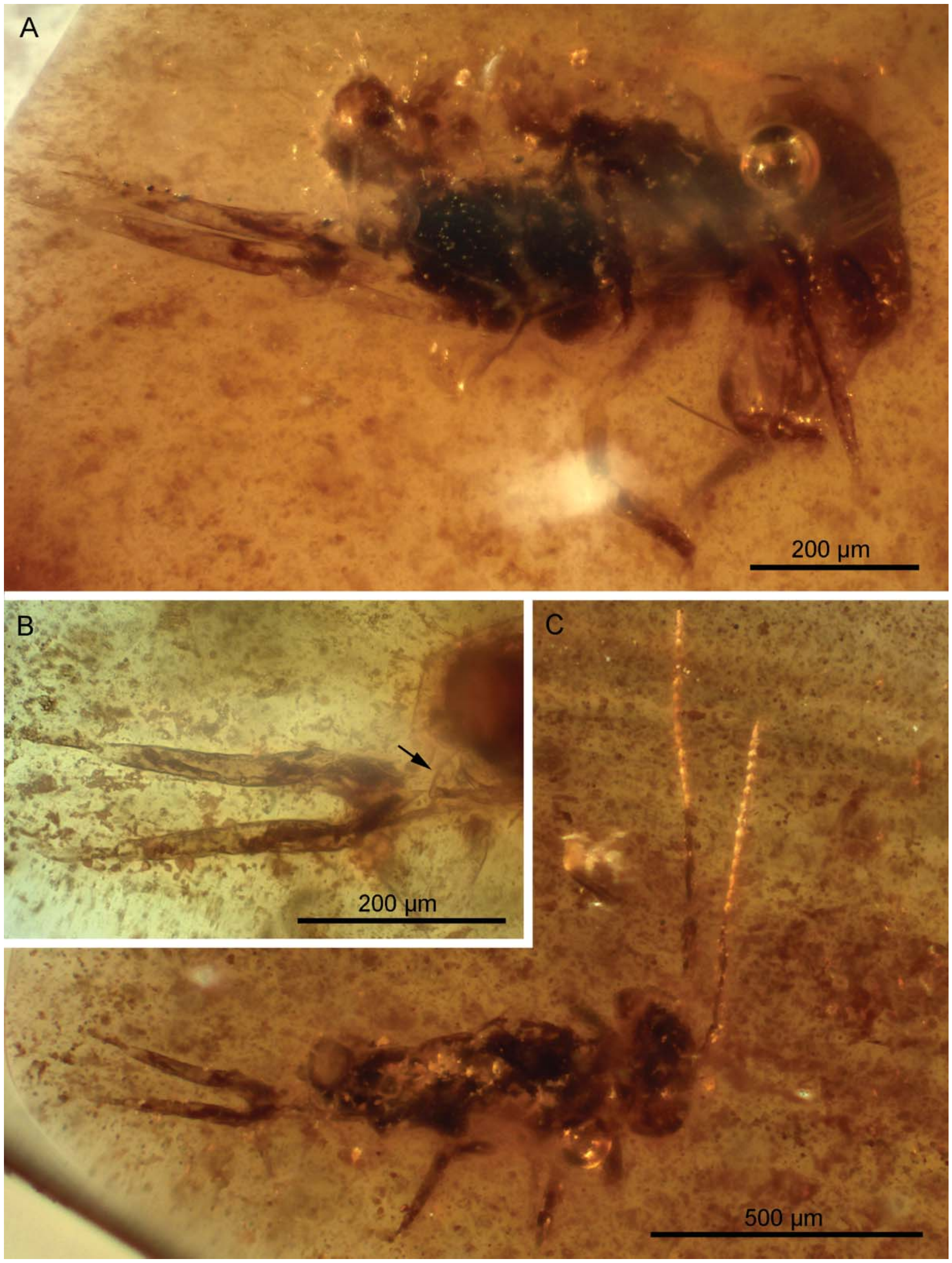

Figure 11. Photomicrographs of the holotype female of *Katiannasminthurus xenopygus* gen. et sp. nov., MCNA 10048. **A,** ventro-lateral habitus; **B,** detail of furcula; arrow points to the subanal appendage; **C,** dorso-lateral habitus. Figures made from consecutive pictures taken at successive focal planes.

Derivation of name. The specific epithet is considered an adjective and is a combination of the Greek terms *ξένος*, meaning 'strange' and *πυγος*, meaning 'rump', and as a reference to the occurrence of an anal appendage directed to the genital orifice (a character of the Katianniformia), but otherwise combined with characters indicative of the Sminthuridae (Sminthuriformia).

Type material. Holotype ♀, MCNA 10048, virtually complete. Preserved in a clear yellow turbid piece of amber trimmed to 0.7 × 0.1 × 0.1 cm (in an epoxy resin trapezoid 1.3 × 0.9 × 0.1 cm), and accompanied by particles of detritus and bubbles. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Female. Total length as preserved 744 µm; habitus sminthuroid.

