AMERICAN MUSEUM NOVITATES

Number 3974, 32 pp. August 6, 2021

Terrestrial Isopods from Spanish Amber (Crustacea: Oniscidea): Insights into the Cretaceous Soil Biota

ALBA SÁNCHEZ-GARCÍA,[1, 2] ENRIQUE PEÑALVER,[3] XAVIER DELCLÒS,[4] AND MICHAEL S. ENGEL[1, 5]

ABSTRACT

Terrestrial isopods (Crustacea: Oniscidea) are a model group for studying the colonization of land. However, their fossil record is remarkably scarce and restricted to amber inclusions, and therefore amber deposits represent valuable windows to their past diversity and morphology. Here we present a new collection of 11 terrestrial isopod specimens preserved in Albian-aged amber from the Peñacerrada I outcrop, northern Spain, which collectively represent the most thoroughly documented fauna of Mesozoic Oniscidea. The three new genera and species identified belong to three of five major groups of the Oniscidea: *Eoligiiscus tarraconensis*, new genus and species (Ligiidae), *Autrigoniscus resinicola*, new genus and species (Synocheta: Trichoniscidae), and *Heraclitus helenae*, new genus and species (Crinocheta: Detonidae?). These taxa significantly expand the known fossil record of Oniscidea and demonstrate that considerable cladogenesis had already transpired by the Albian. The assemblage represents the earliest-known diversification of Oniscidea, extending direct evidence of terrestrialization in the group back to the late Early Cretaceous. These new taxa exhibit some characteristics that may inform hypotheses relating to general patterns of terrestrial isopod evolution. A discussion is provided about different aspects of the paleo-

[1] Division of Invertebrate Zoology, American Museum of Natural History.
[2] Departament de Botànica i Geologia, Universitat de València, València, Spain.
[3] Museo Geominero, Instituto Geológico y Minero de España, València, Spain.
[4] Departament de Dinàmica de la Terra i de l'Oceà, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain.
[5] Division of Entomology, Natural History Museum, and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence.

 ISSN 0003-0082

ecology and biology of the fossils compared to the Recent fauna. The new species indicate that Cretaceous isopods were a group of considerable adaptive diversity, exhibiting innovations analogous to what Recent isopods would exhibit 105 million years later.

INTRODUCTION

The Oniscidea (terrestrial isopods, often referred to as woodlice) are considered a suborder of Isopoda, with overwhelming morphological evidence demonstrating their monophyly (Schmalfuss, 1974, 1989). In the modern fauna, Oniscidea are currently represented by over 3700 recognized species (Schmalfuss, 2003; Sfenthourakis and Taiti, 2015), and are distinct from the predominantly marine crustaceans in their adoption of a terrestrial way of life (e.g., Schmidt, 2002, 2003, 2008; Hornung, 2011). This distinctive clade exhibits a wide array of specializations for terrestriality, notably a reduction in size, water-resistant cuticle, diverse surface morphology, water-conducting system, reduced antennules, a simplification of the buccal maxilla to a unique plate, mandible without palp, pereopod without annular coxa, pleopodal lungs, modification of the endopodial plate of the male copulatory organ's second pleopod, and styliform uropods not forming a range with the pleotelson. Oniscidea are widely represented in various terrestrial habitats, preferably those with considerable moisture, but some are capable of living in arid regions, others are amphibious along seashores, and a few species have become secondarily adapted and returned to aquatic habitats (Schmidt, 2008). Most species often constitute an important part of the soil fauna, where they play a significant role as primary decomposers (Davis, 1984; Grünwald, 1988).

Oniscidea are organized into five groups (Erhard, 1995, 1996, 1997, 1998)—Ligiidae (Diplocheta), Tylidae (Tylida), Mesoniscidae (Microcheta), Synocheta, and Crinocheta (the latter four often considered as infraorder Holoverticata). Relationships among these groups have been contentious (Tabacaru and Danielopol, 1996), but the Synocheta and Crinocheta are generally considered sister groups (Legrand, 1946). Overall, phylogenetic relationships within Oniscidea are still debated and the subject of ongoing discussion.

The fossil record of Oniscidea is scant, largely biased toward preservation in amber and, until recently, almost entirely restricted to the Cenozoic (fig. 1). To date, the earliest oniscidean described is a single individual from Early Cenomanian amber of northern Myanmar (Broly et al., 2015). However, there are Cenozoic deposits that shed light on early woodlice history and have records of all major families. Woodlice have been described from Eocene Rovno, Baltic and Bitterfeld ambers, and Miocene Dominican and Mexican ambers (e.g., Van Straelen, 1928; Schmalfuss, 1980, 1984a; Spahr, 1993; Perkovsky et al., 2010; Weitschat and Wichard, 2010; Broly et al., 2017, 2018).

While there are a number of Cretaceous amber deposits, woodlice from this period are exceedingly rare and not particularly speciose. Along with the Burmese specimen, woodlice are known from approximately contemporaneous Charentese amber (Perrichot, 2004), and from Early Cretaceous Spanish amber (Delclòs et al., 2007), although none of them have been thoroughly documented. In the case of Spanish amber, woodlice comprise 11 individuals, whereas 12 and six individuals have been recorded from French (Perrichot, 2004) and Burmese ambers

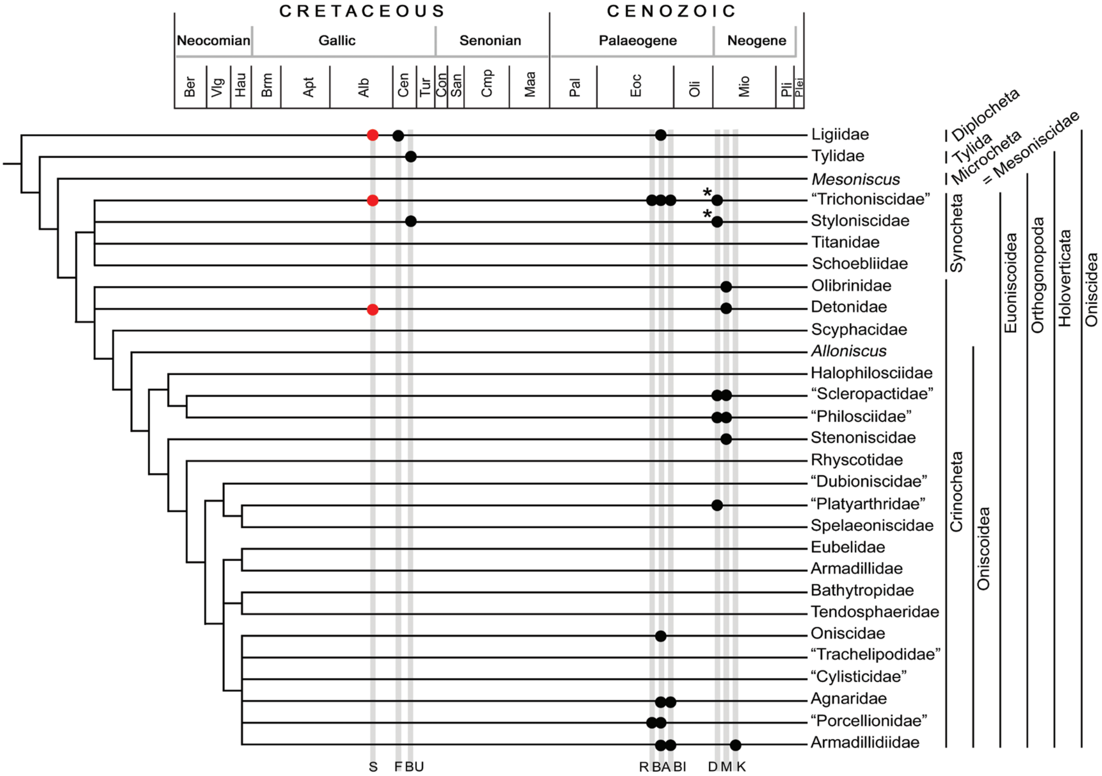

FIGURE 1. Phylogenetic hypothesis of Oniscidea based on Schmidt (2008) and Dimitriou et al. (2019) combined with a synthesis of the Oniscidea amber fossil record. Circles indicate the known fossil records; those in red are the new records from Spanish amber, while black circles are those taxa recorded previously. Abbreviations: **BA,** Baltic amber (Van Straelen, 1928; Spahr, 1993; Weitschat and Wichard, 2010); **BI,** Bitterfeld amber (Schumann and Wendt, 1989; Spahr, 1993; Dunlop, 2010); **BU,** Burmese amber (Broly et al., 2015, 2016); **D,** Dominican amber (Schmalfuss, 1980, 1984a; the family Pseudarmadillidae = Delatorreidae has also been recorded); **F,** French amber (Perrichot, 2004); **K,** Kerala (India) amber (Srivastava et al., 2006); **M,** Mexican amber (Broly et al., 2017, 2018); **R,** Rovno amber (Perkovsky et al., 2010); **S,** Spanish amber (Delclòs et al., 2007; this paper). Age is approximately the same for Rovno, Baltic, and Bitterfeld ambers; the same occurs for Mexican and Dominican ambers (Solórzano-Kraemer et al., 2020). *dubious assignment.

(Broly et al., 2016), respectively. Aside from body fossils, traces of terrestrial locomotion putatively assigned to isopods have been recorded from the Late Jurassic (Gaillard et al., 2005). Unfortunately, the scant number of specimens provides little data for describing or resolving patterns of early woodlice diversification, and the systematic characterization of more fossils as they are discovered is needed to enrich our perspective. Here we describe three new genera and species including representatives of three of five principal groups of the Oniscidea, suggesting that by the late Early Cretaceous much oniscidean diversification had already taken place.

Amber from the Peñacerrada I and II outcrops in Burgos and Álava provinces, respectively, also called "Álava amber," is now known to be 105 Ma (Late Albian) based on palynomorph dating (Barrón et al., 2015). Both amber-bearing outcrops are found in the eastern area of the Basque-Cantabrian Basin. In this area, continental-transitional deposits can be differentiated into three subunits that are represented by a deltaic succession, with a vertical tendency toward a regression of the deltaic system in the lower-middle subunits and a vertical transgression in the upper subunit. Amber is always associated with coal and lignitic beds or organically rich clay levels from the middle subunit, coinciding with the boundary between the maximum regression and the beginning of the transgression, and it is mainly present at the top of filling sequences of interconnected channels within deltaic bays. The amber from the Peñacerrada I outcrop has yielded the present oniscidean specimens as well as thousands of other arthropod inclusions. The specimens reported here represent the largest assemblage of Cretaceous Oniscidea known to date.

MATERIAL AND METHODS

The amber pieces were cut and embedded in a transparent epoxy resin (Epo-tek 301); the preparations were polished once the polymer hardened (Nascimbene and Silverstein, 2000). Fossils were examined under two lenses, i.e., a Motic BA310 and an Olympus BX41 optical microscopes, with reflected and transmitted light, and measurements were taken with Image J software. All measurements were recorded in millimeters. Subsequently, photomicrography was performed with a Moticam 2500 digital camera attached to a Motic BA310 optical microscope with Motic Images Plus 2.0 software. All photographs were stacked with Helicon Focus and edited with Adobe Photoshop CS3. Drawings were prepared with the aid of a camera lucida attached to the Olympus BX41 microscope.

Morphological terminology used in species descriptions is mainly based on Vandel (1960, 1962), Leistikow (2001), and Campos-Filho et al. (2014). Terminology of the cuticle ornamentation follows the definitions given in Schmidt (2002) for "aesthetascs" (stick-shaped sensory hairs on the antennae), "setae" (structures of various shape, always composed of a sensory hair and an additional sheathlike epicuticle portion), "scales" (plates on the surface of the epicuticle, probably consisting of a waxlike material), and "scale setae" (setae with a scalelike shape due to the enlarged sheath). Additionally, we have followed the traditional use of "spines" for relatively inflexible, thornlike structures, in keeping with their etymology. Material is deposited at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain (herein abbreviated as MCNA).

SYSTEMATIC PALEONTOLOGY

Class Malacostraca Latreille, 1802

Order Isopoda Latreille, 1817

Suborder Oniscidea Latreille, 1829

With a total of 11 specimens—representing three new genera and species—the Isopoda fauna from Early Cretaceous Spanish amber is assignable to Oniscidea based on the presence of: (1) a body more or less depressed, oval or oblong in form, sometimes able to conglobate; (2) tergites with scale setae; (3) a cephalon generally small, more or less sunk into the first pereonite, exhibiting no true rostral projection, with the lateral parts more or less expanded; (4) a pereon composed of seven well-defined and rather uniform segments, the lateral parts of which are generally expanded to thin fornicate plates; (5) a pleon variably shaped, composed of six segments, the lateral parts of which are similarly expanded as those of the pereonites, the two first and the last segments smaller than the three middle segments; (6) a very short pleotelson, only slightly longer than a pleon segment; (7) antennulae inserted between the antennae, always quite small, with only three articles, the distal article often rudimentary; (8) antennae of moderate length, seldom exceeding half the length of the body, composed of five peduncular articles and a flagellum generally divided into a restricted number of articulations; (9) seven pairs of ambulatory pereopods, of uniform appearance (e.g., first pereopod never subchelate); (10) five pairs of pleopods, the inner plate of the second and often also of the first pair peculiarly modified in males to serve for copulatory purposes; and (11) uropods generally biramous, with uniarticulate rami projected more or less caudally (Sars, 1899; Schmidt, 2008).

Family Ligiidae Brandt, 1833

Eoligiiscus, new genus

Type species: *Eoligiiscus tarraconensis*, new species.

