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Three new species of Echinoderidae (Kinorhyncha: Cyclorhagida) from two seamounts and the adjacent deep-sea floor in the Northeast Atlantic Ocean

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Abstract: Three new species of *Echinoderes* (Kinorhyncha: Cyclorhagida: Echinoderidae) are described from two Northeast Atlantic seamounts and the adjacent deep-sea floor. *Echinoderes apex* sp. nov. from the Great Meteor Seamount and the Sedlo Seamount is characterized by a combination of: a small trunk length (165-215 µm); middorsal acicular spines on segments 4, 6, and 8; tubes ventrolaterally on segment 2, lateroventrally on segment 5, and laterodorsally on segment 10; lateroventral acicular spines on segments 6-9; long lateral terminal spines, 60.0-80.2% of trunk length; and type-2 glandular cell outlets subdorsally on segment 2, sublaterally on segment 6, and lateral accessorily on segment 8. *Echinoderes bathyalis* sp. nov. from the deep-sea floor near the Sedlo Seamount is characterized by a combination of: a small trunk length (224-243 µm); middorsal acicular spines on segments 4-8 with a spine on segment 8 being very long (ca. 50% of trunk length); lateral accessory tubes on segment 5; lateroventral acicular spines on segments 6-9; and type-2 glandular cell outlets midlaterally on segment 2. *Echinoderes meteorensis* sp. nov. from the Great Meteor Seamount differs from its congeners in a combination of: a small trunk length (157-196 µm); presence of middorsal acicular spines on segments 4, 6, and 8; tubes lateroventrally on segment 5, lateral accessorily on segment 8, and laterodorsally on segment 10; lateroventral acicular spines on segments 6-9; and type-2 glandular cell outlets in subdorsal and lateral accessory positions on segment 2. *Echinoderes apex* occurs on two seamount summits, whereas *E. meteorensis* occurs on one seamount summit, and no species occur both on a seamount summit and on the deep-sea floor.

Résumé : *Trois nouvelles espèces d'Echinoderidae (Kinoryncha: Cyclorhagia) provenant de deux monts sous-marins et du fonds marin adjacent dans le nord-est de l'Océan Atlantique*. Trois nouvelles espèces d'*Echinoderes* (Kinorhyncha: Cyclorhagida: Echinoderidae) sont décrites des montages sous-marines du nord-est de l'Atlantique et du fonds marin adjacent. *Echinoderes apex* sp. nov. des monts marins Great Meteor et Sedlon est caractérisé par une combinaison de : une petite longueur de tronc (165-215 µm) ; des épines aciculaires médiodorsales sur les segments 4, 6 et 8 ; des tubes ventrolatéraux sur le segment 2, latéroventraux sur le segment 5 et latérodorsaux sur le segment 10, des épines aciculaires latéroventrales sur les segments 6-9, des épines terminales latérales longues, 60.0-80.2% de la longueur du tronc, et des sortes de cellules glandulaires de type 2 subdorsales sur le segment 2, de manière sublatérale sur le segment 6, et accessoirement latérale sur le segment 8. *Echinoderes bathyalis* sp. nov. du fond marin près du mont Sedlo se caractérise par une combinaison de: une petite longueur de tronc (224-243 µm); des épines aciculaires médio-dorsales sur les segments 4-8 avec une épine sur le

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segment 8 très longue (environ 50% de la longueur du tronc); des tubes accessoires latéraux sur le segment 5; des épines aciculaires lateroventrales sur les segments 6-9; et des sortes de cellules glandulaires de type 2 dans la partie médiane du segment 2. *Echinoderes meteorensis* sp. nov. du mont Great Meteor diffère de ses congénères par une combinaison de: une petite longueur de tronc (157-196 μm); la présence d'épines aciculaires médiodorsales sur les segments 4, 6 et 8; des tubes latéroventraux sur le segment 5, accessoirement latéraux sur le segment 8, et plus latérodorsaux sur le segment 10; des épines aciculaires lateroventrales sur les segments 6-9; des sorte cellule glandulaire de type 2 dans les positions auxiliaires subdorsales et latérales du segment 2. *Echinoderes apex* se trouve sur les deux monts, tandis qu'*E. meteorensis* se trouve sur un sommet, et aucune espèce ne se trouve à la fois sur un sommet montagneux et sur le fonds marin.

Keywords: *Echinoderes* ● Meiofauna ● Taxonomy ● Fauna ● Biogeography

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Introduction

Knowledge on metazoan meiofauna on seamounts has accumulated since the report of an entoproct species, *Loxomespilon perezi* from the Great Meteor Seamount by Emschermann (1971). To date, 13 phyla and more than 350 meiofaunal species have been recorded from several seamounts, and the number of the species is still increasing. A recent review about meiofauna on seamounts by George (2013) also indicated a remarkable potential for endemism of seamount-meiofauna, with over 90% of recognized species being reported only from seamounts but not from surrounding areas. Kinorhyncha is one of the phyla that occurs on many seamounts, and also represents one of the dominant meiofaunal taxa there (e.g., George, 2013). However, there were only two reports which identified the kinorhynch specimens to species-level (Bauer-Nebelsick, 1996; Kristensen, 2005). In the other kinorhynch records from seamounts, specimens were identified only to phylum-level, and mentioned just as "Kinorhyncha" (e.g., Zeppilli et al., 2013).

Seamounts have also attracted attention for the distribution mechanism of meiofauna. Despite the low possible dispersal abilities of meiofauna because of the lack of free-swimming life history stages, some taxa show a wide distribution pattern (e.g., Giere, 2009), and seamounts possibly act as stepping stones and/or trapping stones for their dispersal. The "stepping stones" hypothesis proposes that seamounts help shallow-water fauna distributing widely beyond the deep sea as being intermediate habitats between shallow waters. In contrast, the "trapping stones" hypothesis suggests that (1) deep-sea floors prevent random exchanges of shallow-water meiofaunal populations, (2) meiobenthic organisms rarely reach a new habitat at a seamount, but if they do then they are trapped there, (3) if the new habitat on a seamount is a survivable place for the organisms, they will establish new populations and even speciate (George, 2013). To determine the actual role of seamounts for meiofaunal dispersal, sufficiently large sets of faunal data for various taxa from summits of multiple seamounts as well as the data from the geographically adjacent areas are required (George, 2013).

In this paper, we report two new echinoderid kinorhynchs from the Great Meteor Seamount and from the Sedlo Seamount (Northeast Atlantic Ocean), as well as one new species from the deep-sea floor adjacent to the Sedlo Seamount. This paper is the first in a series about Kinorhyncha from Northeast Atlantic and Mediterranean seamounts and surrounding areas.

Material and Methods

Kinorhynchs were obtained from meiofauna samples collected from the Sedlo Seamount and an adjacent deep-sea station on RV METEOR expedition M60/1 (OASIS) in 2003 and from the Great Meteor Seamount on RV POSEIDON cruise P397 (GROMET) in 2010 (Fig. 1 & Table 1). The sediment samples were taken with a multicorer, a boxcorer, and a Van Veen grab. The sediment from the Great Meteor Seamount was fixed by adding 10% formaldehyde to the same volume of sediment resulting in a concentration of 5% formaldehyde in the fixed samples. The sediment from Sedlo Seamount and the surrounding area wasfixed in 4-8% formaldehyde. The samples were washed with tap water through a 40 μm mesh sieve in the laboratory. Subsequently, the meiofauna was extracted from the sediment by centrifuging with a colloidal silica polymer (H.C. Stark, Levasil 200/40%, density 1.17 g.cm^{-3}) and Kaolin. After the extraction, the meiofauna was rinsed with tap water and sorted under a stereomicroscope.

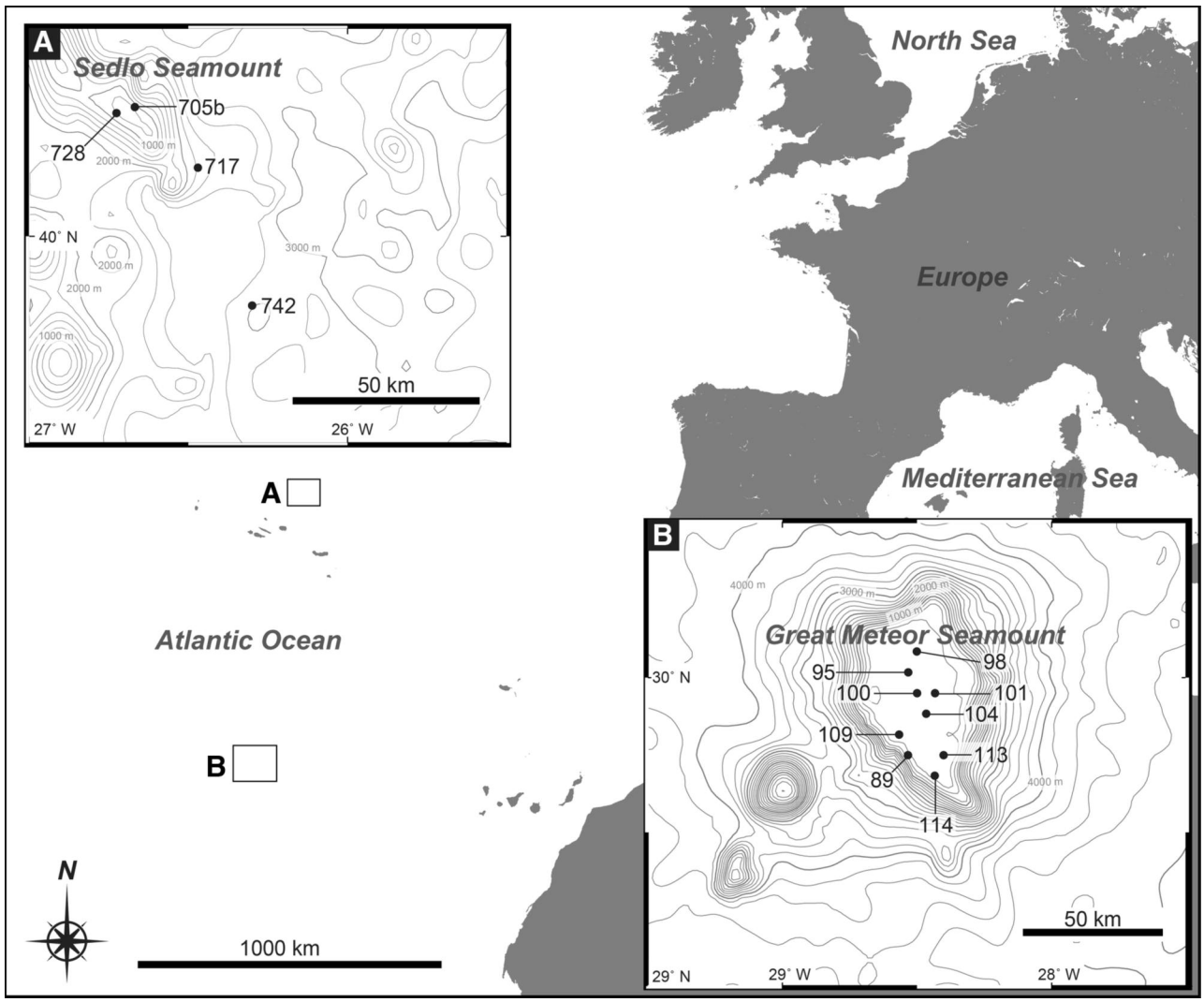

Figure 1. Map of the sampling localities. **A.** Enlarged map of the Sedlo seamount and surrounding deep-sea floor. **B.** Enlarged map of .the Great Meteor Seamount.

After the specimens were sorted, they were transferred into 4% formaldehyde.

Specimens for light microscopy (LM) were mounted as glycerol-paraffin slides on Cobb aluminum frames. LM specimens were observed with a Zeiss Axioskop 50 microscope equipped with Nomarski differential interference contrast, an Optovar 1.6×, objectives Plan-Neofluar 63/0.90 Korr. and 100/1.30 oil, and a camera lucida for drafts of line illustrations and measurements. Final line illustrations were drawn with Adobe Illustrator CS6 based on the drafts. Specimens were photographed with a Zeiss AxioCam MRc5 and objectives Plan-Neofluar 40×/0.75 and 100×/1.30 Ph3 oil attached to a microscope Zeiss Axioplan 2 mot.

Specimens for scanning electron microscopy (SEM) were transferred to distilled water through a graded series of ethanol, postfixed with OsO_4 in 0.05 M phosphate buffer (pH = 7.3) with 0.3 M sodium chloride and 0.05% sodium azide for 2.5 hours, dehydrated through a graded series of ethanol, critical-point dried, mounted on aluminum stubs, sputter-coated with gold-palladium, and observed with a Zeiss EVO LS 10 scanning electron microscope.

The terminology follows Neuhaus & Higgins (2002), Sørensen & Pardos (2008), and Neuhaus (2013). For comparison, ten specimens of *Echinoderes* cf. *ferrugineus*, which were collected at Sicily, Italy and reported in Dal Zotto & Todaro (2016), were given on loan by Dr Matteo Dal Zotto (University of Modena and Reggio Emilia). All specimens have been deposited in the Museum für Naturkunde Berlin (= ZMB, former Zoological Museum Berlin), Germany and catalogued in the collection "Vermes" in the "Generalkatalog Freilebende Würmer".

Table 1. Data on sampling stations.

Station	Seamount	cruise	date	depth (m)	latitude	longitude	gear	Species
89	Great Meteor Seamount	P397	14.03.2010	316	29°44'59.70"N	28°32'0.13"W	Van Veen-grab	*Echinoderes apex* sp. nov.; *Echinoderes meteorensis* sp. nov.
95	Great Meteor Seamount	P397	16.03.2010	287	30° 1'1.13"N	28°31'57.61"W	Van Veen-grab	*Echinoderes apex* sp. nov.; *Echinoderes meteorensis* sp. nov.
98	Great Meteor Seamount	P397	17.03.2010	309	30° 5'1.75"N	28°30'2.88"W	Van Veen-grab	*Echinoderes apex* sp. nov. *Echinoderes meteorensis* sp. nov.
100	Great Meteor Seamount	P397	18.03.2010	287	29°57'0.61"N	28°29'59.93"W	Van Veen-grab	*Echinoderes apex* sp. nov. *Echinoderes meteorensis* sp. nov.
101	Great Meteor Seamount	P397	18.03.2010	307	29°57'0.54"N	28°25'59.70"W	Van Veen-grab	*Echinoderes apex* sp. nov.
104	Great Meteor Seamount	P397	19.03.2010	300	29°52'58.62"N	28°27'57.24"W	Van Veen-grab	*Echinoderes apex* sp. nov. *Echinoderes meteorensis* sp. nov.
109	Great Meteor Seamount	P397	20.03.2010	309	29°48'59.15"N	28°34'0.48"W	Van Veen-grab	*Echinoderes apex* sp. nov. *Echinoderes meteorensis* sp. nov.
113	Great Meteor Seamount	P397	21.03.2010	292	29°44'59.82"N	28°24'2.88"W	Van Veen-grab	*Echinoderes apex* sp. nov.; *Echinoderes meteorensis* sp. nov.
114	Great Meteor Seamount	P397	21.03.2010	288	29°40'57.72"N	28°26'3.05"W	Van Veen-grab	*Echinoderes apex* sp. nov.; *Echinoderes meteorensis* sp. nov.
705b	Sedlo Seamount	M60/1	23.11.2003	774	40°19'0.00"N	26°40'0.00"W	multicorer	*Echinoderes apex* sp. nov
728	Sedlo Seamount	M60/1	23.11.2003	856	40°18'30.00"N	26°41'60.00"W	box corer	*Echinoderes apex* sp. nov
717	Sedlo Seamount	M60/1	24.11.2003	2.721	40°10'60.00"N	26°33'6.00"W	box corer	*Echinoderes bathyalis* sp. nov.
742	deep-sea plain near Sedlo Seamount	M60/1	29.11.2003	2.875	39°50'0.00"N	26°17'54.00"W	multicorer	*Echinoderes bathyalis* sp. nov.

