

Research article

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***Echinoderes xiphophorus* sp. nov. – the first deep-water representative of Echinoderidae in the Sea of Japan (Kinorhyncha: Cyclorhagida)**Andrey V. ADRIANOV ¹ & Anastassya S. MAIOROVA ^{2,*}^{1,2}A.V. Zhirmunsky National Scientific Center of Marine Biology,
Far Eastern Branch of Russian Academy of Sciences, Vladivostok 690041, Russia.*Corresponding author: anastasia.mayorova@gmail.com¹ Email: avadr@mail.ru¹urn:lsid:zoobank.org:author:8D252A04-2DE8-48A9-85BE-353CE8DE70C0²urn:lsid:zoobank.org:author:C7691069-EC28-4FBE-A80D-02902686C364

Abstract. A new species of echinoderid kinorhynchs, *Echinoderes xiphophorus* sp. nov. collected from oxidized brown silt at the deepest depression in the Sea of Japan, North-West Pacific, is described and illustrated using light and electron microscopy. This new representative of the most speciose kinorhynch genus is characterized by the unique set of spines and tubes and can easily be distinguished from most of its congeners. The second trunk segment bears three pairs of tubes in subdorsal, midlateral and ventrolateral position in both sexes; one pair of tubes on trunk segment 5 in lateroventral position and on trunk segment 8 in sublateral position; aciculate lateroventral spines on trunk segments 6–9; aciculate middorsal spines on trunk segments 4, 6, 8. This species is well recognized by very long tergal extensions of the posteriormost segment, some of the longest within the family Echinoderidae. Males of *Echinoderes xiphophorus* sp. nov. are well distinguished from all the congeners by extremely long sword-like appendages dorsally to three pairs of penile spines. The species constitutes the first deep-sea representative of the Echinoderidae in the Sea of Japan and the deepest representative of the Kinorhyncha in this sea.

Keywords. North-West Pacific, deep sea, bathyal, meiofauna, kinorhynchs, species description.

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Introduction

Kinorhynchs are meiobenthic free-living segmented worms, from 0.2 to 1.2 mm in length. They are worldwide in distribution, inhabiting the upper few centimeters of various marine sediments from the littoral zone to the hadal depth up to 9538 m (see Adrianov & Maiorova 2019). Currently, the Kinorhyncha Reinhard, 1881 is considered a phylum in Scalidophora (Lemburg, 1995) or as a class of the phylum Cephalorhyncha Adrianov & Malakhov, 1995 (see Adrianov & Malakhov 1999; Neuhaus 2013).

As reported in some recent papers, kinorhynchs are very common and numerous in the abyss and even in the hadal zone (see Neuhaus 2013; Adrianov & Maiorova 2015, 2016, 2018a, 2018b, 2019, 2020; Sørensen *et al.* 2018; Yamasaki *et al.* 2018a, 2018b, 2018c). Nevertheless, information on the species composition in the deep sea is still very limited.

Only six species of *Echinoderes* Claparède, 1863 have been described from the Sea of Japan: *E. filispinosus* Adrianov, 1989 and *E. multisetosus* Adrianov, 1989 from the Peter the Great Bay, and *E. ulsanensis* Adrianov, 1999, *E. koreanus* Adrianov, 1999, *E. obtuspinosus* Sørensen *et al.*, 2012 and *E. songae* Sørensen & Chang, 2020 off the east coast of the Korean Peninsula (see Adrianov & Malakhov 1999; Sørensen *et al.* 2012, 2020). Three other species, *E. tchefouensis* Lou, 1934; *E. cernunnos* Sørensen *et al.*, 2012 and *E. microaperturus* Sørensen *et al.*, 2012, were found in the Korean Strait (between Tsushima Island and the Korean mainland) between the Sea of Japan and the East-China Sea, and *E. sensibilis* Adrianov, Murakami & Shirayama, 2002 was reported from Tsugaru Strait between the Sea of Japan and the Pacific (see Sørensen *et al.* 2012, 2020; Yamasaki *et al.* 2014). All these echinoderids are shallow-water species, found in intertidal and subtidal environments only (from 0 to 140 m depth).

On the slope of the deepest depression in the Sea of Japan, near the Russian coast, at a depth of 1530 m, we found a new species of echinoderid kinorhynchs with unique morphological characters. The purpose of this paper is to describe the new species as the first deep-sea representative of the genus *Echinoderes* in the Sea of Japan and the first bathyal species of the genus in the North-West Pacific.

Material and methods

The specimens here described as a new species, *Echinoderes xiphophorus* sp. nov., were collected from an oxidized brown clay taken by multiple corer (MUC) on a slope at the deepest depression in the western part of the Sea of Japan at a depth 1530 m (44.7942° N and 137.2550° E). Sediments were collected during the SoJaBio voyage (Russian-German deep-sea expedition) of the RV “*Akademik M.A. Lavrentyev*” in August–September 2010 alongside the deep-water transect from 500 to 3660 m near the Russian coast of the Sea of Japan.

