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Original Article

Taxonomy of the enigmatic genus *Acanthoniscus* Gosse, 1851 (Isopoda: Oniscidea: Armadillidae), from Jamaica, with the description of a new species

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ABSTRACT

A body entirely covered with long and sharp-pointed spines makes *Acanthoniscus spiniger* Gosse, 1851, one of the rarest and most ornamented terrestrial isopods in the world. The original description of this species was based on a single specimen collected by the British naturalist Philip Henry Gosse in Jamaica in 1845 and deposited in the British Museum (currently The Natural History Museum, London). A second specimen, presumably of this species, was collected by the American entomologist Henry Guernsey Hubbard in 1877 and deposited in the United States National Museum, Smithsonian Institution, which served as the basis for a further description by Richardson (1909). After Gosse and Hubbard specimens, no additional material appears to have reached any museum collection. Due to the scarce available information on this genus, it has been indistinctly placed in at least four different families through history, without a consensus on its definitive placement to date. Herein, we describe a new species of *Acanthoniscus* Gosse, 1851, based on a population discovered in the Blue Mountains, Jamaica, above 1,200 m elevation and more than 150 km eastward of *A. spiniger*'s type locality. We also emend the authorship and diagnoses of the genus *Acanthoniscus* and its type species. Finally, we discuss the possible relationships of *Acanthoniscus* at the family level, concluding that, despite some putative autapomorphies, it belongs to Armadillidae, as its present-day status.

KEYWORDS

Bluefields, Blue Mountains, Crinocheta, Crustacea, Greater Antilles, systematics.

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INTRODUCTION

The Jamaican endemic spiny isopod, *Acanthoniscus spiniger* Gosse, 1851, is one of the rarest and most ornamented Oniscidea in the world, due to its body being entirely covered with long and sharp-pointed spines arranged in longitudinal rows (Kinahan, 1859; Richardson, 1909). The holotype of *A. spiniger* was collected by the British naturalist Philip Henry Gosse during his stay in Jamaica from December 5th, 1844 to June 19th, 1846 (Gosse, 1851). It was supposed to have been described by the naturalist Adam White from the British Museum. However, White (1847: 99) limited his text to naming and listing the specimen, declaring that it was a new species from Jamaica, but he never included an accompanying description. The only information provided by White (1847: 99) reads as follow:

> "Acanthoniscus, White.
> Acanthoniscus spiniger, n. s.
> Jamaica. From the collection of Mr. Gosse."

Referring to the most remarkable West Indian isopod fauna, Schomburgk (1848: 658) wrote: "amongst the Isopoda, an interesting spined species found by Mr. Gosse in Jamaica, is named *Acanthoniscus spiniger*, White, List of Crustacea in British Museum, p. 99." A few years after his return to England, Gosse mentioned in his book on his voyage to Jamaica: "Some other interesting animals were found under stones in this locality ["Bluefields Mountains," see 'Remarks' under *A. spiniger*], though not all at the same time. A curious little dark grey Oniscus, every segment of which is armed with two spines, was numerous; it has been described by my friend, Mr. Adam White, of the British Museum, under the name of *Acanthoniscus spiniger*" (Gosse, 1851: 65).

Kinahan (1859) provided what is considered the original description of the genus and its type species, based on the specimen deposited in the British Museum. Despite Kinahan (1859) considering that White was the author of the genus and species, the lack of a formal description in White (1847) renders *"Acanthoniscus spiniger* White, 1847", a nomen nudum. This fact was first noted and emended by Richardson (1909), who attributed the genus and species authorship (keeping the original binomen) to Kinahan (1859), since he included an important number of characters and the first illustrations of the species in his description, and this has been followed since (e.g., Arcangeli, 1927; Van Name, 1936; Schmalfuss, 2003; Schmidt and Leistikow, 2004; Jass and Klausmeier, 2006). The exception to the latter is Clark and Presswell (2001: 154), who listed "*Acanthoniscus* White (in Kinahan, 1859)" and "*Acanthoniscus spiniger* (in Kinahan, 1859)." Richardson (1909) redescribed *A. spiniger* based on a second specimen collected by the American entomologist Henry Guernsey Hubbard in Jamaica, in 1877, and received by the United States National Museum in 1908, after Hubbard's death (see also Van Name, 1936: 403). Nonetheless, the precise locality of this second specimen is unknown (see 'Discussion'); the original label accompanying it only reads: "*Oniscus spiniger*. Jamaica" (Richardson, 1909: 431). The Gosse and Hubbard specimens seem to be the only known material of *Acanthoniscus* Gosse, 1851, so far studied and deposited in museum collections until the present contribution. It is remarkable that new specimens of *Acanthoniscus* became available now, more than 175 years since the holotype of *A. spiniger* was collected by Gosse, more than 140 years since the last specimen of the genus was collected by Hubbard, and over 110 years after the last comprehensive contribution on the genus (Richardson, 1909). It is fairly "strange" (as noted also by Richardson, 1909) because it seems not to be a rare animal but a "numerous" isopod in Jamaica (Gosse, 1851: 65).

Moreover, the placement of *Acanthoniscus* at the family level has been controversial through history, mainly because of its unique combination of characters and some putative autapomorphies (e.g., unique shape and pattern of pleotelson and uropod) that make it difficult to fit entirely within any of the families currently recognized based on the morphological characters traditionally used. Kinahan (1859) was unable to assign it to a specific family, and later it was indistinctly placed in at least four different families (i.e., Oniscidae Latreille, 1802, Armadillidae Brandt, 1831, Delatorreidae Verhoeff, 1938, and Scleropactidae Verhoeff, 1938; Stebbing, 1893; Budde-Lund, 1879; 1885; 1910; Richardson, 1901; 1905; 1909; Van Name, 1936; Schmalfuss, 2003; Schmidt and Leistikow, 2004; Jass and Klausmeier, 2006; Boyko et al., 2008).

In November 2013, a new population of *Acanthoniscus* was discovered in the Blue Mountains, above 1,200 m elevation and more than 150 km eastward from the *A. spiniger's* type locality. Herein, we describe a new species of *Acanthoniscus* based on the specimens found in the Blue Mountains and emend the diagnoses of the genus and its type species. We also discuss the most satisfactory placement of *Acanthoniscus* at the family level, concluding that, despite some putative autapomorphies, it fits best in Armadillidae, as its present-day status.

MATERIALS AND METHODS

All measurements are expressed in millimeters and were taken under a Zeiss® stereomicroscope with a coupled ×10 widefield measuring eyepiece (20×, 40×). Small pieces such as mouth parts, antennae and pleopods were first clarified with KOH (3%, for about one hour at room temperature) and then mounted on slides with glycerin for observation under a higher magnification under an Olympus® compound microscope (80×, 400×). Photographs of preserved specimens and structures were taken with an Olympus® compact digital camera coupled to an eyepiece. Bright/contrast adjustments of photographs, stacking, cutting out of images and highlighting of some structures were made with Adobe Photoshop® CS. The distribution maps where first obtained from Quantum GIS® ver. 3.22 and Google Earth, and then processed with Adobe Photoshop® CS; datum for all coordinates is WGS 84.

Nomenclature largely follows Schmidt (2002; 2003; 2008). We considered the minimum adult size based on the smallest male with well-differentiated pleopods 1 and 2. The diagnosis and redescription of *A. spiniger* is based on high-resolution photographs of the holotype taken by The Trustees of the Natural History Museum (BMNH), London, England, U.K. (formerly British Museum), as we did not examine it directly and no additional specimens were examined. We evaluated the conservation statuses of the taxa treated following the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Subcommittee, 2019). The material examined was collected as part of the large-scale Caribbean Biogeography (CarBio) project and is deposited in the zoological collection (CZACC) of the Instituto de Ecología y Sistemática (IES), Havana, Cuba. Other acronyms and abbreviations are as follow: USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (= United States National Museum); MYA = Million years ago.

SYSTEMATICS

Order *Isopoda* Latreille, 1817

Suborder *Oniscidea* Latreille, 1802

Section *Crinocheta* Legrand, 1946

Family *Armadillidae* Brandt, 1831

Genus *Acanthoniscus* Gosse, 1851

(Figs. 1–8)

Acanthoniscus White, 1847: 99 (Nomen nudum). — Schomburgk, 1848: 658 (Nomen nudum).

Acanthoniscus Gosse, 1851: 65.

Acanthoniscus Kinahan, 1859: 197–198, plate 200–201. — Budde-Lund, 1879: 5. — Budde-Lund, 1885: 241. — Richardson, 1901: 562, 569. — Richardson, 1905: 636–637 (repeated the description of Kinahan, 1859). — Richardson, 1909: 432. — Budde-Lund, 1910: 11. — Arcangeli, 1927: 135. — Van Name, 1936: 401–402. — Clark and Presswell, 2001: 154. — Schmalfuss, 2003: 4. — Schmidt and Leistikow, 2004: 4. —Boyko et al., 2008.

Type species. *Acanthoniscus spiniger* Gosse, 1851, by monotypy.

Other species included. *Acanthoniscus richardsonae* sp. nov.

Diagnosis (emended). Body of fragile general appearance, with endoantennal conglobation ability involving all body segments (Figs. 2–4); coxal plates enlarged and fused with tergites, with more or less complex inner tooth-like processes forming cleft or schisma (except coxal plate 4, which lacks tooth-like processes) (Figs. 2C, 4F–G). Cephalothorax with upper margin of frontal shield irregular, forming lateral