Diagnosis: Sex unknown. An oniscidean with the following unique combination of characters: Body size small (<2 mm), oval, with pleon not abruptly contracted; dorsal surface moderately convex, with epimeral plates only moderately prominent, smooth. Cephalon broad, not sunk into first pereonite. Eyes large and convex (with at least 10 ommatidia). Antenna rather stout, short, with flagellum composed of only four articles. Pereopods all alike, slender and cylindrical, armed with short thick spines; dactylus hirsute, with two claws; dactylar setae unbranched, quite short. Uropod greatly elongate, distinctly surpassing length of pleon; protopod long and stout, not produced inside pleotelson, with endopod and exopod inserted at same level; endopod and exopod styliform, exopod only slightly longer and stouter than endopod, each with a single apical spine.

Etymology: The new genus group name is a combination of Greek Ἠώς (*Eos*), goddess of the dawn; *Ligia* Fabricius, type genus of the family; and the Greek suffix *-iskos*, a diminutive commonly applied as a suffix to woodlice generic names (as in *Oniscus*: itself a combination of Greek ὄνος [*onos*], meaning, "woodlouse"), and *-iskos*). The gender of the name is masculine.

Eoligiiscus tarraconensis, new species

Figures 2, 3

Diagnosis: As for the genus (above).

Description: Body (fig. 2A, C–D) oval, attenuated caudally, but with pleon not abruptly contracted, of "runner" habitus; small sized, total length 1.35 mm (from tip of cephalon to tip of pleon), twice as long as broad; dorsal surface only moderately convex, smooth; gland pores not visible as preserved.

Cephalon (fig. 2B) transversely semioval, fairly broad, not sunk into first pereonite; length 0.21 mm as preserved, about 0.15× of body length, maximum width 0.49 mm, with front evenly rounded, lacking lateral lobes; antennal lobes absent. Eyes large and convex, diagonal 0.10 mm, consisting of multiple ommatidia (at least 10 as preserved).

Pereon about 0.70× of body length; pereonites overlapping, lamellar; lateral parts of pereonites (i.e., epimeral plates) only moderately prominent, those of posterior pereonites with posterior corners acutely triangular. Pleon about 0.27× of body length, narrower than pereon, lateral parts of two anterior pleonites concealed; pleotelson short, subtriangular, with rounded apex and uropod insertions on posterior corners.

Mouthparts not visible as preserved.

Antennule not visible as preserved.

Antenna (fig. 3A) not very spinose in appearance, rather stout, with five peduncular articles and a multiarticulate flagellum, reaching posteriorly to middle pereonite 2, elbowed between fourth and fifth articles; first article partly obscured by head; second article short and stout, 0.07 mm long, about as long as broad, with two visible thick spines distally; third article short and stout, as long as preceding article, about as long as broad, with one visible thick spine distally; fourth article only slightly elongate, stout, 0.09 mm long, 1.29× length of preceding article, 1.50× longer than broad, with one visible thick spine distally; fifth article only slightly elongate, stout, 0.12 mm long, 1.33× length of preceding article, 3.00× longer than broad; flagellum short, with only four subequal articles, distal article tapering distally and without visible aesthetascs.

Pereopods all alike, slender and cylindrical, without sexual modifications; basis and ischium mostly obscured by body; merus with at least three short thick spines distally; carpus with at least four short thick spines distally; propodus longer than carpus, without visible spines; dactylus (fig. 3B) with large outer claw and smaller inner claw; dactylar setae unbranched, glabrous, very short and hirsute; ungual setae (usually arising between both claws) not visible as preserved.

Pleopods not visible as preserved.

Uropod greatly elongate, about 0.41× of body length, distinctly surpassing length of pleon, freely projecting caudally; protopod not produced inside pleotelson, subrectangular, long and stout, 0.18 mm long, 0.10 mm width, with endopod and exopod inserted at same level; exopod styliform, long and slender, 0.38 mm long, only slightly longer than endopod, 0.04 mm width, with one short slender seta apically (0.03 mm long); endopod styliform, long and slender, 0.34 mm long, 0.04 mm width, with one long slender spine apically (0.16 mm long).

Holotype: MCNA 9751, sex unknown, virtually complete. Preserved in a 8.5×8.0×1.0 mm section of dark-orange amber (in an epoxy trapezoid 15.5×8.2×1.1 mm), surrounded by numerous pseudoinclusions interpreted as droplets of emulsified phloem sap in Lozano et al. (2020), particles of detritus and fungal hyphae; no other major inclusions.

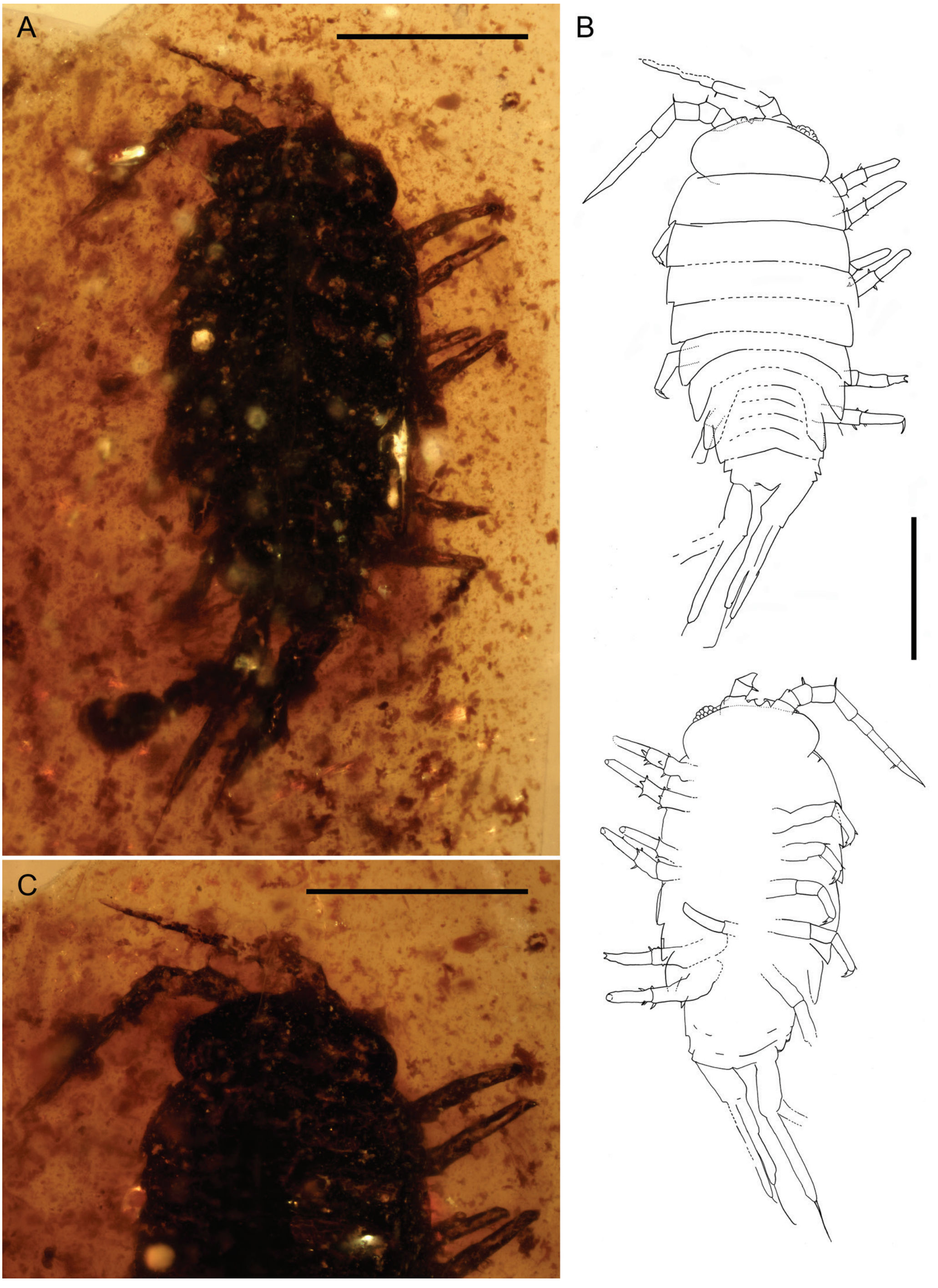

FIGURE 2. *Eoligiiscus tarraconensis*, new genus and species, family Ligiidae (holotype, MCNA 9751, sex unknown). **A.** Microphotograph in dorsal habitus. **B.** Camera lucida drawings of dorsal (top) and ventral (bottom) habitus. **C.** Microphotograph of head in dorsal view. Figures made with consecutive photographs taken at successive focal planes. Scale bars = 0.5 mm.

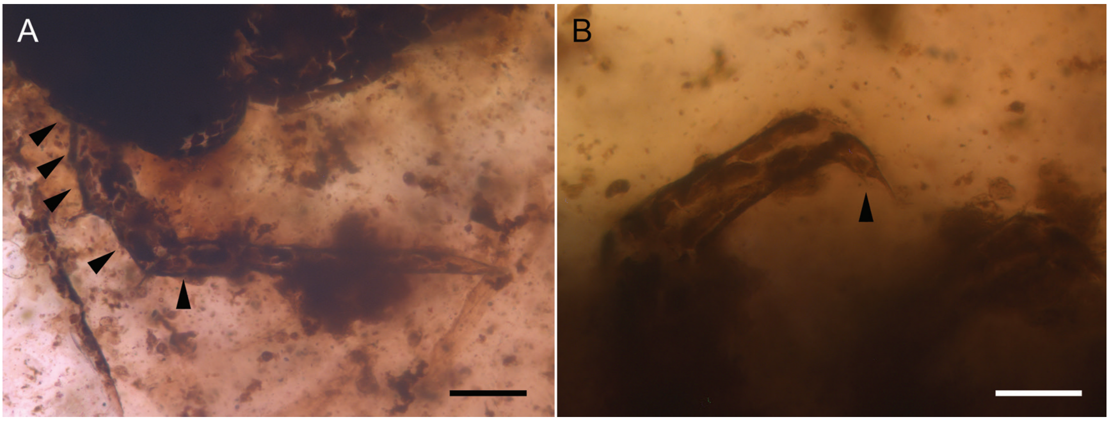

FIGURE 3. Microphotographs of *Eoligiiscus tarraconensis*, new genus and species, family Ligiidae (holotype, MCNA 9751). **A.** Detail of antenna in dorsal view; note five peduncular articles pointed with arrowheads. **B.** Detail of dactylus of left pereopod 1 in ventral view; note small inner claw of dactylus pointed with an arrowhead. Figures made with consecutive photographs taken at successive focal planes. Scale bars: A = 0.1 mm; B = 0.05 mm.

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

Etymology: The specific epithet is taken from the Roman name for the province Hispania Tarraconensis, which encompassed the Peñacerrada I amber site.

Remarks: The family Ligiidae comprises the extant genera *Caucasoligidium* Borutzky, *Ligia* Fabricius, *Ligidioides* Wahrberg, *Ligidium* Brandt, *Tauroligidium* Borutzky, and *Typhloligidium* Verhoeff.

Eoligiiscus tarraconensis may be placed clearly within the family Ligiidae on the basis of the following morphological features (Sars, 1899): (1) oval-shaped body, somewhat convex, with lamellar segments; (2) cephalon without lateral lobes, with the front rounded and not distinctly defined from the epistome; (3) eyes well developed or wanting; and, (4) uropods freely projecting caudally, with both endopod and exopod styliform. Species of Ligiidae also share well-developed antennae, with a multiarticulate flagellum. However, *E. tarraconensis* is readily distinguished from the aforementioned genera in the possession of only four articles to the antennal flagellum (refer to Discussion, below). Unfortunately, no details of the antennulae, mouthparts, and pleopods are visible in the holotype of *E. tarraconensis*, preventing further comparison with extant Ligiidae until better preserved specimens are discovered.

Morphotype I

Figure 4

Description: Body (fig. 4) oval, attenuated caudally, but with pleon not abruptly contracted, of "runner" habitus; medium sized, total length 5.28 mm, about 2.54× longer than broad; dorsal surface only moderately convex, smooth, with very small semicircular scales; gland pores not visible as preserved.

FIGURE 4. Morphotype I, family Ligiidae (MCNA 9513, sex unknown). **A.** Microphotograph in dorsal habitus. **B.** Camera lucida drawing in dorsal habitus. Figure made with consecutive photographs taken at successive focal planes. Scale bar = 1 mm (both panels to the same scale).

Cephalon transversely semioval, partly flanked by side plates of first pereonite; maximum width 0.97 mm, with front evenly rounded, lacking lateral lobes; antennal lobes absent. Eyes not visible as preserved.

Pereon about 0.70× of body length; pereonites overlapping, lamellar; lateral parts of pereonites (i.e., epimeral plates) more pronounced than in *E. tarraconensis*, those of posterior segments with posterior corners acutely triangular, all edged with few very small triangular-shaped scale setae. Pleon poorly visible as preserved, narrower than pereon, with lateral parts of pleonites acutely triangular.

Mouthparts not visible as preserved.

Antennule not visible as preserved.

