Gracilideres mawatarii, a new genus and species of Franciscideridae (Allomalorhagida: Kinorhyncha): a kinorhynch with thin body cuticle, adapted to the interstitial environment

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Gracilideres mawatarii, a new genus and species of Franciscideridae (Allomalorhagida: Kinorhyncha) - a kinorhynch with thin body cuticle, adapted to the interstitial environment

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Abstract

A new genus and species of Kinorhyncha, *Gracilideres mawatarii* gen. et sp. nov. is described from coarse subtidal sand, west of Tanegashima Island, Japan. The genus and species is characterized by a cylindrical neck with sparsely arranged longitudinal crimps at surface; segments 1–10 each consisting of a single cylindrical cuticular plate; middorsal and ventromedial string-like glandular cells on segments 1–9; primary pectinate fringes with pectinate fringe teeth on segments 1–10; lateral accessory pores on segments 2–10; unpaired dorsal spines on segments 3–11 or 4–11, of which those on segments 3–9 are alternatingly laterally displaced left or right to paradorsal positions, and those on segments 10 and 11 in middorsal position; lateral accessory acicular spines on segment 5; lateroventral acicular spines on segments 4, 6–10; and tubes in lateroventral position on segments 2 and 5 and in ventrolateral position on segment 1. Together with the description of *G. mawatarii* gen. et sp. nov., emended diagnoses for the family Franciscideridae and the genus *Franciscideres* are provided. The introvert morphology of *G. mawatarii* gen. et sp. nov. is unique within Kinorhyncha, but showing some similarities to those of *Franciscideres* and *Cateria*, suggesting a close relationship between these three genera. The thin and flexible trunk cuticle in *G. mawatarii* gen. et sp. nov., *Franciscideres*, Neocentrophyidae, and some kentrorhagids would be related to the adaptation of interstitial environment. The thickening or thinning of cuticle has evolved independently at least twice in the kinorhynch lineages.

Keywords

Evolution; introvert; meiofauna; morphology; taxonomy; thin cuticle

1. Introduction

The phylum Kinorhyncha is comprised of marine, meiobenthic, and segmented animals. So far, the phylum accommodates 30 genera and 277 species (Sørensen et al., 2015; Sánchez et al., 2016; Yamasaki, 2016; Adrianov and Maiorova, 2018; Yamasaki et al., 2018). Of these, several were discovered and described as new genera and/or new species within the last decade (e.g., Sørensen and Rho, 2009; Sørensen and Thormar, 2010; Herranz et al., 2012; Dal Zotto et al., 2013; Sánchez et al., 2014; Yamasaki, 2016; Adrianov and Maiorova, 2018), and the number will definitely increase in the coming years. The recent phylogenetic studies of kinorhynchs based on molecular, morphological, and/or total evidence data aimed at understanding their phylogenetic relationships, have led to a revision of the classification system of the phylum. Accordingly, it is now composed of two classes, three orders, and eleven families (Dal Zotto et al., 2013; Yamasaki et al., 2013; Sørensen et al., 2015). Nevertheless, phylogenetic relationships of some groups, e.g., the position of the genus *Cateria* Gerlach, 1956, relationships within Echinoderidae Zelinka, 1894, and those within Kentrorhagata Sørensen et al., 2015, have not been well resolved yet, and further analyses with improved data, and/or more comprehensive taxon sampling are desired (Sørensen et al., 2015).

In the above-mentioned phylogenetic studies, one genus referred as “Undescribed genus” or “New Genus” was included in the analyses (Yamasaki et al., 2013; Dal Zotto et al., 2013; Sørensen et al., 2015). While the genus showed a close relationship to the aberrant kinorhynch genus *Franciscideres* Dal Zotto et al., 2013 in the all analyses, and information on its morphology was briefly given in these studies (Yamasaki et al., 2013; Dal Zotto et al., 2013; Sørensen et al., 2015), the genus has not been officially described yet.

In this paper, I describe this “Undescribed genus” as a new genus and species. Together with the description of the new genus and species, the emended diagnoses of the family Franciscideridae Sørensen et al., 2015 and the genus *Franciscideres* are provided. In addition, the unique introvert morphology of the new genus is compared to those of *Franciscideres* and *Cateria*. The presence of thin cuticle on trunk segments in the new genus as well as some other kinorhynch genera, and its evolutionary process are also discussed.

2. Material and methods

A sediment sample of coarse sand was collected at 55 m depth, west off Tanegashima Island, Japan (30°34'13"N, 130°51'54"E) on 23 May 2012 using a dredge (TR/V Toyosho-maru). Kinorhynchs were extracted from the sample with the bubbling and blot technique (Higgins, 1988; Sørensen and Pardos, 2008), and preserved in 99% EtOH. Later on, the extracted specimens were sorted under a stereomicroscope.

Specimens for light microscopy (LM) were put in glycerol, mounted in Hoyer's medium in H-S plastic frames, and observed with a Zeiss Axioskop 50 microscope. Line art illustrations were made with a mounted camera lucida. Final line art illustrations were drawn with Adobe Illustrator CS6 based on the drafts. Measurements were made through a camera lucida. Specimens were photographed with a Zeiss AxioCam MRc5.

Specimens for scanning electron microscopy (SEM) were transferred to 100% EtOH, dried with a Hitachi HCP-2 CO2 critical-point drier, mounted on aluminum stubs, sputter-coated with gold with a JEOL JFC-1100 ion sputter coater, and observed with a Hitachi S-3000N scanning electron microscope.

Total genomic DNA was extracted from three specimens for DNA sequencing. Extractions were performed on single individuals with a DNeasy Tissue Kit (Qiagen, Tokyo), following the protocol of Yamasaki et al. (2013). Parts of the nuclear 18S rRNA (18S) and 28S rRNA (28S) genes and the mitochondrial cytochrome *c* oxidase subunit I gene (COI) were amplified by PCR with the primer sets used by Yamasaki (2015). PCR conditions were as reported in Yamasaki & Fujimoto (2014). All nucleotide sequences were determined by direct sequencing with a BigDye Terminator Kit ver. 3.1 (Life Technologies, Co., USA) and a 3730 DNA Analyzer (Life Technologies, Co., USA). Sequence fragments were assembled by using MEGA 5 (Tamura et al., 2011). Of the determined sequences, 18S and 28S sequences for one specimen had already been published in Yamasaki et al. (2013) with GenBank accession numbers AB738378 and AB738379, respectively. The remaining sequences were newly deposited in GenBank.

The terminology follows Neuhaus and Higgins (2002), Sørensen and Pardos (2008) and Neuhaus (2013). All specimens have been deposited in the Invertebrate Collection at the Hokkaido University, Japan (ICHUM).

3. Results

Class Allomalorhagida Sørensen et al., 2015

3.1. Family Francisciderida Sørensen et al., 2015

3.1.1. Emended family diagnosis

Trunk slender, circular in cross-section, with thin and extremely flexible cuticle; pachycycli absent; neck cylindrical, without differentiated placids; neck and segment 1 divided by transverse cuticular folding; small pores present at least on trunk segments; segment 11 with middorsal, lateral terminal, and lateral terminal accessory spines, but without midterminal spine.

3.1.2. Genera included

Franciscideres Dal Zotto et al., 2013
Gracilideres gen. nov.

3.2. Genus *Franciscideres*

3.2.1. Emended diagnosis

Neck with densely and regularly arranged longitudinal crimps; trunk segments 1, 2, and 11 appear as closed rings; segments 3–10 with weak indication of midsternal junction; posterior margins of segments 1–10 with broad or narrow lopes; middorsal acicular spines on segments 1–11; lateral accessory acicular spines on segment 5; lateroventral acicular spines on segment 3, 4, and 6–10; tubes in lateroventral positions on segments 2 and 5, and in lateral accessory position on segment 8.

3.3. Genus *Gracilideres*

urn:lsid:zoobank.org:act:00997653-DB9F-47E3-9292-C75BA8B52B56

3.3.1. Diagnosis

Neck with sparsely arranged longitudinal crimps; segments 1–11 each consisting of a single cylindrical cuticular plate without longitudinal articulation; middorsal and ventromedial string-like glandular cells on segments 1–9; lateral accessory pores on segments 2–10; primary pectinate fringes present on segments 1–10, with pectinate fringe teeth on segments 1–4 very short and indistinct, and those on segments 5–10 thin, long and conspicuous; unpaired dorsal spines on segments 3–11 or 4–11; dorsal spines on segments 3–9 alternatingly lateral displaced left or right to paradorsal positions; dorsal spines on segments 10 and 11 in middorsal position; lateral accessory acicular spines on segment 5; lateroventral acicular spines on segments 4, 6–10; tubes in lateroventral position on segments 2 and 5, and in ventrolateral position on segment 1.

3.3.2. Etymology

The generic name is masculine, of which the prefix “*Gracili*-” is derived from a Latin word “*gracilis*” meaning thin, slim or slender, which refers to the thin cuticle as well as the slender body of the genus. The suffix ‘-*deres*’ is derived from the Ancient Greek meaning neck, which is often used in generic names of Kinorhyncha.

3.4. *Gracilideres mawatarii* gen. et sp. nov.

urn:lsid:zoobank.org:act:4221FF32-3F45-41F9-A864-3C0AC347713C

3.4.1. Synonym list

Undescribed genus: Yamasaki et al. (2013), Dal Zotto et al. (2013), Sørensen et al. (2015)
N. gen. n. sp.: Dal Zotto et al. (2013)
New Genus: Sørensen et al. (2015)

3.4.2. Diagnosis

Same as generic diagnosis.

3.4.3. Etymology

This species epithet is named after Dr. Shunsuke F. Mawatari, a Japanese taxonomist, who has trained many taxonomists including the author of this study and greatly contributed to the taxonomy in Japan.

