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Kinorhyncha from the Caribbean, with the description of two new species from Puerto Rico and Barbados

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Abstract :

Two new kinorhynch species from Puerto Rico (Greater Antilles) and Barbados (Lesser Antilles) are described herein from Dr R. P. Higgins unexamined Caribbean meiofaunal samples, which have been stored in the Smithsonian Institution collections. The species from Puerto Rico, Cristaphyes cornifrons sp. nov., belongs to the class Allomalorhagida, whereas the species from Barbados, Echinoderes barbadensis sp. nov., belongs to the class Cyclorhagida. Cristaphyes cornifrons sp. nov. is easily distinguished from most of its congeners by the presence of lateral terminal spines and the absence of male, sexually dimorphic, ventromedial tubes on segment 2, as only other two species of the genus lack these features. Of these, C. cornifrons sp. nov. may be easily differentiated by its pattern of paradorsal, ventrolateral and ventromedial setae. Echinoderes barbadensis sp. nov. is unique among its congeners by the combined presence of middorsal spines on segments 4–8, lateroventral spines on segments 6–9, lateral accessory tubes on segment 8, lateroventral tubes on segment 5, ventrolateral tubes on segment 2 and type 2 glandular cell outlets in subdorsal position on segment 2 and in midlateral position on segment 4.

Keywords : Kinorhynchs, biodiversity, meiofauna, morphology, taxonomy

1. Introduction

Kinorhynchs, commonly known as mud dragons, are small, holobenthic, meiofaunal organisms that inhabit the spaces and crevices between the sediment particles of worldwide oceans (Neuhaus, 2013; Sørensen and Pardos, 2008). Much of the currently known biodiversity of the phylum includes intertidal to circalittoral species, biased by samplings being done in the most accessible marine areas (Neuhaus, 2013; Sørensen et al., 2018). However, many shoreline regions still remain poorly studied, as it is the case of the Caribbean Basin. The Caribbean is a tropical sea bounded by Mexico and Central America to the west and south west, by the Greater Antilles to the north, by the Lesser Antilles to the east and by the northern coast of South America to the south (Miloslavich et al., 2010). To date, a total of 30 species have been reported for the whole Basin (Higgins, 1983; Kirsteuer, 1964; Pardos et al. 2016b; Sørensen, 2006), but the study of several samples from different Caribbean localities stored at the Smithsonian National Museum of Natural History (NMNH) has revealed a still unknown, rich diversity of Caribbean kinorhynchs (Cepeda et al., this issue b, this issue c).

The present contribution is part of an extensive survey of Caribbean Kinorhyncha that take advantage of the series of samples deposited by Dr R. P. Higgins during several decades, samples that still remain unsorted and unexamined in the NMNH. Specifically, this paper focuses on Puerto Rico, part of the Greater Antilles, and Barbados, which is part of the Lesser Antilles, locations where the kinorhynch fauna is completely unknown. The present study describes two species new to science.

2. Material and methods

Studied kinorhynchs were collected by Dr R. P. Higgins at two different localities throughout the Caribbean Antilles (Fig. 1A): La Parguera (Puerto Rico) in 1967 (Fig. 1B) and St. James (Barbados) in 1968 (Fig. 1C). All the samplings were done using a meiobenthic dredge (Higgins, 1988).

After sampling, meiofauna was extracted from sediment using the bubble and blot method defined by Higgins (1964). Meiofaunal specimens were fixed in 4% formalin and finally preserved in Carosafe®. Fixed kinorhynchs were picked up with an

Irwin loop using a Motic® SMZ-168 stereo zoom microscope and washed with distilled water to remove remnants of formalin. For light microscopy (LM), specimens were dehydrated though a series of 25%, 50%, 75% and 100% glycerine and mounted on glass slides using Fluoromount G® sealed with Depex®. Mounted specimens were studied and photographed using an Olympus® BX51-P microscope equipped with differential interference contrast (DIC) optics and an Olympus® DP-70 camera. Morphometrics were obtained with Olympus cellSens® software. For scanning electron microscopy (SEM), specimens were transferred to 70% ethanol and progressively dehydrated through a graded series of 80%, 90%, 95% and 100% ethanol. Hexamethyldisilazane (HMDS) was used for chemical drying through a HMDS-ethanol series. Specimens were finally coated with gold and mounted on aluminium stubs to be examined with a JSM® 6335-F JEOL SEM at the ICTS Centro Nacional de Microscopía Electrónica (Complutense University of Madrid, Spain). Type material is deposited at the NMNH, Smithsonian Institution, Washington, while non-type material is deposited at the Invertebrates Collection of the Meiofaunal Laboratory at the Universidad Complutense de Madrid (UCM), Spain. Line drawings and image plates composition were done using Adobe® Photoshop CC-2014 and Illustrator CC-2014 software.

3. Results and discussion

Class Allomalorhagida Sørensen et al., 2015

Family Pycnophyidae Zelinka, 1896

Genus *Cristaphyes* Sánchez et al., 2016

3.1. *Cristaphyes cornifrons* sp. nov.

urn:lsid:zoobank.org:act:5F5572D9-EB13-4205-8706-6D3BC6413DC3.

(Figs. 2–5 and Tables 2–3)

3.1.1 Type material

Holotype, adult female, collected by Dr R. P. Higgins on 7 June 1967 at La Parguera, Puerto Rico, western Atlantic Ocean (L1): 17º57´00´´N, 67’03´00´´W (Table 1; Fig. 1A-B), 15 m depth, mud; mounted in Fluoromount G®, NMNH accession number:

115 USNM 1550583. Two paratypes, one adult male and one adult female, with same
116 collecting data as holotype, mounted in Fluoromount G®, NMNH accession numbers:
117 USNM 1550584 and 1550585.

118 *3.1.2 Non-type material*

119 Two additional specimens with same collecting data as holotype and paratypes,
120 prepared for SEM, deposited at the Invertebrates Collection of the Meiofaunal
121 Laboratory of the Universidad Complutense de Madrid (UCM), Spain.

122 *3.1.3 Diagnosis*

123 *Cristaphyes* with middorsal processes on segments 2–9, with small pointed projection
124 of the tergal plate of segment 10. Anterior margin of first segment strongly denticulated,
125 with "teeth" of different sizes. Unpaired paradorsal setae on segments 2, 4 and 6. Paired
126 paralateral setae on segment 1; paired laterodorsal setae on segments 2–9; paired
127 lateroventral setae on segments 2, 4, 6, 8 and 10; paired ventrolateral setae on segments
128 2, 3 (in some specimens mesially shifted to ventromedial position on segment 3) and 5
129 (females furthermore with sexually dimorphic, ventrolateral setae on segment 10);
130 paired ventromedial setae on segments 4–9. Lateral terminal spines long, about 34% of
131 total trunk length.

132 *3.1.4 Etymology*

133 From the latin "cornifrons", which refers to the lateral anterior horn-shaped extensions
134 of segment 1 that are markedly elongated, curved and pointed.

135 *3.1.5 Description*

136 See Table 2 for measurements and dimensions, and Table 3 for summary of cuticular
137 process, seta, glandular cell outlet, nephridiopore, spine and sensory spot locations.

138 Head with retractable mouth cone and introvert (Fig. 3C-D). Although two of
139 the examined specimens had the introvert completely everted, oral styles and scalids
140 tended to be collapsed when mounted for LM (Fig. 3C-D), so only some details can be
141 provided. External ring of mouth cone (ring 00) with nine equally-sized outer oral styles
142 (Fig. 3C), arranged as one anterior to each introvert sector except for the middorsal
143 sector 6 where a style is missing. Each outer oral style composed of a single, very
144 flexible, superficially smooth piece with a basal, short, fringed sheath (Fig. 3C). Ring

01 with ten primary spinoscalids, each one composed of a basal sheath and a distal, elongated piece; basal sheath equipped with a median, dense fringe (Fig. 3D). Remaining rings of introvert (rings 02-06) with regular scalids morphologically similar to the primary spinoscalids but shorter (Fig. 3D).

Neck with four dorsal and two ventral, sclerotized placids (Figs. 2A-B and 3E-F). Dorsal placids rectangular; mesial ones broader than lateral ones (Figs. 2B and 3E). Ventral placids much more elongated and trapezoidal, getting thinner towards the lateral sides (Figs. 2A and 3F). Fourteen elongated, hairy trichoscalids are present, without trichoscalid plates (Fig. 3D).

