Ryuguderes iejimaensis, a new genus and species of Campyloderidae (Xenosomata: Cyclorhagida: Kinorhyncha) from a submarine cave in the Ryukyu Islands, Japan

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***Ryuguderes iejimaensis*, a new genus and species of Campyloderidae (Xenosomata: Cyclorhagida: Kinorhyncha) from a submarine cave in the Ryukyu Islands, Japan**

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Abstract

Ryuguderes iejimaensis gen. et sp. nov. (Xenosomata: Cyclorhagida: Kinorhyncha) is described from the Daidokustu submarine cave off Iejima Island, Ryukyu Islands, Japan. The species is characterized by the presence of outer oral styles with incompletely fused proximal parts and separate distal parts; primary spinoscalids with several internal septa; spinoscalids in ring 02 short; 14 placids, with the midventral one broadest and six broader placids alternating with seven narrower ones; middorsal acicular spines on segments 2–11 in males and on segments 2–9 in females; lateroventral acicular spines on segments 4, 6–7, and 9; short, blunt lateroventral spines on segment 5; midterminal, lateral terminal and lateral terminal accessory spines with a thick proximal cuticle around a central cellular cavity. The placid numbers and morphology of the outer oral styles, spinoscalids, and lateral terminal accessory and midterminal spines suggest *Ryuguderes* to be closely related with *Campyloderes*. In addition, morphological similarities between *Ryuguderes*, *Campyloderes*, and different genera of Kentrorhagata suggest Xenosomata and Kentrorhagata to be closely related.

Keywords

meiofauna, submarine cave, taxonomy, morphological evolution

1. Introduction

Exploration of submarine caves in the past decades have revealed the existence of numerous biologically interesting organisms, including sponges, polychaetes, bryozoans, brachiopods, crustaceans, and molluscs, that otherwise are known mostly from the deep-sea (e.g., Browman and Iliffe, 1985; Harmelin, 1997; Hayami and Kase, 1992; Iliffe et al. 1984; Kano and Kase, 2008; Vacelet et al. 1994; Yager, 1981). Such species previously detected in Daidokutsu, a submarine cave east of Iejima Island, Ryukyu Islands, Japan, include representatives of Tardigrada (Fujimoto, 2015), Ostracoda (Tabuki and Hanai, 1999), and Mollusca (Kase and Hayami, 1992). While the macrofauna of several submarine caves have been investigated, few surveys have focused at the meiofauna. The only previous account of a new submarine cave-dwelling kinorhynch was an *Echinoderes* species from Australia (Sørensen et al., 2000).

Campyloderidae, which currently contains only the genus *Campyloderes*, is one of 11 kinorhynch families (Sørensen et al., 2015). Campyloderids occupy various habitats, including fine sand, coarse sand, coral sand, and the holdfasts of kelps and calcareous algae (Moore, 1973; Neuhaus and Sørensen, 2013; Sánchez et al., 2012), are distributed worldwide from equatorial to polar regions, and range in depth from 0.2 m to 5118 m (Neuhaus and Sørensen, 2013). Unique synapomorphies for *Campyloderes* are fused outer oral styles, primary spinoscalids with several septa, and unusually long lateroventral spines on segment 1

(Neuhaus and Sørensen, 2013; Sørensen et al., 2015). Recent phylogenetic studies based on molecular, or combined molecular and morphological, have indicated monophyly for the group and that the campyloderid clade comprises one of the three major clades in the class Cyclorhagida (Dal Zotto et al., 2013; Sørensen et al., 2015; Yamasaki et al., 2013).

In this paper, I describe a new campyloderid genus and species from Daidokutsu and discuss the phylogenetic position and morphological evolution of the genus.

2. Material and methods

A mud sediment sample was collected by SCUBA at 28–30 m depth on 25 April 2015 in the Daidokustu submarine cave (24°43.492'N, 127°49.873'E). Kinorhynchs and other meiofauna were extracted from the sample by a combination of decantation (Higgins and Thiel, 1988) and floatation (Giere, 2009) with Ludox® HS-40, and preserved in 10% formalin. After a week, the organisms were transferred to 70% EtOH and sorted under a stereomicroscope.

Eleven specimens to be used for light microscopy (LM) were transferred into a solution of 70% ethanol, 25% distilled water, and 5% glycerol. After evaporation of the ethanol and water, specimens were mounted individually in Fluoromount G® between two cover slips attached to a plastic H-S slide and sealed with Canada balsam. The LM specimens were observed, sketched, and photographed with an Olympus BX51 microscope equipped with a Nikon DS-Fi1c camera and a drawing tube. Line illustrations based on scanned camera lucida drawings of mounted specimens were prepared with Adobe Illustrator CS5. Measurements were made with a Nikon DS-L3 camera control unit.

Five specimens were prepared for scanning electron microscopy (SEM). Two of them were dehydrated in a graded ethanol series, immersed in 100% t-butyl alcohol for about 30 minutes, freeze-dried, mounted on aluminum stubs, sputter-coated with gold-palladium, and observed with a JEOL JSM-6060LV scanning electron microscope at the University of the Ryukyus (Okinawa, Japan). The remaining three specimens were postfixed with OsO4 in 0.05 M phosphate buffer (pH = 7.3) with 0.3 M sodium chloride and 0.05% sodium azide for 2.5 hours, dehydrated through a graded series of ethanol, and critical point dried, mounted on aluminum stubs, sputter coated with gold-palladium, and observed with a Zeiss EVO LS 10 scanning electron microscope in Museum für Naturkunde (Berlin, Germany).

The terminology herein follows Neuhaus and Higgins (2002), Sørensen and Pardos (2008), and Neuhaus (2013). LM specimens were deposited in the invertebrate collection of the Hokkaido University Museum, Hokkaido University, Sapporo, Japan (catalogue numbers ZIHU-5081–5087); the University Museum (Fujukan), University of the Ryukyus, Okinawa, Japan (catalogue numbers RUMF-ZK-00022–00023); and the Natural History Museum of Denmark, Copenhagen, Denmark (catalogue numbers ZMUC KIN-920–921).

3. Results

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

Order Xenosomata Zelinka, 1907

3.1. Family Campyloderidae Remane, 1929

3.1.1. Diagnosis

Outer oral styles fused proximally; primary spinoscalids (=ring 01) of adult with at least 8 internal septae; ring 02 scalids short and acicular; 14 placids present; midventral placid broadest, with the rest comprising small, triangular placids alternating with broader, rounded placids; middorsal acicular spines at least on segments 2–11 in males and at least on segments 2–9 in females; laterodorsal to sublateral acicular spines on segment 10 in males only; lateral terminal spines; midterminal spine with thick proximal cuticle around central cavity and an area of thin cuticle dorsally; lateral terminal accessory spines with thick proximal cuticle around central cavity and two dorsal areas of thin cuticle.

3.1.2. Genera included

Campyloderes Zelinka, 1907; *Ryuguderes* gen. nov.

3.2. Genus *Campyloderes* Zelinka, 1907 [Japanese name: Nise-mitsuotogekawa]

3.2.1. Diagnosis

Proximal part of outer oral styles fused completely and each style indistinct at proximal part; middorsal acicular spines on segments 1–11 in males and on segments 1–9 in females; lateroventral acicular spines on segments 1, 3–7, 9; lateroventral spines on segment 1 conspicuously long; lateroventral blunt spines on segment 2; ventrolateral blunt spines on segments 1 and 5.

3.3. Genus *Ryuguderes* gen. nov. [Japanese name: Ryugu-togekawa]

3.3.1. Diagnosis

Proximal part of outer oral styles fused at least their surface, but each style distinct in LM; distal part of the outer oral styles with ca. 10 lateral filiform cuticular elements; middorsal acicular spines on segments 2–11 in males and on segments 2–9 in females; lateroventral acicular spines on segments 4, 6–9; lateroventral short blunt spines on segment 5.

