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Investigation of echinoderid kinorhynchs described 90 years ago: redescription of *Echinoderes capitatus* (Zelinka, 1928) and *Echinoderes ferrugineus* Zelinka, 1928

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Abstract

The two kinorhynch species *Echinoderes capitatus* (Zelinka, 1928) and *Echinoderes ferrugineus* Zelinka, 1928 are redescribed herein, based on specimens collected at different Mediterranean locations. *Echinoderes capitatus* is characterized by the presence of middorsal acicular spine on segment 4 and lateroventral acicular spines on segments 6–9; at least three pairs of tubes on segment 2 (subdorsal, midlateral, and ventrolateral); subdorsal tubes on segment 8; laterodorsal tubes on segment 10; lateral accessory tubes on segments 5 and 8; subdorsal sensory spots on segments 1 and 3–11; and ventromedial sensory spots on segments 2 and 5–7, often additionally on 8; occurrence of subdorsal tubes on segments 6 and 7, laterodorsal tubes on segment 2, midlateral tubes on segments 7 and 8, and ventromedial tubes on segment 8 showing intraspecific variation; and the absence of the type-2 gland cell outlets. The pattern of the additional tubes is relatively well-preserved within a population but differs among populations. *Echinoderes ferrugineus* is characterized by the presence of middorsal acicular spines on segment 4–8; lateroventral acicular spines on segments 6–9; lateral accessory tubes on segment 5; type-2 gland cell outlets in subdorsal, laterodorsal, sublateral, and ventrolateral position on segment 2, subdorsal and midlateral position on segment 4, midlateral position on segment 5, and midlateral position on segment 8; long lateral terminal spines (ca. 140–180 μm, 45–63% of trunk length). Comments are provided on the intraspecific variation in tube pattern in *Echinoderes capitatus*, and its potential importance in a speciation and evolutionary context.

Keywords

meiofauna; Mediterranean Sea; morphological variation; polymorphism; Kinorhyncha; mud

dragons

1. Introduction

Mud dragons are exclusively meiobenthic animals, composing the phylum Kinorhyncha. To date, more than 270 species have been described from various environments. They are most commonly found in marine, muddy sediments, but may also occur in various other substrates and habitats, such as sandy beaches, coarse sand bottoms, brackish waters, continental shelves, deep-sea floors, sea mounts, submarine caves. They have been reported from all parts of the world and the discovery of new species has increased significantly in the recent years (e.g., Sørensen and Pardos, 2008; Neuhaus, 2013; Dal Zotto, 2015; Yamasaki, 2016; Yıldız et al., 2017; Adrianov and Maiorova, 2018; Grzelak and Sørensen, 2018; Herranz et al., 2018; Landers et al., 2018; Sánchez et al., 2018; Sørensen et al., 2018; Yamasaki et al., 2018a, b). Dr Carl Zelinka (1859–1946) published the first monograph on Kinorhyncha describing and naming 56 new species (Zelinka, 1928). Although many of them subsequently were synonymized or regarded as *nomina dubia* in later studies, twelve species in the monograph are still considered as valid species.

Both *Echinoderes capitatus* (Zelinka, 1928) and *Echinoderes ferrugineus* Zelinka, 1928 were originally described in Zelinka's monograph (Zelinka, 1928). He described the species based on specimens collected from the Gulf of Trieste and from the Bay of Naples (Fig. 1), however, the original material does not exist any longer (Neuhaus et al., 2013). Subsequently, Remane (1954) reported *E. ferrugineus* from the Bay of Kiel, Germany, and later Nebelsick (1992b) redescribed *E. capitatus* based on specimens from the Gulf of Trieste and from off Rovinj, Istria, relatively close to the Gulf of Trieste (northern Adriatic Sea). She also investigated the fine structure of the species, e.g., sensory spots, introvert, mouth cone, and nervous system, with using scanning and transmission electron microscopes (Nebelsick, 1992a, 1992b, 1993). More recently, the two species have been recorded at several localities in Italian waters by Dal Zotto and Todaro (2016), Dal Zotto et al. (2016, this issue).

During a project of kinorhynchs on seamounts funded by the Deutsche Forschungsgemeinschaft DFG (GE 1086/20-1, NE 931/6-1), specimens of *E. capitatus* and *E. ferrugineus* from Italian waters were examined in order to compare and distinguish seamount kinorhynchs. Consequently, several new taxonomic characters in both species as well as intraspecific morphological variations in *E. capitatus* were discovered. This paper provides these newly-found morphological characters, suggesting emended diagnoses for each of the two species, and discusses about the intraspecific variations in *E. capitatus*.

2. Material and methods

Apart from topotypic material kindly provided by Dr. Monika Bright (see below), the specimens analysed in the present study were collected during two different environmental monitoring projects, led in the Gulf of Castellammare, off the town of Castellammare del Golfo (Tyrrhenian Sea, Sicily, southern Italy), and off Chioggia (Adriatic Sea, Veneto, northern Italy), respectively. For detailed information on the former monitoring project see Dal Zotto et al. (2016). The sediment samples were collected with a hand-held piston corer (3.40 cm inner diameter x 5.00 cm height for the sample from the Gulf of Castellammare; 2.75 cm inner diameter x 5.00 cm height for the samples from off Chioggia). Further information on each sampling station is listed in Table 1. The fauna was narcotized using a 7% magnesium chloride solution and fixed on site with a 10% buffered formalin solution. In the laboratory, some samples were stained with Rose Bengal for subsequent sorting (Todaro et al., 2006). Each sample was filtered using two sieves, 1 and 0.045 mm, respectively. The 45 µm fraction was kept for study, and meiofauna was extracted three times using silica gel gradient centrifugation (LUDOX® AM, density: 1.210; Pfannkuche and Thiel 1988; Todaro et al., 2001). Kinorhynchs were isolated under stereomicroscopes WILD M8 and stored in 5% buffered formalin. Before the following observations, all specimens were transferred from formalin to 75% EtOH.

Specimens for light microscopy (LM) were dehydrated in glycerol and mounted as glycerol-paraffin slides on Cobb aluminum frames and observed with a Zeiss Axioskop 50 microscope. A camera lucida equipped with the microscope was used to make drafts for line art illustrations. 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 from ethanol to distilled water through a graded series of ethanol, postfixed with OsO_4 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, critical-point dried with a BalTec CPD 030, mounted on aluminum stubs, sputter-coated with gold-palladium with a Polaron SC 7640, and observed with a Zeiss EVO LS 10 scanning electron microscope.

The additional topotypic specimens stored in the Museum für Naturkunde Berlin (= ZMB, former Zoological Museum Berlin), Germany, which were originally collected by Dr Monika Bright (University of Vienna) and donated to Dr Birger Neuhaus (ZMB) were also observed. The specimens were collected on 12 March 1987 off Trieste, northern Adriatic Sea, and mounted in an unknown mounting media either on Cobb aluminum frame or on glass slides. Further information on the sampling locality, e.g., coordinates, depth, and sediment type, could not be obtained.

The terminology follows Neuhaus and Higgins (2002), Sørensen and Pardos (2008) and Neuhaus (2013). The classification system follows Sørensen et al. (2015). All specimens have been deposited in ZMB and catalogued in the collection “Vermes” in the “Generalkatalog Freilebende Würmer”.

3. Results and discussion

Class Cyclorhagida Zelinka, 1896

Order Echinorhagata Sørensen et al., 2015

Family Echinoderidae Zelinka, 1894

Genus *Echinoderes* Claparède, 1863

3.1. *Echinoderes capitatus* (Zelinka, 1928) (Figs 2–5 and Tables 2 and 3)

3.1.1. Synonymy

Echinoderella capitata: Zelinka (1912) [nomen nudum], Zelinka (1928); *Echinoderes capitata*: Karling (1954); *Echinoderes capitatus*: Higgins (1983), Nebelsick (1992a, 1992b, 1993), Dal Zotto and Todaro (2016), Dal Zotto et al. (2016); *Habroderella capitata*: Zelinka (1928); *Habroderella trispinosa*: Remane (1936); *Hapaloderes minimus*: Nyholm (1947)

3.1.2. Emended diagnosis

Echinoderes with middorsal acicular spines on segment 4 and lateroventral acicular spines on segments 6–9; at least three pairs of tubes on segment 2 (subdorsal, midlateral, and ventrolateral position); subdorsal tubes on segment 8; laterodorsal tubes on segment 10; lateral accessory tubes on segments 5 and 8; additional tubes present not always but in some specimens: subdorsally on segments 6 and 7, laterodorsally on segment 2, midlaterally on segments 7 and 8, and/or ventromedially on segment 8; subdorsal sensory spots on segments 1 and 3–11; ventromedial sensory spots on segments 2 and 5–7, often additionally on 8; without type-2 gland cell outlets and lateral terminal accessory spines in both sexes.

3.1.3. Material examined

Non-type: one female (ZMB XXXXXX), collected from off Trieste, northern Adriatic Sea (coordinates unknown), mounted in unknown mounting medium on a Cobb aluminum frame; one male and one female (ZMB XXXXXX), collecting data as above mentioned specimen, mounted in unknown mounting medium on glass slide; seven males and three females (ZMB XXXXXX), collected from off Chioggia, northern Adriatic Sea, mounted as glycerol-paraffin slide on a Cobb aluminum frame; three males and one female (ZMB XXXXXXX), collected from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea, mounted as glycerol-paraffin slide on a Cobb aluminum frame; three males and four females collected from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea, on an aluminum stub for SEM observation.

3.1.4. Description

This chapter describes the typical morphology of *Echinoderes capitatus*, as observed in specimens from Trieste. See “3.1.7. Variation” for polymorphic characters in specimens from other localities.

Adult with head, neck, and eleven trunk segments (Figs 2A, B, 3A, and 4A). See Table 2 for measurements. Table 3 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Head consisting of retractable mouth cone and introvert (Figs 3A–C and 5). Mouth cone with inner and nine outer oral styles (Figs 3B and 5). Detailed arrangement of inner oral style not observed. Each outer oral style consisting of rectangular basal part and triangular distal part, with basal part alternating in length between five larger basal parts in odd sectors and four smaller ones in even sectors (Figs 3B and 5). Basal part covered with six long spinose processes bifurcated at their tips (Fig. 3B). One pair of short spinose processes originating slightly more anteriorly and laterally on either side of each basal part (Fig. 3B). Introvert composed of one ring of primary scalids, five rings of spinoscalids, and one ring of trichoscalids (Figs 3C and 5). Arrangement of spinoscalids in each ring summarized in Fig. 5. Each primary spinoscalid consisting of basal sheath and distal end piece (Fig. 3C). Basal sheath comprises two layers of proximal fringes. End piece long with smooth surface, bluntly ending at distal tip. Each spinoscalid of rings 02–05 composed of basal sheath with fringed edge and distal long-spinose end piece (Fig. 3C). Spinoscalids in rings 02 and 03 longer than those in rings 04–06. Trichoscalids arising from trichoscalid plates. Each trichoscalid covered with long hairs.

Neck with 16 placids (Figs 2A, B, 4B, C, and 5). Midventral placid broadest. Remaining placids similar in size. Two trichoscalid plates present ventrally and four dorsally, each associated with ventromedial, subdorsal, and laterodorsal placid, respectively (Figs 2A, B, 4B, and C).

Segment 1 consisting of complete cuticular ring (Figs 2A, B, 4A–C). Sensory spots present in subdorsal, laterodorsal, and ventromedial position (Figs 2A, B, 3D, E, 4B, and C). Sensory spots on this and following segments oval, composed of single pore surrounded by numerous micropapillae (Fig. 3D–M). Type-1 gland cell outlets situated in middorsal and lateroventral position (Fig. 4B and C). Non-bracteate cuticular hairs arising from perforation sites covering whole segment except for anterior quarter of ventral area (Figs 2A, B, 3D, and E). Posterior part of this and following nine segments with primary pectinate fringe (Figs 2A, B, 3D, and E). Pectinate fringe teeth of primary pectinate fringe short and thin (Fig. 3D–F).