Results

Class Cyclorhagida (Zelinka, 1896) Sørensen et al., 2015
Order Echinorhagata Sørensen et al., 2015
Family Echinoderidae Zelinka, 1894
Genus *Echinoderes* Claparède, 1863
Echinoderes apex sp. nov.
(Figs 2-7 & Tables 2-3)

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Diagnosis

Echinoderes with short trunk (165-215 µm); middorsal acicular spines on segments 4, 6, and 8; ventrolateral tubes on segment 2; lateroventral tubes on segment 5; lateroventral acicular spines on segments 6-9; laterodorsal tubes on segment 10; lateral terminal spine relatively long, 60.0-80.2% of trunk length; type-2 glandular cell outlets in subdorsal position on segment 2, sublateral position on segment 6, and lateral accessory position on segment 8.

Etymology

The species name is derived from Latin "*apex*", meaning "top" or "summit", and refers to the species occurring on the summits of two seamounts.

Material examined

Holotype: Female (ZMB 11561), collected at station 109 (Table 1) on the Great Meteor Seamount, mounted as glycerol-paraffin slide on a Cobb aluminum frame.

Paratypes: 14 males, 11 females, one recently moulted male, one recently moulted female, and one exuvia of a male. Two males (ZMB 11562b & c) and one female (ZMB 11562a), collected at station 89 on the Great Meteor

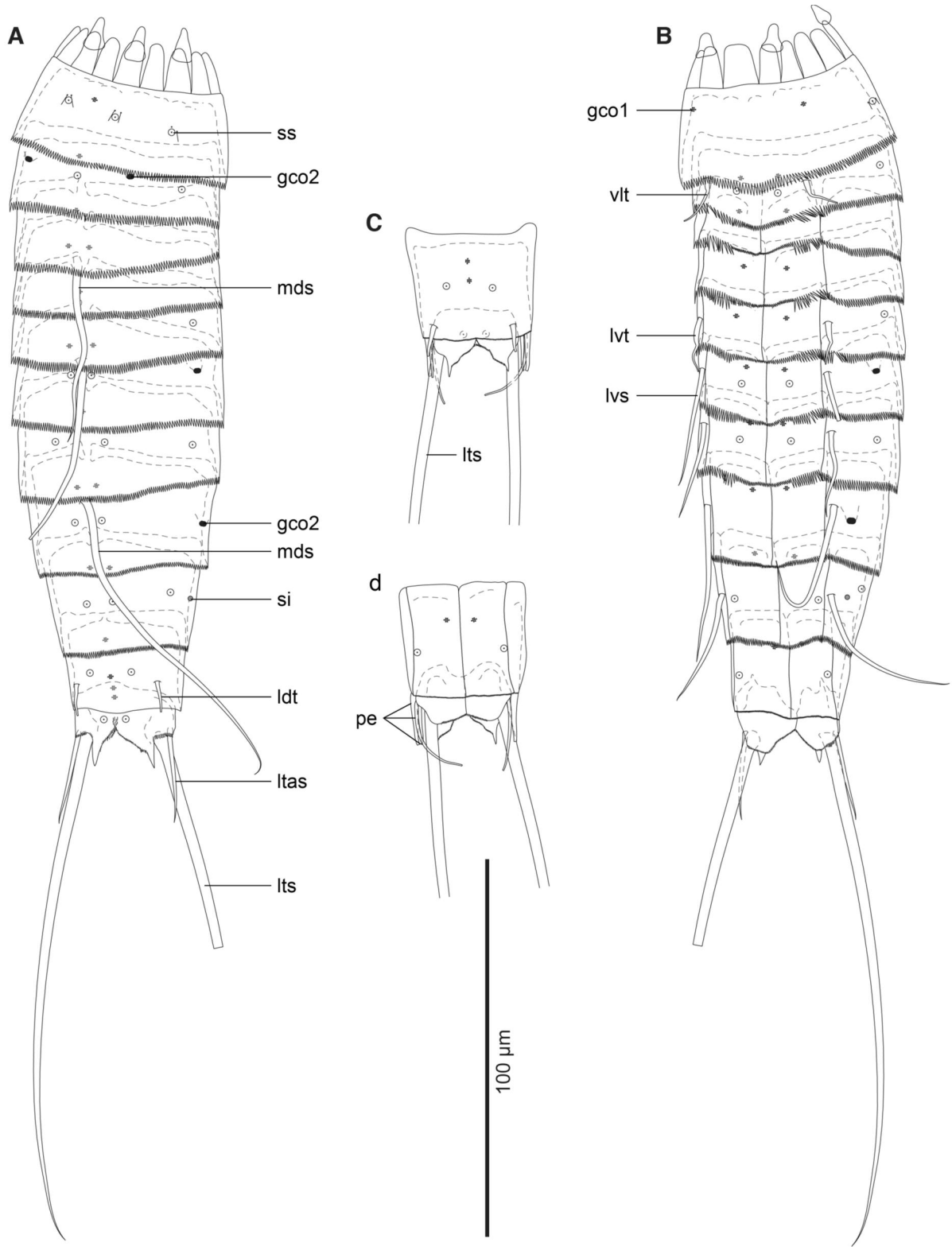


Figure 2. *Echinoderes apex* sp. nov. Camera lucida drawings. **A & B.** Holotype, female (ZMB 11561), entire animal, dorsal and ventral view of segments 1-11, respectively. **C & D.** Paratype, male (ZMB 11564d), segments 10 and 11, dorsal and ventral view, respectively. Abbreviations: gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine; si, sieve plate; ss, sensory spot; vlt, ventrolateral tube.

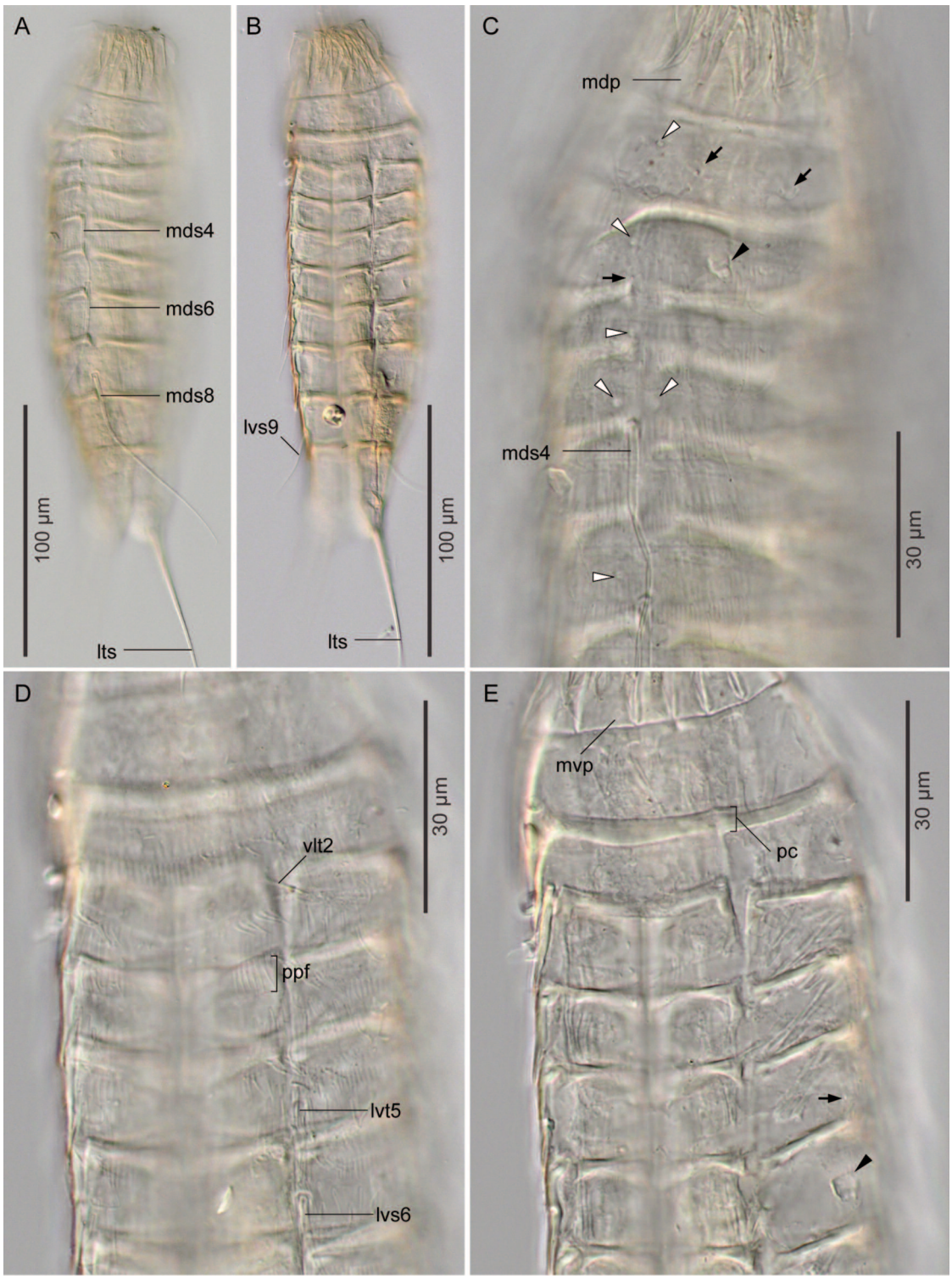


Figure 3. *Echinoderes apex* sp. nov. Nomarski photomicrographs of the holotypic female (ZMB 11561). **A.** Entire animal, dorsal view. **B.** Entire animal, ventral view. **C.** Neck and segments 1-6, dorsal view. **D.** Segments 1-6, ventral view, focusing on cuticular surface. **E.** Neck and segments 1-6, ventral view, focusing on subcuticular structures. Black arrows, white arrowheads, and black arrowheads indicate sensory spot, type-1 glandular cell outlet, and type-2 glandular cell outlet, respectively. Abbreviations: lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mdp, middorsal placid; mds, middorsal acicular spine; mvp, midventral placid; pc, pachycyclus; ppf, primary pectinate fringe; vlt, ventrolateral tube. Digits after abbreviations indicate the corresponding segment number.

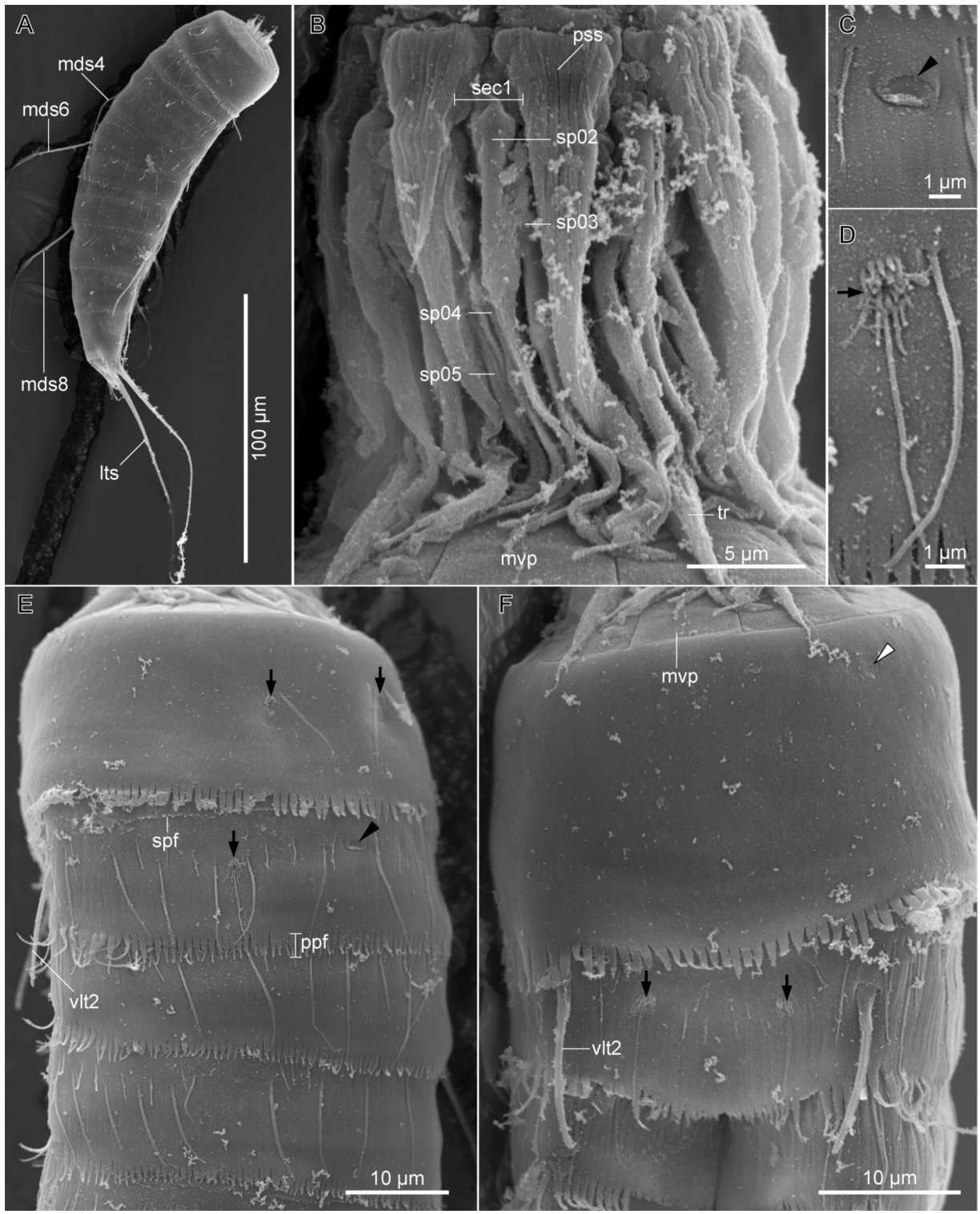


Figure 4. *Echinoderes apex* sp. nov. Scanning electron micrographs of males. **A.** Entire male animal, lateral view (right side). **B.** Introvert, ventral view. **C.** Close-up of subdorsal type-2 glandular outlet on segment 2. **D.** Close-up of midlateral sensory spot on segment 2. **E.** Segments 1-4, lateral view (left side). **F.** Segments 1-3, ventral view. Black arrows, white arrowhead, and black arrowheads indicate sensory spot, type-1 glandular cell outlet, and type-2 glandular cell outlet, respectively. Abbreviations: lts, lateral terminal spine; mds, middorsal acicular spine; mvp, midventral placid; ppf, primary pectinate fringe; pss, primary spinoscalids; sec, sector number; sp, spinoscalid; spf, secondary pectinate fringe; tr, trichoscalid; vlt, ventrolateral tube. Digits after abbreviations indicate sector number, ring number, or the corresponding segment number.