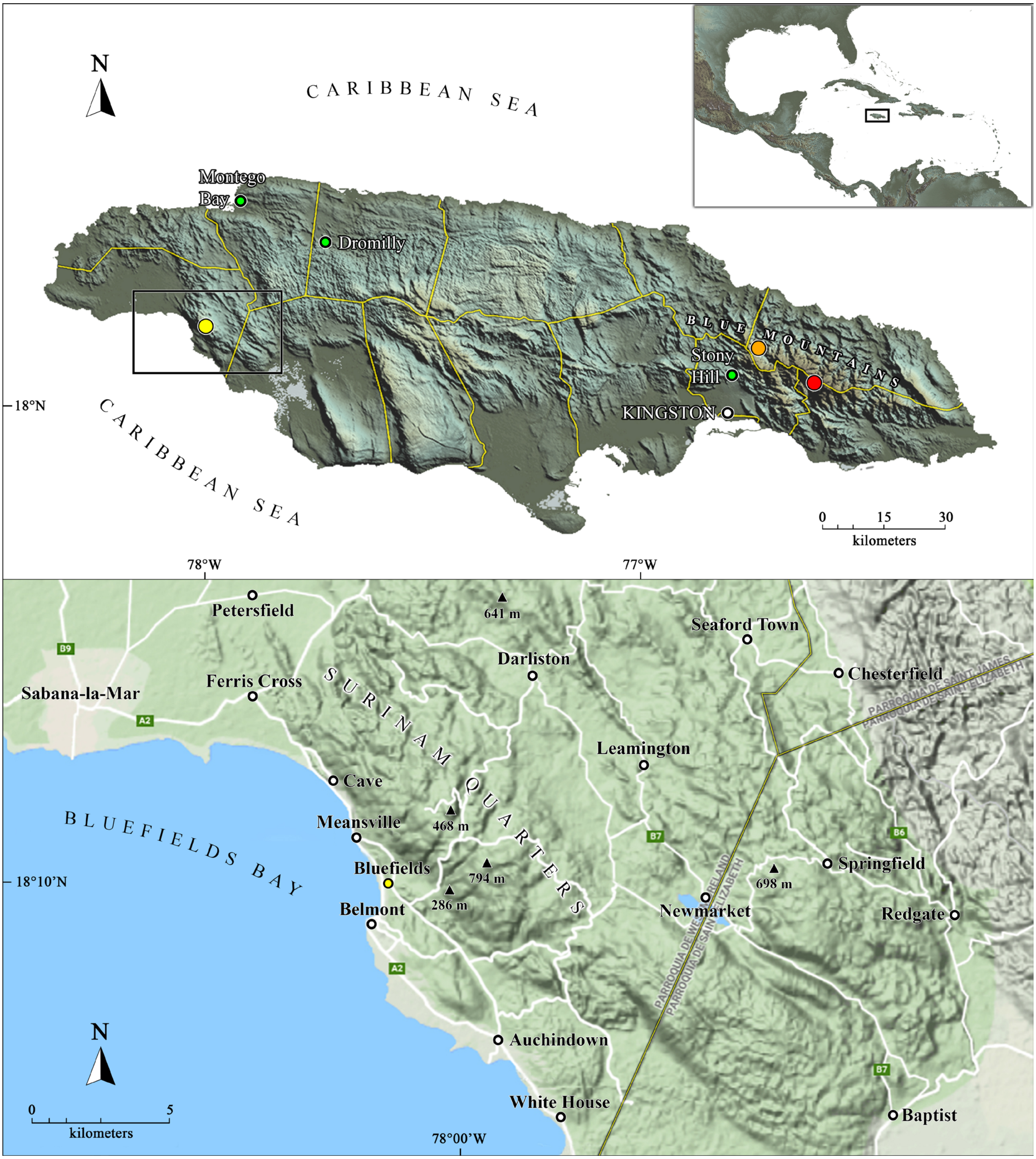

Figure 1. Distribution of the genus *Acanthoniscus* in Jamaica. Above: type locality of *A. spiniger* at the hills near Bluefields (yellow dot), the type locality of *A. richardsonae* sp. nov. in the Blue Mountains (red dot), and a second location in the Blue Mountains where a specimen presumably of *A. richardsonae* sp. nov. was photographed (orange dot). The main collection sites of Henry G. Hubbard in 1877 are depicted by green dots, notice the proximity of Stony Hill to the distribution of *A. richardsonae* sp. nov. Below: The hills known as Surinam Quarters near Bluefields, referred by Gosse (1851) as "Bluefields Mountain," Westmoreland Parish, constitute the type locality of *A. spiniger.*

and median lobes (not antennal lobes); profrons with wide shallow depressions on each side divided by very low median ridge holding second antennae; dorsal surface with small spiniform tubercles and/or medium-sized, club-like spines (Figs. 2, 4). Eyes composed of 16 ommatidia (Figs. 2, 4). Pereon tergites covered with long, slightly sinuous dorsolateral spines and smaller posteromedian and lateral spines, sometimes with paramedian spiniform tubercles; with lateral spiniform tubercle near anterior margin of pereonites 2–7 and directed forward, as part of outer structures involved during conglobation; epimera 1 enlarged, with posterior angle and outer margin broadly rounded, anterior angle more acutely produced; epimera 2–7 enlarged and with acutely produced outer angle; male sternite 7 simple, without bilobed caudal process (Figs. 2–4, 8). Pleon tergites 3–4 with pair of small posteromedian spines or spiniform tubercles; epimera of pleonites 3–5 enlarged and acutely produced (Figs. 2–4). Pleotelson "hourglass-shaped," with basal part wider than distal part, distal margin broadly convex and ending in 2 triangular projections separated by notch, basal half with 2 dorsal spines 1.3–1.5 times as long as pleotelson, widely surpassing its distal margin and uropod exopodite tip (Figs. 2, 4, 8). Uropod sympodite asymmetric and dorsoventrally flattened, filling gap between pleotelson and fifth pleon epimera, broader at base, medial margin deeply concave and irregular, with inner lobe above and basal with respect to insertion point of exopodite which, together with wide transversal dorsal furrow, engaging with pleotelson, outer margin from slightly to widely convex, and medial-posterior angle acutely produced (more or less sharp-pointed); uropod endopodite laterally compressed (outer surface concave to engage with medial margin of uropod sympodite), inserted near base of sympodite and not surpassing distal margin of pleotelson, but it may surpass posterior margin of uropod sympodite (e.g., *A. spiniger*); uropod exopodite extremely long (longer than sympodite), narrow, and slightly curved (stick-shaped), inserted on medial margin of sympodite (visible dorsally and ventrally) and widely surpassing posterior margin of sympodite (by 60–80% of its length) and posterior margin of pleotelson (Figs. 2, 4, 8). Pereiopod dactylus with simple, straight to curved dactylar seta, inner claw, sickle-shaped ungual seta (shorter than inner claw and not surpassing basal half of outer claw length), and other smaller setae similar to aesthetascs of antennae (Fig. 5I, J). First antenna 3-jointed (Fig. 5E–F). Second antenna long and slender, sum of its articles being 2.5 times width of cephalothorax, flagellum 2-jointed and with 2 groups of aesthetascs on distal article (Fig. 5A–D). Pleopods with single spiracle lungs (Fig. 7).

Distribution. Jamaica (Fig. 1).

Comparisons. The genus *Acanthoniscus* very much resembles other specialized (spiny) forms of Old World Armadillidae, such as the genera *Calmanesia* Collinge, 1922, *Echinodillo* Jackson, 1933, *Laureola* Barnard, 1960, *Pseudolaureola* Kwon, Ferrara and Taiti, 1992, and *Tridentodillo* Jackson, 1933 (e.g., Collinge, 1922; Jackson, 1933; Barnard, 1958; 1960a; 1960b; Green, 1963; Vandel, 1977; Kwon et al., 1992; Dalens, 1998). However, *Acanthoniscus* can be readily distinguished from all those other genera by the combination of its unique pleotelson-uropod pattern and its spine arrangement (see Diagnosis above).

Remarks. Schmalfuss (2003) tentatively listed *Acanthoniscus* and its type species, *A. spiniger*, under the family Delatorreidae (it is still listed as such by Boyko et al., 2008, an on-line database), probably because several species in this family (genera *Pseudarmadillo* de Saussure, 1857 and *Cuzcodinella* Armas and Juarrero de Verona, 1999) have the body covered with long and sharp-pointed spines similar to *Acanthoniscus* (see Vandel, 1973a; Armas and Juarrero de Varona, 1999; Juarrero de Varona and Armas, 2003a; 2003b; Armas and Rodríguez-Cabrera, 2016). However, Delatorreidae strongly differ from Armadillidae in the cephalothorax (presence of antennal lobes and furrows in Delatorreidae), number of eye ommatidia (six in Delatorreidae), and the uropod pattern (exopodite very short and inserted on the inner corner of the posterior margin of the sympodite in Delatorreidae) (Armas and Juarrero de Varona, 1999; Schmidt, 2003).

The general pattern of the uropod in *Acanthoniscus* led Schmidt and Leistikow (2004: 4) to suggest that it might belong to the heterogeneous family Scleropactidae (Schmidt, 2002; 2003; 2007; 2008). The flagellum of the second antenna may be either 2-jointed or 3-jointed in Scleropactidae (Schmidt, 2003; 2007; 2008). In Scleropactidae and *Acanthoniscus* the uropod exopodite is inserted on the medial margin of the sympodite and widely surpasses its posterior margin (see Discussion for other divergent forms in Armadillidae; Fig. 8), but the pleotelson in Scleropactidae is subtriangular and much shorter than the uropod sympodite, with the uropod endopodite widely surpassing the distal margins of both the uropod sympodite and the pleotelson.

In a key to the genera of the Oniscidae, Richardson (1901: 562) included *Acanthoniscus* as having "the flagellum of the external antennae quadri-articulate." However, this information must be erroneous, since the flagellum of the second antenna in this genus was unknown until the present contribution, as stated also by Kinahan (1859: 198) and Richardson (1909: 432).

Acanthoniscus spiniger **Gosse, 1851**

(Figs. 1–2)

Acanthoniscus spiniger White, 1847: 99 (Nomen nudum). Schomburgk, 1848: 658 (Nomen nudum).

Acanthoniscus spiniger Gosse, 1851: 65.

Acanthoniscus spiniger Kinahan, 1859: 197–198, plate 200–201 (erroneously designated as the original description by Richardson, 1909). — Budde-Lund, 1879: 5. — Budde-Lund, 1885: 241. — Stebbing, 1893: 432. — Richardson, 1901: 569. — Richardson, 1905: 637 (repeated the description of Kinahan, 1859). — William T. Calman in Richardson, 1909: 434 (see Remarks). — Budde-Lund, 1910: 11 (partim). — Richardson, 1910: 495 (partim). — Arcangeli, 1927: 135 (partim). — Van Name, 1936: 402–403 (partim). — Clark and Presswell, 2001: 154. — Schmalfuss, 2003: 4 (partim). — Schmidt and Leistikow, 2004: 4 (partim). — Jass and Klausmeier, 2006: 4, 6, 25 (partim).

Type material. 1 ♀, holotype, BMNH 1973.478.1. Jamaica. Examined by means of high-resolution pictures.

Diagnosis (emended). Total length: 9.9 mm (holotype). Cephalothorax with angulate lateral lobes and small, triangular median lobe (shorter than lateral lobes); dorsal surface with 2 small posteromedian spiniform tubercles (Fig. 2D, G–I). Pereonites 1–7 with pair of small posteromedian spiniform tubercles, one on either side of median line (Fig. 2A, D, F, M); epimera 2–7 similar and subtriangular (Fig. 2B–D); coxal plates 5–7 with medium-sized submarginal tooth-like process, in basal position, just posterior to pereiopod junction, forming schisma (Fig. 2C); the latter as single schisma engaging with contiguous posterior pereon epimera during conglobation. Pleonites 3–4 with pair of very small posteromedian spiniform tubercles; pleon epimera 3–5 with anterior margin slightly convex (Fig. 2E). Pleotelson with posterior margin ending in 2 prominent triangular projections separated by deep notch (Fig. 2D, J–K). Uropod sympodite "subtriangular," outer margin slightly convex, medial-posterior angle triangular and not reaching distal margin of pleotelson; endopodite widely surpassing posterior margin of sympodite and almost reaching distal margin of pleotelson (not visible dorsally) (Fig. 2J–L).

Cephalothorax (Fig. 2G–I). More than 3 times (3.2) as wide as long, with angulate lateral lobes and small, triangular median lobe (shorter than lateral lobes). Dorsal surface with 2 small, posteromedian spiniform tubercles (one on either side of the median line) close to eyes.