Segment 2 with complete cuticular ring as segment 1 (Figs 2A, B, 4B, and C). This and following eight segments with very thick pachycyclus at anterior margin of each segment. Tubes present in subdorsal, laterodorsal, midlateral, and ventrolateral position (Figs 2A, B, 3D–F, and 4B, and C). Sensory spots in middorsal and ventromedial position (Figs 2A, B, 3E, F, 4B, and C). Type-1 gland cell outlets located in middorsal and ventromedial position (Figs 2A, B, 4B, and C). Bracteate cuticular hairs arising from perforation sites cover whole segments. One row of secondary pectinate fringe present on anterior part of this and following eight segments, often covered by preceding segment (Fig. 3F).

Segment 3 and following eight segments consisting of one tergal and two sternal plates (Fig. 2A, B). Sensory spots present in subdorsal and midlateral position (Figs 2A, B, 3D, F, G, and 4B). Type-1 gland cell outlets situated in middorsal and ventromedial position (Figs 2A, B, 4B, and C). Bracteate cuticular hairs arising from perforation sites on this and following seven segments covers whole segment except for ventromedial area (Figs 2A, B, and 3D–M). Ventromedial area covered with minute cuticular hairs without perforation sites (Fig. 3E).

Segment 4 with middorsal acicular spine (Figs 2A, and 3G). Sensory spots present in subdorsal position (Figs 2A, and 3G). Type-1 gland cell outlets in paradorsal and ventromedial position (Figs 2A, B, and 4D).

Segment 5 with lateral accessory tubes (Figs 2B, 3H, I, and 4D). Sensory spots in subdorsal, midlateral, and ventromedial position (Figs 2A, B, 3H, I, and 4D). Type-1 gland cell outlets present in middorsal and ventromedial position (Figs 2A, B, and 4D).

Segment 6 with lateroventral acicular spines and subdorsal tubes (Figs 2A, B, 3H, I, and 4D). Sensory spots present in paradorsal, subdorsal, midlateral, and ventromedial position (Figs 2A, B, 3H–J, and 4D). Type-1 gland cell outlets present paradorsally and ventromedially (Figs 2A, B, and 4D).

Segment 7 with lateroventral acicular spines (Figs 2A, B, 3H, K, and 4E). Sensory spots present in subdorsal, midlateral, and ventromedial position (Figs 2A, B, 3H, J, and 4E). Type-1 gland cell outlets present middorsally and ventromedially (Fig. 2A and B).

Segment 8 with acicular spines in lateroventral position and tubes in subdorsal, midlateral, lateral accessory, and ventromedial position (Figs 2A, B, 3J, K, 4E, and F). Sensory spots present paradorsally and subdorsally (Figs 2A, 4H, J, K, and 4F). Type-1 gland cell outlets present in paradorsal and ventromedial position (Figs 2A, B, and 4E).

Segment 9 with lateroventral acicular spines (Figs 2B, D, 3K, and 4G). Paradorsal, subdorsal, midlateral and ventrolateral sensory spots present (Figs 2, 3K, L, 4F, and G). Type-1 gland cell outlets present in paradorsal and ventromedial position (Figs 2 and 4G). Small rounded sieve plates present in sublateral position (Fig. 2B–D).

Segment 10 with short laterodorsal tubes (Figs 2A, C, and 3M). Tube length slightly longer in males than females. Subdorsal and ventrolateral sensory spots present (Figs 2, 3L, M, and 4G). Two type-1 gland cell outlets aligned middorsally (Fig. 2A and C). Additional pair of type-1 gland cell outlets present in ventromedial position (Figs 2B, D, 4G).

Segment 11 with lateral terminal spines (Figs 2, 3A, L, M, and 4G). Three pairs of penile spines present in males, with two pairs being long and tube-like and one pair thick and relatively short (Figs 2C, D, and 3L). Lateral terminal accessory spines absent in both sexes. Subdorsal sensory spots present (Fig. 2A and C). Type-1 gland cell outlets present middorsally (Fig. 2A and C). Tergal extensions triangular and sternal extensions rounded (Fig. 2).

3.1.5. Intraspecific variation

Among specimens from off Trieste, one specimen lacks ventrolateral tube on right side on segment 2 and has ventrolateral sensory spot on right side on segment 9 being slightly relocated to anterior and median line (Figs 2B, 4C, and G).

Compared to specimens from Trieste, those from Chioggia differ in absence of subdorsal tubes on segment 6 and midlateral and ventromedial tubes on segment 8, and in presence of ventromedial sensory spots on segment 8. One out of ten specimens from Chioggia shows midlateral tubes instead of sensory spots on segment 7.

Specimens from off Castellammare (Sicily) differ from those from Trieste in absence of laterodorsal tubes on segment 2, subdorsal tubes on segment 6, midlateral sensory spots on segment 7, and midlateral and ventromedial tubes on segment 8, and in presence of laterodorsal sensory spots on segment 2, midlateral tubes on segment 7, and ventromedial sensory spots on segment 8 (Fig. 3D, and I–K). Only one out of eleven specimens from

Castellammare shows midlateral sensory spots instead of tubes on segment 7.

3.1.6 Discussion: *E. capitatus*

3.1.6.1. Comparison with the previous descriptions

Echinoderes capitatus was originally described based on the specimens from the Gulf of Trieste and the Bay of Naples by Zelinka in his monograph in 1928 (Zelinka, 1928). In the monograph, he described the species as having a body with segments 1 and 2 broadened and not tapered as in most *Echinoderes* as well as lacking any spine on its body (Zelinka, 1928). However, the latter feature might have been a misinterpretation of the author, likely deriving from the observation with a microscope of that time and the spines being relatively short and hidden by thick pachycycli. Subsequently, Nebelsick (1992b) redescribed the species based on the specimens from Gulf of Trieste (one of the type localities) and from off Rovinj, Istria (relatively close to the Gulf of Trieste), and reported additional characters including spines, tubes, sensory spots and gland cell outlets. The redescription was based on detailed observations, and was documented with high-quality photographs and illustrations. Hence, the information in Nebelsick (1992b) has been used for the identification of the species, and to distinguish it from congeners. Nebelsick (1992b) also stated that “The number, pattern of distribution, cellular arrangement, and fine structure of all cuticular structures of the trunk region…are species constant character-states in *Echinoderes capitatus*”.

Most characters of the specimens in the present study appeared in line with the description by Nebelsick (1992b) (Table 3). However, when the characters of each specimen were thoroughly examined, it appeared that the morphology was mostly congruent within a population, whereas slightly different among populations, and none of the newly-observed specimens were identical to the description in Nebelsick (1992b), inclusive those from the Gulf of Trieste. The differences among populations and the description in Nebelsick (1992b) are related to the position and presence/absence of tubes, sensory spots, and type-1 gland cell outlets (Table 3). Of these, the additional middorsal type-1 gland cell outlets on segments 4, 10, and 11 might have been overlooked or eventually irregularly present/absent in the specimens examined by Nebelsick (1992b); in fact, these gland cell outlets are often overlapped by the preceding segment and not easily observed or distinguished. The occurrence of tubes and sensory spots among populations is undoubtedly inconsistent, even between populations which are geographically very close to each other (e.g., those of Chioggia and Trieste, both in the northern Adriatic Sea). Although none of the newly-observed specimens are completely identical to the redescription in Nebelsick (1992b) and the specimens observed in Nebelsick (1992b) are not available for re-examination, we suppose specimens of the population in a part of the Gulf of Trieste and Rovinj show the morphological pattern described in Nebelsick (1992b).

3.1.6.2. Intraspecific variation or different species?

Notwithstanding the specimens with different pattern in tubes and sensory spots could represent different species, we regard such differences as intraspecific variations and put all specimens in a same species in this study. As mentioned in the previous chapter, the differences concerning tubes and sensory spots seem to characterize even geographically-neighboring populations, such as those from Trieste and Chioggia, and those collected in the Gulf of Trieste at different times. In addition, a low degree of variation was detected even within the same population (e.g., populations of Chioggia and of Castellammare del Golfo). Due to the complexity of the situation – inclusive the differences between the specimens from Trieste examined by Nebelsick (1992b) and those analyzed in the present study – and the availability only of morphological data so far, it is impossible to provide a clear threshold between species, except for either regarding all types of different tube/sensory spot patterns as characterizing different species (= 6 species in total, some of which very similar and sympatric) or considering all of them as the same species showing variation. Further analyses, inclusive of populations genetics, will hopefully shed light on the existence of a single species or of a potential *E. capitatus* species group. Until these investigations, we find premature to split the differing specimens and populations into just as many species. The risk of splitting the species at this stage would be an eventual necessity to reunify at least some new taxa in the future. Thus, in this study we regard all morphotypes as a polymorphism in *E. capitatus*.

3.1.6.3. Comparison with congeners

Although new morphological information as well as the inconsistent occurrence of some characters were detected, *E. capitatus* still possesses a unique spine/tube pattern among species of *Echinoderes*. The presence of acicular spines only middorsally on segment 4 and lateroventrally on segments 6–9 allow discrimination of the species from congeners, except for three species, *Echinoderes charlotteae* Sørensen et al., 2016 found in the Gulf of Mexico (Sørensen et al., 2016), *Echinoderes isabelae* G^{a}Ordóñez et al., 2008 reported from various Atlantic and Mediterranean Spanish locations (see Sánchez et al., 2012), and *Echinoderes reicherti* Neves et al., 2016, described from the southern coast of Portugal (Neves et al., 2016). Among these species, *E. charlotteae* and *E. reicherti* are easily distinguished from *E. capitatus* by the presence/absence of the type-2 gland cell outlets. *E. charlotteae* and *E. reicherti* have type-2 gland cell outlets on segment 2, whereas *E. capitatus* completely lacks these characters (Neves et al., 2016; Sørensen et al., 2016). The presence of numerous tubes in *E. capitatus* also helps to discriminate it from these two species. The fusiform-shaped trunk of *E. charlotteae* and *E. reicherti* is different from the trunk shape of *E. capitatus* appearing as a stick-like and anteriorly-plump body (Neves et al., 2016; Sørensen et al., 2016).

Echinoderes capitatus shows closest resemblance with *E. isabelae* in the spine and tube pattern. The two species share the presence of more than three pairs of tubes on segment

2, lateral accessory/lateroventral tubes on segment 5, subdorsal and lateral accessory tubes on segment 8 (GªOrdóñez et al., 2008). They are also similar in the presence of large, oval sensory spots, and the absence of lateral terminal accessory spines, which are otherwise usually present in females of most echinoderid species (GªOrdóñez et al., 2008). In addition, both species have a trunk with almost uniform sternal width on segments 1–10, appearing as a stick-like or an anteriorly-plump body (GªOrdóñez et al., 2008; see also Figs 2, 3A, 4A, and Table 2). GªOrdóñez et al. (2008) considered the presence of subdorsal tubes on segment 6 and 7 and ventromedial tubes on segment 8 in *E. capitatus* as differential characters to discriminate it from *E. isabelae*. Due to their inconsistent occurrence in *E. capitatus* we highlight that these features may be ambiguous for distinguishing the two species. Based on our investigation, the two species can still be distinguished by the following characters: the laterodorsal tubes on segment 10 (present in *E. capitatus*, absent in *E. isabelae*) and sensory spots positions. Especially for the sensory spots, those in the subdorsal positions (present on segments 1 and 3–11 in *E. capitatus* whereas limited only to segments 3–6 and 9 in *E. isabelae*) and those in the ventromedial positions (present on segments 2 and 5–7 or 8 in *E. capitatus* whereas present on segments 3–9 in *E. isabelae*) are the easiest characters to be detected and used to distinguish the two species (GªOrdóñez et al., 2008; Table 3).