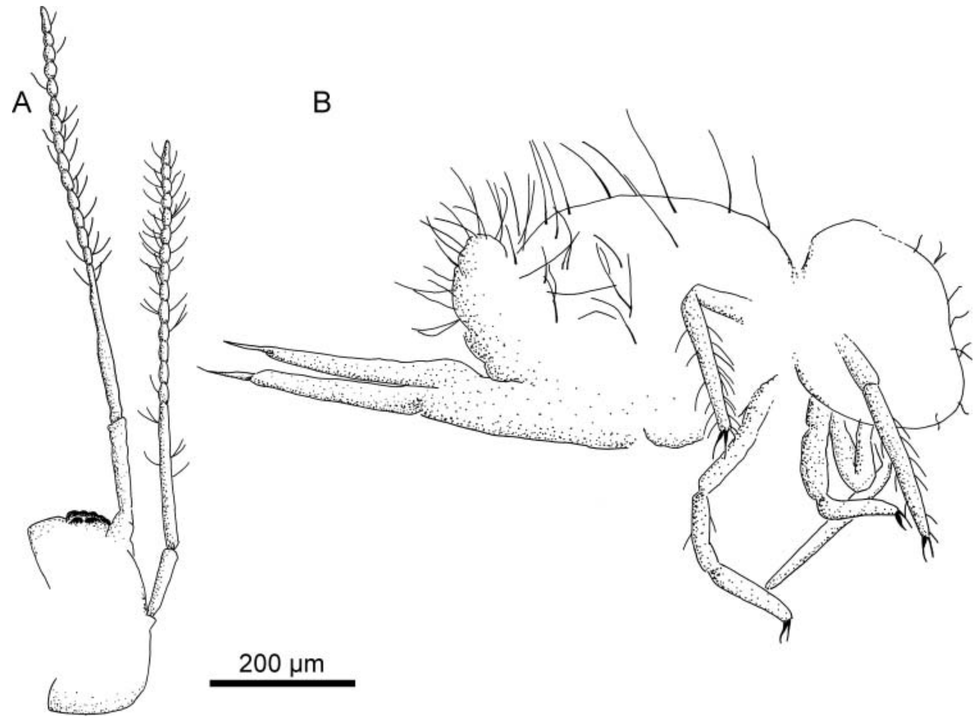

Figure 12. Camera lucida drawings of the holotype female of *Katiannasminthurus xenopygus* gen. et sp. nov., MCNA 10048. **A,** head in dorso-lateral view; **B,** ventro-lateral habitus.

Head. Dorsoventrally exposed preventing cephalic diagonal measurement, length 193 µm as preserved; eyes poorly visible, with at least five ommatidia visible in left eyepatch.

Antennae. Very long and slender; length about 3.32× cephalic length; antennomere lengths in µm approximately: IV, 399; III, 164; II, 77; fourth antennomere with 14 subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (such setae approximately as long as maximum width of subsegments, except for some that are twice diameter of subsegments); third antennomere with long, scattered setae; second antennomere without visible setae; first antennomere poorly visible.

Collophore. Not visible.

Retinaculum. Not visible.

Legs. Legs mostly obscured by adjacent body mass; coxa and trochanter not visible; femora poorly visible and angled preventing measurements; length of mesotibiotarsus: 215 µm; length of metatibiotarsus: 208 µm; tibiotarsus with numerous small, slender acuminate setae; tibiotarsal organ not visible; unguis small and thin, with a basal tunica; unguiculus apparently not reaching apex of unguis.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 595 µm as preserved; greater abdomen and thorax clothed largely with very long, somewhat curved, coarse, spine-like setae, such setae becoming longer and more numerous posteriorly; lesser abdomen sharply demarcated from greater abdomen, projecting upward, with numerous long and slender circumanal setae; bothriotrichia not distinguishable from surrounding setae; subanal appendage long, anteriorly recurved and downwardly directed towards genital orifice, apparently smooth, not branched at apex, apically pointed.

Furcula. Long and slender; manubrium length 114 µm, without visible setae; dens length 219 µm, without visible setae; mucro simple, slender, length 76 µm, pointed in lateral view; mucronal lamellae narrow and unequal, with edges smooth; ventral axis of rachis smooth; mucronal seta absent. Ratio of mucro, dens, manubrium: 1.00:2.90:1.49.

Male. *Latet*.

Remarks. This form is mainly distinguished from the others in having very long coarse spine-like setae on the abdomen, and the peculiar combination of a sminthuroid habitus and a katiannid-like subanal appendage. Unfortunately, several critical characters are simply not discernible as preserved in the only available specimen (e.g.

number, form and arrangement of the abdominal bothriotrichia; chaetotaxy and form of the tibiotarsus and pretarsus, etc.). Given the peculiar combination of traits we have left the species as incertae sedis until such time as more completely preserved specimens are discovered. Regardless, the species is distinctive for is unusual combination of traits and it is greatly hoped that more finely preserved material will be discovered so as to permit a characterization of its bothriotrichial pattern, among other traits.

Genera and species indeterminate

We studied two other specimens from Peñacerrada amber that were too badly preserved to ascertain confidently whether they belonged to any described species or were of undescribed taxa. Accordingly, we have left these specimens as indeterminate, though we provide below a short description and illustration of visible features that might aid future comparative studies.

Specimen MCNA 10016 (Figs 13, 14) was originally preserved as a syninclusion with an as of yet undetermined entomobryomorphan springtails (in MCNA 10070 and MCNA 10071), in a clear yellow turbid piece of amber trimmed to 0.2 × 0.1 × 0.05 cm (in a microscopic slide preparation), and accompanied by particles of detritus and bubbles. The specimen is laterally exposed, and although a vague outline of the long legs, collophore and furcula can be seen, these are so thoroughly obscured through preservation or by the adjacent body mass as to afford no useful delineation of features. Worthy of some note are the large body (total length as preserved 590 μm), and the relative length proportions between the head and opisthosoma (opisthosoma length as preserved 475 μm, cephalic diagonal 193 μm). The specimen also possesses a long antenna, about 2.40× as long as the cephalic diagonal, that is elbowed between antennomeres II and III and between the first subsegments of the fourth antennomere (although preservational), a fourth antennomere with at least 16 subsegments and a whorl of smooth, acuminate setae on each subsegment. The lengths of the individual antennomeres in μm are approximately: IV, 296; III, 76; II, 63; I, 27. Although a relatively large eye patch can be distinguished under the highest magnification of reflected light, ommatidia are not visible, nor are other details of the head capsule. The specimen also has a small and weakly demarcated lesser abdomen, and no setae are visible throughout the body. Simón-Benito *et al.* (2002) tentatively placed MCNA 10016 in the extant genus *Sminthurus* (Sminthuridae: Sminthurinae), and in particular noted putative similarities in pattern of colouration with the extant species *Sminthurus nigromaculatus* Tullberg, 1871, as well as its general size and similar number of