Pereon (Fig. 2A–D, F). Pereonite 1, 2.2 times as wide and 1.9 times as long as cephalothorax, with 2 very long, slightly sinuous dorsolateral spines (broken, but probably more than twice length of pereonite 1), pair of small posteromedian spiniform tubercles (one on either side of the median line), and smaller lateral spine on either side near posterior margin, directed backward; pereonites 2–7 similar, 3.5 times as wide as long (pereonite 7 slightly narrower), with 2 very long slightly sinuous dorsolateral spines (twice the length of pereonite 1), pair of small posteromedian spiniform tubercles (one on either side of median line), smaller lateral spine on either side near posterior margin, slightly curved and directed backward (gradually increasing in length posteriorly, being lateral spines of seventh tergite about half as long as dorsolateral spines), and spiniform tubercle near anterior margin and directed forward (engaging with previous tergite during conglobation, decreasing in size posteriorly,

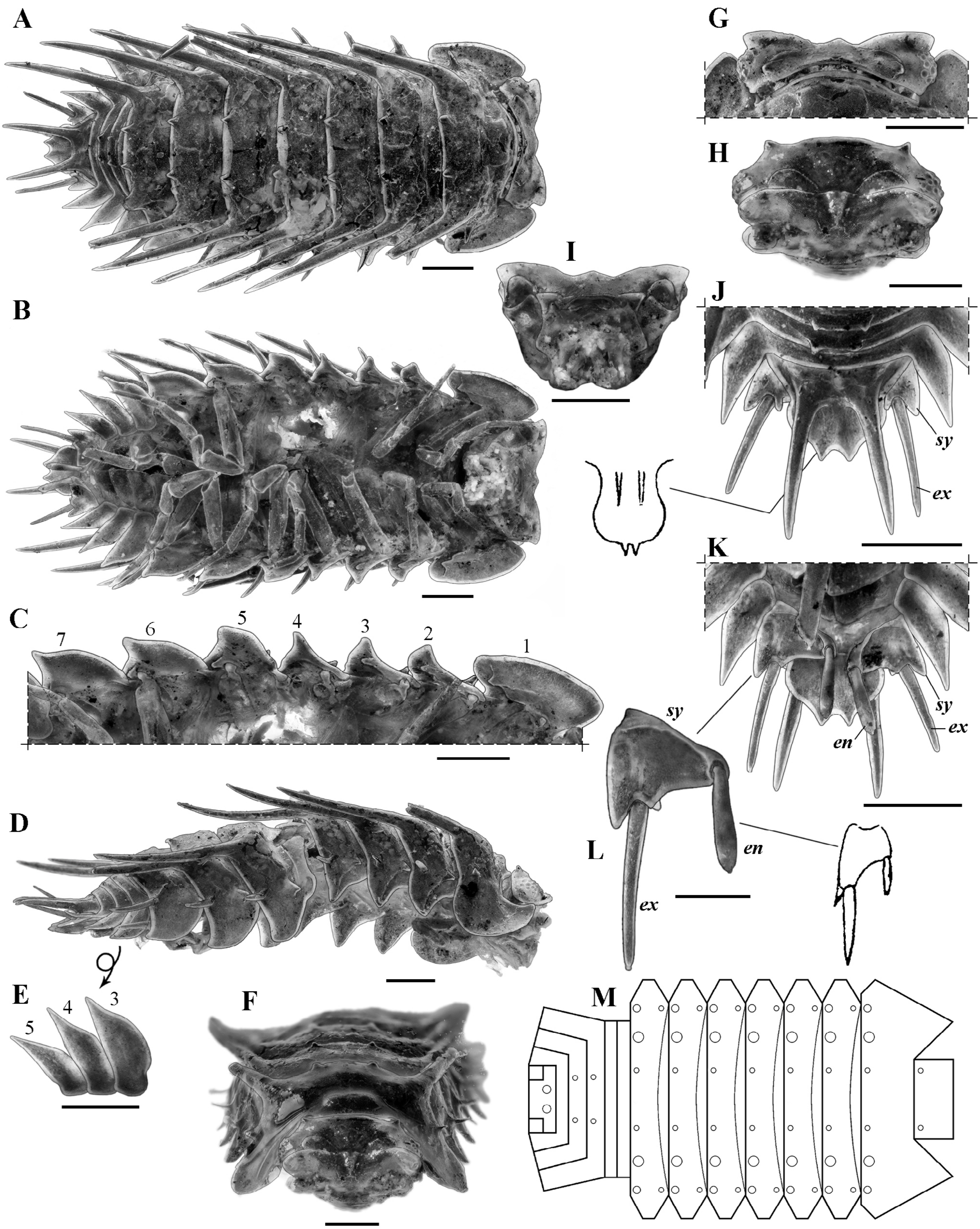

Figure 2. Body parts of *Acanthoniscus spiniger* (female holotype BMNH 1973.478.1). **A**, Overall, dorsal view; **B**, overall, ventral view; **C**, right pereon-epimera 1–7 in ventral view; **D**, overall, lateral view; **E**, right pleon-epimera 3–5 in ventral view ; **F**, overall, frontal view; **G**, cephalothorax in dorsal view; **H**, cephalothorax in frontal view; **I**, cephalothorax in ventral view; **J**, pleotelson and uropods in dorsal view ; **K**, pleotelson and uropods in ventral view; **L**, right uropod in ventral view; **M**, arrangement of dorsal spines, the diameters of the circles correspond to the relative size of the spines. Drawings of the corresponding structures modified from Kinahan (1859) are included in J and L. Abbreviations: sympodite (*sy*), endopodite (*en*), and exopodite (*ex*). Scale bars = 1 mm (A–K), 0.5 mm (L). Original photographs by The Trustees of the BMNH.

vestigial on pereonite 7). Epimera 1 with posterior angle and outer margin broadly rounded, anterior angle more acutely produced, dorsal surface concave; epimera 2–4 similar and subtriangular (epimera 4 only slightly differentiated from epimera 2–3), with anterior margin slightly concave and posterior margin slightly convex, outer angle acutely produced; epimera 5–7 more or less subtriangular, with anterior margin moderately convex and posterior margin concave, outer angle acutely produced and directed backward. Coxal plates 1–3 with small inner tooth-like process near posterior margin and directed backward, in medial position, forming small schisma and, in coxal plate 1, extending into shallow transversal groove toward base of coxa; coxal plate 4 without tooth-like processes; coxal plates 5–7 with medium-sized submarginal tooth-like process, in basal position, just posterior to pereiopod junction, forming schisma; the latter as single schisma engaging with contiguous posterior pereon epimera during conglobation.

Pleon (Fig. 2A–B, D–E). Tergites 1, 2, and 5 without spines; tergites 3 and 4 with pair of very small posteromedian spiniform tubercles (one on either side of median line); epimera of pleonites 3–5 acutely produced, similar in shape and size, with anterior margin slightly convex, posterior margin straight, and outer angle acutely produced (sharp-pointed).

Pleotelson (Fig. 2D, J–K). Basal part 1.7 times wider than distal part, 1.4 times as wide as long, with both dorsal spines 1.3 times as long as pleotelson; distal margin ending in 2 prominent triangular projections, separated by deep notch (0.8 times as deep as median diameter of pleotelson spines).

Uropods (Fig. 2J–L). Sympodite subtriangular, 1.2 times as long as wide, ventral surface slightly concave (although it might be a consequence of dehydration during the time it was preserved dry, see Remarks), outer margin slightly convex, medial-posterior angle triangular and not reaching posterior margin of pleotelson, medial margin with well-developed, produced inner lobe above and basal with respect to insertion of exopodite; endopodite widely surpassing posterior margin of sympodite and almost reaching distal margin of pleotelson (not visible dorsally); exopodite nearly 1.5 times as long as sympodite and surpassing posterior margin of sympodite by 80% of its length.

Distribution. Known only from the type locality, "Bluefields Mountain" (sensu Gosse, 1851), which most certainly refers to the hills known as Surinam Quarters, immediately eastward and northward of Bluefields, Westmoreland Parish, southwestern Jamaica (Fig. 1; see Remarks).

Natural history. According to Gosse (1851), the area where *A. spiniger* was found (see Remarks) was in part covered with forest at the collection time (early February, 1845), but he made reference to the high level of disturbance because of agriculture (e.g., coffee, pimento, fruits, sugarcane), logging and livestock farming (see also Curtin, 1991; 2010; Scolaro, 2013). Indeed, he secured the isopod, together with some land snails, earthworms, and a small onychophoran, under stones "in a piece of ground just reclaimed from the forest, cleared and burnt over, but not yet planted, full of blackened stumps and stones" (Gosse, 1851: 65).

Remarks. The holotype of *A. spiniger* is exceptionally well preserved given the time span since its collection (> 175 years); only the second antennae were missing, some pereiopods, mouth pieces, and some of the longest spines on the pereon were broken (two on pereonite 1, left on pereonite 4, and right on pereonite 7) (Fig. 2). It was originally preserved dry and later it was transferred to ethanol, but it remains very rigid and the pleopods cannot be manipulated without risk of rupture, and the pin hole still can be observed in the right side of pereonite 4 (Miranda Lowe, in litt. 24.IX.2021; Fig. 2A–D).

Schmidt and Leistikow (2004) were the first authors to mention the catalog numbers associated with the holotype of *A. spiniger* deposited at the BMNH. The current catalog number appears in the Crustacea register (1969–1976, p. 119), as well as in the current on-line catalog (Natural History Museum, 2014). Previous registration numbers: BMNH 1845.110 (Entomology register: Annulosa Vol. II, 1840–1849, p. 195: it says six crustacea specimens purchased from Mr. Gosse; Locality: Jamaica; but the remaining five specimens do not correspond to this species: Miranda Lowe, in litt. 24.IX and 7.XII.2021); White's catalog no. 1024 (White's Catalogue of Crustacea, Vol. III, 1845–1847?,

p. 1024: the precise date for this catalog is unknown, but falls within the previous range). The registration no. "1845.118" allocated by Ms. Joan Ellis (see also Schmidt and Leistikow, 2004: 4) is incorrect, the result of a mistake when doing the cross referencing, it should have said 1845.110, since 1845.118 is allocated also to another batch of specimens in the same catalog (Crustacea register 1969–1976; Miranda Lowe, in litt. 24.IX and 7.XII.2021).

Jass and Klausmeier (2006) wrongly stated that "Richardson [1909] redescribed the species under the genus *Oniscus*," probably because she cited the content of the original accompanying label that reads "*Oniscus spiniger*," which does not constitute a published work and therefore it must not be considered a valid synonym (ICZN, 1999: Art. 9); see Additional material under *A. richardsonae* sp. nov.

According to ICZN (1999: Art. 12), "To be available, every new name published before 1931 must satisfy the provisions of Article 11 and must be accompanied by a description or a definition of the taxon that it denotes, or by an indication." The way Schomburgk (1848) referred to the species ("spined"), seems most likely an extraction of evident information from the Latin name. However, "little dark grey Oniscus, every segment of which is armed with two spines," as stated by Gosse (1851: 65), satisfies the concept of description before 1931 (e.g., ICZN, 1999: Arts. 12 and 13), plus all the additional information provided by this author regarding the type locality and habitat (he was the collector of the type specimen, see below). Following the Principle of Priority (ICZN, 1999: Art. 23), the author of *A. spiniger*, and therefore of the genus *Acanthoniscus*, must be Gosse (1851) and not Kinahan (1859). Gosse's (1851) book is a published work within the meaning of the Code (Art. 8). Gosse in the same work wrote: "Twenty-four new species of animals are described in the following pages, distributed nearly equally through the classes of Mammalia, Reptiles, and Fishes." Many of those taxa are still recognized in the present day: i.e., the fishes *Gambusia melapleura* (Gosse, 1851) (Poeciliidae), *Jenkinsia lamprotaenia* (Gosse, 1851) (Clupeidae), *Parexocoetus hillianus* (Gosse, 1851) (Exocoetidae), and *Trinectes inscriptus* (Gosse, 1851) (Achiridae), the frog *Eleutherodactylus luteolus* (Gosse, 1851) (Eleutherodactylidae), the snakes *Hypsirhynchus ater* (Gosse, 1851) and *H. callilaemus* (Gosse, 1851) (Dipsadidae), and the bat *Pteronotus macleayii griseus* (Gosse, 1851) (Mormoopidae) (Wilson and Reeder, 2005; Froese and Pauly, 2021; Uetz et al., 2022; AmphibiaWeb, 2022). Furthermore, this is an unusual case in that there is an objective continuity in the taxonomic concept of Gosse (1851) and Kinahan (1859), since they refer to the same specimen and kept the binomen given by White (1847). This taxonomic concept was simply improved by Kinahan (1859), then by Richardson (1909) and now in the present contribution. Clark and Presswell (2001: 154) cited "*Acanthoniscus* White (in Kinahan, 1859)" and "*Acanthoniscus spiniger* White (in Kinahan, 1859)," which is wrong, since Kinahan (1859) just recognized a source that did not include a description, same as Gosse (1851).