Based on the affinities between *E. capitatus* and *E. isabelae*, as well as the inconsistency of the tube pattern in *E. capitatus*, and also considered the presence of *E.*

isabelae in the Mediterranean Sea (off Gerona; Sánchez et al., 2012), we can't exclude the existence of a single species, including specimens currently recognized as "*E. capitatus*" and "*E. isabelae*", with a high degree of variation. In this case, the above mentioned differences would be regarded as intraspecific variations. However, we do not have enough elements to support this hypothesis at the present stage and prefer not to speculate further, fostering the continuation of the analyses to this respect.

3.1.6.4. Intraspecific variation in the occurrence of spines and tubes

The position and patterns of spines and tubes in adult kinorhynchs is usually well preserved and consistent within a species, therefore traditionally used for species discrimination. Main exceptions are the sexual dimorphic spines/tubes, i.e., lateral terminal accessory spines and penile spines, as well as the different length of laterodorsal tubes on segment 10 in Echinoderidae (e.g., Neuhaus and Blasche, 2006; Herranz et al., 2012; Grzelak and Sørensen, 2018; Sørensen et al., 2018; Yamasaki et al., 2018a, b); middorsal and subdorsal/laterodorsal spines on segment 10 in kentrorhagid and campyloderid species (e.g., Neuhaus and Sørensen, 2013; Herranz et al., 2014; Yamasaki, 2016; Neuhaus, 2017; Sørensen and Landers, 2018); and ventromedial tubes on segment 2 and penile spines in pycnophyid species (e.g., Sánchez et al., 2016, 2018; Sørensen and Grzelak, 2018). More recently, intraspecific variation of middorsal and midlateral spines on segment 10 was documented also between different adult stages of *Centroderes* and *Condyloderes* (Neuhaus et al., 2014; Sørensen et al., this issue).

However, variation in spine/tube pattern not related to the sexual and/or developmental dimorphism was observed in species of *Campyloderes*, *Centroderes*, and *Condyloderes* (Neuhaus and Sørensen, 2013; Neuhaus et al., 2013, 2014, 2019; Dal Zotto et al., this issue). The major variation occurring in species of *Condyloderes* regards cuspidate spines (Neuhaus et al., 2019; Dal Zotto et al., this issue), which are hypothetical homologous to the tubules in *Franciscideres kalenesos* Dal Zotto et al., 2013 (e. g., Dal Zotto et al., 2013) and possibly to the tubes in species of Echinoderidae, too.

Other variation not deriving from sexual and/or developmental dimorphism was also recently reported from some echinoderid species: *Echinoderes dubiosus* Sørensen et al., 2018 with the tubes on segment 8 switching between midlateral and lateral accessory positions; *Echinoderes daenerysae* Grzelak and Sørensen, 2017 in Grzelak and Sørensen (2018): ventrolateral tubes on segment 2 present/absent; *Echinoderes rhaegali* Grzelak and Sørensen, 2017 in Grzelak and Sørensen (2018): sublateral tubes on segment 2 present/absent; *Echinoderes eximus* Higgins and Kristensen, 1988: sublateral tubes on segment 9 present/absent; *Echinoderes levanderi* Karling, 1954: subdorsal tubes on segment 2 present/absent; and *Fissuroderes higginsi* Neuhaus, 2006 in Neuhaus and Blasche (2006): dorsal tubes on segment 2 switching between laterodorsal and subdorsal positions (Grzelak and Sørensen, 2018; Sørensen, 2018; Sørensen et al., 2018). Although our knowledge about intraspecific variation of spine/tube patterns has increased recently, the taxonomic studies on different populations of a single species are rare (e. g., Yamasaki et al., 2018a), and the relationship between such variation on species and population level is still unclear.

Echinoderes capitatus seems to be the first example of a species with a tube-pattern showing a relatively high degree of intraspecific variation between populations and a few variations within the same population. Considering the variation between geographically close populations (e.g., Chioggia versus Trieste), and the limited number of populations investigated so far, there may still be undiscovered populations with different tube-patterns. Further investigations in gap areas in Tyrrhenian Sea, Adriatic Sea, and the adjacent seas are required for a wider understanding of the intraspecific variation-patterns in *E. capitatus*.

If the existence of a single species with variation will be confirmed, it is likely that the differences between populations of *E. capitatus* could be related to adaptations to the local environments, and exhibit an ongoing speciation process. Alternatively, the presence or absence of tubes could be poorly or not affected by selection pressure, allowing *E. capitatus* to possess high variation in the tube pattern. Irrespective of these hypotheses, *E. capitatus* or, eventually, *E. capitatus* species group, could be a good model for studying the mechanisms at the basis of morphological diversity in meiofaunal organisms. However, we have currently no idea of the factors affecting the number and position of tubes, of the function of different tube patterns, and whether and/or to what extent populations with different tube-patterns are genetically differentiated. Functional morphological and ecological studies aimed at detecting the correlation between tube patterns and environmental factors, as well as population genetic studies will help determine its potential influence on polymorphism.

3.2. *Echinoderes ferrugineus* Zelinka, 1928 (Figs 6–9 and Tables 4 and 5)

3.2.1. Synonymy

Echinoderes ferrugineus: Zelinka (1928); Remane (1954); Dal Zotto and Todaro (2016); Dal Zotto et al. (2016)

3.2.2. Emended diagnosis

Echinoderes with middorsal acicular spines on segments 4–8 and lateroventral acicular spines on segments 6–9; lateral accessory tubes on segment 5; type-2 gland cell outlets in subdorsal, laterodorsal, sublateral, and ventrolateral position on segment 2, subdorsal and midlateral position on segment 4, midlateral position on segment 5, and midlateral position on segment 8; lateral terminal spines elongated (ca. 140–180 µm, 45–63% of trunk length).

3.2.3. Material examined

Non-type: one female (ZMB XXXXXX), collected from off Trieste, northern Adriatic Sea (coordinates unknown), mounted in unknown mounting medium on a Cobb aluminum frame; two males and two females (ZMB XXXXXX), collecting data as above mentioned specimen, mounted in unknown mounting medium on glass slide; two males and three females (ZMB XXXXXX), collected from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea, mounted as glycerol-paraffin slide on a Cobb aluminum frame; two males and two females (ZMB XXXXXX), collected from off Chioggia, northern Adriatic Sea, mounted as glycerol-paraffin slide on a Cobb aluminum frame; three males and one female collected from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea and one female from off Chioggia, northern Adriatic Sea on an aluminum stub for SEM observation.

3.2.4. Description

Adult with head, neck, and eleven trunk segments (Figs 6A, B, 7A, 8A, and B). See Table 4 for measurements. Table 5 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Head consisting of retractable mouth cone and introvert (Figs 7B and 9). Mouth cone with nine outer oral styles, each consisting of rectangular basal part and triangular distal part (Fig. 7B). Basal part slightly alternating in length between five larger parts in odd sectors and four smaller ones in even sectors (Figs 7B and 9). Inner oral styles and ornaments of outer oral styles not observed. Introvert composed of one ring of primary scalids, five rings of spinoscalids, and one ring of trichoscalids (Figs 7B and 9). Arrangement of spinoscalids in each ring summarized in Fig. 9. Each primary spinoscalid consists of basal sheath and distal end piece. Basal sheath comprises of layer of proximal fringes. End piece long with smooth surface and spinose distal tip (Fig. 7B). Each spinoscalid of rings 02–05 composed of basal sheath with fringed edge and distal long-spinose end piece (Fig. 7B). Spinoscalids in rings 02 and 03 longer than those in rings 04–06. Trichoscalids arising from trichoscalid plates (Fig. 7B). Each trichoscalid covered with relatively short hairs.

Neck with 16 placids (Figs 6A, B, 7B, and 9). Midventral placid broadest. Remaining placids similar in size. Two trichoscalid plates present ventrally and four dorsally, each associated with ventromedial, subdorsal, and laterodorsal placid, respectively (Fig. 6A and B).

Segment 1 consisting of complete cuticular ring (Fig. 6A and B). Sensory spots located in subdorsal, laterodorsal, and ventromedial position: each sensory spot with short micropapillae surrounding single pore with single cilium (Figs 6A, B, 7C, and 8C). Type-1 gland cell outlets present in middorsal and lateral accessory position (Figs 6A, B, and 8C). Non-bracteate cuticular hairs arising from perforation sites cover whole segment except for anterior half of ventral side (Figs 6A, B, and 7C). Posterior part of this and following ten segments with primary pectinate fringe (Figs 6A, B, 7C, D, 8C, and D). Pectinate fringe teeth of primary pectinate fringe longer in midlateral to midventral areas than those in middorsal to laterodorsal areas (Figs 6A, B, and 7C).

Segment 2 with complete cuticular ring as segment 1 (Fig. 6A and B). This and following eight segments with thick pachycyclus at anterior margin of each segment. Two pairs of sensory spots present in laterodorsal position (Figs 6B, 7C, D, and 8D). Additional sensory spots present in middorsal and ventromedial position (Figs 6A, B, and 7C). Sensory spots of this and following eight segments with short micropapillae surrounding single pore and single long micropapilla (Fig. 7D). Type-1 gland cell outlets present in middorsal and ventromedial position (Fig. 6A and B). Type-2 gland cell outlets in subdorsal, laterodorsal, sublateral, and ventrolateral position (Figs 6A, B, 7C, D, and 8A–D). Bracteate cuticular hairs cover posterior three quarters of segment (Figs 6A, B, and 7C). Primary pectinate fringe as on segment 1. Single row of secondary pectinate fringe on anterior part of this and following eight segments often covered by preceding segment (Fig. 7C).

Segment 3 and following eight segments consisting of one tergal and two sternal plates (Figs 6A, B, 8A, and B). Sensory spots present in subdorsal and midlateral position (Figs 6A, B, 7C, 8C, D). Type-1 gland cell outlets situated in middorsal and ventromedial position (Fig. 6A and B). Cuticular hairs of this and following seven segments as those on segment 2, except for being absent in ventromedial area. Primary pectinate fringe of this and following six segments with long pectinate fringe teeth.

Segment 4 with middorsal acicular spine (Figs 6B, 7C, 8B, D, and E). No sensory spots present. Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 6A and B). Type-2 gland cell outlets present subdorsally and midlaterally (Figs 6A, B, 7C, 8A, and C–E).

Segment 5 with middorsal acicular spine and lateral accessory tubes (Figs 6A, B, 7E, F, 8B, C, and E). Sensory spots present in subdorsal and ventromedial position (Figs 6A, B, 7C, E, and 8C–E). Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 6A and B). Type-2 gland cell outlets located in midlateral position (Figs 6A, B, 7C, and F).

Segment 6 with middorsal and lateroventral acicular spines (Figs 6A, B, 7E–G, 8A, B, E, and F). Sensory spots present in paradorsal, subdorsal, midlateral, and ventromedial position (Figs 6A, B, 7E–G, 8B, E, and F). Type-1 gland cell outlets present paradorsally and ventromedially (Figs 6A, B, and 8E).

Segment 7 with middorsal and lateroventral acicular spines (Figs 6A, B, 7E, G, H, 8A, B, E, and F). Sensory spots present in paradorsal, midlateral, and ventromedial position (Figs 6A, B, 7E–H, 8B, E, and F). Type-1 gland cell outlets present paradorsally and ventromedially (Figs 6A, B, and 8E).

Segment 8 with middorsal and lateroventral acicular spines (Figs 6A, B, 7H–J, 8A, B, E, and F). Sensory spots present in paradorsal position (Figs 6B, 7I, and 8B, and E). Type-1 gland cell outlets present in paradorsal and ventromedial position (Figs 6A, B, and 8E). Type-2 gland cell outlets present in midlateral position (Figs 6A, B, 7G, I, and J).

