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Dal Zotto, Matteo
Department of Life Sciences, University of Modena and Reggio Emilia

Neuhaus, Birger
Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity

Yamasaki, Hiroshi
Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity

Todaro, M. Antonio
Department of Life Sciences, University of Modena and Reggio Emilia

The genus *Condyloderes* (Kinorhyncha: Cyclorhagida) in the Mediterranean Sea, including the description of two new species with novel characters

MATTEO DAL ZOTTO[1,2*], BIRGER NEUHAUS[3], HIROSHI YAMASAKI[3,4], M. ANTONIO TODARO[1]

[1] Department of Life Sciences, University of Modena and Reggio Emilia, via Campi 213/d, I-41125 Modena, Italy
[2] Consortium for the Interuniversity Center of Marine Biology and Applied Ecology, viale N. Sauro 4, I-57128 Livorno, Italy
[3] Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity, Invalidenstr. 43, D-10115 Berlin, Germany
[4] Senckenberg am Meer, Abt. Deutsches Zentrum für Marine Biodiversitätsforschung DZMB, Südstrand 44, D-26382 Wilhelmshaven, Germany

[*] Corresponding author: matteo.dalzotto@unimore.it

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Running head
The genus *Condyloderes* in the Mediterranean Sea

Abstract
Two new species of Kinorhyncha belonging to the genus *Condyloderes* (Cyclorhagida: Centroderidae) are described herein. The specimens were collected in the Gulf of Castellammare (Tyrrhenian Sea, Sicily, Southern Italy) and off Livorno (Ligurian Sea, Tuscany, Central Italy), respectively. The new taxa represent the first species of *Condyloderes* described from the Mediterranean basin. *Condyloderes agnetis* sp. nov. is distinguished from its congeners by bearing cuspidate spines on segment 3 – a character never reported before for Cyclorhagida – in subdorsal position, paradorsally and sublaterally on segment 7, an extremely short midterminal spine, and a combination of cuspidate spines in lateral accessory position on segments 2 and 9, ventrolaterally slightly displaced ventromedially on segment 5, and ventrolaterally on segment 8. *Condyloderes clarae* sp. nov. is characterized by a combination of cuspidate spines on segments 5, 8, and 9 only, cuspidate spines ventrolaterally on segment 8 and in a lateral accessory position on segment 9, ventromedial appendages on segments 5, 6, and 7 in females. Both species exhibit the recently described type-6 sensory spots. Furthermore, the female morphology and data on the distribution of *C. multispinosus* (McIntyre, 1962) within the Mediterranean Sea are reported, along with the record of the co-occurrence of different species of *Condyloderes* at the same site. We report a certain degree of intraspecific variation of taxonomically diagnostic characters like the presence or absence of cuspidate spines and sensory spots on some segments in *C. agnetis* sp. nov. and *C. multispinosus*. The presence of regularly arranged cuticular hairs on most trunk segments and of an acicular spine in lateral accessory position on segment 1, along with the absence of an area of micropapillae on segment 9 in females of *C. agnetis* sp. nov. and *C. clarae* sp. nov., unique within the genus, suggest the existence of distinct evolutionary lines within *Condyloderes*. The discovery of the two new species highlights the potential species richness of a genus considered species-poor until recently. Our findings underscore the importance of promoting further studies even in rather well investigated areas, such as the Mediterranean basin. Beyond the taxonomic and biogeographical interest, the data reported herein provides additional

insights for ongoing taxonomic and phylogenetic investigations on the Centroderidae and allies, and on the whole Cyclorhagida.

Keywords
biogeography; kinorhynch; meiofauna; morphology; taxonomy; variation

1. Introduction

Even though kinorhynchs are found worldwide, from intertidal to abyssal depths, their distribution is far from being fully known and the greater part of their diversity has likely not been discovered. To date this phylum comprises over 270 species based on descriptions of adults. In the past decade, several taxa above species level were discovered (Dal Zotto et al., 2013; Sørensen, 2013; Sánchez et al., 2014b, 2016; Yamasaki, 2016, this issue; Adrianov and Maiorova, 2018). Two thirds of the almost 180 species comprised in the class Cyclorhagida belong to the genus *Echinoderes*, while each of the remaining 17 cyclorhagid genera accounts only for one to eight species. A particular consideration is directed to the species-poor genera both for their taxonomic and phylogenetic relevance. Herein we describe two new species of the rare genus *Condyloderes*, report the presence of *C. multispinosus* (McIntyre, 1962) from the Mediterranean Sea and describe the female morphology of adult stage of this species, which was not known before (McIntyre, 1962; Higgins, 1969; Neuhaus et al., 2019). The genus *Condyloderes* currently consists of six species (Neuhaus et al., 2019) plus two additional formally described species by Sørensen et al. (this issue), and belongs to a phylogenetically debated order and family, i.e., Kentrorhagata and Centroderidae, respectively (Dal Zotto et al., 2013; Neuhaus, 2013; Yamasaki et al., 2013; Neuhaus et al., 2014; Sørensen et al., 2015). Traditionally, *Condyloderes* together with *Centroderes* and *Campyloderes* composed the family Centroderidae. Recent analyses based on molecular and total evidence data highlighted that *Condyloderes* and *Centroderes* may have to be considered as sister taxa, whereas the third genus, *Campyloderes*, seems to be phylogenetically less closely related to the former two genera mainly based on molecular characters (Dal Zotto et al., 2013; Yamasaki et al., 2013; Sørensen et al., 2015). Sørensen et al. (2015) proposed to maintain *Condyloderes* and *Centroderes* in the family Centroderidae and in the order Kentrorhagata, whilst including *Campyloderes* in the family Campyloderidae Remane, 1929 and in the order Xenosomata Zelinka, 1907. The latter study suggested that this genus may be basal within Cyclorhagida. An additional issue was the following erection of the genus *Ryuguderes*, very likely a sister taxon of *Campyloderes* (see Yamasaki, 2016). In this context, the information from the two new species of *Condyloderes* described herein and from the female specimens of *C. multispinosus* assumes a particular relevance towards future more comprehensive phylogenetic analyses.

This study is part of an ongoing comparison of Kinorhyncha from the continental shelves and from seamounts in the deep sea of the Mediterranean Sea and of the eastern Atlantic Ocean (comp. Yamasaki et al., 2018a, b, c, this issue; Yamasaki and Dal Zotto, this issue).

2. Material and methods

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 Livorno (Ligurian Sea, Tuscany, Central Italy), respectively (Fig. 1). Further information on the former monitoring project is reported extensively by Dal Zotto et al. (2016).

The specimens analysed herein from the Gulf of Castellammare were collected during two surveys, in June 2006 and June 2007. Sediment samples were collected subcoring the sediment collected with a box corer with a hand-held piston corer (inner diameter: 3.40 cm; height: 5.00 cm). The specimens from off Livorno (ca. 12 nautical miles from the coastline, close to the continental shelf edge) were collected during four different surveys led from 2014 to 2017. Sediment samples were collected subcoring the sediment collected with a box corer with a hand-

held piston corer (inner diameter: 2.75 cm; height: 3.00 cm). The coordinates, depths, and sediment characteristics of the sites where the kinorhynchs were found are reported in Table 1, together with additional information on sampling and specimen processing.

The fauna was narcotized using a 7% magnesium chloride solution, fixed on site with a 4% buffered formaldehyde solution, stained with rose Bengal, and stored for later checking (Todaro et al., 2006). In the laboratory, each sample was filtered using two sieves, 1 mm and 0.045 mm, respectively, laid one upon the other and fauna was extracted trice from the finer fraction using the silica gel gradient centrifugation technique (LUDOX® AM, density = 1.210; Pfannkuche and Thiel 1988; Todaro et al., 2001). Kinorhynchs were isolated, counted, transferred and mounted between two coverslips as glycerin-paraffin slides on Cobb aluminum frames as described in Neuhaus and Kegel (2015); coverslips were subsequently sealed with Glyceel. The majority of the specimens were conserved as glycerin-paraffin slides, while others were removed from the slide after observation and stored in formalin for future studies. Specimens were observed using a Nikon Eclipse 90i microscope or a Zeiss Axioskop 50 microscope both equipped with Nomarski differential interference contrast. During observation specimens were photographed with a DS-5M digital camera and measured using the ACT-2U v.4 Nikon software or with a Zeiss AxioCam MRc5 attached to a Zeiss Axioplan 2 mot. Additional specimens were prepared for SEM, therefore dehydrated through a graded ethanol series, critical point dried using carbon dioxide with a CPD 010-Balzer, mounted on aluminum stubs, sputter-coated with Au/Pd (Sputter Coater E24, Balzer) and observed with a Philips XL 40 scanning electron microscope (SEM) in Modena. Additional specimens were postfixed with OsO_4 in 0.67 M phosphate buffer (pH = 7.3) for 2 hours, dehydrated through a graded series of ethanol, critical-point dried with a BalTec CPD 030 or with a Leica EM CPD30, mounted on aluminum stubs, sputter coated with Au/Pd (Polaron SC 7640) or with gold (Quantum Quorum Q150R S) and examined with a Zeiss EVO LS 10 SEM in Berlin.

Specimens of *C. multispinosus* (McIntyre, 1962) Higgins, 1969 from off Rovinj (northern Adriatic Sea) and off Banyuls-sur-Mer (Gulf of Lion) were borrowed from the National Museum of Natural History, Smithsonian Institution, Washington D.C. One specimen (USNM 1562540) was already mounted by R. P. Higgins, while the others were mounted in the present study. This material was examined under a Zeiss Axioskop 50 microscope with Nomarski differential interference contrast. The sampling sites of the specimens of *C. agnetis* sp. nov., *C. clarae* sp. nov., and *C. multispinosus* examined in the present study are shown in Fig. 1.

Measurements of two specimens of *Condyloderes agnetis* sp. nov. prepared subsequently first for light microscopy and then for SEM allowed to report that the dehydration process led to an overall approximate 6% reduction of trunk and segment length, but no or very little variation of the measures of body structures like spines was detected.

All specimens of the new species were deposited at the Museum of Natural History Berlin in the collection "Vermes".

The availability of quantitative data of the kinorhynch fauna associated to the samples collected off Castellammare del Golfo allowed to investigate the potential correlation among the abundances of *Condyloderes agnetis* sp. nov. and the co-occurring kinorhynch species. The software PRIMER 6.0 (PRIMER-E Ltd, Plymouth, UK; Clarke and Gorley, 2006) was used for this analysis.

3. Results
Class Cyclorhagida Zelinka, 1896
Order Kentrorhagata Sørensen et al., 2015
Family Centroderidae Zelinka, 1896
Genus *Condyloderes* Higgins, 1969

Emended diagnosis

Mouth cone with 9 individual outer oral styles with broader base and thin and flexible anterior part; 14 trichoscalids each originating from a trichoscalid plate and accompanied anteriorly by two pointed filamentous appendages; 16 placids with broader midventral placid, neighboured by two narrower placids and alternatingly a broader and a narrower placid; all placids with knobby projections (= condyles) in one or two lateral rows in narrower placids and two or three lateral rows in broader placids; midventral placid with two or three apical condyles, zero or two in intermediate lateral row, and 3−6 in basal lateral row; ventromedial to midventral free flap and primary pectinate fringe of segment 1 at least partly reduced; acicular spine middorsally on segments 1−9, midterminally on segment 11 (= midterminal spine), lateroventrally on segments 2−9, lateroventrally or in lateral accessory position on segment 1, laterodorsally on segment 10 in male and in stage-1 female (in species with more than one adult life history stage), and lateral accessorily on segment 11 (= lateral terminal accessory spine); cuspidate spines present on two or more segments from 1 to 9; type-3 sensory spot ventrolaterally next to lateral terminal accessory spine and subdorsally or laterodorsally on segment 11; type-6 sensory spot elevated above trunk surface giving the impression to be half-drowned in the trunk cuticle; ventromedial appendage at least on two segments of segments 5−8 in female.

3.1. *Condyloderes agnetis* sp. nov.

http://zoobank.org/8D20EDE4-FD6E-4251-AF4F-539F88DC1831
(Figs 2–7; Figs S1, S2; Tabs 1–3; Tabs S1, S2)
Condyloderes sp. − Dal Zotto et al. (2008)
Condyloderes sp. 1 − Dal Zotto and Todaro (2016), Dal Zotto et al. (2016)

3.1.1. Diagnosis

Condyloderes with two lateral rows of condyles in broader placids, two apical and three basal condyles in midventral placid, two basal and two apical condyles in remaining broader placids; longitudinal rows of cuticular hairs regularly arranged on trunk segments 1−9; acicular spines in lateral accessory position on segment 1; cuspidate spines in lateral accessory position on segment 2; subdorsal cuspidate spines on segment 3; ventrolateral slightly displaced ventromedially cuspidate spines on segment 5; pairs of paradorsal and sublateral cuspidate spines on segment 7; ventrolateral cuspidate spines on segment 8; lateral accessory cuspidate spines on segment 9; thick and short lateroventral acicular spines on segment 10 in females; ventromedial appendages on segments 6−8 in females; laterodorsal acicular spines on segment 10 in males.

3.1.2. Examined material

Holotype: female, mounted as glycerol-paraffin slide on a Cobb aluminium frame, ZMB 11763. Paratypes: 14 females and 31 males, mounted as glycerol-paraffin slide on a Cobb aluminium frame. Additional non-type material consists of five females and 12 males, also mounted for light microscopy or on SEM stubs. Catalogue numbers for types and non-types: ZMB 11764 to 11825. One male non-type mounted for light microscopy, USNM 1484169. Information on localities of the type and non-type material is reported in Table 1.

3.1.3. Type locality

Mediterranean Sea, southern Tyrrhenian Sea, Sicily, Gulf of Castellammare, off Castellamare del Golfo, 38°02'59.80" N, 012°52'44.91" E, 43 m depth, silt to very fine sand.

3.1.4. Etymology

The species is named after the first daughter of the first author, Agnese, and follows the Latinized wording *Agnes* and its genitive *Agnetis*.

3.1.5. Description

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The description refers to females. See chapter "3.1.6. Sexual dimorphism" for male characters which are different from female ones. Figures and tables show both male and female characters (see figure and table legends). Adult specimens consist of head, neck, and 11 trunk segments (Figs 2, 3A–B, 4A, 6A, B, 7A; Fig S1A, B). See Table 2 for a summary of spine and sensory spot positions, and Table 3 for measurements and dimensions.

Head. The head is made up of a retractable mouth cone and an introvert (Figs 4E, 5, 6C–E; Fig. S1A, B). The pharyngeal crown consists of 10 lobular extensions at the anterior end of the pharynx and becomes visible in specimens with extremely protruded mouth cone (Fig. 6D). The mouth cone is characterized by the presence of a mouth cone weir (Fig. 6E). At least two rings with five inner oral styles in each were detected (rings -02 and -01; Fig. 6D, E). Ring 00 is characterized by nine thin outer oral styles, consisting of a single element with a thin distal part (Fig. 6E). The introvert has six rings of scalids and one ring of trichoscalids. Ring 01 bears 10 primary spinoscalids consisting of a sheath-like basis and an elongated distal part. The number of visible scalids in ring 06 is 14, no ring 06 scalids were observed in sectors 5 and 7 (Fig. 5). The posterior part of the introvert is characterized by 14 elongated and fringed trichoscalids. A pair of filamentous appendages is attached anteriorly to each trichoscalid. These structures are thinner than the scalids and do not show external sculpturing (Fig. 6C).

Neck. The neck consists of 16 placids, having irregular, knobby surfaces (condyles), varying in number between narrower and broader placids (Figs 3C, 4F, 6F, 7B). A broader midventral placid is neighboured by two narrower placids, and from thereon a broader and a narrower placid alternate. The midventral placid shows two condyles in the apical lateral row and three condyles in the basal lateral row. The remaining broader placids have two basal and two apical condyles. The narrower placids have one condyle in the basal lateral row, which splits apically into two condyles, whereas the paraventral narrower placids reveal only a single condyle (Tab. S2).

Trunk. The trunk is divided into 11 segments. It appears triangular in cross-section, with the tergosternal junctions located along the lateroventral angles.

Segment 1 is formed by a closed cuticular ring and shows a deep broad and squared midventral indentation at the posterior edge, because the free flap is missing (Figs 2A, 7B). This segment is characterized by the presence of a middorsal hirsute spine and two acicular spines placed in lateral accessory position (Figs 4B, 7A; Fig. S1C). The middorsal spine from this segment through segment 10 is located posteriorly on its segment and originates from a sclerotized anterior keel on a trunk segment; the free flap is missing where a spine inserts (Fig. 3D). Minute cuticular hairs are located along the anterior part of the segment. Paired sensory spots are located anteriorly in subdorsal, laterodorsal, midlateral, sublateral, and ventromedial position. These sensory spots are type-6, hence consisting of a structure emerging from the cuticle and giving the impression of being half-drowned in it (Fig. 6H). In rare cases a cilium, ca. 2 μm long, juts out of the central pore of this sensory spot (Fig. 6G). Similarly to the following segments, the posterior margin of the segment is straight, and shows a free flap overlapping the subsequent segment and terminating in a primary pectinate fringe (Figs 4D). The free flap is interrupted where the spines originate and ventrolaterally to midventrally. This condition is repeated through segments 2 to 11 except for the ventral lack of the free flap, even if the teeth of the primary pectinate fringe are shorter and smaller on segment 10 and, particularly, on segment 11 (Figs 6I, 7B–C, F–G). Elongated cuticular hairs (Figs 6J, 7H) are arranged in longitudinal rows of one to three each originating from the middle part of the segment and continuing beyond the segment's posterior edge (Figs 6C, 7B). Within each row the hairs are arranged one after the other from anterior to posterior. The rows are approximately 16 on the ventral side and 40 on the dorsal side, and are absent midventrally and paraventrally, and partially in a midlateral position. Other irregularly arranged cuticular hairs are present midventrally and ventrolaterally from anterior to posterior.