Trunk markedly rectangular, stout, triangular in cross-section, composed of eleven segments (Figs. 2A-B, 3A-B and 5A-B). Segment 1 with one tergal, two episternal and one trapezoidal, midsternal plate; remaining segments with one tergal and two sternal plates (Figs. 2A-B, 3A-B and 5A-B). Midsternal and tergosternal junctions as conspicuous lines externally on the cuticle (Fig. 2A, C). Sternal plates reach their maximum width at segment 5, but almost constant in width throughout the trunk, slightly tapering at the posterior trunk end (Figs. 2A-B, 3A-B and 5A-B). Sternal plates are relatively narrow (MSW-5:TL average ratio = 23.6%), giving the animal a slender appearance. Middorsal processes on segments 2–9, keel-shaped, with pointed tips that surpass the posterior segment margins, turning progressively longer towards the posterior end (Figs. 2B, D, 3A, 4C-D, F, I and 5A, C-D); segment 10 with a small pointed projection towards the posterior segment margin (Figs. 2B, D and 4C). Segments 1–10 with oval-shaped glandular cell outlets in subdorsal and ventromedial position (Figs. 2A-D, and 4A-J). Segments 2–10 with paired cuticular ridges in laterodorsal position, not always detectable, followed by one small glandular cell outlet; segments 2–10 furthermore with paired cuticular ridges at the ventrolateral-ventromedial limit, followed by small glandular cell outlets with two cuticular openings (Figs. 2A-D and 5G). Cuticular hairs acicular, distributed all over the trunk cuticle, except the mesial halves of the episternal plates. Muscular scars very conspicuous as superficially smooth, hairless, rounded to oval-shaped areas on the cuticle, in laterodorsal and ventromedial positions (Figs. 2A-D and 4A-J). Pachycycli and ball-and-socket joints on segments 2–10 (Fig. 2A-B). Apodemes not observed. Posterior margin of segments straight, showing poorly-developed primary pectinate fringes with a very weak serration (Fig. 2A-D). Secondary pectinate fringes developed as three

transverse, wavy rows with a very weak dentation, two of them located near the anterior margin of segments, one of them located near the posterior margin of segments (Fig. 2A-D). Some specimens were found carrying epibiontic Ciliophora on both tergal and sternal plates throughout the trunk.

Segment 1 without middorsal process (Figs. 2B and 4A). Anterolateral margins of the tergal plate large, elongated as horn-shaped extensions, curved inwards, distally pointed (Figs. 2A-B, 3A-B, F, 4B and 5A-B). Anterior margin of the tergal plate strongly denticulated, with projections of different sizes, followed by a smooth area (Figs. 2B, 3A and 5A). Paired setae in paralateral position (Figs. 2B and 4A). Paired sensory spots in subdorsal position, posterior to the dorsal cuticular scars; in laterodorsal position, lateral to the dorsal cuticular scars; and in ventrolateral position, lateral to the ventral muscular scars (Figs. 2A-B and 4A-B). Sensory spots on this and remaining segments rounded to oval, with several rings of cuticular papillae surrounding a central pore (similar to Fig. 5F, I).

Segment 2 with keel-like middorsal process that surpasses the posterior segment margin, with a median, densely-covered fringe of cuticular hairs (Figs. 2B, 4D and 5D). Unpaired seta in paradorsal position, and paired setae in laterodorsal, lateroventral and ventrolateral positions, the former immediately lateral to the dorsal muscular scars (Figs. 2A-B, 4D-E and 5D-E). Two pairs of sensory spots in subdorsal and ventromedial positions, the latter lateral to the ventral muscular scars; plus one pair of sensory spots in paradorsal and laterodorsal positions, the latter lateral to the laterodorsal setae (Figs. 2A-B, 4D-E and 5D-E). Sexually dimorphic male tubes absent.

Segment 3 with middorsal process as on preceding segment (Figs. 2B, 4F and 5D). Paired setae in laterodorsal and ventrolateral positions (Figs. 2A-B, 4F-G and 5D, F), the latter showing intraspecific variation as one of the examined specimens had this pair of setae mesially shifted to ventromedial position (Fig. 5E). Paired sensory spots in paradorsal, subdorsal, laterodorsal and ventromedial positions (Figs. 2A-B, 4F-G and 5D-F).

Segment 4 with middorsal process as on the preceding segment (Figs. 2B and 4I). Unpaired seta in paradorsal position, plus paired setae in laterodorsal, lateroventral and ventromedial positions (Figs. 2A-B and 4I-J). Paired sensory spotrs in paradorsal, subdorsal, laterodorsal and ventromedial positions (Figs. 2A-B and 4I-J).

Segment 5 with tergal plate similar to that of segment 3 and sternal plates similar to those of segment 4 but also with paired ventrolateral setae (Figs. 2A-B and 4I-J).

Segment 6 similar to segment 4 (Figs. 2A-B and 4I-J).

Segment 7 with tergal plate similar to that of segment 3 and sternal plates similar to those of segment 4 (Figs. 2A-B, 4I-J and 5I).

Segment 8 similar to segment 4, but lacking paradorsal seta (Figs. 2A-B, 4C, H and 5C).

Segment 9 with tergal plate similar to that of segment 3, but with lateroventral nephridiopores present, and sternal plates similar to those of segment 4 (Figs. 2A-B and 4C, H).

Segment 10 with small pointed projection towards the posterior margin of the tergal plate (Figs. 2B, D and 4C). Paired setae in lateroventral position; females furthermore with sexually dimorphic, paired setae in ventrolateral position (Figs. 2A-D and 4C, H). Two pairs of sensory spots in laterodorsal position, plus one pair of sensory spots in paradorsal, subdorsal, ventrolateral and ventromedial positions (Figs. 2A-D, 4C, H and 5H).

Segment 11 with two pairs of type 3 sensory spots, one in subdorsal and one in laterodorsal position (Figs. 2B, D and 4C). Males with two pairs of stout, penile spines and genital pores surrounded by tuft of long hairs (Figs. 2A and 5H). Lateral terminal spines long (LTS:TL average ratio = 34.0%), stout, wide, apparently flexible (Figs. 2A-D, 3A-B and 5B).

3.1. 6 Remarks on diagnostic characters

Of the 23 species currently belonging to *Cristaphyes*, the newly described species may be distinguished from eight of them by the possession of lateral terminal spines, as *C. anomalus* (Lang, 1953), *C. belizensis* (Higgins, 1983), *C. harrisoni* Pardos et al., 2016, *C. panamensis* Pardos et al., 2016 (in Pardos et al. 2016a), *C. phyllotropis* (Brown and Higgins, 1983), *C. rabaulensis* (Adrianov, 1999 in Adrianov and Malakhov, 1999), *C. spinosus* (Lang, 1949) and *C. yushini* (Adrianov, 1989) lack these structures. Additionally, males of *C. cornifrons* sp. nov. do not have ventral tubes on segment 2, whereas males of eleven of the remaining congeners do, namely *C. abyssorum* (Adrianov and Maiorova, 2015), *C. arctous* (Adrianov, 1999 in Adrianov

and Malakhov, 1999), *C. carinatus* (Zelinka, 1928), *C. chukchiensis* (Higgins, 1991), *C. cristatus* (Sánchez et al., 2013), *C. cryopygus* (Higgins and Kristensen, 1988), *C. dordaidelosensis* Sørensen and Grzelak, 2018, *C. furugelmi* (Adrianov, 1999 in Adrianov and Malakhov, 1999), *C. glaurung* Sørensen and Grzelak, 2018, *C. odhneri* (Lang, 1949) and *C. scatha* Sørensen and Grzelak, 2018. Male specimens of *C. nubilis* (Sánchez et al., 2014) are unknown, so this species cannot be assumed to lack these tubes. Of the four remaining congeners, *C. chilensis* (Lang, 1953) and *C. nubilis* possess middorsal processes from segment 1, unlike *C. cornifrons* sp. nov. that has these structures from segment 2. Moreover, both species differ from the new species by keel-shaped middorsal process at segment 10 clearly surpassing beyond the posterior margin of the segment (Lang, 1953; Sánchez et al., 2014).

Cristaphyes cornifrons sp. nov. is most similar to *C. fortis* Cepeda et al., this issue (in Cepeda et al., this issue a) and *C. longicornis* (Higgins, 1983) as all three of them share the presence of lateral terminal spines and the lack of ventral tubes on segment 2 in males. However, there are some remarkable differences in the setae arrangement, which justifies the erection of the new species: *C. cornifrons* sp. nov. possesses unpaired setae in paradorsal position on segments 2, 4 and 6, whereas *C. longicornis* carries these structures on segments 2, 4, 6 and 8. Additionally, *C. cornifrons* sp. nov. has paired setae in ventrolateral position on segments 2-3, 5 and 10 (only in females) and in ventromedial position on segments 4–9, while *C. longicornis* bears ventrolateral setae on segments 2, 5 and 10 and in ventromedial position on segments 1 and 3–9. Main morphological differences in the setae location between *C. cornifrons* sp. nov. and *C. fortis* are found in the sternal plates. Thus, *C. cornifrons* sp. nov. is characterized by a single pair of ventrolateral setae on segments 2–3, 5 and 10 (only in females), while *C. fortis* has two pairs of ventrolateral setae on segment 5 and a single pair on segments 2–4, 6–7 and 10. Moreover, *C. cornifrons* sp. nov. has ventromedial setae on segments 4–9 whereas *C. fortis* bears these structures only on segments 8–9.

Additionally, *Cristaphyes longicornis* and *C. fortis* are larger species than *C. cornifrons* sp. nov. (TL average of *C. cornifrons*: 447.9 μm; *C. fortis*: 644.5 μm; *C. longicornis*: 636.7 μm), and although the three species are characterized by having the anterolateral margins of segment 1 forming horn-shaped extensions, these are much more elongated and curved inwards in *C. cornifrons* sp. nov. than those of *C. fortis* and

C. longicornis. *Cristaphyes fortis* also has the pachycycly and ball-and-socket joints much more developed than *C. cornifrons* sp. nov, being thicker and stouter in the former, but this could be related to the age of the type specimens of *C. fortis*. Finally, *C. longicornis* possesses conspicuous apodemes in segments8–10, which are absent in *C. cornifrons* sp. nov.