3.4.4. Material examined

Holotype: gender uncertain, (ICHUM 04304), collected from coarse sand at 55 m depth west of Tanegashima Island, Japan (30°34'13"N, 130°51'54"E), mounted in Hoyer's medium in H-S plastic frames.

Paratypes: three specimens of uncertain gender (ICHUM 04301, 04302, 04303), collected at same locality as holotype, mounted in Hoyer medium in H-S plastic frames.

Additional material: one specimen of possible female (ICHUM 04299) and three specimens of uncertain gender for SEM (ICHUM 04297, 04298, 04300), collected at same locality as holotype, mounted on aluminum stubs.

Sequences: three specimens collected at same locality as holotype. The loci 18S, 28S and COI were sequenced and deposited in GenBank under following accession numbers: Specimen 1: 18S (1765 bp) - AB738378, 28S (3231 bp) - AB738379 (AB738378 and AB738379 already published by Yamasaki et al. (2013), and used in used in analyses of Yamasaki et al. (2013), Dal Zotto et al. (2013), and Sørensen et al. (2015)), and COI (658 bp) - XXXXXXX; specimen 2: 18S (1765 bp) - XXXXXX; specimen 3: 18S (1765 bp) - XXXXXX and COI (658 bp) – XXXXXX.

3.4.5. Description

Adult with head, neck, and eleven trunk segments (Figs 1 and 2A). See Table 1 for measurements. Table 2 indicates positions of cuticular structures (sensory spots, spines, and tubes).

Head consisting of retractable mouth cone and introvert (Fig. 2B). Mouth cone with inner and nine outer oral styles (Figs 2B and 3A). Exact number and arrangement of inner oral styles not observed. Each outer oral style consists of triangular distal and rectangular basal part (Figs 2B and 3A). Distal tip of oral style flexible, often bending interiorly (Figs 2B and 3A). Basal parts alternating in size between five larger ones in odd sectors and four slightly thinner and shorter ones in even sectors (Figs 2B and 3A). Fringe composed of three long spinose processes present at bases of outer oral styles (Figs 2B and 3A). Introvert composed of five rings of scalids (Figs 2C, 3B, and 4). Ring 01 with ten primary scalids each consisting of one basal sheath and one distal end piece (Figs 2C, 3B, and 4). Basal sheath serrated on lateral edge, and bifurcated along most of its length (Figs 2C and 3B). Distal end pieces with smooth surface and blunt tip. Primary scalids conspicuously longer and thicker than scalids in following rings (Figs 2C and 3B). Ring 02 with 10 long and thin spinoscalids without basal sheaths (Figs 2C, 3B, and 4). Ring 03 with 20 scalids, probably composed of only basal sheath (Figs 2C, 3B, and 4). Ring 04 with 10 spinoscalids composed of basal sheath and spinose distal end piece (Figs 2C, 3B, and 4). Ring 05 with 10 spinoscalids similar to spinoscalids in ring 04, but present only in odd sectors (Figs 2C, 3B, and 4). Posterior surface of head densely covered by thin hair-like structures (Figs 2C and 3C). Trichoscalids absent. Bacteria attaching on scalids found in two SEM specimens (ICHUM 04297 and ICHUM 04299) (Fig. 3B, C).

Neck formed by cylindrical cuticular plate with smooth surface except for longitudinal crimps aligning on surface (Figs 1, 2, and 3C). Longitudinal crimps aligned sparsely with wide smooth surfaces in between, and present only at surface, hence not forming differentiated placids (Figs 2 and 3C). The crimps and thin cuticle make the neck area more flexible, enabling it to move like accordion, in order to act as a closing apparatus when the head retracts into the trunk (Fig. 3D).

Segment 1 consisting of complete cuticular ring. Cuticle very thin and flexible on this and all remaining segments. String-like structures in middorsal and ventromedial position (Figs 1, 2B, 3E–G, and 4A–C), which would represent glandular cells, however, glandular openings could not be observed probably because of its smallness and debris attaching on specimens. String-like glandular cells present in central part, reaching neither anterior nor posterior margins, and only observable in LM specimens (Figs 1, 2B, 3E–G, and 4A–C). Pachycycli absent on this and all remaining segments. Short tape-like tubes present in ventrolateral position (Figs 1, 3E–F, and 4C). Cuticular scales covering segment (Fig. 3F). Scales smaller and more well-arranged in anterior third part of segment, whereas more elongate and more irregularly-arranged in posterior part. Posterior edge of this and following three segments with primary pectinate fringe with very short and indistinct pectinate fringe teeth (Figs 1, 3F, G, and 5C). Secondary pectinate fringe absent on this and all remaining segments.

Segment 2 and following 9 segments with complete cuticular ring as segment 1 (Figs 1, 2A, B, 3E, G, and 5A–C). This and following eight segments with middorsal and ventromedial string-like glandular cells as on segment 1 (Figs 1 and 5C). Ventromedial string-like glandular cells located more mesially toward posterior segments, except for those on segment 9 situated in same positions as those on segment 1 (Figs 1, 5C, and 7C). Small pores in lateral accessory position on this and following eight segments. Pores very small, only observable in SEM specimen (Fig. 6B and C). Tubes present in lateroventral position (Figs 1, 3E, F, and 5C). Sensory spots in sublateral position (Figs 1, 3E, 5C, and 6B). Each sensory spot of this and following segments rounded, neighbouring a notch in free flap, and comprised of numerous micropapillae with single pore often equipped with a cilium, representing type-1 sensory spot (Figs 1, 5C, 6B–F, 7C–E, 8A, and B). Cuticular scales on whole dorsal side and posterior part of ventral side as on segment 1. Anterior part of ventral side covered with minute cuticular hairs.

Segment 3 with single paradorsal acicular spine either on right or left side (Figs 1A, 5A, D, and 6A). Paradorsal spine never be there in one out of the eight examined specimens (ICHUM 04301). Notch in free flap present at base of each acicular spine on this and following seven segments (Figs 1, 5D–F, 6, 7C–F, and 8). Sensory spots present in lateral accessory position (Figs 1, 5C, 6B, and C). Minute cuticular hairs covering this and following segments. Cuticular hairs more densely arranged in anterior third part and more sporadically arranged in posterior part of each segment.

Segment 4 with single paradorsal acicular spine, located at opposite side of spine on segment 3 (Figs 1A, 5A, D, and 6A). Additional acicular spines present lateroventrally (Figs 1, 5B, E, 6B–D). Sensory spots in lateral accessory position (Figs 1, 5E, 6B–D). Pectinate fringe teeth of primary pectinate fringe slightly longer than those on preceding segments (Fig. 6C).

Segment 5 with single paradorsal acicular spine, located at same side as spine on segment 3 (Figs 1A, 5A, F, and 6F). Lateral accessory acicular spines and lateroventral tubes present (Figs 1, 5E, 6E, and 7B). Pectinate fringe teeth of primary pectinate fringe on this and following five segments longer and more conspicuous than those on segments 1–4 (Figs 1, 5E, and 6E).

Segment 6 with single paradorsal acicular spine, located at same side as spine on segment 4 (Figs 1A, 5A, F, 6F, and 7A). Lateroventral acicular spines present (Figs 1, 5B, 6E, and 7B). Sensory spots present in subdorsal and lateral accessory position (Figs 1, 5F, 6E, F, and 7A).

Segment 7 with single paradorsal acicular spine, located at same side as spine on segment 3 (Figs 1A, 5A, F, 6F, 7A, and D). Lateroventral acicular spines present (Figs 1, 5B, 6E, 7B, and C). Sensory spots in lateral accessory position (Figs 1, 6E, and 7C).

Segment 8 with single paradorsal acicular spine, located at same side as spine on segment 4 (Figs 1A, 7A, D, E, and 8A). Lateroventral acicular spines present (Figs 1, 7A–C, and 8B). Sensory spots in subdorsal position (Figs 1A, 5F, 7A, D, and 8A).

Segment 9 with single paradorsal acicular spine, located at same side as spine on segment 3 (Figs 1A, 7A, D–F, and 8A). Lateroventral acicular spines present (Figs 1, 7B, C, F, and 8B). Sensory spots in subdorsal, lateral accessory, and ventromedial position (Figs 1, 7A–E, 8A, and B).

Segment 10 with middorsal and lateroventral acicular spines (Figs 1, 7A, B, E, F, 8C, and D). Sensory spots absent.

Segment 11 with middorsal acicular spine, lateral terminal accessory spines, and lateral terminal spines (Figs 1, 7A, B, E, F, 8C, and D). Oval area without cuticular hairs in ventrolateral position found only in one SEM specimen (Fig. 8D), which may be female gonopore. Cuticular plate on dorsal area separated middorsally, extending posteriorly, and forming tergal extension (Figs 1, 8C, and D). Tergal extensions triangular and pointed posteriorly (Fig. 8C).

4. Discussion

4.1. Affiliation of *Gracilideres* to Franciscideridae and comparison with *Franciscideres*

Both morphological and molecular data indicate the close relationship between *Gracilideres mawatarii* gen. et sp. nov. and *Franciscideres kalenesos* Dal Zotto et al., 2013. The two species are morphologically similar in the slender trunk body with thin and flexible cuticle, the introvert surface posterior to scalids densely covered with hair-like structures, the primary scalids with bifurcated structures which terminate into two tips, the neck with longitudinal crimps but not divided into independent placids, very small pores present on the surface of the trunk segments, and segment 11 with lateral terminal spines, lateral terminal accessory spines, and middorsal spine, but no midterminal spine (Dal Zotto et al., 2013; Dal Zotto pers. comm.). Especially, the latter three features are known only from *G. mawatarii* gen. et sp. nov. and *F. kalenesos*. Previous phylogenetic analyses based on molecular data (Dal Zotto et al., 2013; Sørensen et al., 2015), morphological data (Sørensen et al., 2015), and total evidence data (Sørensen et al., 2015) strongly supported the close relationship between the two species (Dal Zotto et al., 2013; Sørensen et al., 2015), and allow the inclusion of *Gracilideres mawatarii* gen et sp. nov. into the family Franciscideridа.