Segment 2 consists of a tergal and two sternal plates (Figs 3D, 7A). The same condition is repeated through segments 3 to 10. This segment bears a middorsal spine, two lateroventral acicular spines, and two cuspidate spines in lateral accessory position next to the edge of the

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sublateral position (Figs 4B, 7A, B, C; Fig. S1C). Pairs of type-6 sensory spots are located posteriorly in subdorsal, laterodorsal, midlateral, sublateral and ventromedial position (Figs 3D, 4B, 7B, C; Fig. S1C). Similarly to segment 1, long cuticular hairs arranged in longitudinal rows of three to five each originate from the middle part of the segment and continue beyond the segment's posterior edge. Approximately 9–12 rows are present on each sternal plate and 38–42 rows on the tergal plate. These rows are absent close to the midsternal junction and also in part of the midlateral area. The same condition is repeated through segments 3 to 9 (Figs 3E, 4D, 6A–B, I, 7A–F). Segments 10 and 11 do not bear the rows of cuticular hairs (Figs 4D, 6I, 7G).

Segment 3 has a middorsal spine, two subdorsal cuspidate spines (Figs 3D, 6A–B, 7C–E) and two lateroventral acicular spines. Three pairs of type-6 sensory spots are placed laterodorsally, sublaterally, and ventromedially (Figs 4B, 7C; Fig. S1C).

Segment 4 bears one middorsal spine and two lateroventral acicular spines. Paired type-6 sensory spots are present paradorsally, a pair of type-6 sensory spots is located laterodorsally and another pair ventromedially (Figs 4B, 7C; Fig. S1C). Ovaries almost reaching the junction between this segment and segment 3 (Fig. 3H).

Segment 5 shows one middorsal spine, two lateroventral acicular spines, and two ventrolateral cuspidate spines slightly displaced ventromedially (Figs 2A, 7A; Fig. S1D). The cuspidate spines are located next to the edge of the ventromedial position (Figs 4C, 6B, 7A, F). Pairs of type-6 sensory spots are located laterodorsally and sublaterally. No ventral sensory spots were detected.

Segment 6 bears one middorsal spine and two lateroventral acicular spines (Fig. 4C). Pairs of type-6 sensory spots are located paradorsally, laterodorsally, sublaterally, and ventromedially (Fig. 7F, I; Fig. S1D). Females bear ventromedial appendages on this segment (Figs 4C, 7A, F, H).

Segment 7 has one middorsal spine, two pairs of cuspidate spines located paradorsally and sublaterally (Figs 3E, 6A, 7D, E, I; Fig. S1G), and two lateroventral acicular spines. A pair of type-6 sensory spots is located laterodorsally and a second pair ventromedially (Figs 4C, D, 7F, I; Fig. S1D). Females bear ventromedial appendages (Figs 2A, 87F).

Segment 8 bears one middorsal spine, two lateroventral acicular, and two ventrolateral cuspidate spines (Figs 3E, F, 4D, 6A, 7A, D; Fig. S1A). Pairs of type-6 sensory spots are placed paradorsally, laterodorsally, and ventromedially (Figs 4D, 7F; Fig. S1D. Females bear ventromedial appendages (Figs 2A, 7F).

Segment 9 has one middorsal spine, two lateroventral acicular spines, and two cuspidate spines in lateral accessory position (Figs 3E–G, 4D, 6A, I, 7A; Fig. S1E). Pairs of type-6 sensory spots are located paradorsally, laterodorsally, and ventromedially (Figs 4D, 6I, 7G; Fig. S1E). A structure very likely representing the protonephridial opening, marked by minute cuticular papillae, is present in sublateral position (Figs 6I–J). Ventromedial areas of micropapillae are absent.

Segment 10 is characterized by the presence of a middorsal spine (Figs 3B, E, 6B, 7G). A pair of paradorsal type-6 sensory spot is present (Fig. 6I). The teeth of the primary pectinate fringe are shorter and smaller than those on segments 1–9. Females bear two thick and short lateroventral acicular spines (Figs 3A, G, 6I, 7G; Fig. S1A). Short cuticular hairs are arranged irregularly especially on the sternal plates (Figs 6I, 7G).

Segment 11 is formed by one tergal and one sternal plate. The latter seems to show a midventral to paraventral cuticular thickening, appearing optically separated from the remaining plate because of a paraventral fold in the cuticle (Figs 4H, 7G). This segment bears a relatively short midterminal spine and two elongated lateral terminal accessory spines each with two thin areas in the basal part (Figs 3A, 4H, 6A). Two pairs of type-3 sensory spots, each composed of a conical base and terminal cuticular papillae, are placed laterodorsally and ventrolaterally (Fig. 7G, J). The former are located more centrally on the segment, while the latter are placed posteriorly. Two ventromedial sensory spots are placed anteriorly on the segment, partially hidden by the free flap of segment 10. We could not assign these sensory spots to any specific

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type of sensory spot, even though they resemble type-6. Similar structures have been observed in *Condyloderes shirleyi* Neuhaus and Higgins, 2019 in Neuhaus et al., 2019 (fig. 42D, F).

The teeth of the primary pectinate fringe are much shorter and smaller than on segments 1–9. Females show cuticularized gonopores at the anterior margin of the sternal plate, almost at the junction between segments 10 and 11 (Figs 3A, G, 7G).

It was noted that a single female specimen had an indistinct mass of material which may be interpreted as a spermatophore attached to the terminal part of its trunk (Fig. S1A). This would be the second report of potential spermatophore in a cyclorhagid, after the finding in *Centroderes drakei* Neuhaus, Pardos, Sørensen and Higgins, 2014 (see Neuhaus et al., 2014). The spermatophore was present in both females and male in the species of this closely related genus.

3.1.6. Sexual dimorphism

Males possess a pair of laterodorsal acicular spines on segment 10, extending beyond the posterior edge of segment 10 (Figs 4G, 6A–B, 7J; Fig. S1F). The acicular spines on segment 10 are thinner than the acicular spines on other segments (Fig. 4G, Fig. S1F). In addition, males lack gonopores on segment 11, lateroventral acicular spines on segment 10, and ventromedial appendages on segments 6, 7, and 8 (Fig. 4C, D), all of which are present only in females (see chapter 3.1.5.).

3.1.7. Variation

Out of 46 specimens mounted for light microscopy and in a condition to check variation of trunk characters, variation is observed in 22 specimens (= 48%) (Fig. S2A–I; Tab. S1). Ten specimens vary in one character, seven in two characters, three in three characters, and one each in five and seven characters. Most variation results from the absence of a cuspidate spine paradorsally on one or both sides of segment 7 and of a type-6 sensory spot sublaterally on segment 5 (Fig. 7E, I; Fig. S2A, D, E; Tab. 2; Tab. S1). In two specimens, the paradorsal cuspidate spine is missing on one side of segment 7 and replaced by a sensory spot. One specimen reveals a very short middorsal and laterodorsal spine on segment 10 (Fig. S2H). Another specimen possesses a crippled lateral terminal accessory spine on one side (Fig. S2I). One specimen shows an acicular spine lateroventrally on the right side of segment 5 but a cuspidate spine on the left side of this segment; the ventrolateral cuspidate spine of the left side is missing (Fig. S2C). Three specimens lack a laterodorsal sensory spot on one side of segments 6 or 9 and possess an additional spot paradorsally on the same side of these segments (Fig. S2B, E; Tab. S1). A type-6 sensory spot may occur in an unusual position on one side only, e. g., lateroventrally on segment 1 (Fig. S2F). Little variation has been found in the arrangement of placids. One specimen shows two narrower placids instead of one broader placid next to the middorsal placid (Fig. S2G).

3.1.8. Ecology

Beyond the type locality of *Condyloderes agnetis* sp. nov., the species was found also at four more sites off Castellammare del Golfo and off the town of Trappeto, a second location placed over 12 km to the east, within the Gulf of Castellammare Sicily, southern Tyrrhenian Sea (see chapter 3.4.8. and Tab. 1). The species was collected from both the two areas (off Castellammare and off Trappeto) during four different surveys led from June 2006 to December 2007. The bottom depths of the sampling sites ranged from 32 to 50 m. Sediment was made up on average of silt to very fine sand off Castellammare del Golfo, and very fine sand to coarse silt off Trappeto.

Condyloderes agnetis sp. nov. co-occurred with other kinorhynchs, i.e.: *Paracentrophyes quadridentatus* (Zelinka, 1928), *Cristaphyes carinatus* (Zelinka, 1928), *Pycnophyes communis* Zelinka, 1908, *Pycnophyes giganteus* (Zelinka, 1928), *Pycnophyes robustus* Zelinka, 1928, *Semnoderes armiger* Zelinka, 1928, *Condyloderes multispinosus* (off Trappeto only; see chapter 3.4.8), *Echinoderes capitatus* (Zelinka, 1928), *E. ferrugineus* Zelinka, 1928, and *E. gerardi*

Higgins, 1978 (Dal Zotto and Todaro, 2016). The other meiobenthic taxa associated with *C. agnetis* sp. nov. were mainly nematodes, harpacticoids, polychaetes, turbellarians, tanaidaceans, ostracods, amphipods, cumaceans, tardigrades, gastropods, bivalves, and cnidarians (Dal Zotto et al., 2016).

The densities of *C. agnetis* sp. nov. ranged from 1 to 6 individuals/10 cm^2. Compared to the other associated kinorhynch species it was relatively scarce, but it was also rather common, because it was found at seven out of eight investigated sites off Castellammare del Golfo (Dal Zotto et al., 2016).

Any clear correlations among the abundances of *C. agnetis* sp. nov. and other co-occurring kinorhynch species were found, with Pearson correlation coefficients varying from -0.18 (*C. agnetis* sp. nov. – *Semnoderes armiger*) to 0.44 (*C. agnetis* sp. nov. – *Pycnophyes* spp. juveniles).

One male of *C. agnetis* sp. nov. from a sample collected at 42 m depth off Rovinj (Croatia, northern Adriatic Sea) was found among the specimens of *Condyloderes* on loan from the National Museum of Natural History, Smithsonian Institution, Washington D. C. (see Table 1; Fig. S1B–G).

3.1.9. Note on epizoic protozoa

Six epizoic protozoans attached on segments 1 and 7–9 to a male specimen from off Rovinj, northern Adriatic Sea (Fig. S1B, G).

3.2. *Condyloderes clarae* sp. nov.

http://zoobank.org/A8E22442-31E0-4A5C-A9DD-CA1E62880B56
(Figs 5, 8–12; Tabs 1, 2, 4; Tab. S2)
Condyloderes sp. 2 (Ligurian Sea) – Dal Zotto and Todaro (2016)

3.2.1. Diagnosis

Condyloderes with two lateral rows of condyles in broader placids, two apical and three basal condyles in midventral placid, two apical and two large basal condyles in remaining broader placids, and two basal condyles in narrower placids, apart from the two neighbouring the midventral placid with only one basal condyle; longitudinal rows of cuticular hairs regularly arranged on trunk segments 1–10, fewer and with shorter hairs on segment 10; acicular spines lateral accessorily on segments 1 and 11, lateroventrally on segments 2–9 (on segment 10 in females only), laterodorsally on segment 10 in males only; cuspidate spines ventrolaterally slightly displaced ventromedially on segment 5, ventrolaterally on segment 8, and lateral accessorily on segment 9; ventromedial appendages on segments 5–7 in females only; type-6 sensory spots paradorsally on segments 1 and 7, sublaterally on segments 3 and 6, and ventromedially on segment 8.

3.2.2. Examined material

Holotype: female, mounted as glycerol-paraffin slide on a Cobb aluminium frame, ZMB 11826. Allotype: male, mounted as glycerol-paraffin slide on a Cobb aluminium frame, ZMB 11827. Paratype: one male ZMB 11828 mounted as glycerol-paraffin slide on a Cobb aluminium frame. Non-type: one juvenile ZMB 11829, mounted as glycerol-paraffin slide on a Cobb aluminium frame. One non-type male ZMB 11830 mounted on aluminium stub for scanning electron microscopy. Information on localities of the type and non-type material is reported in Table 1.

3.2.3. Type locality

Mediterranean Sea, Ligurian Sea, Tuscany, off Livorno (Leghorn), 43°37'35" N, 009°59'18" E, 112 m depth, sandy mud.

3.2.4. Etymology

The species is named after the second daughter of the first author, Chiara, and follows the Latinized wording *Clara* and its genitive *Clarae*.

3.2.5. Description

The description refers to female. No variation was observed in the examined material except for the midventral placid (see below). See chapter "3.2.6. Sexual dimorphism" for male characters that differ from female ones. Figures and tables show both male and female characters (see figure and table legends). The analysed adult specimen consists of head, neck, and 11 trunk segments (Figs 8, 9A, B, 10A, 11A). See Table 2 for a summary of spine and sensory spot position, and Table 4 for measurements and dimensions.

Head. The head is made up of a retractable mouth cone and an introvert (Fig. 10B). The introvert has six rings of scalids and one ring of trichoscalids. Ring 01 bears 10 primary spinoscalids, consisting of a sheath-like basis and an elongated distal part. Rings 02 to 05 bear 5, 15, 15, and 15 scalids, respectively. The number of scalids in ring 06 is more than 12, even though the exact number could not be detected because those in sectors 3, 5, 7, and 9 could not be observed. Generally, the scalid arrangement appeared very similar and is most likely identical to *C. agnetis* sp. nov. (Fig. 5). The posterior part of the introvert is characterized by 14 elongated and fringed trichoscalids (Figs 11C, 12F). A pair of filamentous appendages is attached anteriorly to each trichoscalid. These structures are thinner than the scalids and do not show external sculpturing (Fig. 10B).

Neck. The neck consists of 16 placids, having irregular, knobby surfaces (condyles), varying in number between narrower and broader placids (Figs 9C, 10D, 11C). A broader midventral placid is neighboured by two narrower placids, and from thereon a broader and a narrower placid alternate. The midventral placid shows 5–6 condyles arranged in an apical lateral row with two condyles and a basal lateral row with three condyles in the female holotype and in the male allotype (Fig. 10D), whereas the male mounted for SEM reveals four basal condyles (Fig. 11C). The remaining broader placids have two apical and two basal condyles; the basal condyles are very large and seem to possess apically three smaller condyles (Fig. 11C). The narrow placids have two basal condyles, apart from the two closest to the midventral placid, which bear only one basal condyle (Fig. 11C; Tab. S2).

Trunk. The trunk is divided into 11 segments. It appears triangular in cross-section, with the tergosternal junctions located along two of the lateroventral angles.

Segment 1 is formed by a closed cuticular ring and shows a broad and squared midventral indentation, because the free flap is missing (Figs 8A, 9D, 10D, 11C). This segment is characterized by a middorsal hirsute spine and two acicular spines placed in lateral accessory position (Fig. 9D). The middorsal spine from this segment through segment 10 is located posteriorly on a segment and originates from a sclerotized anterior keel on a trunk segment; the free flap is missing where a spine inserts (Fig. 9B). Minute cuticular hairs are located along the anterior part of the segment. Paired type-6 sensory spots are located anteriorly in subdorsal, laterodorsal, midlateral, sublateral, and ventromedial position (Fig. 9C, D, 10D, 11C, 12D). Similar to the following segments, the posterior margin of the segment is straight, and shows a free flap overlapping the subsequent segment and terminating in a primary pectinate fringe (Figs 11D, 12C). The free flap is interrupted where the spines originate and ventrolaterally to midventrally. This condition is repeated through segments 2 to 11 except for the ventral lack of the free flap (Figs 11D, 12C), even if the teeth of the primary pectinate fringe are shorter and smaller on segments 10 and 11. Very long cuticular hairs are arranged in longitudinal rows of three to five each originating from the anterior to the central part of the segment and continuing beyond the segment's posterior edge on the dorsal side (Fig. 9F). There are approximately 18–20 rows. In addition, many irregularly arranged cuticular hairs are present midventrally and ventrolaterally from anterior to posterior.

Segment 2 consists of a tergal and two sternal plates. The same condition is repeated through segments 3 to 10. The segment bears a middorsal spine and two lateroventral acicular spines.

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Pairs of type-6 sensory spots are located in subdorsal, laterodorsal, midlateral, sublateral, and ventromedial position (Figs 9D, 11C, D, 12D). The subdorsal and sublateral sensory spots are placed posteriorly, whereas the laterodorsal, midlateral and ventromedial are located more medially on the segment (Fig. 11D). Long cuticular hairs arranged in longitudinal rows of normally six each originate from the middle part of the segment and continue beyond the segment's posterior edge. There are approximately 6–7 rows on each sternal plate and 24–26 on the tergal plate. These rows are absent midventrally, paraventrally and midlaterally (Figs 9D–F, 10E, 11A–B, D–E, 12A–B, D–E).

Segment 3 bears a middorsal spine and two lateroventral acicular spines. Two pairs of type-6 sensory spots are placed posteriorly in subdorsal and sublateral position (Fig. 12D, E). No ventral sensory spot was detected (Fig. 11D).

Segment 4 is characterized by one middorsal spine and two lateroventral acicular spines. Pairs of type-6 sensory spots are placed paradorsally, laterodorsally, and ventromedially (Figs 10E, 11B, D, 12E).

Segment 5 shows one middorsal spine, two lateroventral acicular spines, and two ventrolateral cuspidate spines slightly displaced ventromedially (Figs 8A, 9D, 10E, 11B). The cuspidate spines are located next to the edge of the ventromedial position (Figs 9A, D, 10E). A single pair of type-6 sensory spots is located laterodorsally (Fig. 12E). No ventral sensory spot was detected. The female bears ventromedial appendages on this segment (Fig. 9D).

Segment 6 bears one middorsal and two lateroventral acicular spines. Pairs of type-6 sensory spots are located paradorsally, midlaterally, and ventromedially (Figs 8A, 11B, 12A). The female bears ventromedial appendages on this segment (Fig. 9D).

Segment 7 has one middorsal spine and two lateroventral acicular spines. A pair of type-6 sensory spots is located laterodorsally and a second pair of this same type of sensory spots is placed ventromedially (Figs 11B, 12A). The female bears ventromedial appendages on this segment (Fig. 9D).

Segment 8 bears one middorsal spine, two lateroventral acicular, and two ventrolateral cuspidate spines (Fig. 12A). These latter spines are noticeably longer than other cuspidate spines (Figs 9B, 10C, 11A–B; Tab. 5). Pairs of type-6 sensory spots are located in paradorsal, laterodorsal, and ventromedial position (Figs 11B, 12A).

Segment 9 has one middorsal spine, two lateroventral acicular spines, and two lateral accessory cuspidate spines (Figs 9B, 10C, 11A, E, 12B, C). Pairs of type-6 sensory spots are placed paradorsally, laterodorsally, and ventromedially (Figs 11E, 12B, C). A structure with cuticular papillae is present in sublateral position. We assume that this character represent the protonephridial opening (Fig. 12B–C). Ventromedial areas of micropapillae are absent.