Seamount; two males (ZMB 11563e & f), two females (ZMB 11563a & b), one recently moulted male (ZMB 11563c), and one exuvia of a male (ZMB 11563d), collected at station 98 on the Great Meteor Seamount; two males (ZMB 11564c & d) and four females (ZMB 11564a, b, e & f), collected at station 100 on the Great Meteor Seamount; one female (ZMB 11565), collected at station 101 on the Great Meteor Seamount; seven males (ZMB 11566b, c, e, f, g, I & k), three females (ZMB 11566a, h & j), and one recently moulted female (ZMB 11566d), collected at station 109 on the Great Meteor Seamount; two males (ZMB 11567a & b), collected at station 114 on the Great Meteor Seamount (Table 1). All paratypes mounted as glycerol-paraffin slides on Cobb aluminum frames.

Additional material: one male collected at station 728 on the Sedlo Seamount (ZMB 11569) and two females collected at station 705b on the Sedlo Seamount (ZMB 11568a & b), mounted as glycerol-paraffin slides on Cobb aluminum frames for LM observations; 13 males and nine females mounted on aluminum stubs for SEM observations. Four males and two females collected at station 95 on the Great Meteor Seamount; four males and three females collected at station 98 on the Great Meteor Seamount; one male and two females collected at station 104 on the Great Meteor Seamount; four males and two females collected at station 113 on the Great Meteor Seamount (Table 1).

Type locality

The Great Meteor Seamount (29°48'59.15"N-28°34'0.48"W), 309 m depth.

Description

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

Head consisting of retractable mouth cone and introvert. Mouth cone with inner oral styles and nine outer oral styles. Exact number and arrangement of inner oral styles not examined because of withdrawn head in specimens. Each outer oral style consisting of rectangular basal part and triangular distal part, with basal part alternating in size between five larger ones in odd sectors and four smaller ones in even sectors. Introvert composed of at least 6 rings of spinoscalids and one ring of trichoscalids (Fig. 4b). Number of spinoscalids on ring 06 could not be counted completely. Trichoscalids of ring 07 attached to trichoscalid plates. Number and arrangement of outer oral styles, scalids, and placids summarized in figure 5.

Neck with 16 placids (Figs 2A-B, 3C, 4B & F & 5). Midventral placid broadest (ca. 10 µm wide at base). Remaining placids similar in size (ca. 6 µm wide at base).

Table 2. *Echinoderes apex* sp. nov. Measurements for adult (in micrometers) and relations between measurements. Columns N and SD indicate sample size and standard deviation, respectively. Abbreviations: (ac), acicular spine; (f), female condition of sexually dimorphic character; ld, length of laterodorsal tube; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; (m), male condition of sexually dimorphic character; md, length of middorsal spine; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube; vl, length of ventrolateral tube.

Character	N	Range	Mean	SD
tl	25	165-215	186	12.18
msw-8	12	30-38	33	2.56
msw-8/tl	10	17.0-20.2%	18.5%	1.08%
sw-10	13	27-33	29	1.54
sw-10/tl	11	14.3-17.2%	15.8%	0.94%
s1	13	26-30	28	1.28
s2	13	22-25	24	0.84
s3	12	17-20	18	0.91
s4	12	17-20	18	1.07
s5	12	18-20	19	0.63
s6	10	19-23	21	1.01
s7	12	21-28	23	1.84
s8	12	24-28	26	1.24
s9	13	25-31	27	1.50
s10	13	25-32	29	1.66
s11	12	17-23	20	2.13
md4 (ac)	24	42-67	57	5.31
md6 (ac)	20	57-80	73	6.14
md8 (ac)	24	74-99	87	6.77
vl2 (tu)	27	11-16	14	1.51
lv5 (tu)	29	9-19	14	2.30
lv6 (ac)	28	24-34	31	2.41
lv7 (ac)	27	31-41	36	2.94
lv8 (ac)	29	36-48	42	3.10
lv9 (ac)	28	40-52	44	3.15
ld10 (tu) (m)	16	9-19	13	2.55
ld10 (tu) (f)	12	8-12c	10	0.94
lts	24	102-149	127	13.24
ltas	13	21-25	23	1.42
lts/tl	21	60.0-80.2%	68.9%	5.81%
ltas/tl	11	10.5-14.4%	12.2%	1.03%

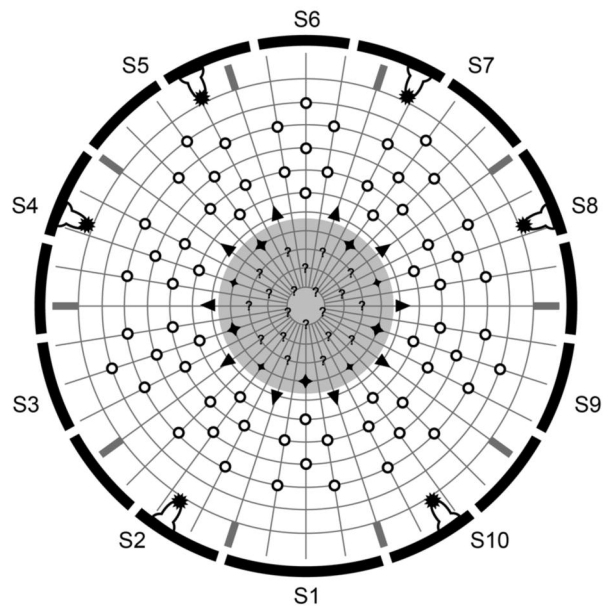
Segment 1 consisting of complete cuticular ring. Sensory spots located in subdorsal and laterodorsal positions: each sensory spot with short micropapillae surrounding single pore, and flanked by one to two non-

Table 3. *Echinoderes apex* sp. nov. Summary of locations of cuticular structures and appendages. Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pd, paradorsal; pe, penile spine; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

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

bracteate cuticular hairs (Figs 2A, 3C & 4E). Additional cuticular hairs absent or a few present near primary pectinate fringe on dorsal side. Type-1 glandular cell outlets present in middorsal and lateroventral positions (Figs 3C & 4F). Posterior part of this and following nine segments with primary pectinate fringe. Fringe tips on this segment medium in length.

Segment 2 with complete cuticular ring as in segment 1. This and following eight segments with thick pachycyclus at anterior margin (Fig. 3E). Ventrolateral tubes present (Figs 3D & 4E-F). Sensory spots present in middorsal, midlateral, and ventromedial positions (Figs 3C & 4D-F). Sensory spots of this and following segments with micropapillae surrounding single pore; single posteriormost micropapilla of each sensory spot elongates and gives the impression of cuticular hair (Fig. 4D). Two lines of bracteate cuticular hairs rising from perforation sites present in middorsal to ventrolateral area on this and following eight segments (Fig. 4E & F). Cuticular hairs of posterior line longer than those of other lines. Additional short bracteate cuticular hairs present in ventromedial area on this and next segment (Fig.4F). Type-1 glandular cell outlet present in middorsal and ventromedial positions (Fig. 3C). Type-2 glandular cell outlets in subdorsal position (Figs 3C, 4C & E). Fringe tips of primary pectinate fringe on middorsal to ventrolateral areas similar to those on segment 1, whereas those on ventromedial to midventral areas shorter on this and following five segments (Figs 2A-B, 3D & 4F). Single line of secondary pectinate fringe present at anterior part of segment on this and following eight segments (Fig. 4E). Primary pectinate fringe of preceding segment overlaps secondary pectinate fringe in most segments of many specimens.



Scalid and style arrangement

Ring/Section	1	2	3	4	5	6	7	8	9	10	Total
00 outer oral styles ✦	1	1	1	1	1	0	1	1	1	1	9
01 primary spinoscalids ▼	1	1	1	1	1	1	1	1	1	1	10
02 spinoscalids o	1	1	1	1	1	1	1	1	1	1	10
03 spinoscalids o	2	2	2	2	2	2	2	2	2	2	20
04 spinoscalids o	1	1	1	1	1	1	1	1	1	1	10
05 spinoscalids o	2	2	2	2	2	2	2	2	2	2	20
06 spinoscalids o	0?	0?	1?	0?	1?	1?	1?	0?	1?	0?	>5
07 trichoscalids ✹	0	1	0	1	1	0	1	1	0	1	6

Figure 5. *Echinoderes apex* sp. nov. Polar-coordinate diagram of mouth cone, introvert and placids. Grey area and heavy line arcs show mouth cone and placids, respectively. The table lists the scalid arrangement by sector.

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Sensory spots absent. Type-1 glandular cell outlets situated in middorsal and ventromedial positions (Fig. 3C).

Segment 4 with middorsal acicular spine (Figs 3A & C, 4A & 6A). Type-1 glandular cell outlets present in paradorsal and ventromedial positions (Figs 3C & 6A). No sensory spots present.

Segment 5 with lateroventral tubes (Figs 3D, 6B & 7A-B). Sensory spots situated in sublateral position (Figs 3E & 7B). Type-1 glandular cell outlets existing in middorsal and ventromedial positions.

Segment 6 with middorsal and lateroventral acicular spines (Figs 3A, 4A, 6A-B & 7A-C). Sensory spots present in paradorsal and ventromedial positions (Figs 6A & 7A-C). Type-1 glandular cell outlets situated paradorsally and ventromedially (Figs 3C & 6A). Type-2 glandular cell outlets placed sublaterally (Figs 3E & 7B-C).

Segment 7 with lateroventral acicular spines (Figs 6B & 7A-B). Sensory spots present in subdorsal, sublateral, and ventromedial positions (Figs 6A & 7A-C). Type-1 glandular cell outlets located middorsally and ventromedially.

Segment 8 with middorsal and lateroventral acicular spines (Figs 3A, 4A, 6A-C & 7B-E). Sensory spots present in paradorsal position (Figs 6A & 7C-D). Type-1 glandular cell outlets situated in paradorsal and ventromedial positions (Fig. 6A). Type-2 glandular cell outlets located in lateral accessory position (Figs 6B & 7B).

Segment 9 with lateroventral acicular spines (Figs 3B, 6B-C & 7D-E). Paradorsal, laterodorsal, and ventrolateral sensory spots present (Fig. 7D & E). Type-1 glandular cell outlets situated in paradorsal and ventromedial positions. Small sieve plates placed in sublateral position.

Segment 10 with laterodorsal tubes, similar in length between males and females (Figs 6E, 7D & F). Subdorsal and ventrolateral sensory spots present (Fig. 7D-F). Two type-1 glandular cell outlets aligned middorsally. Additional pair of type-1 glandular cell outlets situated in ventromedial position. Fringe tips of primary pectinate fringe very short.

Segment 11 with lateral terminal spines (Figs 3A-B, 4A, 6E, 7D & F). Lateral terminal accessory spines present in females (Figs 2A-B, 6D & 7D). Three pairs of penile spines existing in males (Figs 2C-D, 6C & 7F). Penile spines of most dorsal and most lateral pairs thin and long; those of middle pair stout and triangular. Paradorsal sensory spots present (Fig. 7D). Two type-1 glandular cell outlets aligned middorsally. Posterior edges of sternal plates rounded. Posterior edge of tergal plate protruding subdorsally, forming pointed tergal extensions.

Recently moulted specimens similar to more mature adults in morphometry and positions of acicular spines, tubes, glandular cell outlets, and sensory spots, except for thinner trunk cuticle and presence of button-like structures in cuticular flap of segments 1-10 (Fig. 6F).

Remarks

The presence of middorsal spines only on segments 4, 6, and 8 is found in 17 species of the congeners, however, only three of these species lack lateral accessory spines or tubes on segment 8 like in *E. apex* sp. nov. These three species are *Echinoderes arlis* Higgins, 1966, *Echinoderes bermudensis* Higgins, 1982, and *Echinoderes joyceae* Landers & Sørensen, 2016 (see Higgins, 1966a & 1982; Landers & Sørensen, 2016).

Echinoderes apex sp. nov. shares with *E. arlis* having ventrolateral tubes on segment 2 and type-2 glandular cell outlets in subdorsal position on segment 2, but can be distinguished from *E. arlis* in the absence of type-2 glandular cell outlets in sublateral position on segment 2 and presence of sublateral tubes on segment 5 (tubes on segment 5 in *E. arlis* situated more laterally, in sublateral position). These characters were not mentioned in the original description of *E. arlis* (Higgins, 1966a) but were confirmed by a reexamination of the species by Dr Martin V. Sørensen (Sørensen pers. comm.). In addition, *E. apex* sp. nov. and *E. arlis* can be distinguished by their different body sizes (165-215 µm trunk length in *E. apex* sp. nov., whereas 380-420 µm in *E. arlis*) (see Higgins, 1966a).

Echinoderes apex sp. nov. differs from *E. bermudensis* in having laterodorsal tubes on segment 10 and type-2 glandular cell outlets on segment 2, 6, and 8 (Higgins, 1982).

Echinoderes apex sp. nov. is most similar to *E. joyceae*. The two species show a similar trunk length and agree in the same number and position of spines, tubes, type-2 glandular cell outlets on the same segments, suggesting that they are phylogenetically closely related. The conspicuous differences between *E. apex* sp. nov. and *E. joyceae* are the appearances of some sensory spots (e.g., ventromedial ones on segment 2 present in *E. apex* sp. nov., but absent in *E. joyceae*; subdorsal ones on segment 3 absent in *E. apex* sp. nov., but present in *E. joyceae*), and the lengths of lateral terminal spines (102-149 µm and 60.0-80.2% of trunk length in *E. apex* sp. nov., but 72-83 µm and 39.3-42.9% of trunk length in *E. joyceae*) and lateroventral acicular spines (40-52 µm in *E. apex* sp. nov., but 31-34 µm in *E. joyceae*) (Landers & Sørensen, 2016).