Despite the close relationship between the two taxa, *G. mawatarii* gen. et sp. nov. has several unique morphological characters, which make it differ from *F. kalenesos*. The first difference between the two species is the cuticular-plate composition of the trunk segments. In *F. kalenesos*, segments 1, 2, and 11 consist of closed rings and segments 3 to 10 appear to be composed of a single plate with a very weak line which could indicate a midventral joint, while in *G. mawatarii* gen. et sp. nov., segments 1–11 all consist of clearly closed rings (Dal Zotto et al., 2013).

Gracilideres mawatarii gen. et sp. nov. differs from *F. kalenesos* also in the longitudinal crimps/lines in the neck region, and in the shape of the posterior edge of each trunk segment. Although both species are characterized by the presence of longitudinal crimps/lines on the surface of the neck region, those in *G. mawatarii* gen. et sp. nov. are sparser, whereas those in *F. kalenesos* are densely arranged and more regular. In *G. mawatarii* gen. et sp. nov., the posterior edges of the trunk segments terminate into primary pectinate fringes with thin pectinate teeth, while in *F. kalenesos*, they end with a number of lopes (Dal Zotto et al., 2013).

Other differences between the two species are the spine and tube pattern and the presence/absence of string-like glandular cells. Although both species have long acicular spines on their dorsal sides, those in *G. mawatarii* gen. et sp. nov. are located in paradorsal position on segments 3–9 and in middorsal position on segments 10 and 11, whereas those in *F. kalenesos* all are aligned along the middorsal position on segments 1–11. *Gracilideres mawatarii* gen. et sp. nov. and *F. kalenesos* have lateral accessory and lateroventral acicular spines in almost the same positions, however, *G. mawatarii* gen. et sp. nov. lacks lateroventral spines on segment 3, whereas they are present in *F. kalenesos*. Ventrolateral tubes on segment 1 are found only in *G. mawatarii* gen. et sp. nov., and lateral accessory tubes on segment 8 present in *F. kalenesos* are absent in *G. mawatarii* gen. et sp. nov. (Dal Zotto et al., 2013). The string-like glandular cells are conspicuous in *G. mawatarii* gen. et sp. nov., whereas such a structure has not been found in *F. kalenesos* (Dal Zotto et al., 2013).

4.2. Comparison with other kinorhynchs based on selected morphological features

4.2.1. Unique introvert morphology in G. mawatarii *gen. et sp. nov.*

The introvert of *G. mawatarii* gen. et sp. nov. shows a unique morphology: each of its primary spinoscalids is composed of one basal sheath and one distal end piece, with the proximal part of the sheath showing an incomplete cleft at its base, and a complete bifurcation centrally and distally; spinoscalids of ring 02 consist of only long and thin end pieces, whereas those of ring 03 consist of only basal sheaths. Furthermore, the introvert surface posterior to ring 05 is densely covered by thin hair-like structures, and trichoscalids are completely absent.

The only species showing some similarities to *G. mawatarii* gen. et sp. nov. in the introvert morphology are *F. kalenesos*, *Cateria gerlachi* Higgins, 1968, and *Cateria styx* Gerlach, 1956 (Fig. 9). Although the morphology of the introvert in *F. kalenesos* has not been completely described so far, it resembles that of *G. mawatarii* gen. et sp. nov. by the presence of the longitudinal clefts at the base of the primary spinoscalids, with clefts dividing the scalids into a distal bifurcation; scalids of ring 02 are thin and acicular; the introvert surface posterior to scalids densely covered with hair-like structures; and the absence of trichoscalids (Dal Zotto et al., 2013; Dal Zotto pers. comm.). Dal Zotto et al. (2013) also mentioned the presence of two, short flexible spikes flanking each scalid of ring 03. It can be assumed that these short spikes might correspond to the ring 03 scalids in *G. mawatarii* gen. et sp. nov., and the scalids of ring 03 referred in Dal Zotto et al. (2013) would actually be those of ring 04. Regarding *C. gerlachi* and *C. styx*, ten pairs of thin cuticular spines anterior to the primary spinoscalids were described by Neuhaus and Kegel (2015) and Herranz et al. (this issue). These might correspond to the basal sheaths of the primary spinoscalids. The introvert surface posterior to the rings of the spinoscalids covered with short cuticular hairs is found in *G. mawatarii* gen. et sp. nov. as well as in *C. gerlachi* and *C. styx*. However, that area is continuous in *G. mawatarii* gen. et sp. nov., whereas it is divided into 14 patches in *C. gerlachi* and 16 patches in *C. styx* (Neuhaus and Kegel, 2015; Herranz et al., this issue). The presence of a basal and a distal element in each of the spinoscalids of rings 02–05 as well as the presence of trichoscalids in *C. gerlachi* and *C. styx* is more similar to other kinorhynchs than to *G. mawatarii* gen. et sp. nov. (Neuhaus and Kegel, 2015; Herranz et al., this issue).

As mentioned above, the close relationship between *G. mawatarii* gen. et sp. nov.

and *F. kalenesos* has been supported by both morphological and molecular data. While in the previous phylogenetic analyses, the position of *Cateria* is not clarified. The first two molecular phylogenetic analyses of Kinorhyncha did not include any *Cateria* species (Dal Zotto et al., 2013; Yamasaki et al., 2013). Sørensen et al. (2015) used morphological data of *C. gerlachi* and supported its affiliation to the order Kentrorhagata based on the total evidence and morphological analyses with relatively low support values. Future phylogenetic studies of *Cateria* including molecular data and/or an improved morphological matrix may or may not indicate a different phylogenetic relationship of the genus.

Considering the similarities of the introvert morphology and the uncertainty of the phylogenetic relationship of *Cateria*, *Cateria* could be more closely related to Franciscideridae than to other kentrorhagid genera as hypothesized in Dal Zotto et al. (2013), and *Cateria*, *Gracilideres*, and *Franciscideres* could form a monophyletic clade. If this hypothesis is correct, the introvert morphology may provide features of phylogenetic significance, and appear as synapomorphic of this group. These three genera share the presence of a trunk with thin cuticle. However, this trait is also shared with different kentrorhagid genera, and would rather be a homoplastic feature, as discussed in the following section. It should be also noted that *Cateria* shows similarities to other kentrorhagid genera, such as the presence of a midterminal spine, scalids of rings 02 and 03 each composed of a basal and a distal element, and trichoscalids. A neck with separated placids found in *C. gerlachi* is also rather similar to other kentrorhagid genera, however, any separated placid is present in *C. styx* (Herranz et al., this issue). The similarities support the hypothesis of a phylogenetically close relationship of *Cateria*, *Gracilideres*, and *Franciscideres*, however, the conflicting hypothesis of the relationships suggested by Sørensen et al. (2015) cannot be rejected. The relationships of three genera remain open until further phylogenetic analyses based on additional molecular/morphological data are available.

4.2.2. Thin and flexible trunk cuticle in Kinorhyncha

Among all kinorhynch species, the presence of a thin cuticle trunk in the adult stage is known only in some genera and species: most species of *Antygomonas*, all species of *Semnoderes*, *Zelinkaderes*, *Cateria*, *Triodontoderes*, *Tubulideres*, Neocentrophyidae, *Franciscideres*, and *Gracilideres* gen. nov. (Zelinka, 1928; Băcescu and Băcescu, 1956;

Gerlach, 1956, 1969; Higgins, 1967, 1968, 1969, 1983, 1990; Nebelsick, 1990; Bauer-Nebelsick, 1995, 1996; Sørensen, 2007; Sørensen et al., 2007, 2010; Sørensen and Rho, 2009; Dal Zotto et al., 2013; Sánchez et al., 2014; Dal Zotto, 2015; Altenburger et al., 2015; Sørensen and Landers, 2017, 2018; this study) (Fig. 9). Most of these species have been found from relatively coarse substrata, namely fine to coarse sand, coral sand, and/or shell gravel. The only exceptions are *Zelinkaderes floridensis* Higgins, 1990, *Antygomonas* sp. in Sørensen and Landers (2018), some specimens of *Semnoderes armiger* Zelinka, 1928, *Semnoderes lusca* Sørensen and Landers, 2017 in Sørensen and Landers (2018), *Mixtophyes*, *Neocentrophyes*, *Paracentrophyes anurus* Sørensen et al., 2010, and *Paracentrophyes sanchezae* Sørensen and Landers, 2017, which are known from muddy substrates (Higgins, 1969, 1990; Sørensen et al., 2009, 2010; Sánchez et al., 2014; Sørensen and Landers, 2017, 2018). Eventually, it should be noted that the sediment type was not reported for *Semnoderes ponticus* Băcescu and Băcescu, 1956 (Băcescu and Băcescu, 1956).

A body with a thin and flexible cuticle may be an advantage when inhabiting interstices of coarse substrata, where sand grains would be a safer habitat than the surface of the seafloor. The thin cuticle of trunk would make the kinorhynch more flexible, and help it to bend its body when moving through the interstices. The records of most thin-cuticle kinorhynchs from coarse sands also support that the thin-cuticle is related to an adaptation for living in interstices of sand grains.