Antenna not very spinose in appearance, with very small semicircular scales visible in some articles, much longer and slender than in *E. tarraconensis*, with five peduncular articles and a multiarticulate flagellum, at least reaching posteriorly to middle pereonite 3 as preserved, elbowed between fourth and fifth articles; first article partly obscured by head; second article short, not measurable as preserved, with one short thin spine distally; third article short, 0.28 mm long, twice as long as broad, with one long thick spine distally; fourth article elongate, 0.50 mm long, 5.00× times longer than broad, with one long thin spine distally; fifth article elongate, 0.62 mm long, 8.86× longer than broad, with short thin setae sparsely distributed; flagellum long, 0.95 mm long as preserved, with at least nine subequal articles, each article with several short thin setae distally.

Pereopods poorly preserved, all similar in shape and chaetotaxy, slender; dactylus with large outer claw and smaller inner claw.

Pleopods and uropod not visible as preserved.

Material: MCNA 9513, sex unknown. Preserved in a 6.0×5.0×2.2 mm section of dark-orange turbid amber (in an epoxy trapezoid 14.5×5.5×2.2 mm), surrounded by numerous pseudoinclusions (Lozano et al., 2020) and particles of detritus; no other major inclusions.

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

Remarks: The specimen is difficult to place accurately among Oniscidea due to the few observable characters. However, placement within the family Ligiidae seems most appropriate owing to the presence of long antennae with a multiarticulate flagellum. We have avoided formally describing the specimen as a new genus and species until more well-preserved material becomes available. At the least, the above description should permit positive association between this specimen and more completely preserved conspecifics, if they are discovered through future excavations.

Morphotype II

Figure 5

Description: Body (fig. 5A–B) oval, attenuated caudally, but with pleon not abruptly contracted, of "runner" habitus; medium sized, total length 3.09 mm; details of cephalon

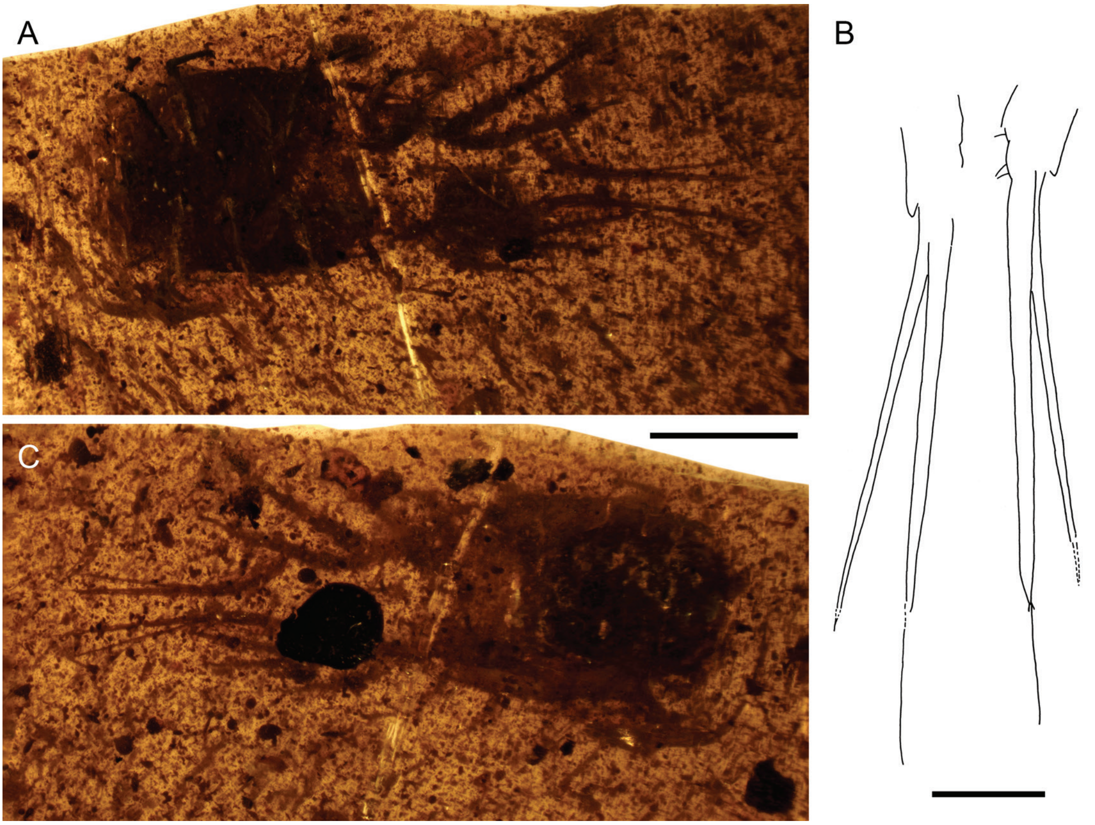

FIGURE 5. Morphotype II, family Ligiidae (MCNA 14274, sex unknown). **A.** Microphotograph in ventral habitus. **B.** Camera lucida drawing of uropods. **C.** Microphotograph in dorsal habitus. Figures A and C made with consecutive photographs taken at successive focal planes. Scale bars: A, C = 1 mm (both panels share the same scale); B = 0.25 mm.

(including antennule, antenna, and mouthparts), pereon and pleon (including pleopods) not visible due to poor preservation of cuticle.

Pereopods poorly preserved, all similar in shape and chaetotaxy, slender; dactylus with large outer claw and smaller inner claw.

Uropod (fig. 5C) greatly elongate, about 0.47× of body length, distinctly surpassing length of pleon, freely projecting caudally; protopod not produced inside pleotelson, subrectangular, long and slender, with outer margin grooved in distal part, 0.44 mm long, 0.13 mm width, with endopod and exopod inserted at same level; exopod styliform, long and slender, 1.00 mm long, subequal in length to endopod but much slender, with one short slender spine apically; endopod styliform, long and slender, 1.00 mm long, 0.04 mm width, with one long slender spine apically.

Material: MCNA 14274, sex unknown. Preserved in a 12×14×1.5 mm section of dark-orange amber (in an epoxy trapezoid 21.5×15.5×2.0 mm), surrounded by numerous pseudoinclusions (Lozano et al., 2020), particles of detritus, fungal hyphae, coprolites, and arthropod and plant remains; other inclusions include a hemipteran and the wing of a hymenopteran.

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

Remarks: The wholly exposed, greatly elongate uropods may serve as an easily recognizable distinguishing character that clearly places specimen MCNA 14274 in the family Ligiidae (Sars, 1899). Among extant Ligiidae, it most closely resembles the genus *Ligia* by having both uropodal rami inserted at the same level. However, the exopod is distinctly slender than the endopod, the reverse of that occurring in Recent Ligiidae (Schmidt, 2008). As for the previous morphotype I, morphotype II is not named here as the number of diagnostic characters available seems insufficient. Nonetheless, this is a unique taxon quite distinct from the others in this deposit and further emphasizes the diversity of the woodlouse fauna in this ancient ecosystem.

Section Synocheta Legrand, 1946

Family Trichoniscidae Sars, 1899

The new genus and species described here (see below) is certainly a member of the clade Synocheta. The main apomorphies of the Synocheta are a fused male genital duct and reduction of the eyes to three or fewer ommatidia (Tabacaru and Danielopol, 1996; Schmalfuss, 2005; Schmidt, 2008). Erhard (1997) also considered the presence of a single pereopod claw as a valid character, but it was not regarded as an autapomorphy of the Synocheta by Schmidt (2008). Among the Synocheta, the Trichoniscidae, spanning the Holarctic region, are assuredly paraphyletic. The new taxon fits in Trichoniscidae sensu stricto by having the first male endopodal pleopod prolonged and bearing a long subterminal seta evolved into an apparent second article of this appendage (Schmalfuss, 2005; Schmidt, 2008). Based on Sars (1899) for the Trichoniscidae, it also has: (1) a more or less elongate body, with the lateral parts of the segments generally not much expanded; (2) cephalon with distinct—though not very large—lateral lobes, with the front more or less produced but scarcely marginate; (3) eyes small or absent; (4) pleon generally much narrower than the pereon, with pleotelson forming a thin projecting plate; (5) antennule minute, with the distal article well developed and tipped with sensory aesthetascs; (6) antenna moderately elongate, minutely spinulose throughout, the flagellum composed of only a restricted number of articles which are less distinctly defined than those in the Ligiidae, the last one terminating in a tuft of delicate setae; (7) pereopods moderately elongate, coarsely spinous, with simple dactylus (i.e., with only one claw); (8) opercular plates of pleopods exceptionally thin, without air chambers or any branchial structure, with the inner plate lobular except on the two anterior pairs; (9) sexual appendage of simple conic shape; (10) endopod of both first and second pairs of pleopods transformed for copulatory purposes; and, (11) uropods with the protopod broadly expanded inside, partly covered by the pleotelson, with the endopod and exopod conically tapered, generally terminating in a tuft of slender setae.

Below the family level, placement in the Haplophthalminae is unsupported due to the new genus' highly developed ornamentation and well developed epimera of pleonites 3–5 or 4–5

(Vandel, 1960), and in the Buddelundiellinae due to their ability to roll into a ball (Vandel, 1960). Placement in the Trichoniscinae is more likely owing to the combination of a smooth or tuberculate body (without longitudinal ridges), and the pleon distinctly narrower than pereon (usually abruptly contracted) due to the reduction of the epimera of pleonites 1 to 5 (Vandel, 1960). Nevertheless, this subfamily is certainly an artificial group in need of phylogenetic clarification.

Autrigoniscus, new genus

Type species: *Autrigoniscus resinicola*, new species.

Diagnosis: **Male.** An oniscidean with the following combination of characters: Body size small (<2 mm), more or less oblong, with pleon much narrower than pereon; dorsal surface moderately convex dorsally, with epimeral plates only moderately prominent, relatively smooth in appearance, covered with small semicircular scales and sparsely arranged, small triangular-shaped scale setae. Eyes small but distinct (with at least three ommatidia). Antennule with three articles, distal article shorter than second and bearing a tuft of apical aesthetascs. Antenna rather stout, with flagellum composed of six articles. Pereopods not all alike, of moderate size, armed with elongate, thick, nearly straight spines arranged in a longitudinal row on sternal margin; carpus modified having a large distal process on tergal margin with a row of scales; dactylus simple (i.e., with one claw); dactylar setae unbranched, glabrous, long and slender (i.e., flagellar). First pair of pleopods modified; endopod biarticulate, with proximal article very short, and distal article long and slender, styliform. Uropod moderately elongate, not surpassing length of pleon; protopod rather short and stout, produced inside pleotelson, with endopod and exopod inserted at same level; endopod and exopod conical, exopod much longer and stouter than endopod, each with a terminal tuft of setae. **Female.** Unknown.

Etymology: The new genus group name is a combination of the pre-Roman tribe Autrigones (who lived in northern Spain near the region of the amber localities along with the Cantabri) and the Greek suffix –*iskos*, denoting a diminutive. The gender of the name is masculine.

Autrigoniscus resinicola, new species

Figures 6–8

Diagnosis: As for the genus (above).

Description: Body (figs 6, 7A–B) more or less oblong, of "clinger" habitus; small sized, total length 1.62 mm, nearly twice as long as broad (1.78×); dorsal surface only moderately convex, of a relatively smooth appearance, covered with small semicircular scales and sparsely distributed small triangular-shaped scale setae arranged in transverse rows (fig. 8B); gland pores not visible as preserved.

Cephalon transversely semioval, maximum width 0.49 mm, with front evenly rounded, and lateral lobes small but distinct; suprantennal line nearly straight medially (in holotype) to

V-shaped (in specimen MCNA 12617); antennal lobes absent. Eyes small but distinct, consisting of at least three ommatidia.

Pereon poorly visible due to blackening of cuticle; pereonites overlapping, lamellar; lateral parts of pereonites (i.e., epimeral plates) only moderately prominent, those of two posterior pereonites with posterior corners acutely triangular, all edged with small appressed spikes and some small triangular-shaped scale setae (as a continuity to those of dorsal surface). Pleon distinctly narrower than pereon (abruptly contracted); pleotelson short, subtriangular, with rounded apex.

Mouthparts not visible as preserved.

Antennule (fig. 8A) with three articles; first article obscured by head, second article partly obscured by head, 0.04 mm long as preserved, without visible setae; third article shorter than second, 0.02 mm long, with a tuft of several short and relatively thick apical aesthetascs.

Antenna not very spinose in appearance, rather stout, with five peduncular articles and a multiarticulate flagellum, reaching posteriorly to middle pereonite 1, elbowed between fourth and fifth articles, with flagellum much shorter than peduncle; first article partly obscured by head, short and stout, 0.08 mm long as preserved, slightly broader than long, with no visible spines; second article short and stout, 0.09 mm long, slightly broader than long, with one visible thick spine distally; third article short and stout, 0.10 mm long, about as long as broad, with up to two visible thick spines distally; fourth article elongate, stout, 0.20 mm long, 2.0× length of preceding article, 2.5× longer than broad, with two visible thick spines distally; fifth article elongate and much slender than fourth article, 0.25 mm long, 1.2× length of preceding article, 6.2× longer than broad; flagellum with six articles, 0.20 mm long, 0.8× length of fifth article of peduncle, flagellar articles gradually tapering distally, distal article without visible aesthetascs.

Pereopods (figs 7C, 8C–D) of moderate size, increasing in length and thickness posteriorly; basis and ischium mostly obscured by body; merus poorly visible, with elongate, thick, nearly straight spines on sternal margin; carpus with elongate, thick, nearly straight spines more or less arranged in a longitudinal row on sternal margin giving it a rippled appearance, spines becoming longer distally; at least carpus of pereopods 4–7 having a large distal process on tergal margin with a row of scales (probably male sexually dimorphic characters, but females unknown) (fig. 8C); propodus longer than carpus, with elongate, thick, nearly straight spines on sternal margin, less numerous than on carpus; dactylus simple, with enlarged outer claw (fig. 8D); dactylar setae unbranched, glabrous, long and slender; ungual setae not visible as preserved.