Segment 10 is characterized by a rather long middorsal spine (Figs 9B, 12B). A pair of paradorsal type-6 sensory spots is present. The teeth of the primary pectinate fringe are shorter and smaller than on segments 1 to 9 (Fig. 11E). Cuticular hairs shorter, and arranged in fewer rows. The female bears two lateroventral acicular spines on this segment (Fig. 9B).

Segment 11 is formed by one tergal and one sternal plate. The latter shows a midventral to paraventral cuticular thickening, appearing optically separated from the remaining plate because of a paraventral fold in the cuticle (Figs 9E, 11E). This segment bears a midterminal spine and two elongated lateral terminal accessory spines each with two thin areas in the basal parts (Figs 9A, B, 10A, 11A, E, 12B). Two type-3 sensory spots, composed of a conical base and terminal cuticular papillae, are placed centrally on the segment in laterodorsal position. Another pair of type-3 sensory spots is placed posteriorly in ventrolateral position (Fig. 10C, G, 11E, 12B). Two ventromedial sensory spots are placed anteriorly on the segment, partially hidden by the free flap of segment 10. We could not assign these structures to any specific type of sensory spot, even though they resemble type-6.

On this segment, the teeth of the primary pectinate fringe are shorter and smaller than on segments 1 to 10, and cuticular hairs are absent. The female shows cuticularized gonopores at the anterior margin of the sternal plate, almost at the junction between segments 10 and 11 (Fig. 9E).

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3.2.6. Sexual dimorphism

The two males bear a pair of laterodorsal acicular spines on segment 10, ending after the posterior edge of the segment (Figs 10F, 12B), and a ventromedial gland cell outlet on segment 10. In addition, the males lack gonopores on segment 11, lateroventral acicular spines on segment 10, and ventromedial appendages on segments 5, 6, and 7 (Fig. 10C, E), all of which are present only in the female (see chapter 3.2.5. Description).

3.2.7. Ecology

Condyloderes clarae sp. nov. was found at different sites off Livorno (Ligurian Sea, Tuscany, Central Italy). The bottom depth of the sampling sites ranged from 111 to 113 m. The sediment was made up on average of sandy mud or loamy sand (see Table 1). *Condyloderes clarae* sp. nov. co-occurred with other kinorhynchs, i.e.: *Paracentrophyes quadridentatus*, *Fujuriphyes* cf. *rugosus* (Zelinka, 1928), *Pycnophyes communis*, *Pycnophyes giganteus*, *Semnoderes armiger*, *Echinoderes* cf. *capitatus*, *Echinoderes* sp. 2, and *Echinoderes* sp. 3 (see Dal Zotto and Todaro, 2016). The other meiobenthic taxa associated with *C. clarae* sp. nov. were mainly nematodes, polychaetes, harpacticoids, tanaidaceans, ostracods, amphipods, cumaceans, gastropods, bivalves, priapulids, and loriciferans.

The densities of *C. clarae* sp. nov. were of 1–2 individuals/10 cm^2. Compared to the other associated kinorhynch species it was rare, found at four out of twelve investigated sites, and scarce.

3.3. Differential diagnosis

Six species of *Condyloderes* have been described to date, i. e., *C. multispinosus* (McIntyre, 1962), *C. paradoxus* Higgins, 1969, *C. setoensis* Adrianov, Murakami and Shirayama, 2002, *C. storchi* Higgins, 2004 in Martorelli and Higgins, 2004, *C. kurilensis* Adrianov and Maiorova, 2016, and *C. shirleyi*. Two additional species are described from off California and the Gulf of Mexico by Sørensen et al. (this issue).

Condyloderes agnetis sp. nov. and *C. clarae* sp. nov. can be distinguished from their congeners by the presence of (1) longitudinal rows of cuticular hairs on segments 1–9 and (2) a lateral accessory acicular spine on segment 1 (Tab. S2; Neuhaus et al., 2019; this paper).

Condyloderes agnetis sp. nov. can be differentiated from all its congeners by (1) a subdorsal cuspidate spine on segment 3, (2) a paradorsal cuspidate spine on segment 7, (3) a sublateral cuspidate spine on segment 7, (4) the lack of a paradorsal type-6 sensory spot on segment 5, and (5) a very short midterminal spine in comparison to the lateral terminal accessory spine (Tab. 7; Neuhaus et al., 2019; this paper).

Condyloderes clarae sp. nov. can be identified from all its congeners by (1) the lack of a paradorsal type-6 sensory spot on segments 1 and 4, (2) the lack of a sublateral type-6 sensory spot on segments 3 and 6, (3) the lack of a ventromedial type-6 sensory spot on segment 8, (4) the existence of a ventromedial female-specific appendage on segment 5, and (5) the lack of a ventromedial female-specific appendage on segment 8 (Tab. S2; Neuhaus et al., 2019; this paper).

Condyloderes agnetis sp. nov. can be distinguished from *C. clarae* sp. nov. by (1) a larger trunk length (302–327 μm *versus* 215–229 μm length), (2) a shorter midterminal spine (18–30 μm *versus* ca. 55 μm length; see Tabs 4 and 5 for average values, MTS/TL, and MTS/LTAS of both species), (3) the existence of a lateral accessory cuspidate spine on segment 2 *versus* its lack, (4) the existence of a subdorsal cuspidate spine on segment 3 *versus* its lack, (5) the existence of paradorsal and sublateral cuspidate spines on segment 7 (but spines may be missing naturally) in *C. agnetis* sp. nov. *versus* their lack in *C. clarae* sp. nov., (6) the existence of a paradorsal type-6 sensory spot on segments 1 and 4 *versus* its lack on these segments, (7) the existence of a ventromedial type-6 sensory spot on segments 3, 8 and 11 *versus* its lack on these segments, (8) the existence of a sublateral type-6 sensory spot on segments 3 and 6 *versus* its

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lack on these segments, (9) the existence of a laterodorsal type-6 sensory spot on segments 3 (but may be missing naturally), 6 and 11 *versus* its lack on these segments, and (10) the existence of a ventromedial female-specific appendage on segments 6–8 *versus* its existence on segments 5–7 (Tab. S2). Additional, though weaker, traits characterizing *C. agnetis* sp. nov. are (1) shorter and less robust cuticular hairs as well as fewer hairs in each longitudinal row (3–5 *versus* 6 hairs per row) and more rows of hairs both on the sternal plates (9 *versus* 6–7 rows) and tergal plates (40–44 *versus* 24–26 rows), (2) the lack of rows of cuticular hairs on segment 10 *versus* their presence in *C. clarae* sp. nov.

3.4. *Condyloderes multispinosus* (McIntyre, 1962) Higgins, 1969
(Figs 13, 14; Fig. S3; Tabs 1, 2, 5; Tab. S2)
Centroderes multispinosus – McIntyre (1962)
Condyloderes multispinosus comb. nov. – Higgins (1969)
Condyloderes multispinosus – Higgins (1971, 1986, 1988), Moore (1973), Brown (1985), Huys and Coomans (1989), Nebelsick (1993), Adrianov and Malakhov (1994, 1999), Bamber (1997), Adrianov et al. (2002), Martorelli and Higgins (2004), Sørensen and Pardos (2008), Sørensen et al. (2010b), Neuhaus (2013), Neuhaus et al. (2019)
Condyloderes sp. 2 (Tyrrhenian Sea) – Dal Zotto and Todaro (2016)

3.4.1. Emended diagnosis
Neck placids with condyles in one lateral row in narrower placids and three lateral rows in broader placids; each narrower placid with one basal condyle; each broader placid with two condyles both in apical, intermediate, and basal lateral row; midventral placid with three apical and three basal condyles and two in intermediate lateral row; acicular spine middorsally on segments 1–9 (on segment 10 in male only), midterminally on segment 11, laterodorsally on segment 10 in male only, lateroventrally on segments 1–9, and laterodorsally on segment 10; cuspidate spine ventrolaterally on segments 2, 5 and 9 and lateral accessorily on segment 8, sometimes also middorsally on segments 5 and/or 7; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally), 2–4 and 6–9, lateroventrally on segment 10, sublaterally on segments 1–3 and 5–9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 4–9; gland cell outlet ventromedially on segment 10; ventromedial appendage on segments 7 and 8 and area of micropapillae ventromedially on segment 9 in female only.

3.4.2. Examined material
One male (USNM 1562541), two females (USNM 1562542, USNM 1562543), and one juvenile (USNM 1562544), from off Banyuls-sur-Mer, Gulf of Lion. One female from off Rovinj, northern Adriatic Sea (USNM 1562540). All specimens mounted for light microscopy (Figs 13–14; Fig. S3; Tab. 5). One male from off Trappeto, Gulf of Castellammare, Sicily, southern Tyrrhenian Sea, lost during observation. Thus only few photographs were available for this specimen.

3.4.3. Brief description
The morphology of the specimens from the Mediterranean Sea agrees widely with that of the recently re-described specimens of *C. multispinosus* from the North Sea, so only differences are mentioned for the Mediterranean specimens here. For illustrations, data and morphological measurements see Figs 13–14, Fig. S3, Tabs 2, 5, and Tab. S2.

Our findings report for the first time a female adult stage for *C. multispinosus*. The female exhibits a ventromedial appendage on each sternal plate of segments 7 and 8, which gives the impression of an extremely elongated sensory spot covered by numerous cuticular micropapillae (Fig. 13E). At its base, each structure shows a sclerotized cuticular duct penetrating the trunk

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cuticle. The duct seems to be surrounded by a cavity. The structures occur ventromedially on segment 7 and slightly more paraventrally on segment 8 (Fig. 13E; Tabs 2, 5; Tab. S2). Each sternal plate of segment 9 possesses a more or less rectangular area with rounded edges and prominent cuticular micropapillae (Fig. 13E; Tabs 2, 5; Tab. S2). Pores and ducts penetrating the trunk cuticle do not seem to exist in this area. A large circular gonopore with a more sclerotized edge at its anterior margin and a less sclerotized edge at the posterior margin occurs on each sternal plate of segment 11 (Fig. 13G).

3.4.4. Sexual dimorphism

Males can be distinguished from females by the lack of the ventromedial appendage on each sternal plate of segments 7 and 8 *versus* its existence in females (Fig. 13E; Tabs 2, 5; Tab. S2), the lack of a more or less rectangular area with prominent cuticular micropapillae on each sternal plate of segment 9 *versus* its existence in females (Fig. 13E; Tabs 2, 5; Tab. S2), the existence of a ventromedial gland cell outlet with a short sclerotized cuticular duct and an intra- and subcuticular cuticle-lined cavity on each sternal plate of segment 10 *versus* the lack of this outlet in females, the possession of a middorsal and a laterodorsal acicular spine on segment 10 thinner than on the remaining segments (Fig. 14G) *versus* the lack of these spines in females (Fig. 14F; Tabs 2, 5; Tab. S2), and in the lack of a large circular gonopore with a sclerotized edge at its anterior and posterior margin on each sternal plate of segment 11 *versus* its existence in females (Fig. 13G).

3.4.5. Variation

Out of the three specimens from the Gulf of Lion, one male (USNM 1562541) shows a middorsal cuspidate spine on segment 5 (Fig. 14D), whereas two females (USNM 1562542, USNM 1562543) reveal a middorsal cuspidate spine on segments 5 and 7 (Fig. 14E). The female from the northern Adriatic Sea (USNM 1562540) lacks any middorsal cuspidate spine.

3.4.6. Juvenile stage

One small specimen (trunk length = 149 μm) possesses a very thin cuticle, has segments 10 and 11 still fused, lacks a free flap but shows a series of postmarginal spicula with a stronger base, and reveals papilla-like sensory spots elevated above the surface of the cuticle (Fig. S3A−D). Based on these observations, this specimen is regarded as a juvenile stage. Placids with condyles exist but are difficult to separate from each other. The trunk is composed of segments 1−9 separated from each other and from segments 10 + 11 which are still fused (Fig. S3B). Segment 1 reveals a single cuticular plate, whereas segments 2−11 probably possess one tergal and one sternal plate (Fig. S3A). Short cuticular hairs with a stronger base cover all segments except ventromedially and midlaterally, where the dorsoventral muscles originate (Fig. S3A, B). A type-3 sensory spot occurs ventrolaterally and subdorsally on segment 11 (Fig. S3B). Type-6 sensory spots appear at least ventromedially on segments 2, 5, and 9, sublaterally on segments 1, 3, 6, 7, and 9, and paradorsally on segments 1 (almost subdorsally), 4 and 6−9 (Fig. S3A−D). Acicular spines are found lateroventrally and middorsally on segments 1−10 as well as in a lateral accessory position and midterminally on segment 11 (Fig. S3A−D). Cuspidate spines are located ventrolaterally on segments 2, 5, and 9, in a lateral accessory position on segments 4 and 8, and middorsally on segment 5 (Fig. S3A−D).

3.4.7. Comparison with previous descriptions

The species was originally described as *Centroderes multispinosus* by McIntyre (1962) and later placed in a new genus and combined as *Condyloderes multispinosus* (McIntyre, 1962) by Higgins (1969). Most recently, Neuhaus et al. (2019) re-described the male holotype and three additional males from the North Sea. The specimens from the Mediterranean Sea differ from the specimens from the North Sea in the possession of a type-6 sensory spot ventromedially on

segments 5 and 11 *versus* the lack of these spots in the specimens from the North Sea and in the existence of a middorsal cuspidate spine on segments 5 and/or 7 at least in some specimens *versus* their lack in the northern population. The juvenile specimen from the Mediterranean Sea possesses a cuspidate spine in a lateral accessory position on segment 4, which is missing in any adult specimen from the North Sea and from the Mediterranean Sea. We regard the above mentioned differences as variation within one and the same species. It should be kept in mind that few specimens of this species are known both from the North Sea and from the Mediterranean Sea (Tab. S2). In any case, this study expands the distribution record of *C. multispinosus* considerably from the North Sea to the Mediterranean Sea suggesting that the species should also occur in the northeastern Atlantic Ocean.

3.4.8. Co-occurrence of *C. multispinosus* and *C. agnetis* sp. nov.

A single male of *C. multispinosus* was collected together with *C. agnetis* sp. nov. at a station off Trappeto, Gulf of Castellammare, Sicily, southern Tyrrhenian Sea (Tab. 1). The two species also occurred in almost the same location off Rovinj, northern Adriatic Sea, but were collected in different years (Tab. 1).

4. Discussion
4.1. Different evolutionary lines in species of *Condyloderes*?

Several characters of *Condyloderes agnetis* sp. nov., *C. clarae* sp. nov., and of *Condyloderes* sp. 1 from the Gulf of Mexico (see Sørensen et al., this issue) were not known for species of *Condyloderes* before, *viz*, (1) broader placids with only two lateral rows of condyles *versus* three lateral rows, (2) longitudinal rows of cuticular hairs on trunk segments *versus* irregularly arranged cuticular hairs, (3) the existence of an acicular spine on segment 1 in a lateral accessory position *versus* a lateroventral position, (4) the existence of a cuspidate spine ventrolaterally on segment 8 plus lateral accessorily to sublaterally on segment 9 *versus* just *vice versa* in the remaining species of *Condyloderes* (but see below), and (5) the lack of a female-specific ventromedial area of micropapillae on segment 9 *versus* its existence (Higgins, 1969; Adrianov et al., 2002; Martorelli and Higgins, 2004; Sørensen et al., 2010, this issue; Adrianov and Maiorova, 2016; Neuhaus et al., 2019; this paper). Whereas the first four characters mentioned above may indicate a closer relationship of these three species, the fifth character seems to have a more disjunct distribution among species of *Condyloderes* (see following chapter). Concerning the fourth character, *C. shirleyi* reveals a previously unknown amount of variation and shows *inter alia* a cuspidate spine ventrolaterally on segment 8 plus lateral accessorily on segment 9 in a range of specimens (Neuhaus et al., 2019).

4.2. Different adult life history stages in species of *Condyloderes*?

Sørensen et al. (this issue) formally describe a new species with two female life history stages. Amazingly, both stages reveal irregularly arranged cuticular hairs on the trunk segments and lack the ventromedial area of micropapillae on segment 9. It cannot be totally excluded at this time that a subsequent female life history stage may exist for this species, for *C. agnetis* sp. nov., and for *C. clarae* sp. nov. revealing a ventromedial area of micropapillae on segment 9. In this connection, one should keep in mind the low amount of specimens available for most species of *Condyloderes*. Alternatively, the observations by Sørensen et al. (this issue) may suggest simply different evolutionary lines within *Condyloderes*.

Whereas the males of all species of *Condyloderes* reveal a middorsal plus a laterodorsal acicular spine on segment 10, the females of *C. agnetis* sp. nov., *C. clarae* sp. nov., and *C. paradoxus* show a middorsal plus a lateroventral acicular spine on segment 10 (see Higgins, 1969; Neuhaus et al., 2019; Sørensen et al., this issue; this paper). Neuhaus et al. (2019) suggested that the existence of acicular spines on segment 10 of females may represent a developmental rather than a species-specific character, and this hypothesis is corroborated by Sørensen et al. (this issue), who document two adult life history stages for one of their formally

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described species. Interestingly, the stage-1 female of this species possesses a middorsal plus a laterodorsal acicular spine on segment, 10 whereas the stage-2 female lacks any spines on this segment. Several specimens of the last juvenile stage of *C. shirleyi* fixed in the process of moulting to the adult stage reveal on segment 10 either 1) a middorsal plus a sublateral to midlateral acicular spine in the last juvenile stage and a middorsal plus a laterodorsal spine in the male or 2) a middorsal plus a lateroventral acicular spine in the last juvenile stage and no spine in the female. Earlier juvenile stages show a middorsal plus a lateroventral spine (Neuhaus, unpubl. obs.). These observations indicate that in *C. shirleyi* the lateroventral spines might "shift" gradually more dorsally from stage to stage from a lateroventral position via a sublateral to midlateral position to a laterodorsal position in the (prospective) male, whereas the (prospective) female seems to lose its lateroventral spine from the last juvenile stage to the adult stage. The gradual "shift" of the position of the spine may be explained by the hypothesis that it may be too difficult for a specimen to develop a laterodorsal spine directly from a lateroventral spine, because the topological difference between these two positions may be too large. The existence of an acicular spine on segment 10 of a female laterodorsally (new species by Sørensen et al., this issue) or lateroventrally (*C. agnetis* sp. nov., *C. clarae* sp. nov, *C. paradoxus*) may suggest either more adult life history stages for species of *Condyloderes* or different evolutionary lines within this genus.