Interestingly, species characterized by a thin cuticle belong to two different lineages, i.e., Kentrorhagata within Cyclorhagida (*Antygomonas*, *Cateria*, *Semnoderes*, *Triodontoderes*, *Tubulideres*, and *Zelinkaderes*), and Neocentrophyidae (*Mixtophyes*, *Neocentrophyes*, and *Paracentrophyes*) plus Franciscideridae (*Franciscideres* and *Gracilideres*) within Allomalorhagida (Fig. 9). Adrianov and Malakhov (1995) and Neuhaus (1995) suggested that thin cuticle would be a plesiomorphic character of Kinorhyncha, and a thicker cuticle evolved independently in the cyclorhagid and homalorhagid (=taxon used at that time, including Pycnophyidae and Neocentrophyidae) lineages. Based on the tree topology by the previous phylogenetic studies, the thick cuticle would be a plesiomorphic condition within the Echinorhagata-Kentrorhagata clade in Cyclorhagida, and the thin cuticle would have evolved within the kentrorhagid lineage(s) (Fig. 9). Plesiomorphic characters of Allomalorhagida are still not clear, due to the unresolved relationships among the Franciscideridae-Neocentrophyidae, Dracoderidae, and Pycnophyidae clades, which also make the plesiomorphic condition for Kinorhyncha uncertain (Fig. 9). Nevertheless, the diversified thickness of the cuticle has most likely evolved independently at least twice in different lineages within Kinorhyncha.

The adaptation to the interstitial environment has occurred in several metazoan lineages, and these evolutionary processes and mechanisms have attracted recent attention (e.g., Laumer et al., 2015; Struck et al., 2015). Although the evolution towards a thinner cuticle in Kinorhyncha is one of the evolutionary processes which might have been linked to their migration into the interstitial environment, further studies of various aspects are necessary to understand the exact mechanisms in depth. The still unresolved phylogenetic relationships within Kentrorhagata and Allomalorhagida as well as the phylogenetic position of *Cateria* should be addressed by phylogenetic or phylogenomic analyses, which will be the basis of the discussion of evolution of the thin body cuticle in kinorhynchs. Ultrastructural and/or evo-devo approaches of kinorhynchs with thin body cuticle could reveal the micromorphological and developmental differences between thinner and thicker cuticle. Further ecological studies focused on kinorhynch communities and environmental factors will probably increase the information on specific preference for a variety of parameters, e.g., sediment granulometry, nutrient, etc. These features have certainly played a crucial role in the evolutionary process of colonization of the coarse-substrate environments. With these studies, the mechanisms of the kinorhynch adaptation to the interstitial environment could be understood, and become a model to study meiofaunal evolution.

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Figure captions

Fig. 1. *Gracilideres mawatarii* gen. et sp. nov., holotype (ICHUM 04304), camera lucida drawings. **A**, **B**, neck and trunk segments, dorsal and ventral views, respectively. Abbreviations: las, lateral accessory acicular spine; ltas, lateral accessory terminal acicular spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; ne, neck; pds, paradorsal acicular spine; po, pore; sgc, string-like glandular cell; ss, sensory spot; tr, trunk; vlt, ventrolateral tube.

Fig. 2. *Gracilideres mawatarii* gen. et sp. nov., holotype (ICHUM 04304), Nomarski photomicrographs. **A**, whole animal including head, neck, and trunk segments 1–11, dorsal view; **B**, head, neck and segments 1 and 2, dorsal view; **C**, introvert and neck, dorsal view. Abbreviations: bs, basal sheath of primary spinoscalid; dep, distal end piece of primary spinoscalid; he, head; hls, area covered with hair like structures; int, introvert; mc, mouth cone; ne, neck; oos, outer oral style; psc, primary spinoscalid; sc, scalid, followed by the ring number; seg, segment followed by number; tr, trunk.

Fig. 3. *Gracilideres mawatarii* gen. et sp. nov., scanning electron micrographs. **A–B**, **E–F**, ICHUM 04299; **C**, ICHUM 04297; **D**, **G**, ICHUM04298. **A**, mouth cone with inner and outer oral styles; **B**, close up of introvert; **C**, introvert, neck, and segment 1; **D**, neck when head retracted, frontal view; **E**, neck and segments 1 and 2, lateroventral view (right side); **F**, close up of segment 1, ventral view; **G**, segments 1–3, ventral view. Black arrow indicates sensory spot. Abbreviations: bac, bacterium; bs, basal sheath of primary spinoscalid; dep, distal end piece of primary spinoscalid; he, head; hls, area covered with hair like structures; ios, inner oral style; lc, longitudinal crimp; lvt, lateroventral tube; ne, neck; oos, outer oral style; psc, primary spinoscalid; sc, scalid with ring number; seg, segment followed by segment number; vlt, ventrolateral tube.

Fig. 4. Diagram of mouth cone, introvert, and placids in *Gracilideres mawatarii* gen. et sp. nov. Grey shaded are and bold line symbolize mouth cone and neck, respectively. The table lists the scalid arrangement by sector.

Fig. 5. *Gracilideres mawatarii* gen. et sp. nov., Nomarski photomicrographs. **A**, **B**, holotype

(ICHUM 04304); **C**, **F**, paratype (ICHUM 04301); **D**, **E**, paratype (ICHUM 04303). **A**, segments 1–8, dorsal view; **B**, segments 1–8, ventral view; **C**, segments 1–4, ventral view; **D**, segments 3–5, dorsal view; **E**, segments 4–6, ventral view; **F**, segments 6–8, dorsal view. Black arrows indicate sensory spots. Abbreviations: las, lateral accessory acicular spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; pds, paradorsal acicular spine; seg, segment followed by segment number; sgc, string-like glandular cell; vlt, ventrolateral tube.

Fig. 6. *Gracilideres mawatarii* gen. et sp. nov., scanning electron micrographs. **A**, **F**, ICHUM 04297; **B**, **D**, ICHUM 04299; **C**, **E**, ICHUM04298. **A**, segments 3–5, dorsal view; **B**, segments 3–5, lateral view (right side); **C**, segments 3–5, ventral view; **D**, segment 4: lateroventral acicular spine and sensory spot in lateral accessory position; **E**, segments 5–7, ventral view; **F**, segments 6–8, dorsal view. Black arrows indicate sensory spots. Abbreviations: las, lateral accessory acicular spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; pds, paradorsal acicular spine; po, pore; seg, segment followed by segment number.

Fig. 7. *Gracilideres mawatarii* gen. et sp. nov., Nomarski photomicrographs. **A**, **B**, **F**, holotype (ICHUM 04304); **C**, **E**, paratype (ICHUM 04301); **D**, paratype (ICHUM 04303). **A**, segments 7–11, dorsal view; **B**, segments 6–11, ventral view; **C**, segments 8–10, ventral view; **D**, segments 8–9, dorsal view; **E**, segments 9–11, dorsal view; **F**, segments 10 and 11, dorsal view. Black arrows indicate sensory spots. Abbreviations: las, lateral accessory acicular spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pds, paradorsal acicular spine; seg, segment followed by segment number; sgc, string-like glandular cell.

Fig. 8. *Gracilideres mawatarii* gen. et sp. nov., scanning electron micrographs. **A**, **C**, ICHUM 04297; **B**, **D**, ICHUM 04299. **A**, segments 8–10, dorsal view; **B**, segments 8–10, ventral view; **C**, segments 10 and 11, dorsal view; **D**, segments 10 and 11, ventral view. Black arrows indicate sensory spots. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pds, paradorsal acicular spine; seg, segment followed by segment number.

Fig. 9. Phylogenetic tree of Kinorhyncha with a focus on selected characters of introvert and cuticle in relation to *Gracilideres mawatarii* gen et sp. nov.. The tree is modified from Sørensen et al. (2015), showing the not well-resolved relationships as polytomies or as dashed lines. Although *Parasemnoderes* was not included in the analyses by Sørensen et al. (2015), the genus is included in the Kentrorhagata clade based on its affiliation of the family Semnoderidae suggested by Adrianov and Maiorova (2018). Character: 1, basal sheath of primary spinoscalid distally bifurcated; 2, ring 02 scalids consisting of only long and thin end piece; 3, ring 03 scalids consisting of basal sheath only; 4, introvert surface posterior to scalids densely covered with hair-like structures; 5, trichoscalids absent. Symbols indicate taxa with characters: White circles = same as *Gracilideres*, black circles = possibly same as *Gracilideres* but further examination required, question mark = unknown, and crosses = different from *Gracilideres*.

Table 1

Table 1. Measurements for adult *Gracilideres mawatarii* gen. et sp. nov. (in micrometers). Mean lengths and standard deviations are calculated based on the specimens except for ICHUM 04302, due to its clearly deviating dimensions, suggesting that the specimen might be juvenile. Columns N and SD indicate sample size and standard deviation, respectively. Abbreviations: (ac), acicular spine; la, lateral accessory spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine/tube; md, middorsal spine; pd, paradorsal spine; s, segment length; tl, trunk length; (tu), tube; vl, ventrolateral tube.

Character	ICHUM 4304 (Holotype)	ICHUM 4301	ICHUM 4302	ICHUM 4303	Specimens except ICHUM 04302		
					N	Mean	SD
tl	500	501	370	534	3	511.6	19.18
s1	46	41	40	41	3	42.8	2.40
s2	38	41	33	41	3	39.9	2.06
s3	40	40	31	44	3	41.2	2.04
s4	45	43	34	49	3	45.4	3.14
s5	54	51	41	58	3	54.1	3.56
s6	61	56	47	63	3	60.1	3.72
s7	64	57	44	67	3	62.9	5.17
s8	60	56	48	66	3	60.8	5.28
s9	58	49	41	58	3	55.2	5.48
s10	60	48	42	64	3	57.5	8.38
s11	46	38	25	43	3	42.4	3.67
pd3 (ac)	47	n.a.	42	38	2	42.7	6.71
pd4 (ac)	51	38	61	41	3	43.2	6.50
pd5 (ac)	65	50	83	47	3	54.2	9.80
pd6 (ac)	67	56	64	51	3	58.0	8.13
pd7 (ac)	76	58	73	60	3	64.7	9.46
pd8 (ac)	77	57	25	65	3	66.0	9.99
pd9 (ac)	61	52	59	64	3	58.7	6.18
md10 (ac)	56	61	broken	64	3	60.7	3.83
md11 (ac)	broken	63	broken	broken	1	63	n.a.
vl1 (tu)	12	11	12	12	3	11.7	0.54
lv2 (tu)	13	11	12	13	3	12.1	0.81
lv4 (ac)	51	32	43	36	3	39.8	10.19
lv5 (tu)	16	18	16	17	3	16.7	1.04
la5 (ac)	45	38	50	36	3	40.0	4.82
lv6 (ac)	46	38	45	39	3	41.2	4.29
lv7 (ac)	56	42	51	45	3	47.7	7.70
lv8 (ac)	57	48	49	52	3	52.3	4.22
lv9 (ac)	57	45	42	51	3	51.2	5.96
lv10 (ac)	42	46	41	43	3	43.8	2.21
lts	99	76	72	85	3	86.6	11.52
ltas	100	75	70	89	3	88.2	12.58
lts/tl	19.8%	15.2%	19.4%	15.9%	3	17.0%	2.48%
ltas/tl	20.1%	15.0%	18.9%	16.6%	3	17.3%	2.58%