The other 14 species with middorsal spines only on segments 4, 6, and 8 differ from *E. apex* sp. nov. in the characters on segment 2 additional to the presence of lateral accessory spines or tubes on segment 8. *Echinoderes abbreviates* Higgins, 1983, *Echinoderes belenae* Pardos et al., 2016a, *Echinoderes hispanicus* Pardos et al., 1998, *Echinoderes intermedius* Sørensen, 2006, *Echinoderes newcaledoniensis* Higgins, 1967, *Echinoderes peterseni*

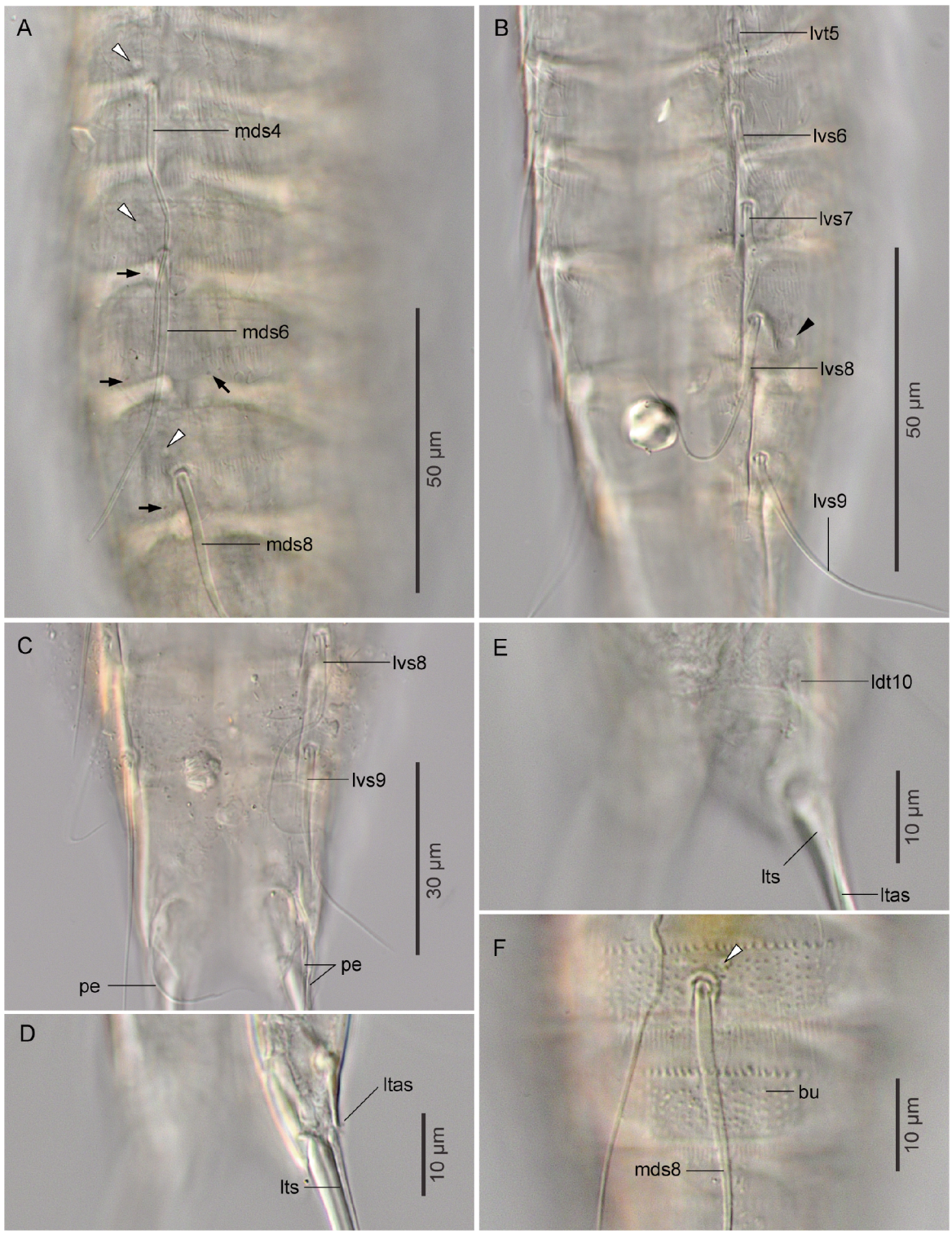


Figure 6. *Echinoderes apex* sp. nov. Nomarski photomicrographs of the holotypic female (ZMB 11561) (A, B, D, E), a paratypic male (ZMB 11564d) (C), and a recently moulted female (ZMB 11566d) (F). **A.** Segments 4-8, dorsal view. **B.** Segments 5-10, ventral view. **C.** Segments 6-11, ventral view. **D.** Segments 11, ventrolateral view. **E.** Segments 10 and 11, dorsal view. **F.** Segments 8 and 9, dorsal view. Black arrows, white arrowheads, and black arrowheads indicate sensory spot, type-1 glandular cell outlet, and type-2 glandular cell outlet, respectively. Abbreviations: bu, button-like structure; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine. Digits after abbreviations indicate the corresponding segment number.

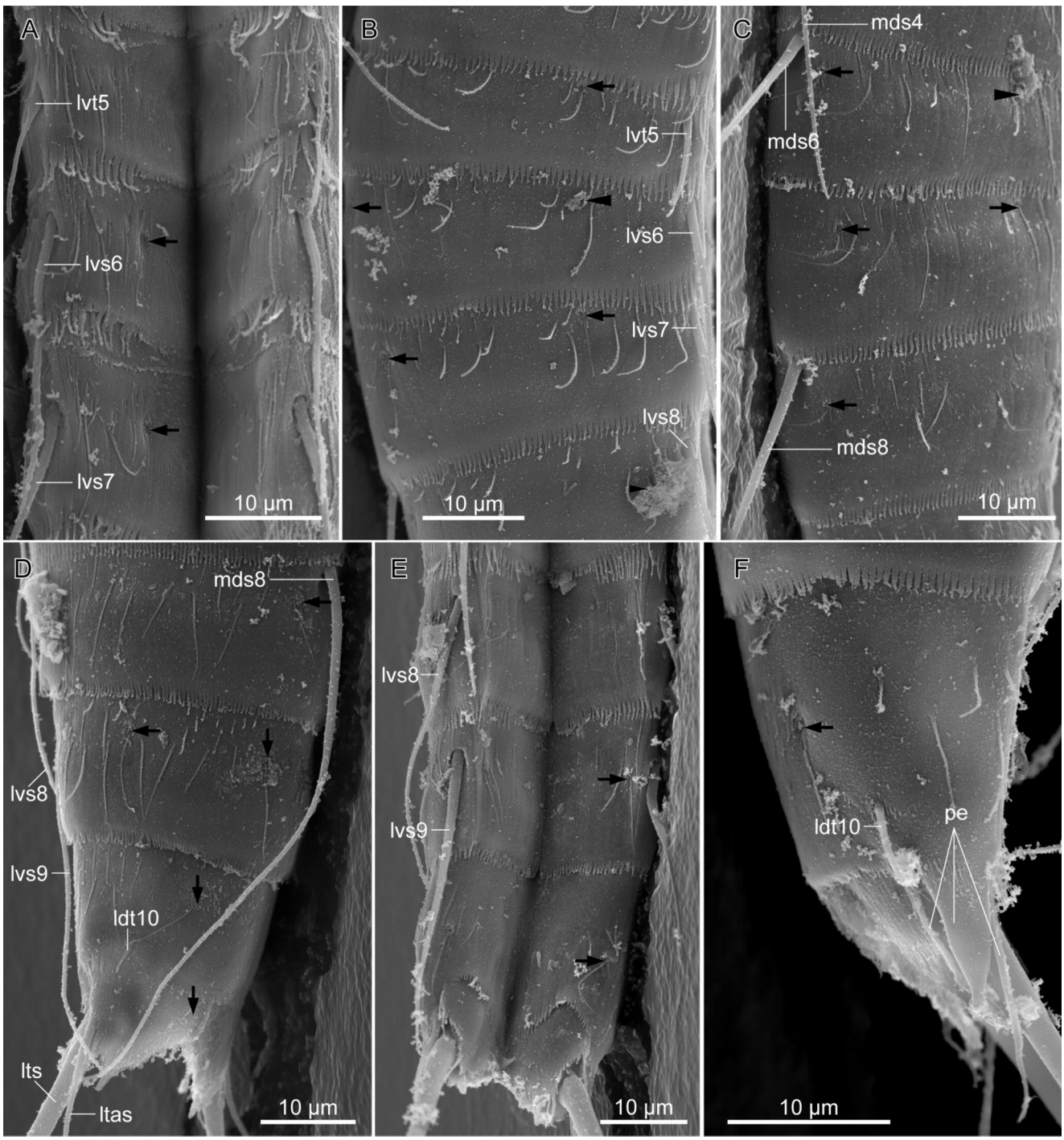


Figure 7. *Echinoderes apex* sp. nov., scanning electron micrographs of males (A-C, E, F) and a female (D). **A.** Segments 5-7, ventral view. **B.** Segments 4-8, lateral view (right side). **C.** Segments 6-8, laterodorsal view. **D.** Segments 8-11, laterodorsal view. **E.** Segments 8-11, ventral view. **F.** Segments 10-11, lateral view (right side). Black arrows and black arrowheads indicate sensory spot and type-2 glandular cell outlet, respectively. Abbreviations: ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine. Digits after abbreviations indicate the corresponding segment number.

Higgins & Kristensen, 1988, *Echinoderes rociae* Pardos et al., 2016b, and *Echinoderes skipperae* Sørensen & Landers, 2014 have two or more pairs of tubes on segment 2, whereas the new species has only one pair of tubes (Higgins, 1967 & 1983; Higgins & Kristensen, 1988; Pardos et al., 1998, 2016a & b; Sørensen, 2006; Sørensen & Landers, 2014). *Echinoderes kristenseni* Higgins, 1985 and *Echinoderes wallaceae* Higgins, 1983 possess type-2 glandular cell outlets in the subdorsal and ventrolateral/lateroventral positions, *Echinoderes higginsi* Huys & Coomans, 1989, *Echinoderes riceae* Herranz et al., 2014, and *Echinoderes riedli* Higgins, 1966b have no type-2 glandular cell outlets, whereas the new species shows type-2 glandular cell outlets only in the subdorsal position (Herranz et al., 2014; Higgins, 1966b & 1978; Huys & Coomans, 1989; Sørensen et al., 2016). *Echinoderes apex* sp. nov. differs from *E. meteorensis* sp. nov. in the presence of ventrolateral tubes on segment 2 (see also below).

Echinoderes bathyalis sp. nov.
(Figs 8-10 & Tables 4-5)

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Diagnosis

Echinoderes with short trunk (224-243 µm); middorsal acicular spines on segments 4-8; middorsal acicular spine on segment 8 very long (more than 100 µm, about half of trunk length); lateral accessory tubes on segment 5; lateroventral acicular spines on segments 6-9; type-2 glandular cell outlets in midlateral position on segment 2 and in lateral accessory position on segment 8 of recently moulted male.

Etymology

The species name "*bathyalis*" is derived from the Greek "*bathys*", meaning "deep", and refers to the species inhabiting the deep-sea floor.

Material examined

Holotype. Female (ZMB 11576), collected at station 742 in the deep-sea plain near the Sedlo Seamount (Table 1), mounted as glycerol-paraffin slide on a Cobb aluminum frame.

Paratypes. Male (ZMB 11577), collected at station 717 at the foot of the Sedlo Seamount; one recently moulted male (ZMB 11578), collected at station 742 in the deep-sea plain near the Sedlo Seamount (Table 1). All paratypes mounted as glycerol-paraffin slides on Cobb aluminum frames.

Type locality

Deep-sea plain near the Sedlo Seamount (39°50'0.00"N-26°17'54.00"W), 2,875 m depth.

Description

Adult with head, neck, and eleven trunk segments (Figs 8A-B & 9A). See table 4 for measurements. Table 5 indicates the positions of cuticular structures (sensory spots, glandular cell outlets, spines, and tubes).

Head consisting of retractable mouth cone and introvert with numerous scalids. Detail structure mouth cone and introvert not examined, because heads of all examined specimens retracted.

Neck with 16 placids (Figs 8A-B & 9B-D). Midventral placid broadest (ca. 12 µm wide at base). Remaining placids similar in size (ca. 8 µm wide at base).

Segment 1 consisting of complete cuticular ring. Sensory spots located in subdorsal and laterodorsal positions (Fig. 8A). Two type-1 glandular cell outlets present in tandem in middorsal position. Additional type-1 glandular cell outlets present lateroventrally (Fig. 9C & D). Posterior part of this and following ten segments with primary pectinate fringe. Fringe tips on this segment short, but proportionally longer in lateroventral to ventrolateral positions (Fig. 8A & B).

Segment 2 with complete cuticular ring as in segment 1. This and following eight segments with thick pachycyclus at anterior margin (Fig. 9B & D). Cuticular hairs originating from perforation sites cover central to posterior area of the segment. Sensory spots present in middorsal and ventromedial positions. Type-1 glandular cell outlet present in middorsal position. Type-2 glandular cell outlets in midlateral position (Fig. 9B). Fringe tips of primary pectinate fringe longer than those on segment 1 (Fig. 8A & B).

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Sensory spots present in subdorsal position. Type-1 glandular cell outlets situated in middorsal and ventromedial positions (Fig. 9D). Cuticular hairs originating from perforation sites cover central to posterior part of whole segment except for paraventral area on this and following seven segments. Cuticular hairs without perforation sites present in paraventral area. Primary pectinate fringe similar to preceding segment.

Segment 4 with middorsal acicular spine (Figs 8A, 9B & 10A). Type-1 glandular cell outlets present in paradorsal and ventromedial positions (Fig. 9B & D). No sensory spots present.

Segment 5 with middorsal acicular spine and lateral accessory tubes (Figs 8A-B, 9C & 10A). Sensory spots present in paradorsal and laterodorsal positions. Type-1 glandular cell outlets present in paradorsal and ventromedial positions (Fig. 9D). Cuticular hairs arranged similar as those on segment 3.