Philip H. Gosse spent most of his time in Jamaica around Bluefields Bay (Fig. 1), in the southwestern part of the island (Gosse, 1851). The holotype was most certainly collected at "Bluefields Mountain," which according to Gosse, refers to "the lofty mountain that rises behind" Bluefields, a town where he stayed for several months (Gosse, 1851). He also commented: "A ride of four or five miles brought me to the brow of the mountain" (Gosse, 1851: 61), which gives an idea of the proximity to Bluefields. Gosse even mentioned that as he "draw nearer the lofty summit […] Savanna-le-Mar [Savanna-la-Mar] […], St. John's Point and even the extreme western headlands, North and South Negril appeared just at hand" (Gosse, 1851: 62). Therefore, this "Bluefields Mountain" must certainly refer to the hills immediately eastward and northward of Bluefields, on the eastern side of Bluefields Bay, within a subcoastal mountainous area known as Suriname Quarters, Westmoreland Parish, southwestern Jamaica (Fig. 1). These hills include elevations such as Bluefields Peak (794 m a.s.l.), Mount Pleasant (468 m a.s.l.), and Shafston (286 m a.s.l.) (Fig. 1; Scolaro, 2013). Gosse even made an estimate of 1,500 feet elevation (> 450 m; Gosse, 1851: 63) near the collection point, which coincides with the heights of the area. Moreover, he mentioned a higher peak nearby "covered with the original forest," shaded and humid, with abundance of lycophytes and tree-ferns (Bluefields Peak?), suggesting that the collection point was not at the highest peak of these mountains (Gosse, 1851: 66).

Despite all the above information provided by Gosse, a precise locality within Jamaica was never mentioned for *A. spiniger*, neither in the description by Kinahan (1859) nor in further contributions redescribing, listing or just mentioning the species (Budde-Lund, 1879; 1885; 1910; Stebbing, 1893; Richardson, 1901; 1905; 1909; 1910; Arcangeli, 1927; Schmalfuss, 2003; Schmidt and Leistikow, 2004; Jass and Klausmeier, 2006). The exception was Van Name (1936), who made reference to Gosse's (1851) writings about the "Bluefields Mountains" as the collection site of this isopod. Therefore, according to the ICZN (1999: Art. 76) and given the impossibility to specify an exact collection point, these hills above 400 m elevation known as Surinam Quarters, immediately eastward and northward of Bluefields (approximate coordinates: 18°10'45"N 78°00'00"W; Fig. 1), Westmoreland Parish, must be considered the type locality of *A. spiniger*.

***Acanthoniscus richardsonae* sp. nov.**

(Figs. 1, 3–8, 10)

ZooBank: urn:lsid:zoobank.org:act:EBB60F4A-ECDB-44F6-8110-8A7C06D2AE78

Acanthoniscus spiniger (partim): Richardson, 1909: 431–434 (misidentification). — Budde-Lund, 1910: 11 (partim). — Richardson, 1910: 495 (partim). — Arcangeli, 1927: 135 (partim). — Van Name, 1936: 402–403 (partim). — Schmalfuss, 2003: 4 (partim). — Schmidt and Leistikow, 2004: 4 (partim). — Jass and Klausmeier, 2006: 4, 6, 25 (partim).

Type material. Holotype: 1 ♂ (CZACC 5.0500), around the ranger station (18°03'12.6"N 76°33'47.2"W, approximately 1,250 m a.s.l.), Blue Mountains, Saint Thomas Parish, Jamaica (Fig. 1), 15 November 2013, Abel Pérez-González and Franklyn Cala Riquelme (collectors' code: "JA 10-2", "1671Caribbean"). Paratypes: 2 ♂♂, 6 ♀♀, 2 juvs. (CZACC 5.0501), same data as the holotype.

Additional material (not paratype). Jamaica (unknown locality), a single specimen collected by Hubbard in 1877, the original label reads: "*Oniscus spiniger*. Jamaica" (Richardson, 1909: 431). The current catalog number is: USNM 41501 (https://n2t.net/ark:/65665/3ac606ed9-99f9-4214-891d-1e92ed7ccbe4). This specimen served as the basis for Richardson's (1909) description, assumed as a redescription of *A. spiniger*. It was not possible for us to review this specimen directly or by pictures.

Diagnosis (Diagnosis and description are the same for the holotype and the paratypes, unless specified). Maximum total length: 7.2 mm in males (holotype) and 8.5 mm in females (see Variation). Cephalothorax with rounded lateral lobes, and a well-developed, deeply notched median lobe, forming two triangular projections, dorsal surface with a pair of small paramedian spiniform tubercles and three medium-sized, club-like, posteromedian spines (Fig. 4C, H–J). Pereonite 1 with two pairs of paramedian spiniform tubercles and three medium-sized posteromedian spines; pereonites 2–7 with a pair of paramedian spiniform tubercles and three medium-sized posteromedian spines (Fig. 4A, C–D, O–P); epimera more or less quadrangular (except epimera 4: subtriangular, very narrow and sharp-pointed), with anterior (epimera 2–3) or posterior (epimera 5–7) margins widely convex and produced (forming an almost square angle) (Fig. 4C, F); coxal plates 5–7 with a medium-sized tooth-like process, in medial position, forming a schisma and extending anteriorly into an oblique, very shallow, longitudinal groove, and with a very small submarginal tooth-like process, in basal position, just posterior to pereiopod's junction, forming a second very small schisma; latter two schisma forming a continuum engaging with the contiguous posterior pereon epimera during conglobation (Fig. 4F). Pleonites 3–4 with a pair of small posteromedian spines; pleon epimera 3–5 with anterior margin widely convex and produced (forming an almost square angle) (Fig. 4E). Pleotelson with posterior margin ending in two small triangular projections separated by a shallow notch (Figs. 4D, K–L, 8F). Uropod sympodite "subtrapezoidal," outer margin widely convex and produced (forming an almost square angle), medial-posterior angle narrow, and approximately at same level or slightly surpassing the distal margin of pleotelson; endopodite surpassing the insertion of exopodite, but not surpassing either the posterior margin of sympodite or the distal margin of pleotelson (Figs. 4K–N, 8G).

Cephalothorax (Fig. 4C, H–J). Nearly three times (2.7) as wide as long, with rounded lateral lobes, and well-developed, deeply notched median lobe, forming 2 triangular projections slightly bent upward. Dorsal surface with pair of small paramedian spiniform tubercles and 3 medium-sized, club-like, posteromedian spines, one on the median line and one on either side close to the eyes; lateral spines about half length of cephalothorax, median spine smaller than lateral ones. Eyes with tiny scale-setae inserted on inter-ommatidia space (observable only at > 80×).

Pereon (Figs. 3, 4A, C–D, F–G, O–P). Pereonite 1, 3 times as wide and 1.5 times as long as cephalothorax, with 2 very long, slightly sinuous dorsolateral spines (twice the length of pereonite 1), 2 pairs of paramedian spiniform tubercles (2 on either side of median line), 3 medium-sized posteromedian spines (0.3 times as long as pereonite 1, 1 on the median line), and smaller lateral spine on either side near posterior margin, directed backward and slightly bent upward; pereonites 2–7 similar, four times as wide as long (pereonite 7 slightly narrower), with 2 very long slightly sinuous dorsolateral spines (twice the length of pereonite 1), pair of paramedian spiniform tubercles (one on either side of median line), 3 medium-sized posteromedian spines, smaller lateral spine on each side near posterior margin, straight and directed backward and slightly outward (gradually increasing in length posteriorly, being lateral spines of seventh tergite about half as long as dorsolateral spines), and spiniform tubercle near anterior margin and directed forward (engaging with previous tergite during conglobation, decreasing in size posteriorly, vestigial on pereonite 7). Epimera 1 with posterior angle and outer margin broadly rounded, anterior angle more acutely produced, dorsal surface concave; epimera 2–3 more or less quadrangular and narrow, with anterior margin concave and posterior margin widely convex, produced distally and then straight toward median region, outer angle acutely produced and directed forward; epimera 4 subtriangular, very narrow and sharp-pointed, and strongly differentiated from epimera 2–3; epimera 5–7 more or less quadrangular, with anterior margin widely convex and produced distally (forming almost square angle), posterior margin concave, and outer angle acutely produced (sharp-pointed) and directed backward. Coxal plates 1–3 with small inner tooth-like process near posterior margin and directed backward, in medial position, forming small schisma and, in coxal plate 1, extending into shallow transverse groove toward base of coxa; coxal plate 4 without tooth-like processes; coxal plates 5–7 with medium-sized tooth-like process, in medial position and near posterior margin, directed backward, forming schisma and extending anteriorly into oblique, very shallow, longitudinal groove, and with very small submarginal tooth-like process, in basal position, just posterior to pereiopod junction, forming second very small schisma; the latter 2 schisma forming continuum engaging with contiguous posterior pereon epimera during conglobation.

Figure 3. Right lateral view of a female paratype *Acanthoniscus richardsonae* sp. nov. showing coloration in alcohol. Scale bar = 1 mm.

Pleon (Fig. 4A, D–E). Tergites 1, 2, and 5 without spines; tergites 3–4 with pair of small posteromedian spines (one on either side of the median line) as long as pleonite length; epimera of pleonites 3–5 acutely produced, similar in shape and size, with anterior margin widely convex and produced medially (forming almost square angle), posterior margin straight, and outer angle acutely produced (sharp-pointed).

Pleotelson (Figs. 4D, K–L, 8F). Basal part 1.7 times wider than distal part, 1.4 times as wide as long, with both dorsal spines 1.3–1.5 times as long as pleotelson; distal margin ending in 2 small triangular projections separated by shallow notch (0.3 times as deep as the median diameter of pleotelson spines).