3.1.7 Associated kinorhynch fauna

Cristaphyes cornifrons sp. nov. co-occurred with the cyclorhagids *Echinoderes astridae* Sørensen, 2014, *E. horni* Higgins, 1983, *E. orestauri* Pardos et al., 2016 (in Pardos et al. 2016b) and *E. spinifurca* Sørensen et al., 2005, and the allomalorhagids *Cristaphyes* sp. and *Dracoderes spyro* Cepeda et al., this issue (in Cepeda et al., this issue b).

Class Cyclorhagida (Zelinka, 1896) Sørensen et al., 2015

Family Echinoderidae Zelinka, 1894

Genus *Echinoderes* Claparède, 1863

3.2 *Echinoderes barbadensis* sp. nov.

urn:lsid:zoobank.org:act:BCF2D1F5-A0AF-480E-B1E1-3E5AB93E1083.

(Figs. 6–8 and Tables 4–5)

3.2.1 Type material

Holotype, adult male, unknown collector, sampling done on 23 Aug 1968 at St. James (Barbados), Caribbean Sea, eastern Atlantic Ocean (L2): 13º13´12´´N, 59º37´12´´W (Table 1; Fig. 1A, C), depth and sediment unknown; mounted in Fluoromount G®, NMNH accession number: USNM 1550576. Paratypes, three adult males and three adult females, with same collecting data as holotype; mounted in Fluoromount G®, NMNH accession numbers: USNM 1550577–1550582.

3.2.2 Non-type material

Six additional specimens with same collecting data as holotype and paratypes, mounted for SEM, deposited at the Invertebrates Collection of the Meiofaunal Laboratory at the Universidad Complutense de Madrid (UCM), Spain.

3.2.3 Diagnosis

Echinoderes with short middorsal spines on segments 4–8, lateroventral spines on segments 6–9, lateral accessory tubes on segment 8, lateroventral tubes on segment 5 and ventrolateral tubes on segment 2. Type 2 glandular cell outlets present in subdorsal position on segment 2 and in midlateral position on segment 4. Cuticular hairs densely distributed through all cuticular surface (except on segment 11), very long, bracteate. Segment 11 with a middorsal, triangular, protuberance-like structure emerging between segments 10 and 11, located near the anterior segment margin. Sternal extensions of segment 11 bearing paired, very long, thick cuticular hairs.

3.2.4 Etymology

The species name refers to Barbados, the type locality where the species was found.

3.2.5 Description

See Table 4 for measurements and dimensions, and Table 5 for summary of spines, tubes, nephridiopores, glandular cell outlets and sensory spots location.

Head with retractable mouth cone and introvert. Although some of the paratypes have the introvert partially everted, oral styles and scalids tended to collapse when mounted for LM; furthermore, specimens for SEM were not suitable for head examination, so details on the exact number, arrangement and morphology of oral styles and scalids cannot be provided.

Neck with sixteen trapezoidal placids, wider at base, with a deep indentation on its anterior margin, and distinguished joint between the neck and segment 1 (Figs. 6A-B and 7B-C). Midventral placid widest (ca. 12–13 μm wide at base) (Figs. 6A and 7C), remaining ones alternate between wider and narrower (ca. 8–10 μm at base) (Figs. 6A-B and 7B-C). Placids situated closely together at base, distally separated by cuticular folds (Figs. 6A-B and 7B-C). Six long, hairy trichoscalids attached to trichoscalid plates present (Figs. 6A-B and 7B-C).

Trunk outline orbicular, stubby, strongly sclerotized, hairy, heart-shaped in cross-section, composed of eleven trunk segments (Figs. 6A-B, 7A and 8A). Segments 1–2 as closed cuticular rings; remaining ones with one tergal and two sternal plates (Figs. 6A-D and 7A). Midsternal and tergosternal junctions as conspicuous lines on the cuticle (Figs. 6A-D and 7A). Tergal anterior plates noticeably bulging middorsally;

posterior ones more flattened, giving the animal a tapering outline in lateral view (Fig. 8A). Sternal plates reach their maximum width at segment 5, slightly tapering towards the last trunk segments (Figs. 6A and 7A). Sternal plates conspicuously wide compared to the total trunk length (MSW-5:TL average ratio = 25.9%), giving the animal a globose, stout appearance (Figs. 6A-B and 7A). Cuticular hairs densely distributed all over the trunk cuticle, except on segment 11, in wavy, continuous, transversely arranged rows along the surface of the cuticle (Figs. 6A-D, 7A-Q and 8A-C, E). Cuticular hairs on all segments bracteate, long, slender, apparently flexible (Figs. 8A-E). Posterior margin of segments straight, with well-developed primary pectinate fringes with an elongated, strongly serrated free flap (Figs. 6A-D, 7A-Q and 8A, C); secondary pectinate fringes absent.

Segment 1 without spines and tubes. Unpaired type 1 glandular cell outlet in middorsal position, near the anterior segment margin; in LM, the glandular cells appear like a row of vertically arranged light refracting granules (Figs. 6B and 7D). Paired sensory spots in subdorsal, laterodorsal and ventrolateral positions, all of them located near the anterior segment margin (Figs. 6A-B and 7D-E). Sensory spots on this and remaining segments are small, circular to oval-shaped areas composed of a ring with few (ca. 8–10) micropapillae varying in size that surround a central pore with an emerging, quite long cilium, not flanked by cuticular hairs (similar to Fig. 8D, F). Cuticular hairs distributed in 7–9 rows (Figs. 6A-B and 7D-E).

Segment 2 with paired tubes in ventrolateral position (Figs. 6A and 7G). Type 1 glandular cell outlet unpaired in middorsal and paired in ventromedial positions, both located near the anterior segment margin, as rows of horizontally arranged light refracting granules (Figs. 6A-B and 7F-G). Paired type 2 glandular cell outlets in subdorsal position, (Figs. 6B, 7F and 8B). Paired sensory spots in laterodorsal position (Figs. 6B and 7F). Cuticular hairs distributed in 5–6 rows (Figs. 6A-B and 7F-G).

Segment 3 without spines and tubes. Type 1 glandular cell outlet unpaired in middorsal and paired in ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7H-I). Paired sensory spots in ventrolateral position (Figs. 6A and 7I). Cuticular hairs distributed as on the preceding segment.

Segment 4 with a short, acicular middorsal spine not exceeding the posterior edge of the segment (Figs. 6B and 7H). Paired type 1 glandular cell outlets in paradorsal

and ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7H-I). Paired type 2 glandular cell outlets in midlateral position, near the posterior segment margin, smaller than those of the second trunk segment (Figs. 6A and 7I). Paired sensory spots in paradorsal and ventrolateral positions, the former anterior to the base of the middorsal spine, the latter near the posterior margin of segment (Figs. 6A-B and 7H-I). Cuticular hairs distributed in 8–10 rows (Figs. 6A-B and 7H-I).

Segment 5 with a short, acicular middorsal spine not exceeding the posterior edge of the segment and paired tubes in lateroventral position (Figs. 6A-B, 7L-M and 8C). Paired type 1 glandular cell outlets in paradorsal and ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7L-M). Paired sensory spots in paradorsal, subdorsal and ventrolateral positions, the former anterior to the base of the middorsal spine, the latter near the posterior margin of segment (Figs. 6A-B and 7L-M). Cuticular hairs distributed in 7–10 rows (Figs. 6A-B and 7L-M).

Segment 6 with a short, middorsal spine not exceeding the posterior edge of the segment and paired spines in lateroventral position (Figs. 6A-B, 7L-M and 8C). Paired type 1 glandular cell outlets in paradorsal and ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7L-M). Paired sensory spots in paradorsal position, located anteriorly to the base of the middorsal spine (Figs. 6B and 7L). Cuticular hairs distributed in 7–9 rows (Figs. 6A-B and 7L-M).

Segment 7 similar to segment 6 but with the cuticular hairs distributed in 9–11 rows (Figs. 6A-B, 7J-K and 8C).

Segment 8 with a middorsal spine not exceeding the posterior margin of the segment and paired spines in lateroventral position (Figs. 6A-B, 7J-K and 8C, E). Paired tubes in lateral accessory position (Figs. 6A, 7K and 8C, E). Paired type 1 glandular cell outlets in paradorsal and ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7J-K). Paired sensory spots in paradorsal, subdorsal and ventrolateral positions, the former anterior to the base of the middorsal spine, the latter close to the lateroventral spines near the anterior margin of segment (Figs. 6A-B, 7J-K and 8D). Cuticular hairs distributed in 9–12 rows (Figs. 6A-B and 7J-K).

Segment 9 with paired spines in lateroventral position (Figs. 6A, 7O and 8C). Cuticular hairs distributed in 10–13 wavy, continuous, transversely arranged rows along the surface of the cuticle (Figs. 6A-B and 7N-O). Paired type 1 glandular cell outlets in

paradorsal and ventromedial positions, similar to those of preceding segments (Figs. 6A-B and 7N-O). Paired sensory spots in subdorsal and ventrolateral positions, the latter close to the lateroventral spines, near the posterior margin of segment (Figs. 6A-B and 7N-O). Paired nephridiopores in sublateral position, as a longitudinally elongated, oval-shaped sieve plate (Fig. 7O).

