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Springtails from the Early Cretaceous Amber of Spain (Collembola: Entomobryomorpha), with an Annotated Checklist of Fossil Collembola

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ABSTRACT

Entomobryomorphan springtails (Hexapoda: Entognatha: Collembola) of the family Isotomidae are the most numerous group of Collembola in Spanish amber, a pattern typical in other studied Cretaceous amber deposits. Here we provide a revision of the Spanish amber springtail fauna, Early Cretaceous (Late Albian) in age, based on 93 specimens sufficiently well preserved to permit specific identification. Three new species are erected within the Isotomidae: Anurophorinae. These are: *Burmisotoma spinulifera*, new species, *Protoisotoma autrigoniensis*, new species, and *Proisotoma communis*, new species. The two former are respectively placed in the Cretaceous genera *Burmisotoma* Christiansen and Nascimbene (previously known from Cenomanian Burmese amber) and *Protoisotoma* Christiansen and Pike (in both Burmese and Canadian ambers), while the last species is indistinguishable from the extant, cosmopolitan genus *Proisotoma* Börner (also recorded in Burmese amber). Low morphological intraspecific variability is described for *P. communis*. Taxa are discussed in relation to other fossil entomobryomorphan lineages as well as their modern counterparts. A catalog of the known fossil springtails is appended. Isotomidae are diverse springtails, putatively basal among Entomobryomorpha and extending back into the Early Devonian. Indeed, taxa described herein are overall remarkably similar to their extant relatives, emphasizing the antiquity and morphological stasis of the group as a whole.

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INTRODUCTION

The springtail family Isotomidae is one of the most diverse in the collembolan order Entomobryomorpha, presently comprising about 1346 species in 108 genera (Janssens and Christiansen, 2011). Isotomids are rather generalized springtails and are usually the most common component of most collembolan communities. Species of the family are abundant in varied kinds of litter, soil, and moss and in all types of undisturbed ecosystems ranging from deserts to polar regions, although they are more numerous in damp and cold conditions (Hopkin, 1997). Together with Hypogastruridae (Poduromorpha), species of Isotomidae comprise the primary component of high-arctic and nival springtail communities (e.g., Christiansen, 1964; Greenslade, 1995; Hopkin, 1997; Babenko, 2000; Stevens et al., 2006b), with some demonstrating considerable activity on snow and ice (Leinaas, 1981; Hågvar and Hågvar, 2011), leading to their moniker as "snow fleas." In sharp contrast, some genera can tolerate the dry conditions of exposed microhabitats, such as tree trunks and rocks, or survive the aridity and high temperatures of xeric regions, although none are truly "xerophilic" (Cassagnau, 1961; Christiansen, 1964; Greenslade, 1981; Sømme, 1995). Isotomids can also be diverse in sandy soils (Thibaud and Christian, 1997), even thriving within the hot and humid soils of compost heaps where some species may form large aggregations (Hopkin, 1997). Neustonic forms may similarily be found in a wide variety of microhabitats, from the sea littoral zone, to the banks of lakes and large rivers, well within bogs, or even along cold-water mountain streams (Potapov, 2001; Deharveng et al., 2008). Lastly, many species are truly euedaphic, moving through sand or deep soil layers (e.g., *Pseudanurophorus* Stach, *Jesenikia* Rusek) (Potapov, 2001). This vast ecological breadth has allowed isotomids to flourish in virtually all areas of the world, and their distribution is truly cosmopolitan with the exception of some equatorial areas in Africa, although this may merely reflect a lack of suitable sampling. Given the preceding, that springtails are vital to most soil biotas and food webs (Peterson and Luxton, 1982; Hopkin, 1997; Rusek, 1998; Hättenschwiler et al., 2005; Whalen and Sampedro, 2010), and the fact that a variety of their morphological traits are intimately tied to their ecological preferences (Christiansen, 1964; Hopkin, 1997), Collembola have the potential to be critical in reconstructing localized palaeofaunal conditions. Isotomidae have also been the subject of considerable taxonomic investigation, the earliest significant one being the posthumously published monograph of Folsom (1937a), a work that treated the Nearctic fauna and provided a general foundation for future endeavors. Stach (1947) modified the familial classification based on his study of the Polish fauna, and this was expanded by the works of Deharveng (e.g., Deharveng, 1977), and ultimately by Potapov (2001) in his comprehensive overview of the Paleartic Isotomidae.

Not surprisingly, given their minute size, the fossil record of springtails is largely confined to preservation in amber, in which organisms hold the potential to fossilize with lifelike fidelity. Aside from a few exceptions, this bias effectively restricts their geological occurrence to the Cretaceous and later as it is from this period onward that suitably fossiliferous ambers are known (Grimaldi and Engel, 2005). Isotomidae are the most abundant and common of springtails in Cretaceous ambers, accounting for more than half of all specimens in Canadian amber and more than a third of all those in Burmese amber (Christiansen and Nascimbene, 2006). Isotomidae are also of considerable antiquity, with the Early Devonian *Rhyniella praecursor*

Hirst and Maulik (1926) presently placed therein (Greenslade and Whalley, 1986), although its familial attribution has shifted from Rhyniellidae (Paclt, 1956), to Neanuridae (Massoud, 1967a), to Protentomobryidae (Scourfield, 1940a, 1940b). Remarkably, the putatively extinct family Protentomobryidae (Folsom, 1937b), in which once *R. praecursor* was placed, is almost assuredly a synonym of Isotomidae (Greenslade and Whalley, 1986), particularly as it is separated from isotomids merely by a single autapomorphy (Delamare-Deboutteville and Massoud, 1968; Christiansen and Pike, 2002a). Interestingly, although Isotomidae are seemingly very ancient, a few phylogenetic studies have suggested the family to be relatively derived among Entomobryomorpha (D'Haese, 2002, 2003a), although this pattern was reversed in the studies of Xiong et al. (2008) and Schneider et al. (2011), with isotomids basal within the order—a placement more intuitively pleasing given their stratigraphic span.

Here we document an Early Cretaceous fauna of isotomid springtails preserved in amber from Burgos Province, northern Spain, and as a companion work to a similar study of the Symphypleona of these same deposits (Sánchez-García and Engel, 2016). Although presently Isotomidae are not as diverse in Spanish amber as in Burmese amber (Christiansen and Nascimbene, 2006), their diversity is significant as it is currently the earliest documented from the Mesozoic. Moreover, in contrast to those putative isotomids from the Devonian and Permian, the Spanish amber springtail fauna is the oldest with sufficient preservation to allow a critical comparison with other faunas and allow for inferences regarding the general habitat in which the amber was exuded. Entomobryomorphan diversity will certainly rise in Spanish amber as new material becomes available from the El Soplao and San Just outcrops. To this treatment we append a catalog of the known fossil and subfossil records of springtails (Appendix).

MATERIAL AND METHODS

The present revision considers the fauna of Entomobryomorphan springtails preserved in Early Cretaceous amber from Spain, complementing the earlier overview of Collembola from these deposits by Simón-Benito et al. (2002). Preparation, photography, and imaging of the amber and its inclusions followed the procedures outlined by Sánchez-García and Engel (2016), which started with initial screening of pieces for biotic inclusions followed by vacuum-embedding in a stable epoxy resin (Epo-tek 301) (Nascimbene and Silverstein, 2000). The embedded amber was then suitable for trimming, grinding, and polishing using a water-fed flat lap. Given the minute proportions of springtails, thin sections of amber were required (epoxy preparations typically between 1.0–4.5 mm thickness, and, when possible, with the inclusion merely microns beneath the amber surface). In order to best visualize details such as setae, integument, and structure of the furcula and tibiotarsal complex, some preparations were positioned between a glass microscope slide and glass coverslip held in place by a thin layer of synthetic resin. Such slide preparations allowed for greater clarity and resolution of individual structures. Inclusions were studied with Motic BA310 and Olympus BX41 compound microscopes, and measurements were taken with the ImageJ software package and recorded in micrometers. Total body length measurements were taken along the midline from the tip of the head to the apex of the abdomen. Microphotographs were taken with a Moticam 2500 digital camera attached to the Motic BA310 compound microscope and per-

formed in Motic Images Plus 2.0 software at the Universitat de Barcelona. The software package Helicon Focus was used to combine different focal layers. Line drawings were prepared with the aid of a camera lucida attached to the Olympus BX41 compound microscope at the University of Kansas. For the systematic work, the higher classifications of Folsom (1937a), Potapov (2001), and Soto-Adames et al. (2008), are followed, and morphological terminology for the descriptions is generally based on Potapov (2001), Fjellberg (2007), and as modified by Sánchez-García and Engel (2016), with descriptions provided in the context of expanding upon evolutionary patterns (e.g., Grimaldi and Engel, 2007). All material is deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain, abbreviated as MCNA herein.

The geological setting was summarized by Peñalver and Delclòs (2010), and is only briefly outlined here. The amber discussed here and in an earlier paper on Symphypleona (Sánchez-García and Engel, 2016), comes from the Peñacerrada I locality in the municipality of Moraza (Burgos Province, northern Spain), while a sister locality, named Peñacerrada II, is present in the municipality of Peñacerrada (in the neighboring Álava Province). Both outcrops are Late Albian in age (Barrón et al., 2015), and take part of the Utrillas Group within the Basque-Cantabrian Basin. These deposits represent deltaic systems dominated by fluvial-deltaic environments with siliclastic input (Martínez-Torres et al., 2003). Within this framework, resin was deposited in paralic environments, as amber is today found within lignitic beds or organically-rich marls, present at the top of filling sequences of channels within deltas, coinciding with the boundary between maximum regression and the start of transgression (Peñalver and Delclòs, 2010). Cretaceous amber localities in Spain are today geographically arranged following an arc from north to east of the Iberian Peninsula that corresponds to the Early Cretaceous seashore (Delclòs et al., 2007).

To date, aside from the isotomid springtails discussed here, the amber from Peñacerrada I has produced thousands of arthropod inclusions representing virtually all orders of Hexapoda, numerous groups of Arachnida, principally mites and spiders, and certain lineages of Crustacea (e.g., Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010; Sánchez-García et al., 2015), making it one of the most important Early Cretaceous Lagerstätten.

SYSTEMATIC PALEONTOLOGY

Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Superfamily Isotomoidea Schäffer, 1896
Family Isotomidae Schäffer, 1896
Subfamily Anurophorinae Börner, 1901
(sensu Potapov, 2001)

Following the concept of Isotomidae as outlined by Folsom (1937a) and Potapov (2001), as well as the last suprageneric classification of Entomobryomorpha by Soto-Adames et al. (2008; whose treatment of Isotomidae followed Potapov, 2001), all the entomobryomorphan springtails from the Spanish Cretaceous amber are assignable to Isotomidae. Collectively, this is based on: **1,** the absence of scales, trochanteral organs, and postocular trichobothria; **2,** the relatively short

antennae, with four antennomeres; **3,** the fourth abdominal segment usually subequal to or longer than the third (erroneously cited as "shorter than the third" in Soto-Adames et al., 2008), with one never more than one and one-half times as long as the other; **4,** the last two or three abdominal segments sometimes fused (e.g., in *Folsomia* Willem, *Folsomina* Denis, and *Pectenisotoma* Gruia); **5,** trichobothria usually absent; and, **6,** a general covering of simple setae, the largest of which are often serrate or fringed, but never clavate or fringed on all margins. In addition, Folsom (1937a) also considered the following characters as diagnostic for Isotomidae: **1,** prothorax membranous and without setae (except in *Guthriella* Börner); **2,** mesothorax not projecting over the head; **3,** postantennal organs almost invariably present, each consisting externally of a simple tubercle; **4,** pretarsi with an unguis and sometimes an unguiculus; **5,** inner edge of unguis always simple, never basally split or doubled; **6,** furcula present (except in *Anurophorus* Nicolet and its allies); **7,** manubrium with setae, seldom bare ventrally; and, **8,** integument generally smooth and with distinct sclerites, except in some taxa in which it can be tuberculate and with less distinctive sclerites. Most of the characters utilized by Potapov (2001) in his system are related to chaetotaxy. The present samples share with his characterization the absence of dorsal prothoracic setae, the body covered with abundant setae (i.e., polychaetotic), and a weak morphological chaetotaxic differentiation expressed by the plesiomorphic condition of two features: a weak differentiation of chaetalike components, and uniformity of the chaetotaxy of body segments.