Segment 9 with lateroventral acicular spines (Figs 6A, 7H, 8A, F, and G). Paradorsal, subdorsal, midlateral, and ventrolateral sensory spots present (Figs 6A, B, 7H–K, 8A, and F). Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 6A and B). Small sieve plates present in sublateral position (Figs 6A, B, and 7J).

Segment 10 with subdorsal and ventrolateral sensory spots (Figs 6, 7K, and 8G). Two type-1 gland cell outlets aligned middorsally (Fig. 6B and C). Additional pair of type-1 gland cell outlets present in ventromedial position (Figs 6A, D, and 8H). Pectinate fringe teeth of primary pectinate fringe shorter than those on preceding segments (Figs 6 and 7K).

Segment 11 with lateral terminal spines (Figs 6, 7A, K–M, 8A, G, and H). Lateral terminal accessory spines present in female (Figs 6C, D, and 8H). Three pairs of penile spines present in males, with two pairs being long, tube-like and one pair thick and cone-like (Figs 6A, B, 7K–M, 8A, and G). Paradorsal sensory spots present (Figs 6B, C, 7K, and L). Posterior edge of tergal plate pointed and protruded subdorsally, forming tergal extensions. Primary pectinate fringe present on areas without tergal extensions on tergal plate, and on ventromedial area on sternal plate.

3.2.5. Discussion: *E. ferrugineus*

3.2.5.1. Comparison with the original description

According to the original description, the species has a relatively small trunk (210–220 μm); adhesive tubes on segment 2, lateral spines on segments 5 to 10 (with shortest spines on segment 6); middorsal spines on segments 4–8, with the spines on segment 8 reaching segment 10; lateral terminal spines, and terminal accessory spines in females (Zelinka, 1928). Of these characters, the adhesive tubes on segment 2 would not be tubes but probably type-2 gland cell outlets because the structures were not illustrated as tube-like but as circular markings in the original illustration. The lateral spines on segment 5 would be tubes considering their thinness. Furthermore, the lateral spines on segment 10 would probably be a misinterpretation of a pair of penile spines. The pigment rings, which were probably type-1 gland cell outlets, were not mentioned in the main text but illustrated middorsally on segments 1–3, 10, and possibly 11, paradorsally on segments 4–9, lateral accessorily or lateroventrally on segment 1, ventrolaterally on segment 2, ventrolaterally or ventromedially on segment 3, and ventromedially on segments 4–10 and possibly 11 (Zelinka, 1928).

Even though the specimens in the present study showed some differences from the original description, they are identified as *E. ferrugineus* based on the fact that one of the investigated localities was relatively close to one of the type localities of the species (the Gulf of Trieste); the presence of middorsal spines on segments 4–8; middorsal spine on segment 8 being the longest and reaching segment 10; lateral accessory tubes on segment 5; lateroventral spines on segments 6–9; type-2 gland cell outlets in ventrolateral position on segment 2; and type-1 gland cell outlets following the pattern of the pigment rings described by Zelinka (1928). The morphometrics of most of spines and tubes overlap those of the original description, with a few exceptions. Remarkable differences between the original description and the specimens examined during our study are: the length of the trunk (210–220 μm in the original description compared to 260–324 μm in this study), the length of the middorsal spines on segments 6 and 7 (25 μm and 27 μm, respectively, in the original one, versus 40–49 μm and 45–56 μm, respectively, in this study); the length of the lateral terminal accessory spines (23 μm in the original one, versus 80–100 μm in this study; we speculate that Zelinka's measurements might be based on penile spines); the presence of the additional type-2 gland cell outlets in subdorsal position on segments 2 and 4, laterodorsal position on segment 2, midlateral position on segments 4, 5, and 6, and sublateral position on segment 2 in this study (absent/not mentioned in the original description); ventral type-1 gland cell outlets on segment 2 and 3 being more laterally placed in the original description than those in this study; and the ventromedial type-1 gland cell outlets on segment 1 (present in the original description whereas absent in this study). Because the specimens described by Zelinka (1928) no longer exist, and none of the other available specimens obtained from the Italian and neighboring waters are similar to the original description of *E. ferrugineus*, we regard the specimens in the current study as *E. ferrugineus* and propose the emended diagnosis of the species based on the new specimens.

3.2.5.2. Comparison with congeners

Echinoderes ferrugineus shares the spine and tube pattern with 14 congeners. However, it can be distinguished from all congeners by the distribution of type-2 gland cell outlets on segments 4, 5, and 8, which in combination is unique. Especially the presence of the two pairs of type-2 gland cell outlets (in subdorsal and midlateral position) on segment 4 in *E. ferrugineus* is unique among these species, thus the most important differential character for the species.

Due to the lack of information on type-2 gland cell outlets in *Echinoderes brevicaudatus* Higgins, 1977, *Echinoderes remanei* (Blake, 1930), and *Echinoderes stockmani* Adrianov, 1999 in Adrianov and Malakhov, 1999, *E. ferrugineus* cannot be differentiated from them based on the type-2 gland cell outlets. Nonetheless, *E. ferrugineus* can be distinguished from *E. brevicaudatus* by having much longer lateral terminal spines (143–181 µm and 45.6–62.3% of trunk length in *E. ferrugineus*, versus 57 µm and 17% of trunk length in *E. brevicaudatus*) and a longer middorsal spine on segment 8 (57–72 µm in *E. ferrugineus*, versus 18 µm as a maximum length of *E. brevicaudatus*) (Higgins, 1966, 1977).

Echinoderes ferrugineus can be distinguished from *E. remanei* by the shape of its primary pectinate fringe on ventral side of segment 1. The pectinate fringe teeth of this segment are similar in width to those of the other segments in *E. ferrugineus*, whereas they are much wider in *E. remanei* (Higgins, 1964). In addition, *E. ferrugineus* differs from *E. remanei* in having shorter lateroventral acicular spines (15–24 µm in *E. ferrugineus*, versus 35–47 µm in *E. remanei*) and longer lateral terminal spines (143–181 µm, 45–63% of trunk length in *E. ferrugineus*, versus 80–110 µm, 24–31% of trunk length in *E. remanei*).

Echinoderes ferrugineus differs from *E. stockmani* by its small trunk size (260–324 µm in *E. ferrugineus*, versus 493 µm in *E. stockmani*) and in the length of the lateral terminal spines (143–181 µm and 45.6–62.3% of trunk length in *E. ferrugineus*, versus 410 µm and 83% of trunk length in *E. stockmani*) (Adrianov and Malakhov, 1999).

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Figure captions

Fig. 1. Map of middle Mediterranean Sea, showing the localities where *Echinoderes capitatus* and *Echinoderes ferrugineus* were reported. The abbreviations of c and f, and asterisks in parentheses indicate the records of *E. capitatus*, that of *E. ferrugineus*, and the original type locality for the species, respectively. Black circles indicate the stations where the specimens examined in this study were collected.

Fig. 2. *Echinoderes capitatus*, camera lucida drawings. A, B, female from the Gulf of Trieste (ZMB XXXXXX), whole animal, dorsal and ventral views, respectively; C, D, male from the Gulf of Trieste (ZMB XXXXXX), segments 9–11, dorsal and ventral views, respectively. Note that the ventrolateral tube on right side on segment 2 is irregularly absent in ZMB XXXXXX, but illustrated with dotted line in B as referencing that in other specimens. Abbreviations: gco1, type-1 gland cell outlet; lat, lateral accessory tube; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; mlt, midlateral tube; pe, penile spine; sdt, subdorsal tube; si, sieve plate; ss, sensory spot; vlt, ventrolateral tube; vmt, ventromedial tube.

Fig. 3. *Echinoderes capitatus* from Castellammare del Golfo, Sicily, scanning electron photomicrographs. A, female, whole body, lateral view (right side); B, close up of the mouth

cone, lateroventral view (right side); C, close up of the introvert, lateral view (right side); D, segments 1–3, lateral view (left side); E, segments 1–4, ventral view; F, segments 1–3, dorsal view; G, segments 3 and 4, dorsal view; H, segments 5–8, ventral view; I, segments 5 and 6, lateral view (left side); J, segments 6–8, dorsal view; K, segments 7–9, lateral view (left side); L, segments 9–11 of male, ventral view; M, segments 10 and 11 of female, lateral view (right side). Black arrows indicate sensory spots. Abbreviations: he, head; lat, lateral accessory tube; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; mlt, midlateral tube; oos, outer oral style; pe, penile spine; pss, primary spinoscalid; sdt, subdorsal tube; sec, sector number; seg, segment number; sp, spinoscalid with ring number; tr, trichoscalid; vlt, ventrolateral tube.

Fig. 4. *Echinoderes capitatus*, female from the Gulf of Trieste (ZMB XXXXXX), Nomarski photomicrographs. A, neck and segments 1–11, dorsal view; B, neck and segments 1–3, dorsal view; C, neck and segments 1 and 3, ventral view; D, segments 4–6, ventral view; E, segments 7 and 8, ventral view; F, segments 8 and 9, dorsal view; G, segments 9–11, ventral view. Black arrows and white arrowheads indicate sensory spots and type-1 gland cell outlets, respectively. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; mdp, middorsal placid; mds, middorsal acicular spine; mlt, midlateral tube; mvp, midventral placid; sdt, subdorsal tube; seg, segment

number; trp, trichoscalid plate; vlt, ventrolateral tube; vmt, ventromedial tube.

Fig. 5. Diagram of mouth cone, introvert, and placids in *Echinoderes capitatus*. Grey shaded area shows mouth cone and bold bent bars symbolize placids. The table lists the scalid arrangement by sector.

Fig. 6. *Echinoderes ferrugineus*, camera lucida drawings. A, B, male from Castellammare del Golfo, Sicily (ZMB XXXXXX), whole animal, ventral and dorsal views, respectively; C, D, female from Castellammare del Golfo, Sicily (ZMB XXXXXX), segments 10 and 11, dorsal and ventral views, respectively. Abbreviations: gco1, type-1 gland cell outlet; gco2, type-2 gland cell outlet; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mdp, middorsal placid; mds, middorsal acicular spine; mvp, midventral placid; pe, penile spine; si, sieve plate; ss, sensory spot.

Fig. 7. *Echinoderes ferrugineus* from Castellammare del Golfo, Sicily, scanning electron photomicrographs. A, male, whole body, lateral view (left side); B, head and neck, lateral view (left side); C, segments 1–5, laterodorsal view (left side); D, close-up of laterodorsal type-2 gland cell outlet and sensory spots; E, segments 5–7, ventral view; F, segments 5–7, laterodorsal view (left side); G, segments 6–8, laterodorsal view (left side); H, segments 7–9,

ventral view; I, segments 8 and 9, lateral view (left side); J, close-up of midlateral to lateroventral areas on segments 8 and 9; K, segments 9–11, laterodorsal view (left side); L, close-up of segment 11, dorsal view; M, close-up of penile spine on segment 11, lateral view (left side). Black arrows and black arrowheads indicate sensory spots and type-2 gland cell outlets, respectively. Abbreviations: lat, lateral accessory tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; oos, outer oral style; pe, penile spine; pl, placid; pss, primary spinoscalid; sec, sector number; seg, segment number; si, sieve plate; sp, spinoscalid with ring number; tr, trichoscalid.

Fig. 8. *Echinoderes ferrugineus*, from Castellammare del Golfo, Sicily, Nomarski photomicrographs. A–G, male (ZMB XXXXXX); H, female (ZMB XXXXXX). A, neck and segments 1–11, ventral view; B, neck and segments 1–11, dorsal view; C, segments 1–5, ventral view; D, segments 1–5, dorsal view; E, segments 4–8, dorsal view; F, segments 6–9, ventral view; G, segments 10 and 11, ventral view; H, segments 10 and 11, ventral view. Black arrows, white arrowhead, and black arrowheads indicate sensory spots, type-1 gland cell outlet, and type-2 gland cell outlets, respectively. Abbreviations: lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pe, penile spine; ppf, primary pectinate fringe; seg, segment number.