Water above the sediment in the core was filtered through a 32 µm mesh sieve. Filtered material was checked under a stereo microscope to collect live specimens.

All specimens were fixed in 10% buffered formalin in seawater.

Six adult specimens were transferred to 70% ethanol-5% glycerol-25% deionized water solution. After evaporation of the ethanol and water, the material was preserved in anhydrous glycerol. All specimens were mounted individually in VECTASHIELD mounting medium for fluorescence microscopy between two circular slips (coverglasses with 18 and 12 mm in diameter, respectively) which enable viewing from both sides. The slips were positioned on Higgins-Shirayama plastic slide frames for further examination using differential interference contrast microscopy (DIC or Nomarski microscopy). The specimens were studied with a Zeiss (Imager.Z2) microscope equipped with an AxioCamHR Rev3 camera.

Four adult specimens were selected for scanning electron microscopy (SEM). These specimens were transferred by an Irwin Loop from 10% formalin to a vessel of distilled water and washed using a detergent to clean the body surface. The cleaned specimens were dehydrated through a graded series of ethanol, transferred to acetone, and critical-point dried. The dried specimens were mounted on aluminum stubs. Uncoated stubs were initially imaged at low vacuum with a Zeiss Sigma scanning electron microscope using a SE2 and a VSPG4 detectors. Stubs were subsequently coated with gold and observed using a regular scanning electron microscope protocol by SEM (Zeiss Sigma).

All microscope facilities were provided by the Far Eastern Center for Electron Microscopy at the NSCMB FER RAS.

In the examination procedures, we followed the standard protocol described by Higgins (1983) and modified more recently by several authors (see Neuhaus 2013). Measurements are summarized in Table 1.

Positions of cuticular structures on the trunk segments follow the terminology used in several recent papers (see Neuhaus 2013; Adrianov & Maiorova 2018a, 2020). Presence and position of cuticular structures are summarized in Table 2.

Type material is deposited at the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology of the Far Eastern Branch of the Russian Academy of Sciences (NSCMB FER RAS) (MIMB).

Results

Taxonomic account

Class Kinorhyncha Reinhard, 1881
 Order Cyclorhagida Zelinka, 1896
 Family Echinoderidae Carus, 1885
 Genus *Echinoderes* Claparède, 1863

Echinoderes xiphophorus sp. nov.

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Figs 1–8

Diagnosis

Trunk length (TL) 290–305 µm; lateral terminal spines (LTS) 142–185 µm; trunk segments 1–2 consisting of closed cuticular rings, and trunk segments 3–11 of one tergal and two sternal plates; trunk segment 2 with three pairs of well-developed tubes in subdorsal, midlateral, and ventrolateral positions; trunk segment 5 with tubes in lateroventral position; trunk segment 8 with tubes in sublateral position; middorsal spines on trunk segments 4, 6, 8; lateroventral acicular spines on trunk segments 6–9; trunk segment 11 with remarkably long tergal extensions (TE) about 15–16% of TL; males with three pairs of penile spines and remarkably long sword-like extensions (about 80% of TE) dorsally to penile spines; females with pair of laterodorsal tubes on trunk segment 10.

Etymology

The species name is derived from the Greek ‘*xiphos*’ (sword) and ‘*phorus*’ (carry) because of very long sword-like appendages in males dorsally to penile spines.

Material examined

Holotype (Fig. 2A–E)

RUSSIA • 1 ♂; Sea of Japan; 44.7942° N, 137.2550° E; depth 1530 m; 14 Aug. 2010; SoJaBio cruise; stn A3-7; multiple corer; oxidized brown clay; MIMB 41347.

Paratypes (Fig. 3A–B)

RUSSIA • 4 adult ♂♂; same locality and station as for holotype; MIMB 41348, MIMB 41349, MIMB 41350, MIMB 41351 • 1 adult ♂; Sea of Japan; 44.9439950° N, 137.2017717° E; depth 515 m; 13 Aug. 2010; SoJaBio cruise; stn A2-5; multiple corer; oxidized brown clay; MIMB 41352.

Other material

RUSSIA • 2 adult ♂♂, 2 adult ♀♀ (mounted for SEM); same locality and station as for holotype.

Table 1. Measurements (μm) of the main characters of six adult specimens of *Echinoderes xiphophorus* sp. nov.: holotype and five paratypes. Number after abbreviation indicates number of trunk segment.