3.3.2. Etymology

The generic name is masculine, derived from the Japanese *Ryugu* or *Ryugu-jou* (mythical submarine dragon palace) and the Greek *deres* (neck), which is commonly used in generic names in the classes Cyclorhagida within Kinorhyncha.

3.3.3. Type species

Ryuguderes iejimaensis sp. nov.

3.4. *Ryuguderes iejimaensis* sp. nov. [Japanese name: Iejima Ryugu-togekawa] (Figs. 1–8 and Tables 1 and 2)

3.4.1. Diagnosis

Same as generic diagnosis.

3.4.2. Etymology

The specific epithet is from Iejima Island.

3.4.3. Type locality

Daidokutsu submarine cave near Iejima Island, Ryukyu Islands, Japan (24°43.492'N, 127°49.873'E), ca. 35 m from the cave entrance, depth 28 m, mud substrate.

3.4.4. Material examined

Holotype: Adult female (ZIHU-5081), mounted in Fluoromount G®. Allotype: Adult male (ZIHU-5082), mounted in Fluoromount G®. Paratypes: One adult female and four adult males (ZIHU-5083–5087), one adult female and one adult male (RUMF-ZK-00022–00023), one adult female and one adult male (ZMUC KIN-920–921), all mounted in Fluoromount G®. Additional material: Two male and three female mounted on aluminum stubs for SEM, in the author’s collection (University of the Ryukyus, Okinawa, Japan).

3.4.5. Description

Adult with head, neck, and 11 trunk segments (Figs. 1A, B and 2A). See Table 1 for measurements. Table 2 indicates positions of cuticular structures (sensory spots, glandular cell outlets type I, nephridial pores, and spines). Positions of some sensory spots and glandular cell outlets type I vary between specimens (see Table 2). Size and shape of glandular cell outlets type I vary between specimens as well as between right and left sides in same specimen.

Head consists of a retractable mouth cone and an introvert (Figs. 2A, B and 3A). Mouth cone with at least ten ring -01 inner oral styles and nine outer oral styles (Figs. 2B, C, 3A, B, and 4). Ring -01 inner oral styles triangular, fused with each other at lateral margins

(Fig. 3B). Each outer oral style without articulation (Fig. 2C). Ring -02 and -03 inner oral styles not examined. Adjacent outer oral styles fused proximally (Figs. 2B, C and 3A, B). Distal part of each outer oral style consists of long triangular area with ca. 10 filiform cuticular elements on each side (Figs. 2A and 3B). Proximal parts of outer oral styles completely fused externally with smooth surface. Even though the proximal parts of the surface of the outer oral styles are fused and appear this way in SEM, the internal parts of still appear as distinct styles in LM (Fig. 2C). Introvert composed of six rings of spinoscalids and one ring of trichoscalids (Figs. 2D, 3C, and 4). Ring 01 includes 10 primary spinoscalids, each with a basal sheath and a long end piece (Figs. 2D, 3C, and 4). Each basal sheath has minute hairs along its midline (Fig. 3C) and distal margin trident (Fig. 3C). End piece of primary spinoscalids' longest unit, with internal septa (Fig. 2D). Rings 02 and 03 with 10 spinoscalids; rings 04–06 with 15 spinoscalids (Figs. 2D, 3C, and 4). Distal part of spinoscalids ring 03–06 with minute hairs (Fig. 3C). Spinoscalids of rings 03–05 longer than those of rings 02 and 06 (Fig. 3C). Posteriormost ring with 14 trichoscalids whole covered with minute hairs.

Neck with 14 placids, with the midventral one broadest (ca. 25 µm in width at base), six of broader (ca. 17 µm in width at base), and seven narrower (ca. 14 µm in width at base) (Figs. 1A, B, 2D, 3C, 4, and 5A, B). Broadest midventral and broader placids rounded, narrower placids triangular (Figs. 1A, B, 2D, and 5A, B). Broadest midventral placid neighbored by narrower ones, and broader and narrower placids neighbored alternately (Figs. 1A, B and 5A, B).

Segment 1 consists of a complete cuticular ring with a thick pachycyclus at the anterior margin (Figs. 1A, B and 5A, B). Central to posterior surface of segment covered with small cuticular scales, visible only with SEM (Fig. 6A). Surface of central middorsal area with densely arranged cuticular bristles. Posterior edge of segment with flexible primary pectinate fringe (Figs. 1A, B, 5C, D, and 6A) with non-, bi-, or multi-furcate fringe tips of variable width (Fig. 6A). Fringe tips longest in sublateral to lateroventral region (Figs. 1A, B and 6A). Sensory spots present in laterodorsal position (Figs. 1A, 5A and 6A). Two pairs of glandular cell outlets type I present in laterodorsal position, and one pair each in subdorsal, ventrolateral, and ventromedial positions (Figs. 1A, B and 5A, B).

Segment 2 and following nine segments consist of one tergal and two sternal plates (Figs. 1A, B, 2A, 5A, B, D, E, and 7A–D). Separation between tergal and sternal plates of segments 2–10 is subcuticular and hence visible only with LM (Figs. 1A, B, 2A, 5B, D, E, 6C, 7A, D, and 8A–C); midsternal junctions visible with both SEM and LM (Figs. 1A, B, 2A, 5B, D, E, 7A, D, and 8C). Middorsal acicular spine present in most specimens, except for two of seven females (Figs. 1A, 5A, C, and 6B). Pachycycli present at anterior and tergosternal margins of each plate on segments 2–10 (Figs. 1A, B, 5A–E, and 7A–D). Cuticular scales cover the entire surface of segments 2–11, except for areas of densely arranged cuticular bristles, primary pectinate fringe, and muscle attachment sites (Figs. 6A–D and 8A–D). Posterior edge of each cuticular scale extends to form minute cuticular hair (Fig. 6E). Surface of central to posterior middorsal line and tergosternal junctions with densely arranged cuticular bristles (Figs. 1A, B, 5C, D, and 6B). Primary pectinate fringe similar to that of preceding segment (Figs. 5A–D and 6A, B). Secondary pectinate fringe form three lines, but sometimes difficult to observe on dorsal side with LM (Figs. 1A, B, 5C, D, and 6B). Sensory spots present at least in laterodorsal and ventromedial positions (Figs. 1A, B, 5A, D, 6A). Posterior paradorsal sensory spots variably present among specimens, i.e., paired, unpaired, or absent (Figs. 1A, 5C, 6B). Glandular cell outlets type I present in subdorsal, laterodorsal, ventrolateral, and ventromedial positions (Figs. 1A, B and 5A–D).

Segment 3 similar to preceding segment, except sensory spots present midlaterally and absent laterodorsally and ventromedially (Figs. 1A, B, 5A, B, and 6A, B).

Segment 4 with middorsal spine and lateroventral acicular spines (Figs. 1A, B, 5A, and 6C). Densely arranged cuticular bristles, and primary and secondary pectinate fringes, similar to segment 2 (Figs. 1A, B, and 6A–C). Unpaired paradorsal sensory spot present on anterior segment in all examined specimens, but presence at right or left side varies between individuals (Figs. 1A, 5A, and 6B). Additional posterior paradorsal sensory spots variably present among specimens, i.e., paired, unpaired, or absent (Figs. 1A, 5A, and 6B). Paired sensory spots present in midlateral and ventromedial positions (Figs. 1A, B, 5A, and 6A).