Uropods (Figs. 4K–N, 8G). Sympodite subtrapezoidal, 1.3 times as long as wide, ventral surface flat, outer margin widely convex and produced (forming almost square angle), medial-posterior angle narrow and approximately at same level, or slightly surpassing, distal margin of

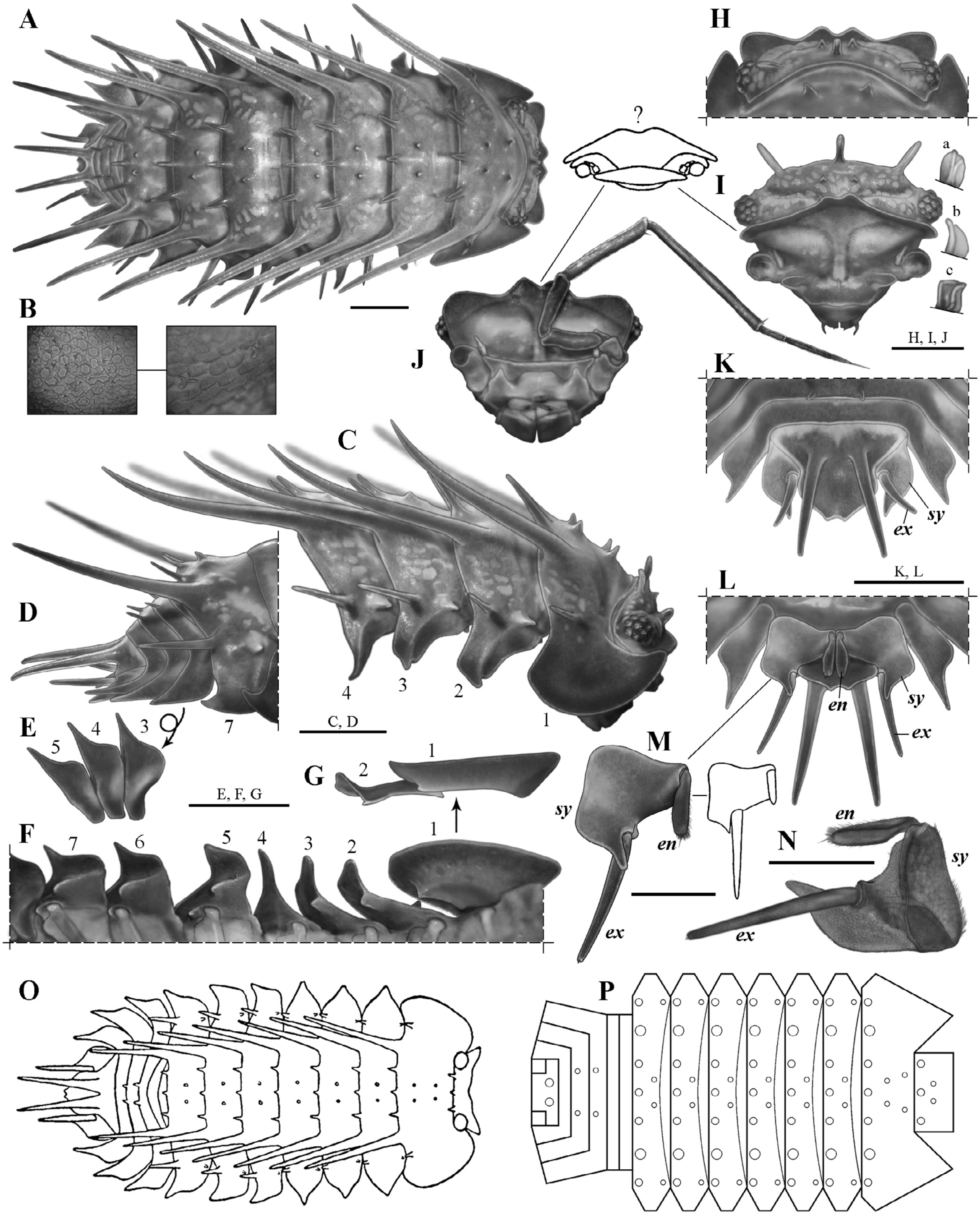

Figure 4. Body parts of *Acanthoniscus richardsonae* sp. nov. **A**, Overall, dorsal view; **B**, detail of the microsculpture of the dorsal tegument (left) and tricorn-like setae (right); **C**, lateral view of the anterior region of the body; **D**, lateral view of the posterior region of the body; **E**, right pleon-epimera 3–5 in ventral view; **F**, right pereon-epimera 1–7 in ventral view; **G**, detail of pereon-epimera 1–2 in a more ventral position; **H**, cephalothorax in dorsal view; **I**, cephalothorax in frontal view (the tiny sensory setae inserted between the ommatidia are illustrated under a magnification of 400×: a, b, c); **J**, cephalothorax in ventral view; **K**, pleotelson and uropods in dorsal view (the uropod exopodites are slightly pointing upward); **L**, pleotelson and uropods in ventral view; **M**, right uropod in ventral view; **N**, right uropod in dorsal view; **O**, drawing of the overall dorsal view modified from Richardson (1909); **P**, arrangement of dorsal spines, the diameters of the circles correspond to the relative size of the spines. Drawings of the corresponding structures modified from Richardson (1909) are included in **I, J** (the question mark means that the position representing the drawing is not totally clear) and in **M**. Abbreviations: sympodite (*sy*), endopodite (*en*), and exopodite (*ex*). Scale bars = 1 mm (**A–L**), 0.5 mm (**M–N**); in some cases, a single scale bar applies to more than one figure (indicated by the letters above the scale bar).

pleotelson, medial margin with very small inner lobe above and basal with respect to insertion of exopodite; endopodite surpassing insertion of exopodite, but not surpassing either posterior margin of sympodite or distal margin of pleotelson (not visible dorsally); exopodite 1.1 times as long as sympodite and surpassing posterior margin of sympodite by 60% of its length.

Antennae (Figs. 4J, 5A–D). First antenna 3-jointed; first article thick, sub-cylindrical, twice the length of second article and 1.6 times as long as third article; second article shortest and sub-conical in shape; third article narrow and asymmetric, slightly curved, with row of eight aesthetascs in subapical position. Second antenna flagellum with distal article 3 times longer

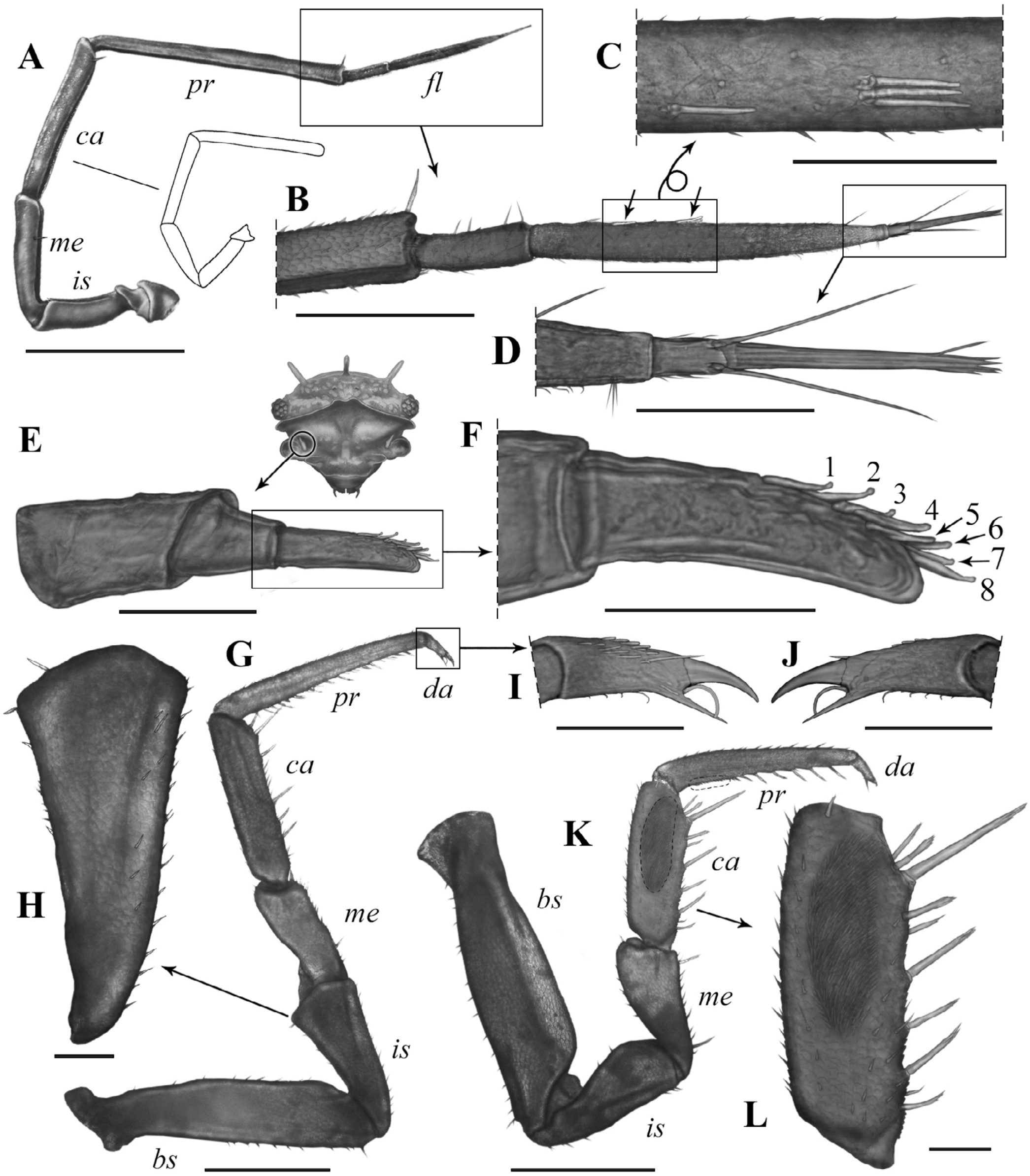

Figure 5. Other appendages of *Acanthoniscus richardsonae* sp. nov. **A**, Second antenna; **B**, detail of flagellum of second antenna depicting position of aesthetasc groups (small arrows); **C**, detail of the distal article of the flagellum of the second antenna slightly turned over showing the aesthetasc groups; **D**, detail of the distal-most portion of the flagellum of the second antenna showing the apical cone; **E**, first antenna; **F**, detail of the third article of the first antenna showing the aesthetascs; **G**, male left seventh pereiopod; **H**, detail of ischium of male seventh pereiopod; **I**, detail of dactylus of male seventh pereiopod in anterior view; **J**, detail of dactylus of male seventh pereiopod in posterior view; **K**, male left first pereiopod, showing the areas on the carpus and propodus covered with the cleaning apparatus or antennal brush (dashed outlines); **L**, detail of carpus of male first pereiopod (anterior surface). Abbreviations: basis (*bs*), ischium (*is*), merus (*me*), carpus (*ca*), propodus (*pr*), flagellum (*fl*), and dactylus (*da*). Drawing of the corresponding structure modified from Richardson (1909) is included in **A**. Scale bars = 1 mm (**A**), 0.5 mm (**G, K**), 0.3 mm (**B**), 0.1 mm (**C–E, H–J, L**), 0.05 mm (**F**).

than basal article, with aesthetasc group on basal-most quarter and other near middle region (formula: 1–3), and tuft of 3 small setae near distal end, apical cone as long as basal article of flagellum and hence 3 times shorter than distal article, with 2 long lateral free sensilla inserted on basal-most quarter and nearly reaching tip of cone; ischium nearly as long as merus, carpus 1.3 times longer than merus, propodus 1.5 times longer than carpus and 1.3 times longer than flagellum; ischium, merus, carpus, and propodus with deep groove along entire inner surface.