Segment 10 without spines and tubes. Two unpaired type 1 glandular cell outlets in middorsal position, one horizontally arranged and near the anterior margin of segment, the other one vertically arranged and posterior to the other outlet (Figs. 6B and 7P). Paired type 1 glandular cell outlets in ventromedial position, near the anterior margin of segment, obliquely arranged (Figs. 6A and 7Q). Paired sensory spots in subdorsal position, not aligned with those of the previous segments, mesially shifted, near the posterior margin of segment (Figs. 6B and 7P). Cuticular hairs distributed in 10–12 rows (Figs. 6A-B and 7P-Q).

Segment 11 with quite short lateral terminal spines (LTS:TL average ratio = 20.1%), stout, rigid, distally pointed, showing a central cavity (Fig. 6A-D and 7A, R). Females with paired lateral terminal accessory spines (LTAS:LTS average ratio = 34.7%), slender, flexible, distally pointed (Fig. 6A-B). Males with three pairs of penile spines, first and third pairs longer and slender, superficially smooth and distally rounded, second pair shorter and stouter, superficially hairy with a distal tuft of hairs (Figs. 6C-D and 8G). Dorsal plate with an anterior, middorsal, triangular, protuberance-like structure that emerges between segments 10 and 11 (Fig. 6B, D). Unpaired type 1 glandular cell outlet in middorsal position, vertically arranged near the posterior margin of segment (Figs. 6B, D and 7P). Tergal extensions quite long, distally elongated and pointed (Figs. 6B, D and 7P). Sternal extensions wide, distally rounded, bearing a basal tuft of thick, long hairs (Figs. 6A, C, 7Q and 8G).

3.2.6 Remarks on diagnostic characters

Echinoderes barbadensis sp. nov. possesses middorsal spines on segments 4–8 and short, robust lateral terminal spines. There are only seven species with this pattern of characters: *E. aquilonius* Higgins and Kristensen, 1988, *E. augustae* Sørensen and Landers, 2014, *E. brevicaudatus* Higgins, 1966, *E. cavernus* Sørensen et al., 2000, *E. lusitanicus* Neves et al., 2016 (only females), *E. obtuspinosus* Sørensen et al., 2012 and *E. ulsanensis* Adrianov, 1999 in Adrianov and Malakhov, 1999. Nonetheless, *E.*

barbadensis sp. nov. can be unambiguously distinguished from the aforementioned congeners by the arrangement of the remaining spines and tubes, and the pattern of type 2 glandular cell outlets.

Echinoderes lusitanicus and *E. ulsanensis* are the species that most differ from *E. barbadensis* sp. nov., as only possess lateroventral spines on segments 8–9 and 6–8 respectively, whereas *E. barbadensis* has lateroventral spines on segments 6–9.

The pattern of tubes allows distinguishing *E. aquilonius* and *E. obtuspinosus* from *E. barbadensis* sp. nov: the first two bear these structures only in lateroventral position on segment 5, whereas the latter has tubes in lateral accessory position on segment 8, lateroventral position on segment 5 and ventrolateral position on segment 2. The pattern of the type 2 glandular cell outlets is also different: *E. aquilonius* bears these structures in subdorsal position on segments 2 and 4, laterodorsal position on segment 10, sublateral position on segment 8, midlateral position on segments 2 and 5, and ventrolateral position on segment 2; *E. obtuspinosus* has the glands in subdorsal position on segments 2 and 4, laterodorsal position on segment 2, sublateral position on segments 2 and 8, and ventrolateral position on segment 2; *E. barbadensis* sp. nov. only has type 2 glandular cell outlets in subdorsal position on segment 2 and midlateral position on segment 4.

Echinoderes augustae, *E. brevicaudatus* and *E. cavernus* are similar to *E. barbadensis* sp. nov. in the possession of lateroventral spines on segments 6–9, lateroventral tubes on segment 5 and lateroventral/ventrolateral tubes on segment 2. However, *E. augustae* also possesses tubes in midlateral position on segment 4, laterodorsal position on segment 10 (only males), and sublateral position on segment 8, whereas *E. barbadensis* sp. nov. carries these structures only in lateral accessory position on segment 8. Additionally, *E. brevicaudatus* and *E. cavernus* lack tubes in lateral accessory position on segment 8 and type 2 glandular cell outlets, structures present in *E. barbadensis* sp. nov. as mentioned above.

3.2.7 Associated kinorhynch fauna

No other kinorhynch species co-occurred with *E. barbadensis* sp. nov. in the studied location.

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The authors declare no conflicts of interest.

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598 TABLES

599 Table 1. Data on sampling localities and habitat of the collected specimens.

Station code	Location	Geographical coordinates	Sampling date	Sediment	Depth (m)
L1	La Parguera (Puerto Rico)	17º57´00´´N 67’03´00´´W	07/06/1967	Mud	15
L2	St. James (Barbados)	13º13´12´´N 59º37´12´´W	23/08/1968	Unknown	Unknown

600

601 Table 2. Measurements of adult *Cristaphyes cornifrons* sp. nov. from Puerto Rico,
602 including number of measured specimens (*n*), mean of data and standard deviation
603 (SD). Abbreviations: LTS, lateral terminal spine; MSW-5, maximum sternal width (on
604 segment 5); S, segment lengths (numbers after S indicate the corresponding segment);
605 SW-10, standard sternal width (on segment 10); TL, total length of trunk.

Character	Range	Mean (SD; *n*)
TL (µm)	422.6–481.8	447.9 (30.5; 3)
MSW-5 (µm)	101.0–111.7	105.3 (5.6; 3)
MSW-5/TL (%)	21.5–24.0	23.6 (2.0; 3)
SW-10 (µm)	76.9–104.2	88.1 (14.3; 3)
SW-10/TL (%)	16.0–23.7	19.8 (3.9; 3)
S1 (µm)	68.5–82.0	76.2 (7.0; 3)
S2 (µm)	35.1–40.6	38.5 (3.0; 3)
S3 (µm)	43.3–50.0	46.0 (3.3; 3)
S4 (µm)	44.7–49.8	47.0 (2.6; 3)
S5 (µm)	45.8–51.6	48.9 (2.9; 3)
S6 (µm)	48.3–53.5	50.6 (2.6; 3)
S7 (µm)	47.1–52.5	48.9 (3.1; 3)
S8 (µm)	47.8–54.5	50.6 (3.5; 3)
S9 (µm)	46.9–58.7	53.4 (6.0; 3)
S10 (µm)	35.5–49.0	43.4 (7.1; 3)
S11 (µm)	24.6–38.7	29.6 (7.8; 3)
LTS (µm)	111.7–181.8	151.6 (36.0; 3)
LTS/TL (%)	25.4–43.0	34.0 (8.8; 3)

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607 Table 3. Summary of nature and arrangement of sensory spots, glandular cell outlets,
608 cuticular processes, setae, nephridiopores and spines in adults of *Cristaphyes cornifrons*

609 sp. nov. Abbreviations: cp, cuticular process; f, female condition of sexually dimorphic
610 character; gco, glandular cell outlet; LD, laterodorsal; lts, lateral terminal spine; LV,
611 lateroventral; m, male condition of sexually dimorphic character; MD, middorsal; ne,
612 nephridiopore; PD, paradorsal; PL, paralateral; ps, penile spine; se, seta; ss, sensory
613 spot; ss3, type 3 sensory spot; SD, subdorsal; VL, ventrolateral; VM, ventromedial; ▲,
614 indicates intraspecific variation between ventrolateral or ventromedial position; *,
615 indicates unpaired structures.

Segment	MD	PD	SD	LD	PL	LV	VL	VM
1			gco, ss	ss	se		ss, gco	
2	cp	se*, ss	gco, ss, ss	gco, se, ss		se	se, gco	ss, ss, gco
3	cp	ss	gco, ss	gco, se, ss			se▲, gco	ss, gco
4	cp	se*, ss	gco, ss	gco, se, ss		se	gco	ss, se, gco
5	cp	ss	gco, ss	gco, se, ss			se, gco	ss, se, gco
6	cp	se*, ss	gco, ss	gco, se, ss		se	gco	ss, se, gco
7	cp	ss	gco, ss	gco, se, ss			gco	ss, se, gco
8	cp	ss	gco, ss	gco, se, ss		se	gco	ss, se, gco
9	cp	ss	gco, ss	gco, se, ss		ne	gco	ss, se, gco
10	cp	ss	gco, ss	gco, ssx, ss		se	se (f), ss, gco	ss, gco
11			ss3	ss3		lts, psx2 (m)		

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617 Table 4. Measurements of adult *Echinoderes barbadensis* sp. nov. from Barbados,
618 including number of measured specimens (*n*), mean of data and standard deviation
619 (SD). Abbreviations: ac, acicular spine; LA, lateral accessory; LTAS, lateral terminal
620 accessory spine; LTS, lateral terminal spine; LV, lateroventral; MD, middorsal; MSW-
621 5, maximum sternal width (on segment 5); S, segment lengths (numbers after S indicate
622 the corresponding segment); SW-10, standard sternal width (on segment 10); TL, total
623 length of trunk; tu, tube; VL, ventrolateral.