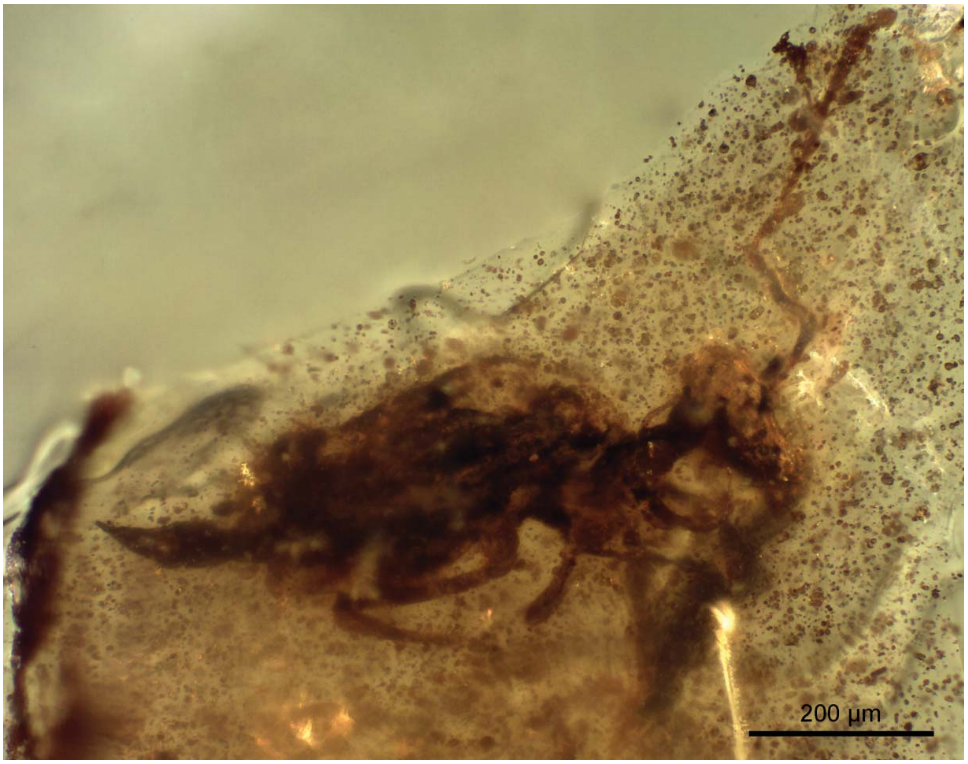

Figure 13. Photomicrograph of the specimen MCNA 10016 (Symphypleona, genus and species indeterminate), in lateral habitus. Figure made from consecutive pictures taken at successive focal planes.

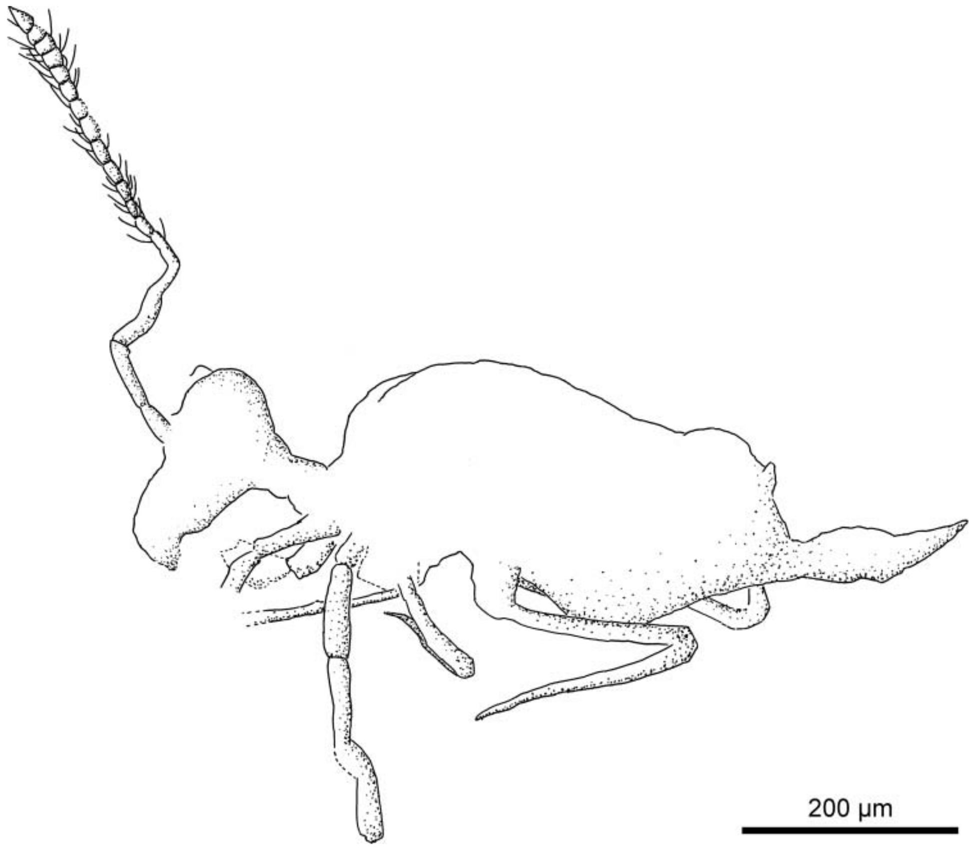

Figure 14. Camera lucida drawing of the specimen MCNA 10016 (Symphypleona, genus and species indeterminate).

subsegments on antennomere IV. However, true colouration is clearly not preserved in MCNA 10016 and the pattern attributed is purely owing to preservation. More importantly, the number of antennomere IV subsegments and the total size of the specimen are highly variable across sminthurids, and Symphypleona in general, with many different genera possessing a similarly subsegmented antennonere IV. Thus, there is no justification for considering MCNA 10016 as similar to *S. nigromaculatus*, or even to *Sminthurus*, from the available character information.

Specimen MCNA 11231.1 is preserved in a thick, dark orange turbid piece of amber trimmed to 1.2 × 0.9 × 0.3 cm (in an epoxy resin trapezoid 2.1 × 1.4 × 0.3 cm) together with more than 45 entomobryomorphan Collembola and much debris, coprolites, fungal hyphae and plant remains (e.g. pollen). Close viewing and therefore accurate description of the specimen is not possible because of its position distant from the amber surface as well as the thickness of the amber piece. Some general measurements are given in Table 2.