Isotomidae are organized into three subfamilies: Isotominae Schäffer, 1896, Anurophorinae Börner, 1901, and Pachyotominae Potapov, 2001 (Potapov, 2001). The three species erected below can be placed among the Anurophorinae owing to the combination of: **1,** absence of secondary granulation over the body; **2,** chaetotaxy oligo- to polychaetotic; **3,** empodium sometimes reduced or outright lacking; **4,** tibiotarsi with seven setae in the distal ring; **5,** manubrium with or without a few anterior setae; **6,** well-developed dens that is continuously narrowed apically, with its posterior side crenulate or tuberculate; and **7,** mucro, if present, usually bidentate. Anal spines may or may not be present among anurophorine taxa. As will be observed from the descriptions below, all the addressed genera have a combination of traits that best suits the Anurophorinae and are, in fact, close to the extant genus *Proisotoma* Börner (with one new species placed within that particular genus).

Genus *Burmisotoma* Christiansen and Nascimbene, 2006

Burmisotoma Christiansen and Nascimbene, 2006: 340. Type species: *Burmisotoma lamellifera* Christiansen and Nascimbene, 2006, by original designation.

Burmisotoma spinulifera, new species

Figures 1–2

Diagnosis: Aside from the general traits of the genus (outlined by Christiansen and Nascimbene, 2006), the new species differs from the type species (*Burmisotoma lamellifera* Christiansen and Nascimbene) by the presence of a long, thick, and straight femoral spine, as well as a ventrally crenulate manubrium.

Description: Total body length as preserved 473 μm. Body slender, thickened in posterior half, of typical isotomid shape. Dorsal integument with distinct, fine reticulation; all body setae smooth.

Head length as preserved 122 μm, about 0.26× length of body; covered largely with sparse, somewhat curved, slender setae; antennae with four antennomeres; fourth antennomere not swollen, densely setaceous, with slender, mostly weakly curved, acuminate, long setae, accompanied by some thick, truncate, cylindrical, long setae on apical half of antennomere; first to third antennomeres mostly obscured preventing measurements. Ommatidia not visible. Postantennal organ not visible (likely not present).

Thorax highly distorted, maximum width 87 μm, without visible setae; prothoracic segment membranous; meso- and metathoracic segments subequal in length.

Legs with trochanter poorly visible, with a few short, weakly curved, acuminate setae; femur length 33 μm, bearing a thick and straight spine, about as long as femoral diameter; tibiotarsus length 43 μm, with several slender setae, setae apparently not clavate nor truncate; unguis and unguiculus not clearly visible, apparently simple, without serration or denticles; unguis length 23 μm, acuminate.

Abdomen swollen and somewhat ovoid, maximum width 153 μm, distinctly wider than thorax, with sparse, straight to somewhat curved, slender setae, such setae becoming longer and more numerous posteriorly; abdominal segments not fused; third and fourth abdominal segments subequal in length, fourth segment only slightly longer than third segment; lengths of abdominal segments III–VI in μm, approximately: III, 43; IV, 49; V, 27; VI, 20. Length, exclusive of appendages 107 μm.

Furcula long and slender (visible in lateral view); manubrium length 36 μm, ventrally crenulate, without visible setae; dens length 84 μm, tapering distally, without visible setae; mucro poorly visible, apparently bidentate.

Holotype: MCNA 12583 (fig. 1), virtually complete, visible dorsally, ventrally, and laterally. Preserved in a clear-yellow, turbid piece of amber trimmed to 1.05 × 0.80 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.20 × 0.10 cm), and included with fungal hyphae, and many arthropod (e.g., scales) and plant remains (e.g., stellate hairs).

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

Etymology: The specific epithet is from the Latin *spinula* (meaning, "small spine") and *fero* (meaning, "bear" or "carry"), and refers to the femoral spine distinctive of the species.

Remarks: The genus *Burmisotoma* was described originally from a single specimen in mid-Cretaceous amber from Myanmar (Burma). *Burmisotoma spinulifera,* n. sp., shares with the type species, *B. lamellifera*, a well-developed furcula lacking ventral manubrial setae, strongly tapered dentes, and the antennae bearing stout, cylindrical, truncate setae. Unfortunately, the ommatidia, details of the setae and tubercles of the dens, and the morphology of the mucrones were not clearly visible in *B. lamellifera*, preventing comparison of these structures with the present specimen. In the new species, the body shape (slender and thickened in the posterior half), general chaetotaxy of the body, antennal structure, and the tarsal complex are all very similar to *B. lamellifera* as illustrated by Christiansen and Nascimbene (2006); there-

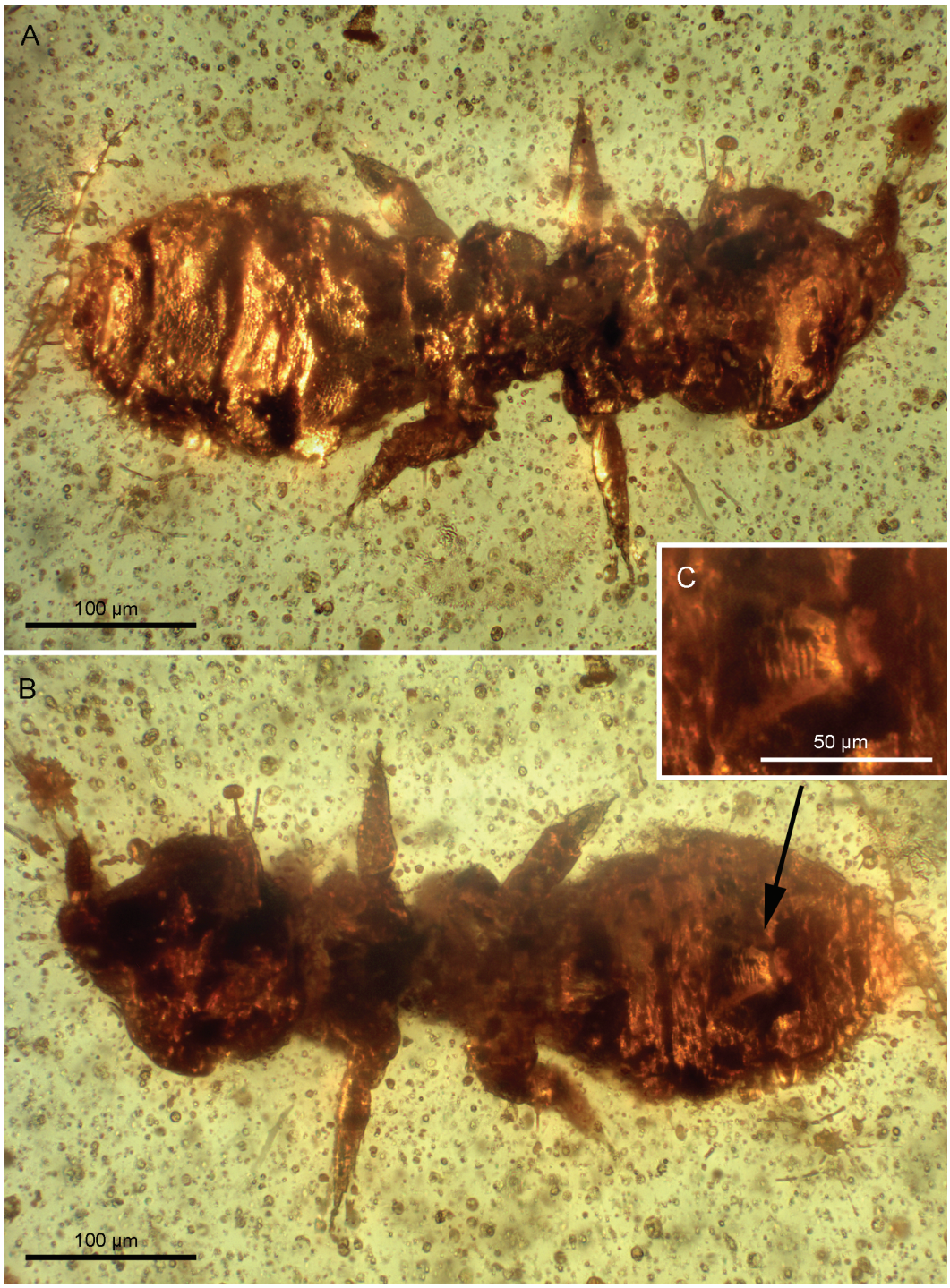

FIGURE 1. Microphotographs of the holotype (MCNA 12583) of *Burmisotoma spinulifera*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes). **A.** Dorsal habitus. **B.** Ventral habitus. **C.** Detail of manubrial crenulation.

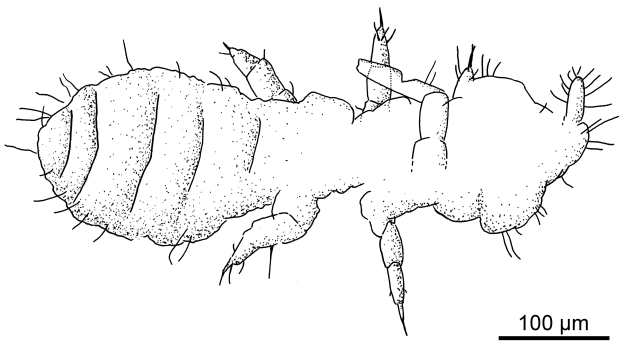

FIGURE 2. Camera lucida drawing of the holotype (MCNA 12583) of *Burmisotoma spinulifera*, new species, in dorsal habitus.

fore, the most reasonable is to consider them congeneric. However, *B. spinulifera* is remarkable in having a thick and straight femoral spine (fig. 2), and a ventrally crenulate manubrium. The dorsal reticulation of the integument is also distinctive of the new species. These features are, however, merely autapomorphic and the establishment of a separate genus based on these comparatively minor differences would serve only to proliferate the number of monospecific genera for otherwise quite similar Cretaceous springtails.

Genus *Protoisotoma* Christiansen and Pike, 2002a

Protoisotoma Christiansen and Pike, 2002a: 171. Type species: *Protoisotoma micromucra* Christiansen and Pike, 2002a, by original designation.

Protoisotoma autrigoniensis, new species

Figures 3–4

Diagnosis: The new species agrees with the characters of the genus (as outlined by Christiansen and Pike, 2002a), but differs from its congeners by the longer third antennomere that is subequal to the fourth antennomere, and the fourth abdominal segment being subequal to or slightly longer than the third segment.

Description (based on holotype): Total body length as preserved 1273 µm. Body slender, not thickened in posterior half, about 5.12× as long as wide, of typical isotomid shape. Dorsal integument smooth; all body setae smooth.

Head length as preserved 192 µm, about 0.15× length of body, largely with long, somewhat curved, slender setae; antennae with four antennomeres; fourth antennomere swollen, length 107 µm, with a few slender, mostly weakly curved and acuminate, short setae; third antennomere about as long as fourth; first and second antennomeres mostly obscured by head, preventing measurements. Ommatidia not visible. Postantennal organ not visible (perhaps not present).

Thorax length 335 µm, about 0.26× length of body, maximum width 235 µm; prothoracic segment indistinct; meso- and metathoracic segments subequal in length; segments densely covered with short, straight to somewhat curved, slender setae.