Segment 5 with middorsal and lateral accessory acicular spines (Figs. 1A, B, 5E, and 6C, D). Blunt spines present in lateroventral position (Figs. 1B, 5E, and 6C, D). Densely arranged cuticular bristles, and primary and secondary pectinate fringes, similar to segment 2 (Figs. 1A, B and 6C, D). Paradorsal sensory spots variable among specimens, paired or unpaired (Fig. 1A). Glandular cell outlets type I present in subdorsal, laterodorsal, ventrolateral, and ventromedial positions (Figs. 1A, B, and 5A).

Segment 6 with middorsal spine and lateroventral acicular spines (Figs. 1A, B, 5E, and 6D). Densely arranged cuticular bristles, and primary and secondary pectinate fringes, similar to segment 2. Paradorsal sensory spots variably present among specimens, i.e., paired, unpaired, or absent. Additional paired sensory spots present in midlateral and ventromedial positions (Figs. 1A, B, 5E, and 6D). Ventromedial papillae present in most females (ventromedial papillae absent in males and one of seven females) (Figs. 1B and 5E, and 6D, E).

Segment 7 similar to preceding segment, except for absence of midlateral and ventromedial sensory spots (Fig. 1A, B). Ventromedial papillae absent in males and two of seven females.

Segment 8 with middorsal and lateroventral acicular spines (Figs. 1A, B, 7A, and 8A, B). Paradorsal sensory spots variably present among specimens, i.e., paired, unpaired, or absent. Paired sensory spots present in midlateral, lateral accessory, and ventromedial positions (Figs. 1A, B, 7A, and 8A). Paired glandular cell outlets type I present in subdorsal, laterodorsal, and ventrolateral positions, and two paired in ventromedial positions (Fig. 1A, B). Other characters similar to the preceding segment.

Segment 9 similar to preceding segment, except for presence of nephridial pores in lateral accessory position and sensory spots in laterodorsal position, and absence of midlateral and lateral accessory sensory spots (Figs. 1A, B, 7A, B, and 8B). Tips of primary pectinate fringe shorter than on preceding segment (Figs. 1A–D and 8A, B).

Segment 10 with acicular spines middorsally and laterodorsally in males, but lacking in females (Figs. 1A–D, 7A–C, and 8D). Tergal and sternal plates only partially differentiated, with tergosternal subcuticular junctions, present anterior to medially, but not posteriorly (Figs. 1B, D and 7A). Primary and secondary pectinate fringes similar to preceding segment, except for the most posterior line of secondary pectinate fringe which is absent (Figs. 1A–D, 7A, B, and 8C). Area of densely arranged cuticular bristles present in middorsal line in males only (Figs. 1C and 8D). Sensory spots present at least in laterodorsal and ventrolateral positions (Figs. 1A–D, 7A–C, and 8C, D). Paradorsal and subdorsal sensory spots present only in some specimens (Figs. 1A, C, 7B, and 8D). Glandular cell outlets type I paired at least in subdorsal and ventrolateral positions (Figs. 1A–D, 7A). Additional paired or unpaired glandular cell outlets type I present in subdorsal and ventrolateral positions in some specimens (Figs. 1A–D and 7A–C).

Segment 11 with midterminal spine, lateral terminal spines, and lateral terminal accessory spines (Figs. 1A–D, 7A–D, and 8C, D). Middorsal acicular spine present only in males (Figs. 1C, 7C, and 8D). Midterminal and lateral terminal accessory spines with thick proximal cuticle around central cellular cavity. Gonopores present in ventrolateral position in females (Figs. 1B, 7D, and 8C). Primary pectinate fringe absent. One line of secondary pectinate fringe present on sternal plates (Figs. 7D and 8C). Sensory spots present in subdorsal position (Figs. 1A, C, 7B, and 8D). Two pairs of glandular cell outlets type I present in ventromedial positions (Figs. 1B, D and 7A, D). Paired or unpaired subdorsal and ventrolateral glandular cell outlets type I present in some but not all specimens (Figs. 1C, D, 7A).

4. Discussion

Ryuguderes gen. nov. is assigned to Campyloderidae based on the morphology of the head, neck, and terminal spines. The outer oral styles are fused; the primary spinoscalids have several internal septa; the 14 placids include one broadest, six broader, and seven narrower ones; and the midterminal and lateral terminal accessory spines have a thick proximal cuticle around a central cellular cavity. This combination of characters is shared only with the campyloderid genus *Campyloderes* (Neuhaus, 2004; Neuhaus and Sørensen, 2013), and these two genera are undoubtedly closely related.

Ryuguderes gen. nov. differs from *Campyloderes* in several ways. In *Ryuguderes*, each distal part of the outer oral styles comprises a long triangular area with ca. 10 filiform cuticular elements on each side, whereas such structures are absent in *Campyloderes*. In *Ryuguderes*, the proximal parts of the outer oral styles are incompletely fused, and have separated or partially fused styles that are visible with LM. Oppositely, *Campyloderes* has outer oral styles being fused both externally and internally, and separation of each style is not visible (Neuhaus and Sørensen, 2013, Neuhaus per. comm.). *Ryuguderes* and *Campyloderes* have the same total number of spinoscalids in each sector of the introvert but differ in the number of spinoscalids in each ring: even sectors in rings 03–05 have 0, 2, and 1 spinoscalids, respectively in *Ryuguderes*, but 2, 1, and 0 in *Campyloderes*. Spine composition also differs between *Ryuguderes* and *Campyloderes*. *Ryuguderes* lacks a middorsal acicular spine on segment 1, and spines in the lateroventral and ventrolateral positions on segments 1–3, whereas *Campyloderes* has a middorsal acicular spine on segment 1, lateroventral acicular or blunt spines on segments 1–3, and ventrolateral blunt spines on segment 1. In *Ryuguderes*, cuticular bristles are densely arranged on the surface of the tergosternal junctions on segments 2–9, in the middorsal line on segments 1–9 in both sexes, and in the middorsal line on segment 10 in males, whereas such cuticular bristles have not been reported from any *Campyloderes* species (Johnston, 1938; Moore, 1973; Neuhaus, 2004; Neuhaus and Sørensen, 2013; Song and Chang, 2001; Zelinka, 1913, 1928).

4.1. Morphological character evolution in Campyloderidae and Cyclorhagida

Sørensen et al. (2015) analyzed the phylogenetic relationships among higher kinorhynch taxa using combined molecular and morphological data, and discussed morphological evolution based on their tree. They hypothesized that Xenosomata/Campyloderidae/*Campyloderes* evolved from the plesiomorphic character states of 16 placids, oral styles fused only proximally, and no markedly long lateroventral spines on segment 1, to the derived states of 14 placids, completely fused oral styles, and markedly long lateroventral spines on segment 1. *Ryuguderes iejimaensis* shows a mixture of plesiomorphic and apomorphic states for these characters: 14 placids (apomorphic), but outer oral styles incompletely fused at proximal part and no lateroventral spines on segment 1 (both plesiomorphic). The presence of this mixture of plesiomorphic/apomorphic states in *R. iejimaensis* would help to detect the morphological evolution of Campyloderidae in the future phylogenetic and evolutionally studies.

Ryuguderes iejimaensis gen. et sp. nov. shows morphological similarities not only to *Campyloderes*, but also to some species in Kentrorhagata. The densely arranged cuticular bristles on the surface of the tergosternal junctions and/or the middorsal line are absent in *Campyloderes*, but present in *Wollunquaderes majkenae* Sørensen and Thormar, 2010 and all *Centroderes* species (Neuhaus et al., 2013, 2014; Sorensen and Thormar, 2010). Ventral papillae are present in *Campyloderes* cf. *vanhoeffeni* Zelinka, 1913 (only in females), all *Centroderes* species except for *Centroderes spinosus* (Reinhard, 1881), *Condyloderes megastigma* Sørensen et al., 2010, and *W. majkenae* (only in females) (Neuhaus and Sørensen, 2013; Neuhaus et al., 2013, 2014; Sørensen and Thormar, 2010; Sørensen et al., 2010). The sexually dimorphic character in which only males have middorsal and subdorsal to sublateral acicular spines on segment 10, is evident in most *Ca.* cf. *vanhoeffeni*, *Centroderes barganigra*, Neuhaus et al., 2014, *Ce. bonnyae* Neuhaus et al., 2014, *Ce. drakei* Neuhaus et al., 2014, *Ce. spinosus* (Reinhard, 1881) (Neuhaus and Sorensen, 2013; Neuhaus et al., 2013, 2014). These similarities suggest a close relationship between Xenosomata and Kentrorhagata in Cyclorhagida, as well as imply that these morphologies are the plesiomorphic conditions in a Xenosomata-Kentrorhagata group.