Fig. 9. Diagram of mouth cone, introvert, and placids in *Echinoderes ferrugineus*. Grey shaded area shows mouth cone and bold bent bars symbolize placids. The table lists the scalid arrangement by sector.

Table 1

Table 1. Records of *E. capitatus* and *E. ferrugineus* and information on sampling stations of the material examined in this study. Asterisks on locality name indicate type locality for each species. Bold font indicates the stations of the material examined in this study.

Region	Locality		reference or sampling date in this study	Depth (m)	Latitude	Longitude	Sediment type	Species	Remarks
Adriatic Sea, Mediterranean Sea	Gulf of Trieste	Barcola*	Zelinka (1928)	19–22	n.a.	n.a.	n.a.	*E. capitatus*	
		Servola*	Zelinka (1928)	18	n.a.	n.a.	n.a.	*E. capitatus*	
		S. Bartolomeo*	Zelinka (1928)	12–22	n.a.	n.a.	n.a.	*E. capitatus*	
		Bay of Capodistria*	Zelinka (1928)	21–23	n.a.	n.a.	n.a.	*E. capitatus*	
		Bay of Pirano*	Zelinka (1928)	18	n.a.	n.a.	n.a.	*E. capitatus*	
		Portorož*	Zelinka (1928)	ca. 3	n.a.	n.a.	algae with yellow mud	*E. ferrugineus*	
		Aurisina	Nebelsick (1992a, 1992b, 1993)	Subtidal	n.a.	n.a.	Muddy sands	*E. capitatus*	
		Trieste	**This study (12.05.1987)**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	***E. capitatus*** **;** ***E . ferrugineus***	**Specimens donated by Dr Monika Bright to Dr Birger Neuhaus**
	Rovinj	Istria	Nebelsick (1992a, 1992b, 1993)	Subtidal	n.a.	n.a.	Muddy sands	*E. capitatus*	
	Chioggia		Dal Zotto and Todaro (2016)	20–29	45°05'44"N	12°35'49"E	Coarse silt	*E. capitatus* ; *E . ferrugineus*	
			This study (01.06.2006)	**29**	**45°05'42"N**	**12°35'43"E**	**Pelitic sand (fine/very fine sand: 74.08%, silt: 13.81%, clay: 12.11%)**	***E. capitatus*** **;** ***E . ferrugineus***	**Specimens stained in rose Bengal**
			This study (01.10.2008)	**29**	**45°05'24"N**	**12°34'49"E**	**Fine sand with mud (fine/very fine sand: 81.24%, silt: 12.30%, clay: 6.47%)**	***E. capitatus*** **;** ***E . ferrugineus***	
			This study (01.07.2015)	**28**	**45°05'18"N**	**12°34'33"E**	**Fine sand with mud (sand: 82.20%, silt: 12.23%, clay: 5.56%)**	***E. capitatus*** **;** ***E . ferrugineus***	
Tyrrhenian Sea, Mediterranean Sea	Bay of Naples	Posillipo*	Zelinka (1928)	35	n.a.	n.a.	n.a.	*E. capitatus* ; *E . ferrugineus*	
		Santa Lucia *	Zelinka (1928)	1	n.a.	n.a.	algae	*E. ferrugineus*	
		Nisida *	Zelinka (1928)	1–2	n.a.	n.a.	algae	*E. ferrugineus*	
	Sicily	Castellammare del Golfo	Dal Zotto and Todaro (2016); Dal Zotto et al., 2016	35–50	38°02'35"N	12°52'58"E	Fine sand-coarse silt	*E. capitatus* ; *E . ferrugineus*	
			This study (01.06.2007)	**43**	**38°02'58"N**	**12°52'58"E**	**Silt to very fine sand (coarse sand: 0.69%, medium sand: 0.65%, fine sand: 4.05%, very fine sand: 24.14%, silt-clay: 70.45%)**	***E. capitatus*** **;** ***E . ferrugineus***	**Specimens stained in rose Bengal**
		Trappeto	Dal Zotto and Todaro (2016)	30–40	38°04'31"N	13°01'12"E	Fine sand-coarse silt	*E. capitatus* ; *E . ferrugineus*	
Ligurian Sea, Mediterranean Sea	Leghorn		Dal Zotto and Todaro (2016)	97–130	43°37'35"N	9°59'32"E	Fine sand-coarse silt	*E. capitatus*	
Baltic Sea	Bay of Kiel		Remane (1954)	n.a.	n.a.	n.a.	coarse gravelly sand with detritus	*E. ferrugineus*	

Table 2. Measurements for adult *Echinoderes capitatus* (in micrometers). Columns N and SD indicate sample size and standard deviation, respectively. Abbreviations: (ac), acicular spine; (f), female condition of sexually dimorphic character; la, lateral accessory tube; ld, laterodorsal tube; lts, lateral terminal spine; lv, lateroventral spine; (m), male condition of sexually dimorphic character; md, middorsal spine; ml, midlateral tube; msw, maximum sternal width; s, segment; sd, subdorsal tube; sw, standard width; tl, trunk length; (tu), tube; vl, ventrolateral tube; vm, ventromedial tube.

Character	N	Range	Mean	SD
tl	16	262–353	307	27.42
msw-7	14	45–55	48	2.90
msw-7/tl	14	13.5–19.3%	15.5%	1.71%
sw-10	15	40-47	43	1.60
sw-10/tl	14	11.7–16.1%	14.0%	1.20%
s1	14	32–40	35	2.19
s2	14	19–27	23	2.49
s3	14	24–30	27	1.52
s4	14	27–32	29	1.52
s5	14	28–33	31	1.47
s6	14	31–40	35	2.23
s7	14	35–41	38	1.79
s8	14	38–49	42	2.39
s9	14	30–45	41	3.66
s10	14	29–39	36	2.84
s11	14	20–35	27	4.03
md4 (ac)	14	11–18	13	2.17
sd2 (tu)	15	11–17	13	1.90
ld2 (tu)	12	9–15	12	2.10
ml2 (tu)	13	10–18	14	1.99
vl2 (tu)	16	10–16	14	1.61
la5 (tu)	14	8–15	11	2.12
sd6 (ac)	2	11–12	11	0.33
lv6 (ac)	16	8–13	11	1.21
ml7 (tu)	3	13–18	15	2.55
lv7 (ac)	16	10–13	12	1.28
sd8 (tu)	14	10–16	13	1.52
ml8 (tu)	3	12–16	14	2.12
la8 (tu)	13	9–15	11	1.82
lv8 (ac)	17	9–14	12	1.43
vm8 (tu)	1	9	n.a.	n.a.
lv9 (ac)	17	10–17	13	1.66
ld10 (tu)	13	6–13	8	2.45
ld10 (tu) (m)	8	6–13	9	2.60
ld10 (tu) (f)	5	6–8	6	0.96
lts	15	75–100	88	8.02
lts/tl	14	25.3–35.1%	29.0%	3.35%

Table 3

Table 3. Summary of position of cuticular structures and spines in *Echinoderes capitatus* . Underlined characters show variational occurrence. Abbreviations: ac, acicular spine; (Ca), specimens from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea; (Ch), specimens from off Chioggia, northern Adriatic Sea; gco1, type-1 gland cell outlet; la, lateral accessory; ld, laterodorsal; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; (*Ne*), characters reported in Nebelsick (1992b), based on specimens from the Gulf of Trieste, northern Adriatic Sea; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; (Tr), specimens from off Trieste, northern Adriatic Sea; tu, tube; vl, ventrolateral; vm, ventromedial. One asterisk (*) means that sensory spots are replaced with tubes in one out of ten specimens from Chioggia, Adriatic Sea. Two asterisks (**) means that tubes are replaced with sensory spots in one out of eleven specimens from off Castellammare del Golfo, Sicily, southern Tyrrhenian Sea.

Position segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
1	gco1		ss	ss				gco1		ss
2	gco1, ss (Ca, Ch, Tr)		tu	tu (*Ne* , Ch, Tr), ss (Ca)	tu				tu	gco1, ss
3	gco1		ss		ss					gco1
4	ac, gco1 (*Ne*)	gco1	ss							gco1
5	gco1		ss		ss		tu			gco1, ss
6		gco1, ss	ss, tu (*Ne* , Tr)		ss			ac		gco1, ss
7	gco1		ss, tu (*Ne*)		ss (*Ne* , Ch*, Tr), tu (Ca**)			ac		gco1, ss
8		gco1, ss	ss, tu		tu (Tr)		tu	ac		gco1, tu (*Ne* , Tr), ss (Ca, Ch)
9		gco1, ss	ss		ss (Ca, Ch, Tr)	si		ac	ss	gco1
10	gco1, gco1 (Ca, Ch, Tr)		ss	tu					ss	gco1
11	gco1 (Ca, Ch, Tr)		ss				pe×3 (m)	lts		

Table 4

Table 4. Measurements for adult *Echinoderes ferrugineus* (in micrometers). Columns N and SD indicate sample size and standard deviation, respectively. Abbreviations: (ac), acicular spine; la, lateral accessory; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; msw, maximum sternal width; s, segment; sw, standard width; tl, trunk length; (tu), tube.