Pleopods poorly visible; pleopodal exopods without respiratory structures; endopod of first pair of pleopods modified, biarticulate; proximal article very short; distal article long and slender, styliform (fig. 8F).

Uropod (fig. 8E) moderately elongate, about 0.27× of body length, not surpassing length of pleon, freely projecting caudally; protopod produced inside pleotelson, rather short and stout, 0.15 mm long, about as long as broad, with endopod and exopod inserted at same level; exopod conical, maximum width at base 0.07 mm and strongly tapered distally, 0.29 mm long (excluding terminal tuft of setae), distinctly longer than endopod, with a tuft of short setae apically (0.07 mm long); endopod conical, maximum width at base 0.06 mm and strongly tapered distally, 0.20 mm long (excluding terminal tuft of setae), with a tuft of long setae apically (0.11 mm long), lengths of endopod and endopodal tuft of setae combined reaching length of exopod (excluding terminal tuft of setae).

Holotype: MCNA 12522, male, virtually complete, exposed dorsally, ventrally, and laterally. Preserved in darkened orange-colored amber, trimmed to 2.5×1.5×1.0 mm (in an epoxy trapezoid 22.5×14.5×1.1 mm), surrounded by numerous pseudoinclusions (Lozano et al., 2020) and particles of detritus; no other major inclusions. The specimen shows indirect evidence of the digestive tract from fossilized fecal matter (termed “cololite”).

Additional material: Specimen MCNA 12678, presumed male, partially complete, exposed ventrally, ventrolaterally, and dorsolaterally. Preserved in darkened orange-colored amber, trimmed to 6.0×2.1×1.2 mm (in an epoxy trapezoid 23.0×13.0×1.2 mm), surrounded by numerous pseudoinclusions (Lozano et al., 2020), particles of detritus and fungal hyphae; no other major inclusions. Specimen MCNA 12617, presumed male, poorly preserved, exposed dorsally, ventrally, and laterally. It shows indirect evidence of the digestive tract from fossilized fecal matter. Preserved in darkened yellow-colored amber, trimmed to 6.9×4.0×1.0 mm (in an epoxy trapezoid 23.1×14.9×1.1 mm), surrounded by numerous pseudoinclusions and particles of detritus; no other major inclusions. Specimen MCNA 13823.1, presumed male, partially complete. Preserved in two darkened orange-colored amber pieces, one trimmed to 10.5×6.0×3.0 and preserving the major part of the body, and the other trimmed to 4.5×4.5×1.0 and consisting of an impression of the cuticle. Syninclusions include one possible rove beetle (Staphylinidae?, MCNA 13823.2).

Specimens MCNA 12678, MCNA 12617, and MCNA 13823.1 match the diagnosis of *Autrigoniscus resinicola* for some characters, but other features remain unclear and we cannot attribute them to this species with complete confidence (refer to Remarks, below).

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

Etymology: The specific epithet refers to the occurrence of the species in plant resins (Latin, *resina*, meaning “resin,” and the suffix *-cola*, meaning “dweller”), which in turn become amber when fossilized.

Remarks: Specimen MCNA 12678 (fig. 9A) closely resembles the holotype of *A. resinicola*, sharing with it the relative head, uropod, and body measurements (total body length is 1.64 mm), the overall morphology of the body (more or less oblong, moderately convex dorsally, with the pleon distinctly narrower than pereon, and the epimeral plates only moderately prominent), the very spinous pereopods (with spines arranged as described for the holotype, and a modified carpus apparently visible in one of the posterior pereopods), the dactylus morphology (with one claw and a flagellar dactylar seta), and a similarly shaped uropodal endopod (conical, distinctly shorter and narrower than exopod, and with an apical tuft of long setae). Despite the similar endopod, the poor preservation of the exopod prevents its comparison with that of the holotype. Moreover, the eyes, antennae, pleopods, and cuticle ornamentation are not visible in MCNA 12678, and the antennulae are poorly preserved due to shrinkage and desiccation during preservation.

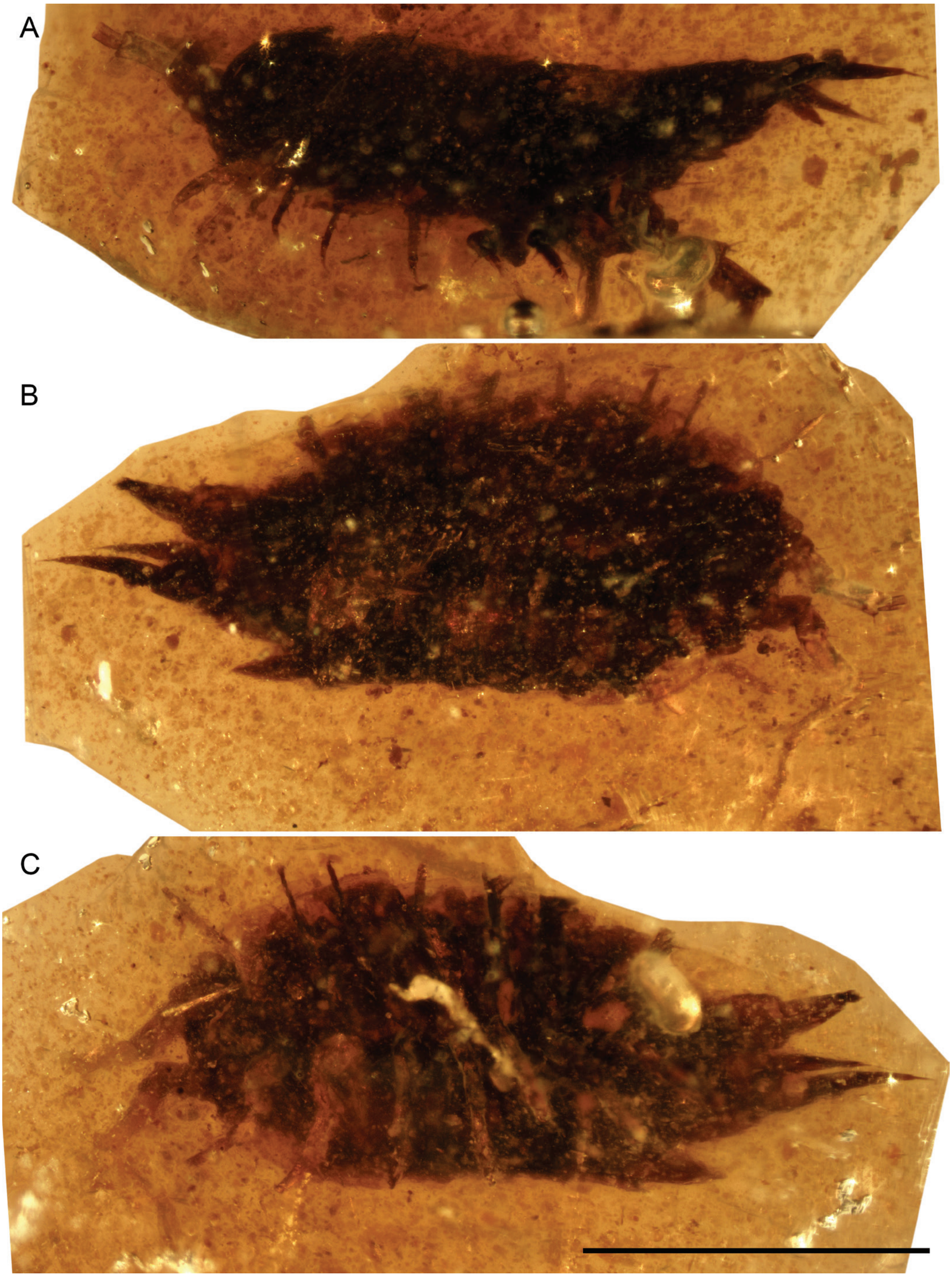

FIGURE 6. Microphotographs of *Autrigoniscus resinicola*, new genus and species, family Trichoniscidae (holotype, MCNA 12522, male). **A.** Lateral habitus. **B.** Dorsal habitus. **C.** Ventral habitus. Figures made with consecutive photographs taken at successive focal planes. Scale bar = 1 mm (all panels to the same scale).

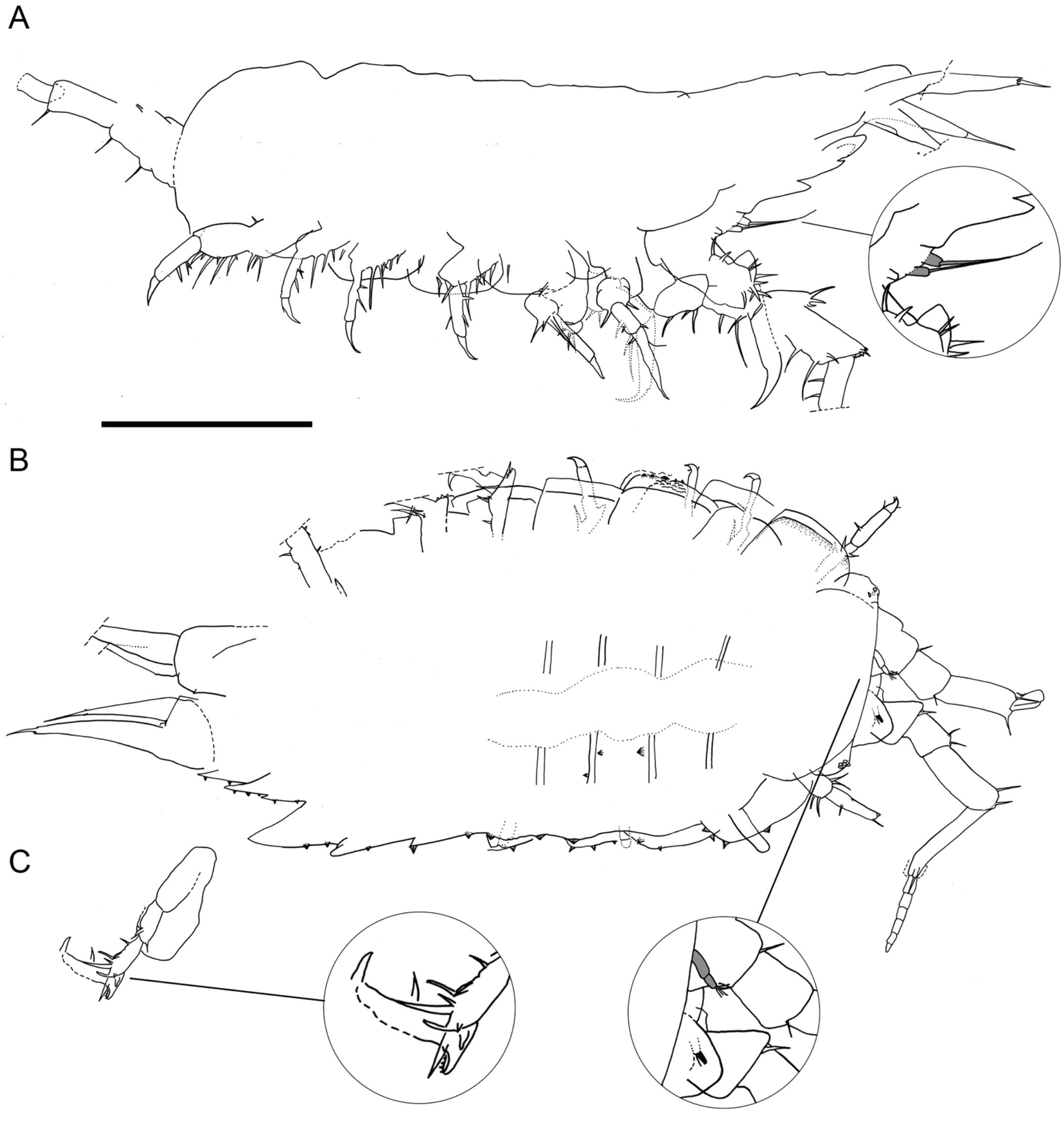

FIGURE 7. Camera lucida drawings of *Autrigoniscus resinicola*, new genus and species, family Trichoniscidae (holotype, MCNA 12522, male). **A.** Lateral habitus, with magnified area showing details of endopod of first pair of pleopods. **B.** Dorsal habitus, with magnified area showing details of antennule. **C.** Fifth pereopod in ventral view, with magnified area showing details of modified carpus. Scale bar = 0.5 mm (all panels to the same scale).