Ryuguderes iejimaensis will be a key taxon for reconstructing morphological evolution in kinorhynchs, especially in Xenosomata and Kentrorhagata. Phylogenetic analyses based on molecular, fine external, and/or internal characters will shed light on the phylogenetic position of *R. iejimaensis*, as well as morphological evolution in Kinorhyncha.

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Figure captions

Fig. 1. *Ryuguderes iejimaensis* gen. et sp. nov., camera lucida drawings. A, B, holotype, female (ZIHU-5081), whole animal, dorsal and ventral views, respectively; C, D, allotype, male (ZIHU-5082), segments 9–11, dorsal and ventral views, respectively. Abbreviations: gco, glandular cell outlet type I; go, gonopore; las, lateral accessory acicular spine; lds, laterodorsal acicular spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvb, lateroventral blunt spine; lvs, lateroventral acicular spine; mdp, middorsal placid; mds, middorsal acicular spine; mts, midterminal spine; mvp, midventral placid; nep, nephridial pore; pa, papilla; ppf, primary pectinate fringe; spf, secondary pectinate fringe; ss, sensory spot.

Fig. 2. *Ryuguderes iejimaensis* gen. et sp. nov., holotype, female (ZIHU-5081), Nomarski photomicrographs. A, whole animal, ventral view; B, head and neck, ventral view; C, close-up of mouth cone, ventral view; D, close-up of introvert, ventral view. Abbreviations: dis, distal part; hea, head; int, introvert; mc, mouth cone; mvp, midventral placid; nec, neck; oos, outer oral style; pro, proximal part; pss, primary spinoscalid; sec, section number; sep, septum; sp, spinoscalid with ring number; tr, trichoscalid; tru, trunk.

Fig. 3. *Ryuguderes iejimaensis* gen. et sp. nov., scanning electron micrographs. A, head and

neck, lateroventral view; B, close-up of mouth cone, lateroventral view; C, close-up of introvert, lateroventral view. Abbreviations: dis, distal part; int, introvert; ios, inner oral style; mc, mouth cone; mvp, midventral placid; oos, outer oral style; pro, proximal part; pss, primary spinoscalid; sec, section number; sp, spinoscalid with ring number; tr, trichoscalid.

Fig. 4. Polar diagram of mouth cone, introvert, and placids in *Ryuguderes iejimaensis* gen. et sp. nov. Grey area and heavy line arcs show mouth cone and placids, respectively. The table lists the scalid arrangement by sector.

Fig. 5. *Ryuguderes iejimaensis* gen. et sp. nov., holotype, female (ZIHU-5081), Nomarski photomicrographs. A, neck and segments 1–5, dorsal view; B, neck and segments 1–4, ventral view; C, close-up of segment 2, subdorsal to middorsal view; D, segments 1 and 2, ventral view; E, segments 5 and 6, ventral view. Dashed circles and black arrowheads indicate sensory spots and glandular cell outlets type I, respectively. Abbreviations: las, lateral accessory acicular spine; lvb, lateroventral blunt spine; lvs, lateroventral acicular spine; mdp, middorsal placid; mds, middorsal acicular spine; mvp, midventral placid; pa, papilla; ppf, primary pectinate fringe; seg, segment number; spf, secondary pectinate fringe.

Fig. 6. *Ryuguderes iejimaensis* gen. et sp. nov., scanning electron micrographs. A, segments

1–4, lateral view; B, segments 2–4, dorsal view; C, segments 4–6, ventral view; D, segments 5 and 6, ventral view of female; E, close-up of papilla on segment 6. Dashed circles indicate sensory spots. Abbreviations: las, lateral accessory acicular spine; lvb, lateroventral blunt spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pa, papilla; ppf, primary pectinate fringe; seg, segment number; spf, secondary pectinate fringe.

Fig. 7. *Ryuguderes iejimaensis* gen. et sp. nov., Nomarski photomicrographs. A, C, allotype, male (ZIHU-5082); B, D, holotype, female (ZIHU-5081). A, segments 8–11, ventral view; B, segments 9–11, dorsal view; C, segments 9–11, dorsal view; D, segment 11, ventral view. Dashed circles and black arrowheads indicate sensory spots and glandular cell outlets type I, respectively. Abbreviations: go, gonopore; lds, laterodorsal acicular spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; mts, midterminal spine; nep, nephridial pore; seg, segment number.

Fig. 8. *Ryuguderes iejimaensis* gen. et sp. nov., scanning electron micrographs. A–C, female; D, male. A, segment 8, lateral view; B, segments 9, lateral view; C, segments 10–11, lateroventral view; D, segments 10 and 11, dorsal view. Dashed circles indicate sensory spots. Abbreviations: go, gonopore; lds, laterodorsal acicular spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular

spine; nep, nephridial pore; seg, segment number; spf, secondary pectinate fringe.

Table 1. Measurements for adult *Ryuguderes iejimaensis* gen. et sp. nov. (in micrometers).
Columns N and SD indicate sample size and standard deviation, respectively. Numbers after characters refer to segment number. Abbreviations: (ac), acicular spine; (bl), blunt spine; LA, lateral accessory acicular spine; LD, laterodorsal acicular spine; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral acicular/blunt spine; MD, middorsal acicular spine; MSW, maximum sternal width; MTS, midterminal spine; S, segment length; SW, standard width; TL, trunk length.

Cahacter	N	Range	Mean	SD
TL	11	441-475	458	10.85
MSW-9	11	78-89	82	3.09
MSW-9/TL	11	17.1-18.9%	18.0%	0.62%
SW-10	11	70-81	74	2.91
SW-10/TL	11	15.2-17.2%	16.1%	0.64%
S1	11	33-41	39	2.38
S2	11	32-38	36	1.89
S3	11	32-38	36	1.76
S4	11	33-40	37	2.09
S5	11	38-42	40	1.37
S6	11	41-47	44	2.32
S7	11	43-50	47	2.11
S8	11	47-55	51	2.41
S9	11	52-59	55	2.27
S10	11	43-51	49	2.10
S11	11	43-49	45	1.62
MD2 (ac)	8	14-17	15	0.92
MD3 (ac)	11	15-18	17	1.17
MD4 (ac)	10	19-22	20	1.16
MD5 (ac)	11	20-25	22	1.40
MD6 (ac)	11	23-27	25	1.38
MD7 (ac)	11	26-31	28	1.72
MD8 (ac)	11	30-34	32	1.62
MD9 (ac)	11	38-43	41	1.63
MD10 (ac)	7	25-33	29	2.85
LD10 (ac)	7	25-29	27	1.60
MD11 (ac)	7	21-25	23	2.09
LV4 (ac)	11	15-19	16	1.20
LV5 (bl)	11	11-14	12	1.00
LA5 (ac)	11	17-22	20	1.39
LV6 (ac)	11	22-26	24	1.59
LV7 (ac)	11	24-28	26	0.95
LV8 (ac)	11	26-30	29	1.11
LV9 (ac)	11	33-35	34	0.80
LTS	11	25-28	27	0.98
LTAS	11	156-171	163	6.21
MTS	11	49-59	54	3.79

Table 2

Table 2. Summary of locations of cuticular structures and spines in *Ryuguderes iejimaensis* gen. et sp. nov. Variable characters (i.e., present in pairs, not in pairs, or absent) marked underlined. Abbreviations: ac, acicular spine; bl, blunt spine; (f), female condition of sexually dimorphic character; gco, glandular cell outlet type I; 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; mts, midterminal spine; nep, nephridial opening; pa, papilla; PD, paradorsal; SD, subdorsal; ss, sensory spot; (u), present in unpair; VL, ventrolateral; VM, ventromedial.