Table 2

Table 2. Summary of locations of cuticular structures and appendages in *Gracilideres mawatarii* gen. et sp. nov. Asterisks indicate unpaired character. The underlined character is absent in one out of eight examined specimens. Abbreviations: ac, acicular spine; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; md, middorsal; ml, midlateral; pd, paradorsal; po, pore; sd, subdorsal; sgc, string-like gland cell; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

Position segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
1	sgc								tu	sgc
2	sgc					ss	po	tu		sgc
3	sgc	ac*					po, ss			sgc
4	sgc	ac*					po, ss	ac		sgc
5	sgc	ac*					po, ac	tu		sgc
6	sgc	ac*	ss				po, ss	ac		sgc
7	sgc	ac*					po, ss	ac		sgc
8	sgc	ac*	ss				po	ac		sgc
9	sgc	ac*	ss				po, ss	ac		sgc, ss
10	sgc						po	ac		
11	sgc						ltas	lts		

Figure 1

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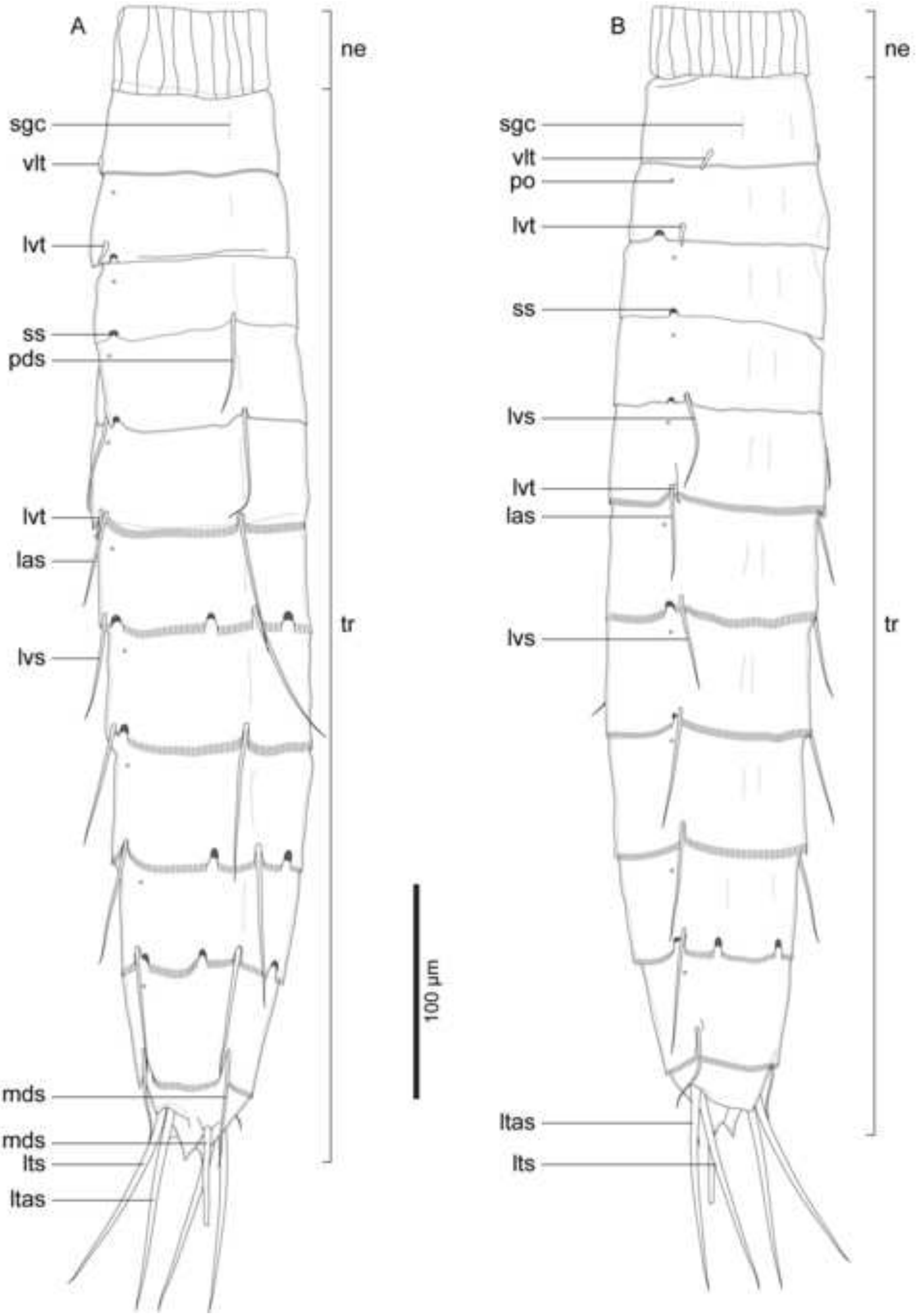

Figure 2

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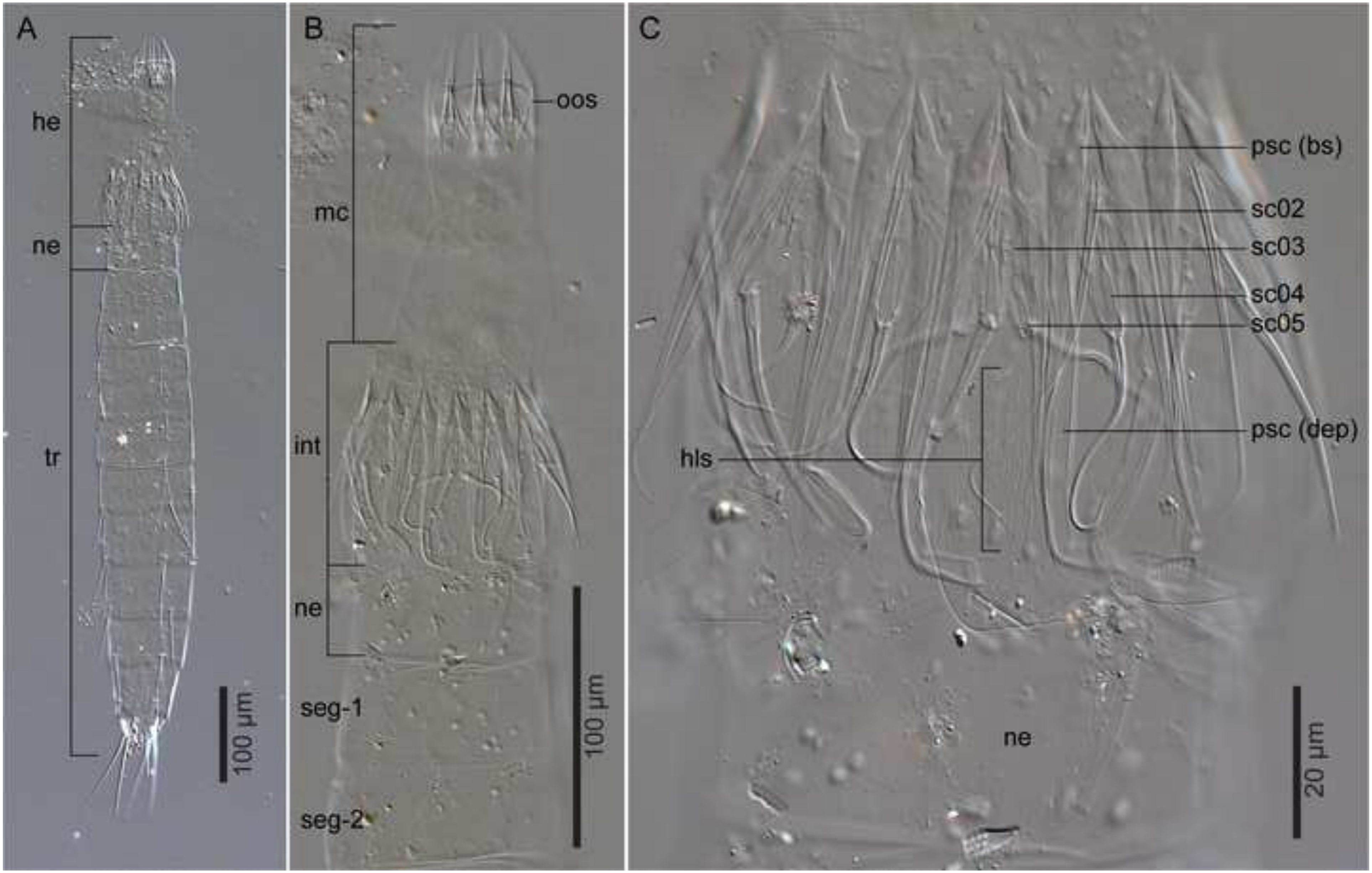