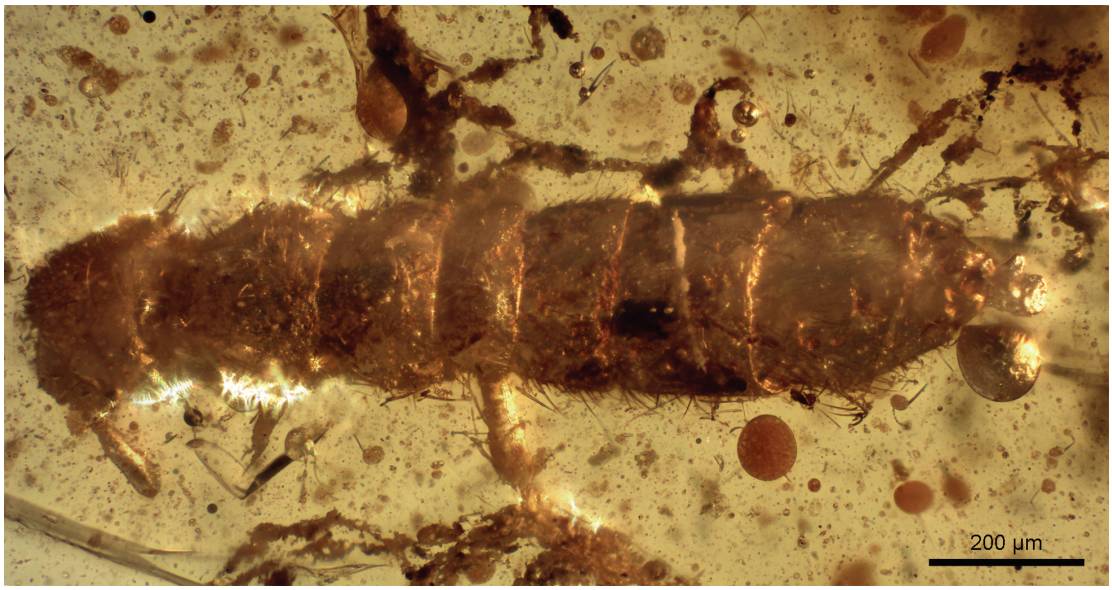

FIGURE 3. Microphotograph in dorsal habitus of the holotype (MCNA 12788.2) of *Protoisotoma autrigoniensis*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes).

Legs poorly visible except for protibiotarsus: tibiotarsus length 109 µm, with a few short, weakly curved, acuminate setae, apparently not clavate nor truncate; unguis simple, without serration or denticles, relatively long, length 58 µm, nearly straight and acuminate; unguiculus simple, half length of unguis (26 µm), nearly straight and acuminate.

Abdomen length 749 µm, about 0.59× length of body, not swollen, maximum width 255 µm, only slightly wider than thorax; abdominal segments not fused; third and fourth abdominal segments subequal in length, fourth segment only slightly longer than third segment; lengths of abdominal segments III–VI in µm, approximately: III, 187; IV, 200; V, 76; VI, 43. Abdominal segments densely covered with short, straight to somewhat curved, slender setae, as well as some long, erect pseudotrichobothria.

Furcula appressed against body (and therefore poorly visible); manubrium without visible setae; dens long and slender, without visible setae; mucro minute, poorly visible.

Holotype: MCNA 12788.2 (fig. 3), virtually complete, visible dorsally and ventrally. Preserved in a clear-yellow, turbid piece of amber trimmed to 1.00 × 0.90 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.20 × 1.50 × 0.20 cm), and accompanied by much debris and arthropod remains (e.g., scales). Syninclusions include three acari and the holotype of the symphypleonan *Pseudosminthurides stoechus* Sánchez-García and Engel (2016). Inclusions in piece MCNA 12788 and a further springtail 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.

Additional material: MCNA 12787.1, virtually complete, visible in profile, with blackened cuticle somewhat altered due to fossilization; preserved in a clear-yellow, turbid piece of amber trimmed to 1.30 × 0.70 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.80 ×

1.80 × 0.10 cm), with syninclusions as detailed for MCNA 12788.2. This specimen agrees in most respects with the holotype but is noticeably smaller (total length 809 μm) and exhibits at least two pairs of anal spines. The shared shape of the furcula, antennae, and chaetotaxy of the body, as well as its preservation as syninclusion with the holotype, all make it seem likely that they represent the same taxon, but this remains unresolved, particularly as the anal spines cannot be discerned in the holotype (owing to its state of preservation).

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

Etymology: The specific epithet is based on the region of Autrigonia, home of the pre-Roman Autrigones who lived in the area of the type locality before their eventual integration into the Empire.

Remarks: Overall, this species exhibits all those traits characteristic of the genus *Protoisotoma*, previously described from species preserved in Cretaceous Canadian and Burmese ambers (Christiansen and Pike, 2002a, 2002b; Christiansen and Nascimbene, 2006). Distinguishing features within the subfamily include the swollen fourth antennomere, simple ungues and unguiculi, elongate dentes, minute mucrones, and a body densely covered with curved, acuminate, smooth setae as well as erect pseudotrichobothria on the abdomen. Unfortunately, the postantennal organ, ommatidia, and details of the furcula cannot be seen, preventing more extensive comparison. Although the dens is elongate in *P. autrigoniensis,* n. sp., no crenulation or setae are visible owing to the nature of preservation of the type. The new species can be distinguished from its congeners (*P. micromucra* Christiansen and Pike from Canadian amber, and *P. burma* Christiansen and Nascimbene from Burmese amber) by its longer third antennomere, which is subequal to the fourth, and the fourth abdominal segment subequal to or slightly longer than the third abdominal segment (rather than the subequal or shorter fourth abdominal segment relative to the third abdominal segment in *P. micromucra* and *P. burma*) (fig. 4). It is remarkable that the other putative specimen of this species, MCNA 12787.1, exhibits two pairs of anal spines, a feature not observed in all other specimens of *Protoisotoma* from Burmese and Canada ambers (this is not a statement of the character's absence from such specimens, merely a condition of it not being observable in such specimens owing to the nature of preservation).

Genus *Proisotoma* Börner, 1901

Proisotoma Börner, 1901: 133. Type species: *Isotoma minuta* Tullberg, 1871, subsequent designation by Börner (1903). Refer to Potapov (2001) and Potapov et al. (2006) for a complete summary of extant synonyms.

Proisotoma communis, new species

Figures 5–6

Micranurida? sp. Simón-Benito et al., 2002: 85: fig. 1a.
Onychiurus? sp. Simón-Benito et al., 2002: 85: fig. 1b.
Anurophorus? sp. Simón-Benito et al., 2002: 85: figs. 1c, d.
Proisotoma (*Ballistura*)? sp. Simón-Benito et al., 2002: 85: figs. 1e–g.
Cryptopygus? sp. Simón-Benito et al., 2002: 87: figs. 2a–d.

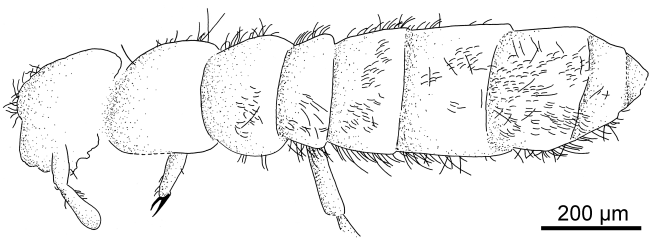

FIGURE 4. Camera lucida drawing of the holotype (MCNA 12788.2) of *Protoisotoma autrigoniensis*, new species, in dorsal habitus.

Diagnosis: The new species has characteristics of the genus and differs from its congeners by the greatly swollen fourth antennomere; the fourth abdominal segment one and a half times the length of the third; the absence of clavate tibiotarsal setae; the simple ungues and unguiculi; the rather slender and elongate dens that is dorsally tuberculate and ventrally bearing thick setae arranged in pairs; and the small, bidentate mucro.

Description (largely based on the type series): Total body length highly variable; body length of holotype 539 µm; body length of paratypes 514–560 µm. Body slender, not thickened in posterior half, about 4.82× as long as wide, of typical isotomid shape. Dorsal integument smooth; all body setae smooth.

Head length 145 µm, about 0.26× length of body; largely with long, somewhat curved, slender setae; antennae with four antennomeres, with few slender, mostly weakly curved and acuminate, short setae; fourth antennomere swollen, length 46 µm, longer than combined lengths of third and second antennomeres; third and second antennomeres subequal in length, 19 and 19 µm, respectively; first antennomere shortest, usually obscured by head. Eyes poorly visible, with at least four ommatidia. Postantennal organ not visible (perhaps not present).

Thorax length 113 µm, about 0.20× length of body, prothoracic segment indistinct; meso- and metathoracic segments subequal in length; densely covered with short, straight to somewhat curved, slender setae.

Legs usually poorly visible, and often obscured by body; trochanter, femur, and tibiotarsus subequal in length, tibiotarsus with a few short, weakly curved, acuminate setae, apparently not clavate nor truncate; unguis simple, without serration or denticles, rather small, nearly straight and acuminate; unguiculus simple, half length of unguis, nearly straight and acuminate.

Abdomen length 300 µm, about 0.54× length of body, not swollen, only slightly wider than thorax; abdominal segments not fused; fourth abdominal segment 1.55× length of third segment; lengths of abdominal segments III–VI in µm, approximately: III, 53; IV, 82; V, 37; VI, 33. Abdominal segments densely covered with short, straight to somewhat curved, slender setae, as well as some longer setae on distal part of abdomen.

Furcula long and slender; manubrium length 22 µm, with several scattered setae; dens length 79 µm, tapering distally, with numerous small tubercles dorsally, and thick ventral setae arranged in pairs; mucro small, generally poorly visible, bidentate, without lamellae.

Holotype: MCNA 9273.1 (fig. 5A), in piece with three specimens (2 paratypes, vide infra), the holotype visible in profile and virtually complete, total length 539 µm, and one disarticulated leg of a possible symphypleonan springtail. Preserved in a clear-yellow, turbid piece of

FIGURE 5. Microphotographs of the holotype and two paratypes of *Proisotoma communis*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes). **A.** Holotype (MCNA 9273.1) in lateral habitus, and paratype (MCNA 9273.2) in ventral habitus. **B.** Paratype (MCNA 9273.3) in dorsal habitus.

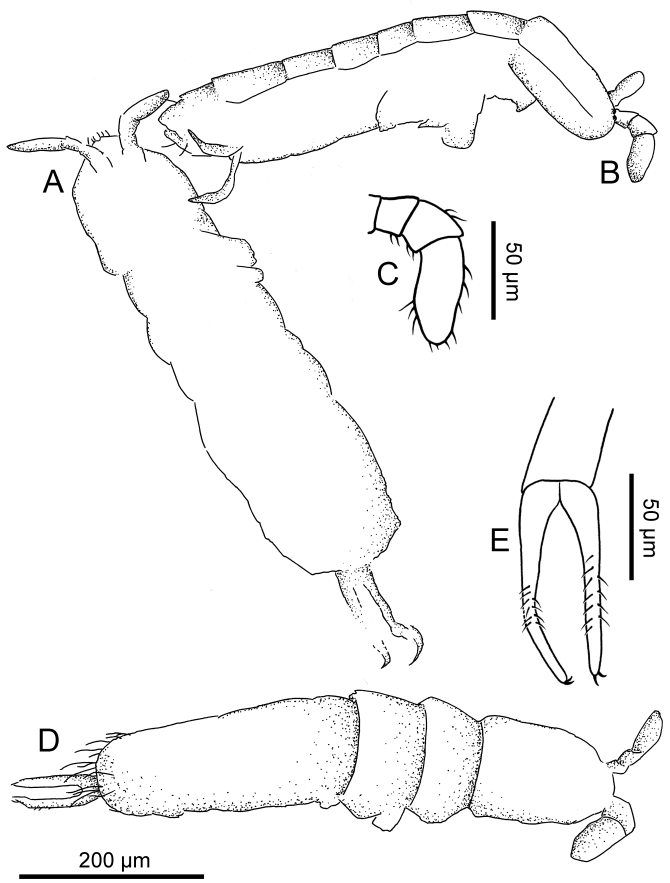

FIGURE 6. Camera lucida drawings of the holotype and two paratypes of *Proisotoma communis*, new species. **A.** Paratype (MCNA 9273.2) in ventral habitus. **B.** Holotype (MCNA 9273.1) in lateral habitus. **C.** Detail of right antenna of holotype (MCNA 9273.1). **D.** Paratype (MCNA 9273.3) in dorsal habitus. **E.** Ventral detail of furca of paratype (MCNA 9273.3).

amber trimmed to 0.90 × 0.40 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.30 × 0.10 cm), and included with many arthropod and plant remains (e.g., stellate hairs).