Position segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1			gco	gco, gco, ss				gco	gco
2	ac	ss	gco	gco, ss				gco	gco, ss
3	ac	ss	gco	gco	ss			gco	gco
4	ac	ss (u), ss	gco	gco	ss		ac	gco	gco, ss
5	ac	ss	gco	gco		ac	bl	gco	gco
6	ac	ss	gco	gco	ss		ac	gco	gco, pa (f), ss
7	ac	ss	gco	gco			ac	gco	gco, pa (f)
8	ac	ss	gco	gco	ss	ss	ac	gco	gco, gco, ss
9	ac	ss	gco	gco, ss		nep	ac	gco	gco, gco, ss
10	ac (m)	ss	gco, gco, ss	ss, ac (m)				gco, gco, ss	
11	ac (m), mts		gco, ss			ltas	lts	gco	gco, gco

Figure 1

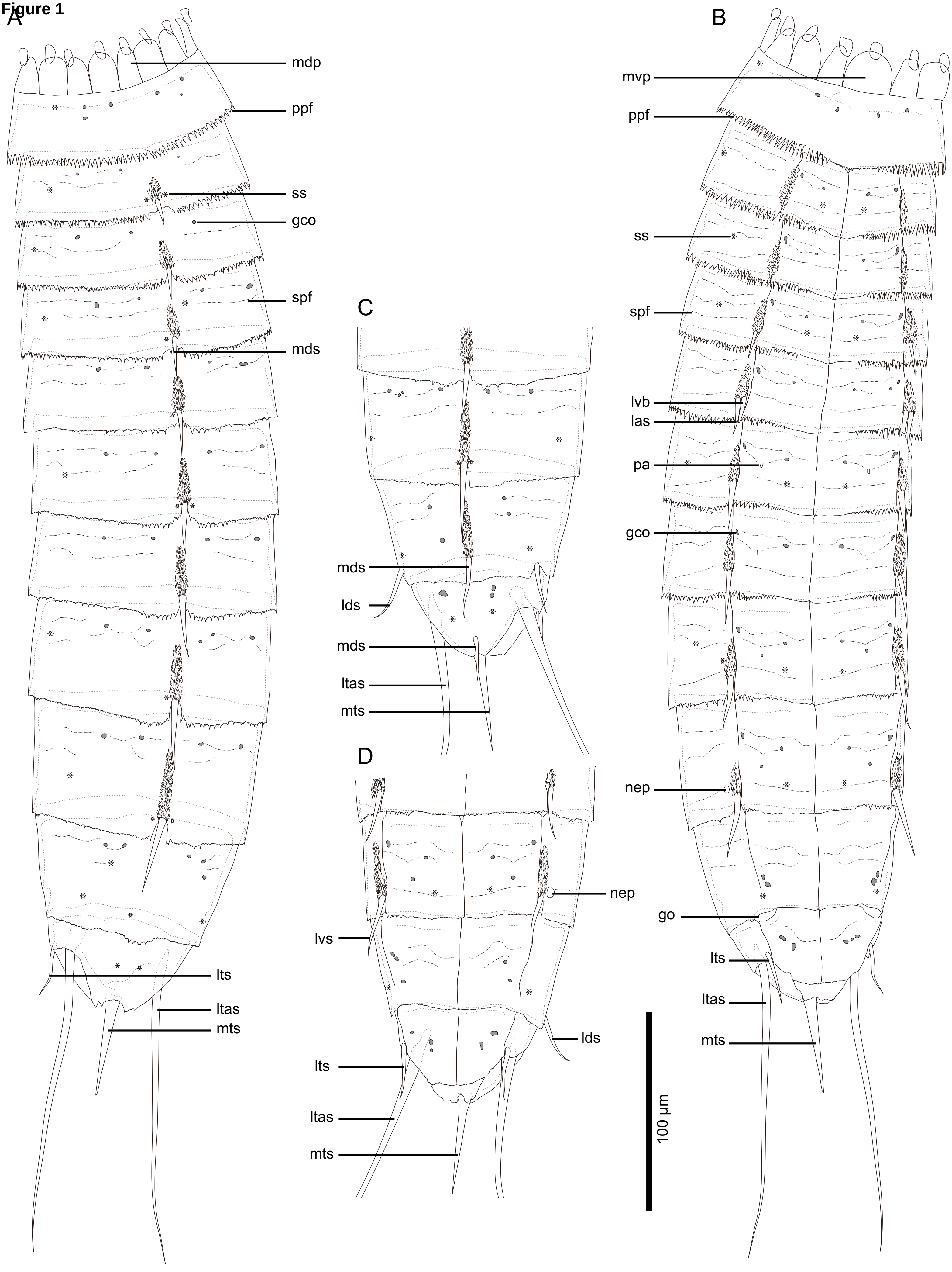
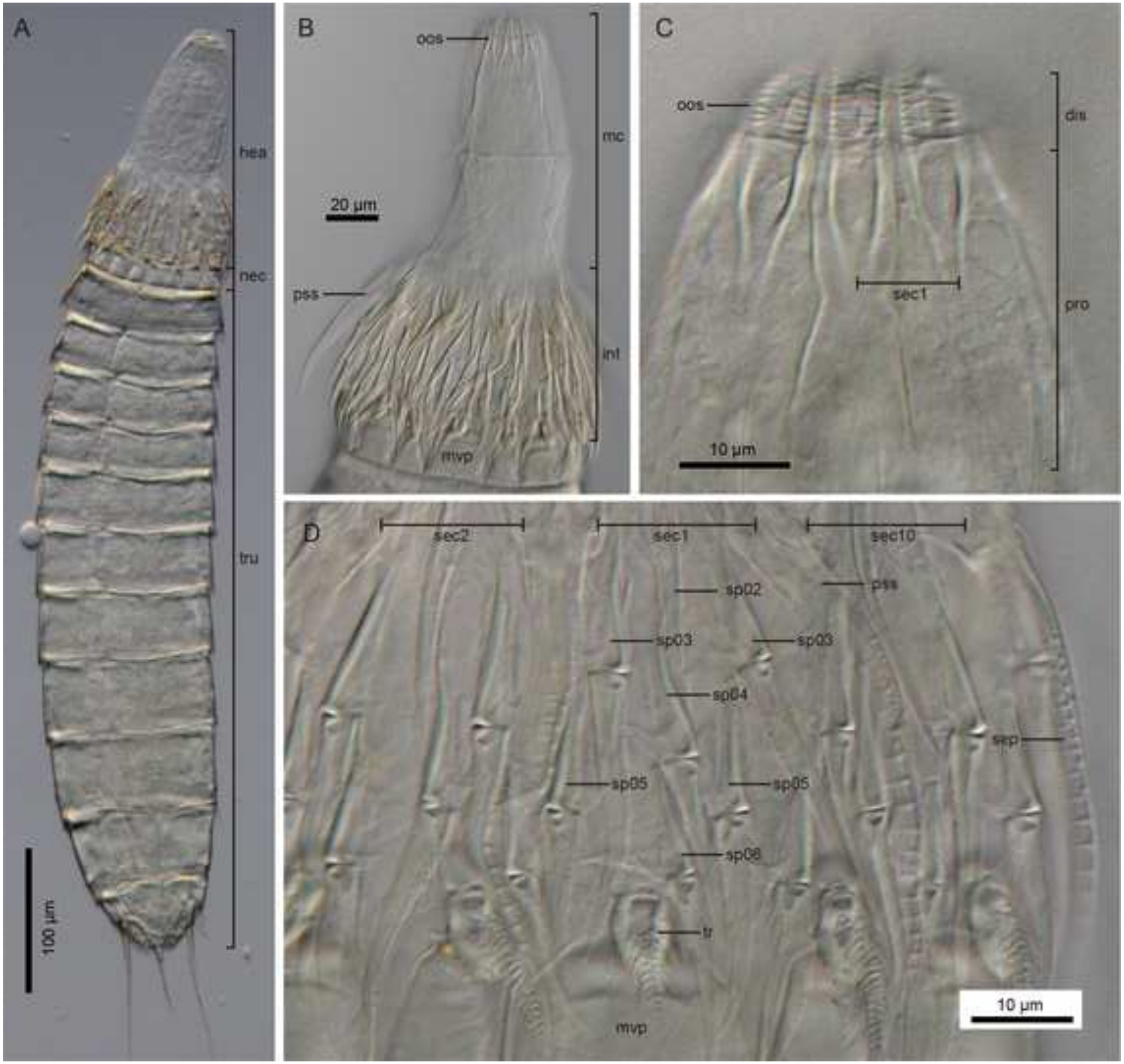