The observation of more than one adult life history stage seems to be uncommon in species of both *Centroderes* and *Condyloderes* irrespective of whether a more comprehensive number of specimens could be studied (Neuhaus et al., 2014: tab. 8) or a low number (Sørensen et al., this issue: tab. 1), and a more substantial number of investigated specimens does not guarantee finding different adult life history stages (Neuhaus et al., 2019: tab. 1 for *C. shirleyi*; this paper, Tab. 1). It remains uncertain which event or situation may trigger development of more than one adult life history stage. If the trigger would be seasonal, e. g., one would find different adult stages at a given time – or not at all. Most descriptions of species of *Centroderes* and *Condyloderes* are based on samples taken at one or few time slots (Higgins, 1969; Adrianov et al., 2002; Martorelli and Higgins, 2004; Sørensen et al., 2010, this issue; Adrianov and Maiorova, 2016; Neuhaus et al., 2014, 2019; this paper).

In summary, four characters new for the genus *Condyloderes* may hint to at least two different evolutionary lines within *Condyloderes*, whereas the fifth character may be explained by the hypothesis of more than one adult life history stage in species of *Condyloderes* as has been documented also for species of *Campyloderes* and *Centroderes*, which may or may not be closely related (Neuhaus and Sørensen, 2013; Neuhaus et al., 2013, 2014). Future descriptions of new species should take into consideration that species should not be discriminated solely by the existence or lack of female-specific characters like a ventromedial area of micropapillae on segment 9 or acicular spines on segment 10.

4.3. Notes on intraspecific variation

Both intraspecific and intrapopulational variation has been documented for various species of *Condyloderes* and may range from 48% of the specimens studied by LM (*C. agnetis* sp. nov.) to 94% (*C. shirleyi*; Neuhaus et al., 2019). Variation refers mainly to the presence or absence of cuspidate spines and type-6 sensory spots. Cuspidate spines may be missing, e. g., middorsally on segments 5 and 7 (*C. multispinosus*, *C. shirleyi*), lateral accessorily on segment 4 (*C. multispinosus*, *C. setoensis*), paradorsally on segment 7 (*C. agnetis* sp. nov.), or switch position between lateral accessorily and ventrolaterally on segments 6, 7, and 9 (*C. shirleyi*) (Neuhaus et al., 2019; this paper). Sensory spots may be lacking ventromedially on segment 5 (*C. multispinosus*) or segment 6 (*C. setoensis*), sublaterally on segment 5 (*C. agnetis* sp. nov.), or in several positions (*C. agnetis* sp. nov., *C. shirleyi*) (Neuhaus et al., 2019).

The existence of intraspecific variation has been reported also for species of *Antygomonas* (see Nebelsick, 1990; Sørensen et al., 2009), *Campyloderes* (see Neuhaus and Sørensen, 2013), *Cateria* (see Neuhaus and Kegel, 2015), *Centroderes* (see Neuhaus et al., 2013, 2014), and

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Echinoderes (see Yamasaki et al., 2018a; Yamasaki and Dal Zotto, this issue). *Antygomonas incomitata* Nebelsick, 1990, originally described from a single specimen with a ventrolateral cuspidate spine on one side of segment 9 only (Nebelsick, 1990), turned out to bear a cuspidate spine on both sides after the investigation of a higher number of specimens (Sørensen et al., 2009). The studies on species of *Condyloderes* revealed for the first time that such variation may be of importance for discriminating species by, e. g., the existence or lack of cuspidate spines within the population of *C. shirleyi* from a single locality (Neuhaus et al., 2019; this paper). The taxonomic description of new species is further complicated by the finding of more than one adult life history stage in species of *Campyloderes*, *Centroderes*, and *Condyloderes* with spine patterns differing between adult stages (Neuhaus and Sørensen, 2013; Neuhaus et al., 2013, 2014, 2019; Sørensen et al., this issue).

The aforementioned findings of variation of taxonomically significant characters underscore the importance of observation of a high number of specimens, if available, in order to detect variation in a species and the necessity to reevaluate these characters as taxonomic characters. The information gathered will be of much importance for further taxonomic and phylogeographic studies. Along with the morphological information, the availability of molecular data within and between populations may be crucial for the understanding of actual thresholds between species.

4.4. Biogeographical account

The Mediterranean Sea represents probably one of the best known areas worldwide for marine diversity (Coll et al., 2010). Although this had been the case for the kinorhynch fauna thanks to some pioneering studies led in the 19th century (e.g., Metschnikoff, 1865; Reinhard, 1881, 1887) and the monographic work by Zelinka (1928), very recent studies showed that the diversity of this area was far from being fully known (see e.g., Sánchez et al., 2018; Yamasaki and Durucan, 2018), especially in scarcely investigated habitats, such as the abyssal depths and seamounts (Yamasaki et al., 2018a, c). The majority of kinorhynch studies in this ecoregion dealt with taxonomic and biogeographic topics (e. g., d'Hondt, 1973; Higgins, 1978; Nebelsick, 1990, 1992, 1993; Sørensen et al., 2009, 2010a; Sánchez-Tocino et al., 2011; Herranz et al., 2012; Sánchez et al., 2012, 2014a, 2018; Dal Zotto, 2015; Dal Zotto and Todaro, 2016; Dal Zotto et al., 2016; Sönmez et al., 2016; Yildiz et al., 2016; Yamasaki et al., 2018a, b; Yamasaki and Durucan, 2018; Yamasaki and Dal Zotto, this issue), whereas a few investigations focused on ecological data, normally addressing kinorhynchs as undetermined "Kinorhyncha" (e.g., Dinet et al., 1973; Cibic et al., 2009; Mirto et al., 2012), except for one study referring to them at species level (Dal Zotto et al., 2016).

In total, kinorhynchs were reported at genus or even species level from almost 50 locations in the Mediterranean Sea, of which 36 species are known as valid species until this study. Nevertheless, none of these 36 species belonged to the genus *Condyloderes*. In the present study, we describe *C. agnetis* sp. nov. and *C. clarae* sp. nov., referred to as undescribed *Condyloderes* species in Dal Zotto and Todaro (2016) and Dal Zotto et al. (2016), and we report the new finding of *C. multispinosus*. This latter is the first record of the species in the Mediterranean Sea, expanding its distribution pattern from North Sea to the Mediterranean basin. The finding of three species of *Condyloderes* in a single bioregion, which is considered a well-investigated area, stimulates to hypothesize a presence of species of *Condyloderes* in some other less intensely investigated areas of the Mediterranean Sea, as well as to expect further reports of new kinorhynch taxa from this region in future studies.

Supplemenatry material
The article contains three supplementary figures (Figs S1–S3) and two supplementary tables (Tab. S1 and S2).

Acknowledgements

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Figure captions

Fig. 1. Maps of the sampling sites of the specimens of *Condyloderes agnetis* sp. nov., *C. clarae* sp. nov., and *C. multispinosus* reported in the present study. **A**, Map of the central Mediterranean Sea. **B**, Enlarged map of the Gulf of Castellammare, southern Tyrrhenian Sea, Sicily.
Preferred size: full page width

Fig. 2. *Condyloderes agnetis* sp. nov., line art illustrations. **A**, Female, habitus, dorsal view. **B**, Female, habitus, ventral view. **C**, Male, segments 6−11, ventral view. **D**, Male, segments 6−11, dorsal view. Abbreviations: **ac**, acicular spine; **ap**, female-specific appendage; **bpl**, broad placid; **cu**, cuspidate spine; **gp**, gonopore; **ld10**, male-specific laterodorsal acicular spine on segment 10; **ltas**, lateral terminal accessory spine; **lv10**, female-specific lateroventral acicular spine on segment 10; **mts**, midterminal spine; **ne**, protonephridial opening; **npl**, narrow placid; **rch**, longitudinal rows of regularly arranged cuticular hairs; **ssp3**, type-3 sensory spot; **ssp6**, type-6 sensory spot. Scale bar: 100 µm.
Preferred size: full page width

Fig. 3. *Condyloderes agnetis* sp. nov., female holotype, ZMB 11763. Light micrographs. **A**, Habitus, ventral view. **B**, Habitus, dorsal view. **C**, Neck with placids and segment 1, dorsal view. **D**, Segments 1−3, dorsal view. **E**, Segments 7−10, dorsal view. **F**, Segments 8−9, ventral view. **G**, Segments 9−11 with gonopores. **H**, Close-up of the trunk (segments 5−6) with an oocyte. Arrowheads in **C**−**D** mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **gp**, gonopore; **lacu**, lateral accessory cuspidate spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **npl**, narrow placid; **oo**, oocyte; **pdcu**, paradorsal cuspidate spine; **s**, segment; **rch**, longitudinal rows of regularly arranged cuticular hairs; **sdcu**, subdorsal cuspidate spine; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A, B = 100 µm; C, G, F = 20 µm; D, E = 50 µm.
Preferred size: full page width

Fig. 4. *Condyloderes agnetis* sp. nov., male paratype, ZMB 11778. Light micrographs. **A**, Habitus, ventral view. **B**−**D**, Segments 3−5 (**B**), 5−7 (**C**), and 7−10 (**D**), ventral view. **E**, Introvert, ventral view. **F**, Neck with placids, ventral view. **G**, Segments 10−11, dorsal view, with male-specific laterodorsal spines on segment 10. **H**, Segment 11, ventral view. Arrowheads in **B**−**D** mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **ff**, free flap; **la**, lateral accessory acicular spine; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **mvpl**, midventral placid; **npl**, narrow placid; **pss**, primary spinscalid; **rch**, longitudinal rows of regularly arranged cuticular hairs; **s**, segment; **se1**, introvert sector 1; **sp**, spinoscalid (followed by the spinoscalid-ring number); **tr**, trichoscalid; **vlcu**, ventrolateral cuspidate spine. Numbers, except for sector and spinoscalid-ring numbers, refer to the segment number. Scale bars: A = 100 µm; B−D = 50 µm; E−H = 20 µm.
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Fig. 5. *Condyloderes agnetis* sp. nov. and *C. clarae* sp. nov., scheme of the mouth cone (central grey shaded area), introvert, and placids in indicating the distribution of oral styles, scalids, and placids. Placids are symbolized by the bent bars around the introvert diagram.
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Fig. 6. *Condyloderes agnetis* sp. nov., scanning electron micrographs. **A**, Male, habitus in dorsal view. **B**, Male, habitus in lateral view. **C**, Introvert, ventral view. **D**, Close-up of the pharyngeal

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crown. **E**, Close-up of the mouth cone, note the mouth cone weir (we). **F**, Neck with placids and almost completely retracted introvert. **G**, Type-6 sensory spot with a cilium jutting out of the central pore. **H**, Type-6 sensory spot lacking cilium. **I**, female, segments 9−10, lateral view, with longitudinal rows of cuticular hairs on segment 9 only. **J**, Close-up of the protonephridial opening in sublateral position on segment 9. Arrowheads in **F**, **I** mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **ci**, cilium; **ch**, cuticular hair; **fa**, filamentous appendage; **ios**, inner oral style; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **mvpl**, midventral placid; **ne**, protonephridial opening; **npl**, narrow placid; **oos**, outer oral style; **pc**, pharyngeal crown; **pss**, primary spinoscalid; **rch**, longitudinal rows of regularly arranged cuticular hairs; **s**, segment; **se1**, introvert sector 1; **sp**, spinoscalid (followed by the spinoscalid-ring number); **tr**, trichoscalid; **vlcu**, ventrolateral cuspidate spine; **we**, mouth cone weir. Numbers, except for sector and spinoscalid-ring numbers, refer to the segment number. Scale bars: A, B = 100 μm; C, F = 20 μm; D, I = 10 μm; E, J = 5 μm; G, H = 1 μm.
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Fig. 7. *Condyloderes agnetis* sp. nov., scanning electron micrographs. **A**, female, habitus in ventral view. **B**, Neck with placids and segments 1−2, ventral view. **C**, Segments 3−4, lateral view, with subdorsal cuspidate spine on segment 3 and longitudinal rows of cuticular hairs. **D**, Segments 7−9, dorsal view with pairs of paradorsal and sublateral cuspidate spines on segment 7. **E**, Segments 7−8, dorsal view, showing variation in the lack of paradorsal cuspidate spines. **F**, Segments 6−8 with female-specific ventromedial appendages. **G**, Segments 9−11 with female-specific lateroventral acicular spines on segment 10 and gonopores (gp) on segment 11. **H**, Close-up of a female-specific ventromedial appendage and of some cuticular hairs (ch). **I**, Segments 5−7, lateral view; note the absence of type-6 sensory spot sublaterally on segment 5 (dotted circle), and cuspidate spine paradorsally on segment 7 replaced by type-6 sensory spot. **J**, Type-3 sensory spot. Arrowheads in **B**, **C**, **F**, **G**, **I** mark type-6 sensory spots. Arrows in **G** mark type-3 sensory spots. Abbreviations: **ap**, female-specific appendage; **ch**, cuticular hair; **gp**, gonopore; **la**, lateral accessory acicular spine; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **mvi**, midventral indentation; **mvpl**, midventral placid; **pdcu**, paradorsal cuspidate spine; **rch**, longitudinal rows of regularly arranged cuticular hairs; **s**, segment; **sdcu**, subdorsal cuspidate spine; **slcu**, sublateral cuspidate spine; **ssp3**, type-3 sensory spot; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A = 100 μm; B−E, G = 10 μm; F = 20 μm; H, J = 1 μm; I = 10 μm.
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Fig. 8. *Condyloderes clarae* sp. nov., line art illustrations. **A**, Female, habitus, dorsal view. **B**, Female, habitus, ventral view. **C**, Male, segments 5−11, ventral view. **D**, Male, segments 9−11, dorsal view. Abbreviations: **ac**, acicular spine; **ap**, female-specific appendage; **bpl**, broad placid; **cu**, cuspidate spine; **gc**, gland cell outlet of male; **gp**, gonopore; **ld10**, male-specific laterodorsal acicular spine on segment 10; **ltas**, lateral terminal accessory spine; **lv10**, female-specific lateroventral acicular spine on segment 10; **mts**, midterminal spine; **ne**, protonephridial opening; **npl**, narrow placid; **rch**, longitudinal rows of regularly arranged cuticular hairs; **ssp3**, type-3 sensory spot; **ssp6**, type-6 sensory spot. Scale bar: 100 μm.
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Fig. 9. *Condyloderes clarae* sp. nov., female holotype, ZMB 11826, light micrographs. **A**, Habitus, ventral view. **B**, Habitus, dorsal view. **C**, Neck with placids and segment 1, dorsal view. **D**, Segments 1−7, ventral view with female-specific ventromedial appendages and longitudinal

rows of cuticular hairs. **E**, Segments 10–11 with gonopores and midventral cuticular thickening on segment 11. **F**, Close-up of rows of regularly arranged cuticular hairs. Arrowheads in **C**–**D** mark type-6 sensory spots. Abbreviations: **ap**, female-specific appendage; **bpl**, broad placid; **ct**, cuticular thickening; **gp**, gonopore; **la**, lateral accessory acicular spine; **lacu**, lateral accessory cuspidate spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **mvi**, midventral indentation; **npl**, narrow placid; **s**, segment; **rch**, longitudinal rows of regularly arranged cuticular hairs; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A, B = 100 μm; C, E = 20 μm; D = 20 μm; F = 10 μm.

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Fig. 10. *Condyloderes clarae* sp. nov., male paratype (**A**–**C**), ZMB 11827 and juvenile non-type (**D**), ZMB 11829, light micrographs. **A**, Habitus, ventral view. **B**, Introvert, ventral view. **C**, Segments 8–11, ventral view. Note the elongated ventrolateral cuspidate spine on segment 8. **D**, Neck with placids and segment 1, ventral view. **E**, Segment 5, ventral view with ventrolateral cuspidate spines. **F**, Segments 10–11, dorsal view. Note male-specific laterodorsal acicular spine. **G**, Segments 8–11, lateral view. Note the laterodorsal and the ventromedial type-3 sensory spots on segment 11. Arrows in **C**, **G** mark type-3 sensory spots. Arrowheads in **D**, **E** mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **fa**, filamentous appendage; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **mvpl**, midventral placid; **npl**, narrow placid; **pss**, primary spinoscalid; **rch**, longitudinal rows of regularly arranged cuticular hairs; **s**, segment; **se1**, introvert sector 1; **sp**, spinoscalid (followed by the spinoscalid-ring number); **tr**, trichoscalid; **vlcu**, ventrolateral cuspidate spine. Numbers, except for sector and spinoscalid-ring numbers, refer to the segment number. Scale bars: A = 100 μm; B–G = 20 μm.

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Fig. 11. *Condyloderes clarae* sp. nov., male, ventral view, scanning electron micrographs. **A**, Habitus. **B**, Segments 4–8. **C**, Neck and segment 1. **D**, Segments 2–4. **E**, Segments 10 and 11. Arrowheads in B–E mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **ff**, free flap; **lacu**, lateral accessory cuspidate spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **mts**, midterminal spine; **mvpl**, midventral placid; **npl**, narrow placid; **rch**, longitudinal rows of cuticular hairs; **s**, segment; **ssp3**, type-3 sensory spot; **tr**, trichoscalid; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A = 100 μm; B–E = 10 μm.

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Fig. 12. *Condyloderes clarae* sp. nov., male, lateral (**A**–**E**) and frontal (**F**) view, scanning electron micrographs. **A**–**E**, Segments 6–8 (**A**), 9–11 (**B**), 9 (**C**), 1–3 (**D**), and 4–5 (**E**). **F**, Head. Arrowheads in A–E point to type-6 sensory spots. Abbreviations: **d**, dorsal side; **ff**, free flap; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **ne**, protonephridial opening; **rch**, longitudinal rows of cuticular hairs; **ssp3**, type-3 sensory spot; **tr**, trichoscalid; **v**, ventral side; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A–F = 10 μm.