Paratypes: Four paratypes in total. Two paratypes, MCNA 9273.2–3 (figs. 5A, 5B) in same piece as holotype, both virtually complete, visible dorsally and ventrally, total lengths 540 (MCNA 9273.2, fig. 5A) and 556 (MCNA 9273.3, fig. 5B) µm, respectively; other details of piece provided under account of holotype.

One paratype, MCNA 9324: Total length 560 µm, virtually complete, visible dorsally and ventrally, showing details of furcula. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.10 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles; the amber is darkened near the inclusion.

One paratype, MCNA 10070: Total length 514 µm, virtually complete, visible dorsally and ventrally, showing details of body setae, segmentation, and ommatidia (at least four ommatidia visible). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.15

× 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles. Syninclusions include two springtails of the same morphotype now in MCNA 10071, and a symphypleonan springtail (genus and species indeterminate) (Sánchez-García and Engel, 2016) now in MCNA 10016.

Additional material: MCNA 8969.1–2 (among which one was labeled as MCNA 8969a in Simón-Benito et al., 2002): Two specimens, one visible dorsally and ventrally, the other visible ventrally and laterally, total lengths 361 and 530μm, respectively; highly distorted but showing details of furcula and legs. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.20 × 0.20 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.05 × 1.30 × 0.10 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include one springtail of the same morphotype now in MCNA 9148.

MCNA 9148: Total length 563 μm, visible dorsally and ventrally, cleared but showing details of furcula (tubercles, setae, and small mucro). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.20 × 0.05 cm (in a microscopic slide preparation). Syninclusions as for MCNA 8969.

MCNA 9162: Total length 739 μm, visible dorsally and ventrally, highly distorted, cleared but showing details of furcula (tubercles and setae). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.40 × 0.15 × 0.05 cm (in a microscopic slide preparation), and included with fungal hyphae, and many arthropod and plant remains.

MCNA 9464.1–2: Two specimens (total length of one specimen 418 μm, visible dorsally and ventrally, showing details of antennae and body setae; the other cleared and not measurable for its length, but showing details of legs and furcula, visible laterally); preserved together with disarticulated remains of a third springtail (disembodied head, antennae, and furcula), fungal hyphae, and many arthropod (e.g., scales) and plant remains (e.g., stellate hairs) in a clear-yellow, turbid piece of amber trimmed to 0.55 × 0.20 × 0.05 cm (in a microscopic slide preparation). Further syninclusions include one springtail of the same morphotype now in MCNA 10061 and one fly (Diptera) now in MCNA 10062.

MCNA 9612.1–7 (among which one was labeled as MCNA 9612a in Simón-Benito et al., 2002): Seven specimens of which six are virtually complete (total lengths of each: 265, 298, 331, 348, 391, and 484 μm), and one nearly complete; some specimens are cleared. Preserved together with disarticulared remains of further springtails of the same morphotype (a cleared body and two disembodied heads), plus one disarticulated leg of a possible symphypleonan springtail. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.55 × 0.55 × 0.05 cm (set into an epoxy trapezoid of dimensions 1.05 × 1.10 × 0.10 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include a paratype of the bethylid wasp *Cretepyris martini* Ortega-Blanco and Engel (2013) (Hymenoptera: Chrysidoidea), now segregated as piece MCNA 9613.

MCNA 10061: Total length 477 μm, visible dorsally and ventrally, highly distorted. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.30 × 0.15 × 0.05 cm (in a microscopic slide preparation), and included with fungal hyphae, and many arthropod and plant remains. Syninclusions as for MCNA 9464.

MCNA 10040.28, 30–35, 37–49: Up to 20 specimens (total length ranging from 246–530 μm), virtually complete. Preserved in a thick, dark-orange, turbid piece of amber trimmed to 1.80 × 0.85 × 0.20 cm (set into an epoxy trapezoid of dimensions 1.80 × 0.85 × 0.45 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include 20 flies (Diptera), one wasp (Hymenoptera), two mites (Acari), one partial roach (Blattaria), and two jumping bristletails (Archaeognatha).

MCNA 10071.1–2: Two specimens (total length of one specimen 408 μm, visible dorsally and ventrally; the other not measurable in length), showing details of body setae. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.15 × 0.15 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles. Syninclusions as for MCNA 10070.

MCNA 10744.2: Total length 418 μm, visible dorsally and ventrally. Preserved in a dark-orange, turbid piece of amber trimmed to 0.90 × 0.60 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.50 × 0.20 cm), and accompanied by much debris, fungal hyphae, and plant remains (e.g., stellate hairs). Further syninclusions include the paratype of the scelionid wasp *Amissascelio temporarius* Ortega-Blanco et al. (2014) (Hymenoptera: Platygastroidea: Scelionidae).

MCNA 11231.2–46: Up to 45 specimens (total length ranging from 186–597 μm, likely representing varied instars) among which 42 are virtually complete, and three are nearly complete; preserved together with disarticulated remains of several further springtails of the same morphotype (at least three disembodied heads, one furcula, and two partially preserved abdomens), a symphypleonan springtail (genus and species indeterminate) (Sánchez-García and Engel, 2016), and much debris, fungal hyphae and plant remains (e.g., pollen) in a thick, dark-orange, turbid piece of amber trimmed to 1.20 × 0.90 × 0.30 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.40 × 0.30 cm).

MCNA 12609: Total length 371 μm, visible dorsally and ventrally, highly distorted. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.10 × 0.10 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles.

MCNA 12674.1: Total length 491 μm, visible in profile. Preserved in a dark-orange, turbid piece of amber trimmed to 0.90 × 0.70 × 0.15 cm (set into an epoxy trapezoid of dimensions 2.05 × 1.35 × 0.25 cm), and included with fungal hyphae, many arthropod and plant remains (e.g., stellate hairs), and one disarticulated roach (Blattaria). Further syninclusions include one fly (Diptera) now in MCNA 12675.

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

Etymology: The specific epithet is taken from the Latin *communis*, meaning "common" or "universal," and refers to the abundance of this species in Spanish amber.

Remarks: The historical concept of the genus *Proisotoma*, as conceived by Gisin (1960), Fjellberg (1980), and others, has recently undergone significant revision, with many species reallocated to other genera (Potapov, 2001; Potapov et al., 2006, 2009). The group has been subdivided at times into different subgenera, which are often raised to generic status (Christiansen and Nascimbene, 2006; Potapov et al., 2006). Following Potapov (2001), the genus *Proisotoma* has generally been defined as containing all species of Isotomidae with: **1,** a normal

or slender habitus, ranging from rather small to large; **2,** a sometimes weakly reticulate or wrinkled integument lacking secondary granulation; **3,** ommatidia present; **4,** antennae bearing a postantennal organ, but lacking an apical bulb; **5,** empodia present; **6,** clavate tibiotarsal setae present or absent; **7,**, abdominal segments IV, V, and VI separate, and lacking anal spines; **8,** a fully developed furcula, with the mucro separated from the dens; **9,** a manubrium with a few setae on the anterior surface; **10,** a usually stout dens, sometimes rather slender, crenulate, and continuously narrowed; **11,** a mucro bi- or tridentate, without seta, and sometimes with lamellae; **12,** setae usually short, macrosetae differentiated at least on the apicalmost abdominal segments; and, **13,** ventromedial setae of the thorax present or absent.

The genus *Proisotoma* makes up 96% approximately of all the entomobryomorphans, and 87% of the whole collembolan record in Spanish amber. It is remarkable that, in spite of the great number of specimens, not a single individual displayed all the characters of the genus and species clearly, likely owing to the darkness and frequent debris in Spanish amber as well as the often dessicated nature of many specimens. Overall, the new species is distinguished by the morphology of the antennae and dens (the latter with characteristic chaetotaxy and tubercles), the small and bidentate mucro, simple ungues and unguiculi, and the relative proportions of the third and fourth abdominal segments (fig. 6). The number of ommatidia cannot be established exactly although at least four have been observed in some specimens. Intraspecific variability in these characters is low, and that variation observed mainly concerns the relative size of specimens.

Simón-Benito et al. (2002) described some of the specimens of *P. communis,* n. sp., as belonging to five genera in three families (see table 1): *Onychiurus* Gervais (Poduromorpha: Onychiuridae), *Micranurida* Börner (Poduromorpha: Neanuridae), and *Anurophorus*, *Cryptopygus* Willem, and *Proisotoma* (Entomobryomorpha: Isotomidae). However, after repreparing all the amber samples and examining further specimens of *P. communis* (not examined by Simón-Benito et al., 2002), it was revealed that they correspond to the same morphotype. Moreover, after suitable preparation it is clear that some structures of this species were not observed or were misinterpreted by Simón-Benito et al. (2002), accounting for their broad misidentifications. Their assignment of some specimens to the Poduromorpha (D'Haese, 2003b) (genera *Onychiurus* and *Micranurida*) clearly was unsupported based on numerous traits, most notably: **1,** the greatly reduced prothorax that never bears setae (instead of well developed and bearing dorsal setae in the Poduromorpha); and, **2,** the fourth abdominal segment generally longer than the third segment (instead of subequal in size in the Poduromorpha). Specimen MCNA 9162, classified as "*Onychiurus* sp." by Simón-Benito et al. (2002), was briefly described as lacking a furcula when in fact a well-developed furcula showing details of setae and tubercles is actually present. In other cases, such as the three specimens classified as "*Anurophorus* sp." by Simón-Benito et al. (2002) (one specimen in MCNA 10070, and two specimens in 10071), the inability to discern a furcula is due to the position of the specimens as fossilized rather than a real absence. While the lateral profile, observable in some specimens, appears to be ideal for seeing the furcula, even when it is appressed to the body, the structure is often not visible in some of the dorsoventrally exposed individuals. Apart from the absence of the furcula, the extant genus *Anurophorus* is diagnosed by the presence of an apical bulb on antennomere IV (Potapov, 2001), which is absent in *P. communis*. The free abdominal segments

TABLE 1. List of available Early Cretaceous Spanish amber pieces with springtails of the order Entomobryomorpha, including previous identifications by Simón-Benito et al. (2002).

Piece No.	No. of specimens (total = 93)	Previous identification (Simón-Benito et al., 2002)	Identification herein (all species are new)
MCNA 12583	1	not examined	*Burmisotoma spinulifera*
MCNA 12787	1	not examined	*Protoisotoma autrigoniensis*?
MCNA 12788	1	not examined	*Protoisotoma autrigoniensis*
MCNA 8969	2	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9148	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 9162	1	*Onychiurus*? sp.	*Proisotoma communis*
MCNA 9273	3	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9324	1	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9464	2	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 9612	7	5 *Cryptopygus*? 2 *Micranurida*? sp.	*Proisotoma communis*
MCNA 10040	20	not examined	*Proisotoma communis*
MCNA 10061	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 10070	1	*Anurophorus*? sp.	*Proisotoma communis*
MCNA 10071	2	*Anurophorus*? sp.	*Proisotoma communis*
MCNA 10744	1	not examined	*Proisotoma communis*
MCNA 11231	45	not examined	*Proisotoma communis*
MCNA 12609	1	not examined	*Proisotoma communis*
MCNA 12674	1	not examined	*Proisotoma communis*
MCNA 9560	1	not examined	Entomobryomorpha form 1

V and VI (rather than fused) prevent attribution of the two specimens in MCNA 8969, three specimens in MCNA 9273, one specimen in MCNA 9324, and five specimens in MCNA 9612 to *Cryptopygus*. Remarkably, the separation of *Cryptopygus* and *Proisotoma* is far from clear, and *Cryptopygus* are mainly differentiated from the latter only by the fusion of abdominal segments V and VI (Linnaniemi, 1912; Gisin, 1944; Palissa, 1964), and the genus as a whole is assuredly composed of various unrelated lineages (e.g., Rusek, 2002; Stevens et al., 2006a). Some authors rely on putative differences in the morphology of the dens, with those of *Cryptopygus* long and slender, rather than the shorter and stouter form found in *Proisotoma* (Stach, 1947; Gisin, 1960; Fjellberg, 1980).