Character	Range	Mean (SD; *n*)
TL (µm)	223.7–307.0	275.0 (18.6; 20)
MSW-5 (µm)	62.5–86.6	71.0 (4.8; 20)
MSW-5/TL (%)	23.2–32.1	25.9 (2.0; 20)
SW-10 (µm)	53.6–67.0	59.2 (4.1; 20)
SW-10/TL (%)	20.0–24.5	21.6 (1.8; 20)
S1 (µm)	29.0–33.9	31.1 (1.3; 20
S2 (µm)	27.2–33.5	30.1 (1.7; 20)

S3 (µm)	29.7–35.9	32.9 (1.7; 20)
S4 (µm)	26.5–40.4	36.8 (2.9; 20)
S5 (µm)	31.8–42.1	37.1 (2.3; 20)
S6 (µm)	32.6–42.7	38.8 (2.4; 20)
S7 (µm)	37.1–42.6	40.5 (1.4; 20)
S8 (µm)	40.3–44.3	42.4 (1.4; 20)
S9 (µm)	39.4–46.9	44.2 (1.8; 20)
S10 (µm)	41.1–48.7	45.8 (1.8; 20)
S11 (µm)	22.3–39.2	31.7 (3.9; 20)
MD4 (ac) (µm)	6.5–12.6	9.6 (1.6; 18)
MD5 (ac) (µm)	6.8–12.2	9.7 (1.4; 19)
MD6 (ac) (µm)	7.7–13.6	10.5 (1.7; 19)
MD7 (ac) (µm)	6.7–14.8	11.0 (2.1; 19)
MD8 (ac) (µm)	7.3–12.8	10.5 (1.2; 20)
VL2 (tu) (µm)	6.3–11.5	8.6 (1.4; 15)
LV5 (tu) (µm)	6.3–11.1	8.4 (1.2; 19)
LV6 (ac) (µm)	8.0–13.6	11.0 (1.4; 20)
LV7 (ac) (µm)	8.0–13.7	10.4 (1.3; 20)
LV8 (ac) (µm)	9.1–15.0	10.6 (1.4; 20)
LA8 (tu) (µm)	6.3–10.9	7.7 (1.0; 20)
LV9 (ac) (µm)	9.5–13.4	11.3 (1.3; 19)
LTS (µm)	48.4–58.3	55.1 (2.5; 19)
LTS/TL (%)	17.4–24.9	20.1 (1.9; 19)
LTAS (µm)	17.2–21.6	19.0 (1.2; 10)
LTAS/LTS (%)	31.8–44.6	34.7 (3.5; 10)

Table 5. Summary of nature and arrangement of sensory spots, glandular cell outlets, spines, tubes and nephridiopores in adults of *Echinoderes barbadensis* sp. nov. Abbreviations: ac, acicular spine; f, female condition of sexually dimorphic character; gco1/2, glandular cell outlet type 1/2; LA, lateral accessory; LD, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; LV, lateroventral; m, male condition of sexually dimorphic character; MD, middorsal; ML, midlateral; ne, nephridiopore; PD, paradorsal; pr, protuberance; ps, penile spine; SD, subdorsal; SL, sublateral; ss, sensory spot; t, tube; VL, ventrolateral; VM, ventromedial.

Segment	**MD**	**PD**	**SD**	**LD**	**ML**	**SL**	**LA**	**LV**	**VL**	**VM**
1	gco1		ss	ss					ss	
2	gco1		gco2	ss					t	gco1

3	gco1							ss	gco1
4	ac	gco1, ss		gco2				ss	gco1
5	ac	gco1, ss	ss				t	ss	gco1
6	ac	gco1, ss					ac		gco1
7	ac	gco1, ss					ac		gco1
8	ac	gco1, ss	ss			t	ac	ss	gco1
9		gco1	ss		ne		ac	ss	gco1
10	gco1, gco1		ss						gco1
11	pr, gco1					psx3 (m), ltas (f)	lts		

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652 FIGURE LEGENDS

653 **Fig. 1.** General map (A) showing the sampling localities (B-C) through the Caribbean
654 Sea (western Atlantic Ocean).

655 **Fig. 2.** Line art illustrations of *Cristaphyes cornifrons* sp. nov. (A) Male, ventral
656 overview; (B) Male, dorsal overview; (C) Female, segments 10-11, ventral view; (D)
657 Female, segments 10-11, dorsal view. Abbreviations: dcr, dorsal cuticular ridge; dpl,
658 dorsal placid; gco, glandular cell outlet; ldgco, laterodorsal glandular cell outlet; ldms,
659 laterodorsal muscular scar; ldse, laterodorsal seta; ldss, laterodorsal sensory spot; ldss3,
660 laterodorsal type 3 sensory spot; lts, lateral terminal spine; lvse, lateroventral seta;
661 mdcp, middorsal cuticular process; pdse, paradorsal seta; pdss, paradorsal sensory spot;
662 plse, paralateral seta; ppf, primary pectinate fringe; ps, penile spine; S, segment
663 followed by number of corresponding segment; sdgco, subdorsal glandular cell outlet;
664 sdss, subdorsal sensory spot; sdss3, subdorsal type 3 sensory spot; spf, secondary
665 pectinate fringes; vcr, ventral cuticular ridge; vlse, ventrolateral seta; vlss, ventrolateral
666 sensory spot; vmgco, ventromedial glandular cell outlet; vmms, ventromedial muscular
667 scar; vmse, ventromedial seta; vmss, ventromedial sensory spot; vpl, ventral placid.

668 **Fig. 3**. Light micrographs showing trunk overviews and details in the head and neck of
669 female holotype USNM 1550583 (A-B) and male paratype USNM 1550585 (C-F) of
670 *Cristaphyes cornifrons* sp. nov. (A) Dorsal overview of trunk; (B) ventral overview of
671 trunk; (C) mouth cone, showing the outer oral styles (ring 00); (D) introvert, showing
672 primary spinoscalids (ring 01), regular scalids and neck's trichoscalids (ring 07); (E)
673 dorsal view of neck, showing the dorsal placids; (F) ventral view of neck, showing the
674 ventral placids. Abbreviations: dpl, dorsal placid; lts, lateral terminal spines; oos, outer
675 oral style; psc, primary spinoscalid; sc, scalid; ts, trichoscalid; vpl, ventral placid.

676 **Fig. 4**. Light micrographs showing trunk cuticular details of male paratype USNM
677 1550585 of *Cristaphyes cornifrons* sp. nov. (A) Left half of tergal plate of segment 1;
678 (B) ventrolateral and ventromedial views on left half of segment 1; (C) left halves of
679 tergal plates of segments 8-11; (D) left half of tergal plate of segment 2; (E) left sternal
680 plate of segment 2; (F) left half of tergal plate of segment 3; (G) left sternal plate of
681 segment 3; (H) lateroventral to ventromedial view on left sternal plates of segments 8-
682 11; (I) left halves of tergal plates of segments 4-7; (J) left sternal plates of segments 4-7.
683 Abbreviations: ldse, laterodorsal seta; lvne, lateroventral nephridiopore; lvse,

lateroventral seta; mdcp, middorsal cuticular process; mdcpr, middorsal cuticular projection; pdse, paradorsal seta; plse, paralateral seta; vlse, ventrolateral seta; vmse, ventromedial seta; sensory spots are marked as closed circles, and glandular cell outlets as dashed circles; numbers after abbreviations indicate the corresponding segment.