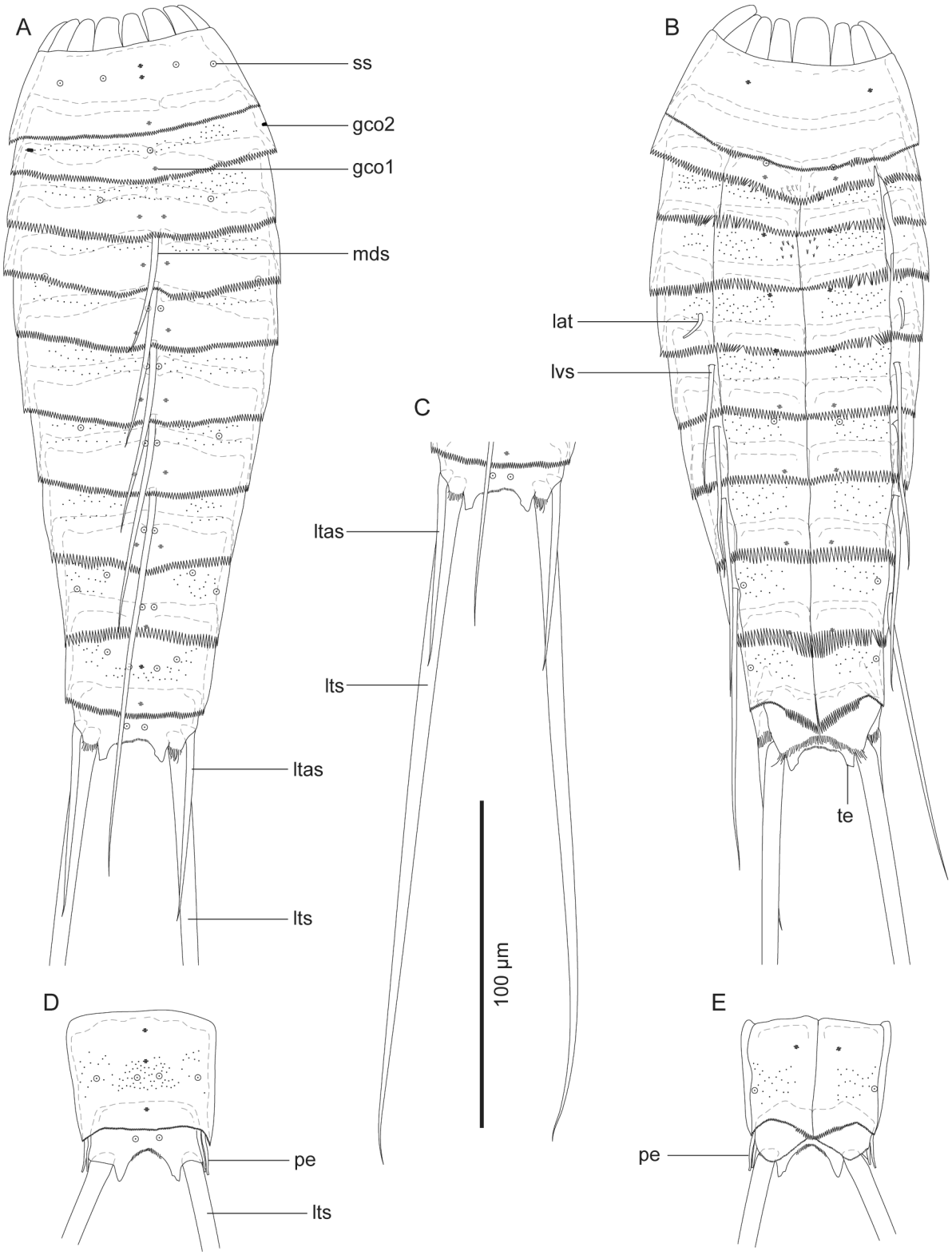

Figure 8. *Echinoderes bathyalis* sp. nov. Camera lucida drawings. **A-C.** Holotype, female (ZMB 11576), entire animal, dorsal and ventral view of segments 1-11 and dorsal view of segment 11 with lateral terminal spines, respectively. **D & E.** Paratype, male (ZMB 11577), segments 10 and 11, dorsal and ventral view, respectively. Abbreviations: gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pe, penile spine; ss, sensory spot; te, tergal extension.

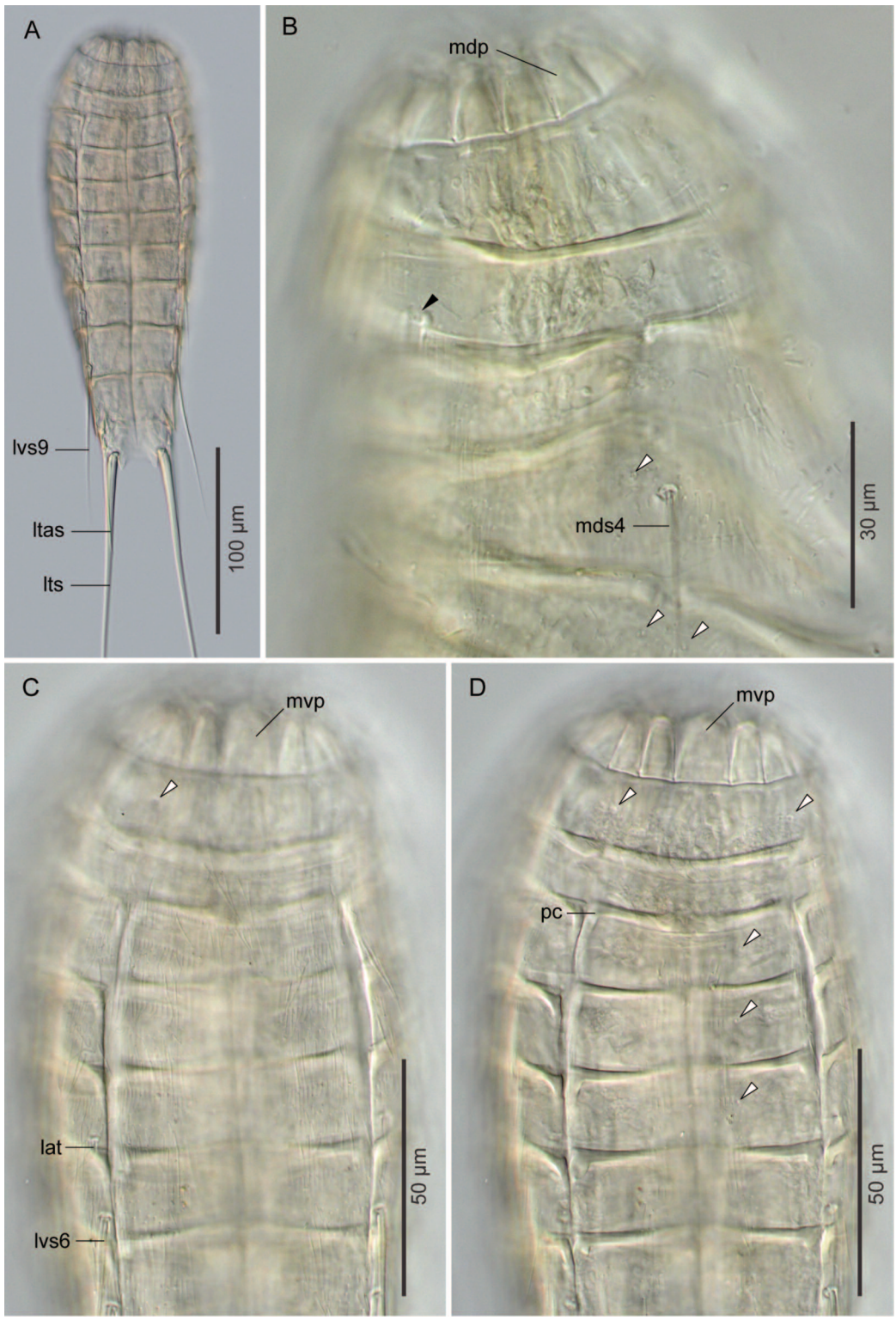

Figure 9. *Echinoderes bathyalis* sp. nov. Nomarski photomicrographs of the holotypic female (ZMB 11576) (A, C, D) and a paratypic male (ZMB 11577) (B). **A.** Entire animal, ventral view. **B.** Neck and segments 1-5, dorsal view. **C.** Segments 1-7, ventral view, focusing on the cuticle surface. **D.** Segments 1-7, ventral view, focusing on different focal plane. White and black arrowheads indicate type-1 and type-2 glandular cell outlets, respectively. Abbreviations: lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mdp, middorsal placid; mds, middorsal acicular spine; mvp, midventral placid; pc, pachycyclus. Digits after abbreviations indicate the corresponding segment number.

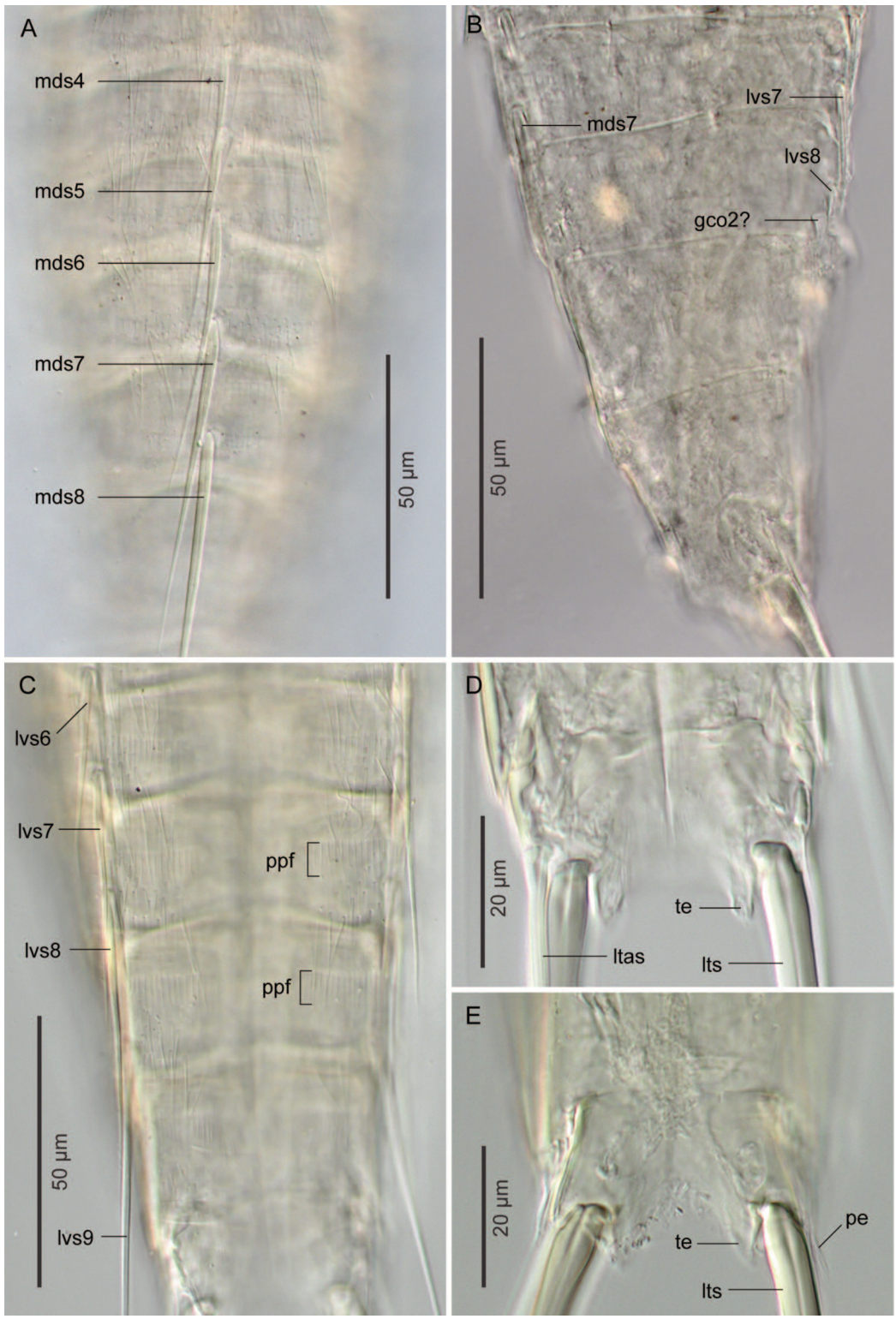

Figure 10. *Echinoderes bathyalis* sp. nov. Nomarski photomicrographs of the holotypic female (ZMB 11576) (A, C, D), a paratypic male (ZMB 11577) (E), and a paratypic recently moulted male (ZMB 11578) (B). **A.** Segments 4-8, dorsal view. **B.** Segments 7-11, lateral view (right side). **C.** Segments 7-11, ventral view. **D.** Segment 11 of female, ventral view. **E.** Segment 11 of male, ventral view. Abbreviations: gco2, type-2 glandular cell outlet; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; pe, penile spine; ppf, primary pectinate fringe; te, tergal extension. Digits after abbreviations indicate the corresponding segment number.

Table 4. *Echinoderes bathyalis* sp. nov. Measurements for adult (in micrometers) and relations between measurements. Column SD indicates standard deviation. Abbreviations: (ac), acicular spine; la, length of lateral accessory tube; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine; md, length of middorsal spine; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube.

Character	ZMB 11576 Holotype female	ZMB 11577 Paratype male	Mean	SD
tl	224	243	234	13.49
msw-6	54	52	53	1.80
msw-6/tl	24.3%	21.3%	22.8%	2.09%
sw-10	42	39	41	1.96
sw-10/tl	18.7%	16.1%	17.4%	1.84%
s1	32	33	32	0.33
s2	25	26	25	0.16
s3	23	25	24	1.64
s4	25	26	25	0.33
s5	27	25	26	1.31
s6	29	27	28	1.64
s7	33	32	33	0.65
s8	26	33	34	2.13
s9	42	35	38	4.75
s10	40	34	37	4.26
s11	25	19	22	3.60
md4 (ac)	40	40	40	0.33
md5 (ac)	47	51	49	2.62
md6 (ac)	59	55	57	2.78
md7 (ac)	70	65	67	3.27
md8 (ac)	125	113	119	8.02
la5 (tu)	13	n.a.	n.a.	n.a.
lv6 (ac)	38	36	37	1.96
lv7 (ac)	48	43	45	3.60
lv8 (ac)	62	61	62	0.82
lv9 (ac)	94	82	88	8.18
lts	219	224	222	3.37
ltas	62	n.a.	n.a.	n.a.
lts/tl	97.9%	92.2%	95.0%	4.04%
ltas/tl	27.8%	n.a.	n.a.	n.a.

Segment 6 with middorsal and lateroventral acicular spines (Figs 8A-B, 9C, 10A & C). Sensory spots present in paradorsal position. Additional sensory spots present in subdorsal position only in males. Type-1 glandular cell outlets present paradorsally and ventromedially.

Segment 7 with middorsal and lateroventral acicular spines (Figs 8A-B & 10A-C). Sensory spots present in paradorsal and ventromedial positions. Additional sensory spots present in subdorsal position only in female. Type-1 glandular cell outlets present paradorsally and ventromedially.

Segment 8 with middorsal and lateroventral acicular spines (Figs 8A-B & 10A-C). Middorsal acicular spine extraordinary long (Fig. 8A). Sensory spots present in paradorsal position. Type-1 glandular cell outlets present in paradorsal and ventromedial positions. Potential type-2 glandular cell outlets present in lateral accessory position at least in one specimen of recently moulted male (Fig. 10B), but this could not be confirmed in two more mature adult specimens.