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Fig. 13. *Condyloderes multispinosus*, female USNM 1562540 from the northern Adriatic Sea (**A**–**E**) and females USNM 1562543 (**F**) and USNM 1562542 (**G**) from the Gulf of Lion, in ventral view, light micrographs. **A**, Habitus. **B**, Neck with placids. **C**–**E**, Segments 1–3 (**C**), 4–6

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(**D**), and 7–9 (**E**). Arrows in **C** point to spinose extensions of free flap. **F**, Sternal plates of segments 2–4; arrows mark paraventral area of micropapillae. **G**, Segments 9–11 with gonad and gonopores. Arrowheads in **C**–**E** mark type-6 sensory spots. Abbreviations: **amp**, female-specific area of micropapillae; **ap**, female-specific appendage; **bpl**, broad placid; **fa**, filamentous appendage; **ff**, free flap; **gc**, gland cell; **go**, female gonad; **gp**, gonopore; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **mts**, midterminal spine; **mvpl**, midventral placid; **npl**, narrow placid; **pa**, pachycyclus; **s**, segment; **st**, sternal plate; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A = 100 µm; E = 50 µm, valid for B–G; F = 30 µm.

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Fig. 14. *Condyloderes multispinosus*, female USNM 1562540 from the northern Adriatic Sea (**A**–**C**, **H**) and male USNM 1562541 (**D**, **G**) and female USNM 1562542 (**E**, **F**) from the Gulf of Lion, in dorsal view, light micrographs. **A**–**B**, Anterior segments, left side (**A**), and right side (**B**); arrows mark tergal extensions of free flap. **C**, Lateral terminal accessory spine with two thin areas (arrows). **D**–**E**, Segments 6–8 (**D**) and 5–7 (**E**) with middorsal cuspidate spine (arrows) on segment 5 (**D**) and segments 5 and 7 (**E**). **F**–**G**, Segments 9–11. **H**, Segment 9 with protonephridial openings (arrows). Arrowheads in **A**–**B, E**, and **H** mark type-6 sensory spots. Abbreviations: **bpl**, broad placid; **epi**, epizoic protozoan; **ltas**, lateral terminal accessory spine; **ld**, laterodorsal acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **npl**, narrow placid; **pa**, pachycyclus; **s**, segment; **ssp3**, type-3 sensory spot. Numbers, except for sensory-spot type, refer to the segment number. Scale bars: C = 20 µm; G = 50 µm, valid for A, B, and D–H.

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Captions for supplementary figures

Fig. S1. *Condyloderes agnetis* sp. nov., adult female from off Castellammare del Golfo, Gulf of Castellammare, southern Tyrrhenian Sea (**A**) and adult male USNM 1484169 from off Rovinj, northern Adriatic Sea (**B**−**G**), light micrographs. **A**, Habitus, ventral view with spermatophore. **B**, Habitus. **C**−**F**, Segments 1−4, ventral view (**C**), 5−8, ventral view (**D**), 10 and 11, ventral view (**E**), and 10 and 11, dorsal view (**F**). **G**, Epizoic protozoans. Arrows in B mark epizoic protozoans, and arrowheads in C−E mark type-6 sensory spots. Abbreviations: **ff**, free flap; **hd**, head; **la**, lateral accessory acicular spine; **lacu**, lateral accessory cuspidate spine; **ld**, laterodorsal acicular spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **mc**, mouth cone; **mts**, midterminal spine; **s**, segment; **slcu**, sublateral cuspidate spine; **spp**, spermatophore; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: A−B = 100 μm, E = 50 μm, valid for C−D; F = 20 μm; G = 50 μm.
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Fig. S2. *Condyloderes agnetis* sp. nov., variation of characters. **A**, Segments 4−6, ventral and right side. Note lack of laterodorsal and sublateral sensory spot but existence of subdorsal spot on segment 5. Cuspidate spine of segment 5 artificially displaced. **B**, Segments 9 and 10, ventral and left side. Notice lack of laterodorsal sensory spot but existence of doubled paradorsal spot. **C**, Segments 5 and 6, ventral view. Note lack of left lateroventral acicular spine and of left ventrolateral cuspidate spine but existence of left lateroventral cuspidate spine on segment 5. **D**, Segments 7−9, dorsal view. Note lack of left paradorsal cuspidate spine on segment 7 and lack of right laterodorsal sensory spot on segment 8. **E**, Segments 7−10, ventral and right side. Note lack of laterodorsal sensory spot but existence of doubled paradorsal spot on segment 6, lack of paradorsal cuspidate spine on segment 7, lack of laterodorsal sensory spot and sublateral cuspidate spine on segment 9, and existence of lateroventral cuspidate spine on segment 10. **F**, Segment 1, ventral view. Note additional lateroventral sensory spot on right side. **G.** Neck, dorsal view. Note two narrow placids next to middorsal placid. **H**, Segment 10, dorsal view. Note very short middorsal and laterodorsal spine. **I**, Segment 11, right side. Note artificially developed lateral terminal accessory spine. Arrowheads in A, B, and D−F mark type-6 sensory spots. Abbreviations: **ap**, female-specific appendage; **bpl**, broader placid; **ff**, free flap; **ld**, laterodorsal spine; **ltas**, lateral terminal spine; **lv**, lateroventral acicular spine; **lvcu**, lateroventral cuspidate spine; **md**, middsorsal spine; **mts**, midterminal spine; **ne**, protonephridial cavity and opening; **npl**, narrower placid; **pdcu**, pardorsal cuspidate spine; **st**, sternal plate; **tp**, tergal plate; **tr**, trichoscalid; **vlcu**, ventrolateral cuspidate spine. Numbers refer to segment number. Scale bars: C = 30 μm; I = 30 μm, valid for A, B, and D−I.
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Fig. S3. *Condyloderes multispinosus*, juvenile USNM 1562544 from the Gulf of Lion in ventral (**A**, **B**) and dorsal view (**C**, **D**), light micrographs. **A**−**B,** Segments 1−7 (A) and 8−11 (**B**); arrows mark postmarginal spicula. **C**−**D**, Segments 1−8 (**C**) and 8−11 (**D**) with middorsal cuspidate spine on segment 5 (arrow in **D**). Note that segments 10 and 11 appear still fused (**B**, **D**). Arrowheads in **A**−**D** mark sensory spots. Abbreviations: **lacu**, lateral accessory cuspidate spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral acicular spine; **md**, middorsal acicular spine; **mts**, midterminal spine; **s**, segment; **ssp3**, type-3 sensory spot; **vlcu**, ventrolateral cuspidate spine. Numbers refer to the segment number. Scale bars: **D** = 50 μm, valid for **A**−**D**.
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Tables

Table 1. Location and processing data of the examined specimens of *Condyloderes* from the Mediterranean Sea. Abbreviations: USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (previously United States National Museum); ZMB, collection "Vermes" of Museum für Naturkunde Berlin (previously Zoological Museum Berlin).

Species	Station data (location, georeferences, field station#; depth; sediment)	Collection date; gear	Collector	Specimens; remarks
Condyloderes agnetis sp. nov.	Tyrrhenian Sea, off Castellammare del Golfo, 38°02'58.00"N, 012°52'58.20"E, station NW100; depth 43 m; 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%)	VI.2007; box corer and piston corer	M. Dal Zotto	holotype ♀: ZMB 11763; paratype ♀: ZMB 11764; paratypes ♂: ZMB 11765–11770; non-types ♀: ZMB 11771–11773; non-types ♂: ZMB 11774–11777
	Location: see above, 38°02'55.72"N, 012°52'50.52"E, station SE100; depth 39 m; mud to very fine sand (coarse sand: 0.63%, medium sand: 0.48%, fine sand: 5.27%, very fine sand: 25.85%, silt-clay: 67.75%)			paratype ♀: ZMB 11780; paratypes ♂: ZMB 11778, 11779
	Location: see above, 38°02'46.54"N, 012°53'1.42"E, station CT2; depth 35 m; mud to very fine sand (coarse sand: 0.47%, medium sand: 0.48%, fine sand: 3.50%, very fine sand: 18.33%, silt-clay: 77.22%)	VI.2006; box corer and piston corer	G. Renda and A. Santulli	paratypes ♂: ZMB 11809–11812
	Location: see above, 38°03'26.03"N,; 012°52'14.41"E, station CT1; depth 45 m			paratypes ♂: ZMB 11803–11808
	Location: see above, 38°02'57.26"N, 012°52'48.44"E, station SE25; depth 40 m	VI.2007; box corer and piston corer	M. Dal Zotto	paratypes ♀: ZMB 11781–11783; paratypes ♂: ZMB 11784–11787
	Location: see above, 38°02'56.68"N, 012°52'49.10"E, station SE50; depth 40 m			paratypes ♀: ZMB 11788–11791; paratype ♂: ZMB 11792; non-types ♀: ZMB 11793, 11794; non-types ♂: ZMB 11795–11802
	Location: see above, 38°02'36.89"N, 012°53'12.98"E, station CT3; depth 35 m			paratypes ♀: ZMB 11813–11817; paratypes ♂: ZMB 11818–11825
	Adriatic Sea, Rovinj, RABAC-3; depth 42 m	04.VIII.1980	J. Vidakovic	1 non-type ♂: USNM 1484169

Table 1. (continued)

Species	Station data (location, georeferences, field station#; depth; sediment)	Collection date; gear	Collector	Specimens; remarks
C. clarae sp. nov.	Ligurian Sea, off Livorno, 43°37'35"N, 009°59'18"E, station MG10; depth 112 m; sandy mud (gravel: 1.50%, medium to very fine sand: 25.50%, silt: 42.00%, clay: 31.00%)	III.2014; box corer and piston corer	L. Pacciardi and M. Pertusati	holotype ♀: ZMB 11826
	Location: see above, 43°38'40"N, 009°59'24"E, station MG13; depth 113 m; sandy mud (medium to very fine sand: 23.00%, silt: 31.00%, clay: 46.00%)	III.2016; box corer and piston corer		paratype ♂: ZMB 11827
	Location: see above, 43°38'40"N, 009°59'16"E, station MG12; depth 111 m; muddy sand (gravel: 5%, medium to very fine sand: 46.00%, silt: 21.50%, clay: 27.50%)	VIII.2016; box corer and piston corer	M. Dal Zotto	paratype ♂: ZMB 11828
	Location: see above, 43°38'30"N, 009°59'20"E, station MG8; depth 112 m; sandy mud (gravel: 4%, medium to very fine sand: 31%, silt: 30%, clay: 35%).	VIII.2017; box corer and piston corer		1 juvenile: ZMB 11829, 1 non-type ♂: ZMB 11830
C. multispinosus	Tyrrhenian Sea, off Trappeto, 38°05'14.87"N, 013°03'17.73"E; depth 33 m; mud to very fine sand (coarse sand: 0.33%, medium sand: 0.14%, fine sand: 0.98%, very fine sand: 31.87%, silt-clay: 66.68%)	VI.2007; box corer and piston corer	M. Dal Zotto	1 non-type ♂: lost during investigation
	Adriatic Sea, Rovinj, RAJA-4	14.IX.1983	J. Vidakovic	1 non-type ♀: USNM 1562540
	Gulf of Lion, off Banyuls-sur-Mer, 42°38'20''N, 003°20'35''E; depth 95 m; coarse sand	10.IV.1991; meiodredge	R.P. Higgins and V. Storch	1 ♂: USNM 1562541, 1 ♀: USNM 1562542, 1 recently moulted ♀: USNM 1562543, 1 juvenile: (USNM 1562544)

Please arrange the 2 pages of this Tables on opposite pages.

Table 2. Characters of *Condyloderes agnetis* sp. nov., *C. clarae* sp. nov., and *C. multispinosus* present in the majority of specimens of a given species. Number of studied specimens mounted for light microscopy provided in ( ) after species name; for *C. multispinosus* including specimens from Neuhaus et al. (2019). Features appearing anteriorly on a segment do not show any background, features located centrally on a segment are indicated by a grey background, and characters occurring posteriorly on a segment are marked in black. Characters found in one gender only are indicated. Characters occupying an intermediate position to two reference positions are arranged right or left in a column (on segment 7: paradorsally to subdorsally; on segments 5, 8 and 9: ventrolaterally to ventromedially). Positions of more frequent variation of organ (n ≥ 5) are highlighted by oblique hatching. Information for *C. multispinosus* also taken from Neuhaus et al. (2019). Abbreviations: **[ ]**, indicates variation in minority of specimens; **ac**, acicular spine; **amp**, area of micropapillae; **ap**, appendage; **gc**, gland cell outlet; **la**, lateral accessory; **ld**, laterodorsal; **ltas**, lateral terminal accessory spine; **lv**, lateroventral; **md**, middorsal; **ml**, midlateral; **mts**, midterminal spine; **ne**, nephridial openings; **pd**, paradorsal; **pv**, paraventral; **sd**, subdorsal; **sh**, short; **sl**, sublateral; **ssp3**, type-3 sensory spot; **vl**, ventrolateral; **vm**, ventromedial.

Position / Segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
Condyloderes agnetis sp. nov. (15 ♀, 31 ♂, 6 juveniles)										
1	ac		ssp6	ssp6	ssp6	ssp6	ac			ssp6
2	ac		ssp6	ssp6	ssp6	ssp6	cu	ac		ssp6
3	ac		cu	ssp6		ssp6		ac		ssp6
4	ac	ssp6		ssp6				ac		ssp6
5	ac			ssp6		ssp6 [−]		ac	cu	
6	ac	ssp6		ssp6		ssp6		ac		ssp6 ; ♀: ap
7	ac	cu [−]		ssp6		cu [−]		ac		ssp6 ; ♀: ap
8	ac	ssp6		ssp6				ac	cu	ssp6 ; ♀: ap
9	ac	ssp6		ssp6	ne		cu	ac		ssp6
10	ac	ssp6		♂: ac				♀: ac (sh)		
11	mts (sh)			ssp3			ltas		ssp3	ssp(6?)
C. clarae sp. nov. (1 ♀, 3 ♂, 1 juvenile)										
1	ac		ssp6	ssp6	ssp6	ssp6	ac			ssp6
2	ac		ssp6	ssp6	ssp6	ssp6		ac		ssp6
3	ac		ssp6			ssp6		ac		
4	ac	ssp6		ssp6				ac		ssp6
5	ac			ssp6				ac	cu	♀: ap
6	ac	ssp6			ssp6			ac		ssp6 ; ♀: ap
7	ac			ssp6				ac		ssp6 ; ♀: ap
8	ac	ssp6		ssp6				ac	cu	ssp6
9	ac	ssp6		ssp6	ne		cu	ac		ssp6
10	ac	ssp6		♂: ac				♀: ac		♂: gc
11	mts			ssp3			ltas		ssp3	ssp(6?)
C. multispinosus (3 ♀, 5 ♂, 1 juvenile)										
1	ac	ssp6		ssp6	ssp6	ssp6		ac		ssp6
2	ac	ssp6		ssp6	ssp6	ssp6		ac	cu	ssp6
3	ac			ssp6		ssp6		ac		ssp6
4	ac	ssp6		ssp6				ac		ssp6
5	ac [cu]	ssp6		ssp6		ssp6		ac	cu	[ssp6]
6	ac	ssp6		ssp6		ssp6		ac		ssp6
7	ac [cu]	ssp6		ssp6		ssp6		ac		ssp6 ; ♀: ap
8	ac	ssp6		ssp6		ssp6	cu	ac		ssp6 ; ♀: ap
9	ac	ssp6		ssp6	ne ; ssp6			ac	cu	ssp6 ; ♀: amp
10	♂: ac		ssp6	♂: ac				ssp6		♂: gc
11	mts		ssp3				ltas		ssp3	[ssp(6?)]

Please do not change position of abbreviations within a column, because this has a certain meaning.

Table 3. *Condyloderes agnetis* sp. nov. Morphometric measurements, including number of measured specimens (N), averages (AV) and standard deviations (SD), for female holotype ZMB 11763 and for selected paratypes. Lengths are reported in μm. Abbreviations: **ac**, acicular spine; **cu**, cuspidate spine; **la**, lateral accessory spine; **ld**, laterodorsal spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral spine; **md**, middorsal spine; **ml**, midlateral spine; **mts**, midterminal spine; **pd**, paradorsal spine; **s**, segment (followed by the segment number 1 to 11); **sd**, subdorsal spine; **sl**, sublateral; **sw**, average sternal width; **tl**, trunk length, **vl**, ventrolateral spine; ♂, males only; ♀, females only; −, character missing naturally.

Character	♀ ZMB 11763 (holotype)	N	Range	AV	SD
tl	312	15	302−337	325.5	9.1
s1	28	15	20−28	24.0	2.4
s2	28	15	21−28	24.9	1.7
s3	30	15	20−30	26.2	2.4
s4	32	15	25−35	29.3	3.2
s5	34	15	25−34	29.9	3.6
s6	38	15	30−38	32.8	2.9
s7	39	15	28−39	33.6	3.8
s8	39	15	32−39	35.5	2.7
s9	38	15	31−38	34.6	2.7
s10	34	15	27−34	29.9	1.5
s11	22	15	15−23	19.8	3.2
sw-6	81	15	75−90	83.8	5.5
sw-8	81	15	77−83	81.2	3.1
sw-10	68	15	56−68	62.7	4.9
md1 (ac)	18	15	14−19	16.4	2.3
md2 (ac)	22	15	15−22	18.9	2.8
md3 (ac)	21	15	14−21	18.2	2.5
sd3 (cu)	14	15	13−20	17.0	2.1
md4 (ac)	22	15	13−22	19.2	2.9
md5 (ac)	21	15	16−28	20.3	3.4
md6 (ac)	22	15	19−23	21.3	1.1
md7 (ac)	20	15	19−23	21.4	1.8
pd7 (cu)	18	14	15−19	17.2	1.3
sl7 (cu)	16	15	12−19	17.5	2.5
md8 (ac)	21	15	15−24	21.2	3.4
md9 (ac)	21	15	20−31	23.3	3.7
md10 (ac)	28	15	20−28	24.4	2.9
ld10 (ac) ♂	−	10	18−27	22.4	3.7
la1 (ac)	16	15	12−17	15.3	1.6
la2 (cu)	17	15	14−20	16.6	1.9
lv2 (ac)	20	15	14−20	17.1	1.8
lv3 (ac)	21	15	16−20	18.0	1.5
lv4 (ac)	22	15	16−23	19.2	2.0
vl5 (cu)	18	15	13−20	17.0	2.0
lv5 (ac)	18	15	16−23	19.6	1.9
lv6 (ac)	19	15	17−21	19.0	1.6
lv7 (ac)	20	15	17−24	19.5	1.6
vl8 (cu)	23	15	21−27	24.1	2.6
lv8 (ac)	23	15	15−23	19.9	2.6
la9 (cu)	19	15	15−23	20.2	2.6
lv9 (ac)	20	15	17−22	20.7	1.5
lv10 ♀	18	5	11−18	15.7	2.6

|					
ltas	169	15	140−169	152.5	6.8
mts	30	14	18−30	24.5	3.7
mts/ltas	0.18%	15	0.16–0.18%	0.17%	0.14%
mts/tl	0.10%	15	0.05–0.10%	0.07%	0.02%

Table 4. *Condyloderes clarae* sp. nov. Morphometric measurements. Lengths are reported in µm. Abbreviations: **ac**, acicular spine; **cu**, cuspidate spine; **la**, lateral accessory spine; **ld**, laterodorsal spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral spine; **md**, middorsal spine; **mts**, midterminal spine; **s**, segment (followed by the segment number 1 to 11); **sw**, average sternal width; **tl**, trunk length, **vl**, ventrolateral spine; ♂, males only; ♀, female only; –, character missing naturally; N/A, information not available.