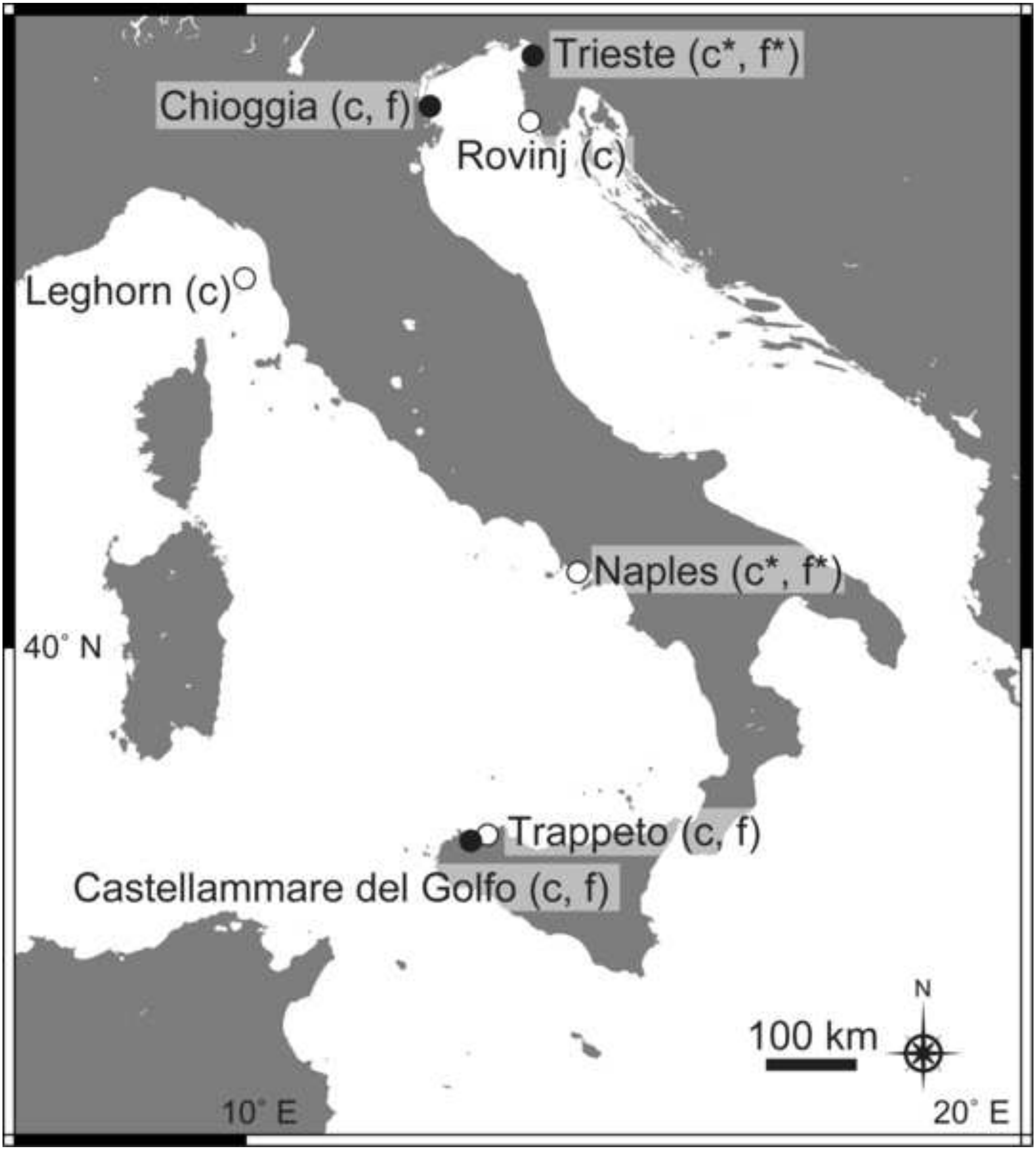
Character	N	Range	Mean	SD
tl	14	260–324	304	19.32
msw-6	10	47–56	52	2.55
msw-6/tl	10	16.2–18.9%	17.2%	0.87%
sw-10	11	37–45	42	2.54
sw-10/tl	11	12.6–15.3%	13.9%	0.89%
s1	11	29–37	32	2.12
s2	11	24–29	27	1.48
s3	11	22–26	25	1.28
s4	11	26–28	27	0.78
s5	11	27–31	29	0.96
s6	11	30–35	32	1.62
s7	11	32–37	35	1.66
s8	11	35–41	37	1.68
s9	11	35–40	37	1.78
s10	11	39–47	44	2.12
s11	11	24–33	29	2.41
md4 (ac)	12	22–36	28	3.41
md5 (ac)	11	29–47	37	4.86
md6 (ac)	11	40–49	45	2.79
md7 (ac)	10	45–56	51	3.36
md8 (ac)	10	57–72	64	4.43
la5 (tu)	13	10–16	13	2.11
lv6 (ac)	13	15–20	17	1.47
lv7 (ac)	14	17–21	19	1.19
lv8 (ac)	14	18–24	20	1.57
lv9 (ac)	14	16–22	19	1.54
lts	13	143–181	162	13.24
ltas	7	80–100	90	7.79
lts/tl	13	45.6–62.3%	53.1%	5.16%
ltas/tl	7	26.3–35.7%	29.1%	3.32%

Table 5

Table 5. Summary of locations of cuticular structures and spines in *Echinoderes ferrugineus* . Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 gland cell outlet; gco2, type-2 gland cell outlet; 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; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm,

Position segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
1	gco1		ss	ss			gco1			ss
2	gco1, ss		gco2	ss, gco2, ss		gco2			gco2	gco1, ss
3	gco1		ss		ss					gco1
4	ac	gco1	gco2		gco2					gco1
5	ac	gco1	ss		gco2		tu			gco1, ss
6	ac	gco1, ss	ss		ss			ac		gco1, ss
7	ac	gco1, ss			ss			ac		gco1, ss
8	ac	gco1, ss			gco2			ac		gco1
9		gco1, ss	ss		ss	si		ac	ss	gco1
10	gco1, gco1		ss						ss	gco1
11	gco1, gco1	ss					pe×3 (m), ltas (f)	lts		

Figure 1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Chioggia (c, f)
Rovinj (c)
Leghorn (c)
Naples (c*, f*)
40° N
Trappeto (c, f)
Castellammare del Golfo (c, f)
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100 km
10° E
20° E