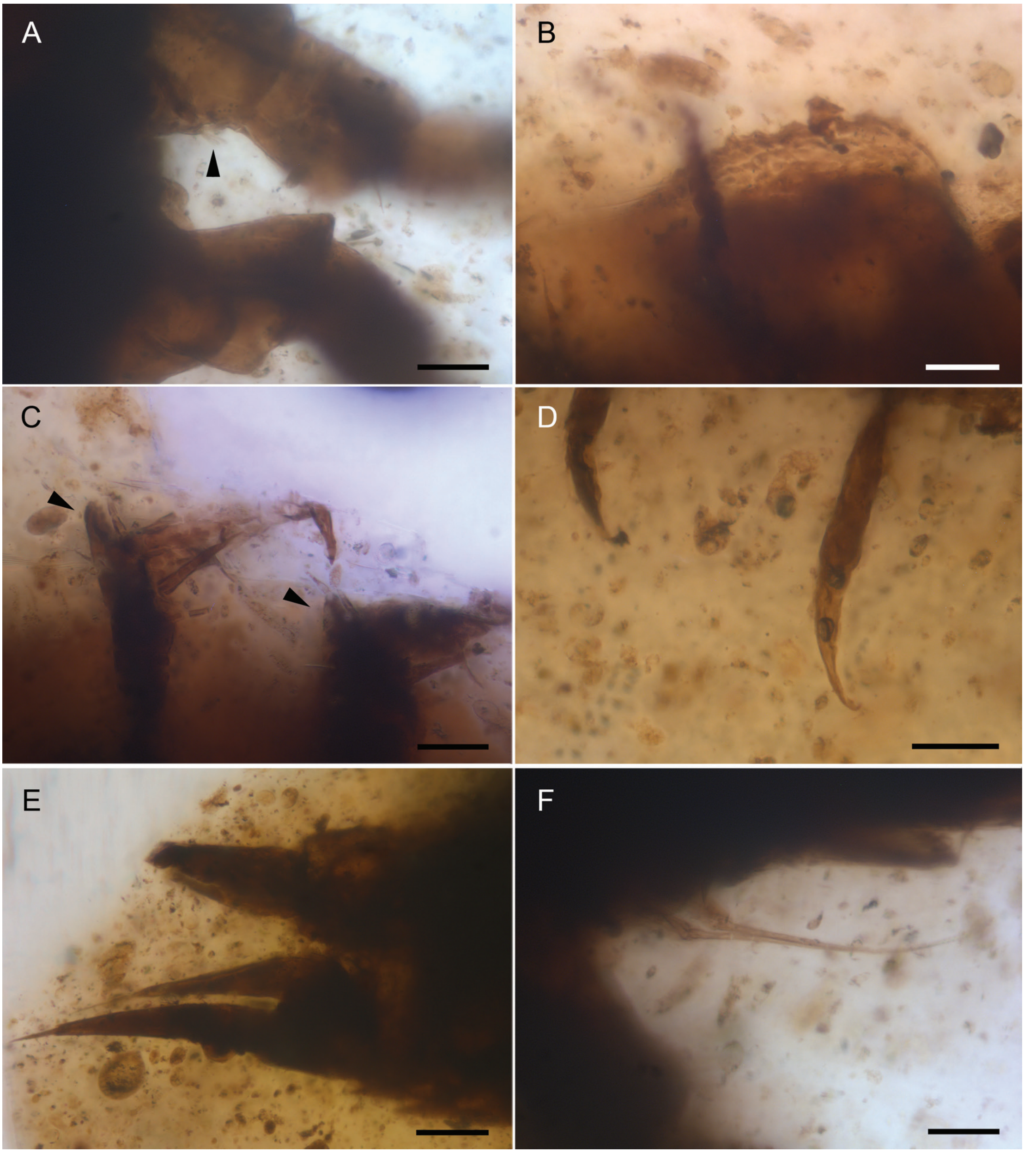

FIGURE 8. Detail microphotographs of *Autrigoniscus resinicola*, new genus and species, family Trichoniscidae (holotype, MCNA 12522, male). **A.** Head in dorsal view, showing the antennule (arrowhead). **B.** Semicircular scales and triangular-shaped scale setae in ventral view. **C.** Carpus of pereopods 5 and 6 in ventral view, showing the distal process (arrowheads). **D.** Simple dactylus of pereopods 2 and 3 in lateral view. **E.** Uropods in dorsal view. **F.** Endopod of first pair of pleopods in lateral view. Figures made with consecutive photographs taken at successive focal planes. Scale bars: A–D, F = 0.05 mm; E = 0.1 mm.

Specimen MCNA 12617 (fig. 8B–D) shares with the holotype the overall morphology of the body and the cuticle ornamentation (i.e., dorsal surface with small semicircular scales and small triangular-shaped scale setae, and lateral parts of the pereonites edged with small appressed spikes). The total length is 1.26 mm, nearly twice as long as broad (1.94×), and thus the specimen is slightly smaller than the holotype. However, the cephalon differs in having a V-shaped supra-antennal line, and the lateral lobes are broadly rounded and larger than in the holotype. The pereopods seems less spinous than the holotype (probably an artifact of preservation), and the pattern of the spines cannot be assessed because of the hidden position of the pereopods. However, the distinctive modified carpus of *A. resinicola* is clearly visible in a posterior pereopod, and the dactylus is identical to those described for the holotype (fig. 8D). Unfortunately, the ommatidia, antennae, antennulae, pleopods, and uropods are not visible in MCNA 12617, preventing comparison of these structures with the holotype.

Specimen MCNA 13823.1 has few characters visible. The cuticle shows the ornamentation as described for *A. resinicola* (although more pronounced than in the holotype), and a modified carpus is visible on some posterior pereopods.

All the shared features listed lead us to consider MCNA 12678, MCNA 12617, and MCNA 13823.1 as conspecific, but this remains somewhat unresolved, and so we have not designated them as a part of the type series. Hopefully, more complete material will eventually be recovered to permit a more thorough characterization of the species and a critical test as to whether these three specimens are correctly placed within *A. resinicola*.

Section Crinocheta Legrand, 1946

Family Detonidae? Budde-Lund, 1906

Heraclitus, new genus

Type species: *Heraclitus helenae*, new species.

Diagnosis: Sex unknown. An oniscidean with the following combination of characters: Body size small (<2 mm), more or less oblong, with pleon much narrower than pereon; dorsal surface convex, with epimeral plates only moderately prominent, rough, covered with large semicircular scales and densely crowded prominent triangular-shaped scale setae. Antenna rather stout, with flagellum composed of at least three articles. Pereopods all alike, of moderate size, armed with elongate, thick, nearly straight spines arranged in a longitudinal row on sternal margin; dactylus with two claws, inner claw minute; dactylar setae unbranched, glabrous, long, and slender, distinctly expanded distally. Uropod moderately elongate; protopod long and stout, produced inside pleotelson, with endopod and exopod inserted at same level; exopod styliform, much longer than endopod; endopod conical, with a terminal tuft of setae.

Etymology: The genus group name honors the pre-Socratic philosopher Heraclitus of Ephesus (ca. 535–475 B.C.E.), early rationalist, empiricist, and founder of philosophical ontology. We have used the common Latinized form of his Greek name. The gender of the name is masculine.

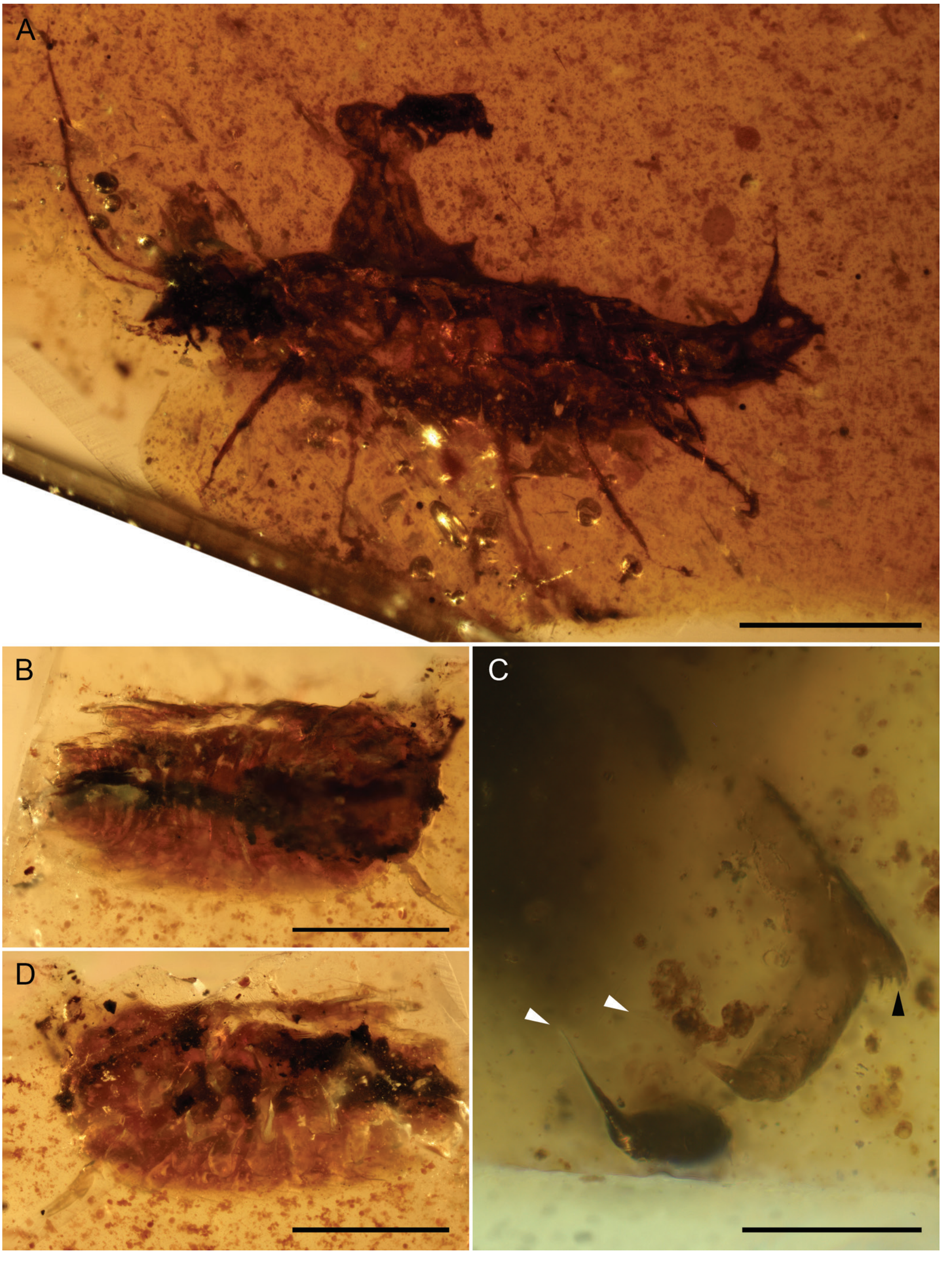

FIGURE 9. Microphotographs of two specimens tentatively assigned to *Autrigoniscus resinicola*, new genus and species, family Trichoniscidae. **A.** Specimen MCNA 12678 (presumed male), in ventrolateral habitus. **B.** Specimen MCNA 12617 (presumed male) in dorsal habitus. **C.** Specimen MCNA 12617; detail of a posterior pereopod in lateral view showing the modified carpus (black arrow) and simple dactylus (white arrows). **D.** Specimen MCNA 12617 in ventral habitus. Figures made with consecutive photographs taken at successive focal planes. Scale bars: A–C = 0.5 mm; D = 0.1 mm.

Heraclitus helenae, new species

Figures 10, 11

Diagnosis: As for the genus (above).

Description: Body (fig. 10) more or less oblong, of "clinger" habitus; small sized, total length 1.76 mm, width not measurable due to orientation in amber; dorsal surface convex, rough, covered with large semicircular scales and densely crowded prominent triangular-shaped scale setae arranged in transverse rows; gland pores not visible as preserved.

Cephalon rounded, rather arcuate, rough, with same ornamentation as described for body (fig. 11B); lateral lobes not visible as preserved (probably small); antennal lobes absent. Eyes not visible as preserved.

Pereon about 0.73× of body length; pereonites overlapping, lamellar; lateral parts of pereonites (i.e., epimeral plates) only moderately prominent, those of two posterior pereonites with posterior corners acutely triangular, all edged with small appressed spikes and distinctly prominent triangular-shaped scale setae (as a continuity to those of dorsal surface). Pleon about 0.24× of body length, distinctly narrower than pereon (abruptly contracted); pleotelson short, subtriangular, with rounded apex bearing two short distal setae.

Mouthparts considerably well developed but without visible details.

Antennule poorly visible; distal article with three short thick spines distally.

Antenna (fig. 11A) very spinose in appearance, packed with small scale setae and spines, rather stout, with five peduncular articles and a multiarticulate flagellum; articles 1–3 partly obscured by head, apparently short and stout; fourth article elongate, stout, 0.18 mm long, 2.25× longer than broad; fifth article elongate and much slender than fourth article, 0.22 mm long, 1.22× length of preceding article, 5.5× longer than broad; flagellum partially preserved, with at least three articles not clearly delimited.

Pereopods all alike, of moderate size; all pereopods without sexual modifications; basis and ischium mostly obscured by body; merus, carpus, and propodus with elongate, thick, nearly straight spines generally arranged in a longitudinal row on sternal margins giving them a rippled appearance; propodus and carpus length apparently subequal; dactylus with enlarged outer claw and minute inner claw; dactylar setae unbranched, glabrous, long, and slender, distinctly expanded distally; ungual setae not visible as preserved.

Pleopods not visible as preserved.

Uropod (fig. 11C) moderately elongate, about 0.28× of body length as preserved, freely projecting caudally; protopod produced inside pleotelson, subrectangular, long and stout, 0.15 mm long, with endopod and exopod inserted at same level; exopod styliform, long and slender, width not measurable due to poor preservation, 0.35 mm long as preserved (distal part not preserved), distinctly longer than endopod, with some very short thin setae sparsely distributed; endopod conical, maximum width at base 0.03 mm, tapering distally, 0.21 mm long (excluding terminal tuft of setae), with some very short thin setae sparsely distributed, and a tuft of long setae apically (0.10 mm long).