Discussion

While the Symphypleona from Peñacerrada I are not numerically abundant, the nine specimens available reveal a rather remarkable breadth of diversity spanning the phylogenetic space of the order. This diversity highlights the fact that the considerable cladogenesis across Symphypleona had already transpired by the Albian and, indeed, many of the genera described here are remarkably similar to their counterparts in the modern fauna, further emphasizing the antiquity of the group (Fig. 15). Collectively this is not surprising given that the group as a whole dates back to the Early Devonian, and all of those fossils discovered and described from the Cenozoic can be placed easily in extant genera (e.g. Handschin 1926; Christiansen 1971; Mari Mutt 1983; Lawrence 1985). However, the considerable morphological stasis of the euedaphic lineages is largely understandable given its significant consistency over expanses of geological time, resulting in a higher probability of bradytely within such groups (Simpson 1953), as is observed in many clades that live in such stable settings (e.g. Engel & Grimaldi 2002; Cognato & Grimaldi 2008; Chatzimanolis *et al.* 2013; Engel *et al.* 2016). Epedaphic species, such as most among the Symphypleona, are more prone to perturbations or shifts in habitat or climate and are thus expected to change more than others. However, the moist leaf litter to riparian environments occupied by several species of this ecomorphological group are still comparatively stable relative to the niches experienced by host specialists or others, except during episodes of considerable drying (which may

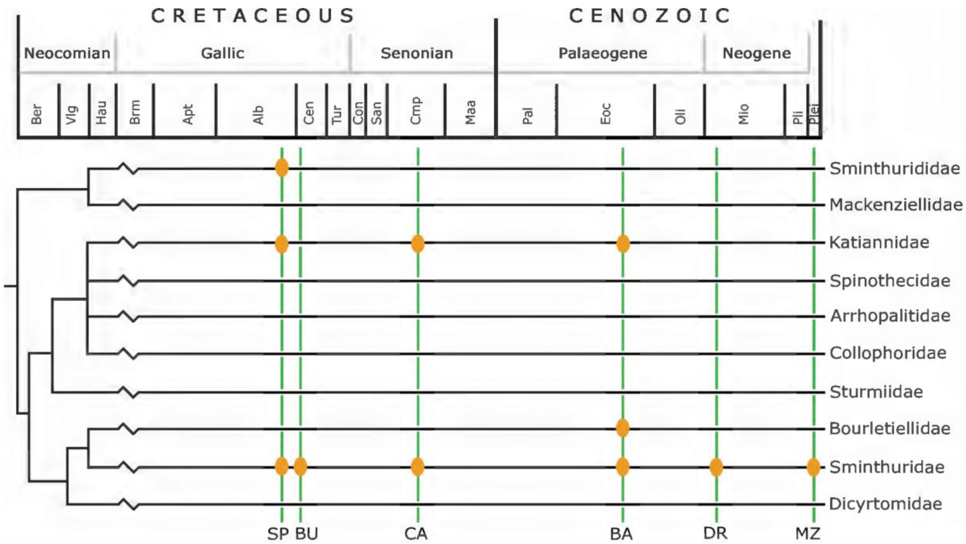

Figure 15. Phylogeny of Symphypleona. Basal divergences predate the Cretaceous, and the long branches are contracted with zig-zags. Ellipses indicate the known fossil records. Abbreviations: SP, Spanish amber; BU, Burmese amber; CA, Canadian amber; BA, Baltic amber; DR, Dominican amber; MZ, Mizunami copal.

account for those cave-dwelling lineages of Collembola as such subterranean areas remain more humid). Such factors may account for the remarkable similarity between modern Symphypleona and those from the Early Cretaceous, and the same is generally observed in the few species of this order described from earliest Cenomanian amber of Myanmar (*Grinnellia ventis* Christiansen & Nascimbene, 2006, *Sminthuricinus deceptus* Christiansen & Nascimbene, 2006, *Mucrovirga incompleta* Christiansen & Nascimbene, 2006 and *Sminthurconus grimaldi* Christiansen & Nascimbene, 2006, all of the Sminthurinae), and Campanian amber of Cedar Lake, Canada (a species of sminthurine, *Brevimucronus anomalus* Christiansen & Pike, 2002b, and one katiannid, *Keratopygos megalos* Christiansen & Pike, 2002b) (Christiansen & Pike 2002a). Although the available material is too little to make the pattern significant, it is interesting to note that among the studied Cretaceous amber deposits, Symphypleona are progressively more diverse in the gradually older resins. Unlike the aforementioned deposits, which include almost exclusively species of the relatively derived sminthurines (assuming that these taxa are properly placed; unfortunately the available descriptions and figures overlook many important details) (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006), the fauna preserved in Spanish amber embodies at least four families and subfamilies, with the first Mesozoic records of Sminthurididae and Sphyrothecinae. Unfortunately, given that chaetotaxy and mouthpart traits are vital in understanding the identity of and relationships within Collembola, it is challenging, if not impossible, for the Mesozoic taxa to be incorporated meaningfully into phylogenetic studies with living species. Although we were able to discern in the fossils the presence and form of several important bothriotrichia or other minute structures (e.g. unguis, mucro, anal appendages), much vital information remains inaccessible. Given their exceedingly diminutive proportions, it is unlikely at present that technologies such as micro-computed tomography scanning would have sufficient resolution to reveal the form of individual setae, although truly minute animals can be rendered with remarkable fidelity (e.g. Engel *et al.* 2013b).

It might be assumed from the simple presence of springtails in amber that such species were arboreal, and reflective of the many species that live in the vegetation of both temperate and tropical forests and which potentially come into contact with extruded resin, as was presumed for the Canadian and most of the Burmese amber representatives of the order (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006). However, fossiliferous resins are equally likely to sample soil and litter faunas and even nearby aquatic habitats (e.g. Perrichot 2004; Schmidt & Dilcher 2007), microenvironments in which Collembola are particularly abundant and diverse (Hopkin 1997). Among the species described here, only *P. stoechus* has an elongate unguis and large mucronal lamellae, both features typically associated with neustonic lifestyles (Christiansen 1961), and an elongate unguis is also seen in the Burmese amber species *G. ventis* and *S. deceptus* (Christiansen & Nascimbene 2006). In the case of *P. stoechus* this is intuitively pleasing as it is the sole sminthuridid in the Spanish amber fauna, and this family is today largely found living on water surfaces (Hopkin 1997). The presence of at least one potentially semi-aquatic springtail among the diversity of Symphypleona parallels the finding of tanaids (Malacostraca) in the same deposit, a group that either lived in exceptionally moist leaf litter and/or was similarly neustonic (Sánchez-García *et al.* 2015). There are also various other arthropods preserved in these same deposits that are indicators of a litter-dwelling fauna, and, moreover, that the general environment was likely near water or perhaps even representative of a swamp owing to the occurrence of Oniscidea, Archaeognatha, Dermaptera, some Blattaria and semi-aquatic Heteroptera, among others (e.g. Engel *et al.* 2015; Sánchez-García *et al.* 2016; unpubl. data). Given the above, it is possible that other species among the Spanish amber Symphypleona were also semi-aquatic, although it is not immediately obvious from their morphology as preserved. Nonetheless, despite the presence of pieces entrapping clearly forest floor or even 'aquatic'-like elements, many pieces of amber from Peñacerrada I do represent a sampling of taxa from above the forest floor (e.g. Peñalver & Delclòs 2010), and so it remains possible that some of the Symphypleona described here may truly have been arboreal taxa, much as was presumed for the Canadian and most of the Burmese amber representatives of the order (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006).