A
mdp
ppf
ss
gco
spf
mds
lts
ltas
mts
B
mvp
ppf
ss
spf
lvb
las
pa
gco
nep
go
lts
ltas
mts
C
mds
lds
mds
ltas
mts
D
nep
lvs
lds
lts
ltas
mts
100 µm

Figure 2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D
sec2
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sp03
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sep
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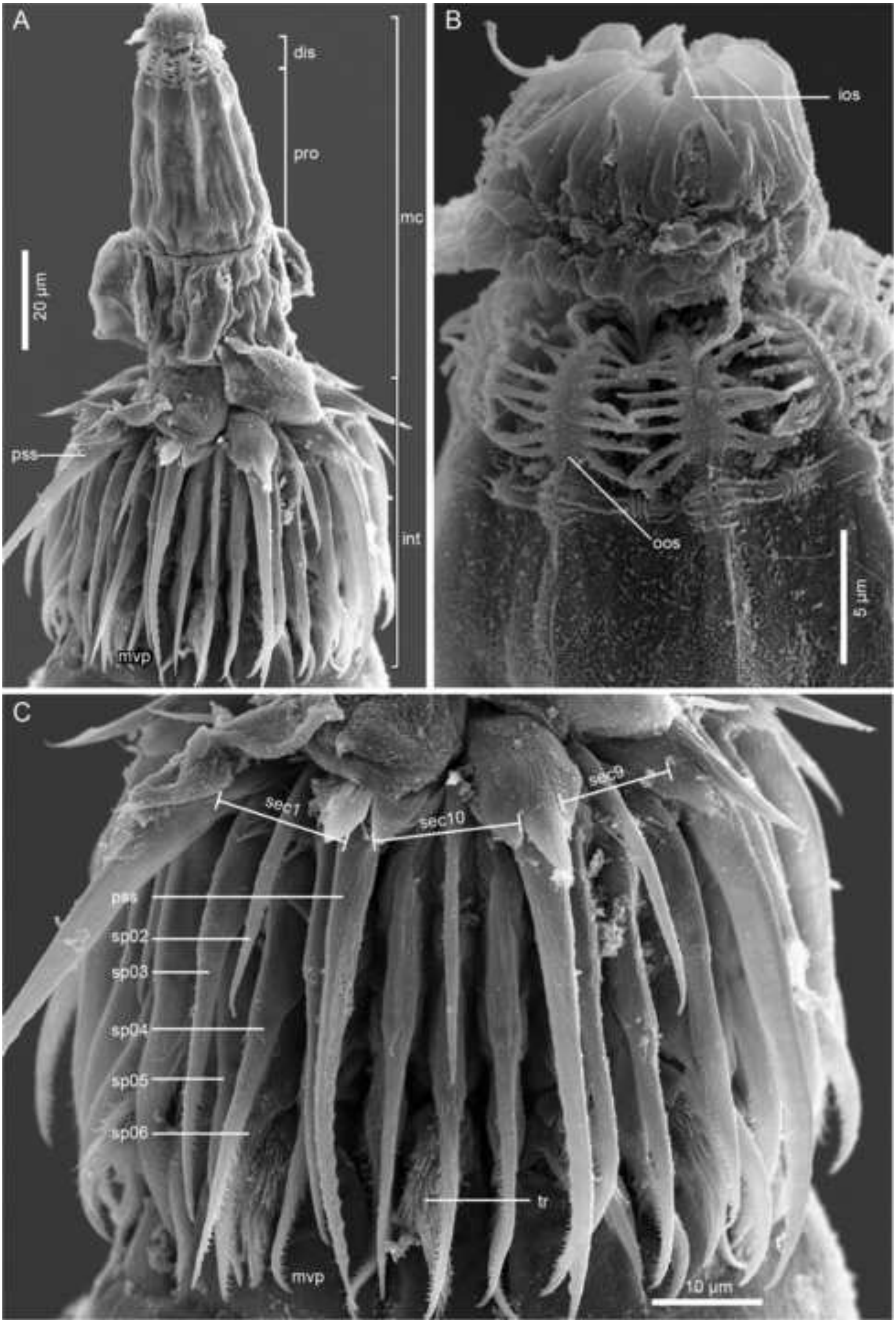
sp06
tr
mvp
10 µm

Figure 3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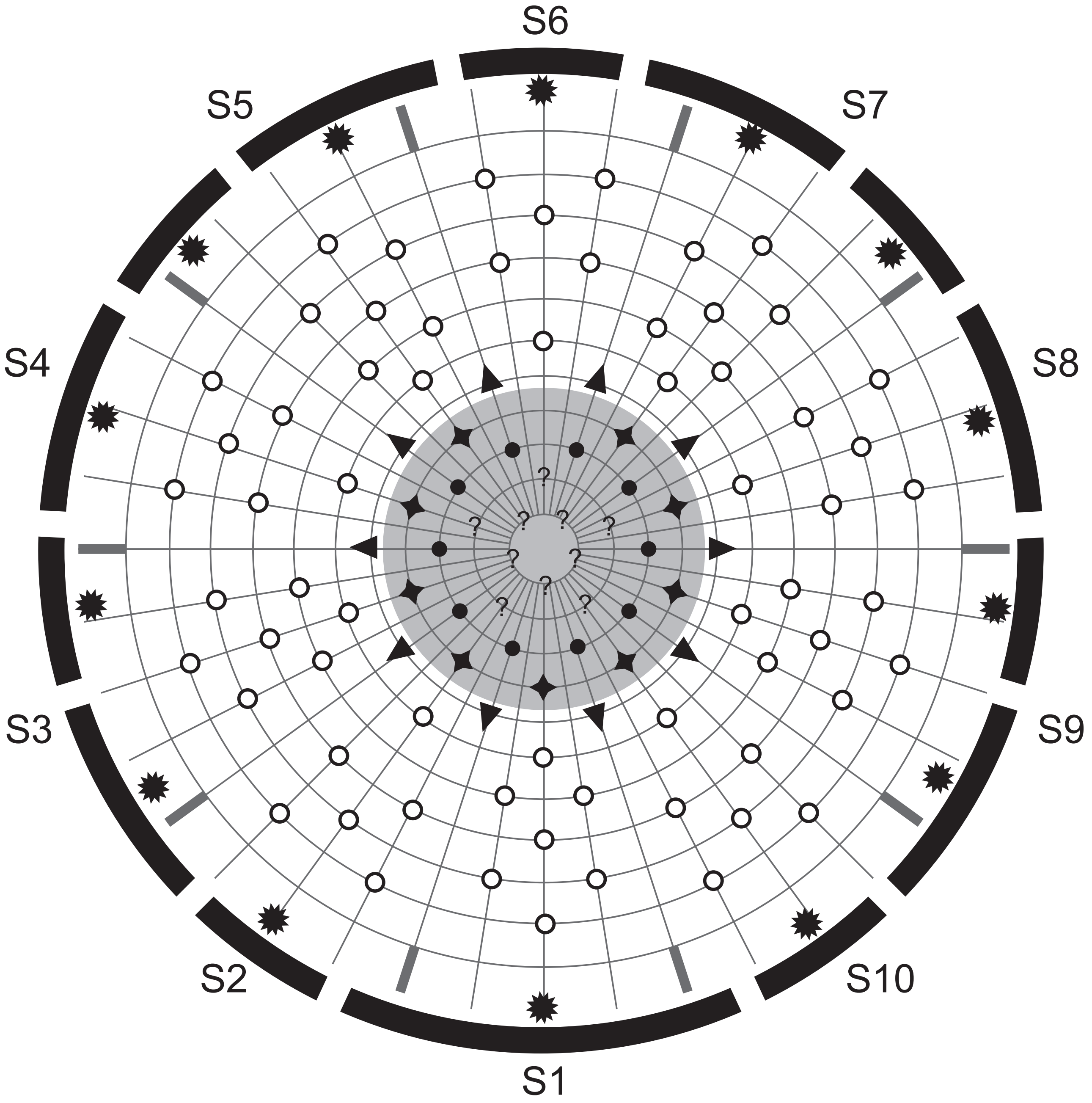
tr
mvp
10 µm