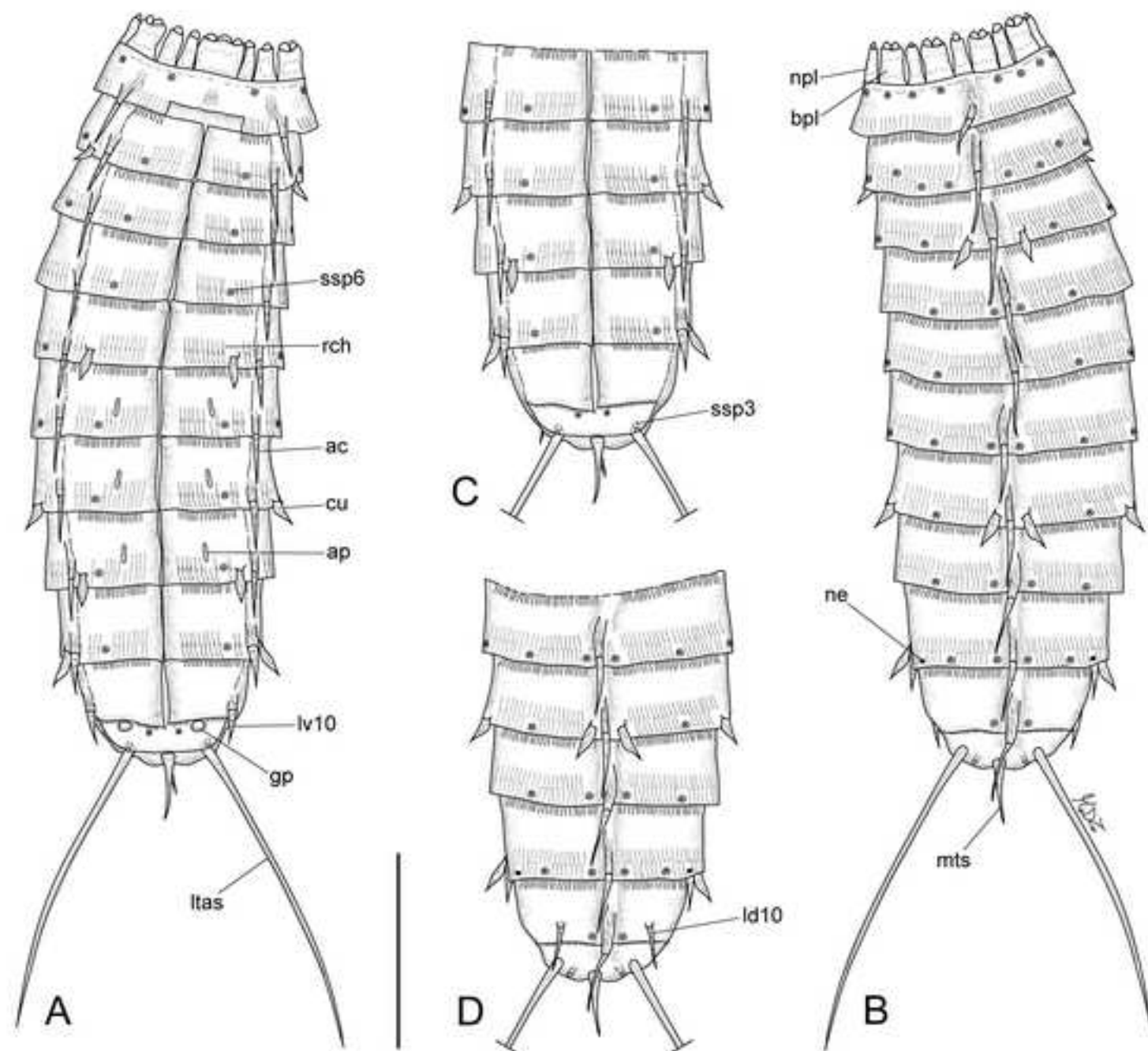| Specimen Character	♀ ZMB 11826 (holotype)	♂ ZMB 11827 (paratype)	♂ ZMB 11828 (paratype)
tl	229	215	223
s1	23	16	22
s2	22	20	22
s3	22	21	22
s4	24	21	23
s5	23	25	23
s6	26	26	24
s7	27	27	29
s8	31	31	31
s9	29	30	28
s10	26	25	22
s11	23	19	21
sw-6	57	62	56
sw-8	53	61	53
sw-10	42	47	46
md1 (ac)	16	17	16
md2 (ac)	16	18	16
md3 (ac)	19	19	19
md4 (ac)	23	18	20
md5 (ac)	22	19	21
md6 (ac)	broken	19	22
md7 (ac)	23	18	23
md8 (ac)	25	21	25
md9 (ac)	27	26	21
md10 (ac)	30	broken	25
ld10 (ac) ♂	–	23	20
la1 (ac)	15	16	14
lv2 (ac)	15	16	15
lv3 (ac)	17	18	16
lv4 (ac)	21	17	18
lv5 (ac)	15	15	16
vl5 (cu)	23	17	21
lv6 (ac)	21	18	17
lv7 (ac)	20	18	17
lv8 (ac)	25	20	18
vl8 (cu)	25	28	29
la9 (cu)	22	19	18
lv9 (ac)	25	24	22
lv10 (ac) ♀	27	–	–
lts (ac)	130	126	130
mts	55	broken	54
mts/ltas	0.42%	N/A	0.41%
mts/tl	0.24%	N/A	0.24%

Table 5. *Condyloderes multispinosus*, morphometric measurements (data given for left/right side if applicable) of specimens from Banyuls-sur-Mer (Banyuls), Rovinj and Trappeto in the Mediterranean Sea, with USNM catalogue numbers (USNM 1562540–1562543) of National Museum of Natural History, Smithsonian Institution, when applicable. Lengths are reported in μmAbbreviations: [1], specimen lost after investigation; **ac**, acicular spine; **cu**, cuspidate spine; **la**, lateral accessory spine; **ld**, laterodorsal spine; **ltas**, lateral terminal accessory spine; **lv**, lateroventral spine; **md**, middorsal spine; **mts**, midterminal spine; **S**, segment (followed by the segment number 1 to 11); **sw**, average sternal width; **tl**, trunk length, **vl**, ventrolateral spine; ♂, males only; ♀, females only; −, character missing naturally.

| Specimen	♂ 1562541	♀ 1562542	♀ 1562543	♀ 1562540	♂[1]
Location	Banyuls	Banyuls	Banyuls	Rovinj	Trappeto
Character					
tl	246	272	220	290	298
s1	14	15	14	15	18
s2	26	23	21	26	28
s3	28	26	26	28	26
s4	29	29	28	28	27
s5	28	30	28	31	30
s6	29	32	27	31	33
s7	32	33	31	33	36
s8	33	33	29	33	35
s9	35	35	30	37	36
s10	28	31	24	31	32
s11	16	18	20	23	25
sw-8	68	68	n. a.	70	71
sw-10	55	57	n. a.	58	61
md1 (ac)	37	45	38	41	33
md2 (ac)	40	34	45	39	30
md3 (ac)	38	39	42	41	30
md4 (ac)	40	42	45	38	32
md5 (ac)	43	45	48	43	33
md5 (cu)	17	n. a.	18	−	−
md6 (ac)	43	48	50	46	n. a.
md7 (ac)	43	55	50	44	43
md7 (cu)	−	n. a.	18	−	−
md8 (ac)	53	55	50	52	48
md9 (ac)	57	75	65	63	49
md10 (ac)	40	−	−	−	41
ld10 (ac) ♂	37/42	−	−	−	40/41
lv1 (ac)	33/32	37/38	38/39	35/43	34/36
vl2 (cu)	13/n. a.	15	16/15	13/ n. a.	10/n. a.
lv2 (ac)	37/31	41/39	37/34	n. a./33	34/37
lv3 (ac)	36/36	38/41	42/n. a.	34/ 36	41/40
lv4 (ac)	36/35	n. a./41	39/34	37/40	42/40
vl5 (cu)	16/15	n. a.	18	16/ n. a.	15/18
lv5 (ac)	43/41	42/44	43/36	43	41/41
lv6 (ac)	43/44	46	43	45/48	n. a./43
lv7 (ac)	45/42	45/48	46/45	45/47	44
lv8 (ac)	48/44	52/54	36/48	48/50	46/44
la8 (cu)	21/20	21/23	25	21/23	23/23
vl9 (cu)	18/21	18/19	19/20	16/n. a.	21/n. a.
lv9 (ac)	57/55	63/62	58/60	58/60	42/45
ltas (ac)	182/180	166/171	183/179	broken	180/181
mts (ac)	94	82	82	80	93
mts/tl	0.38%	0.30%	0.37%	0.28%	0.31%