Large-scale vicariant patterns among epedaphic Collembola are not generally expected, despite their age, given that such species are often capable of remarkable dispersal. Not only can individuals jump distances by repeated use of their furcula (e.g. Grinsbergs 1960; Christian 1978, 1979; Christian & Völlenkle 1979; Sudo *et al.* 2013a, b), but they also may be dispersed as 'aerial plankton' (Freeman 1952; Gressitt *et al.* 1960; Farrow & Greenslade 1992; Hawes *et al.* 2007). Although Symphypleona predate the separation of Laurasia and Gondwana, as well as the subsequent fragmentation of each, such events are not reflected in the patterns of cladogenesis among families or subfamilies of the order, and it is not uncommon for larger groups to be widespread given the influence of dispersal. It is likely that the Cretaceous faunas, like most modern springtail communities, comprised a rather healthy mix of endemics as well as cosmopolitan species (at least among epedaphic groups), and long-distance dispersal must have aided the formation of a diverse fauna at Peñacerrada I. Although Christiansen & Pike (2002b) emphasized the uniqueness of the Canadian Late Cretaceous springtail fauna, the reality is that data are not available to know whether or not those species were more extensively distributed during the Campanian, and the same could be said for the Burmese amber diversity. Cretaceous springtails certainly could have been highly endemic, although for those epedaphic, and particularly arboreal, groups this seems the least likely scenario given the ease with which Collembola may disperse by air. Accordingly, it would appear that it is safe to entertain a working hypothesis that the Spanish amber fauna was at least partly composed of widespread, if not cosmopolitan, taxa. Whatever the factors influencing its composition, the Symphypleona known thus far from Spanish amber provide the most extensive glimpse into the diversity of globular springtails during the Cretaceous.

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References

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.

Azar, D. 2000. *Les Ambres Mésozoïques du Liban*. Unpublished PhD thesis, Université Paris-Sud, 202 pp.

Azar, D., **Gèze, R.** & **Acra, F.** 2010. Lebanese amber. Pp. 271−298 in D. Penney (ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.

Barrón, E., **Peyrot, D.**, **Rodríguez-López, J. P.**, **Meléndez, N.**, **López del Valle, R.**, **Najarro, M.**, **Rosales, I.** & **Comas-Rengifo, M. J.** 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.

Betsch, J.-M. 1980. Éléments pour une monographie des Collemboles Symplyplêones (Hexapodes, Aptérygotes). *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série A, Zoologie*, **116**, 1−227.

Bitsch, C. & **Bitsch, J.** 1998. Internal anatomy and phylogenetic relationships among apterygote insect clades (Hexapoda).

Annales de la Société Entomologique de France, **34**, 339−363.

Bitsch, C. & **Bitsch, J.** 2000. The phylogenetic interrelationships of the higher taxa of apterygote hexapods. *Zoologica Scripta*, **29**, 131−156.

Börner, C. 1900. Vorläufige Mitteilung zur Systematik der Sminthuridae Tullb., insbesondere des genus *Sminthurus* Latr. *Zoologischer Anzeiger*, **23**, 609−618.

Börner, C. 1901. Zur Kenntnis der Apterygoten-Fauna von Bremen und der Nachbardistrikte. Beitrag zur einer Apterygoten-Fauna Mitteleuropas. *Abhandlungen herausgegeben des Naturwissenschaftlichen Verein zu Bremen*, **17**, 1−140.

Börner, C. 1904. Zur Systematik der Hexapoden. *Zoologischer Anzeiger*, **27**, 511−533.

Börner, C. 1906. Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, **23**, 147−188.

Börner, C. 1913. Die Familien der Collembolen. *Zoologischer Anzeiger*, **41**, 315−322. [A translation of Börner's system is provided by Shoebotham (1917).]

Boudreaux, H. B. 1979. *Arthropod phylogeny, with special reference to insects*. Wiley, New York, viii + 320 pp.

Bretfeld, G. 1986. Phylogenetic systematics of the higher taxa of Symphypleona Börner, 1901 (Insecta, Entognatha, Collembola). Pp. 307−311 in R. Dallai (ed.) *Second international symposium on Apterygota*. University of Siena, Siena.

Bretfeld, G. 1994. *Sturmius epiphytus* n. gen. n. spec. from Colombia, a taxon of the Symphypleona (Insecta, Collembola) with an unexpected character combination. *Journal of Zoological Systematics and Evolutionary Research*, **32**, 264−281.

Bretfeld, G. 1999. Symphypleona [Synopses on Palaearctic Collembola, Volume 2]. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **71**, 1−318.

Bretfeld, G. 2005. Collembola Symphypleona (Insecta) from the Republic of Yemen. Part 2: samples from the isle of Socotra. *Abhandlungen und Berichte des Naturkundesmuseums Görlitz*, **77**, 1−56.

Cassagnau, P. 1971. La phylogenie des Collemboles à la lumiere des structures endocrines retrocerebrales. *Acta Salamanticensia, Ciencias*, **36**, 333−349.

Chatzimanolis, S., **Newton, A. F.**, **Soriano, C.** & **Engel, M. S.** 2013. Remarkable stasis in a phloeocharine rove beetle from the Late Cretaceous of New Jersey (Coleoptera, Staphylinidae). *Journal of Paleontology*, **87**, 177−182.

Christian, E. 1978. The jump of springtails. *Naturwissenschaften*, **65**, 495−496.

Christian, E. 1979. Der Sprung des Collembolen. *Zoologische Jahrbücher für Physiologie*, **83**, 457−490.

Christian, E. & **Völlenkle, W.** 1979. Collembolensprung-Absprung bei *Heteromurus*, *Lepidocyrtus*, *Isotoma* und *Hypogastrura*. *Wissenschaftliche Film*, **23**, 11−18.