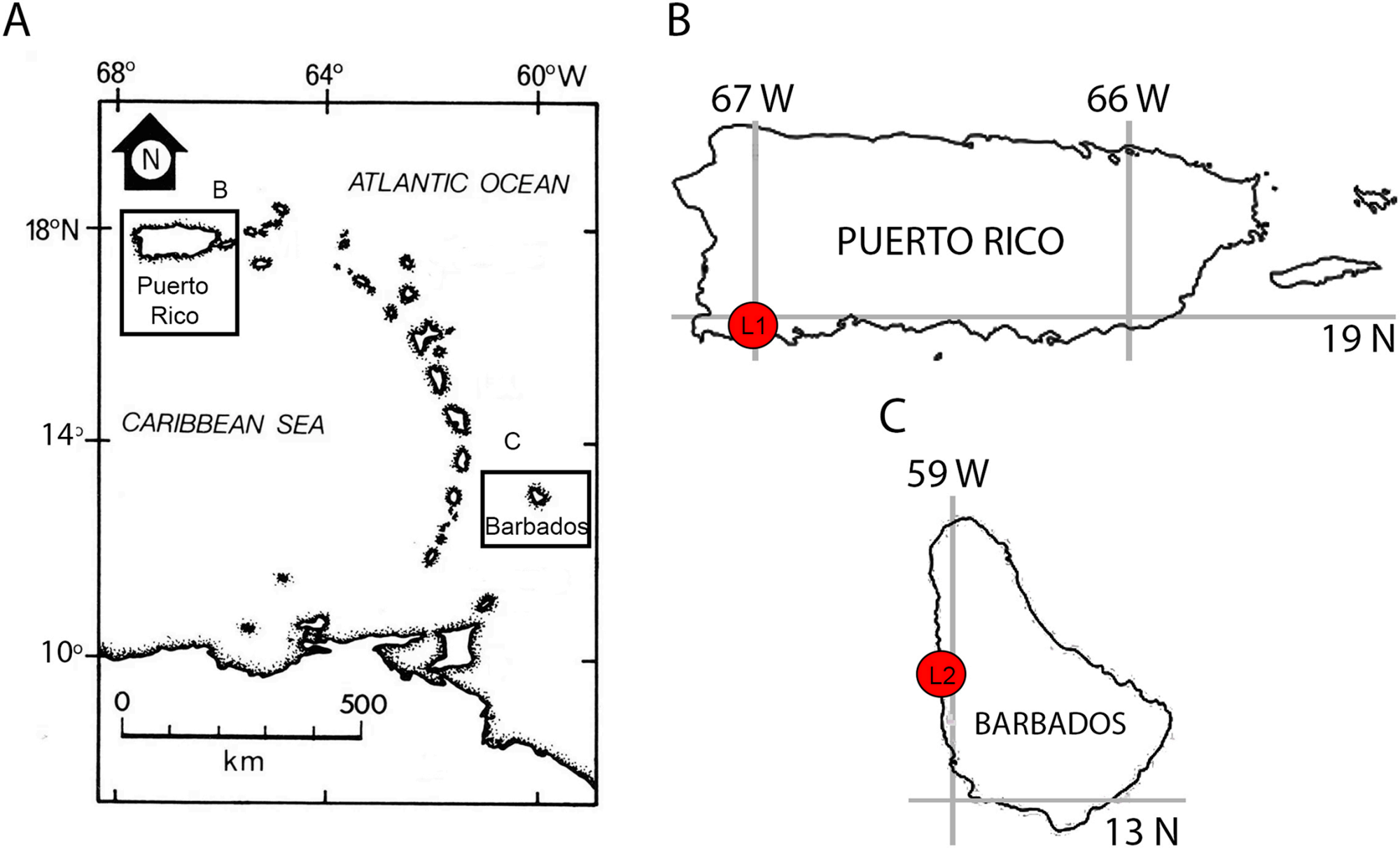
Fig. 5. Scanning electron micrographs showing general overviews and details of the cuticular trunk morphology of non-type male of *Cristaphyes cornifrons* sp. nov. (A) Lateral overview of trunk; (B) ventral overview of trunk; (C) paradorsal view on right half of segment 8, with detail of the middorsal process and the paradorsal sensory spot; (D) subdorsal to lateroventral view on right half of segments 2-3; (E) left sternal plates of segments 2-3; (F) detail of ventrolateral seta and ventromedial sensory spot of segment 3; (G) left sternal plates of segment 7, with detail of the ventral cuticular ridge and the associated glandular cell outlets; (H) left sternal plates of segments 10-11, showing the male penile spines; (I) ventromedial view on left half of segment 7, with detail of the ventromedial seta and the ventromedial sensory spot. Abbreviations: ldse, laterodorsal seta; lvse, lateroventral seta; ps, penile spine; vlse, ventrolateral seta; vmse, ventromedial seta; sensory spots are marked as closed circles, and glandular cell outlets as dashed circles; numbers after abbreviations indicate the corresponding segment.

Fig. 6. Line art illustrations of *Echinoderes barbadensis* sp. nov. (A) Female, ventral overview; (B) Female, dorsal overview; (C) Male, segments 10-11, ventral view; (D) Male, segments 10-11, dorsal view. Abbreviations: ch, cuticular tuft of hairs; dpl, dorsal placid; lat, lateral accessory tube; ldss, laterodorsal sensory spot; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mdgco1, middorsal type 1 glandular cell outlet; mdpb, middorsal protuberance; mds, middorsal spine; mlgco2, midlateral type 2 glandular cell outlet; mvp, midventral placid; ne, nephridiopore; pdgco1, paradorsal type 1 glandular cell outlet; pdss, paradorsal sensory spot; ppf, primary pectinate fringe; ps, penile spine; S, segment followed by number of corresponding segment; sdgco2, subdorsal type 2 glandular cell outlet; sdss, subdorsal sensory spot; te, tergal extension; tsp, trichoscalid plate; vlss, ventrolateral sensory spot; vmgco1, ventromedial type 1 glandular cell outlet; vlt, ventrolateral tube; cuticular hairs are drawn as grey dotes to make the interpretation of the remaining cuticular characters easier.

Fig. 7. Light micrographs showing overviews, neck and trunk cuticular details and structures of male holotype USNM 1550576 of *Echinoderes barbadensis* sp. nov. (A)

Ventral overview of trunk; (B) dorsal view of neck, showing the dorsal placids; (C) ventral view of neck, showing the ventral placids; (D) middorsal to laterodorsal view on left half of segment 1; (E) lateroventral to ventromedial view on left half of segment 1; (F) middorsal to laterodorsal view on left half of segment 2; (G) lateroventral to ventromedial view on left half of segment 2; (H) left halves of tergal plates of segments 3-4; (I) sublateral to ventromedial view on left half of segments 3-4, (J) middorsal to subdorsal view on left half of segments 7-8; (K) lateroventral to ventromedial view on left half of segments 7-8; (L) middorsal to subdorsal view on left half of segments 5-6; (M) lateroventral to ventromedial views on left half of segments 5-6; (N) middorsal to subdorsal view on left half of segment 9; (O) lateroventral to ventromedial view on left half of segment 9; (P) left halves of tergal plates of segments 10-11; (Q) left sternal plates of segments 10-11; (R) lateral terminal spine. Abbreviations: lat, lateral accessory tube; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; mvpl, midventral placid; slne, sublateral nephridiopore; vlt, ventrolateral tube; sensory spots are marked as closed circles, and glandular cell outlets as dashed circles; numbers after abbreviations indicate the corresponding segment.