Figure 3

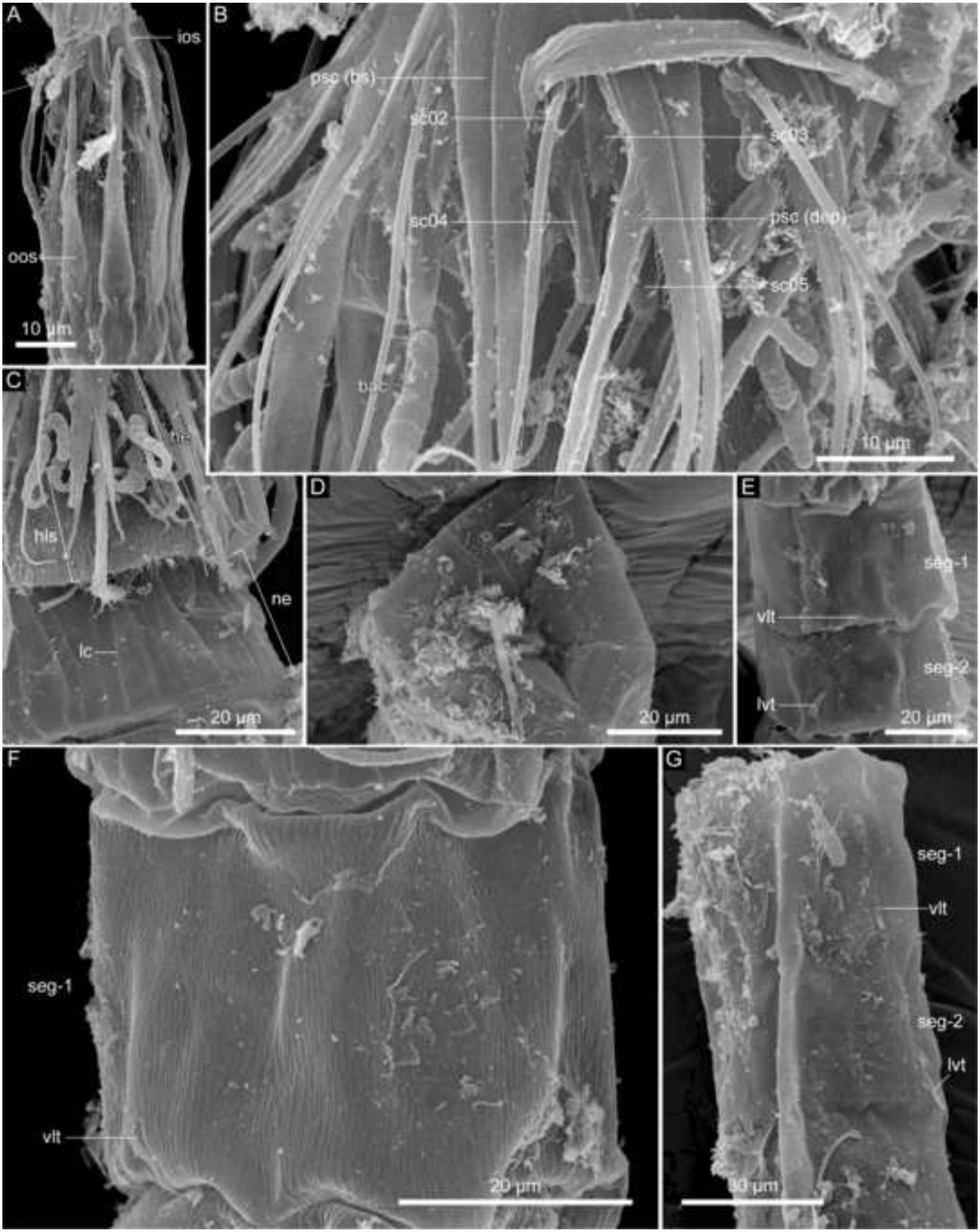
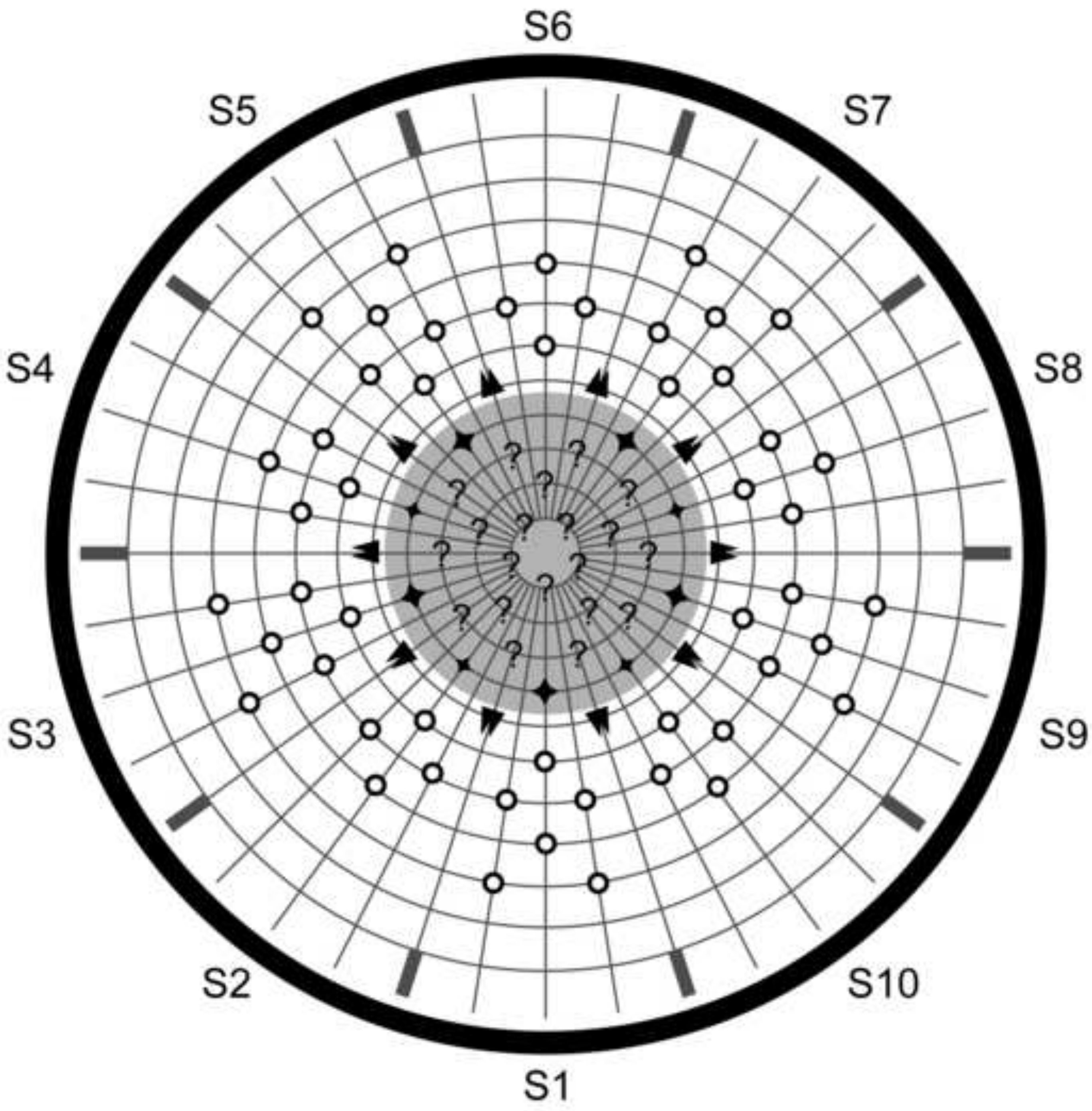

A
ios
oos
10 µm
B
psc (bs)
sc02
sc03
sc04
psc (dep)
sc05
bac
10 µm
C
ne
his
ne
lc
20 µm
D
20 µm
E
seg-1
vlt
seg-2
lvt
20 µm
F
seg-1
vlt
20 µm
G
seg-1
vlt
seg-2
lvt
30 µm

Figure 4



Scalid and style arrangement

Ring/Sector	1	2	3	4	5	6	7	8	9	10	Total
00 outer oral styles ✦	1	1	1	1	1	0	1	1	1	1	9
01 primary scalids ▼	1	1	1	1	1	1	1	1	1	1	10
02 scalids ○	1	1	1	1	1	1	1	1	1	1	10
03 scalids ○	2	2	2	2	2	2	2	2	2	2	20
04 scalids ○	1	1	1	1	1	1	1	1	1	1	10
05 scalids ○	2	0	2	0	2	0	2	0	2	0	10