Christiansen, K. 1961. Convergence and parallelism in cave Entomobryinae. *Evolution*, **15**, 288−301.

Christiansen, K. 1964. Bionomics of Collembola. *Annual Review of Entomology*, **9**, 147−178.

Christiansen, K. 1971. Notes on Miocene amber Collembola from Chiapas. *University of California Publications in Entomology*, **63**, 45−48.

Christiansen, K. & **Nascimbene, P.** 2006. Collembola (Arthropoda, Hexapoda) from the mid Cretaceous of Myanmar (Burma). *Cretaceous Research*, **27**, 318−363.

Christiansen, K. & **Pike, E.** 2002a. A preliminary report on the Cretaceous Collembola. *Pedobiologia*, **46**, 267−273.

Christiansen, K. & **Pike, E.** 2002b. Cretaceous Collembola (Arthropoda, Hexapoda) from the Upper Cretaceous of Canada. *Cretaceous Research*, **23**, 165−188.

Cognato, A. I. & **Grimaldi, D. A.** 2008. 100 million years of morphological conservatism in a bark beetle (Coleoptera: Curculionidae; Scolytinae). *Systematic Entomology*, **34**, 1−8.

Coulson, S. J. 2007. The terrestrial and freshwater invertebrate fauna of the High Arctic archipelago of Svalbard. *Zootaxa*, **1448**, 41−58.

Coulson, S. J., **Fjellberg, A.**, **Gwiazdowicz, D. J.**, **Lebedeva, N. V.**, **Melekhina, E. N.**, **Solhøy, T.**, **Erséus, C.**, **Maraldo, K.**, **Miko, L.**, **Schatz, H.**, **Schmelz, R. M.**, **Søli, G.** & **Stur, E.** 2013. The invertebrate fauna of anthropogenic soils in the High-Arctic settlement of Barentsburg, Svalbard. *Polar Research*, **32**, 1−12.

Deharveng, L. 2004. Recent advances in Collembola systematics. *Pedobiologia*, **48**, 415−433.

Delamare-Deboutteville, C. 1961. Matériaux pour une révision des Collemboles Symphypléones II. Le genre *Spinotheca* Stach 1956 et la sous-famille des Spinothecinae, subfam. nov. *Revue Francaise d'Entomologie*, **28**, 101−111.

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

D'Haese, C. A. 2002. Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. *Proceedings of the Royal Society, Series B,* **269**, 1143−1151.

Engel, M. S. 2015. Insect evolution. *Current Biology*, **25**, R868−R872.

Engel, M. S. & **Delclòs, X**. 2010. Primitive termites in Cretaceous amber from Spain and Canada (Isoptera). *Journal of the Kansas Entomological Society*, **83**, 111−128.

Engel, M. S. & **Grimaldi, D. A.** 2002. The first Mesozoic Zoraptera (Insecta). *American Museum Novitates*, **3362**, 1−20.

Engel, M. S. & **Grimaldi, D. A.** 2004. New light shed on the oldest insect. *Nature*, **427**, 627−630.

Engel, M. S., **Ortega-Blanco, J.** & **McKellar, R. C.** 2013a. New scolebythid wasps in Cretaceous amber from Spain and Canada, with implications for the phylogeny of the family (Hymenoptera: Scolebythidae). *Cretaceous Research*, **46**, 31−42.

Engel, M. S., **Peris, D.**, **Chatzimanolis, S**. & **Delclòs, X.** 2015. An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain. *Insect Systematics and Evolution*, **46**, 291−300.

Engel, M. S., **Ortega-Blanco, J.**, **Soriano, C.**, **Grimaldi, D. A**. & **Delclòs, X**. 2013b. A new lineage of enigmatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). *American Museum Novitates*, **3771**, 1−23.

Engel, M. S., **Breitkreuz, L.C.V.**, **Cai, C.-Y.**, **Alvarado, M.**, **Azar, D**. & **Huang, D.-Y**. 2016. The first Mesozoic microwhip scorpion (Palpigradi): a new genus and species in mid-Cretaceous amber from Myanmar. *The Science of Nature*, **103**, 19.

Farrow, R. A. & **Greenslade, P.** 1992. A vertical migration of Collembola. *Entomologist*, **11**, 38−45.

Fjellberg, A. 2007. The Collembola of Fennoscandia and Denmark, Part II: Entomobryomorpha and Symphypleona. *Fauna Entomologica Scandinavica*, **42**, 1−264.

Folsom, J. W. 1937. Order Collembola. *University of Toronto Studies, Geological Series*, **40**, 14−17.

Freeman, J. A. 1952. Occurrence of Collembola in the air. *Proceedings of the Royal Entomological Society of London, Series A, General Entomology*, **27**, 28.

Giribet, G., **Edgecombe, G. D.**, **Carpenter, J. M.**, **D'Haese, C. A**. & **Wheeler, W. C.** 2004. Is Ellipura monophyletic? A combined analysis of basal hexapod relationships with emphasis on the origin of insects. *Organisms, Diversity and Evolution*, **4**, 319−340.

Gisin, H. 1943. Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. *Revue Suisse de Zoologie*, **50**, 131−224.

Gisin, H. 1960. *Collembolenfauna Europas*. Muséum d'Histoire Naturelle de Genève, Geneva, 312 pp.

Greenslade, P. & **Whalley, P. E. S**. 1986. The systematic position of *Rhyniella praecursor* Hirst & Maulik (Collembola). The earliest known hexapod. Pp. 319−323 in R. Dallai (ed.) *Second International Symposium on Apterygota*. University of Siena, Siena.

Gressitt, J. L. 1967. *Entomology of Antarctica*. American Geophysical Union, Washington, DC, xii + 395 pp.

Gressitt, J. L., **Leech, R. E**. & **O'Brien, C. W.** 1960. Trapping of air-borne insects in the Antarctic area, I. *Pacific Insects*, **2**, 245−250.

Grimaldi, D. & **Engel, M. S.** 2005. *Evolution of the insects*. Cambridge University Press, Cambridge, xv + 755 pp.

Grimaldi, D. A. & **Engel, M. S.** 2007. Why descriptive science still matters. *BioScience*, **57**, 646−647.