Holotype: MCNA 12546, sex unknown, exposed dorsolaterally, ventrolaterally, and laterally. Preserved in darkened orange-colored amber, trimmed to 3.5×1.7×1.2 mm (in an epoxy

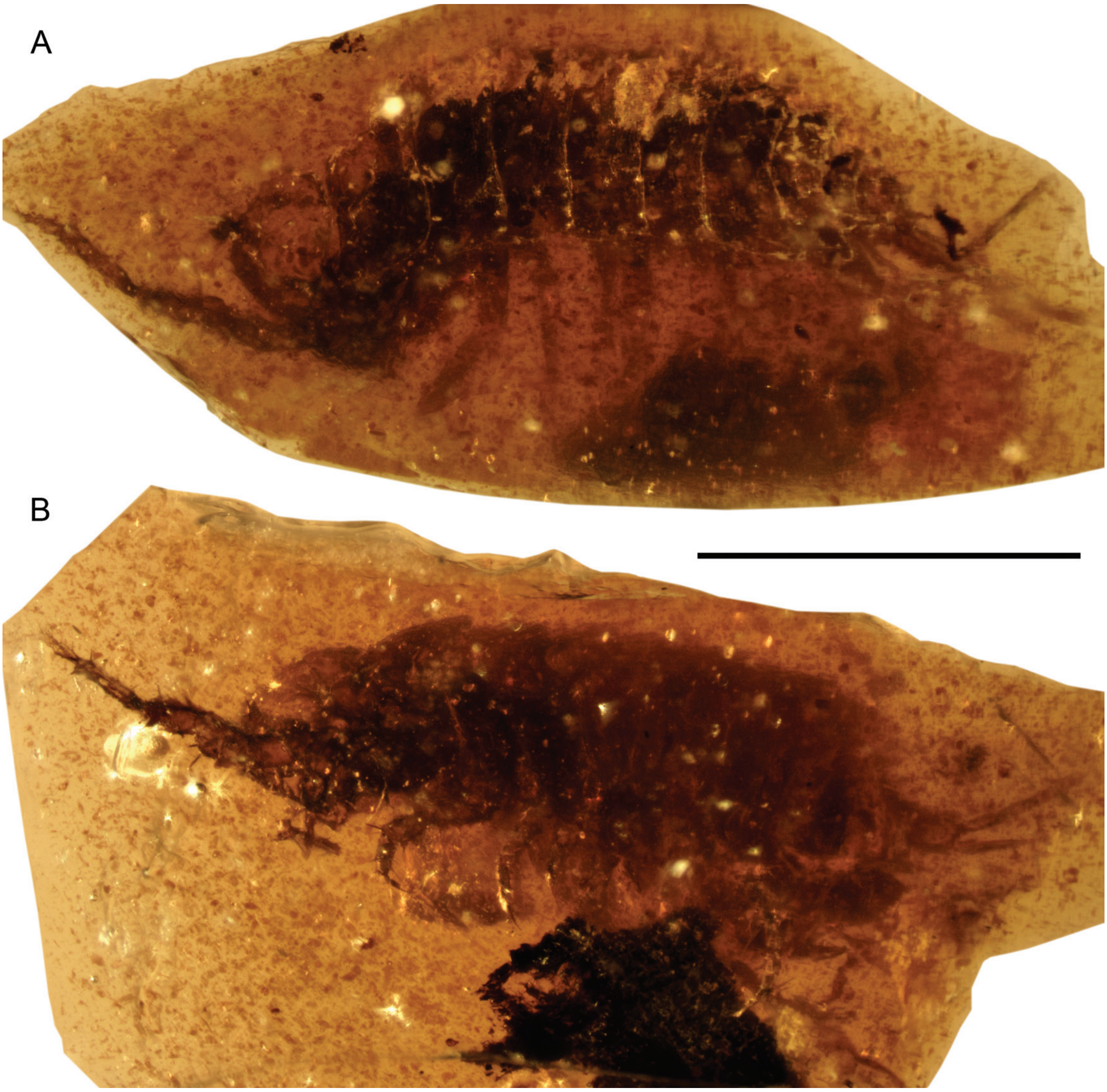

FIGURE 10. Microphotographs of *Heraclitus helenae*, new genus and species, family Detonidae? (holotype, MCNA 12546, sex unknown). **A.** Lateral habitus. **B.** Ventrolateral habitus. Figures made with consecutive photographs taken at successive focal planes. Scale bar = 1 mm (both panels to the same scale).

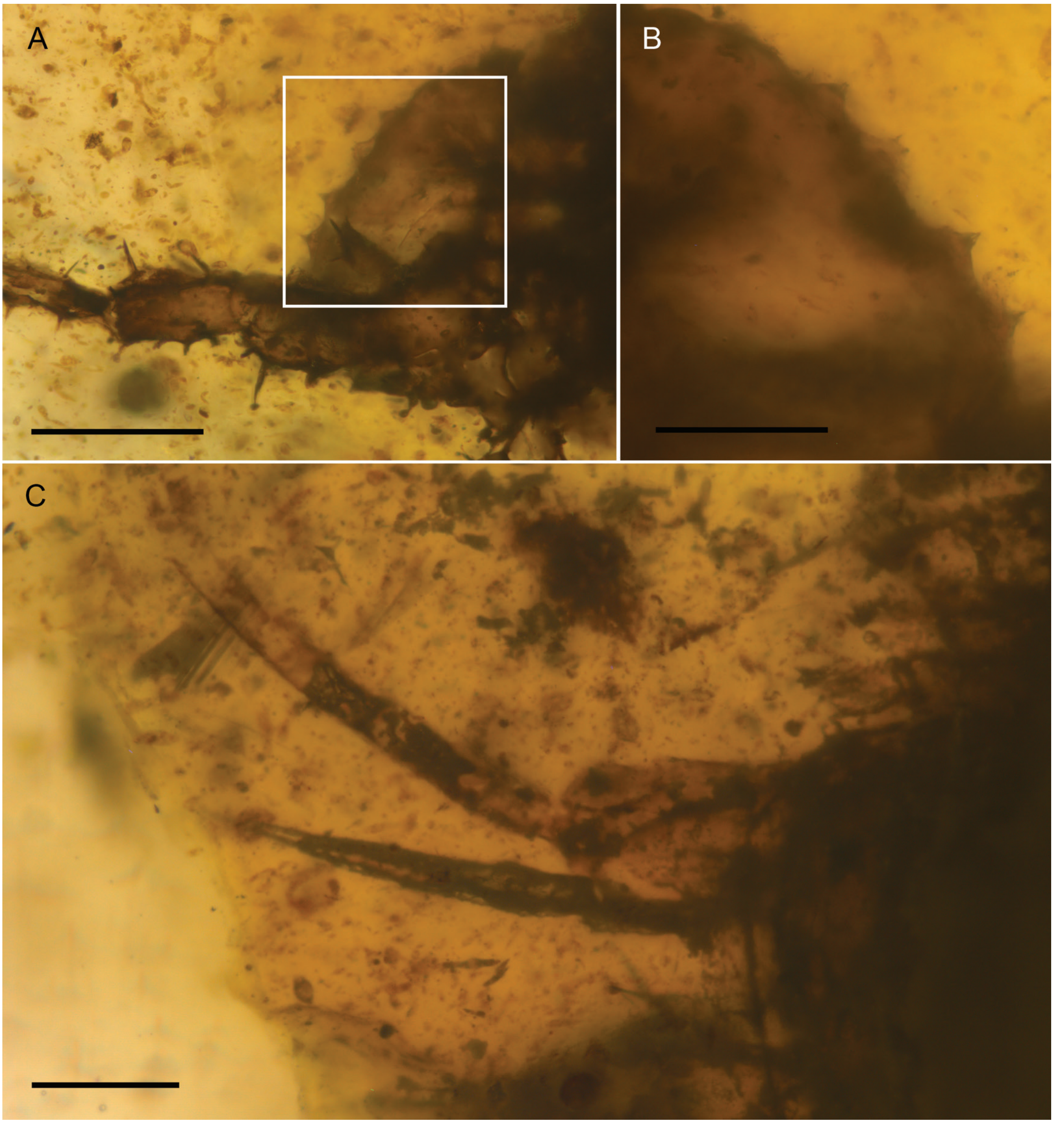

FIGURE 11. Detail microphotographs of *Heraclitus helenae*, new genus and species, family Detonidae? (holotype, MCNA 12546). **A.** Head and antenna in ventrolateral view; box indicates that section magnified in B. **B.** Prominent triangular-shaped scales in A, photographed from the other side. **C.** Uropods in dorsolateral view. Figures made with consecutive photographs taken at successive focal planes. Scale bars: A = 0.2 mm; B, C = 0.1 mm.

trapezoid 23.0×15.0×1.5 mm), surrounded by numerous pseudoinclusions (Lozano et al., 2020) and particles of detritus; no other major inclusions. The specimen is nearly complete, but some areas are poorly visible owing to the position of the animal during fossilization. The distal parts of the uropodal endopod and the antennulae are not preserved.

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

Etymology: The specific epithet refers to Helen of Troy, a figure from Greek mythology known for her considerable beauty and having "launched a thousand ships" (à la Marlowe) as Menelaus and Agamemnon initiated the Trojan War to return her to Achaea.

Remarks: *Heraclitus helenae* may be clearly differentiated from *A. resinicola* by the roughened cuticle, the spinose antennulae, the dactylus with two claws, and the longer uropodal endopod. It is perhaps a representative of Crinocheta: Detonidae? owing to the antennule with a 5-jointed peduncle and a 4-jointed flagellum, the antennulae with conspicuous scaly tubercles, the inner claw small, the uropodal protopod surpassing the pleotelson, the exopodites leaf shaped, and the endopodites styliform (Schmidt, 2002).

Oniscidea Indet.

Specimen MCNA 14907: (fig. 12A) is preserved in darkened orange-colored amber, trimmed to 10.5×6.0×1.5 mm (in an epoxy trapezoid 21.1×13.5×2.2 mm), and surrounded by numerous pseudoinclusions (Lozano et al., 2020), particles of detritus, fungal hyphae, and three coprolites. The specimen is exposed dorsally and ventrally, poorly preserved, with the cuticle virtually degraded except for the lateral parts of the segments, which are edged with small appressed spikes and some small triangular-shaped scale setae. Worthy of note are the oval-shaped medium-sized body (total length 4.27 mm as preserved, maximum width 2.27 mm), and the moderately large eyes composed of multiple ommatidia (only the left eye is visible). The specimen also possesses a partly preserved antenna (cut just below the articulation between the fourth and fifth articles) that is elbowed between the fourth and fifth articles. The first peduncular article is partly concealed by the head, whereas the measurements of the rest of articles are as follows: second article 0.22 mm long, about as long as broad; third article 0.25 mm long, 1.25× longer than broad, with one long, thick spine; fourth article elongate, 0.58 mm long, 4.83× longer than broad. Only some anterior pereopods are visible, but these are so thoroughly obscured owing to preservation as to provide no useful delineation of features. However, long, thick, nearly straight spines, a dactylus with two claws (the inner claw minute, distinctly smaller than in *H. helenae*), and an unbranched, glabrous, long, and slender dactylar seta are visible on some pereopods. The specimen is difficult to place accurately among Oniscidea, but placement within the family Ligiidae seems most appropriate owing to the presence of large eyes composed of multiple ommatidia, the comparatively elongate antennae, and a dactylus with two claws. Interestingly, the specimen corresponds with the anterior half of an exuvia. Isopods perform a biphasic molt, which consists of the shedding of the posterior and then the anterior half of

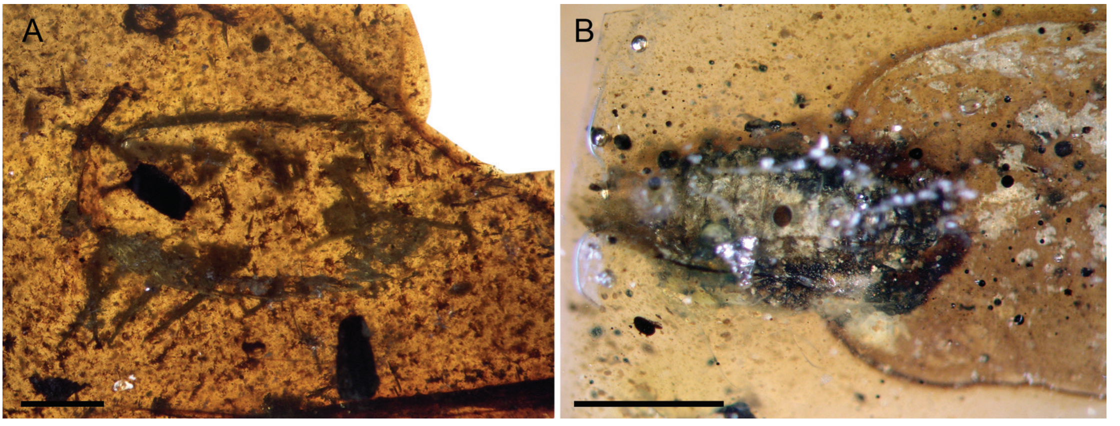

FIGURE 12. Microphotographs of indeterminate Oniscidea. **A.** Specimen MCNA 14907 in dorsal habitus, sex unknown. **B.** Specimen MCNA 9458 in dorsal habitus, sex unknown. Figures made with consecutive photographs taken at successive focal planes. Scale bars = 1 mm.

the body. The boundary between the two halves is between the fourth and fifth pereonites, which agrees with that observed in the fossil.