Figure 5

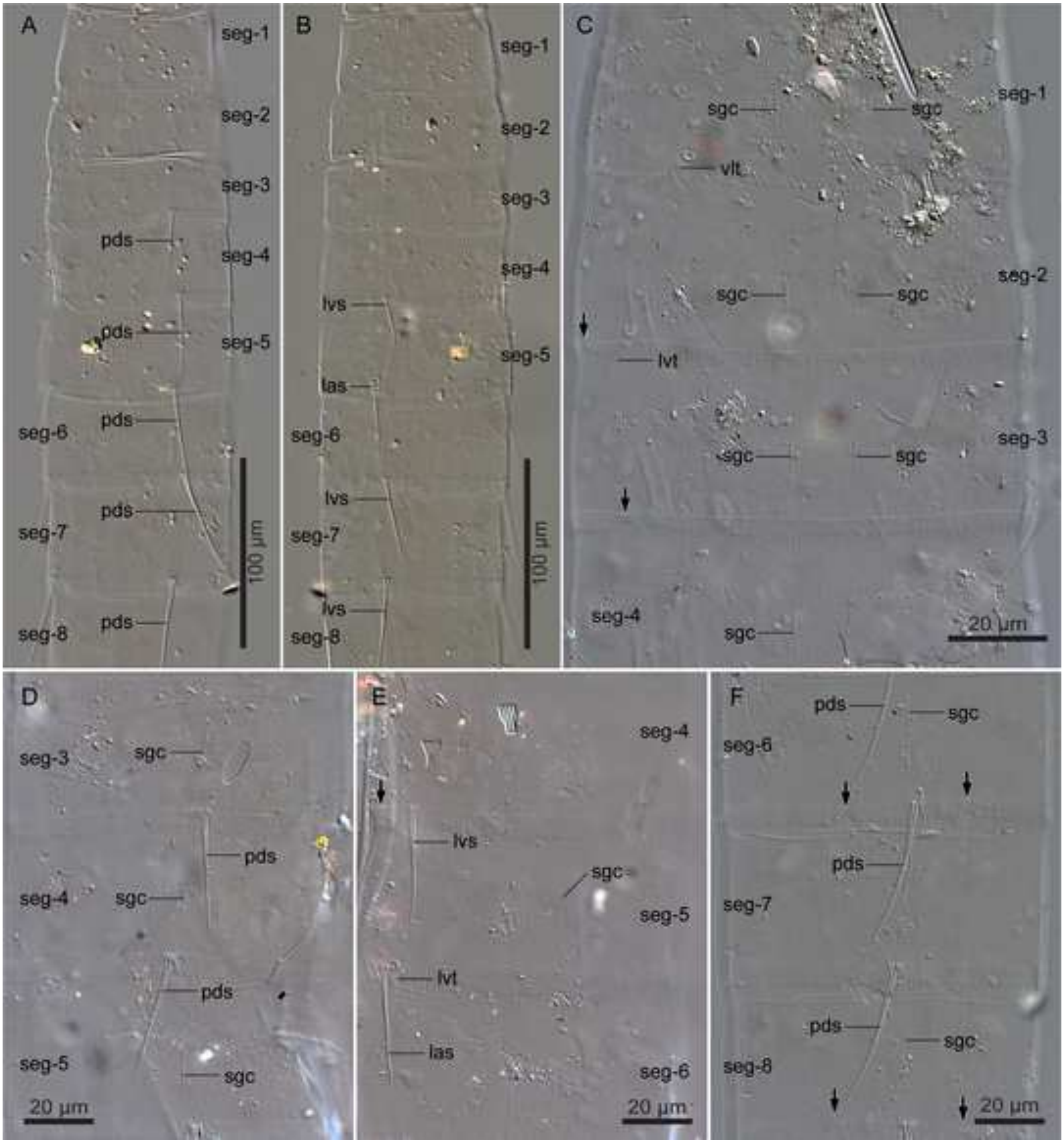

A
seg-1
seg-2
seg-3
pds
seg-4
pds
seg-5
seg-6
pds
pds
seg-7
100 µm
pds
seg-8
B
seg-1
seg-2
seg-3
seg-4
lvs
las
seg-5
seg-6
lvs
seg-7
100 µm
lvs
seg-8
C
seg-1
sgc
sgc
vlt
seg-2
sgc
sgc
lvt
seg-3
sgc
sgc
seg-4
sgc
20 µm
D
seg-3
sgc
pds
seg-4
sgc
pds
seg-5
sgc
20 µm
E
seg-4
lvs
sgc
seg-5
lvt
las
seg-6
20 µm
F
pds
sgc
seg-6
pds
seg-7
pds
sgc
seg-8
20 µm

Figure 6

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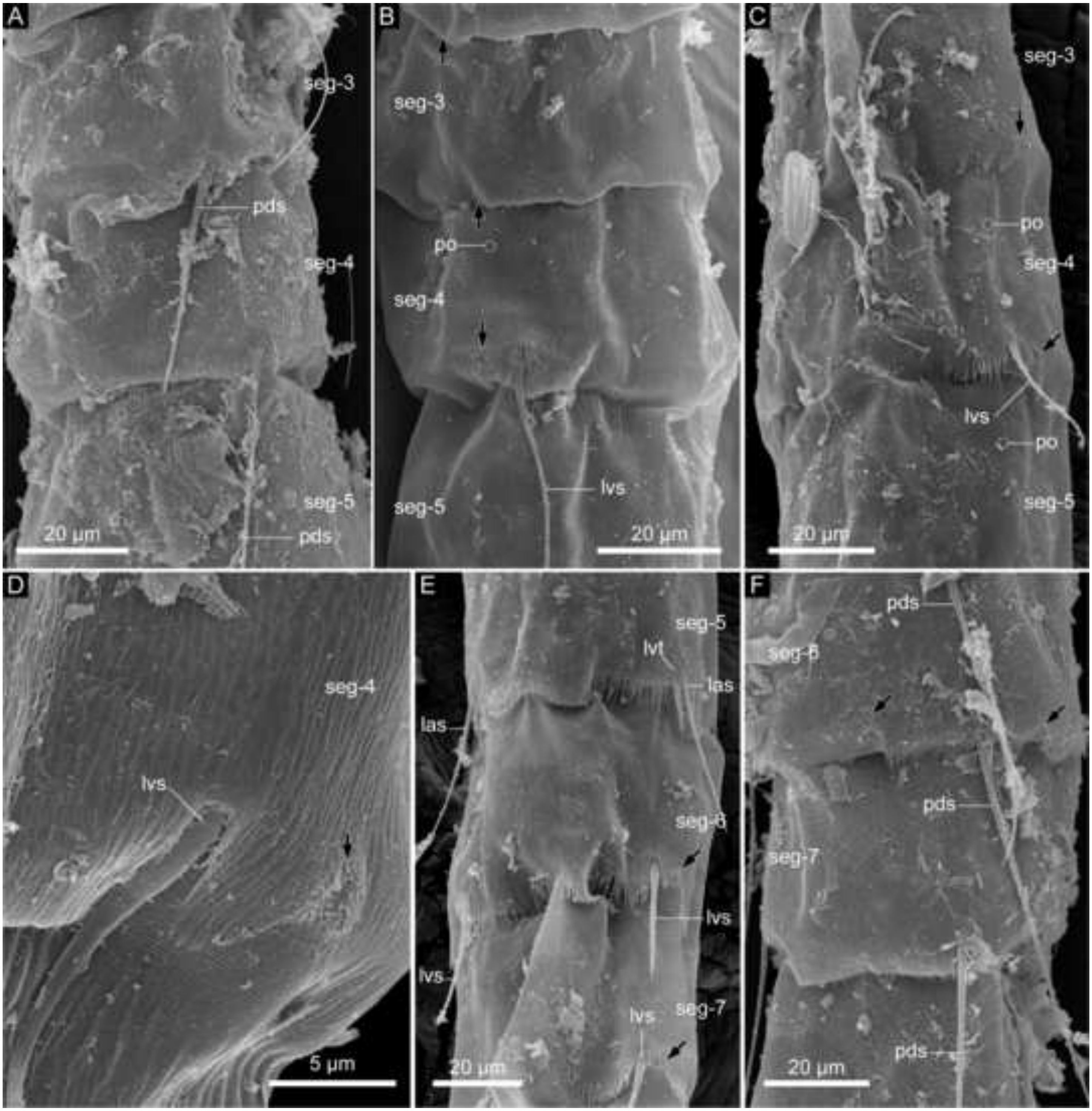

Figure 7

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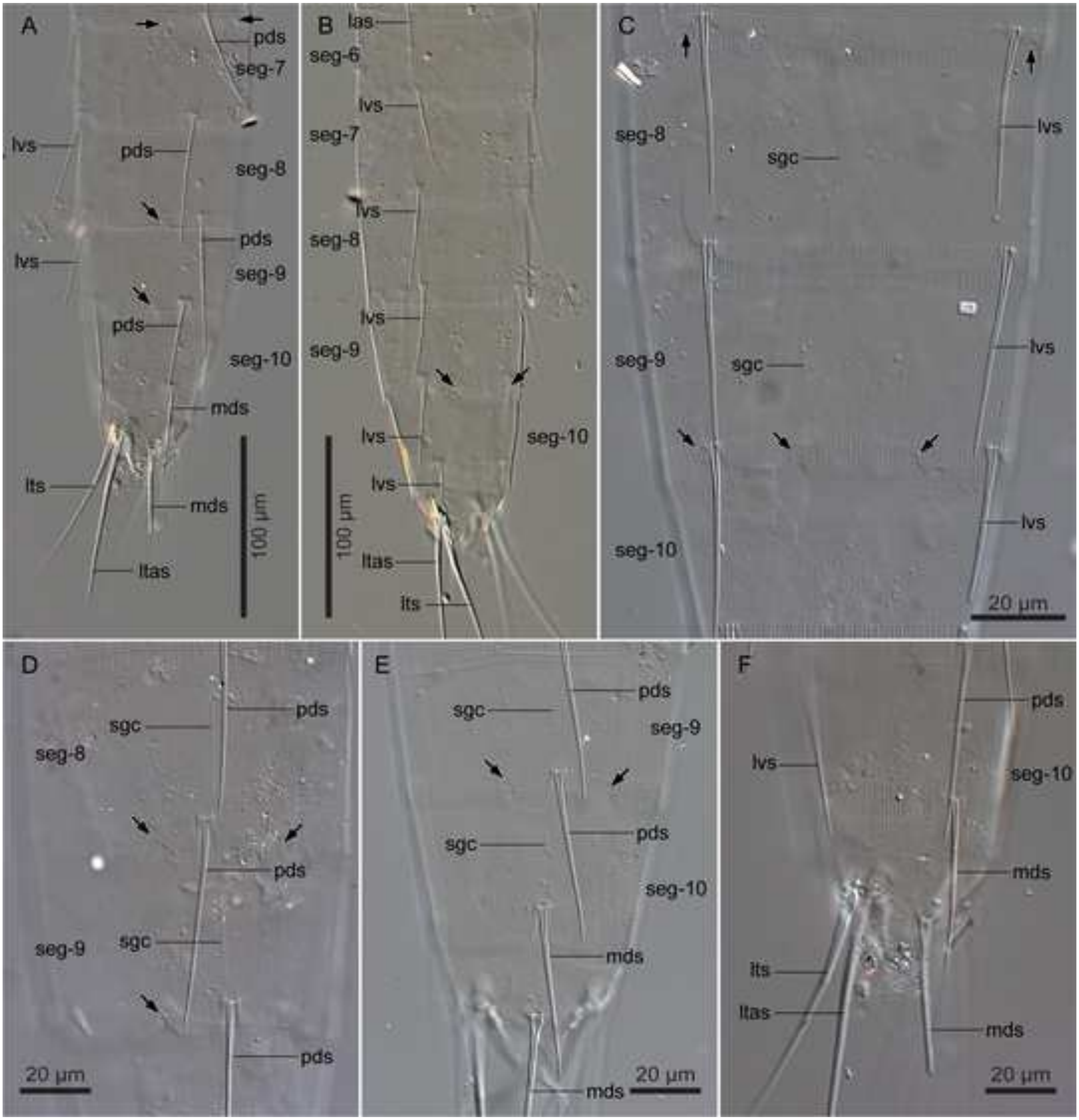