Proisotoma communis is the only known species of Cretaceous Spanish Collembola ascribable to an extant genus. Interestingly, the genus is also known in Burmese and Canadian ambers (Christiansen and Pike, 2002a; Christiansen and Nascimbene, 2006), and as noted by those authors, it is possible that if finer details of the sensory structures were discernible, then the Cretaceous representatives might better be classified in a separate genus. However, in the absence of such data we have adopted the conservative position of considering them congeneric. Despite this, extant genera are not unheard of from Cretaceous ambers. Mesozoic representatives of still-surviving hexapod genera include examples from among the rove and bark beetles (Cognato and Grimaldi, 2008; Chatzimanolis et al., 2013), zorapterans (Engel and

Grimaldi, 2002), biting midges (Borkent, 2001; Szadziewski and Arillo, 2003; Pérez-de la Fuente et al., 2011), among others. Perhaps the most remarkable example is the genus *Alavesia* Waters and Arillo, originally described from fossils in Spanish amber (Waters and Arillo, 1999; Peñalver and Arillo, 2007) and then recorded in Burmese amber (Grimaldi et al., 2002), which was recently discovered alive and well in Namibia, southern Africa (Sinclair and Kirk-Spriggs, 2010). Such bradytely is likely attributable to the conservatism and long-term consistency of their microhabitat preferences.

Genus and Species Indeterminate

Figure 7

Entomobryomorpha form 1 (fig. 7): Specimen MCNA 9560 is preserved in a piece of clear yellow amber trimmed to 0.90 × 0.50 × 0.05 cm (in an epoxy trapezoid of dimensions 2.15 × 1.30 × 0.10 cm), and without syninclusions. The specimen is observable laterally as well as dorsally and ventrally, but not much more than an external profile is visible, preventing suitable comparison. Nonetheless, the morphology of the antennae and legs correspond to a morphotype distinct from those described above. The body length as preserved is 407 μm. The head shape is cylindrical, distinctly narrower than the body, and 79 μm in length as preserved. The well-preserved antennae are slightly longer than the head, with four antennomeres; the first and fourth antennomeres are subequal in length; the second and third antennomeres are subequal in length, together not reaching the length of the first or fourth antennal segments; the fourth antennomere is slightly swollen, with a few slender, short, mostly weakly curved and acuminate setae; the antennomere lengths in μm are approximately: IV, 32; III, 11; II, 10; I, 30. The tibiotarsus and femur are subequal in length, and the trochanter is distinctly longer and inflated; some slender setae, apparently not clavate or truncate, are visible distally on the tibiotarsus, and although the unguis and unguiculus are not clear, they are apparently simple, without teeth, very short, and acuminate. Other features cannot be seen because of the poor state of preservation of this specimen. Hopefully further, more finely preserved, material will be discovered at a later date and permit a full characterization and identification of this form.

DISCUSSION

The main challenge for any study of fossil Collembola, and even more so for entomobryomorphans, is the comparatively low number of specific characters that are observable. The diminutive size of the inclusions, and their frequent dessicated state within the amber, hinders the visualization of even chaetotaxonomic traits unless preparations are exceedingly thin and the amber is relatively clear. Unfortunately, the amber in which many of the springtails are preserved is frequently turbid, darkly colored (possibly as a result of contact with litter), or has ill-positioned bubbles that prevent an optimal view of some structures. Despite these hurdles, diagnostic characters based on the general shape of the body and proportions of segments, morphology of the antennae and furculae, and especially chaetotaxy are possible to discern,

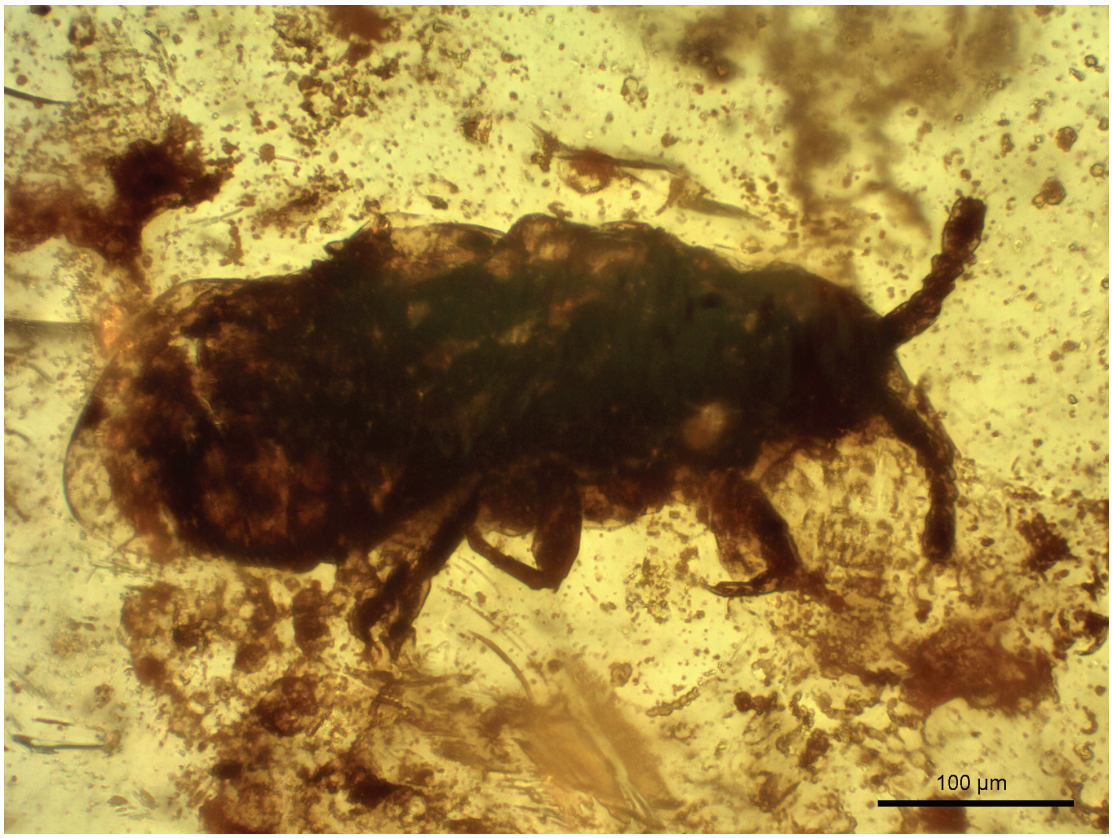

FIGURE 7. Microphotograph in dorsal habitus of specimen MCNA 9560 (Entomobryomorpha form 1) (image combining consecutive photographs taken at successive focal planes).

albeit not universally. In spite of these limitations, nonetheless it is possible to make remarkably robust comparisons between amber entomobryomorphans and, to some extent, between them and their living relatives as well.

Perhaps not surprisingly, there are similarities in the generic composition of the Spanish and Burmese amber faunas of Entomobryomorpha, with all three genera discussed herein present in each deposit (Christiansen and Nascimbene, 2006). Such similarities are not uncommon for these ambers. For example, there are various genera of stigmaphronid and mymarommatoid wasps (Ortega-Blanco et al., 2011a, 2011b) and chimeromyiid and tethepomyiid flies (Grimaldi et al., 2009, 2011) shared between Spanish and Burmese amber, and sometimes also with Lebanese and Canadian amber. Christiansen and Nascimbene (2006) speculated that *Protoisotoma* were widespread during the Cretaceous, and this is borne out by the discovery of a further species in Spanish amber. Although, these authors indicated that *Protoisotoma* were closely related to various austral genera, such a relationship is entirely speculative and in the absence of a phylogenetic analysis of living and fossil Anurophorinae there is little evidence to support their conclusion that the genus was more widespread than its Tertiary and modern counterparts (Christiansen and Nascimbene, 2006). The genus *Protoisotoma* is widespread, but so are other modern genera, and while some do have more restrictive distributions, a cladistic relationship between those clades

and *Protoisotoma* has not been established. *Protoisotoma* are dominant in the Late Cretaceous amber of Canada and the mid-Cretaceous amber of Myanmar (Christiansen and Pike, 2002a; Christiansen and Nascimbene, 2006). However, a different pattern is observed in the Early Cretaceous amber of Spain, where the extant genus *Proisotoma* is the most abundant. Assuming that this paleofaunistic difference is not the result of sampling bias, it perhaps reflects some underlying paleoecological or temporal factor, resulting in the pervasiveness of one genus in Spanish amber and the other in Burmese and Canadian amber. Currently it is unclear what paleoecological parameters might result in the observed difference, but the question is worthy of further inquiry as more becomes known about the three paleoecosystems. Not surprisingly, there are no shared faunal elements at the generic level between the Cretaceous springtail faunas and those of the Cenozoic, which include only extant genera (appendix), although the faunas of Baltic, Dominican, and Mexican ambers are in need of modern revision.

Christiansen and Nascimbene (2006) noted that, while the Entomobryidae of their study appeared arboreal, the attributes of *Protoisotoma*, *Burmisotoma*, and *Proisotoma* as documented in Spanish, Burmese, and Canadian ambers are of neustonic to litter- or soil surface-living ecomorphologies, as supported by the lamellate mucrones, the few to absent clavate setae, and the tuberculate dentes (Christiansen, 1964). Indeed, the available evidence supports the conclusion that these taxa were semiaquatic to epedaphic, or less likely hemiedaphic, and likely came into contact with the resin as it accumulated at the base of trees in a generally moist or even boglike environment. Such an environmental reconstruction is consistent with the pattern observed for the Symphypleona (Sánchez-García and Engel, 2016), as well as with the presence of other litter-dwelling, semiaquatic lineages in similar pieces (e.g., Heteroptera: Sánchez-García et al., 2016; Archaeognatha: Sánchez-García et al., in prep.; Dermaptera: Engel et al., 2015), and the capture of tanaid crustaceans (Sánchez-García et al., 2015) and woodlice (Sánchez-García et al., in prep.). Such a microhabitat sampling is analogous to the fragmentary springtail fauna preserved in the slightly younger amber of France (Perrichot, 2004), and it would be interesting to monograph that fauna and do a comparative analysis as there are many similarities between the Early to mid-Cretaceous ambers of Spain and France in regards to their litter fauna representation.

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APPENDIX

A Checklist of the Fossil Collembola

Appended here is an annotated checklist of documented occurrences of fossil and subfossil Collembola. We have not attempted to trace every passing mention of a springtail or those fossils so poorly preserved as to prevent description or attribution below the level of family (unless the same material was subsequently placed more precisely), but instead we list only those papers with attempts at some degree of identification at the generic level. In addition, we have not repeated entries from general catalogs or inventories (e.g., Keilbach, 1982; Spahr, 1990; Arillo and Ortuño, 2005), unless such secondary references presented unique data not found in a primary source. The arrangement of suprageneric groups is generally based on that of Bretfeld (1999), Deharveng (2004), Soto-Adames et al. (2008), and Janssens and Christiansen (2011). Daggers (†) denote taxa described as extinct, while an asterisk (*) indicates attribution of a particular fossil specimen to an extant species. While those extant species recorded as subfossils in copal are likely conspecific with modern populations, those attributed to specimens in amber, particularly middle Eocene Baltic amber, are almost assuredly not truly representative of the species. Such specimens should be restudied and properly described, and at that time it is almost certain that they will be found to represent extinct species perhaps similar to modern forms. The Baltic amber fauna was significantly confused by Olfers (1907), and the detailed treatments by Handschin (1926a, 1926b, 1926c, 1926d, 1926e) made great strides to clarify the mess. Unfortunately, much of the material upon which this work was made was lost, although small elements do survive. A thorough and modern revision of the Baltic amber Collembola is needed, followed by a new consideration of those in Miocene amber from southern Mexico and the Dominican Republic.

Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Superfamily Isotomoidea Schäffer, 1896
Family Isotomidae Schäffer, 1896
Subfamily Anurophorinae Börner, 1901

†*Burmisotoma lamellifera* Christiansen and Nascimbene

†*Burmisotoma lamellifera* Christiansen and Nascimbene, 2006: 342.

Type species of †*Burmisotoma* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-818-A2, specimen 7 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Burmisotoma spinulifera* Sánchez-García and Engel

†*Burmisotoma spinulifera* Sánchez-García and Engel, herein: 5 (above).