Figure 1
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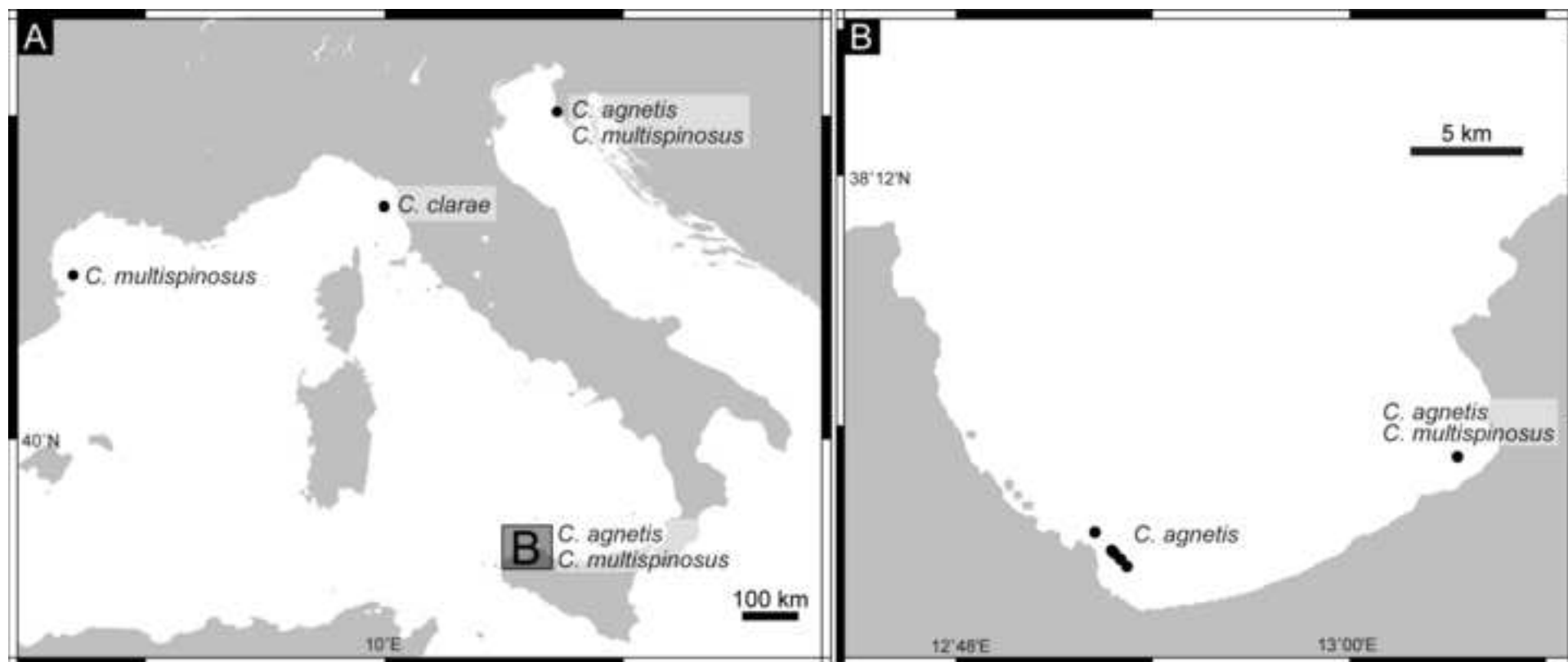
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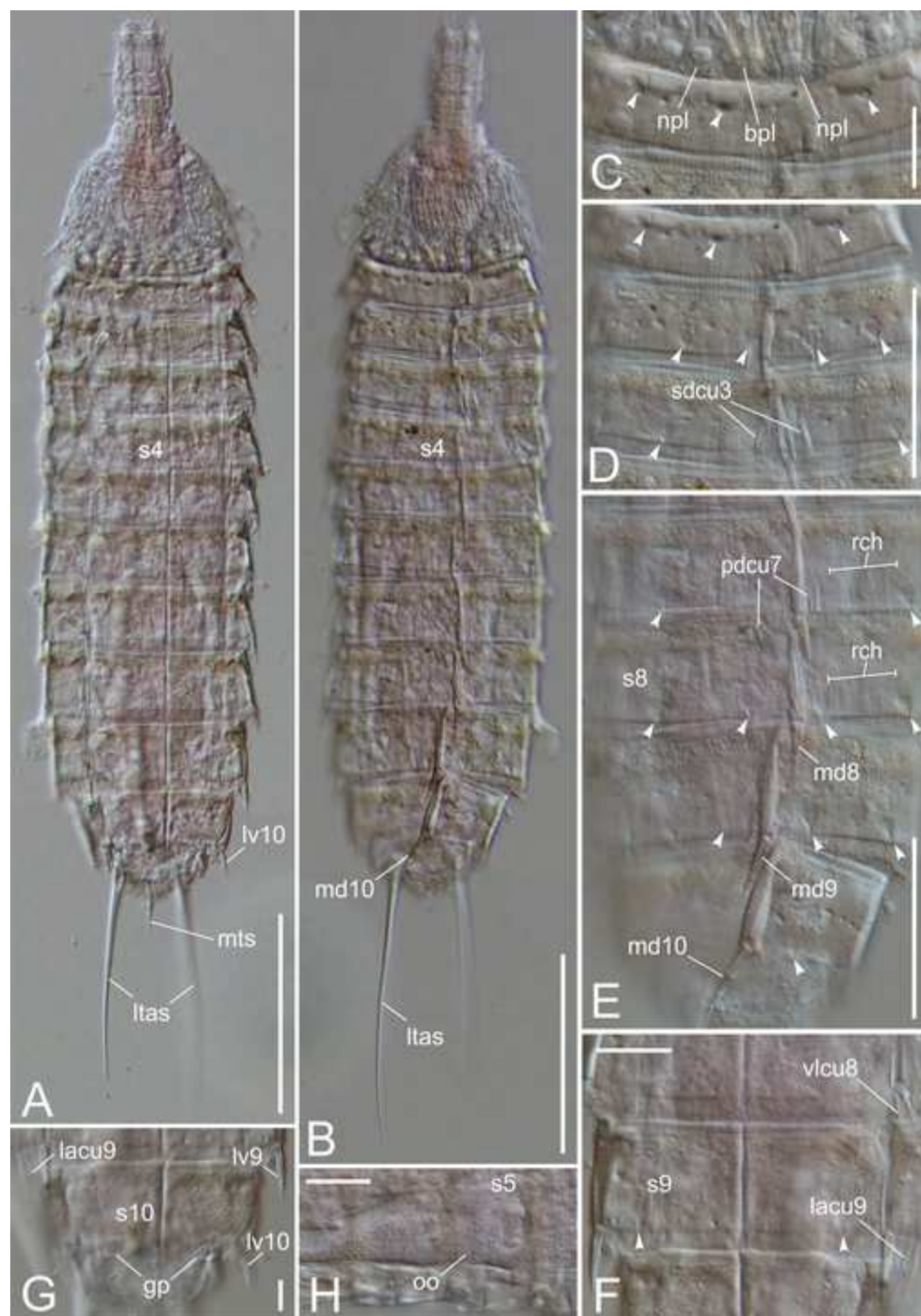
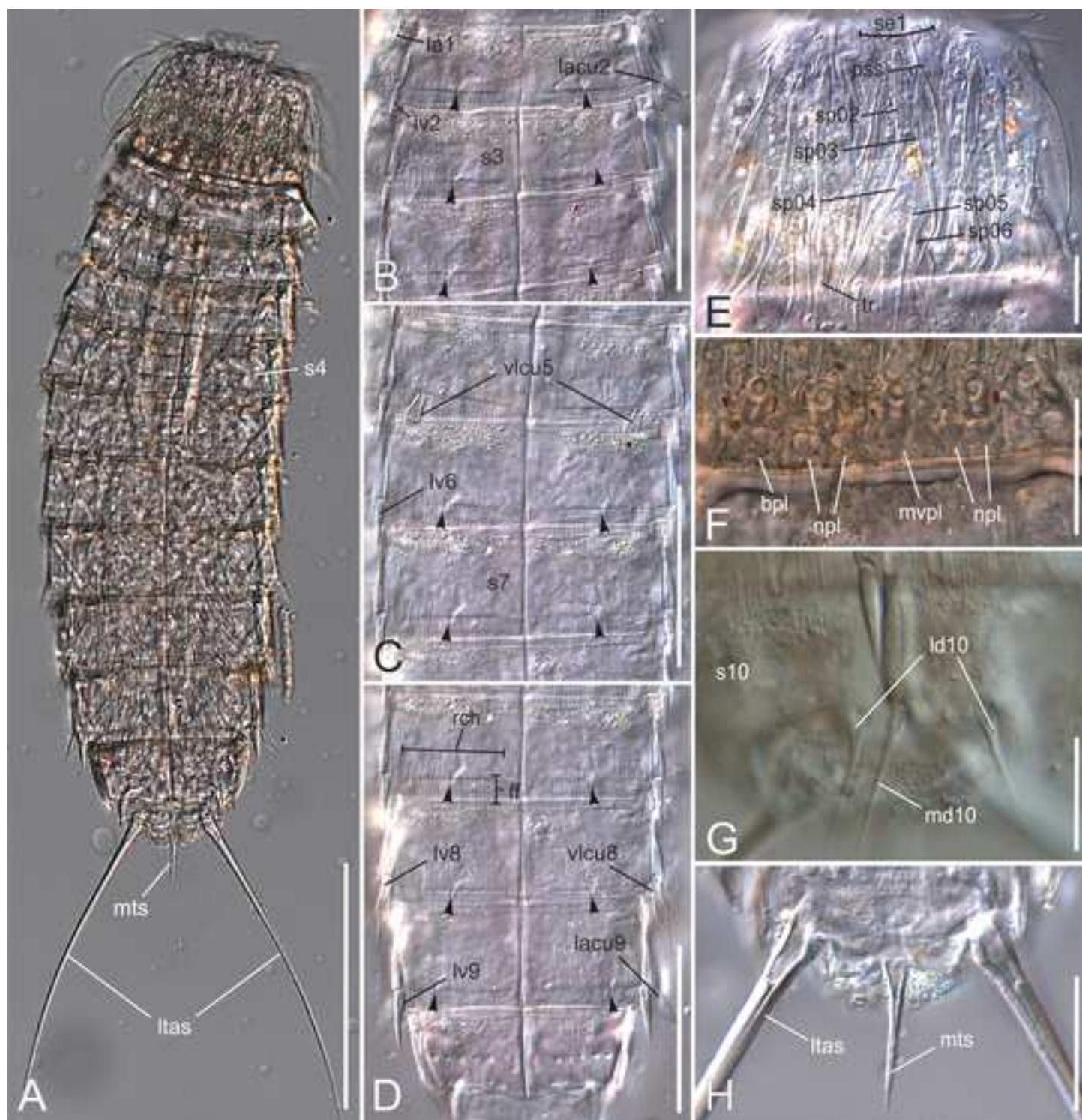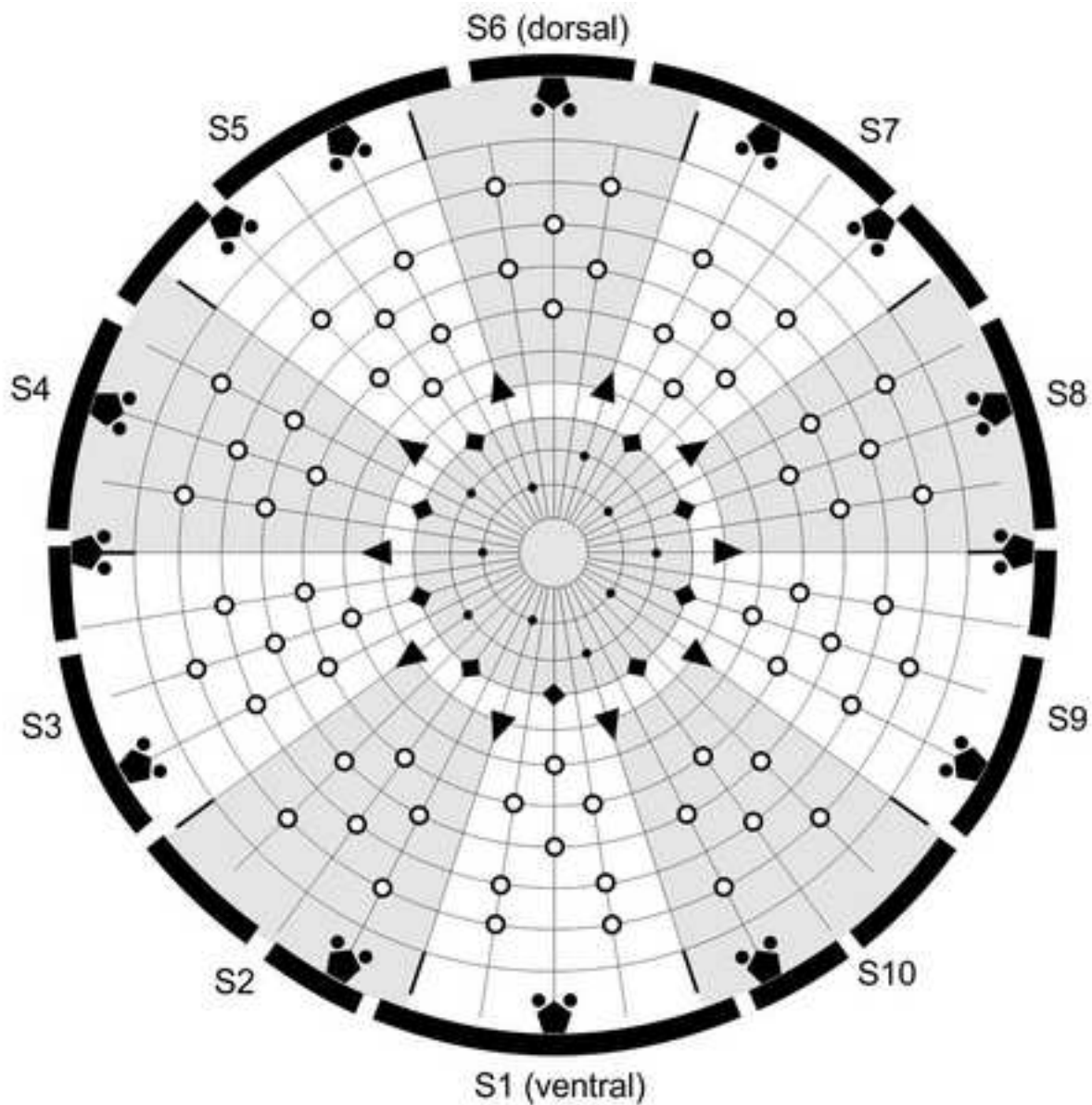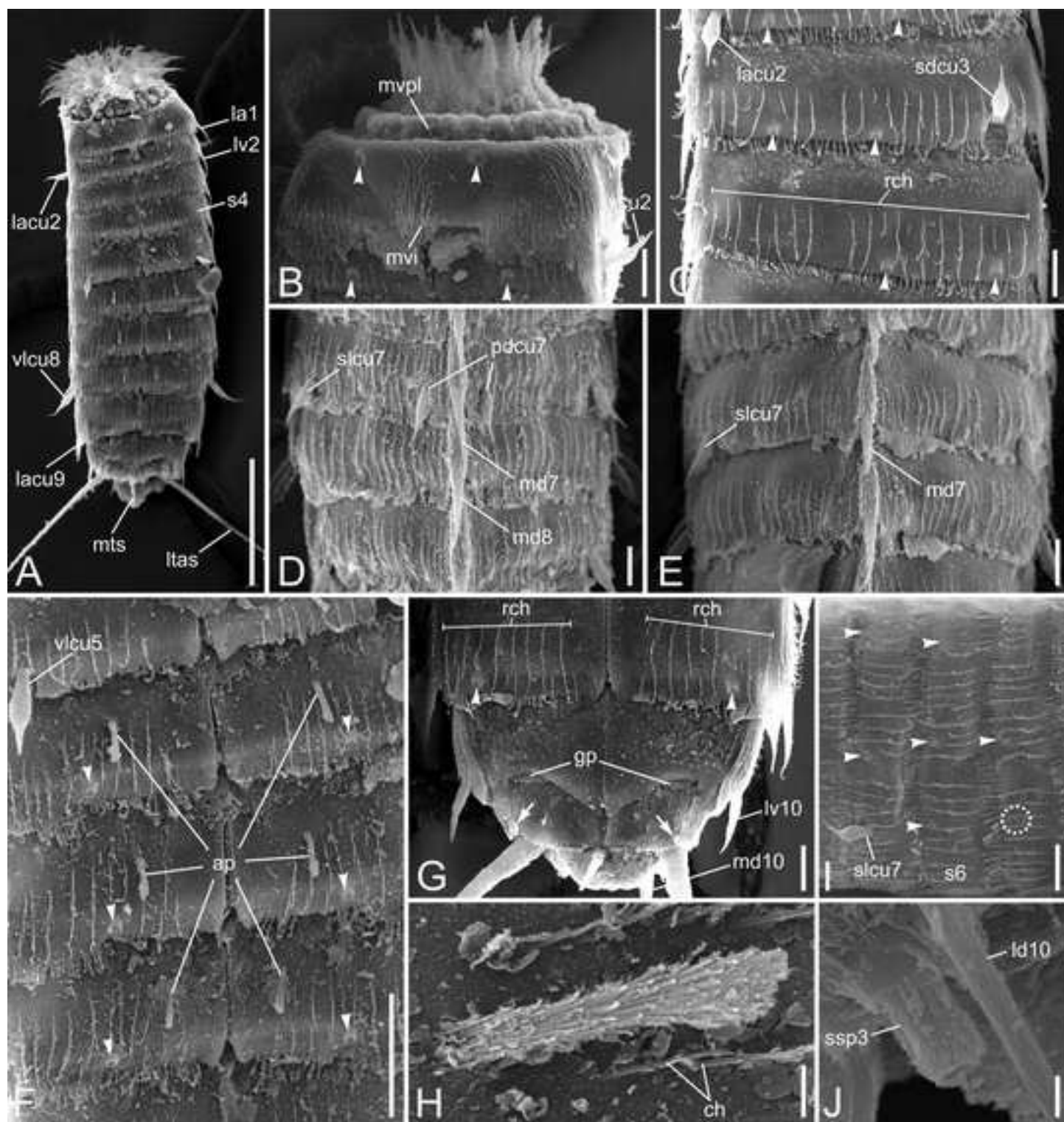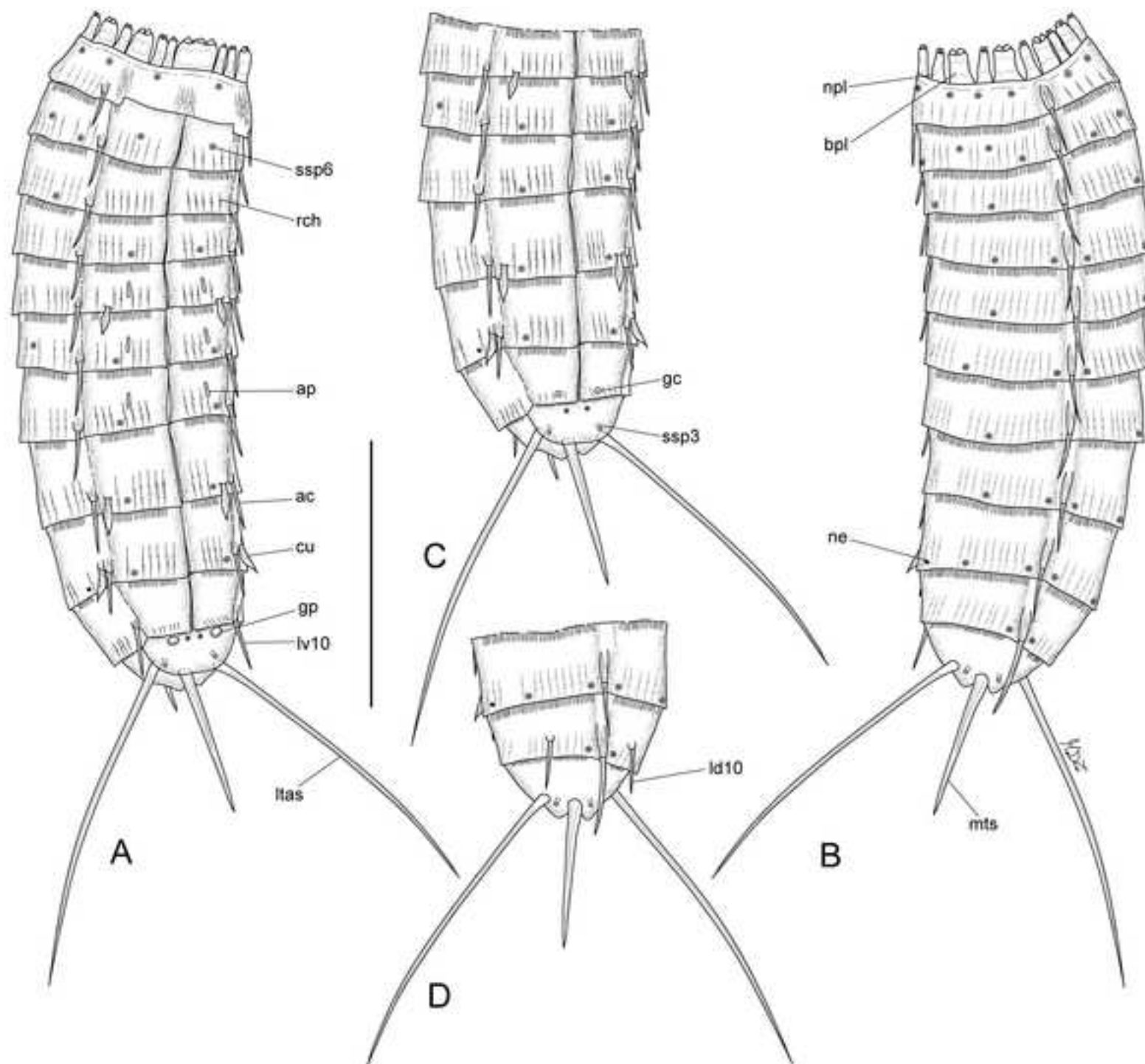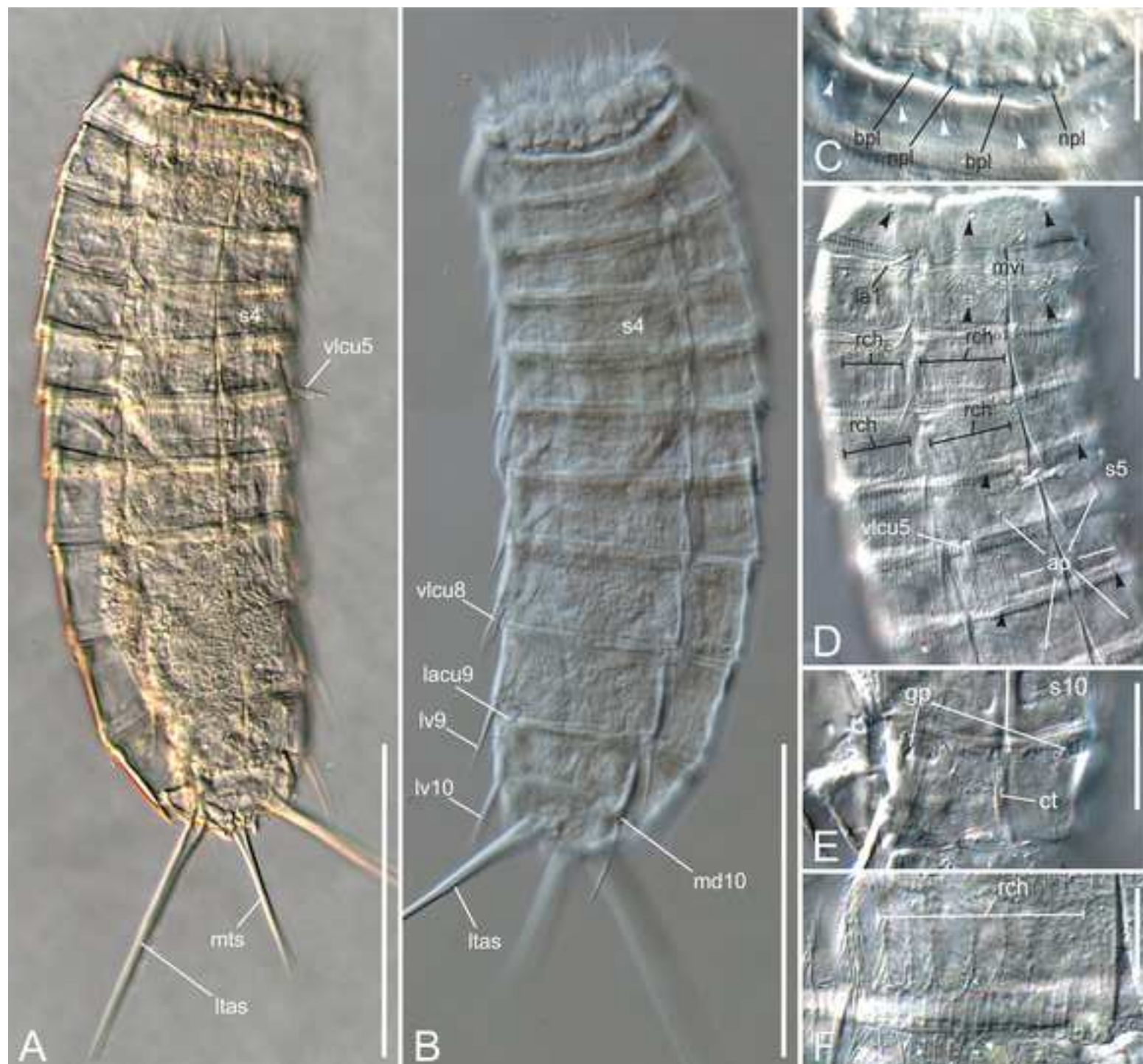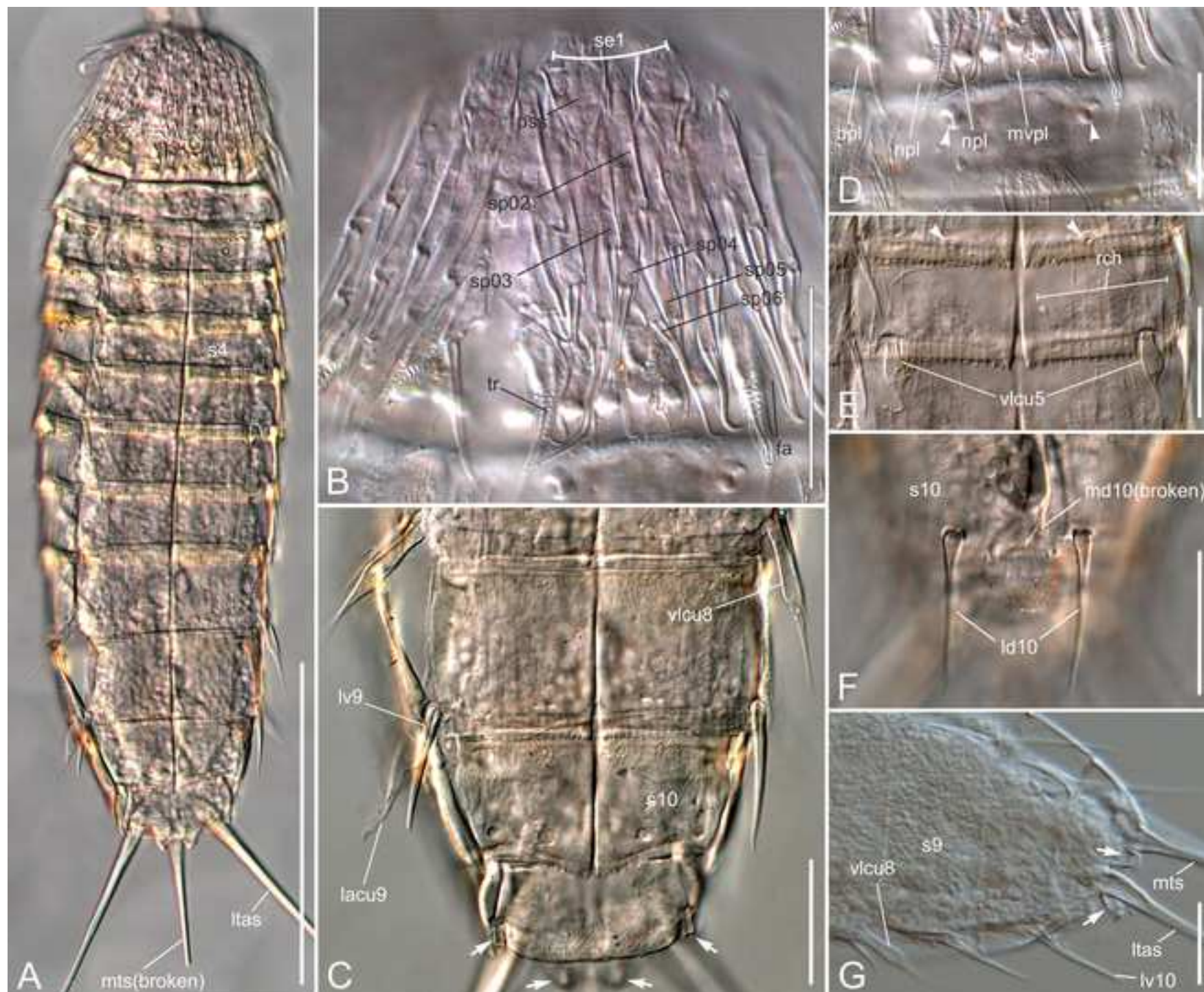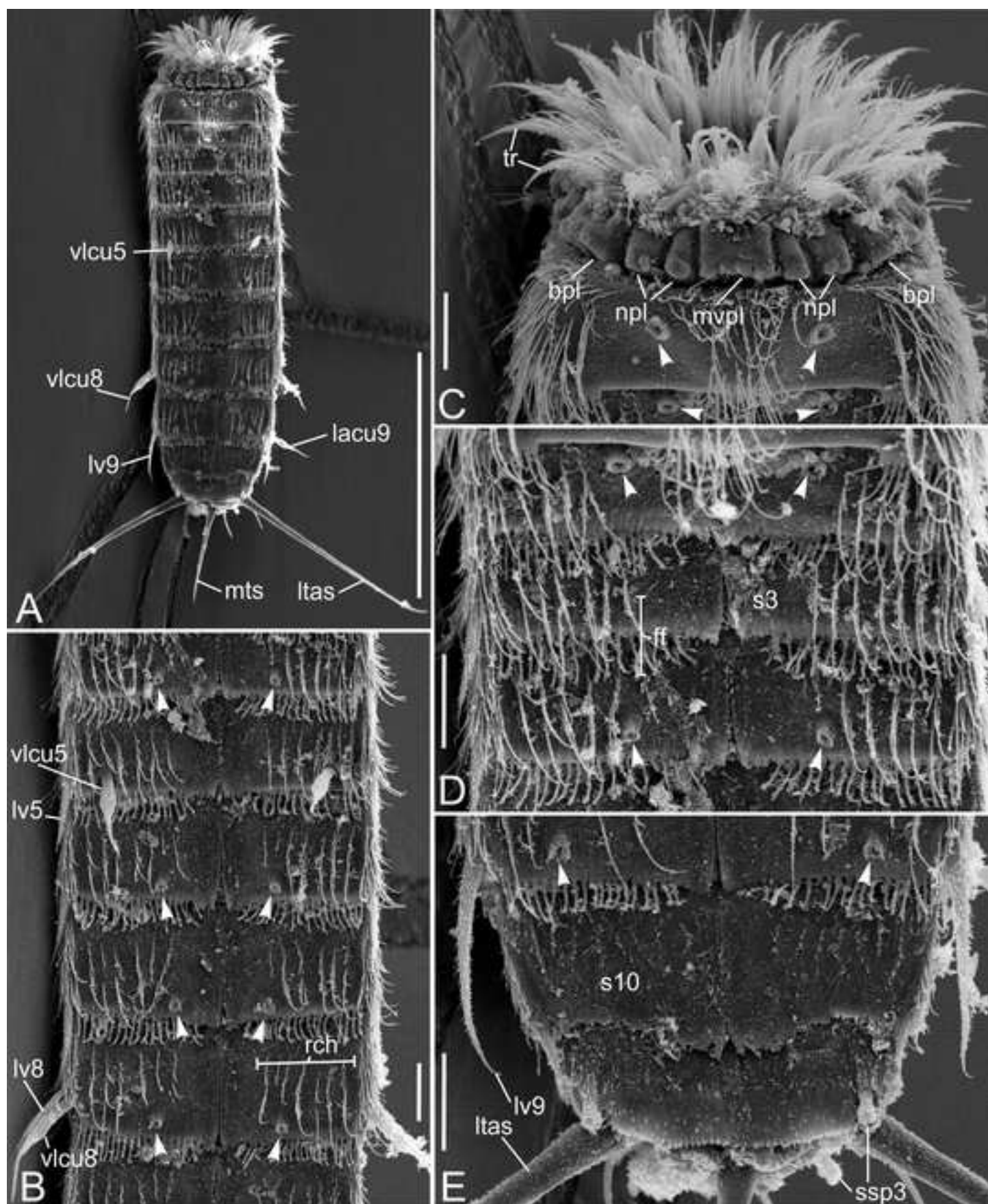**Figure 4**
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Figure 5