Mouthparts (Fig. 6). Left mandible in anterior view (in distal-proximal order) with a narrow quadricuspid incisor process, lacinia mobilis bicuspid with smaller inner lobe, hairy lobe bearing 2 penicils, 1 free penicil, and tuft of hairy setae as molar process. Right mandible in anterior view (in distal-proximal order) with wider quadricuspid incisor process, oval hyaline process, hairy lobe bearing 2 penicils, and tuft of hairy setae as molar process. Hypopharynx with middle lobe notched at tip, with groups of relatively large setae along outer margin of lateral lobes, inner margin of lateral lobes densely hirsute. First maxilla outer endite with outer margin deeply curved distally and with marginal fringe of small setae and 10 simple tooth-like setae of approximately equal in length: outer group composed of 4 strong setae (lateral-most considerably stronger) and small triangular lobe, inner group composed of 6 slender setae, with very small subapical seta between both groups of tooth setae; inner endite with 2 subapical thickset penicils and slightly produced, rounded laterodistal corner.

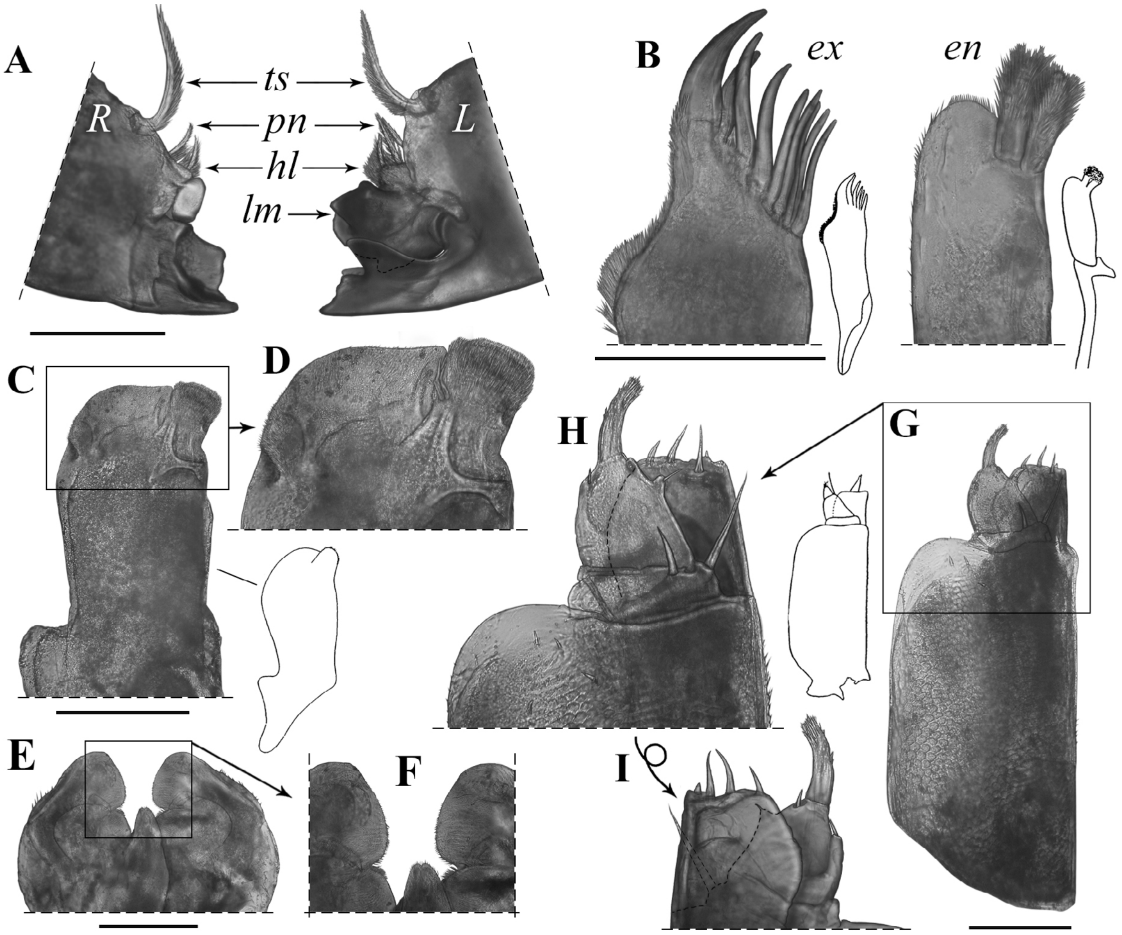

Figure 6. Mouthparts of *Acanthoniscus richardsonae* sp. nov. **A**, Distal portion of right (*R*) and left (*L*) mandibles in anterior views, showing lacinia mobilis (*lm*), hairy lobe (*hl*), penicils (*pn*), and tuft of setae (ts); **B**, first maxilla, with detail of distal portion of outer endite (*ex*) and inner endite (*en*); **C**, second maxilla; **D**, detail of the distal-most portion of the second maxilla; **E**, hypopharynx; **F**, detail of the median region of hypopharynx; **G**, maxilliped; **H**, detail of the distal-most portion of maxilliped in posterior view; **I**, detail of the distal-most portion of maxilliped in anterior view. Drawings of the corresponding structures modified from Richardson (1909) are included in **B, C**, and **G**. Scale bars = 0.25 mm.

Second maxilla outer lobe wider and sensilla scattered, with outer notch; inner lobe narrower, with sensilla concentrated in dense field on mediodistal corner; with 2–3 differentiated setae in incision between both lobes, on medial margin of inner lobe. Maxilliped basipodite with nearly parallel outer and inner margins and wide lamella on distal portion of outer margin, with scaly surface and scattered small setae; endite apically truncate, with 3 enlarged subapical setae on posterior surface and outer corner with 2 small rounded lobes, one of them ending in tiny button-like seta; palpus with middle and distal article fused; basal article bearing 2 strong setae, outer one nearly reaching distal margin of endite; middle article with 2 "tufts" on medial margin bearing small single seta each (basal-most one on produced lobe), and single seta on outer-distal margin; apical article narrow and bent inward, ending in tuft of setae and with tiny subapical seta on outer margin.

Pereiopods (Fig. 5G–L). Basis of pereiopod 1 with dorsal ridge and dorsal surface with longitudinal groove; carpus ventral surface with 9 multi-apex setae, with one in subapical position nearly duplicating size of others; cleaning apparatus, antennal brush, or antenna-grooming brush broad and covering slightly over half of carpus anterior surface and also present on ventral surface of basal-most third of propodus. Male pereiopod 7 without special modifications, with 6 multi-apex setae on ventral surface of carpus, one in subapical position duplicating size of the others; ischium sub-conical, 2.3 times as long as wide.

Pleopods (Fig. 7). Exopodites 1–5 with tracheal structures and single elongate spiracle; first female endopodite absent, first exopodite vestigial. Endopodite 1 in males slightly curved outward distally, 3.7 times as long as wide, distal part without spines; exopodite 1 in males asymmetric, 1.5 times as long as wide, with narrower inner margin, tiny setae

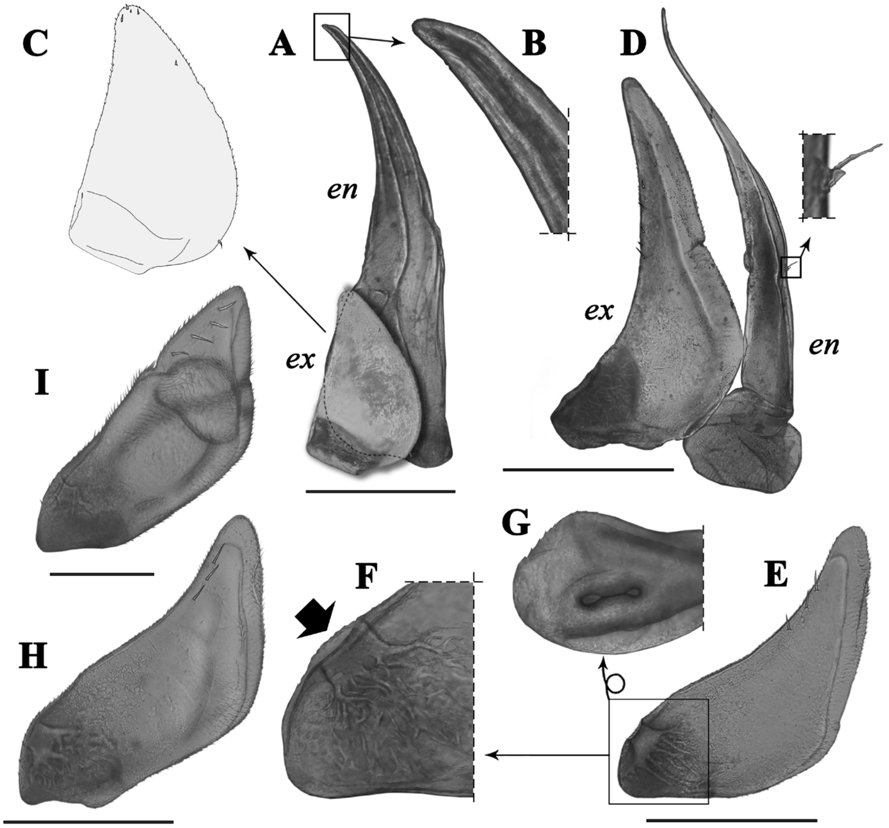

Figure 7. Pleopods of a male *Acanthoniscus richardsonae* sp. nov. **A**, First pleopod; **B**, detail of first pleopod endopodite tip; **C**, detail of first pleopod exopodite; **D**, second pleopod, with detail of the two setae on exopodite outer margin (arrow); **E**, third pleopod exopodite; **F**, detail of the outer-basal region of the third pleopod exopodite showing the respiratory structures (thick arrow indicates the position of the spiracle); **G**, detail of the outer-basal region of the third pleopod exopodite showing the spiracle partially closed from above; **H**, fourth pleopod exopodite; I, fifth pleopod exopodite. Abbreviations: endopodite (*en*) and exopodite (*ex*). Scale bars = 0.5 mm (**A–H**), 0.25 mm (**I**).