Referred material: Holotype, MCNA 12583 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

Cryptopygus spp.

Cryptopygus sp. Mari Mutt, 1983: 578.

Referred material: Nos. 30 and 32 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotomina sp. Christiansen, 1971: 48.

Referred material: UCMP Nos. 13521 and 13522 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Proisotoma communis*** Sánchez-García and Engel

Micranurida? sp. Simón-Benito et al., 2002: 85.

Onychiurus? sp. Simón-Benito et al., 2002: 85.

Anurophorus? sp. Simón-Benito et al., 2002: 85.

Proisotoma (*Ballistura*)? sp. Simón-Benito et al., 2002: 85.

Cryptopygus? sp. Simón-Benito et al., 2002: 87.

†*Proisotoma communis* Sánchez-García and Engel, herein: 10 (above).

Referred material: Holotype, MCNA 9273.1 (visible in profile); paratypes, MCNA 9273.2–3 (two specimens visible dorsally and ventrally), MCNA 9324, MCNA 10070; additional material, MCNA 8969.1–2 (two specimens), MCNA 9148, MCNA 9162, MCNA 9464.1–2 (two specimens), MCNA 9612.1–7 (seven specimens), MCNA 10061, MCNA 10040.28, 30–35, 37–49 (20 specimens), 10071.1–2 (two specimens), MCNA 10744.2, MCNA 11231.2–46 (45 specimens), MCNA 12609, and MCNA 12674.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†***Proisotoma pettersonae*** Christiansen and Nascimbene

†*Proisotoma pettersonae* Christiansen and Nascimbene, 2006: 340.

Referred material: Holotype: AMNH Bu-818-A1, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Protoisotoma autrigoniensis*** Sánchez-García and Engel

†*Protoisotoma autrigoniensis* Sánchez-García and Engel, herein: 8 (above).

Referred material: Holotype, MCNA 12788.2; additional material, MCNA 12787.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†***Protoisotoma burma*** Christiansen and Nascimbene

†*Protoisotoma burma* Christiansen and Nascimbene, 2006: 343.

Referred material: Holotype, AMNH Bu-1074-A1, specimen 1; paratypes, AMNH Bu 1074-A1, specimens 3 and 4; Bu-1074-A2, specimens 2 and 3; Bu-1074-A3 specimens 1 and 2 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Protoisotoma micromucra* Christiansen and Pike

†*Protoisotoma micromucra* Christiansen and Pike, 2002a: 171.

New genus A, family Isotomidae Christiansen and Pike, 2002b: 269.

Type species of †*Protoisotoma* Christiansen and Pike, 2002a.

Referred material: Holotype, TMP 91.148.482, slide 2, specimen 13; paratypes TMP 91.148.482, slide 1, specimens 1, 2, 5, and 6; TMP 82.15.53, slide 1, specimens 2 and 3; TMP 91.148.714 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†*Protoisotoma* spp.

†*Protoisotoma* form 2 Christiansen and Pike, 2002a: 174.

Referred material: TMP 91.148.482, slide 1, specimens 4 and 9; TMP 91.148.482, slide 2, specimens 11, 15, and 16; TMP 91.148.769, specimens 2 and 4; TMP 90.147.31; TMP 91.148.764, specimens 2 and 3; TMP 91.148.481, specimen 2 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†*Protoisotoma* form 3 Christiansen and Pike, 2002a: 174.

Referred material: TMP 91.148.685; TMP 91.148.761; TMP 89.15, specimen 1 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Tetracanthella sp.

Tetracanthella sp. Lawrence, 1985: 102.

Referred material: Two specimens in piece no. 18007 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Villusisotoma brevis* Christiansen and Nascimbene

†*Villusisotoma brevis* Christiansen and Nascimbene, 2006: 335.

Type species of †*Villusisotoma* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-818-A2, specimen 6; paratype, AMNH Bu-818-A2, specimen 10 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Villusisotoma longa* Christiansen and Nascimbene

†*Villusisotoma longa* Christiansen and Nascimbene, 2006: 336.

Referred material: Holotype, AMNH Bu-8181-A2, specimen 8; paratype, AMNH Bu-8181-A2, specimen 11 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Subfamily Isotominae Schäffer, 1896

†*Isotoma crassicornis* Handschin

†*Isotoma crassicornis* Handschin, 1926b: 214.
Degeeria juvenile Olfers, 1907: 20, *ad partem*.
Lepidocyrtus juvenile Olfers, 1907: 22, *ad partem*.
†*Isotoma crassicornis* Handschin; Stach, 1972: 418.
†*Isotoma crassicornis* Handschin; Larsson, 1978: 104.

Referred material: Syntypes, K537, K551, K8068, K8070 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Isotoma spp.

Isotoma sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Isotoma sp. Lawrence, 1985: 102.

Referred material: Nos. 18009, 18012, 18013, 18014 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Isotoma sp. Yosii, 1974: 410.

Referred material: No. 104-f (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Desoria spp.

Isotoma (*Desoria*) sp. 1 Mari Mutt, 1983: 578.

Referred material: Nos. 31 and 33 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotoma (*Desoria*) sp. 2 Mari Mutt, 1983: 578.

Referred material: 18 specimens in piece no. 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotoma (*Desoria*) sp. Yosii, 1974: 409.

Referred material: Nos. 1, 110-b, 144-a (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

†*Vertagopus protocinereus* (Handschin)

†*Isotoma* (*Vertagopus*) *protocinerea* Handschin, 1926b: 213.
†*Isotoma* (*Vertagopus*) *protocinerea* Handschin; Stach, 1972: 418.
†*Isotoma protocinerea* Handschin; Larsson, 1978: 104.

Referred material: Syntypes, K8045, F411, and F417 (ex amber: Klebs and Fritsch Collections, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

******Isotomurus retardatus* Folsom

**Isotomurus retardatus* Folsom; Christiansen, 1971: 48.

Referred material: UCMP no. 13054 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Protodesoria granda*** Christiansen and Nascimbene

†*Protodesoria granda* Christiansen and Nascimbene, 2006: 346.

Type species of †*Protodesoria* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-1452C, specimen 9; paratype, AMNH Bu-1452C, specimen 11 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Subfamily Pachyotominae Potapov, 2001

†***Propachyotoma conica*** Christiansen and Nascimbene

†*Propachyotoma conica* Christiansen and Nascimbene, 2006: 344.

Type species of †*Propachyotoma* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-818-A2, specimen 12; paratype, AMNH Bu-818-A1, specimen 4 (ex amber: American Museum of Natural History; New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Isotomidae

Subfamily Incertae sedis

†***Rhyniella praecursor*** Hirst and Maulik

†*Rhyniella praecursor* Hirst and Maulik, 1926: 71.
†*Rhyniella praecursor* Hirst and Maulik; Tillyard, 1928: 65.
†*Rhyniella praecursor* Hirst and Maulik; Scourfield, 1940a: 799.
†*Rhyniella praecursor* Hirst and Maulik; Scourfield, 1940b: 115.
†*Rhyniella praecursor* Hirst and Maulik; Paclt, 1956: 1.
†*Rhyniella praecursor* Hirst and Maulik; Salmon, 1964: 644.
†*Rhyniella praecursor* Hirst and Maulik; Massoud, 1967a: 497.
†*Rhyniella praecursor* Hirst and Maulik; Delamare-Deboutteville and Massoud, 1967: 625.
†*Rhyniella praecursor* Hirst and Maulik; Crowson, 1970: 65.
†*Rhyniella praecursor* Hirst and Maulik; Whalley and Jarzembowski, 1981: 317.
†*Rhyniella praecursor* Hirst and Maulik; Greenslade and Whalley, 1986: 319.
†*Rhyniella praecursor* Hirst and Maulik; Crowson, 1985: 97.

†*Rhyniella praecursor* Hirst and Maulik; Greenslade, 1988: 115.
†*Rhyniella praecursor* Hirst and Maulik; Grimaldi and Engel, 2005: 116.

Type species of †*Rhyniella* Hirst and Maulik, 1926 (type genus of †Rhyniellidae Paclt, 1956).
Referred material: Type series and additional material (ex chert: Natural History Museum, London).
Deposit: Rhynie chert, Rhynie, Aberdeenshire, Scotland; Early Devonian (Pragian).

Family †Protentomobryidae Folsom, 1937b

†*Protentomobrya walkeri* Folsom

†*Protentomobrya walkeri* Folsom, 1937b: 17.
†*Protentomobrya walkeri* Folsom; Delamare-Deboutteville and Massoud, 1968: 623.
†*Protentomobrya walkeri* Folsom; Greenslade and Whalley, 1986: 321.
†*Protentomobrya walkeri* Folsom; Christiansen and Pike, 2002a: 167.
†*Protentomobrya walkeri* Folsom; Christiansen and Pike, 2002b: 268.

Type species of †*Protentomobrya* Folsom, 1937b (type genus of †Protentomobryidae Folsom, 1937b).
Referred material: No number (ex amber: Royal Ontario Museum, Toronto, Canada).
Deposit: Cedar Lake, Manitoba, Canada (the amber from Cedar Lake in western Manitoba is a secondary deposit of the amber from Grassy Lake: McKellar et al., 2008); Late Cretaceous (Campanian).
Note: Protentomobryidae is assuredly a synonym of Isotomidae (Greenslade and Whalley, 1986).

Superfamily Entomobryoidea Schäffer, 1896

Family †Praentomobryidae Christiansen and Nascimbene, 2006

†*Cretacentomobrya burma* Christiansen and Nascimbene

†*Cretacentomobrya burma* Christiansen and Nascimbene, 2006: 357.

Type species of †*Cretacentomobrya* Christiansen and Nascimbene, 2006.
Referred material: Holotype, AMNH Bu-1452B, specimen 9; paratype, AMNH Bu-1452C, specimen 10 (ex amber: American Museum of Natural History, New York).
Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Praentomobrya avita* Christiansen and Nascimbene

†*Praentomobrya avita* Christiansen and Nascimbene, 2006: 356.

Type species of †*Praentomobrya* Christiansen and Nascimbene, 2006 (type genus of †Praentomobryidae Christiansen and Nascimbene, 2006).
Referred material: Holotype, AMNH Bu-818-A2, specimen 5 (ex amber: American Museum of Natural History, New York).
Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Family Cyphoderidae Börner, 1913

Cyphoderus spp.

Cyphoderus sp. 1 Mari Mutt, 1983: 581.

Referred material: 14 specimens in piece 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Cyphoderus sp. 2 Mari Mutt, 1983: 581.

Referred material: Two specimens in piece 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Family Entomobryidae Schäffer, 1896

Subfamily Entomobryinae Schäffer, 1896

Drepanura sp.

Drepanura sp. Christiansen, 1971: 47.

Referred material: No. 13513 (ex amber: University of California Museum of Paleontology; Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

****Entomobrya decora*** (Nicolet)

**Entomobrya decora*? (Nicolet); Christiansen, 1971: 46.

Referred material: Nos. 13502, 13503 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Entomobrya kirkbyae*** Pierce

†*Entomobrya* (*Entomobrya*) *kirkbyae* Pierce, 1960: 40.

Referred material: Holotype, no. 5-303 (ex calcareous nodule: Ruth Kirkby Collection, Riverside, California).

Deposit: Calcareous nodule, Switchback Canyon, Calico Mountains, San Bernardino County, California; Miocene.

****Entomobrya litigiosa*** Denis

**Entomobrya litigiosa*? Denis; Christiansen, 1971: 46.

Referred material: Nos. 13506, 13507 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Entomobrya pilosa*** (Koch and Berendt)

†*Podura pilosa* Koch and Berendt, 1854: 120.

†*Machilis acuminata* (Koch and Berendt); Olfers, 1907: 14, *ad partem*.