Segment 9 with lateroventral acicular spines (Figs 8B, 9A & 10C). Paradorsal, subdorsal, laterodorsal, and ventrolateral sensory spots present. Type-1 glandular cell outlets present in paradorsal and ventromedial positions. Small sieve plates present in midlateral position.

Segment 10 with paradorsal, subdorsal, and ventrolateral sensory spots (Fig. 8A-B & D-E). Two type-1 glandular cell outlets aligned middorsally. Additional pair of type-1 glandular cell outlets present in ventromedial position. Fringe tips of primary pectinate fringe in ventromedial to midventral area conspicuously longer than those on middorsal to ventrolateral area in female (Fig. 8B).

Segment 11 with lateral terminal spines (Figs 8A-E, 9A & 10D-E). Lateral terminal accessory spines present in female (Figs 8A-C & 10D). At least two pairs of penile spines present in males (Figs 8D-E & 10E). Paradorsal sensory spots present. Sternal plates and middorsal to paradorsal, laterodorsal, and lateroventral areas of tergal plate with primary pectinate fringe. Posterior edge of tergal plate pointed and protruded subdorsally, forming tergal extensions.

Recently moulted male similar to more mature adults in morphometry and positions of acicular spines, tubes, type-1 glandular cell outlets, type-2 glandular cell outlets on segment 2, and sensory spots. Type-2 glandular cell outlets in lateral accessory position on segment 8 confirmed only in recently moulted male (Fig. 10B). These type-2 glandular cell outlets may be present in the remaining two adults, but are difficult to observe in the dorso-ventrally mounted specimens, because the structures are usually covered by the lateroventral acicular spines and the thick pachycycli. Recently moulted male particularly differing from more mature adults in thinner trunk cuticle and presence of button-like structures in cuticular flap of segments 1-10.

Table 5. *Echinoderes bathyalis* sp. nov. Summary of locations of cuticular structures and appendages. Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pd, paradorsal; pe, penile spine; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

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

Remarks

Echinoderes bathyalis sp. nov. shares the presence of middorsal acicular spines on segments 4-8 and of lateroventral or lateral accessory spines/tubes on segments 5-9 as well as the lack of any other spines or tubes with the following ten species: *Echinoderes angustus* Higgins & Kristensen, 1988; *Echinoderes aquilonius* Higgins & Kristensen, 1988; *Echinoderes brevicaudatus* Higgins, 1977; *Echinoderes cernunnos* Sørensen et al., 2012; *Echinoderes ferrugineus* Zelinka, 1928; *Echinoderes obtuspinosus* Sørensen et al., 2012; *Echinoderes pennaki* Higgins, 1960; *Echinoderes remanei* (Blake, 1930); *Echinoderes romanoi* Landers & Sørensen, 2016; *Echinoderes stockmani* Adrianov, 1999 (see Zelinka, 1928; Higgins, 1960, 1964,1966b & 1977; Higgins & Kristensen, 1988; Adrianov & Malakhov, 1999; Sørensen et al., 2012; Landers & Sørensen, 2016). The presence of the tubes on segment 2 in *E. ferrugineus* was noted in the original description of Zelinka (1928) (the character was mentioned as "Klebröhre"). However, the re-examination of new material from Sicily Island, Italy confirmed that the species does not possess any spines/tubes on the segment. Thus, we include *E. ferrugineus* here for comparison.

Echinoderes bathyalis sp. nov. can be easily distinguished from *E. angustus*, *E. aquilonius*, *E. brevicaudatus*, *E. obtuspinosus*, *E. pennaki*, and *E. stockmani* by its small body size (224-243 µm in *E. bathyalis* sp. nov., *versus* 320-475 µm in *E. angustus*, 363-465 µm in *E. aquilonius*, 318-417 µm in *E. brevicaudatus*, 341-357 µm in *E. obtuspinosus*, 390-430 µm in *E. pennaki*, 493 µm in *E. stockmani*) and by its extraordinary long middorsal spine on segment 8 (92.2-97.9% of trunk length in *E. bathyalis* sp. nov., whereas ca. 24% of trunk length on average in *E. angustus* and *E. aquilonius*, 3-6% of trunk length in *E. brevicaudatus*, 12% of trunk length in *E. obtuspinosus*, 17% of trunk length in *E. pennaki*, ca. 20% of trunk length in *E. stockmani*). *Echinoderes bathyalis* sp. nov. also differs from these species, except for *E. stockmani*, in having relatively longer lateral terminal accessory spines (over 90% of trunk length in *E. bathyalis* sp. nov., whereas 13.7-21.7% of trunk length in *E. angustus*, 9.3-18.5% of trunk length in *E. aquilonius*, 17.2% of trunk length in *E. brevicaudatus*, 14.1-14.8% of trunk length in *E. obtuspinosus*, less than 50% of trunk length in *E. pennaki*) (Higgins, 1960, 1966b & 1977; Higgins & Kristensen, 1988; Adrianov & Malakhov, 1999; Sørensen et al., 2012). In addition to the metric differences, *E. bathyalis* sp. nov differs from *E. angustus, E. aquilonius*, *E. obtuspinosus*, and *E. pennaki* in the positions of type-2 glandular cell outlets: *E. bathyalis* has them midlaterally on segment 2 and lateral accessorily on segment 8, whereas *E. angustus* shows type-2 glandular cell outlets subdorsally on segments 2 and 4, *E. aquilonius* reveals them subdorsally and lateroventrally/ventrolaterally on segment 2 and sublaterally on segment 8, *E. obtuspinosus* yields four pairs of them on segment 2, *E. pennaki* has them subdorsally and ventrolaterally on segment 2 and subdorsally on segment 4 (Sørensen et al., 2016; Sørensen pers. comm.)

Echinoderes bathyalis sp. nov. differs from *E. cernunnos* in having fewer type-2 glandular cell outlets: *E. bathyalis* has type-2 glandular cell outlets in midlateral position on segment 2 and lateral accessory position on segment 8, whereas *E. cernunnos* possesses those in subdorsal, laterodorsal, sublateral, and ventrolateral positions on segment 2, midlateral position on segments 5 and 7, and sublateral position on segment 8 (Sørensen et al., 2012).

Echinoderes bathyalis sp. nov. differs from *E. ferrugineus* in having relatively longer lateral terminal spines (over 90% of trunk length in *E. bathyalis* sp. nov., whereas 46.9-60.5% of trunk length in *E. ferrugineus*) and long lateroventral spines on segment 9 (82-94 µm in in *E. bathyalis* sp. nov., whereas 16-19 µm in in *E. ferrugineus*), and lacking type-2 glandular cell outlets on segments 4, 5, and 8 (Yamasaki, Dal Zotto & Neuhaus, unpubl.).

Echinoderes bathyalis sp. nov. can be clearly distinguished from *E. remanei* in proportionally longer lateral terminal spines (92.2-97.9% of trunk length in *E. bathyalis* sp. nov., whereas 24-55% of trunk length in *E. remanei*) (Higgins, 1964).

Echinoderes bathyalis sp. nov. and *E. romanoi* are similar in trunk length, but can be distinguished by the numbers and positions of type-2 glandular cell outlets on segment 2 (present only in midlateral position in *E. bathyalis* sp. nov., whereas present in subdorsal, laterodorsal, sublateral, and ventrolateral positions in *E. romanoi*). *Echinoderes bathyalis* sp. nov. also differs from *E. romanoi* in bearing a quite longer middorsal acicular spine on segment 8 and lateroventral acicular spines on segment 9 (lengths of middorsal acicular spine on segment 8 and lateroventral acicular spines on segment 9 are 113-125 µm and 82-94 µm, respectively, in *E. bathyalis* sp. nov., whereas 48-73 µm and 19-46 µm, respectively, in *E. romanoi*) (Landers & Sørensen, 2016).

Echinoderes meteorensis sp. nov.
(Figs 11-16 & Tables 6-7)

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Diagnosis

Echinoderes with short trunk (157-196 µm); middorsal acicular spines on segments 4, 6, and 8; lateroventral tubes on segment 5; lateroventral acicular spines on segments 6-9; lateral accessory tubes on segment 8; laterodorsal tubes on segment 10; type-2 glandular cell outlets in subdorsal and lateral accessory positions on segment 2.

Etymology

The specific epithet "*meteorensis*" refers to the type locality of the species, the Great Meteor Seamount.

Material examined

Holotype. Female (ZMB 11570), collected at station 109 on the Great Meteor Seamount (Table 1), mounted as glycerol-paraffin slide on a Cobb aluminum frame.

Paratypes. Five males, seven females, and three recently moulted males. One male (ZMB 11571c) and two females (ZMB 11571a & b), collected at station 89 on the Great Meteor Seamount; one male (ZMB 11572a), two females (ZMB 11572b & e), and two recently molted males (ZMB 11572c & d), collected at station 98 on the Great Meteor Seamount; one male (ZMB 11573b), one female (ZMB 11573a), and one recently moulted male (ZMB 11573c) collected at station 100 on the Great Meteor Seamount; one male (ZMB 11574a) and one female (ZMB 11574b), collected at station 109 on the Great Meteor Seamount; one male (ZMB 11575b) and one female (ZMB 11575a), collected at station 114 on the Great Meteor Seamount (Table 1). All paratypes mounted as glycerol-paraffin slide on Cobb aluminum frames.

Additional material: four males and six females mounted on aluminum stubs for SEM observations. Two females collected at station 95 on the Great Meteor Seamount; one male and two females collected at station 98 on the Great Meteor Seamount; one male and two females collected at station 104 on the Great Meteor Seamount; two males collected at station 113 on the Great Meteor Seamount (Table 1).

Type locality

The Great Meteor Seamount (29°48'59.15"N-28°34'0.48"W), 309 m depth.

Description

Adult with head, neck, and eleven trunk segments (Figs 11A-B, 12A & 13A). See Table 6 for measurements. Table 7 indicates the positions of cuticular structures (sensory spots, glandular cell outlets, spines, tubes, and sieve plates).

Head consisting of retractable mouth cone and introvert (Fig. 13B). Mouth cone with inner oral styles and nine outer oral styles. Exact number and arrangement of inner oral styles not examined. Each outer oral style consisting of rectangular basal part and triangular distal part, with basal part alternating in size between five larger ones in odd sectors and four smaller ones in even sectors (Fig. 13B). Introvert composed of at least six rings of spinoscalids and one ring of trichoscalids (Fig. 13B). Number of spinoscalids on ring 06 could not be counted completely. Ring 07 with six trichoscalids attached with trichoscalid plates. Number and arrangement of outer oral styles, scalids, and placids summarized in figure 14.

Neck with 16 placids (Figs 11A-B, 12B, 13B & 14). Midventral placid broadest (ca. 10 µm wide at base). Remaining placids similar in size (ca. 6 µm wide at base).

Segment 1 consisting of complete cuticular ring. Sensory spots located in subdorsal and laterodorsal positions (Fig. 13C). One to two long cuticular hairs present beside each sensory spot. Type-1 glandular cell

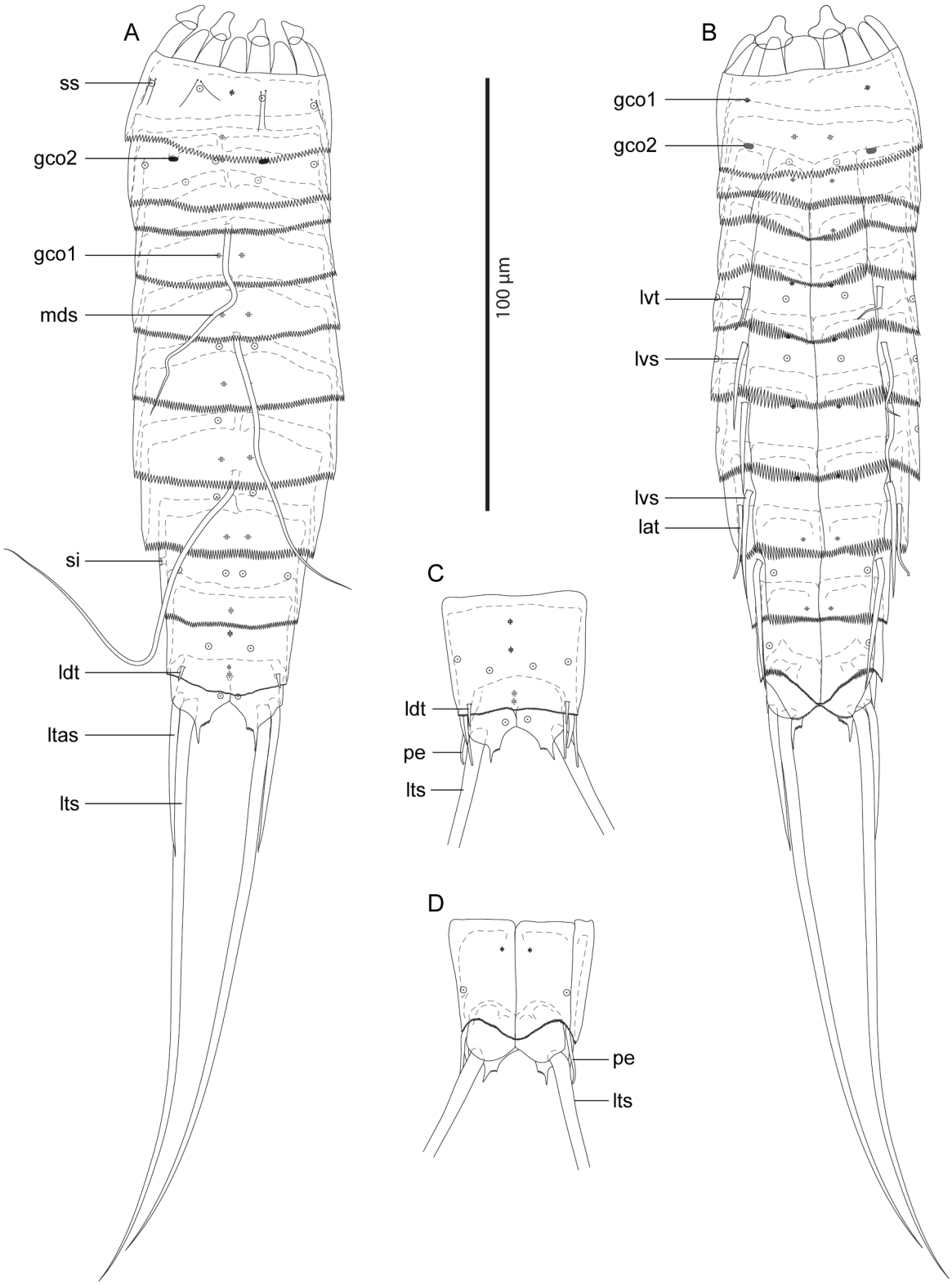


Figure 11. *Echinoderes meteorensis* sp. nov. Camera lucida drawings. **A & B.** Holotype, female (ZMB 11570), entire animal, dorsal and ventral view of segments 1-11, respectively. **C & D.** Paratype, male (ZMB 11571c), segments 10 and 11, dorsal and ventral view, respectively. Abbreviations: gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine; si, sieve plate; ss, sensory spot.