Figure 2

Click here to download high resolution image

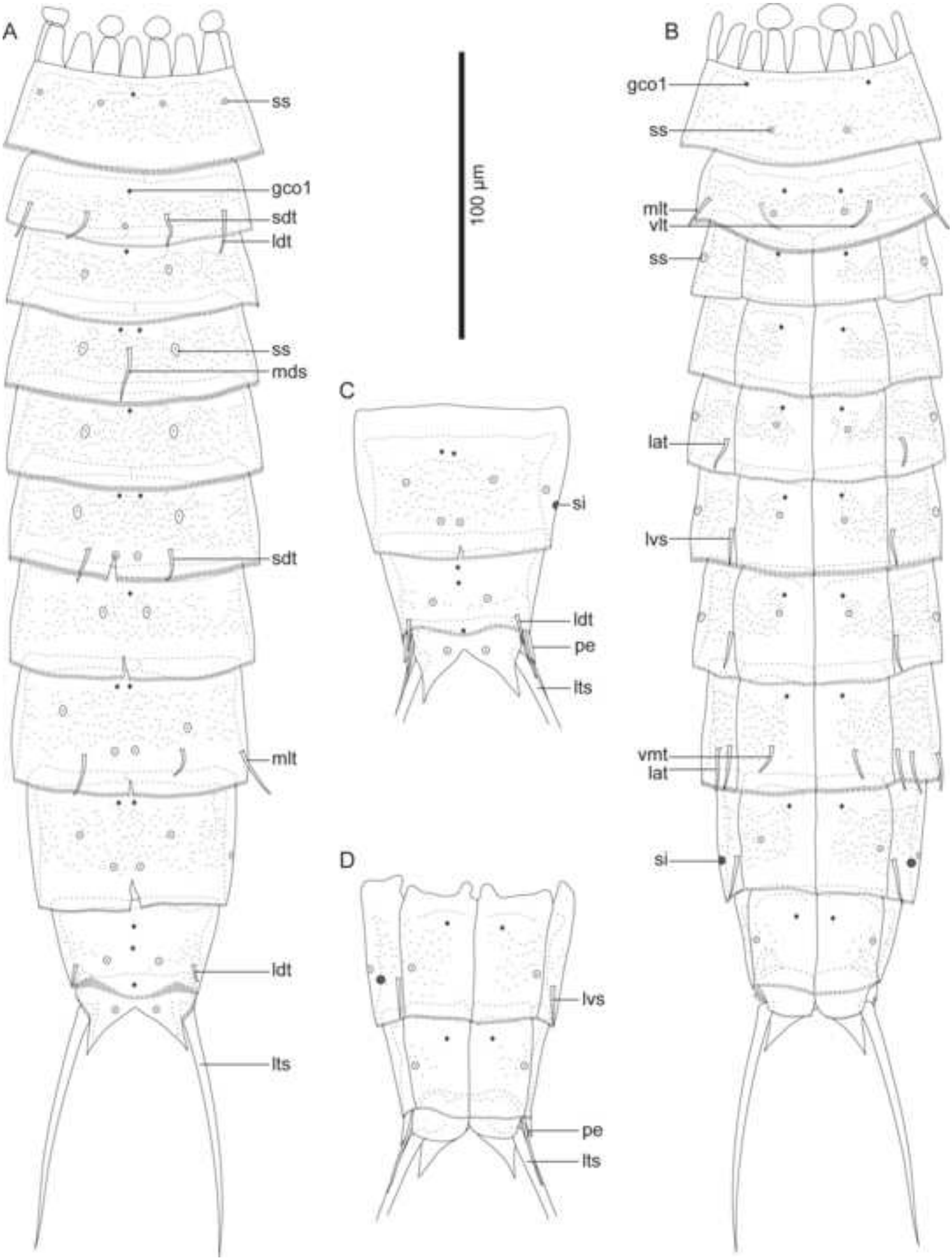

Figure 3

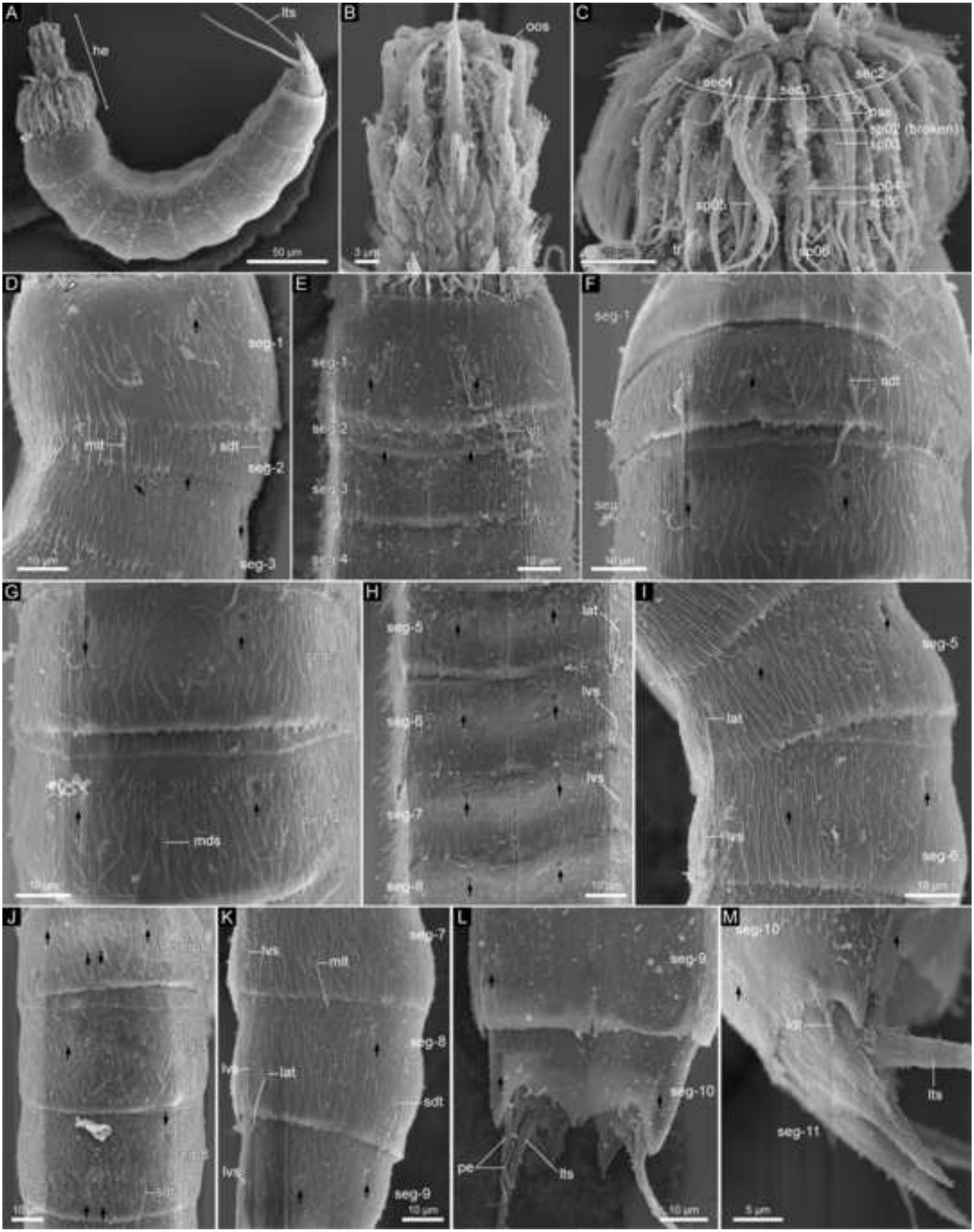
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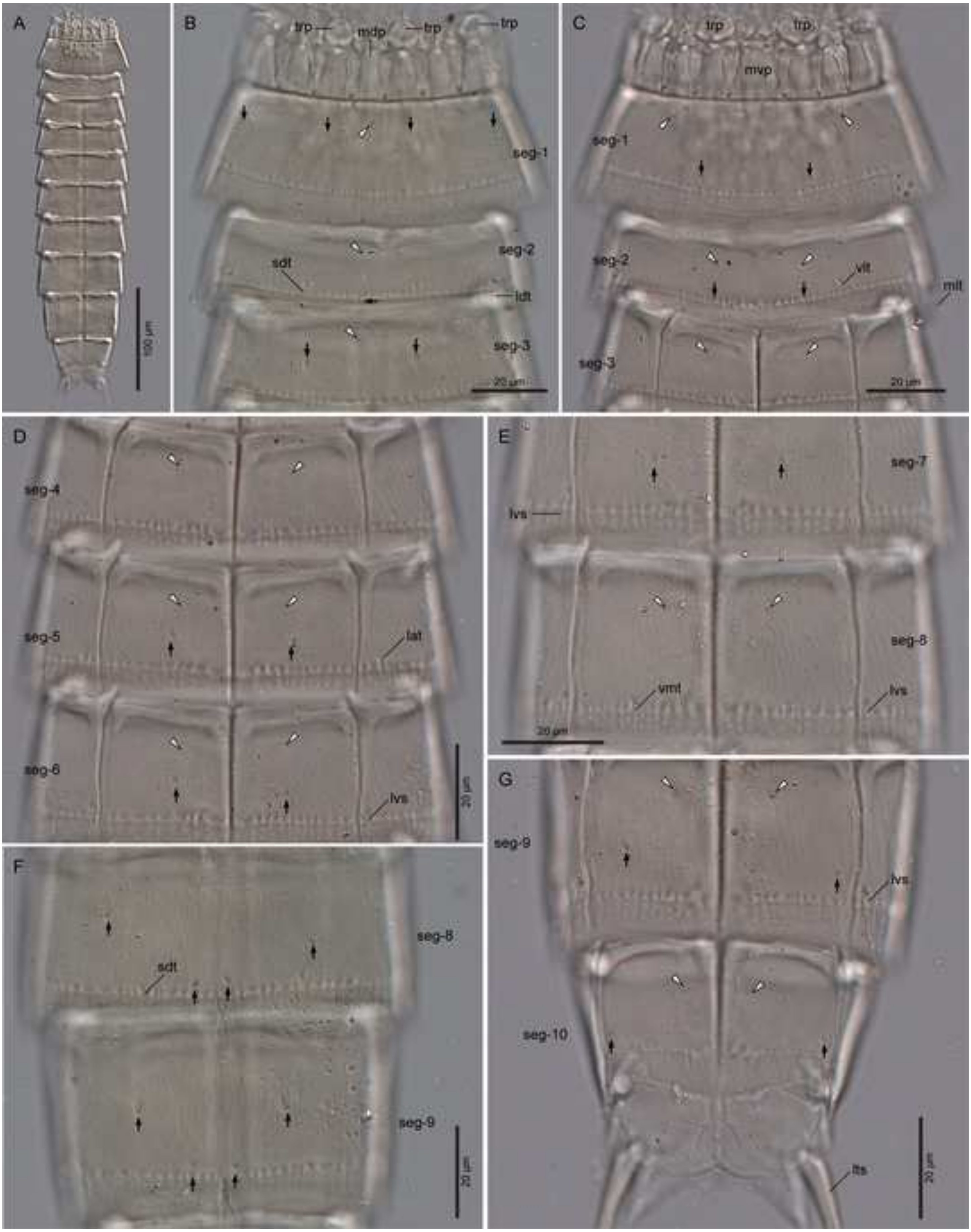
Figure 4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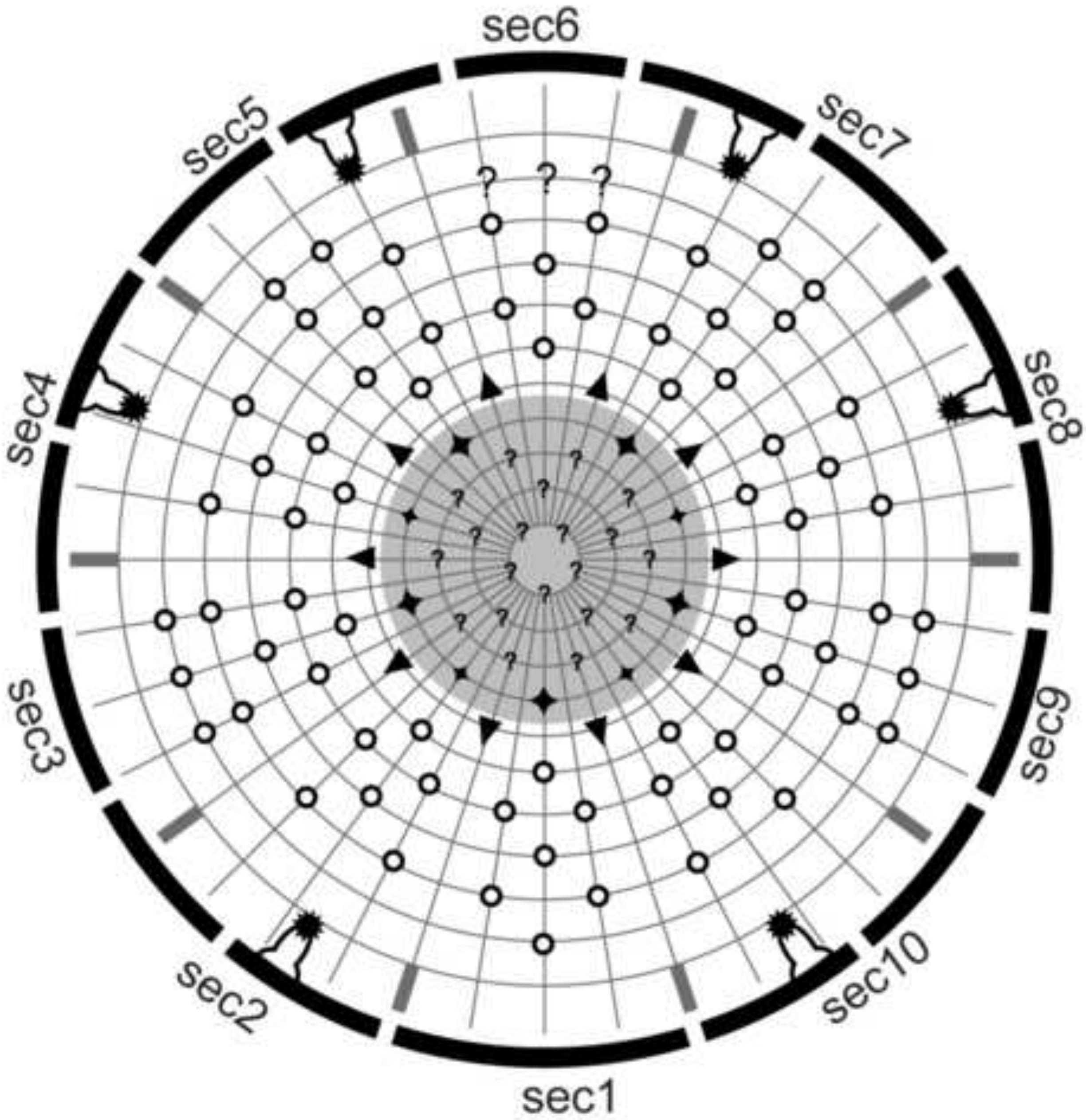
20 µm

Figure 5



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 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	2	2	2	2	2	2	2	2	2	20
04 spinoscalids	○	1	1	1	1	1	1	1	1	1	1	10
05 spinoscalids	○	2	2	2	2	2	2	2	2	2	2	20
06 spinoscalids	○	1	0	3	0	2	?	2	0	3	0	>11
07 trichoscalids	✸	0	1	0	1	1	0	1	1	0	1	6