Figure 8

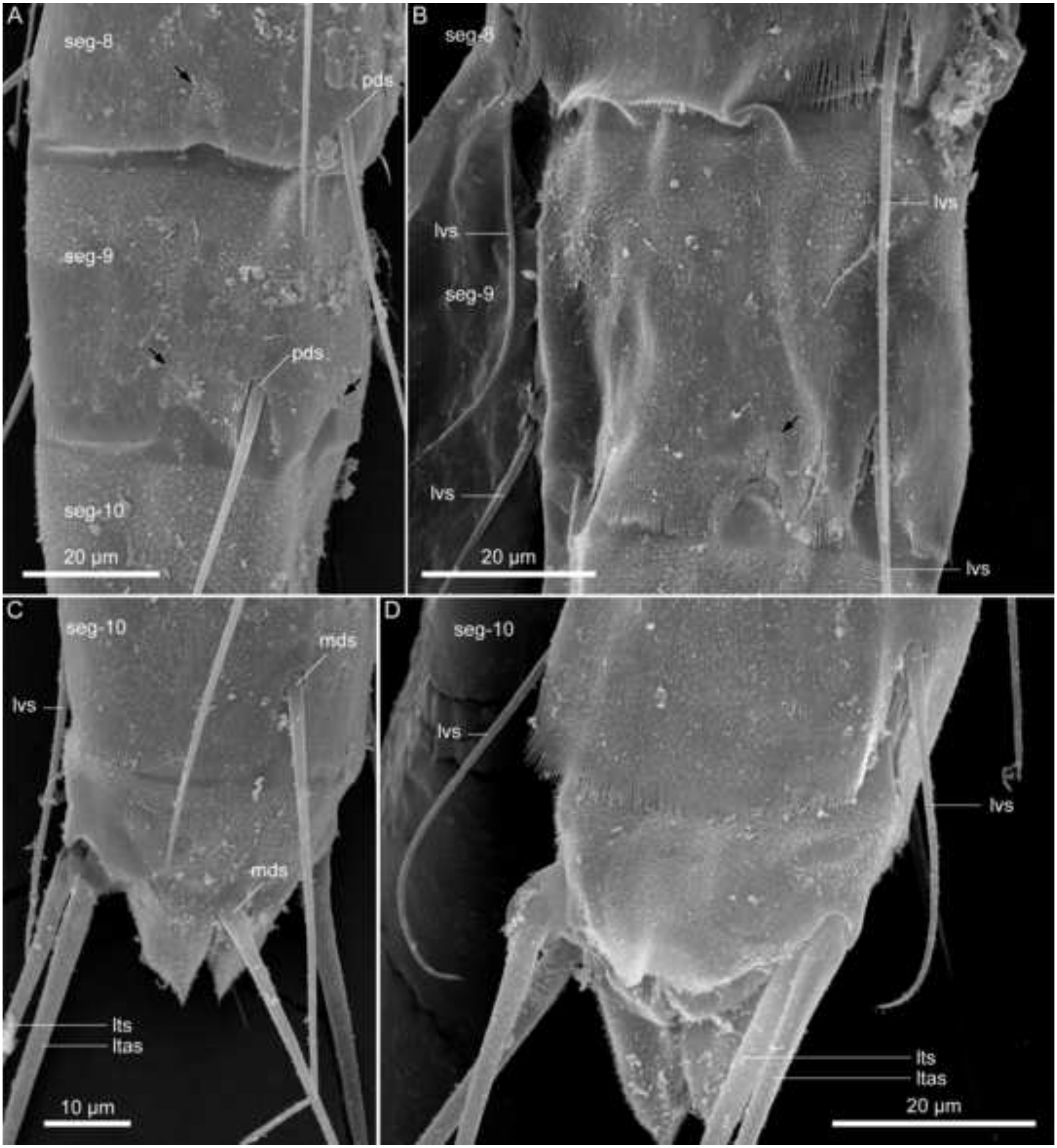
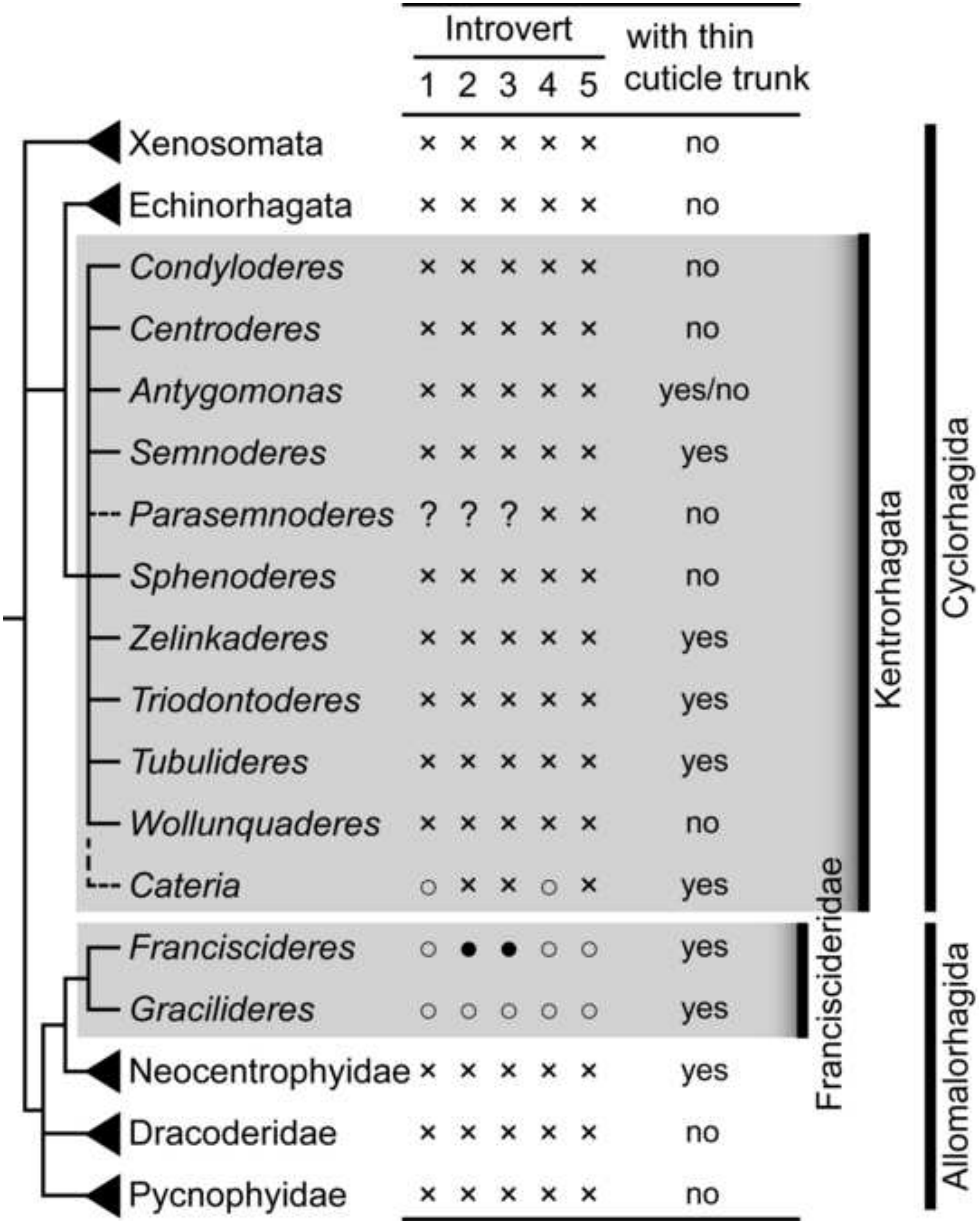

A
seg-8
pds
seg-9
pds
seg-10
20 µm
B
seg-8
lvs
lvs
seg-9
lvs
20 µm
lvs
C
seg-10
mds
lvs
mds
lts
ltas
10 µm
D
seg-10
lvs
lvs
lts
ltas
20 µm

Figure 9



	Introvert 1	2	3	4	5	with thin cuticle trunk
Xenosomata	×	×	×	×	×	no
Echinorhagata	×	×	×	×	×	no
Condyloderes	×	×	×	×	×	no
Centroderes	×	×	×	×	×	no
Antygomonas	×	×	×	×	×	yes/no
Semnoderes	×	×	×	×	×	yes
Parasemnoderes	?	?	?	×	×	no
Sphenoderes	×	×	×	×	×	no
Zelinkaderes	×	×	×	×	×	yes
Triodontoderes	×	×	×	×	×	yes
Tubulideres	×	×	×	×	×	yes
Wollunquaderes	×	×	×	×	×	no
Cateria	○	×	×	○	×	yes
Franciscideres	○	●	●	○	○	yes
Gracilideres	○	○	○	○	○	yes
Neocentrophyidae	×	×	×	×	×	yes
Dracoderidae	×	×	×	×	×	no
Pycnophyidae	×	×	×	×	×	no