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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. (Sminthuridae), 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 eudaphic 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 microorganisms, 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 collombolan 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 Neolepoea (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 Alethoarthropoda), 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 collombolan 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-Beníto 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 (Yosi 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-Beníto 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 Eusymphyleona). Most species are exceptional jumpers and some have a prominent and conspicuous colophore.
(‘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 Peñasos 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 Alava 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 summarises our preferred, simplified classification of families of Symphypleona.

<table>
<thead>
<tr>
<th>Superfamily</th>
<th>Börner, 1901</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sminthuridoidea</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Family</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Pseudosminthurides</td>
<td>gen. nov.</td>
</tr>
</tbody>
</table>

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 interocellar 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

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

<table>
<thead>
<tr>
<th>Order Symphypleona</th>
<th>Börner, 1901</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suborder Sminthuridida</td>
<td>Bretfeld, 1986</td>
</tr>
<tr>
<td>Superfamily Sminthuridoidea</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Family Sminthuridae</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Family Mackenziellidae</td>
<td>Yosii, 1961</td>
</tr>
<tr>
<td>Suborder Appendiciphora</td>
<td>Bretfeld, 1986</td>
</tr>
<tr>
<td>Infraorder Katianniformia</td>
<td>Bretfeld, 1986</td>
</tr>
<tr>
<td>Superfamily Katiannoidea</td>
<td>Börner, 1913</td>
</tr>
<tr>
<td>Family Katiannidae</td>
<td>Börner, 1913</td>
</tr>
<tr>
<td>Family Spinothecidae</td>
<td>Delamare-Deboutteville, 1961</td>
</tr>
<tr>
<td>Family Arrhopalitidae</td>
<td>Stach, 1956</td>
</tr>
<tr>
<td>Family Collophoridae</td>
<td>Bretfeld, 1999</td>
</tr>
<tr>
<td>Superfamily Sturmioida</td>
<td>Bretfeld, 1994</td>
</tr>
<tr>
<td>Family Sturmiidae</td>
<td>Bretfeld, 1994</td>
</tr>
<tr>
<td>Infraorder Sminthuriformia</td>
<td>Bretfeld, 1986</td>
</tr>
<tr>
<td>Superfamily Sminthuroidea</td>
<td>Lubbock, 1862a</td>
</tr>
<tr>
<td>Family Bourletiellidae</td>
<td>Börner, 1913</td>
</tr>
<tr>
<td>Family Sminthuridae</td>
<td>Lubbock, 1862a</td>
</tr>
<tr>
<td>Subfamily Sminthurinae</td>
<td>Lubbock, 1862a</td>
</tr>
<tr>
<td>Subfamily Songhaicinae</td>
<td>subfam. nov.</td>
</tr>
<tr>
<td>Subfamily Spinothecinae</td>
<td>Betsch, 1980</td>
</tr>
<tr>
<td>Superfamily Dicyrtomoida</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Family Dicyrtomidae</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Subfamily Dicyrtominidae</td>
<td>Börner, 1906</td>
</tr>
<tr>
<td>Subfamily Ptenothricinae</td>
<td>Richards, 1968</td>
</tr>
</tbody>
</table>

*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 στωχος, 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 Entomobryo-Porphamorpha and to be treated in a subsequent work focusing on that order: Sánchez-García & Engel in press).
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 acuminated 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 clasp 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

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**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.
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 times length of tibiotarsus, nearly straight and sharp apicly; 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 times 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 claspers 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 clasper organ, and the second antennomere bears a simple 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 habitat, 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, Ortúñ & 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](image.png)  
**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.
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 $1.51 \times$ as long as cephalic diagonal; antennomere lengths in $\mu$m 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.

Opisthosaoma. Opisthosaoma lacking traces of thoracic segmentation, length 217 $\mu$m 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 bothriothrix (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 $\mu$m; dens length 182 $\mu$m, with numerous setae at least on outer margin; mucro simple, length 42 $\mu$m, 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, 8A. Sánchez-García and M. S. Engel

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.
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 important, 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 anulated 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 (Spinotheriidae 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 (Colphoridae 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× micro 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 Sphyrotheta Börner, 1906, type genus of the subfamily, and the masculine diminutive Greek suffix, ισκος. 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.
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...
mesotibiotarsus: 36, 57 and 103 μm; lengths of metatibia 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

Figure 6. Camera lucida drawings of the holotype of Sphyrotheciscus senectus gen. et sp. nov., MCNA 9311, sex unknown. A, ventrolateral habitus; B, dorso-lateral habitus.
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, ἀρχ=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 δόλoς, meaning ‘long’ and ποδός, 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
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 prototibiotarsus: 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 prototibiotarsus apparently with numerous slender, acuminate, straight to slightly curved setae, longest about as long as widest width of prototibiotarsus (visible in paratype); unguis small and thin, with a basal tunica; unguiculus apparently not reaching apex of unguis.

**Colophore.** Not visible.
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
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.
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).

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Species</th>
<th>Total length</th>
<th>Opisthosoma</th>
<th>Head</th>
<th>IV</th>
<th>III</th>
<th>II</th>
<th>I</th>
<th>Manubrium</th>
<th>Dens</th>
<th>Mucro</th>
<th>Mucro/dens ratio</th>
</tr>
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<tbody>
<tr>
<td>MCNA 12788.1</td>
<td>Pseudosminthurides stoechus</td>
<td>631</td>
<td>471</td>
<td>160</td>
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<td>Cretokatianna bucculenta</td>
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<td>217</td>
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<td>210</td>
<td>75</td>
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<td>255</td>
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<td>189</td>
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<td>37</td>
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<td>246</td>
<td>293</td>
<td>122</td>
<td>67</td>
<td>41</td>
<td>75</td>
<td>195</td>
<td>63</td>
<td>3.07</td>
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<td>A. dolichopoda?</td>
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<td>252</td>
<td>285</td>
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<td>Katiannasminthurus xenopygus</td>
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<td>399</td>
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<td>219</td>
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</table>
Derivation of name. The specific epithet is considered an adjective and is a combination of the Greek terms \( \xi\epsilon\nu\omicron\varsigma \), meaning ‘strange’ and \( \pi\upsilon\gamma\omicron\varsigma \), 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 \( \varphi \), MCNA 10048, virtually complete. Preserved in a clear yellow turbid piece of amber trimmed to \( 0.7 \times 0.1 \times 0.1 \) cm (in an epoxy resin trapezoid \( 1.3 \times 0.9 \times 0.1 \) 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 \( \mu \)m; habitus sminthuroid.

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.
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, acuminete 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 acuminete 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.

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.
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 its 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 entomobryomorph 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.](image-url)
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 antennomere 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

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*Figure 14.* Camera lucida drawing of the specimen MCNA 10016 (Symphypleona, genus and species indeterminate).
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, *Sminthuricus deceptus* Christiansen & Nascimbene, 2006, *Macrovirga incompleta* Christiansen & Nascimbene, 2006 and *Sminthuronus grimaldi* Christiansen & Nascimbene, 2006, all of the Sminthurinæ), 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 Sminthurinidae 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 microcomputed 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 sminthurid 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, Archaeogryphus, 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 entraping clearly forest floor or even ‘aquatic’-like elements, many pieces of amber from Peñañerrada I do represent a sampling of taxa from above the forest floor (e.g. Peñalver & Delclós 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 & Nascimbène 2006). Large-scale vicariant patterns among epedaphic Colembola 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 & Völlken 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 Peñañerrada 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 Colembola 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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