Figure 6

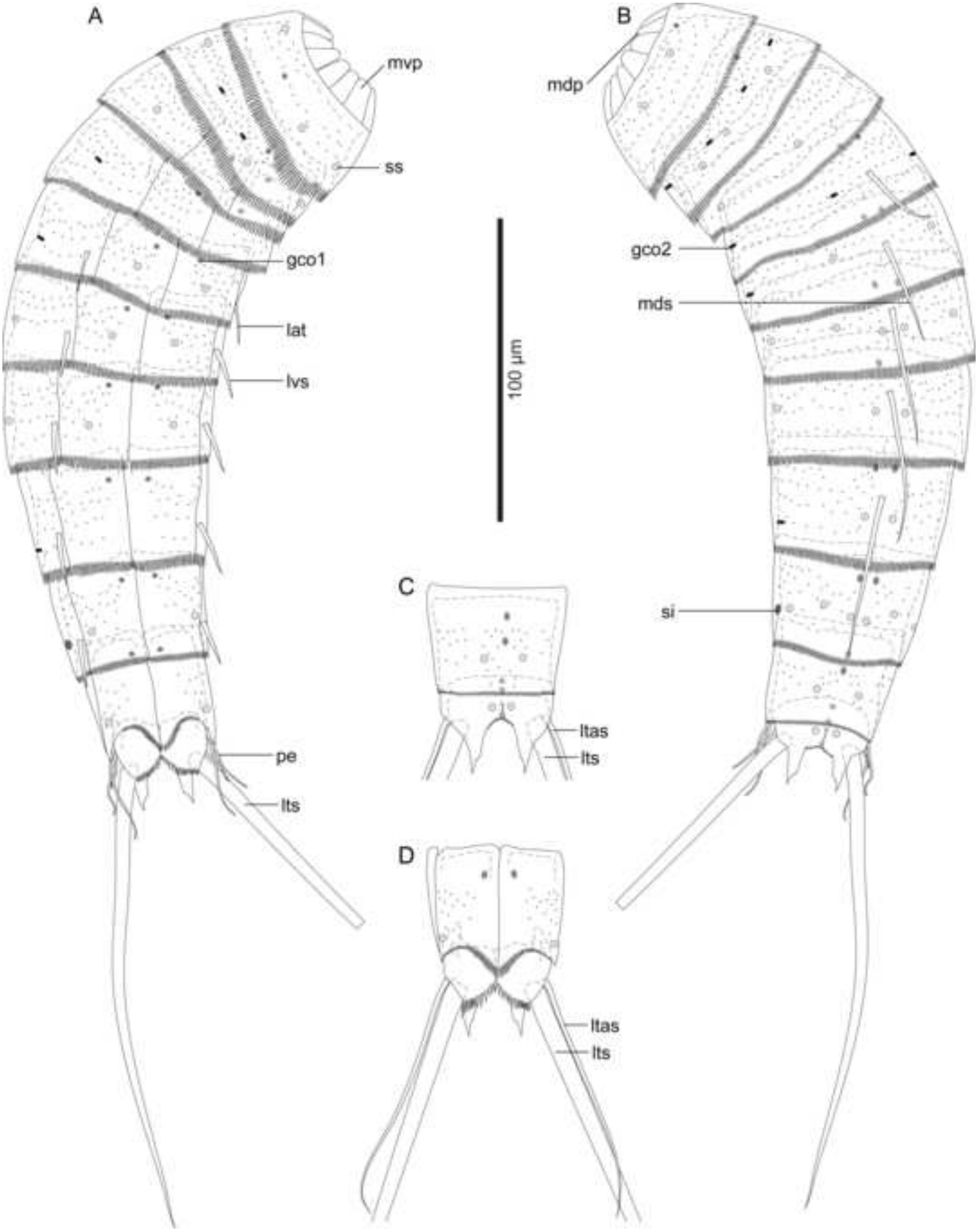

A
B
mvp
mdp
ss
gco1
gco2
mds
lat
lvs
100 µm
C
si
ltas
lts
pe
lts
D
ltas
lts

Figure 7

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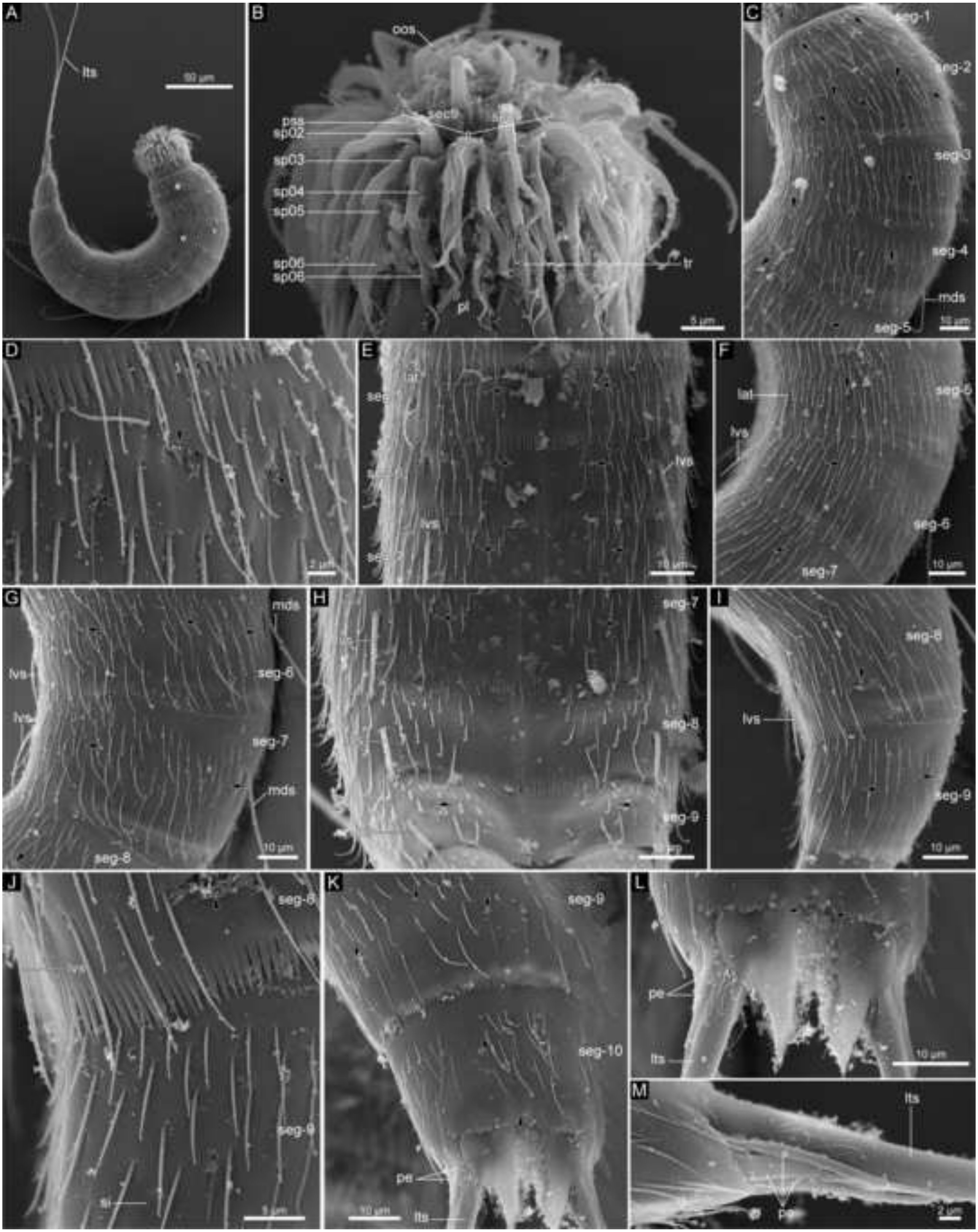

Figure 8

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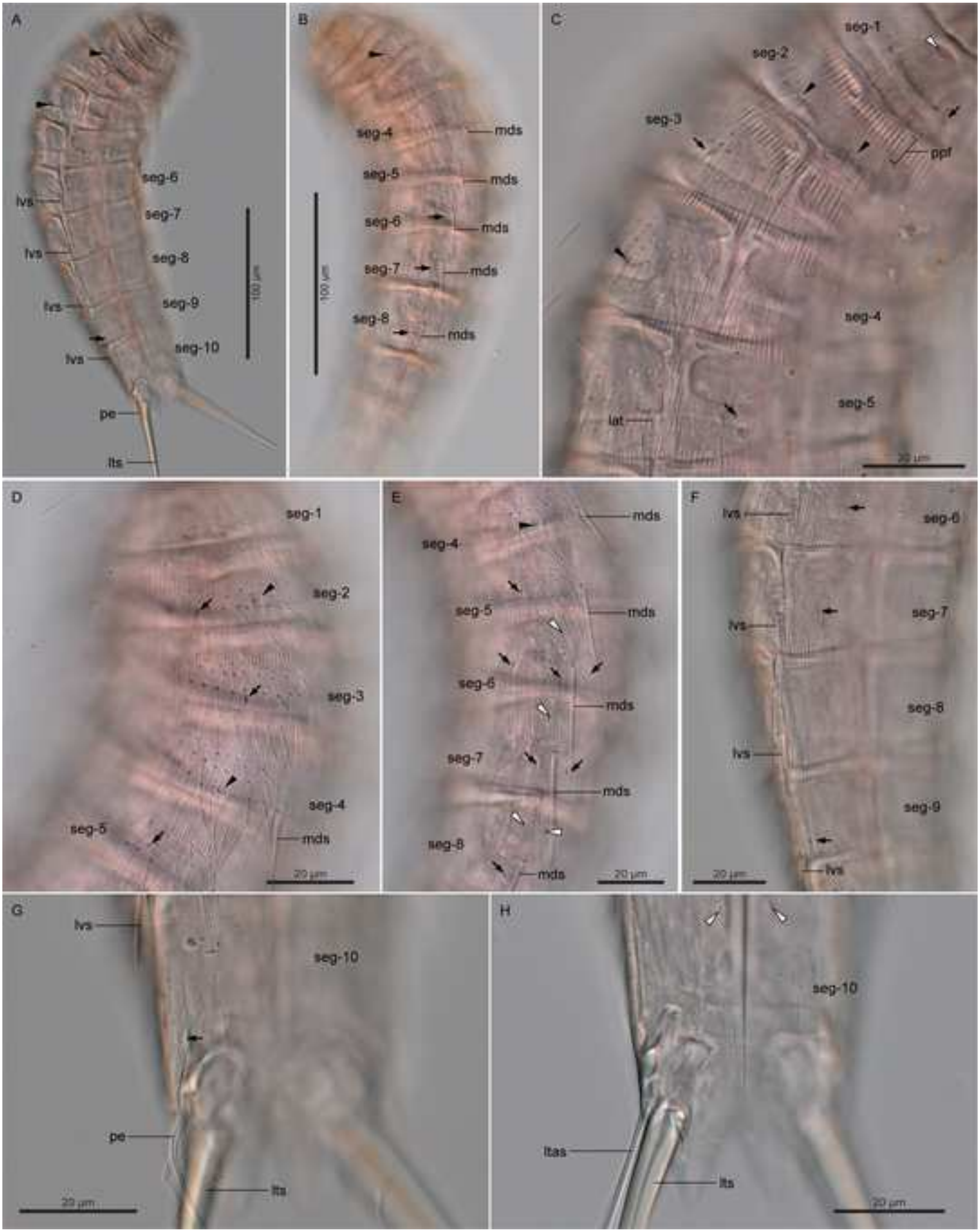

Figure 9

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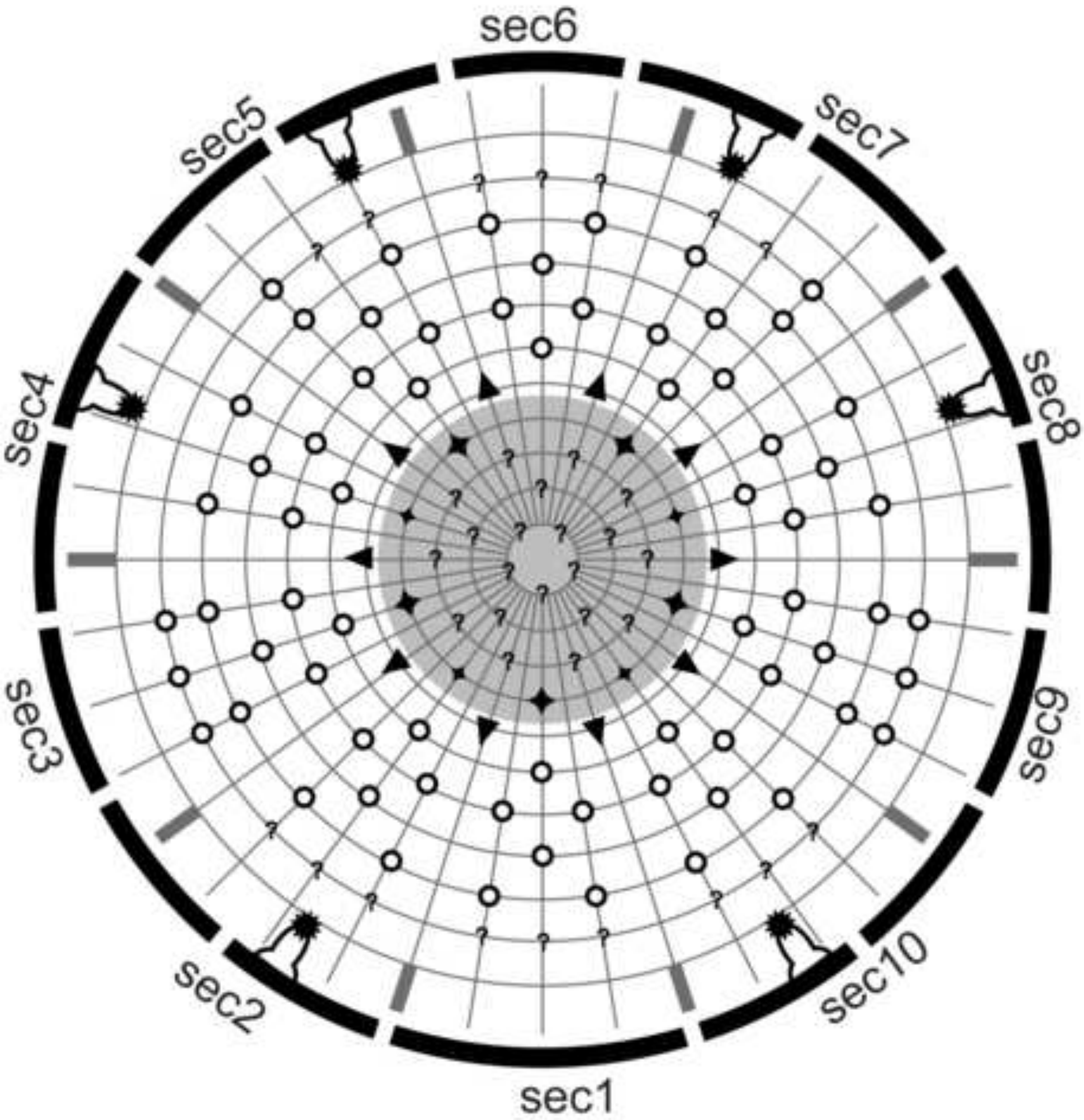

Scalid and style arrangement

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 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	2	2	2	2	2	2	2	2	2	20
04 spinoscalids ○	1	1	1	1	1	1	1	1	1	1	10
05 spinoscalids ○	2	2	2	2	2	2	2	2	2	2	20
06 spinoscalids ○	?	?	3	0	>1	?	>1	0	3	?	>8
07 trichoscalids ✸	0	1	0	1	1	0	1	1	0	1	6