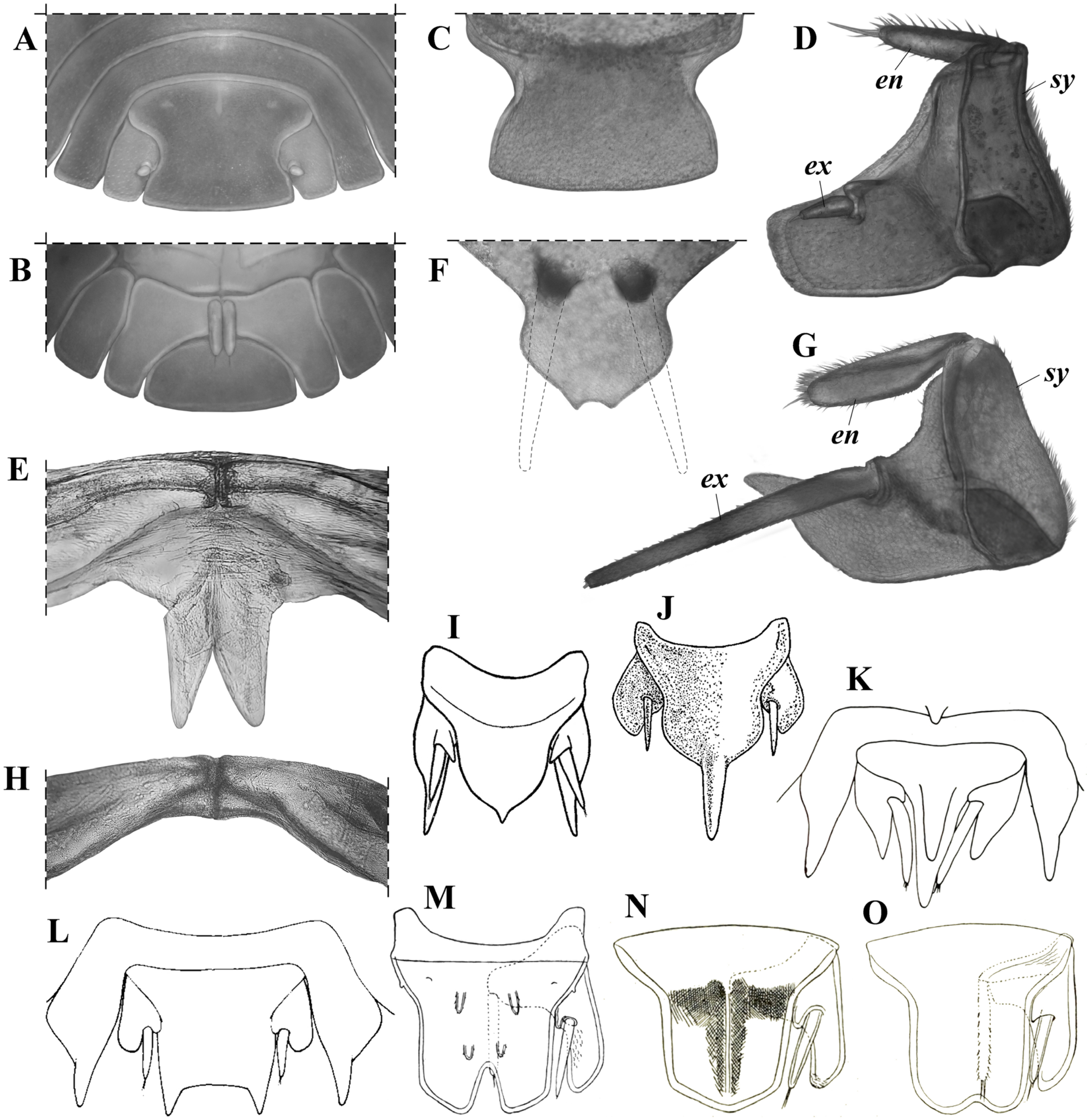

Figure 8. Selected body parts of *Acanthoniscus* for comparison with other taxa within Armadillidae. *Cubaris murina* Brandt, 1833, showing the ground pattern in Armadillidae (**A**–**E**): **A**, Posterior region of the body in dorsal view; **B**, posterior region of the body in ventral view; **C**, pleotelson in dorsal view; **D**, uropod in dorsal view; **E**, middle region of the sternite 7 of a male showing the bilobed caudal process on the posterior margin, which is considered an autapomorphy of Armadillidae. *Acanthoniscus richardsonae* sp. nov. (**F**–**H**): **F**, pleotelson in dorsal view; **G**, uropod in dorsal view; **H**, middle region of the sternite 7 of a male. Drawings of the pleotelson and uropods in dorsal views of some morphologically divergent taxa within Armadillidae. **I**, *Echinodillo cavaticus* Green, 1963; **J**, *Echinodillo montanus* Jackson, 1933; **K**, *Laureola vietnamensis* Kwon, Ferrara and Taiti, 1992; **L**, *Laureola dubia* Schmalfuss and Ferrara, 1983; **M**, *Schismadillo rouxi* Verhoeff, 1926; **N**, *Merulanella wahrbergi* Verhoeff, 1926; **O**, *Nesodillo incisus* Verhoeff, 1926. Drawings modified from Verhoeff (1926) (**M**–**O**), Jackson (1933) (**J**), Green (1963) (**I**), Schmalfuss and Ferrara (1983) (**L**), and Kwon et al. (1992) (**K**). Abbreviations: endopodite (*en*), exopodite (*ex*), sympodite (*sy*).

distributed along entire margin, 1 larger apical seta on inner narrow margin, 3 subapical setae, 1 seta on outer margin and 1 submarginal seta one-third before apex. Exopodite 2 in males very wide basally and narrow distally, 1.8 times as long as wide, with 5 submarginal setae; inner margin with tiny setae and notch in middle region; endopodite 2 in males slightly surpassing tip of exopodite 2 and with 2 setae on outer margin near median region (one of them long and slender and the other short and spatulate). Exopodites 3–4 with 3 submarginal setae near outer-distal margin. Exopodite 5 widely convex, with 4 submarginal setae near outer-distal margin.

Tegument (Figs. 4–6). Dorsal tegument of cephalothorax, pereon and pleon, as well as that of second antenna, pereiopods and maxilliped basipodite, bearing scaly microsculpture, with tricorn-like setae on some areas.

Variation. Adult size varied from 5.6–8.5 mm in total length, but males (5.6–7.2, n = 3) tend to be smaller than females (5.7–8.5, n = 6) in the sample; juveniles measured 4.8 and 5.0 mm. Two adult females had a small paramedian spine on one side of pleonite 5. One of the juveniles had a very small supernumerary spiniform tubercle between one of the pairs of paramedian tubercles of pereonite 1. The middle article of maxilliped palpus sometimes with two setae in distal position on the medial margin.

Natural history. Specimens of *A. richardsonae* sp. nov. were collected under rocks and in humid leaf litter in closed broadleaf forest, specifically in upper montane rainforest (F. Cala, in litt., 4.IX.2018) (Fig. 9).

Distribution. Know only from the type locality, around the ranger station, Blue Mountains, Saint Thomas Parish, Jamaica (Fig. 1). Nonetheless, on November 19th, 2013, a specimen which at first sight matched the description of *A. richardsonae* sp. nov., was found in a leaf litter sample, photographed alive, and posted on iNaturalist by Sarah C. Crews (https://www.inaturalist.org/observations/484229; S.C. Crews, in litt. 24.IX.2021), from near Hardwar Gap (18°08'05.6"N, 76°43'48.0"W; approximately 980 m a.s.l.), Blue and John Crow Mountains National Park, Portland Parish (Figs. 1, 10).

Figure 9. Habitat of *Acanthoniscus richardsonae* sp. nov. in the Blue Mountains, eastern Jamaica. Photo by Carlos Víquez.

Etymology. The selected epithet is a Latinized patronym honoring Harriet Richardson Searle (1874–1958), Washington D.C., U.S.A., known as the first lady of isopods and one of the first women carcinologists, who made important contributions to isopod taxonomy and made the first description and illustrations of *A. richardsonae* sp. nov., although misidentified as *A. spiniger.*

Color (in alcohol) (Fig. 3). Grayish-brown, with muscle spots whitish-beige on dorsal surface of cephalothorax and on dorsolateral region of pereon tergites, around the base of largest dorsolateral spines; dorsal surface of pereon epimera and pleon tergites uniformly grayish-brown; dorsal surface of pereon epimera 1 sometimes spotted on dark gray. Second antenna uniformly light brown. Pereiopods grayish-brown irregularly spotted on whitish-beige. Apparently, the coloration in life is similar to that in alcohol (Fig. 10).

Figure 10. Specimen of *Acanthoniscus* cf. *richardsonae* sp. nov. observed near Hardwar Gap, Blue and John Crow Mountains National Park, Portland Parish. These are the only available photographs of a live specimen of the genus *Acanthoniscus*. Photos by Sarah C. Crews.

Remarks. The isopods of the genus *Acanthoniscus* are very fragile, therefore, most of the available specimens are fragmented, some of them severely damaged. Our description of *A. richardsonae* sp. nov. largely coincides with that of Richardson (1909), but since the precise locality of her specimen is unknown, we ignore whether its origin is the same as that of the type series of *A. richardsonae* sp. nov. (eastern Jamaica). Richardson (1909: 432) mentioned that her specimen had the cephalothorax "with the front emarginate and the lateral angles acutely produced" (Fig. 4O). However, since all other overall characters she described coincide with the description of *A. richardsonae* sp. nov., we suspect that a different angle while making the drawings could be the cause for such differences.

Conservation status. Apparently, both *A. spiniger* and *A. richardsonae* sp. nov. have restricted distributions (known only from a single or two localities), with severely fragmented and reduced habitats. However, since only three collection events (two in the mid-19th century) and an additional observation exist, it would be premature to make an evaluation of their conservation statuses based on the available information. Therefore, we tentatively consider them as Data Deficient (IUCN Standards and Petitions Subcommittee, 2019). The type locality of *A. richardsonae* sp. nov. falls within the Blue and John Crow Mountains National Park (see Protected Areas System Master Plan: Jamaica 2013–2017; Jamaica's National Ecological Gap Assessment Report, 2009), but that of *A. spiniger* is not included in any protected area. Additional surveys are required to collect data on their distributions, ecology, demographic parameters and threats, in order to make accurate assessments of their conservation statuses.

DISCUSSION

Taiti et al. (1998) and Schmidt (2003) stated that in many specialized forms of Armadillidae in which the body is covered with spines, such as *Laureola* and *Calmanesia*, the telson is not hourglass-shaped, but triangular; the genus *Echinodillo*, could be included in this list as well (Jackson, 1933; Green, 1963) (Fig. 8). Some non-spiny armadillid genera such as *Gabunillo* Schmalfuss and Ferrara, 1983, also have a triangular or T-shaped pleotelson (Schmalfuss and Ferrara, 1983; Souza et al., 2010). A triangular and possibly also other divergent forms of the pleotelson such as that of *Acanthoniscus*, has been regarded as secondary with respect to the hourglass-shaped ground pattern in Armadillidae (Taiti et al., 1998; Schmidt, 2003) (Fig. 8). Given the current placement of several divergent forms within Armadillidae, only the biarticulate antennal flagellum would remain as the definitive diagnostic character for this family. However, the 2-jointed flagellum of the second antenna is not unique to Armadillidae, since many other oniscidean families present this character: i.e., Agnaridae Schmidt, 2003, Armadillidiidae Brandt, 1833, Bathytropidae Vandel, 1952, Cylisticidae Verhoeff, 1949, Delatorreidae, Eubelidae Budde-Lund, 1899 (in part), Porcellionidae Brandt and Ratzeburg, 1831, Paraplatyarthridae Javidkar and King in Javidkar et al., 2015, Platyarthridae Verhoeff, 1949, Rhyscotidae Budde-Lund, 1904, Scleropactidae (in part), Spelaeoniscidae Vandel, 1948, Stenoniscidae