Style and scalid arrangement

Based on the ring:

Ring -02: 5 inner oral styles
Ring -01: 5 inner oral styles
Ring 00: 9 outer oral styles
Ring 01: 10 primary spinoscalids
Ring 02: 5 spinoscalids
Ring 03: 15 spinoscalids
Ring 04: 15 spinoscalids
Ring 05: 15 spinoscalids
Ring 06: 14 spinoscalids
Ring 07: 14 trichoscalids with 2
     filamentous appendages

Based on the sector:

Sector 1: 8 scalids
Sectors 2,4,5,6,7,8: 6 scalids
Sectors 3,9: 7 scalids

Total amount of scalids:

74 spinoscalids
14 trichoscalids

Figure 6
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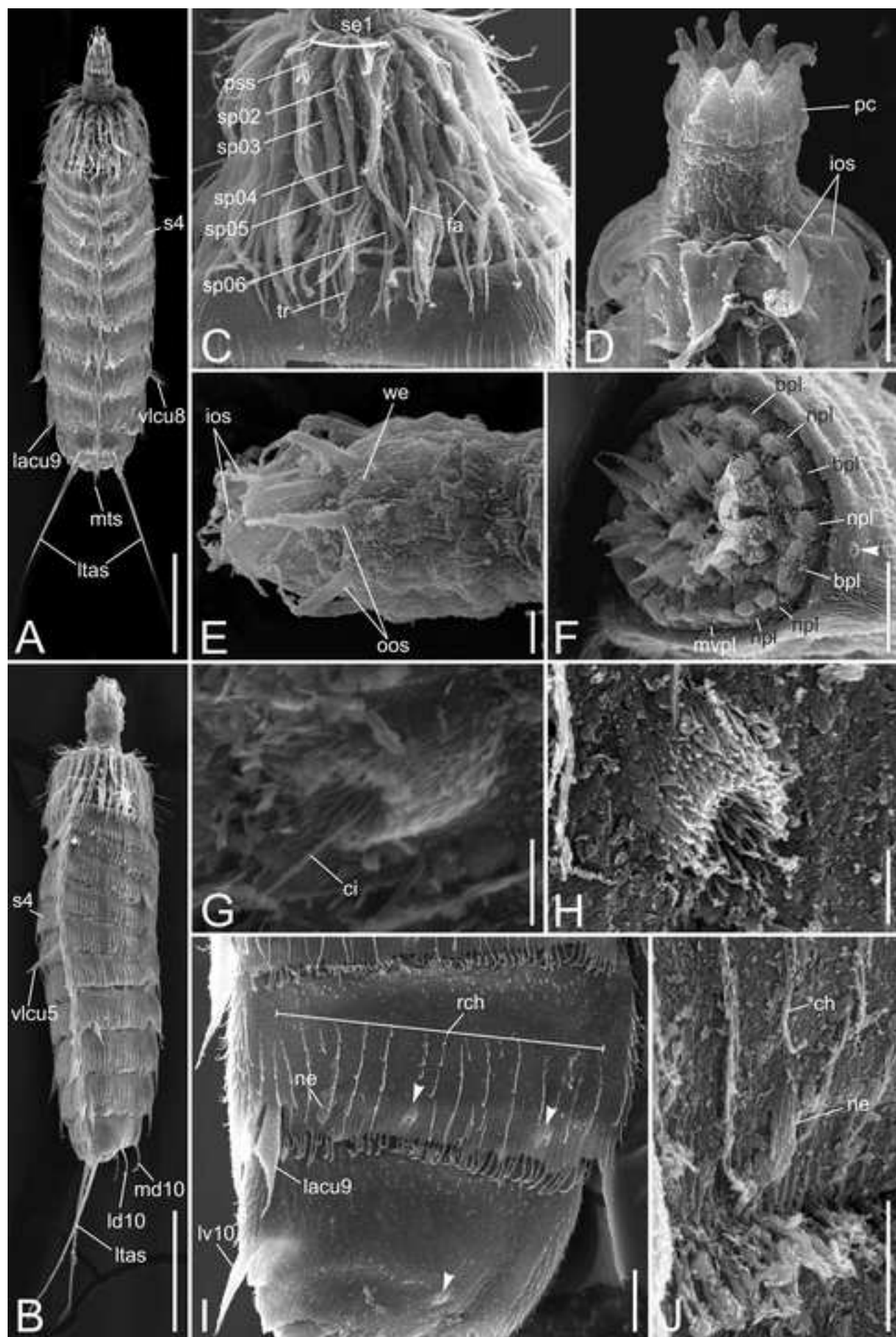
Figure 7
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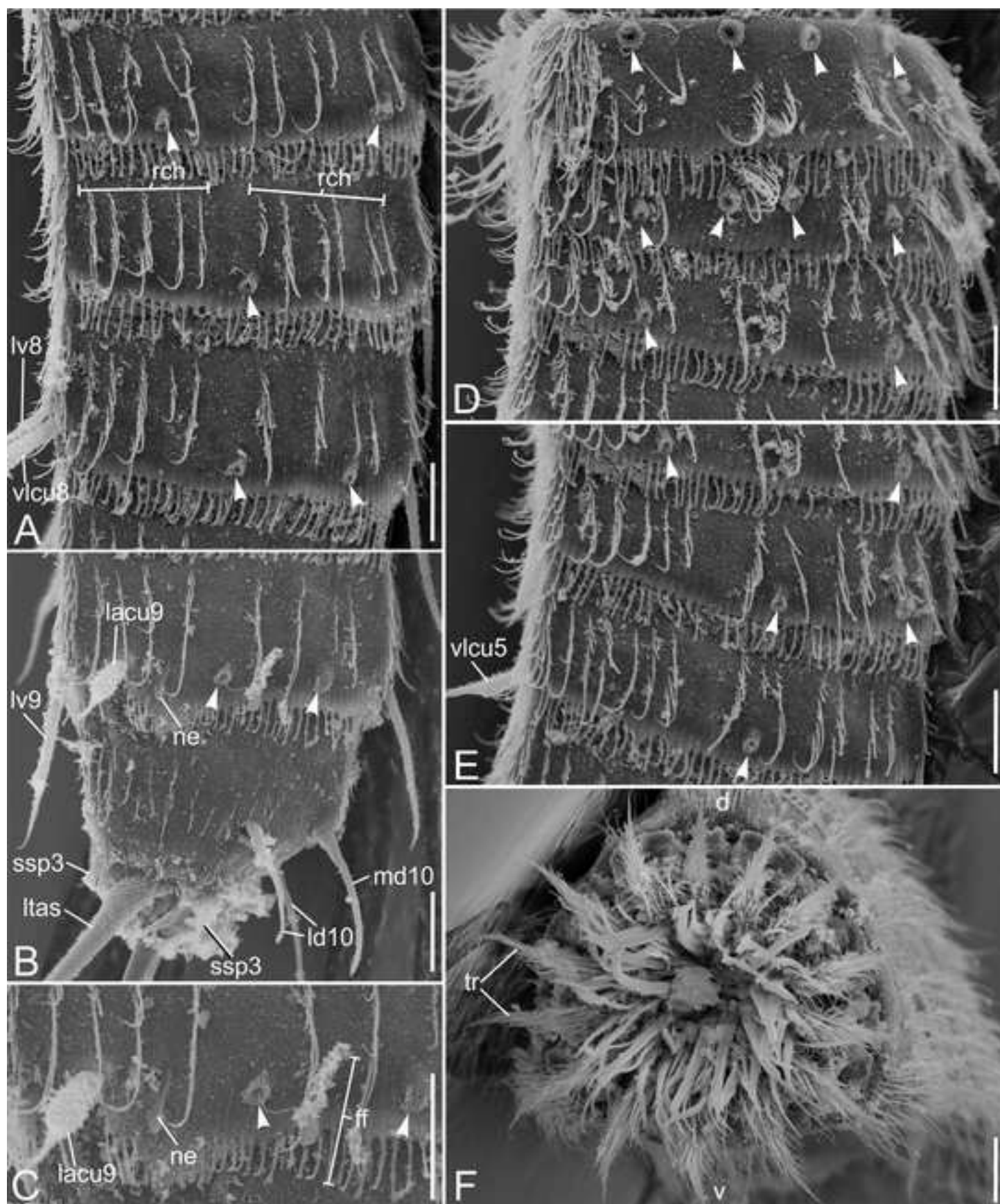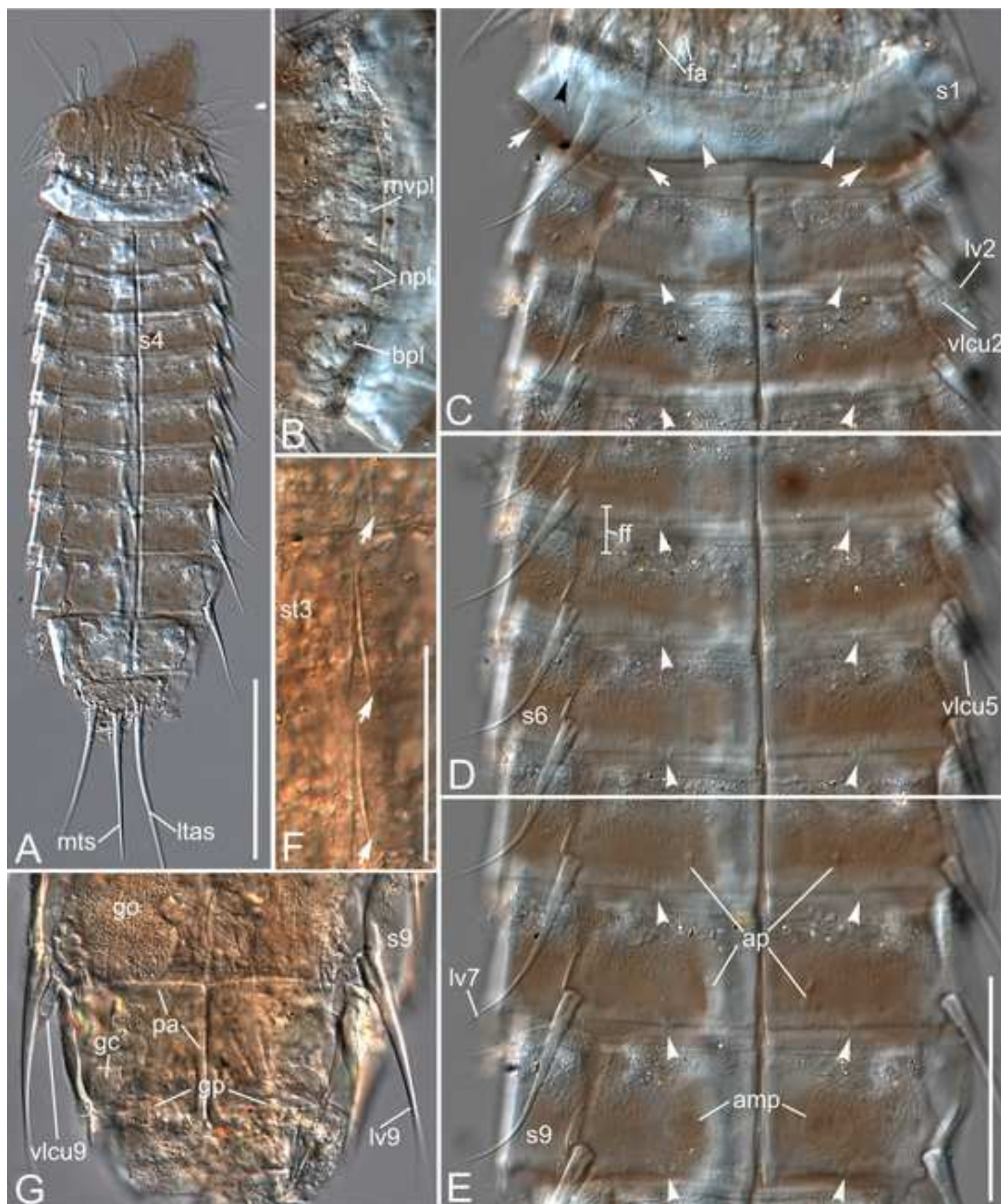**Figure 10**
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