†*Lepismodion machilops* Olfers, 1907: 16, *ad partem*.
Type species of †*Lepismodion* Olfers, 1907.
†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.
Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).
†*Palpigerina sminthuroides* Olfers, 1907: 19, *ad partem*.
†*Palpigerina elongata* Olfers, 1907: 19, *ad partem*.
Included species of †*Palpigerina* Olfers, 1907
†*Palpigeridia longicollis* Olfers, 1907: 19, *ad partem*.
†*Palpigeridia crassula* Olfers, 1907: 19, *ad partem*.
Included species of †*Palpigeridia* Olfers, 1907.
Degeeriadae [sic] sp. Olfers, 1907: 19.
Degeeria juvenile Olfers, 1907: 20, *ad partem*.
†*Degeeria robusta* Olfers, 1907: 20, *ad partem*.
†*Degeeria jubata* Olfers, 1907: 20, *ad partem*.
†*Degeeria signata* Olfers, 1907: 20, *ad partem*.
†*Degeeria gracilis* Olfers, 1907: 20, *ad partem*.
†*Degeeria obesa* Olfers, 1907: 20, *ad partem*.
†*Stylonotus lanuginosus* Olfers, 1907: 21, *ad partem*.
Type species of †*Stylonotus* Olfers, 1907.
†*Omophora tricuspidata* Olfers, 1907: 21, *ad partem*.
Type species of †*Omophora* Olfers, 1907.
†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.
**Orchesella villosa* (Geoffroy); Olfers, 1907: 21, *ad partem*.
†*Seira pachysceles* Olfers, 1907: 21, *ad partem*.
**Templetonia nitida* (Templeton); Olfers, 1907: 22, *ad partem*.
Lepidocyrtus juvenile Olfers, 1907: 22, *ad partem*.
**Lepidocyrtus curvicollis* Bourlet; Olfers, 1907: 22, *ad partem*.
**Lepidocyrtus aeneus* Nicolet; Olfers, 1907: 22, *ad partem*.
**Lepidocyrtus gibbulus* Nicolet; Olfers, 1907: 22, *ad partem*.
**Cremastocephalus trilobatus* Schött; Olfers, 1907: 23, *ad partem*.
**Tomocerus plumbeus* (Linnaeus); Olfers, 1907: 23, *ad partem*.
†*Catastylus calcaratus* Olfers, 1907: 23, *ad partem*.
†*Catastylus crassus* Olfers, 1907: 24, *ad partem*.
†*Catastylus crassicaudatus* Olfers, 1907: 24, *ad partem*.
†*Catastylus nasicornis* Olfers, 1907: 24, *ad partem*.
Included species of †*Catastylus* Olfers, 1907 (type genus of †Catastylidae Olfers, 1907).
†*Cuculliger longistylus* Olfers, 1907: 24.
Type species of †*Cuculliger* Olfers, 1907.
Podura juvenile Olfers, 1907: 25, *ad partem*.
†*Sminthurus* juvenile Olfers, 1907: 40, *ad partem*.
†*Entomobrya pilosa* (Koch and Berendt); Handschin, 1926b: p. 217.
†*Podura pilosa* Koch and Berendt; Stach, 1972: 418.

†*Entomobrya pilosa* (Koch and Berendt); Larsson, 1978: 104.

Referred material: K172, K173, K175, K176, K182, K523, K524, K527, K533, K538, K540, K542, K556, K558, K574, K595, K699, K702, K704, K706, K954–K957, K971, K974, K976, K978, K979, K981, K982, K985–K988, K991–K996, K999, K1000, K1004, K1010, K1014, K1015, K1018, K1019, K1787–K1790, K1792–K1795, K1810–K1813, K1816, K1818, K2690–K2692, K2694, K2710, K3729, K3731, K3737, K3792, K7946–K7954, K7990, K7992, K7994, K8016–K8019, K8027–K8029, K8031, K8039, K8042–K8044, K8046–K8048, K8051, K8052, K8059, K8062, K8063, K8065, K8066, K8113, K8114, α1, α6, α9, α10, α15, α16, α17, α18, α35, α36, χ3, χ10, F239, F242, F355, F369, F385, F388, F394, F397, F410, F418, and B2202, B2208, B2214, B2217, B2246, B2370, B2378, B2380, B2382, B2475, B2488, B2531, B2555, B2623, B2626, B2695, B2734, B2787, B2806, B2841, B2864, B2888, B3016, B3027, B3061, B3176, B3257, B3262, B3412, B3429, B3455, B3506, B3513, B3518, B3575, B3595, B3607, B3723, B3862, B3879, B3931, B4012, B4058, B4068, B4080, B4101, B4113, B4117, B4153, B4208, B4212, B4249, B4262, B5212, B5213, B5252, B5299, B5303, B5307, B5319, B5320, B5323, B5325, B5329, B5330, B5339, B5345, B5358, B5359, B5366, B5373, B5375, B5379, B5410, B5417, B5421, B5448, B5450, B5462, B6059, B6078, B6083, B6140, B6217, B6231, B6242, B6244, B6264, B6274, B6278, B6561, B6587, B6734, B6735, B6738 (ex amber: Berendt Collection, Danzig, Germany; Klebs and Fritsch Collections, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

**Entomobrya trifasciata* Handschin

**Entomobrya trifasciata*? Handschin; Christiansen, 1971: 46.

Referred material: Nos. 13504, 13505 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Entomobrya spp.

Entomobrya sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Entomobrya sp. Lawrence, 1985: 103.

Referred material: Nos. 18015, 18017–18019, 18021–18026, 18028–18031, 18033, 18035–18044, 18046–18055 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Entomobrya sp. Christiansen, 1971: 46.

Referred material: Nos. 13046, 13546, 13547, 13548, 13549, 13550, 13551, 13552, 13553, 13508, 13509, 13510, 13511, 13512 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Entomobrya sp. Yosii, 1974: 410.

Referred material: No. 104-b (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

***Homidia* sp.**

Homidia sp. Yosii, 1974: 410.

Referred material: Nos. 60, 133B-n (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Subfamily Lepidocyrtinae Wahlgren, 1906

†*Lepidocyrtus ambricus* Handschin

†*Lepidocyrtus ambricus* Handschin, 1926b: 220.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

Degeeria sp. Olfers, 1907: 20, *ad partem*.

**Lepidocyrtus curvicollis* Bourlet; Olfers, 1907: 22, *ad partem*.

Tomocerus juvenile Olfers, 1907: 23, *ad partem*.

†*Lepidocyrtus ambricus* Handschin; Stach, 1972: 418.

†*Lepidocyrtus ambricus* Handschin; Larsson, 1978: 104.

Referred material: K983, K1791, K7955, K5807 (juvenile), B3872, B5262, B5437, B6144 (ex amber: Berendt Collection, Danzig, Germany; Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus* cf *geayi Denis

**Lepidocyrtus* cf *geayi* Denis; Christiansen, 1971: 47.

Referred material: No. 13516 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

***Lepidocyrtus* spp.**

Lepidocyrtus sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus sp. Lawrence, 1985: 103.

Referred material: Three specimens in pieces nos. 18034, 18045 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus sp. Christiansen, 1971: 47.

Referred material: Nos. 13515, 13554 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Lepidocyrtus sp. Mari Mutt, 1983: 579.

Referred material: 20 specimens in pieces nos. 17–21 and 37–42 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Lepidocyrtus sp. Yosii, 1974: 410.

Referred material: Nos. 133A-a, 133A-b, 134D-e (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Pseudosinella sp.

Pseudosinella sp. Mari Mutt, 1983: 581.

Referred material: No. 16 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Subfamily Orchesellinae Börner, 1906

Orchesella spp.

Orchesella sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Orchesella sp. Lawrence, 1985: 102.

Referred material: Nos. 18027, 18032 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Orchesella eocaena* Handschin

†*Orchesella eocaena* Handschin, 1926b: 221.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

Degeeriadae [sic] sp. Olfers, 1907: 19.

†*Degeeria jubata* Olfers, 1907: 20, *ad partem*.

†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.

**Orchesella villosa* (Geoffroy); Olfers, 1907: 21, *ad partem*.

**Templetonia nitida* (Templeton); Olfers, 1907: 22, *ad partem*.

**Tomocerus plumbeus* (Linnaeus); Olfers, 1907: 23, *ad partem*.

**Cremastocephalus trilobatus* Schött; Olfers, 1907: 23, *ad partem*.

†*Podura fuscata*? Koch and Berendt; Handschin, 1926b: 221.

†*Orchesella eocaena* Handschin; Stach, 1972: 418.

†*Orchesella eocaena* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K526, K528, K546, K550, K973, K980, K982, K984, K989, K990, K1012, K2713, K7991, K8020, α4, α31, B3090, and B3267 (ex amber: Berendt Collection, Danzig, Germany; Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Subfamily Seirinae Yosii, 1961

Seira frater (Bonet)

**Lepidocyrtinus frater*? Bonet; Christiansen, 1971: 47.

Referred material: Nos. 12635, 13514, 13555, 13556 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Seira sp.

Seira sp. Mari Mutt, 1983: 581.

Referred material: 19 specimens in pieces nos. 1–15, 27–29 and 36 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Entomobryidae Subfamily Incertae sedis

†*Permobrya mirabilis* Riek

†*Permobrya mirabilis* Riek, 1976: 141.

Referred material: Holotype, HI 248 a, b (ex shale compression: Geological Survey, Pretoria, South Africa).

Type locality: Carbonaceous shales, Hammanskraal, near Pretoria, South Africa; Early Permian.

Family Paronellidae Börner, 1913

Paronella spp.

Paronella? sp. Christiansen, 1971: 47.

Referred material: Nos. 13519, 13520 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Paronella sp. Mari Mutt, 1983: 581.

Referred material: Nos. 25, 26, and 44 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

**Salina tristani* Denis

**Salina tristani*? Denis; Christiansen, 1971: 47.

Referred material: Nos. 13517 and 13518 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

***Salina* sp.**

Salina sp. Mari Mutt, 1983: 581.

Referred material: Seven specimens in pieces nos. 22–24 and 41–43 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Family †Oncobryidae Christiansen and Pike, 2002a

†*Oncobrya decepta* Christiansen and Pike

†*Oncobrya decepta* Christiansen and Pike, 2002a: 168.

New family A, new genus F Christiansen and Pike, 200b: 271.

Type species of †*Oncobrya* Christiansen and Pike, 2002a (type genus of †Oncobryidae Christiansen and Pike, 2002a).

Referred material: Holotype, CAS 1094 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Note: The validity of the family Oncobryidae should be reexamined as it likely renders Paronellidae or Oncopoduridae paraphyletic.

Superfamily Tomoceroidea Schäffer, 1896

Family Tomoceridae Schäffer, 1896

†*Entomocerus mirus* Christiansen and Pike

†*Entomocerus mirus* Christiansen and Pike, 2002a: 170.

New genus C, family Tomoceridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Entomocerus* Christiansen and Pike, 2002a.

Referred material: Holotype, CAS 4A (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Cedar Lake, Manitoba, Canada (the amber from Cedar Lake in western Manitoba is a secondary deposit of the amber from Grassy Lake: McKellar et al., 2008); Late Cretaceous (Campanian).

****Tomocerus* cf *minor*** (Lubbock)

Tomocerus cf *minor* (Lubbock); Lawrence, 1985: 102.

Referred material: Nos. 18007, 18011, 18016, 18020 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Tomocerus taeniatus* (Koch and Berendt)

†*Podura taeniata* Koch and Berendt, 1854: 119.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

**Lepidocyrtus curvicollis* Bourlet; Olfers, 1907: 22, *ad partem*.

**Lepidocyrtus gibbulus* Nicolet; Olfers, 1907: 22, *ad partem*.

**Tomocerus plumbeus* (Linnaeus); Olfers, 1907: 23, *ad partem*.

†*Catastylus calcaratus* Olfers, 1907: 23, *ad partem*.

†*Catastylus nasicornis* Olfers, 1907: 24, *ad partem*.

Included species of †*Catastylus* Olfers, 1907 (type genus of †Catastylidae Olfers, 1907).

†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.

†*Tomocerus taeniatus* (Koch and Berendt); Handschin, 1926b: 215.

†*Podura taeniata* Koch and Berendt; Stach, 1972: 418.

†*Tomocerus taeniatus* (Koch and Berendt); Larsson, 1978: 104.