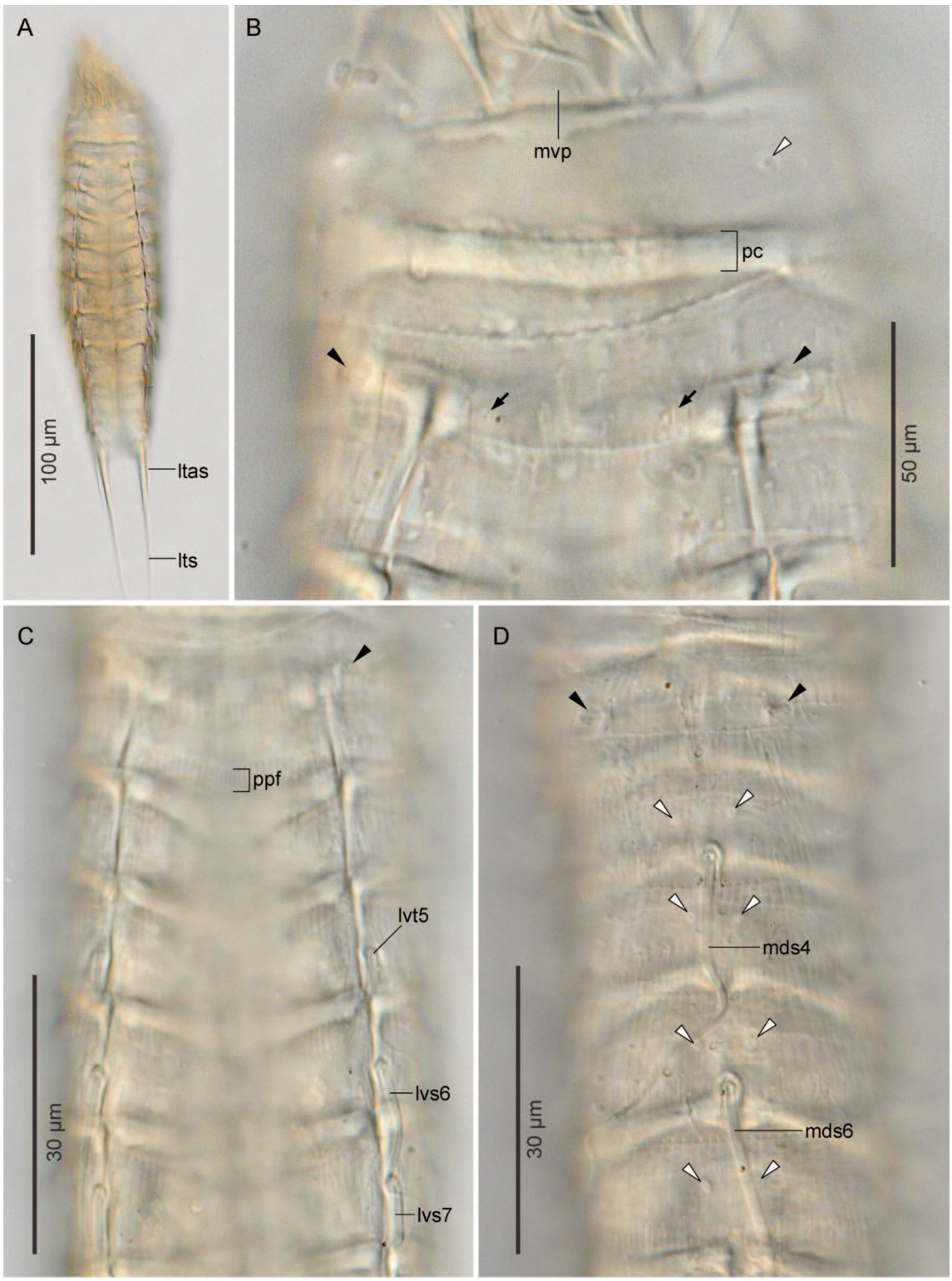


Figure 12. *Echinoderes meteorensis* sp. nov. Nomarski photomicrographs of the holotypic female (ZMB 11570). **A.** Entire animal, ventral view. **B.** Neck and segments 1-3, ventral view. **C.** Segments 2-7, ventral view. **D.** Segments 2-6, dorsal view. Black arrows, white arrowheads, and black arrowheads indicate sensory spot, type-1 glandular cell outlet, and type-2 glandular cell outlet, respectively. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; mvp, midventral placid; pc, pachycyclus; ppf, primary pectinate fringe. Digits after abbreviations indicate the corresponding segment number.

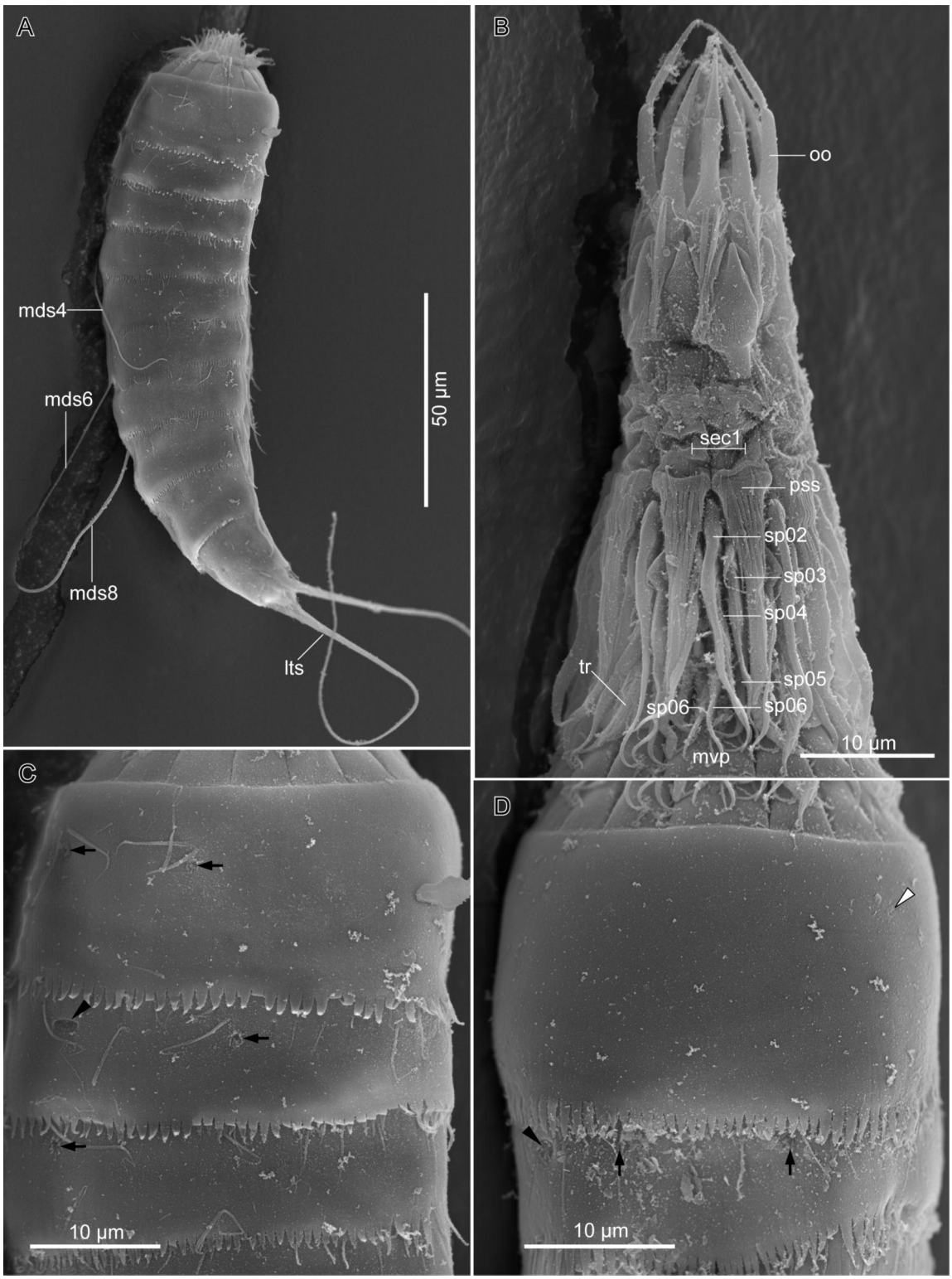


Figure 13. *Echinoderes meteorensis* sp. nov.. Scanning electron micrographs of a male (A, C) and a female (B, D). **A.** Entire male animal, lateral view (right side). **B.** Head, ventral view. **C.** Segments1-3, lateral view (right side). **D.** Segments 1 and 2, ventral view. Black arrows, white arrowhead, and black arrowheads indicate sensory spot, type-1 glandular cell outlet, and type-2 glandular cell outlet, respectively. Abbreviations: lts, lateral terminal spine; mds, middorsal acicular spine; mvp, midventral placid; oo, outer oral style; pss, primary spinoscalids; sec, sector number; sp, spinoscalid; tr, trichoscalid. Digits after abbreviations indicate sector number, ring number, or the corresponding segment number.

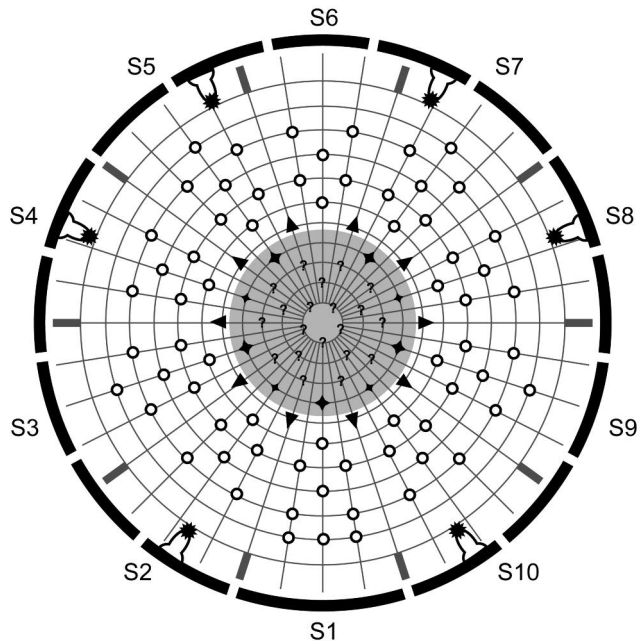
outlets present in middorsal and lateral accessory positions (Figs 12B & 13D). Posterior part of this and following nine segments with primary pectinate fringe. Fringe tips on this segment medium in length.

Segment 2 with complete cuticular ring as in segment 1. This and following eight segments with thick pachycyclus at anterior margin (Fig. 12B). Cuticular hairs rising from perforation sites covering central to posterior area of this and following eight segments. Sensory spots present in middorsal, laterodorsal, and ventromedial positions (Figs 12B & 13C-D). Type-1 glandular cell outlet located in middorsal and ventromedial positions. Type-2 glandular cell outlets in subdorsal and lateral accessory positions (Figs 12B-D & 13C-D). Primary pectinate fringe similar to that on preceding segment. Single line of secondary pectinate fringe present at anterior part of segment on this and following eight segments. Primary pectinate fringe of preceding segment overlaps secondary pectinate fringe in most segments of many specimens.

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Sensory spots present in subdorsal position (Fig. 13C). Type-1 glandular cell outlets situated in middorsal and ventromedial positions. Primary pectinate fringes on this and following six segments similar to those on segment 1, except for lateroventral to ventrolateral areas, which is equipped with longer fringe tips.

Segment 4 with middorsal acicular spine (Figs 12D, 13A & 15A). Type-1 glandular cell outlets placed in paradorsal and ventromedial positions (Fig. 12D). No sensory spot present.

Segment 5 with lateroventral tubes (Figs 12C, 15B & 16A). Sensory spots present in midlateral and ventromedial positions (Fig. 16A). Type-1 glandular cell outlets located in paradorsal and ventromedial positions (Figs 12D & 15A).



Scalid and style arrangement

Ring/Section	1	2	3	4	5	6	7	8	9	10	Total
00 outer oral styles ✦	1	1	1	1	1	0	1	1	1	1	9
01 primary spinoscalids ▼	1	1	1	1	1	1	1	1	1	1	10
02 spinoscalids o	1	1	1	1	1	1	1	1	1	1	10
03 spinoscalids o	2	2	2	2	2	2	2	2	2	2	20
04 spinoscalids o	1	1	1	1	1	1	1	1	1	1	10
05 spinoscalids o	2	2	2	2	2	2	2	2	2	2	20
06 spinoscalids o	3?	0?	1?	0?	1?	0?	1?	0?	1?	0?	>7
07 trichoscalids ✹	0	1	0	1	1	0	1	1	0	1	6

Figure 14. *Echinoderes meteorensis* sp. nov. Polar-coordinate diagram of mouth cone, introvert and placids. Grey area and heavy line arcs show mouth cone and placids, respectively. The table lists the scalid arrangement by sector.