Fig. 8. Scanning electron micrographs showing general overview and details of the cuticular trunk morphology of non-type female (A-B) and male (C-G) of *Echinoderes barbadensis* sp. nov. (A) Lateral overview of trunk; (B) subdorsal to lateroventral view on left half of segments 1-2; (C) lateroventral overview of segments 5-10; (D) detail of ventrolateral sensory spot of segment 8; (E) detail of the lateral accessory tube and the lateroventral spine of right side of tergal plate of segment 8; (F) detail of the ventrolateral sensory spot of sternal plates of segment 8; (G) ventral overview of right sternal plate of segments 10-11, with detail of the penile spines and the elongated, basal, thick cuticular hair of the tergal extensions. Abbreviations: ch, cuticular tuft of hairs; lat, lateral accessory tube; lvs, lateroventral spine; lvt, lateroventral tube; ps, penile spines; sensory spots are marked as closed circles, and glandular cell outlets as dashed circles; numbers after abbreviations indicate the corresponding segment.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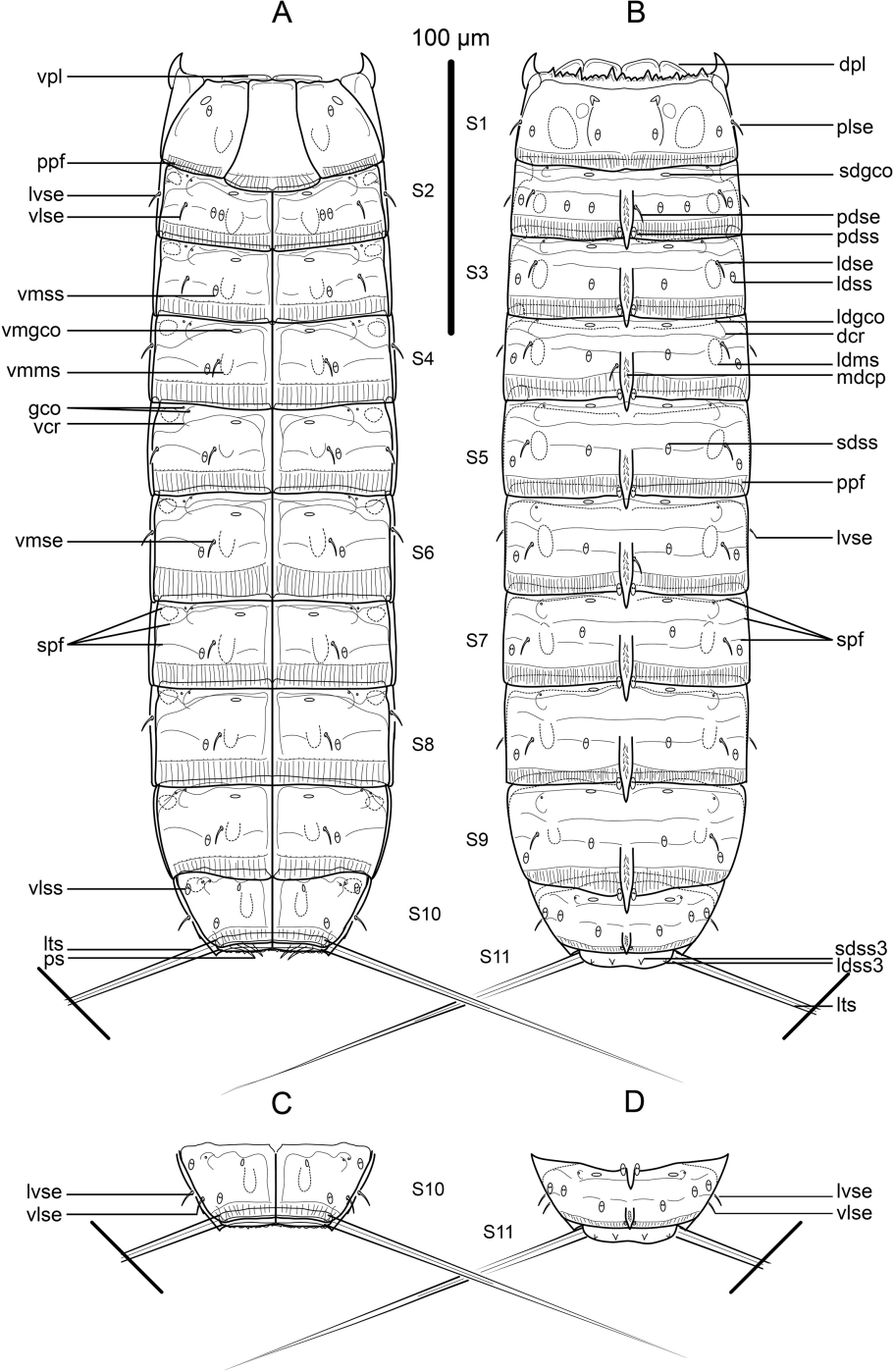
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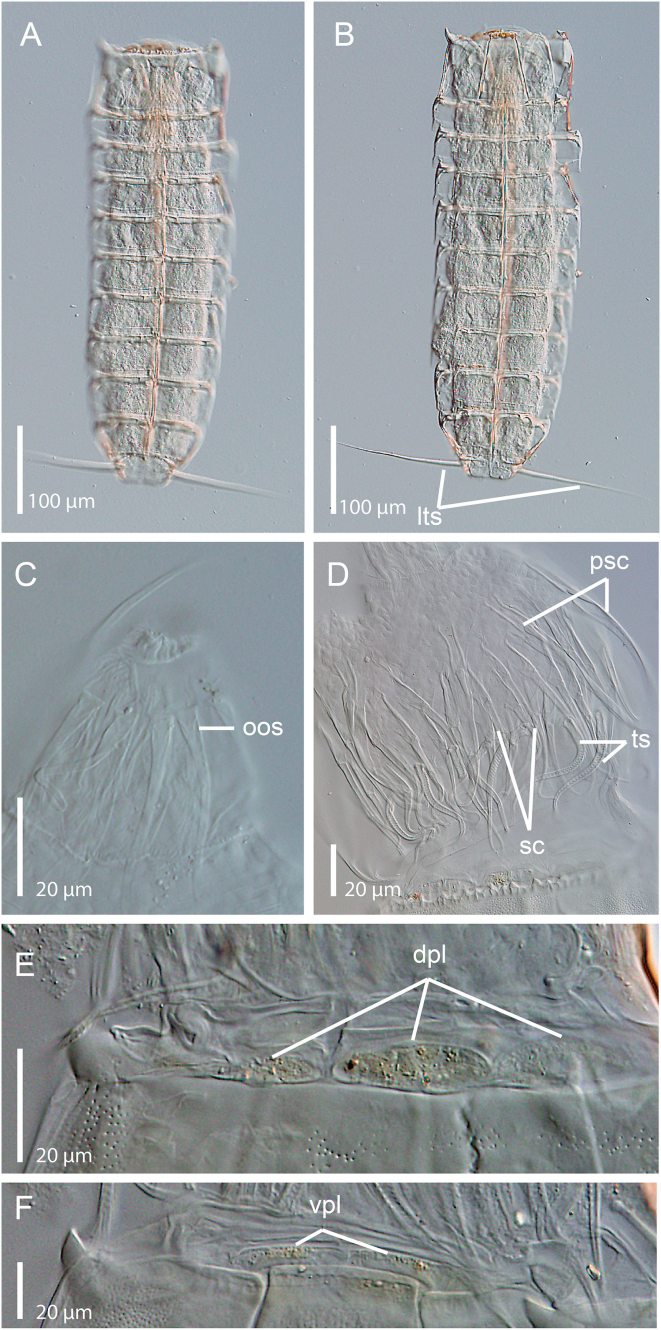
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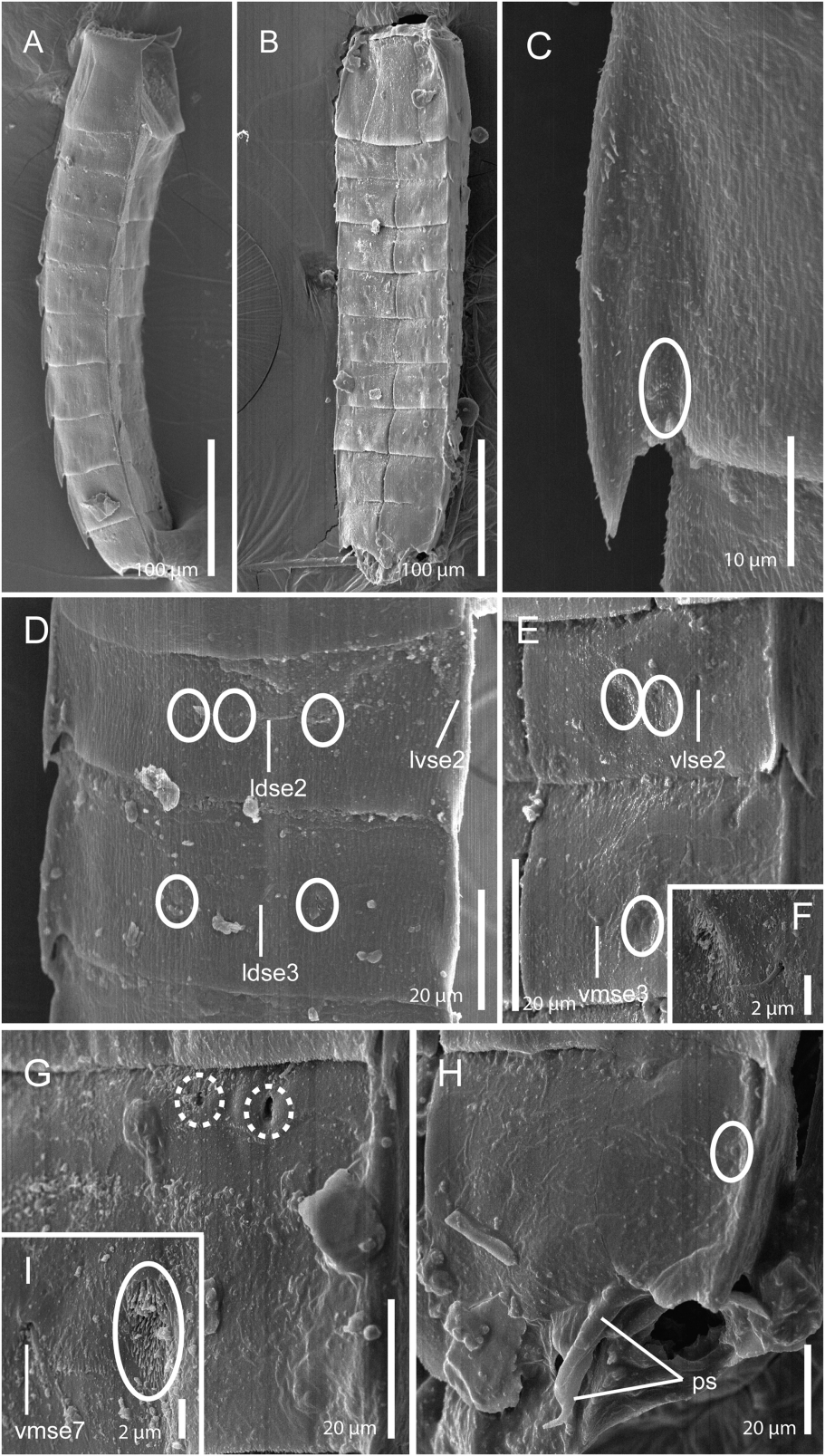
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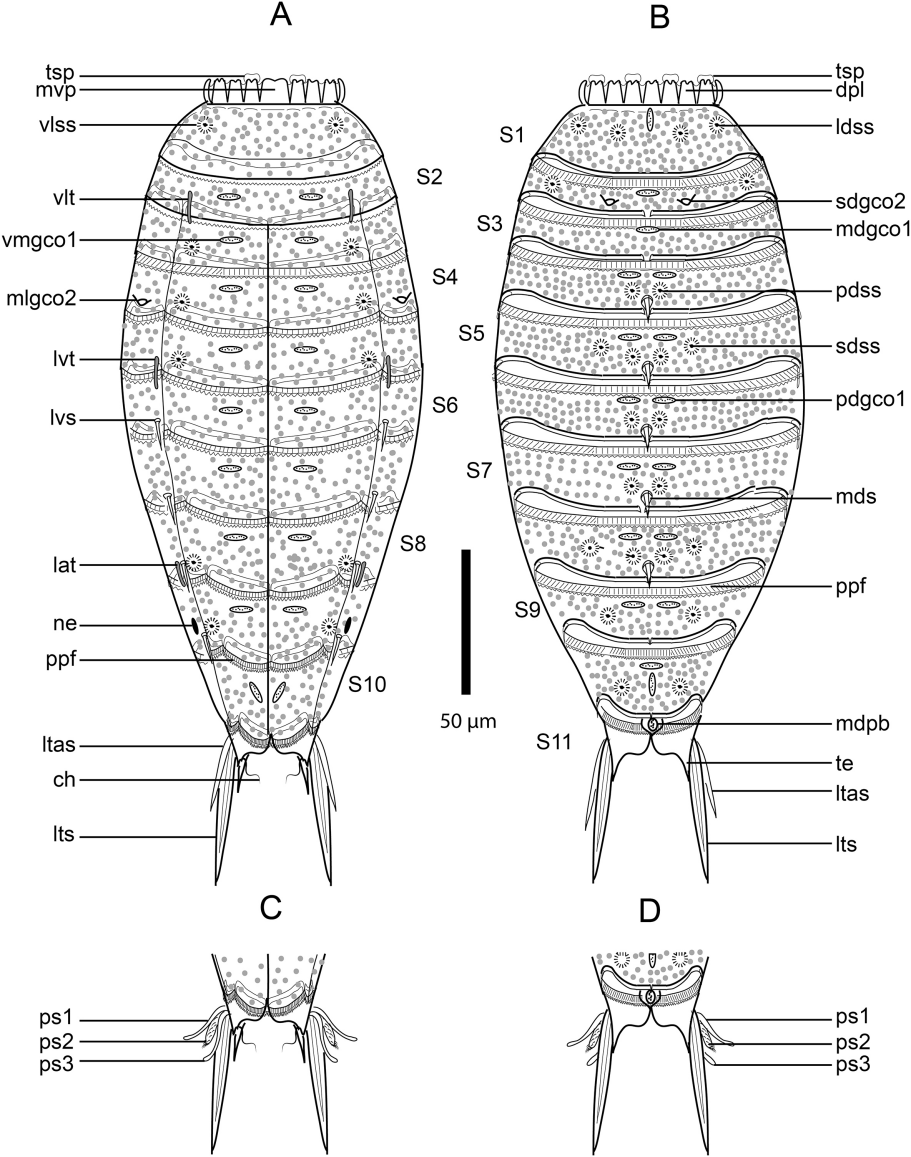
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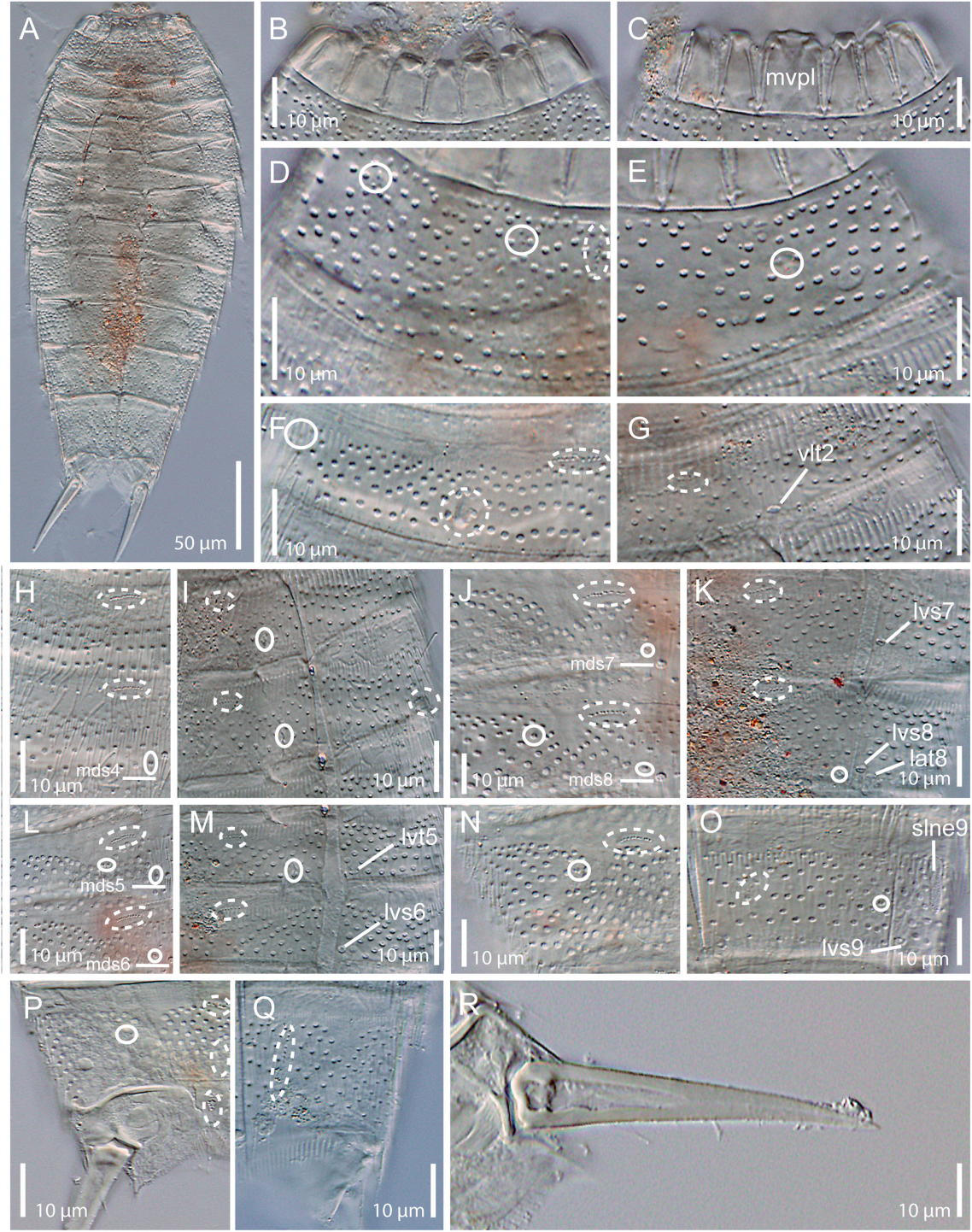
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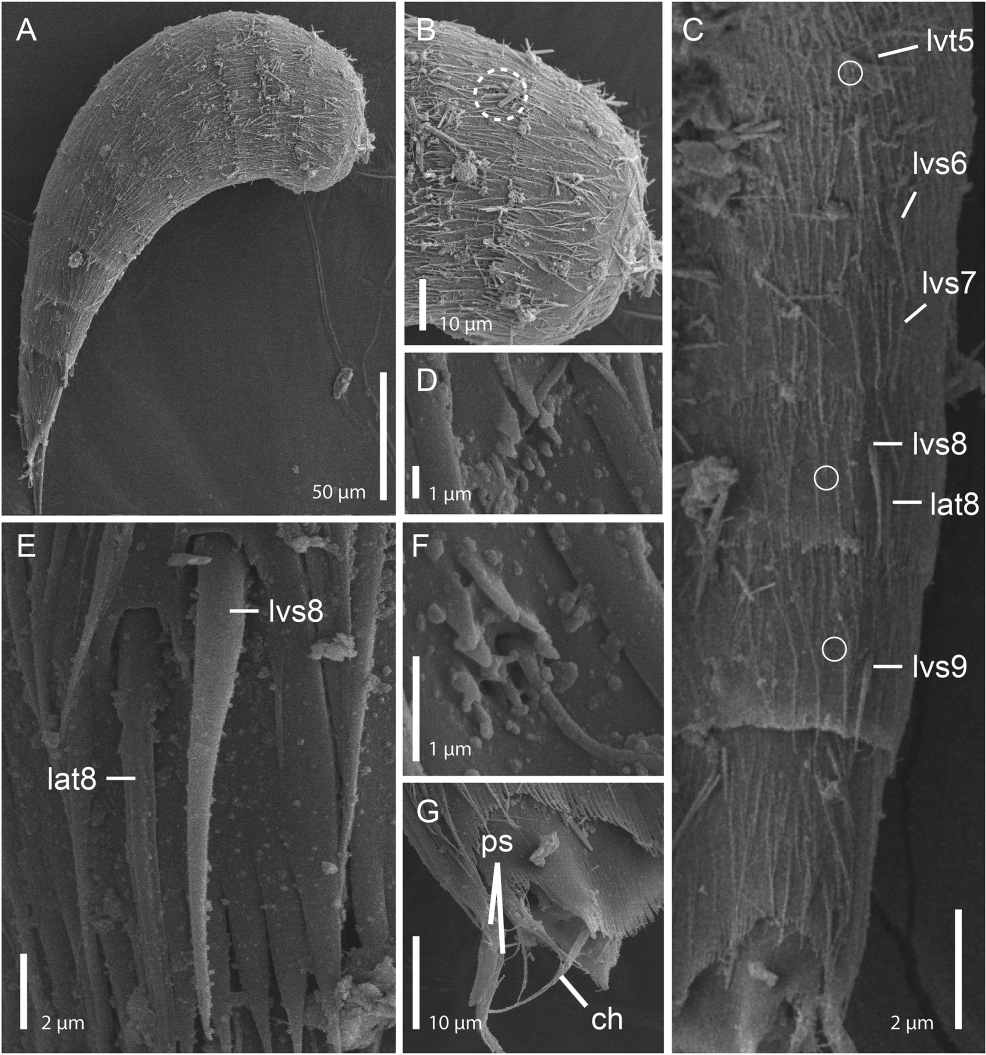
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