Grinsbergs, A. 1960. On mass occurrence and migration of Collembola. *Opuscula Entomologicae*, **25**, 52−58.

Hädicke, C., **Haug, C.** & **Haug, J. T.** 2013. Adding to the few: a tomocerid collembolan from Baltic amber. *Palaeodiversity*, **6**, 149−156.

Handschin, E. 1926. Revision der Collembolen des baltischen Bernsteins. *Entomologische Mitteilungen*, **15**, 161−185, 211−223, 330−342.

Hawes, T. C., **Worland, M. R.**, **Convey, P.** & **Bale, J. S.** 2007. Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. *Antarctic Science*, **19**, 3−10.

Hennig, W. 1981. *Insect phylogeny*. Wiley and Sons, Chichester, xxii + 514 pp.

Hirst, S. & **Maulik, S.** 1926. On some arthropod remains from the Rhynie Chert (Old Red Sandstone). *Geological Magazine*, **63**, 69−71.

Hopkin, S. P. 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press, Oxford, x + 330 pp.

Janssens, F. & **Christiansen, K. A**. 2011. Class Collembola Lubbock, 1870. *Zootaxa*, **3148**, 192−194.

Joseph, S. V., **Bettiga, C.**, **Ramirez, C.** & **Soto-Adames, F. N.** 2015. Evidence of *Protaphorura fimata* (Collembola: Poduromorpha: Onychiuridae) feeding on germinating lettuce in the Salinas Valley of California. *Journal of Economic Entomology*, **108**, 228−236.

Lasebikan, B. A., **Betsch, J.-M**. & **Dallai, R.** 1980. A new genus of Symphypleona (Collembola) from West Africa. *Systematic Entomology*, **5**, 179−183.

Latreille, P. A. 1802. *Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes. Tome troisième.* Dufart, Paris, xii + 467 pp.

Lawrence, P. N. 1985. Ten species of Collembola from Baltic amber. *Prace Muzeum Ziemi PAN*, **37**, 101−104, 2 pls.

Linnaniemi, W. M. 1912. Die Apterygotenfauna Finlands. II. Spezieller Teil. *Acta Societas Scientarum Fennicae*, **40**, 1−361.

Lubbock, J. 1862a. Notes on the Thysanura. *Transactions of the Linnean Society of London*, **23**, 429−448, 2 pls.

Lubbock, J. 1862b. Notes on the Thysanura − Part II. *Transactions of the Linnean Society of London*, **23**, 589−601, 1 pl.

Lubbock, J. 1868. Notes on the Thysanura − Part III. *Transactions of the Linnean Society of London*, **26**, 295−304, 2 pls. [*Nota bene*: This paper was read before the Society 6 June 1867 but appeared in the first part of the 1868 volume.]

Lubbock, J. 1870. Notes on the Thysanura − Part IV. *Transactions of the Linnean Society of London*, **27**, 277−297.

Lubbock, J. 1873. *Monograph of the Collembola and Thysanura*. Ray Society, London, x + 276 pp., 78 pls.

Manton, S. M. 1970. Arthropoda: introduction. Pp. 1−34 in M. Florkin & B. T. Scheer (eds) *Chemical zoology, Volume* **5**: *Arthropoda Part A*. Academic Press, London.

Mari Mutt, J. A. 1983. Collembola in amber from the Dominican Republic. *Proceedings of the Entomological Society of Washington*, **85**, 575−587.

Massoud, Z. 1971. Contribution à la connaissance morphologique et systématique des collemboles Neelidae. *Revue d'Écologie et Biologie du Sol*, **8**, 195−198.

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

Olfers, E. W. M., von. 1907. Die 'Ur-Insecten' (Thysanura und Collembola im Bernstein). *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg*, **48**, 1−40, 25 pls.

Ortega-Blanco, J. & **Engel, M. S.** 2013. Bethylidae from Early Cretaceous Spanish amber (Hymenoptera: Chrysidoidea). *Journal of the Kansas Entomological Society*, **86**, 264−276.

Ortega-Blanco, J., **Delclòs, X**. & **Engel, M. S**. 2011a. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). *Cretaceous Research*, **32**, 762−773.

Ortega-Blanco, J., **Delclòs, X**. & **Engel, M. S.** 2011b. The wasp family Embolemidae in Early Cretaceous amber from Spain (Hymenoptera: Chrysidoidea). *Journal of the Kansas Entomological Society*, **84**, 36−42.

Ortega-Blanco, J., **Delclòs, X**. & **Engel, M. S.** 2011c. A protorhyssaline wasp in Early Cretaceous amber from Spain (Hymenoptera: Braconidae). *Journal of the Kansas Entomological Society*, **84**, 51−57.

Ortega-Blanco, J., **McKellar, R. C**. & **Engel, M. S**. 2014. Diverse scelionid wasps from Early Cretaceous Álava amber, Spain (Hymenoptera: Platygastroidea). *Bulletin of Geosciences*, **89**, 553−571.

Ortega-Blanco, J., **Delclòs, X.**, **Peñalver, E**. & **Engel, M. S**. 2011d. Serphitid wasps in Early Cretaceous amber from Spain (Hymenoptera: Serphitidae). *Cretaceous Research*, **32**, 143−154.

Ortega-Blanco, J., **Peñalver, E.**, **Delclòs, X**. & **Engel, M. S**. 2011e. False fairy wasps in Early Cretaceous amber from Spain (Hymenoptera: Mymarommatoidea). *Palaeontology*, **54**, 511−523.

Paclt, J. 1956. *Biologie der primär flügellosen Insekten*. Gustav Fischer, Jena, 285 pp.

Palacios-Vargas, J. G., **Cuellar, J. L.** & **Vazquez, M. M.** 1999. Two new sminthurids (Collembola: Symphypleona) from humid tropical forests. *Folia Entomológica Mexicana*, **104**, 13–21.

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

Peñalver, E., **Labandeira, C. C.**, **Barrón, E.**, **Delclòs, X.**, **Nel, P.**, **Nel, A.**, **Tafforeau, P.** & **Soriano, C.** 2012. Thrips pollination of Mesozoic gymnosperms. *Proceedings of the National Academy of Sciences, USA*, **109**, 8623–8628.

Peris, D., **Ruzzier, E.**, **Perrichot, V.** & **Delclòs, X.** In press. Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. *Geoscience Frontiers*.