Table 5. *Echinoderes bathyalis* sp. nov. Summary of locations of cuticular structures and appendages. Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pd, paradorsal; pe, penile spine; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

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

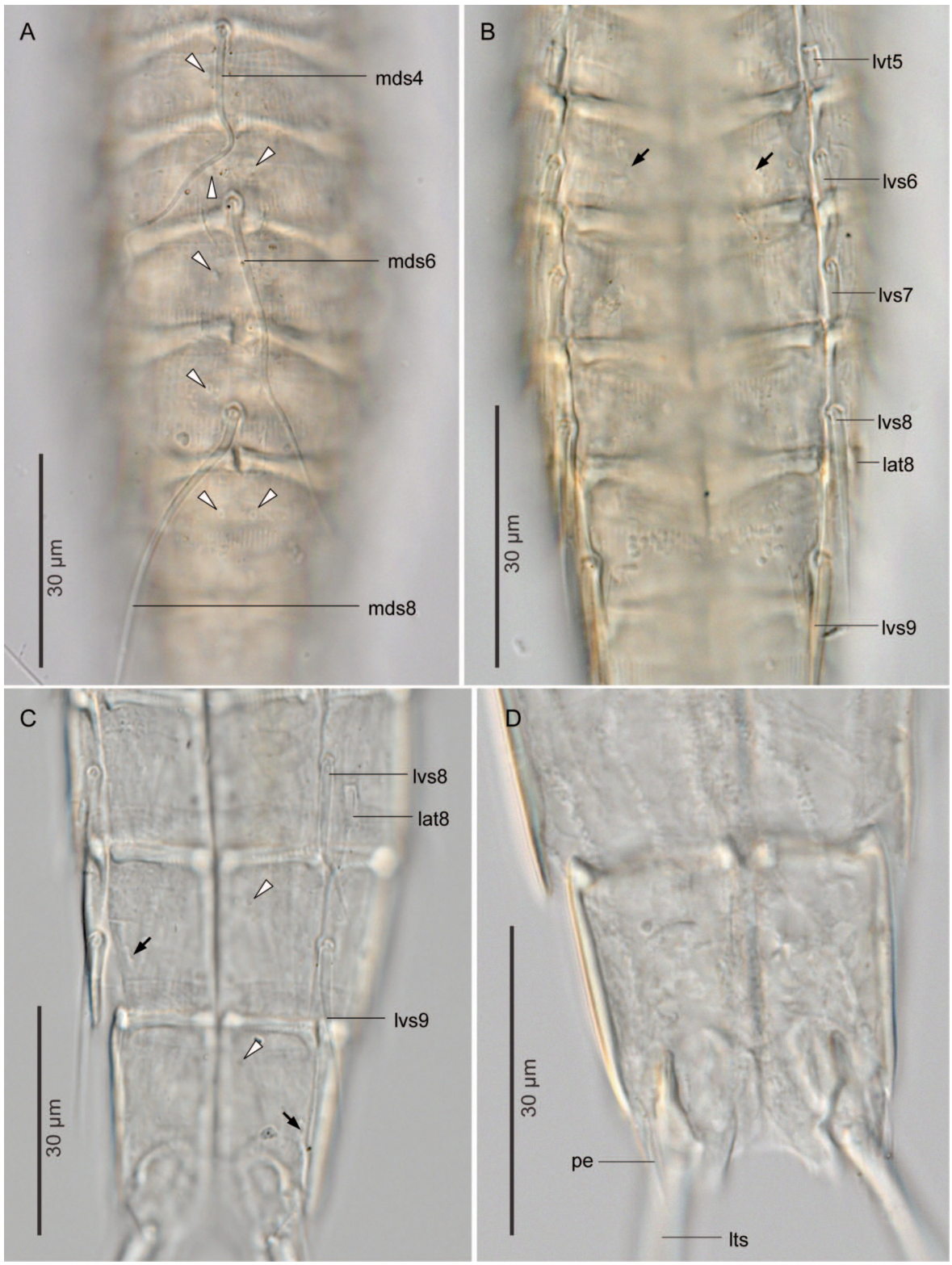


Figure 15. *Echinoderes meteorensis* sp. nov., Nomarski photomicrographs of the holotypic female (ZMB 11570) (A & B) and a paratypic male (ZMB 11571c) (C & D). **A.** Segments 4-9, dorsal view. **B.** Segments 5-9, ventral view. **C.** Segments 8-11, ventral view. **D.** Segments 9-11, dorsal view. Black arrows and white arrowheads indicate sensory spot and type-1 glandular cell outlet, respectively. Abbreviations: lat, lateral accessory tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine. Digits after abbreviations indicate the corresponding segment number.

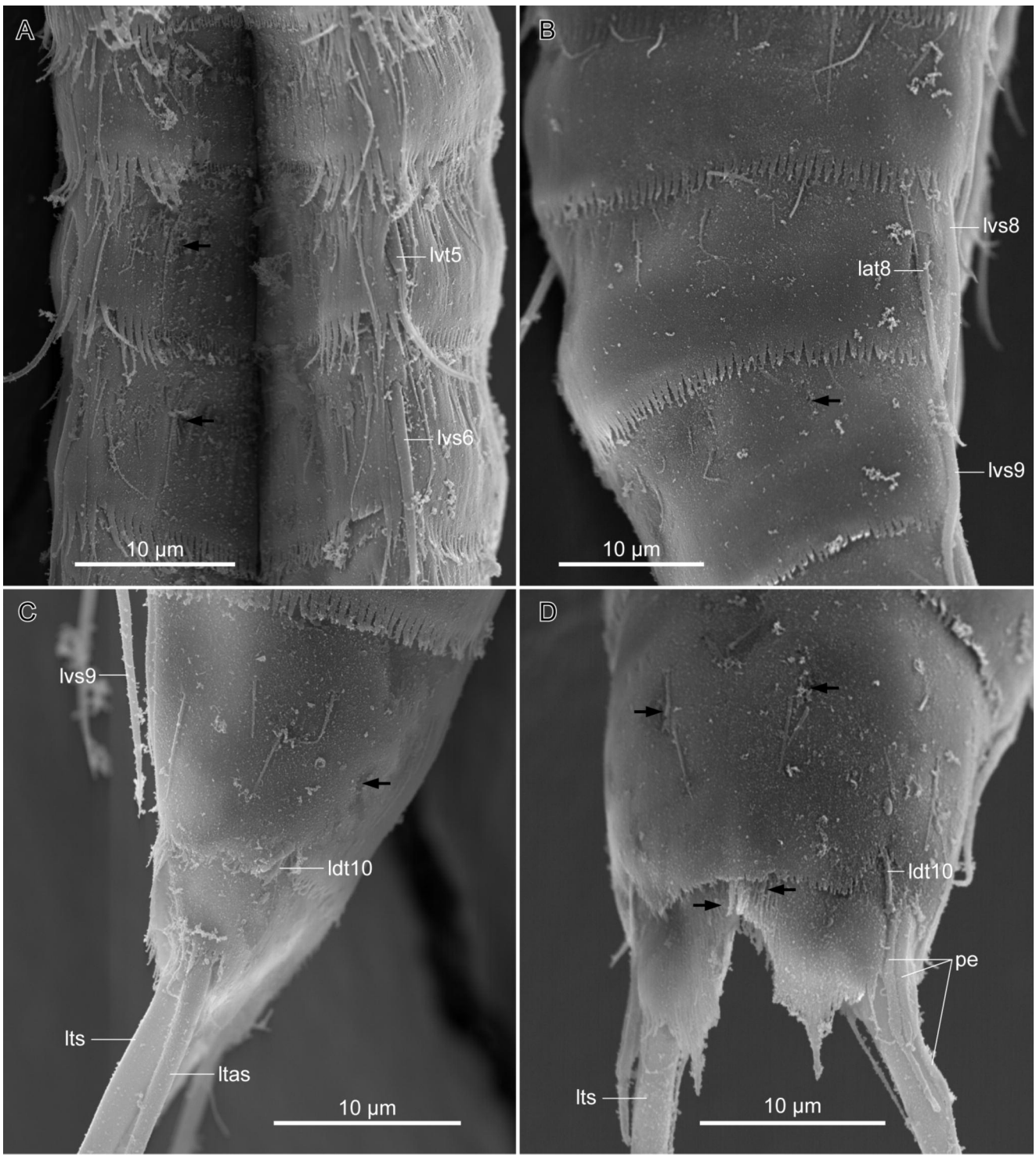


Figure 16. *Echinoderes meteorensis* sp. nov. Scanning electron micrographs of a male (B & D) and a female (A & C). **A.** Segments 4-6, ventral view. **B.** Segments 7-9, lateral view (right side). **C.** Segments 10 and 11, laterodorsal view. **D.** Segments 10 and 11, laterodorsal view. Black arrows indicate sensory spot. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; pe, penile spine. Digits after abbreviations indicate the corresponding segment number.

Table 6. *Echinoderes meteorensis* sp. nov. Measurements for adult (in micrometers) and relations between measurements. Columns N and SD indicate sample size and standard deviation, respectively. Abbreviations: (ac), acicular spine; (f), female condition of sexually dimorphic character; la, length of lateral accessory tube; ld, length of laterodorsal tube; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; (m), male condition of sexually dimorphic character; md, length of middorsal spine; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube.

Character	N	Range	Mean	SD
tl	11	157–196	175	13.78
msw-8	5	30–33	32	1.04
msw-8/tl	5	16.3–20.1%	18.2%	1.54%
sw-10	5	25–27	26	0.87
sw-10/TL	5	13.7–16.0%	15.0%	0.92%
s1	5	25–27	26	0.96
s2	5	23–25	24	0.87
s3	5	18–19	18	0.53
s4	5	18–19	18	0.77
s5	5	18–19	18	0.51
s6	5	20–21	21	0.39
s7	5	22–25	23	0.84
s8	5	24–26	25	0.69
s9	5	25–26	26	0.39
s10	5	28–30	29	0.70
s11	5	18–19	19	0.57
md4 (ac)	12	44–62	51	5.32
md6 (ac)	9	60–79	68	5.48
md8 (ac)	9	79–101	93	7.32
lv5 (tu)	12	8–17	12	3.51
lv6 (ac)	12	17–22	20	1.57
lv7 (ac)	12	18–23	21	1.79
lv8 (ac)	13	24–28	26	1.14
la8 (tu)	11	14–19	16	1.71
lv9 (ac)	13	28–32	30	1.29
ld10 (tu)(m)	5	8–13	10	1.83
ld10 (tu)(f)	7	3–7	5	1.41
lts	11	105–137	123	10.68
ltas	8	33–39	36	1.75
lts/tl	10	53.5–83.5%	70.8%	9.98%
ltas/tl	8	18.1–23.2%	20.8%	1.61%

Segment 6 with middorsal and lateroventral acicular spines (Figs 12D, 13A, 15A-B & 16A). Sensory spots present in paradorsal, midlateral, and ventromedial positions (Figs 15B & 16A). Type-1 glandular cell outlets situated paradorsally and ventromedially (Figs 12D & 15A).

Segment 7 with lateroventral acicular spines (Figs 12C & 15B). Sensory spots present in paradorsal and midlateral positions. Type-1 glandular cell outlets situated paradorsally and ventromedially (Figs 12D & 15A).

Segment 8 with middorsal and lateroventral acicular spines (Figs 13A, 15A-C & 16B). Lateral accessory tubes present (Figs 15B-C & 16B). Sensory spots situated in paradorsal position. Type-1 glandular cell outlets located in paradorsal and ventromedial positions (Fig. 15A).

Segment 9 with lateroventral acicular spines (Figs 15B-C & 16B-C). Paradorsal, laterodorsal, and ventrolateral sensory spots present (Figs 15C & 16B). Type-1 glandular cell outlets situated in paradorsal and ventromedial positions (Fig. 15A & C). Small sieve plates placed in sublateral position.

Segment 10 with laterodorsal tubes (Fig. 16C & D). Tubes in females slightly shorter than those in males (Table 6). Subdorsal and ventrolateral sensory spots present (Figs 15C & 16C-D). Two type-1 glandular cell outlets aligned middorsally. Additional pair of type-1 glandular cell outlets present in ventromedial position (Fig. 15C). Fringe tips of primary pectinate fringe very short, except for slightly longer ones in ventrolateral area.

Segment 11 with lateral terminal spines (Figs 12A, 13A, 15D & 16C-D). Lateral terminal accessory spines present in females (Figs 11A-B, 12A & 16C). Three pairs of penile spines present in males (Figs 11C-D, 15D & 16D). All penile spines thin and long. Paradorsal sensory spots present (Fig. 16D). Two type-1 glandular cell outlets situated middorsally. Posterior edges of sternal plates rounded. Posterior edge of tergal plate protruding subdorsally and forming pointed tergal extensions.

Recently moulted adults similar to more mature adult in morphometries and positions of acicular spines, tubes, glandular cell outlets, and sensory spots, except for thinner trunk cuticle and presence of button-like structures in cuticular flap of segments 1-10.

Remarks

The presence of middorsal spines only on segments 4, 6, and 8 is found in 17 congeners. Of these, the following eleven species share lateroventral spines or tubes on segments 5-9 as well as lateral accessory spines or tubes on segment 8 with *E. meteorensis* sp. nov.: *Echinoderes abbreviatus* Higgins, 1983; *E. belenae*; *E. higginsi*; *E. hispanicus*; *E. intermedius*; *Echinoderes kristenseni* Higgins, 1985; *E. newcaledoniensis*; *E. peterseni*; *E. riedli*; *E. rociae*; *Echinoderes wallaceae* Higgins, 1983 (see Higgins, 1966b, 1967, 1983 & 1985; Higgins & Kristensen, 1988; Huys & Coomans, 1989; Pardos et al., 1998 &

Table 7. *Echinoderes meteorensis* sp. nov. Summary of locations of cuticular structures and appendages. Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 glandular cell outlet; gco2, type-2 glandular cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pd, paradorsal; pe, penile spine; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

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

2016a-b; Sørensen, 2006). But *E. meteorensis* sp. nov. can be easily distinguished from these eleven species by its lack of any tube on segment 2.

Kinorhynch fauna on seamounts

Although kinorhynchs have been reported from several seamounts, all except for *Antygomonas oreas* Bauer-Nebelsick, 1996 and *E. peterseni* were identified only to phylum-level (Bauer-Nebelsick, 1996; Kristensen, 2005; George, 2013). The former species was originally reported from the seamount "Fieberling Guyot" at 500-700 m depth in the East Pacific Ocean (Bauer-Nebelsick, 1996). Subsequently, Sørensen (2001) found an *Antygomonas* species from shallow water (at 3 m depth) in Bermuda, and reported it as "*Antygomonas* cf. *oreas*". However, the paper also mentioned that the morphology of *Antygomonas* from Bermuda differed from the original description of *A. oreas* in the arrangement of lateral spines on segment 11 (= segment 9 in the currently used terminology) (Sørensen, 2001), implying that *Antygomonas* from Bermuda is not *A. oreas*, but an undescribed species with the same spine pattern as *Antygomonas caeciliae* Dal Zotto, 2015, *A. gwenae* Herranz et al., 2014, and *A. paulae* Sørensen, 2007, or identical to them.(Herranz et al., 2014; Dal Zotto, 2015). *Echinoderes peterseni* was originally described from the shallow waters (9 m depth) in Disco Island, west Greenland (Higgins & Kristensen, 1988), and afterwards reported from the seamount "Faroe Bank" in the Northeast Atlantic Ocean (Kristensen, 2005).

Our investigation detected a third and fourth seamount species, *E. apex* sp. nov. and *E. meteorensis* sp. nov. Both species occurred at current knowledge only at seamount summits and were not found in the sample from the adjacent deep-sea floor.

Of these four seamount kinorhynchs, half of them occur at multiple localities, i.e., both on a seamount and on the continental shelf (*E. peterseni*) and on two seamounts (*E. apex* sp. nov.). In comparison to seamount kinorhynchs, only 18 of 357 species of other seamount meiofauna were recorded from multiple localities (George, 2013). No conclusion is drawn at this stage, because this is the first output of our project on kinorhynchs on the North Atlantic and Mediterranean seamounts, and several more species are waiting on our desk for being reported in next papers. Furthermore, only a few seamounts out of many thousands and very small areas of the deep-sea floor have been investigated up to date. It is beyond any doubt that further studies will find more new species as well as detect the connection or the disconnection of the kinorhynch fauna between seamounts, deep-sea floor, and continental shallow waters.

Acknowledgements

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