Figure 4



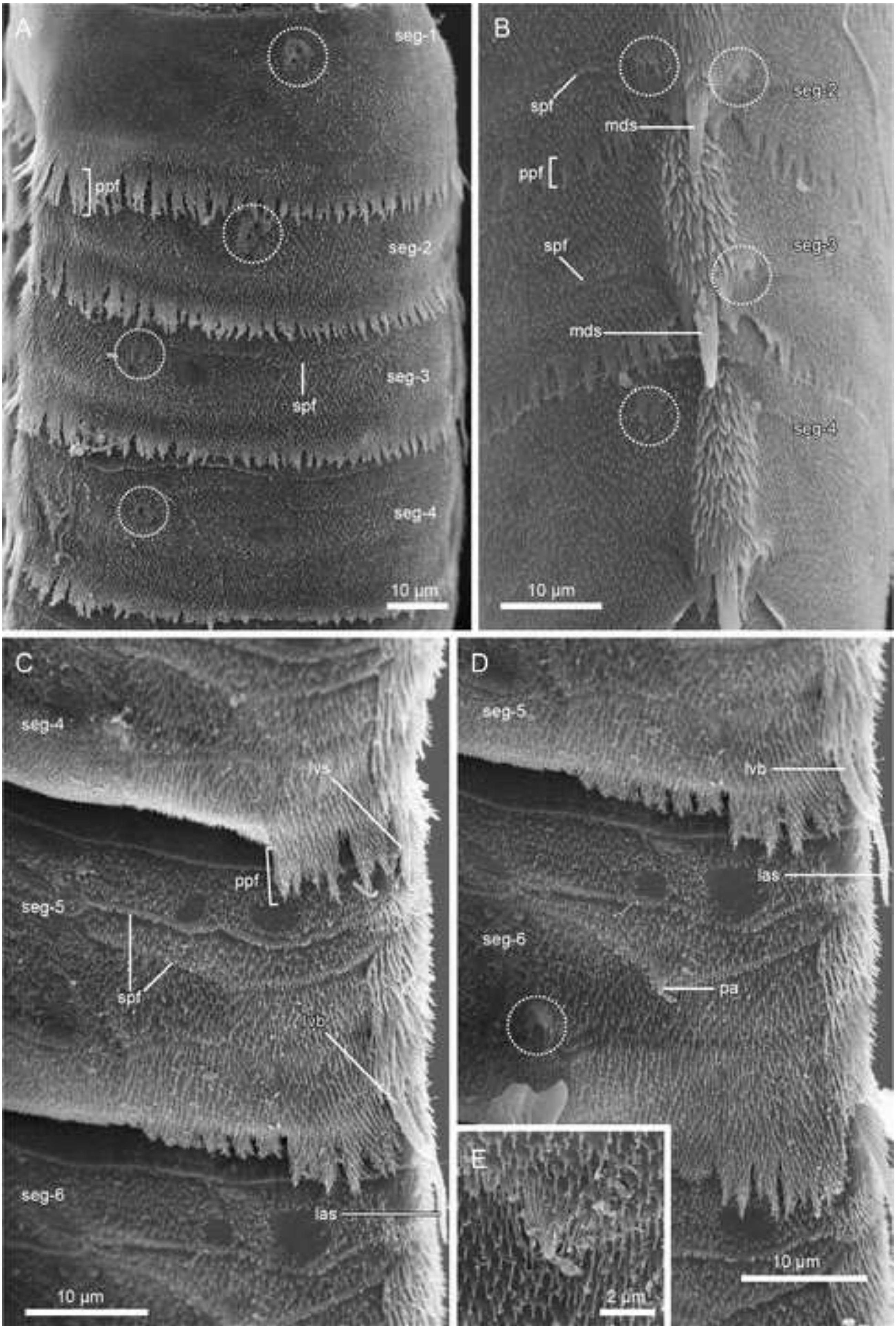
Scalid and style arrangement

Ring/Section		1	2	3	4	5	6	7	8	9	10	Total
-01 inner oral styles	●	1	1	1	1	1	1	1	1	1	1	10
00 outer oral styles	✦	1	1	1	1	1	0	1	1	1	1	9
01 primary spinoscalids	▼	1	1	1	1	1	1	1	1	1	1	10
02 spinoscalids	○	1	1	1	1	1	1	1	1	1	1	10
03 spinoscalids	○	2	0	2	0	2	0	2	0	2	0	10
04 spinoscalids	○	1	2	1	2	1	2	1	2	1	2	15
05 spinoscalids	○	2	1	2	1	2	1	2	1	2	1	15
06 spinoscalids	○	1	2	1	2	1	2	1	2	1	2	15
trichoscalids	✸	1	1	2	1	2	1	2	1	2	1	14

Figure 5


A
mdp
seg-1
seg-2
mds
ppf
seg-3
mds
50 µm
mds
B
mvp
seg-1
seg-2
seg-3
seg-4
50 µm
C
ppf
seg-2
10 µm
mds
D
seg-1
ppf
spf
seg-2
spf
10 µm
E
lvb
las
seg-5
seg-6
pa
lvs
10 µm