Referred material: K535, K557, K560, K575, K594, K709, K953, K1001, K1002, K1003, K1011, K1013, K1798, K1799, K1800, K1801, K1802, K 2697, K2945, K8021, K8022, K8023, K8049, B3209, B3227, B3895, B5073, B5506, F389, F391, and F413 (ex amber: Berendt Collection, Danzig, Germany; Klebs and Fritsch Collections, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Tomocerus* cf. *taeniatus* (Koch and Berendt); Hädicke et al., 2013: 152.

Referred material: PE 61069 (ex amber: Field Museum of Natural History, Chicago).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Tomocerus spp.

Tomocerus sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Tomocerus sp. Yosii, 1974: 410.

Referred material: No. 117 (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Order Poduromorpha Börner, 1913
Superfamily Neanuroidea Börner, 1901
Family Neanuridae Börner, 1901
Subfamily Neanurinae Börner, 1901

Lobella sp.

Lobella sp. Yosii, 1974: 409.

Referred material: Two specimens in piece no. 144-c (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

†*Pseudoxenylla fovealis* Christiansen and Pike

†*Pseudoxenylla fovealis* Christiansen and Pike, 2002a: 176.

New genus C, family Neanuridae Christiansen and Pike, 2002b: 272.

Type species of †*Pseudoxenylla* Christiansen and Pike, 2002a.

Referred material: Holotype: TMP 91.148.296; I–1.19.26 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).
Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Subfamily Pseudachorutinae Börner, 1906

***Pseudachorutes* spp.**
Pseudachorutes sp. Lawrence, 1985: 102.
Referred material: Two specimens in piece no. 18006 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).
Pseudachorutes sp. Yosii, 1974: 409.
Referred material: One specimen in no. 110-c (ex copal: Mizunami Fossil Museum; Japan).
Deposit: Mizunami, Japan; Pleistocene.

Family Odontellidae Massoud, 1967b

†***Protodontella minicornis*** Christiansen and Nascimbene
†*Protodontella minicornis* Christiansen and Nascimbene, 2006: 350.
Type species of †*Protodontella* Christiansen and Nascimbene, 2006.
Referred material: Holotype, AMNH Bu-723C, specimen 2; paratypes, AMNH Bu-723A, specimens 12, 15, and 20 (ex amber: American Museum of Natural History, New York).
Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Family Brachystomellidae Stach, 1949

†***Bellingeria cornua*** Christiansen and Pike
†*Bellingeria cornua* Christiansen and Pike, 2002a: 178.
New genus B, family Brachystomellidae Christiansen and Pike, 2002b: 271.
Type species of †*Bellingeria* Christiansen and Pike, 2002a.
Referred material: Holotype, CAS 724 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).
Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Superfamily Hypogastruroidea Börner, 1906

Family Hypogastruridae Börner, 1906

†***Hypogastrura intermedia*** Handschin
†*Hypogastrura intermedia* Handschin, 1926b: 212.

†*Hypogastrura intermedia* Handschin; Stach, 1972: 418.
†*Hypogastrura intermedia* Handschin; Larsson, 1978: 104.
Referred material: Holotype, K982 (ex amber: Klebs Collection, Königsberg, Russia).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Hypogastrura protoviatica* Handschin

†*Hypogastrura protoviatica* Handschin, 1926b: 211.
†*Hypogastrura protoviatica* Handschin; Stach, 1972: 418.
†*Hypogastrura protoviatica* Handschin; Larsson, 1978: 104.
Referred material: Holotype, F412 (ex amber: Fritsch Collection, Königsberg, Russia).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Hypogastrura (*Ceratophysella*) sp.

Hypogastrura (*Ceratophysella*) sp. Lawrence, 1985: 101.
Referred material: No. 18010 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

**Hypogastrura* (*Schoettella*) cf *ununguiculata* (Tullberg)

Hypogastrura (*Schoettella*) cf *ununguiculata* (Tullberg); Lawrence, 1985: 101.
Referred material: No. 18008 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Superfamily Onychiuroidea Lubbock, 1868

Family Onychiuridae Lubbock, 1868

**Lophognathella choreutes* Börner

**Lophognathella choreutes* Börner; Yosii, 1974: 409.
Referred material: No. 144-b (ex copal: Mizunami Fossil Museum, Japan).
Deposit: Mizunami, Japan; Pleistocene.
Note: Given the young age of the copal, the attribution of this specimen to an extant species is likely accurate.

Entomobryomorpha Incertae sedis

**Hypogastrura bengtssoni* (Ågren)

**Achorutes rufescens* (Nicolet); Olfers, 1907: 27.
Referred material: Unknown (ex amber).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).
Note: Given the general problems with the monograph of Olfers (1907) (Handschin, 1926a) this specimen is assuredly not *Hypogastrura bengtssoni* (Ågren), the currently valid name for *Podura rufescens* Nicolet, and likely not even of the genus *Hypogastrura* Bourlet.

Accordingly, we treat this record as merely incertae sedis despite its positive attribution on the part of Olfers (1907).

†*Isotoma larvata* Olfers

†*Isotoma larvata* Olfers, 1907: 26.

Referred material: Unknown (ex amber).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Order Symphypleona Börner, 1901

Superfamily Sminthuridoidea Börner, 1906

Family Sminthurididae Börner, 1906

†*Pseudosminthurides stoechus* Sánchez-García and Engel

†*Pseudosminthurides stoechus* Sánchez-García and Engel, 2016.

Type species of †*Pseudosminthurides* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 12788.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

Superfamily Katiannoidea Börner, 1913

Family Katiannidae Börner, 1913

†*Cretokatianna bucculenta* Sánchez-García and Engel

Fasciosminthurus? sp. Simón-Benito et al., 2002: 87.

†*Cretokatianna bucculenta* Sánchez-García and Engel, 2016.

Type species of †*Cretokatianna* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 10047 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†*Keratopygos megalos* Christiansen and Pike

†*Keratopygos megalos* Christiansen and Pike, 2002a: 181.

New genus D, family Sminthuridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Keratopygos* Christiansen and Pike, 2002a.

Referred material: Holotype, CAS 110 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Sminthurinus sp.

Sminthurinus sp. Lawrence, 1985: 103.

Referred material: No. 18042 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Superfamily Sminthuroidea Lubbock, 1862

Family Bourletiellidae Börner, 1913

Bourletiella sp.

Bourletiella sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Family Sminthuridae Lubbock, 1862

Subfamily Sminthurinae Lubbock, 1862

†*Allacma plumosa* Handschin

†*Allacma plumosa* Handschin, 1926c: 333.
**Sminthurus fuscus* (De Geer); Olfers, 1907: 29, *ad partem*.
†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.
†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.
†*Papirius verrucosus* Olfers, 1907: 30, *ad partem*.
†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.
†*Allacma plumosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *plumosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K703, K985, K1782, K8011, K8014, K8015, K8025, K8076, α14, α29, and F395 (ex amber: Klebs and Fritsch Collections, Königsberg, Russia).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Allacma plumosetosa* Handschin

†*Allacma plumosetosa* Handschin, 1926c: 332.
**Sminthurus fuscus* (De Geer); Olfers, 1907: 29, *ad partem*.
†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.
†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.
†*Papirius verrucosus* Olfers, 1907: 30, *ad partem*.
†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.
†*Allacma plumosetosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *plumosetosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K537, K552, K553, K592, K701, K966, K968, K1781, K1783, K1784, K2720, K3738, K7995, K8006, K8007, K8026, K8038, α24, α28, α30, and α38 (ex amber: Klebs Collection, Königsberg, Russia).
Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Allacma setosa* Handschin

†*Allacma setosa* Handschin, 1926c: 334.
Sminthurus sp. Olfers, 1907: 29, *ad partem*.

†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Allacma setosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *setosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K525, K596, K7987, K7988, K8037, K8079, α5, α23, α34, and χ10 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Archeallacma dolichopoda* Sánchez-García and Engel

†*Archeallacma dolichopoda* Sánchez-García and Engel, 2016.

Type species of †*Archeallacma* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 13850.4; paratype, MCNA 13850.5 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†*Brevimucronus anomalus* Christiansen and Pike

†*Brevimucronus anomalus* Christiansen and Pike, 2002a: 179.
New genus E, family Sminthuridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Brevimucronus* Christiansen and Pike, 2002.

Referred material: Holotype, CAS 293 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†*Grinnellia ventis* Christiansen and Nascimbene

†*Grinnellia ventis* Christiansen and Nascimbene, 2006: 320.

Type species of †*Grinnellia* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-0117A, specimen 2 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Mucrovirga incompleta* Christiansen and Nascimbene

†*Mucrovirga incompleta* Christiansen and Nascimbene, 2006: 326.

Type species of †*Mucrovirga* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-168; paratype, AMNH Bu-0117B, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Sminthurconus grimaldi* Christiansen and Nascimbene

†*Sminthurconus grimaldi* Christiansen and Nascimbene, 2006: 329.

Type species of †*Sminthurconus* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-854A, specimen 2; paratype, AMNH Bu-1452C, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Sminthuricinus deceptus*** Christiansen and Nascimbene

†*Sminthuricinus decepta* Christiansen and Nascimbene, 2006: 323.

Type species of †*Sminthuricinus* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-810-A (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Sminthurus brevicornis*** Koch and Berendt

†*Smynthurus* [sic] *brevicornis* Koch and Berendt, 1854: 121.

†*Sminthurus brevicornis* Koch and Berendt; Stach, 1972: 418.

Referred material: Syntypes unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Sminthurus longicornis*** Koch and Berendt

†*Smynthurus* [sic] *longicornis* Koch and Berendt, 1854: 121.

†*Sminthurus longicornis* Koch and Berendt; Stach, 1972: 418.

Referred material: Holotype unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Sminthurus longicornis* Koch and Berendt; Poinar, 2000: 229.

Referred material: No. CL-1-4 (ex amber: Poinar Collection, Oregon State University [a personal collection putatively accessible through Oregon State University]).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Sminthurus ovatulus*** Koch and Berendt

†*Smynthurus* [sic] *ovatulus* Koch and Berendt, 1854: 121.

†*Sminthurus ovatulus* Koch and Berendt; Stach, 1972: 418.

Referred material: Syntypes unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Sminthurus succineus*** Stach

†*Sminthurus succineus* Stach, 1923: 55.

†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.

†*Sminthurus gracillimus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus longidens* Olfers, 1907: 29, *ad partem*.

†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.

†*Sminthurus* juvenile Olfers, 1907: 40, *ad partem*.

†*Sminthurus succineus* Stach; Handschin, 1926c: 331.

†*Sminthurus succineus* Stach; Stach, 1972: 418.

†*Sminthurus succineus* Stach; Larsson, 1978: 104.

Referred material: Holotype unnumbered; additional material, K529, K541, K562, K598, K712, K713, K961, K963, K970, K989, K1780, K1805, K1808, K8020, and K8060 (ex amber: Klebs Collection, Königsberg, Russia; Helm Collection, Danziger Naturkundemuseum, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Sminthurus spp.

Sminthurus sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Sminthurus sp. Yosii, 1974: 410.

Referred material: One specimen in no. 140 (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Subfamily Sphyrothecinae Betsch, 1980

Sphyrotheca spp.

Sphyrotheca sp. Mari Mutt, 1983: 585.

Referred material: Nos. 34 and 35 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Sphyrotheca? sp. Penney et al., 2012: 3.

Referred material: No accession number (ex amber: Penney Research Collection, University of Manchester[a personal collection resident at the University of Manchester]).

Deposit: La Bucara mine, Dominican Republic; Early Miocene (Burdigalian).

†*Sphyrotheciscus senectus* Sánchez-García and Engel

Arrhopalites sp. Simón-Benito et al., 2002: 87.

†*Sphyrotheciscus senectus* Sánchez-García and Engel, 2016.

Type species of †*Sphyrotheciscus* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 9311 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

Symphypleona, Family Incertae sedis

†*Katiannasminthurus xenopygus* Sánchez-García and Engel

Sminthurus? sp. 2 Simón-Benito et al., 2002: 87.

†*Katiannasminthurus xenopygus* Sánchez-García and Engel, 2016.

Type species of †*Katiannasminthurus* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 10048 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

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