Verhoeff, 1908, Tendosphaeridae Verhoeff, 1930, and Trachelipodidae Strouhal, 1953 (sensu Schmidt, 2002; 2003; 2007; 2008; Javidkar et al., 2015). In this regard, Schmidt (2003) stated that "the reduction of the flagellar articles [of the second antenna] from 3 to 2 is susceptible to convergence" since it "may have evolved [...] several times within the Oniscoidea, so it is not very useful for phylogenetic speculations." Also, the bilobed process on the posterior margin of sternite 7 that covers and protects the male genital papilla, also called "penes cover" (Lee et al., 2014), has been regarded as an autapomorphy of Armadillidae (Schmalfuss, 1996; Taiti et al., 1998; Schmidt, 2003; 2008). The latter character has not been corroborated in all taxa of Armadillidae, but it is certainly absent in *Acanthoniscus* (and also in *Calmanesia*; S. Taiti, in litt. 21.I.2022) (Fig. 8H). Moreover, Taiti et al. (1998) commented that the evolutionary trend of the uropod in Armadillidae apparently is towards an extreme reduction of the exopodite, which is inserted dorsally near the medial margin of the sympodite (not visible ventrally). Therefore, the extremely long uropod exopodite inserted on the medial margin of the sympodite and widely surpassing both the distal margins of the sympodite and the pleotelson, must be considered a putative autapomorphy of *Acanthoniscus*. Other taxa of Armadillidae, some of them spiny, such as the genera *Echinodillo*, *Laureola*, *Merulanella* Verhoeff, 1926, *Nesodillo* Verhoeff, 1926, and *Schismadillo* Verhoeff, 1926, just to cite some of the most relevant examples, also have relatively well-developed uropod exopodites, sometimes surpassing the distal margin of the sympodite and visible ventrally (e.g., Verhoeff, 1926; Jackson, 1933; Barnard, 1960b; Green, 1963; Vandel, 1973b; Schmalfuss and Ferrara, 1983; Kwon et al., 1992), but in none of those taxa does it parallel that of *Acanthoniscus* (Fig. 8). The phylogenetic relationships of many morphologically divergent taxa within Armadillidae deserve further revision (Taiti et al., 1998; Schmidt, 2008), since this family, as currently recognized, most certainly represents a polyphyletic group. At this point, and after a long time using morphological characters without a definitive consensus, the use of molecular tools would be of much help in resolving the phylogenetic relationships of most taxa within this mega diverse "family." Recent molecular studies in other families such as Porcellionidae, have revealed strong inconsistences with the current systematics of the group based on the morphological characters traditionally used (Dimitriou et al., 2018). Even within the Oniscidea, the phylogenetic relationships among the different families are not totally clear (Lins et al., 2017; Dimitriou et al., 2019). Integrative analyses combining both morphological characters (including scanning electron microscopy) and molecular tools would be helpful to elucidate the phylogenetic relationships of *Acanthoniscus* and other morphologically divergent taxa currently placed in Armadillidae.

The evolutionary and biogeographic histories of *Acanthoniscus* are uncertain. Jamaica has a unique combination of faunal elements when compared to the remaining Greater Antillean islands (e.g., Buskirk, 1985; Crews and Esposito, 2020). It is generally accepted that this island originated in the area currently occupied by the Pacific Ocean and that moved eastward with the Caribbean Plate to its current position during the late Cretaceous, as part of the north-eastern edge of the Nicaragua Rise (for reviews see Pindell, 1994; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2005, 2006; Pindell and Kennan, 2009; Mitchell, 2020). The Cretaceous basement rocks shared by the Western Jamaican Block and the rest of the Nicaragua Rise indicate the same origin. However, the easternmost region of Jamaica (Blue Mountains Block) is structurally and lithologically divisible from the larger central-western region of the island (Clarendon Block and Hanover Block sensu Lewis et al., 1990; Western Jamaican Block sensu Iturralde-Vinent and MacPhee, 1999) (Fig. 11).

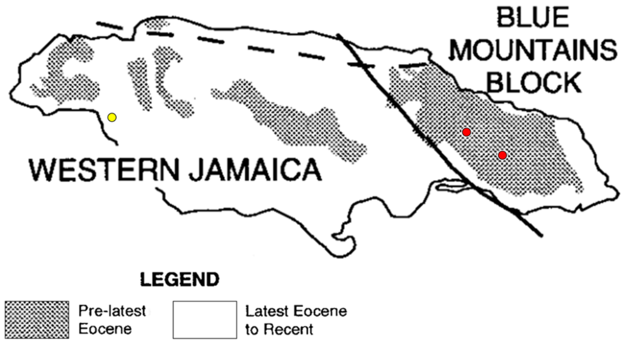

Figure 11. Simplified geological map of Jamaica modified from Iturralde-Vinent and MacPhee (1999), depicting the two main tectonic blocks and the distributions of *Acanthoniscus spiniger* (yellow dot) and of *A. richardsonae* sp. nov. (red dots).

Iturralde-Vinent and MacPhee (1999) suggested that the Blue Mountains Block apparently evolved from the northern Greater Antilles, whereas the Western Jamaican Block originated from the Nicaragua Rise. The Blue Mountains Block is geologically more similar to eastern Cuba and southern Hispaniola, which led Iturralde-Vinent and MacPhee (1999) to suggest that these terrains were connected at some point during the Eocene-Oligocene transition, ca. 33–35 MYA, maybe forming part of GAARlandia (Greater Antilles + Aves Ridge "landspan" sensu Iturralde-Vinent and MacPhee, 1999). Also, whether the Nicaragua Rise (including Jamaican terrains) became completely subaerial at some point during the Miocene or that emerged terrains in this region persisted until the present day is still a subject of much debate (for reviews see Iturralde-Vinent and MacPhee, 1999; Hedges, 2001; 2006; Iturralde-Vinent, 2005; 2006). In any case, the different and complex geological histories of these two main blocks suggest that they remained as separate units at least until the Middle Miocene (> 15 MYA), when they are supposed to have collided, which had strong implications for the biogeography and evolution of their associated biotas (e.g., Domning et al., 1997; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2005; 2006). Further studies are required to clarify whether *Acanthoniscus* has a Central American (via the Nicaragua Rise) or a South American (via GAARlandia) origin. Also, molecular analyses would be helpful to elucidate which region of Jamaica (Blue Mountains Block or Western Jamaican Block) functioned as the primary evolutionary center for *Acanthoniscus*.

The marked differences in geology (volcano-sedimentary and metamorphic rocks in the Blue Mountains vs. white limestone in Bluefields; e.g., Draper, 1986; DeMets and Wiggins-Grandison, 2007; Garrett et al., 2008; Abbott et al., 2013; Domínguez-González et al., 2015; Mitchell 2020;), primary vegetation type (closed broadleaf forest in the Blue Mountains vs. tall open dry forest in Bluefields; e.g., Areces-Mallea et al., 1999; Evelyn and Camirand, 2003; National Forest Management and Conservation Plan 2016–2026), elevation (> 1,200 m in the Blue Mountains vs. approximately 450 m in Bluefields), and the high allopatry (> 150 km), support the hypothesis of these two populations of *Acanthoniscus* representing isolated lineages evolving under different ecological scenarios (Fig. 1). Despite some important diagnostic characters traditionally used in oniscidean taxonomy, such as the male pleopods 1 and 2, the male pereiopod 7, and the flagellum of the second antenna have not yet been described for *A. spiniger*, we consider that the strong differences observed in the overall morphology between *A. spiniger* and *A. richardsonae* sp. nov. warrant the different species status.

Henry G. Hubbard, the collector of Richardson's specimen (Richardson, 1909), visited Jamaica with his uncle in 1877. His unpublished field book gathers notes from March 25 to April 19. However, in published extracts from a letter by him, he mentioned earlier dates ("middle of February" and "March 10, 1877") at which he examined termite nests, at least at Stony Hill, about 10 km N of Kingston (Hubbard, 1877) (Fig. 1). Therefore, his arrival in Jamaica apparently was earlier than what his field notes reflect. According to these notes, he visited a number of localities across Jamaica, but not in all of them he mentioned having collected; some of these collection sites were relatively close to both the Blue Mountains and Bluefields (Fig. 1). In his notes he mentioned having collected and/or observed insects (particularly termites), arachnids, centipedes, freshwater shrimps, land shells, snakes, lizards, birds, bats, plants, and marine animals, among others, but he never mentioned isopods of any kind. The location (near Hardwar Gap) where the specimen presumably of *A. richardsonae* sp. nov. was photographed alive by Sarah C. Crews, is about 20 km NW of the type locality and less than 10 km NE of Stony Hill, one of the collection sites of Hubbard (Hubbard, 1877; Fig. 1). That Stony Hill (and nearby areas) was the collection site of the specimen used by Richardson (1909) in her description, falls within the realm of possibilities, but until further evidence arises its exact location remains uncertain.

Richardson (1909) stated that Kinahan's (1859) representation of the uropod did not coincide with hers, besides other differences in the spine pattern description. She sent a copy of her figures to William Thomas Calman (a carcinologist from the Department of Zoology of the British Museum between 1904–1936) for a comparison with the type specimen, and he answered almost certain that her specimen was *A. spiniger*, despite noticing some differences: i.e., "in the type-specimen there are two teeth instead of three on the posterior margin of the thoracic segments after the first. On the first segment, the middle tooth is extremely small. On the hinder edge of the head are only two teeth, placed a little in front of, not on, the margin. He also noticed a difference in the shape of the uropod, but thinks this may be due to its being in a slightly different position from my sketch" (Richardson, 1909: 434). Despite all the above, both Richardson and W.T. Calman hesitated in considering the specimen collected by Hubbard anything other than *A. spiniger*, assuming such differences as possible intraspecific variation and/or misinterpretation while making the drawings. Richardson also failed in assuming "Jamaica" as the same locality for both specimens, a common mistake when extrapolating the scale and rate at which biogeographical and evolutionary processes take place in continental areas to oceanic islands. As corroborated here, the differences noticed by Richardson and Calman are not only strong enough as to separate both species, but they also overlooked many other important differences in the cephalothorax, pereon and pleon epimera, coxal plates, pleotelson, and uropods.

Finally, both species of *Acanthoniscus* can be easily identified using the following key:

1. Cephalothorax with upper margin of frontal shield forming angulate lateral lobes and a small, triangular median lobe, dorsal surface with two small posteromedian spiniform tubercles; dorsal surface of pereon tergites with only a pair of small posteromedian spiniform tubercles between larger spines, no paramedian spiniform tubercles present; uropod sympodite "subtriangular," with a slightly convex outer margin, medial-posterior angle not reaching distal margin of pleotelson; uropod endopodite long, widely surpassing distal margin of sympodite; pleotelson ending in two prominent triangular projections separated by a deep notch .... *A. spiniger*

-. Cephalothorax with upper margin of frontal shield forming rounded lateral lobes and a well-developed, deeply notched frontal lobe (forming two triangular projections), dorsal surface with a pair of small paramedian spiniform tubercles and three medium-sized, club-like posteromedian spines; dorsal surface of pereon tergites with three medium-sized posteromedian spines, and one (pereonites 2–7) or two (pereonite 1) pairs of paramedian spiniform tubercles; uropod sympodite "subtrapezoidal," outer margin widely convex and produced (forming an almost square angle), medial-posterior angle approximately at same level or slightly surpassing distal margin of pleotelson; uropod endopodite short, not reaching distal margin of sympodite; pleotelson ending in two small triangular projections separated by a shallow notch .... *A. richardsonae* sp. nov.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Conceptualization and Design: TMR-C, LFA. Performed research: TMR-C, LFA. Acquisition of data: TMR-C, LFA. Analysis and interpretation of data: TMR-C, LFA. Preparation of figures/tables/maps: TMR-C. Writing - original draft: TMR-C. Writing– critical review & editing: TMR-C, LFA.

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All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

Competing interests

The authors declare no competing interest.

Data availability

All study data are included in the article.