Figure 6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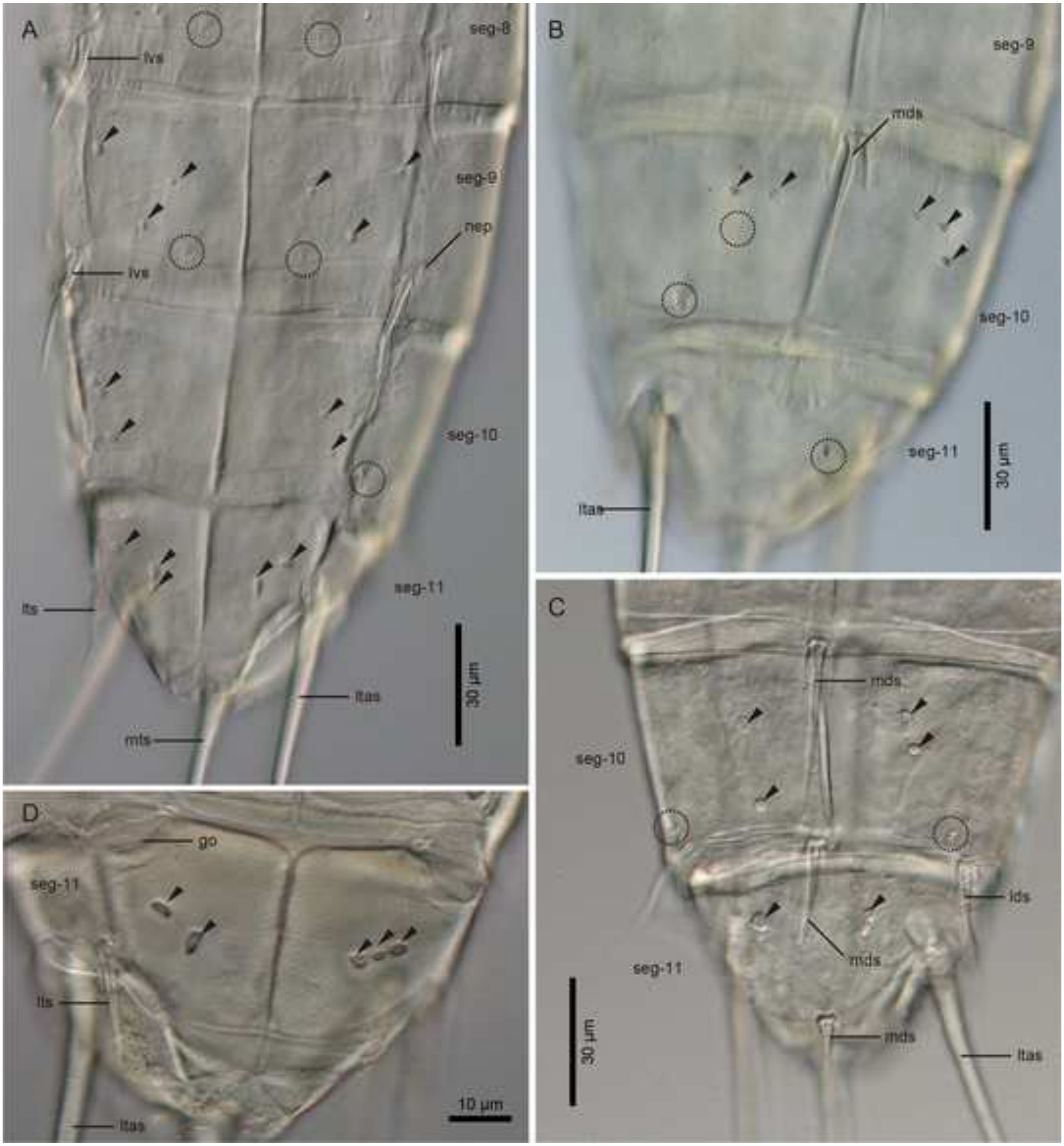
seg-1
ppf
seg-2
seg-3
spf
seg-4
10 µm
B
spf
mds
seg-2
ppf
spf
seg-3
mds
seg-4
10 µm
C
seg-4
lvs
ppf
seg-5
spf
lvb
seg-6
las
10 µm
D
seg-5
lvb
las
seg-6
pa
E
2 µm
10 µm

Figure 7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seg-9
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lvs
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seg-11
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ltas
mts
30 µm
B
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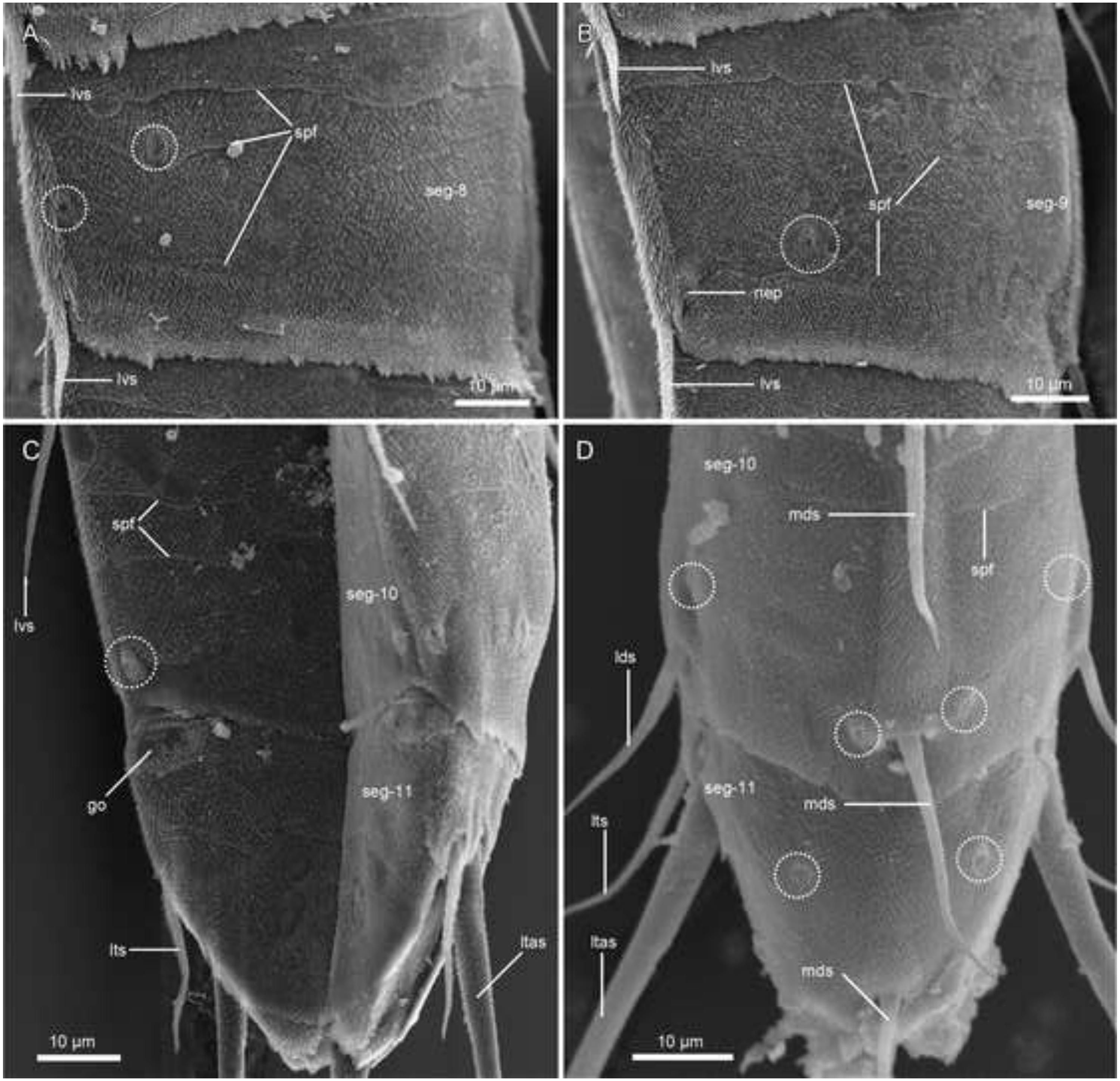
mds
seg-10
seg-11
ltas
30 µm
C
mds
seg-10
lds
mds
seg-11
mds
ltas
30 µm
D
go
seg-11
lts
ltas
10 µm

Figure 8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ltas
mds
10 µm