Specimen MCNA 9458: (fig. 12B) is preserved in darkened yellow-colored amber, trimmed to 5.2×3.5×1.0 mm (in an epoxy trapezoid 19.1×14.1×1.1 mm), and surrounded by numerous pseudoinclusions and particles of detritus; the amber is also darkened near the inclusion. The specimen is exposed dorsally and ventrally, and although a vague outline of the pereopods armed with long, stout, nearly straight spines can be seen, these are so thoroughly obscured owing to preservation and by the adjacent body mass as to provide no useful delineation of features. It possesses a more or less oblong, small body (total length 2.09 mm long as preserved, maximum width 0.87 mm), and some segments of the pereon with some small triangular-shaped scale setae.

Specimen MCNA 9924.2: (fig. 13; previously figured in Delclòs et al., 2007, Broly et al., 2013, and Sánchez-García et al., 2015) is preserved in darkened orange-colored amber, trimmed to 18.0×14.5×3.5 mm (in an epoxy trapezoid 22.5×15.0×4.8 mm). Syninclusions include one acariform Bdellidae, one Blattodea, six Diptera (one Ceratopogonidae, two Dolichopodidae, one Phoridae, two Psychodidae), one Tanaidacea (*Alavatanais margulisae* Sánchez-García, Peñalver, and Delclòs), two Archaeognatha, six coprolites (attributed to termites based on their general shape), and abundant fungal and plant remains (see details of syninclusions in Sánchez-García et al., 2015). The specimen is exposed laterally and partially complete (missing head), with the right side of the body and the right pereopods mostly polished off. The specimen possesses a medium-sized body (total length 3.78 mm as preserved), more or less oblong, only moderately convex dorsally. The pereon is about 0.73× the body length, with the lateral parts of the pereonites only moderately prominent, those of the four posterior segments with posterior corners acutely triangular, all edged with some small appressed spikes. The pleon is about 0.22× of the body length and distinctly narrower than the pereon (abruptly contracted). It also possesses spinous pereopods, a dactylus with two claws (the inner claw minute), and an unbranched, glabrous, long, and slender dactylar seta, distinctly expanded distally. Lastly, an elongate structure that could correspond to a short uropod is sticking out from under the pleon.

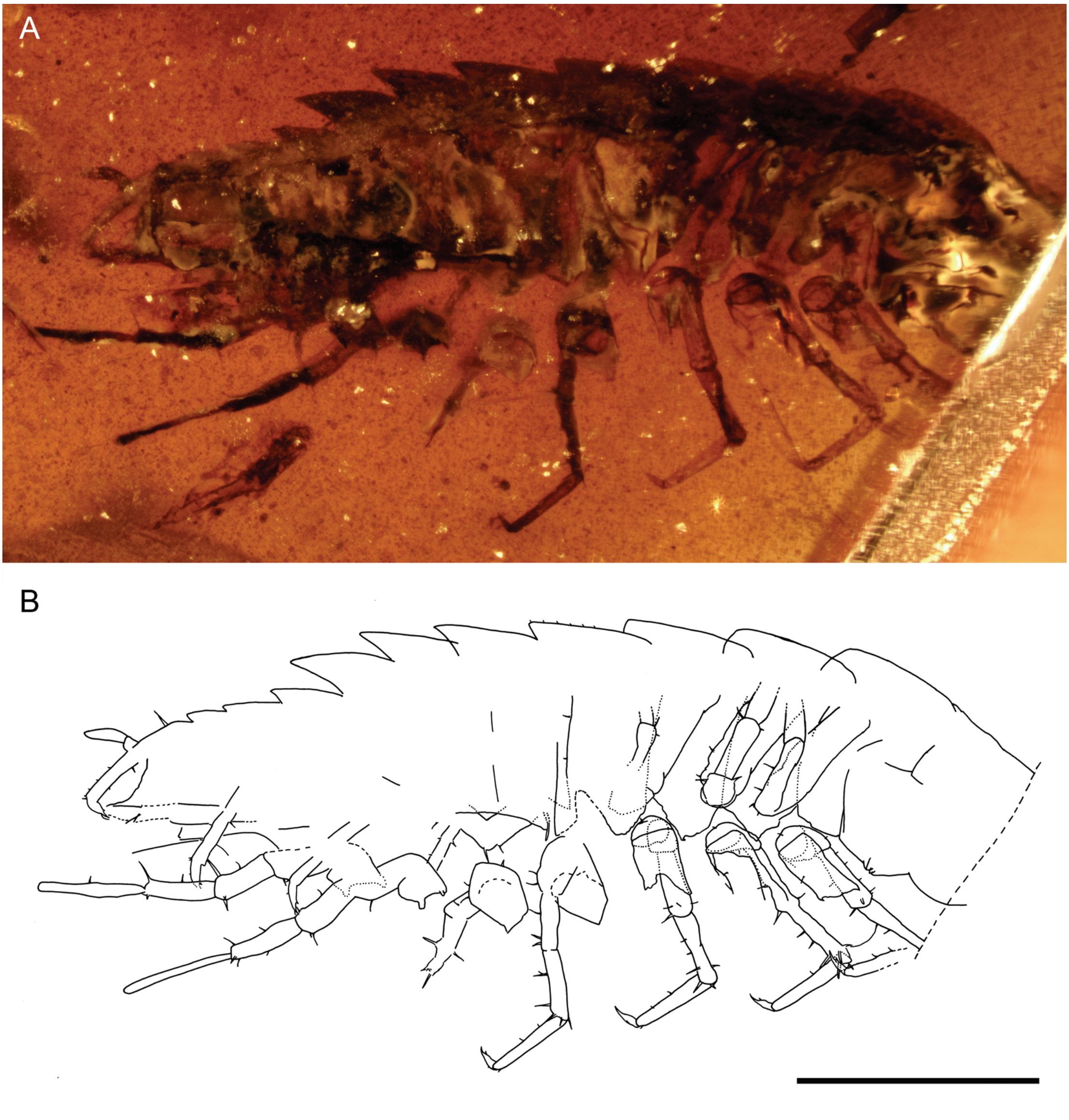

FIGURE 13. Indeterminate Oniscidea specimen MCNA 9924.2, sex unknown. **A.** Microphotograph in ventrolateral habitus. **B.** Camera lucida drawing in ventrolateral habitus. Figures made with consecutive photographs taken at successive focal planes. Scale bar = 1 mm (both panels to the same scale)

DISCUSSION

With a total of three species belonging to three of five major groups of the suborder Oniscidea, and five unnamed morphotypes, the woodlouse fossil fauna described from Spanish amber reveals a significant diversity, and one of considerable phylogenetic breadth in representation. These specimens are some of the earliest evidence of terrestrial Crustacea, confirming the occurrence of land-dwelling crustaceans back to the late Early Cretaceous (next oldest is in the Late Cretaceous; Cenomanian).

Despite a considerable modern diversity, fossil Oniscidea remain comparatively rare. Indeed, they are small animals typical of cryptic habitats (leaf litter, uppermost soil layers, caves) (Hornung, 2011), and their fossil record is strongly biased toward amber. This circumstance is the same as in other litter organisms, and therefore their fossil record has some similarities with several clades such as Diplura, Collembola, and Archaeognatha (e.g., Sánchez-García and Engel, 2016a, 2016b). Compared to insect fossilization in amber, the poor preservation quality of fossil oniscideans is explained by the biochemical properties of their exoskeletons (Hild et al., 2008), more specifically due to reactions occurring between the calcite of the cuticle and the acidic compounds in the fresh resin (Schmalfuss, 1984a). This rendered several characters indistinct and led to an overall degraded (altered) aspect in the Spanish fossils. Because of the rareness of the oniscidean fossil record, any specimen that can be assigned to a certain taxon provides an opportunity for calibrating estimations of clade ages, exploring historical biogeographic patterns, and a unique insight into the diversity and ecology of the past.

From an evolutionary perspective, Oniscidea are of particular importance for studying the evolution of adaptations to terrestrial life. It is generally accepted that oniscideans conquered the terrestrial environment directly from the seashore, i.e., without passing through freshwater (Carefoot and Taylor, 1995). Currently they inhabit a wide array of terrestrial biotopes from high-humidity habitats to arid regions (Hornung, 2011). Living in a terrestrial environment enforces considerable morphological, ecological, and behavioral constraints, and has promoted the evolution of suites of characters related to this specialization. Some of these characters are visible in the studied fossils, such as the severe reduction of the antennule to 1–3 articles or the male endopodite of pleopode 2 modified into a copulatory stylus. The development of a complex copulatory apparatus to guarantee the transfer of sperm may have contributed to the colonization of less humid biotopes, as it minimizes the risk of desiccation and, therefore, the damage of gametes (Erhard, 1995).

Another character that evolved in correlation with the degree of terrestrialization is the reduction of the antennae. The degree to which the flagellar articles become reduced is related to increasing levels of terrestrialization. The shift in habitats from littoral to truly terrestrial biotopes has been accompanied by a reduction in the number of flagellar articles in the antennae (Schmalfuss, 1998). Indeed, the genus *Ligia* is the only oniscidean taxon that still possesses an antennal flagellum with up to 30 articles, whereas in all other taxa the number of flagellar articles is strongly reduced, down to a single article in the most extreme scenario (e.g., *Helleria* von Ebner) (Schmalfuss, 1998). In Ligiidae and some Synocheta the antennae have numerous flagellar articles, while in the Oniscoidea there are three at most, and taxa adapted to less humid conditions have only two flagellar articles (Schmalfuss, 1998; Schmidt, 2008). It is remarkable that in Spanish amber there is a morphotype of Ligiidae in which the flagellum is quite reduced compared to modern taxa. Thus, it is apparent that there was significant Cretaceous diversity and innovation, in this case curiously represented by a severe reduction of the flagellum in *E. tarraconensis* to a degree not known among extant Ligiidae, but occurring in other groups of Oniscidea. The fauna of Cretaceous terrestrial crustaceans reveals that ancient isopods were not morphologically stagnant. Indeed, isopod species from the Cretaceous exhibited species-level radiations comparable to modern day taxa with similar variations of common features. This may be informative in understanding patterns of isopod evolution and development as we now know that Cretaceous isopods appear to have the same innovations as in their modern relatives, particularly antennal reduction.

As for the condition of the dactylus of the pereopodes, it is simple (i.e., with only one claw) in the specimens of Trichoniscidae (i.e., *A. resinicola*), and bifurcate (i.e., with two claws) in *E. tarraconensis* and the other two morphotypes of Ligiidae as well as in the Crinocheta (i.e., *H. helenae*). However, the inner claw in *H. helenae* is smaller than in the ligiid morphotypes. According to Schmidt (2008), the inner claw as present in Ligiidae and Tylidae was lost in the stem group of Orthogonopoda, so that the inner claw present in most Crinocheta evolved secondarily as a new structure. However, others authors do not find support for this hypothesis (Tabacaru and Giurginca, 2019). There is also considerable diversity among comparable species-level traits such as the cuticle structures from nearly smooth (in *E. tarraconensis*) or with small semicircular scales and sparse triangular-shaped small-scale setae (in *A. resinicola*) to distinctly roughened and with a conspicuous ornamentation (in *H. helenae*). Other structures occur only in males, as is the case for the modified carpus of *A. resinicola*.

As previously posed, most fossil isopods are found in amber, i.e., fossilized tree resin. Regarding to the habitats represented in the fossil amber record, preservation in amber directly depends on the proximity to the amber source, which therefore determines the differential representation of taxa (Solórzano Kraemer et al., 2018). For oniscideans, this means that entrapment would favor taxa that inhabit either the leaf litter or the uppermost soil layers near the resin-producing trees. This sampling bias has been reported for other litter organisms preserved in fossil resins and is almost certainly caused by the nature of the resin and the ecological preferences of groups that have higher probabilities of becoming engulfed by it. Indeed, litter-inhabiting arthropods are relatively frequent in other pieces of Spanish amber, suggesting that the resin flows occurred with a certain frequency close to or directly onto the soil (Sánchez-García et al., 2015, 2016, 2017, 2018; Sánchez-García and Engel, 2016a, 2016b).

It is remarkable that most of the Oniscidea morphotypes in Spanish amber are indicative of rather moist environments. The Ligiidae occur preferentially in littoral environments or in terrestrial habitats with a high humidity. They are all representatives of the ecomorphological runner type as described by Schmalfuss (1984b), usually characterized by smooth tergal surfaces, a narrow pleon, small coxal plates, and long slender pereopods and antennae. As for the Trichoniscidae and even the whole Synocheta, they are mainly small isopods typically associated with rather moist environments in modern ecosystems. By contrast, only one species of the section Crinocheta is known from Spanish fossils, even though at least some of these families are species rich in drier terrestrial habitats today. This is particularly significant since the Crinocheta are today the most diversified of terrestrial Isopoda with about 2750 species, and hence about 80% of all described species of Oniscidea (Schmidt, 2008), while the other major groups are distinctly less species rich. Not surprisingly, the section Crinocheta comprises species best adapted to terrestrial life (Schmidt, 2008). We found an opposite pattern in the Spanish amber fauna, reflective of a likely high-humid climate in the region at that time. Indeed, the prevalence of isopod families associated with humid environments in Spanish amber and a near absence of groups related to drier environments is congruent with most prior evidence documented from this paleofauna.

Spanish amber has revealed a wide array of lineages that are indicators of a litter-dwelling to semiaquatic fauna, and that the general environment was likely near water or perhaps even representative of a swamp habitat (Sánchez-García et al., 2015, 2016, 2017, 2018; Sánchez-García and Engel, 2016a, 2016b). Overall, the amber data suggest that a fully diversified woodlouse fauna was established in this ancient humid ecosystem and is in agreement with an old origin of Oniscidea, likely in pre-Pangean times (Broly et al., 2013, 2015).