Pérez-de la Fuente, R., **Saupe E. E.** & **Selden, P. A.** 2013. New lagonomegopid spiders (Araneae: †Lagonomegopidae) from Early Cretaceous Spanish amber. *Journal of Systematic Palaeontology*, **11**, 531–553.

Pérez-de la Fuente, R., **Peñalver, E.**, **Delclòs, X.** & **Engel, M. S.** 2012. Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera). *ZooKeys*, **204**, 1–40.

Perkovsky, E. E., **Rasnitsyn, A. P.**, **Vlaskin, A. P.** & **Taraschuk, M. V.** 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, **48**, 229–245.

Perrichot, V. 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. *Geologica Acta*, **2**, 9–22.

Perrichot, V., **Néraudeau, D.** & **Tafforeau, P.** 2010. Charentese amber. Pp. 192–207 in D. Penney (ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester.

Perrichot, V., **Ortega-Blanco, J.**, **McKellar, R.C.**, **Delclòs, X.**, **Azar, D.**, **Nel, A.**, **Tafforeau, P.** & **Engel, M. S.** 2011. New and revised maimetshid wasps from Cretaceous ambers (Hymenoptera, Maimetshidae). *ZooKeys*, **130**, 421–453.

Porco, D., **Skarżyński, D.**, **Decaëns, T.**, **Hebert, P. D. N.** & **Deharveng, L.** 2014. Barcoding the Collembola of Churchill: a molecular taxonomic reassessment of species diversity in a sub-Arctic area. *Molecular Ecology Resources*, **14**, 249–261.

Richards, W. R. 1968. Generic classification, evolution, and biogeography of the Sminthuridae of the world (Collembola). *Memoirs of the Entomological Society of Canada*, **53**, 1–54.

Riek, E. F. 1976. An entomobryid collembolan (Hexapoda: Collembola) from the Lower Permian of Southern Africa. *Paleontologica Africana*, **19**, 141–143.

Salmon, J. T. 1941. The collembolan fauna of New Zealand, including a discussion of its distribution and affinities. *Transactions of the Royal Society of New Zealand*, **70**, 282–431.

Salmon, J. T. 1964. An index to the Collembola. *Royal Society of New Zealand Bulletin*, **7**, 1–651.

Sánchez-García, A. & **Engel, M. S.** In press. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. *American Museum Novitates*.

Sánchez-García, A., **Arillo, A.** & **Nel, A.** 2016. The first water measurers from the Lower Cretaceous amber of Spain (Heteroptera, Hydrometridae, Heterocleptinae). *Cretaceous Research*, **57**, 111–121.

Sánchez-García, A., **Peñalver, E.**, **Pérez-de la Fuente, R.** & **Delclòs, X.** 2015. A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: palaeobiological implications. *Journal of Systematic Palaeontology*, **13**, 645–676.

Schäffer, C. 1896. Die Collembola der Umgebung von Hamburg und benachbarter Gebiete. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, **13**, 147–216, 4 pls.

Schmidt, A. R. & **Dilcher, D. L.** 2007. Aquatic organisms as amber inclusions and examples from a modern swamp forest. *Proceedings of the National Academy of Sciences, USA*, **104**, 16581–16585.

Schneider, C., **Cruaud, C.** & **D'Haese, C. A.** 2011. Unexpected diversity in Neelipleona revealed by molecular phylogeny approach (Hexapoda, Collembola). *Soil Organisms*, **83**, 383–398.

Sharov, A. G. 1966. *Basic arthropodan stock, with special reference to insects*. Pergamon Press, Oxford, xii + 271 pp.

Shoebotham, J. W. 1917. Notes on Collembola – Part 4. The classification of the Collembola; with a list of genera known to occur in the British Isles. *Annals and Magazine of Natural History, Series 8*, **9**, 425–436.

Simón-Benito, J. C., **Ortuño, V. M.** & **Espantaleón, D.** 2002. Colémbolos (Collembola, Insecta) del ámbar Cretácico de Álava (cuenca vasco-cantábrica, norte de España). *Estudios del Museo de Ciencias Naturales de Álava*, **17**, 83–92.

Simpson, G. G. 1953. *The major features of evolution*. Columbia University Press, New York, 434 pp.

Snider, R. J. 1989. Link between *Sminthurinus* and *Katianna* collected from Alabama (Collembola: Katiannidae). *Florida Entomologist*, **72**, 541–547.

Stach, J. 1923. Eine neue *Sminthurus*-Art aus der Bernsteinfauna. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles, Série B, Sciences Naturelles*, **1922**, 53–61, 1 pl.

Stach, J. 1956. The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Family: Sminthuridae. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1956**, 1–287.

Sudo, S., **Shiono, M.**, **Kainuma, T.**, **Shirai, A.** & **Hayase, T.** 2013a. The kinematics of jumping of globular springtail. *Journal of Aero Aqua Biomechanisms*, **3**, 85–91.

Sudo, S., **Shiono, M.**, **Kainuma, T.**, **Shirai, A.** & **Hayase, T.** 2013b. Observation on the springtail leaping organ and jumping mechanism worked by a spring. *Journal of Aero Aqua Biomechanisms*, **3**, 92–96.

Tullberg, T. 1871. Förteckning öfver Svenska Podurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, **28**, 143–155.

Velasco-Castrillón, A., **Gibson, J. A. E.** & **Stevens, M. I.** 2014. A review of current Antarctic limno-terrestrial microfauna. *Polar Biology*, **37**, 1517–1531.

Wilson, D. J. & **Gerard, P. J.** 2014. Investigating foliar fertiliser effects on the incidence of clover flea (*Sminthurus viridis*) damage on white clover. *New Zealand Plant Protection*, **67**, 245–249.

Xiong, Y., **Gao, Y.**, **Yin, W.-Y.** & **Luan, Y.-X.** 2008. Molecular phylogeny of Collembola inferred from ribosomal RNA genes. *Molecular Phylogenetics and Evolution*, **49**, 728–735.

Yosii, R. 1961. Phylogenetische Bedeutung der Chaetotaxie bei den Collembolen. *Contributions from the Biological Laboratory, Kyoto University*, **12**, 1–37.

Yosii, R. 1974. Fossil Collembola contained in the Mizunami amber (Insecta: Collembola). *Bulletin of the Mizunami Fossil Museum*, **1**, 409–411. [In Japanese.]