ACKNOWLEDGMENTS

The authors express their gratitude to Jesús Alonso, director of the Museo de Ciencias Naturales de Álava (MCNA), and to Arabako Foru Aldundia-Diputación Foral de Álava for permitting the loan of the Spanish amber specimens studied here. Thanks are also given to Rafael López del Valle (MCNA) for the careful preparation of the pieces, and to two anonymous reviewers for their considerable time and care in providing feedback on an earlier version of the work. A.S.-G. is funded by an APOSTD2019 Research Fellowship from the Generalitat Valenciana and the European Social Fund (ESF). This study is a contribution to the Spanish AEI/FEDER, UE Project CRE (CGL2017-84419).

REFERENCES

Barrón, E., et al. 2015. Palynology of Aptian and upper Albian (Lower Cretaceous) amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern Spain). Cretaceous Research 52 (A): 292–312.

Brandt, J.F. 1833. Conspectus monographiæ crustaceorum oniscodorum Latreilleii. Bulletin de la Société Impériale des Naturalistes de Moscou 6: 171–193.

Broly, P., P. Deville, and S. Maillet. 2013. The origin of terrestrial isopods (Crustacea: Isopoda: Oniscidea). Evolutionary Ecology 27: 461–476.

Broly, P., S. Maillet, and A.J. Ross. 2015. The first terrestrial isopod (Crustacea: Isopoda: Oniscidea) from Cretaceous Burmese amber of Myanmar. Cretaceous Research 55: 220–228.

Broly, P., S. Maillet, and A.J. Ross. 2016. Terrestrial isopods: progress in their fossil record. *In* D. Penney and A.J. Ross (editors), Seventh international conference on fossil insects, arthropods and amber, abstracts: 68. Manchester: Siri Scientific Press, 88 pp.

Broly, P., M.L. Serrano-Sánchez, S. Rodríguez-García, and F.J. Vega. 2017. Fossil evidence of extended brood care in new Miocene Peracarida (Crustacea) from Mexico. Journal of Systematic Palaeontology 15 (12): 1037–1049.

Broly, P., M.L. Serrano-Sánchez, and F.J. Vega. 2018. Diversity of the Crinocheta (Crustacea, Isopoda, Oniscidea) from Early Miocene Chiapas amber, Mexico. Revista Mexicana de Ciencias Geológicas 35 (3): 203–214.

Budde-Lund, G. 1906. Die Landisopoden der Deutschen Südpolar-Expedition 1901–1903 mit diagnosen verwandter Arten. *In* E. von Drygalski (editor), Deutsche Südpolar-Expedition 1901–1903 im Auftrage des Reichsamtes des Innern. IX Band. Zoologie I Band: 69–92, + 2 pls [iii, iv]. Berlin: Verlag von Georg Reimer, xii + 567 pp., + 50 pls.

Campos-Filho, I.S., P.B. Araujo, M.E. Bichuette, E. Trajano, and S. Taiti. 2014. Terrestrial isopods (Crustacea: Isopoda: Oniscidea) from Brazilian caves. Zoological Journal of the Linnean Society 172 (2): 360–425.

Carefoot, T.H., and B.E. Taylor. 1995. *Ligia*: a prototypal terrestrial isopod. *In* M. Alikhan (editor), Terrestrial isopod biology (Crustacean Issues 9): 47–60. Rotterdam: A.A. Balken Publishers, 204 pp.

Davis, R.C. 1984. Effects of weather and habitat structure on the population dynamics of isopods in a dune grassland. Oikos 42 (3): 387–395.

Delclòs, X., et al. 2007. Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. Comptes Rendus Palevol 6 (1–2): 135–149.

Dimitriou, A.C., S. Taiti, and S. Sfenthourakis. 2019. Genetic evidence against monophyly of Oniscidea implies a need to revise scenarios for the origin of terrestrial isopods. Scientific Reports 9: 18508 [1–10].

Dunlop, J.A. 2010. Bitterfeld amber. *In* D. Penney (editor), Biodiversity of fossils in amber from the major world deposits: 57–68. Manchester: Siri Scientific Press, 304 pp.

Erhard, F. 1995. Untersuchungen am Skelet-Muskel-System des Landassel-Pleon (Isopoda, Oniscidea). Ein Beitrag zur phylogenetisch-systematischen Stellung der Familie Mesoniscidae. Verhandlungen der Deutschen Zoologischen Gesellschaft 88 (1): 1–144.

Erhard, F. 1996. Das pleonale Skelet-Muskel-System und die phylogenetisch-systematische Stellung der Familie Mesoniscidae (Isopoda: Oniscidea). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 538: 1–40.

Erhard, F. 1997. Das pleonale Skelet-Muskel-System von *Titanethes albus* (Synocheta) und weiterer Taxa der Oniscidea (Isopoda), mit Schlußfolgerungen zur Phylogenie der Landasseln. Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 550: 1–70.

Erhard, F. 1998. Phylogenetic relationships within the Oniscidea (Crustacea, Isopoda). Israel Journal of Zoology 44 (3–4): 303–309.

Gaillard, C., P. Hantzpergue, J. Vannier, A.L. Margerard, and J.M. Mazin. 2005. Isopod trackways from the Crayssac Lagerstätte, Upper Jurassic, France. Palaeontology 48 (5): 947–962.

Grünwald, M. 1988. Adaptation und Dekompostierungsleistung von Landasseln (Isopoda, Oniscidea) an Standorten der großen Brennessel (*Urtica dioica* L.). Hochschulsammlung Naturwissenschaft, Biologie 20: 1–273.

Hild, S., O. Marti, and A. Ziegler. 2008. Spatial distribution of calcite and amorphous calcium carbonate in the cuticle of the terrestrial crustaceans *Porcellio scaber* and *Armadillidium vulgare*. Journal of Structural Biology 163 (1): 100–108.

Hornung, E. 2011. Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. Terrestrial Arthropod Reviews 4 (2): 95–130.

Latreille, P.A. 1802. Histoire naturelle, générale et particuliere des Crustacés et des Insectes. Familles naturelles des genres [tome troisième]. Paris: Dufart, xii + 467 + [i] pp.

Latreille, P.A. 1817. Les crustacés, les arachnides et les insectes. *In* G. Cuvier, Le règne animal distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. Avec figures, dessinées d'après nature [tome III]: 1–653. Paris: Deterville, xxix + 653 pp.

Latreille, P.A. 1829. Les crustacés, les arachnides et les insectes, distribués en familles naturelles [tome I]. Paris: Deterville, xxvii + 584 pp., + 5 pls. [Latreille's work also appeared as volume 4 in G. Cuvier, Le règne animal distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée. Avec figures, dessinées d'après nature (deuxième édition) (tome quatrième)]

Legrand, J.J. 1946. Les coaptations sexuelles des Oniscoidea. Bulletin Biologique de la France et de la Belgique 80: 241–388.

Leistikow, A. 2001. Phylogeny and biogeography of South American Crinocheta, traditionally placed in the family "Philosciidae" (Crustacea: Isopoda: Oniscidea). Organisms, Diversity and Evolution 1 (Electronic Supplement 4): 1–85.

Lozano, R.P., et al. 2020. Phloem sap in Cretaceous ambers as abundant double emulsions preserving organic and inorganic residues. Scientific Reports 10: 9751 [1–15].

Nascimbene, P., and H. Silverstein. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 93–102. Leiden: Backhuys Publishers, viii + 498 pp.

Perkovsky, E.E., V.Y. Zosimovich, and A.P. Vlaskin. 2010. Rovno amber. *In* D. Penney (editor), Biodiversity of fossils in amber from the major world deposits: 116–136. Manchester: Siri Scientific Press, 304 pp.

Perrichot, V. 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. Geologica Acta 2 (1): 9–22.

Sánchez-García, A., and M.S. Engel. 2016a. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. American Museum Novitates 3862: 1–47.

Sánchez-García, A., and M.S. Engel. 2016b. Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona). Journal of Systematic Palaeontology 15 (7): 513–537.

Sánchez-García, A., E. Peñalver, R. Pérez-de la Fuente, and X. Delclòs. 2015. A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: palaeobiological implications. Journal of Systematic Palaeontology 13 (8): 645–676.

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

Sánchez-García, A., A. Nel, A. Arillo, and M.M. Solórzano Kraemer. 2017. The semi-aquatic pondweed bugs of a Cretaceous swamp. PeerJ 5: e3760 [1–32].

Sánchez-García, A., E. Peñalver, X. Delclòs, and M.S. Engel. 2018. Mating and aggregative behaviors among basal hexapods in the Early Cretaceous. PLoS ONE 13 (2): e0191669 [1–13].

Sars, G. 1899. An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. 2, Isopoda. Bergen: Bergen Museum, x + 270 pp., + 104 pls. [Oniscoidea on pp. 153–192, plates 70–83]

Schmalfuss, H. 1974. Skelett und Extremitätenmuskulatur des Isopoden-Cephalothorax. Ein Beitrag zur Klärung von Phylogenie und Systematik der incertae-sedis-Familie Tylidae (Crustacea). Zeitschrift für Morphologie der Tiere 78 (1–2): 1–91.

Schmalfuss, H. 1980. Die ersten Landasseln aus Dominikanischem Bernste in mit einer Revision der Familie Sphaeroniscidae (Stuttgarter Bernsteinsammlung: Crustacea, Isopoda, Oniscoidea). Stuttgarter Beiträge zur Naturkunde, Serie B, (Geologie und Paläontologie) 61: 1–12.

Schmalfuss, H. 1984a. Two new species of the terrestrial isopod genus *Pseudarmadillo* from Dominican amber (Amber-Collection Stuttgart: Crustacea, Isopoda, Pseudarmadillidae). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 102: 1–14.

Schmalfuss, H. 1984b. Eco-morphological strategies in terrestrial isopods. *In* S.L. Sutton and D.M. Holdich (editors), The biology of terrestrial isopods [Symposia of the Zoological Society of London 53]: 49–63. Oxford: Clarendon Press, xxvi + 518 pp.

Schmalfuss, H. 1989. Phylogenetics in Oniscidea. Monitore Zoologico Italiano (N.S.) Monografia 4: 3–27.

Schmalfuss, H. 1998. Evolutionary strategies of the antennae in terrestrial isopods. Journal of Crustacean Biology 18 (1): 10–24.

Schmalfuss, H. 2003. World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie) 654: 1–341.

Schmalfuss, H. 2005. *Utopioniscus kuehni* n. gen., n. sp. (Isopoda: Oniscidea: Synocheta) from submarine caves in Sardinia. Stuttgarter Beiträge zur Naturkunde (Serie A, Biologie) 677: 1–21.

Schmidt, C. 2002. Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 1. (Olibrinidae to Scyphaidae s. str.). Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe 78 (2): 275–352.

Schmidt, C. 2003. Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 2. (Oniscoidea to Armadillidiidae). Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe 79 (1): 3–179.

Schmidt, C. 2008. Phylogeny of the terrestrial Isopoda (Oniscidea): a review. Arthropod Systematics and Phylogeny 66 (2): 191–226.

Schumann, H., and H. Wendt. 1989. Zur Kenntnis der tierischen Inklusen des Sächsischen Bernsteins. Deutsche Entomologische Zeitschrift 36 (1–3): 33–44.

Sfenthourakis, S., and S. Taiti. 2015. Patterns of taxonomic diversity among terrestrial isopods. ZooKeys 515: 13–25.

Solórzano Kraemer, M.M., et al. 2018. Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. Proceedings of the National Academy of Sciences of the United States of America 115 (26): 6739–6744.

Solórzano-Kraemer, M.M., X. Delclòs, M.S. Engel, and E. Peñalver. 2020. A revised definition for copal and its significance for palaeontological and Anthropocene biodiversity-loss studies. Scientific Reports 10: 19904 [1–12].

Spahr, U. 1993. Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und Liste der Bernsteinfossilien. Verschiedene Tiergruppen, ausgenommen Insecta und Araneae. Stuttgarter Beiträge zur Naturkunde (Serie B, Geologie und Paläontologie) 194: 1–77.

Srivastava, G.P., M. Shukla, P. Kumar, M. Kumar, and A. Prakash. 2006. Record of pillbug (*Armadillidium*) and millipede (*Polyxenus*) remains from the resin lumps of Warkali Formation (Upper Tertiary), Kerala Coast. Journal of the Geological Society of India 67 (6): 715–719.

Tabacaru, I., and D.L. Danielopol. 1996. Phylogénie des isopodes terrestres. Comptes Rendus de l'Académie des Sciences à Paris, Sciences de la Vie 319: 71–80.

Tabacaru, I., and A. Giurginca. 2019. Contributions to the study of the Trichoniscidae (Isopoda, Oniscidea). I. Definition and taxonomic position. Travaux de l'Institut de Spéologie "Émile Racovitza" 58: 47–63.

Van Straelen, W. 1928. Contributions à l'étude des isopodes méso- et cénozoïques. Mémoires de l'Académie Royale de Belgique, Classe des Sciences, 2 Série 9 (5): 1–68.

Vandel, A. 1960. Isopodes terrestres (première partie). *In* Faune de France 64: 1–416. Paris: P. Lechevalier, 416 pp.

Vandel, A. 1962. Isopodes terrestres (deuxième partie). *In* Faune de France 66: 417–931. Paris: P. Lechevalier, 417–931.

Weitschat, W., and W. Wichard. 2010. Baltic amber. *In* D. Penney (editor), Biodiversity of fossils in amber from the major world deposits: 80–115. Manchester: Siri Scientific Press, 304 pp.