Character	MIMB 41347 holotype, ♂ Sea of Japan	MIMB 41348 paratype, ♂ 1 Sea of Japan	MIMB 41349 paratype, ♂ 2 Sea of Japan	MIMB 41350 paratype, ♂ 3 Sea of Japan	MIMB 41351 paratype, ♂ 4 Sea of Japan	MIMB 41352 paratype, ♂ 5 Sea of Japan
TL	304	305	295	295	290	broken tergal extensions
MSW-7	56	58	58	63	58	59
MSW-7/TL	18%	19%	20%	21%	20%	–
SW	52	47	46	45	50	53
SW/TL	17%	15%	16%	15%	17%	–
S1	29	29	32	29	31	28
S2	22	23	26	26	22	24
S3	21	23	23	24	23	24
S4	24	26	24	24	23	29
S5	26	28	27	25	27	32
S6	30	31	31	32	30	35
S7	32	31	32	32	32	40
S8	36	36	37	35	33	37
S9	34	39	37	40	35	43
S10	33	31	37	42	32	40
S11 (including TE)	63	60	60	59	54	broken
MD 4	24	24	27	17	12	broken
MD 6	32	33	broken	30	18	29
MD 8	35	40	broken	36	31	31
SDT 2	17	11	14	12	11	17
LVT 5	18	18	15	21	12	17
LVS 6	28	27	27	29	29	32
LVS 7	32	30	28	34	29	34
LVS 8	33	34	37	28	32	36
SLT 8	16	19	20	19	3	15
LVS 9	37	39	39	39	35	31
LTS	185	160	163	142	143	168
LTS/TL	61%	52%	55%	48%	49%	–
TE	51	45	40	45	44	–
TE/TL	17%	15%	14%	15%	15%	–
TE/S11	80%	75%	67%	76%	81%	–
PS1	41	42	40	33	40	39
SWA	35	32	24	broken	28	31
SWA/TE	68%	71%	60%	–	63%	–

Table 2. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes xiphophorus* sp. nov. Abbreviations: ac = acicular spine; exs = excretory sieve plate; gco1 = glandular cell outlet type 1; LA = lateral accessory; LD = laterodorsal; ltas = lateral terminal accessory spine; lts = lateral terminal spine; LV = lateroventral; MD = middorsal; ML = midlateral; PD = paradorsal; pe = penile spines; SD = subdorsal; SL = sublateral; ss = sensory spot; swa = sword-like appendage; tu = tube; VL = ventrolateral; VM = ventromedial; (♀) = female condition of sexually dimorphic character; (♂) = male condition of sexually dimorphic character.

Segment	Position									
	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss						ss, gco1
2	ss		tu	ss	tu			ss	tu	ss, gco1
3	gco1		ss		ss					gco1
4	ac	gco1	ss							gco1
5	gco1		ss	ss				tu		ss, gco1
6	ac	ss, gco1		ss				ac		ss, gco1
7	gco1		ss	ss				ac		gco1
8	ac	ss, gco1				tu		ac		gco1
9		ss, gco1	ss	ss			exs	ac	ss	gco1
10	gco1		ss	swa (♂)					ss	gco1
11	2 × gco1		2 × ss	tu (♀)	3 × pe (♂)		ltas (♀)	lts		ss, gco1

Description

BODY. Adult specimen consists of head, neck and 11 trunk segments. Measurements (μm) and ratios (%) are provided in Table 1. Head consists of retractable mouth cone and eversible introvert. Inner oral styles are arranged in two circlelets (5 large tooth-like outer styles + 10 minute innermost styles). External mouth cone bears nine articulated outer oral styles. Head bears seven rings of spinoscalids and one ring of six trichoscalids. Neck consists of 16 placids. All placids trapezoid in shape, distinctly articulating with the first trunk segment. Midventral placid widest; remaining ones narrower. Two ventral and four dorsal trichoscalid plates present, ventral ones being broader than four dorsal ones.

TRUNK SEGMENT 1. Closed cuticular ring, with three pairs of sensory spots located close to the anterior segment margin in subdorsal and laterodorsal and more posteriorly in ventromedial position (Figs 1A–B, 2A, 3B, 5, 6A–B, 7A); sensory spots rounded in shape, with 15–20 very short petals and one or two pores (Fig. 6A); single glandular cell outlet of type 1 in middorsal position and two outlets in ventromedial position (Figs 1A–B, 2A, 3A–B, 5, 6A–C); glandular cell outlets of type 2 absent as in all trunk segments; posterior margin of segment with pectinate fringe with fringe tips from midventral to ventrolateral position being shorter than others (Fig. 7A); long cuticular hairs on dorsal surface regularly arranged forming a continuous belt of 3–4 distinct transverse rows and irregularly arranged on ventral side (Figs 6A–B, 7B).

TRUNK SEGMENT 2. Closed cuticular ring, without any partial intra- or extracuticular fissures; three pairs of tubes in subdorsal, midlateral and ventrolateral positions; each tube with short and smooth basal part and longer distal part with two wing-like lateral projections (Fig. 6B); one sensory spot in middorsal position and three pairs in laterodorsal, lateroventral and ventromedial position, sensory spots on this and following segments with 10–15 very short petals and 1–2 very long posteriormost petals similar to cilia (Figs 6B, 7C–E); one pair of glandular cell outlets of type 1 in ventromedial position anterior to ventromedial sensory spots (Fig. 3B); ventral hairs on the trunk segment 2 seem to be more regularly

arranged than those on trunk segment 1; pectinate fringe as in the preceding segment. It should be noted that glandular cell outlets at the anterior margin of tergal and sternal plates are usually hidden beneath posterior cuticular fringe of previous segment and seen more easily with DIC (see Figs 2–3).

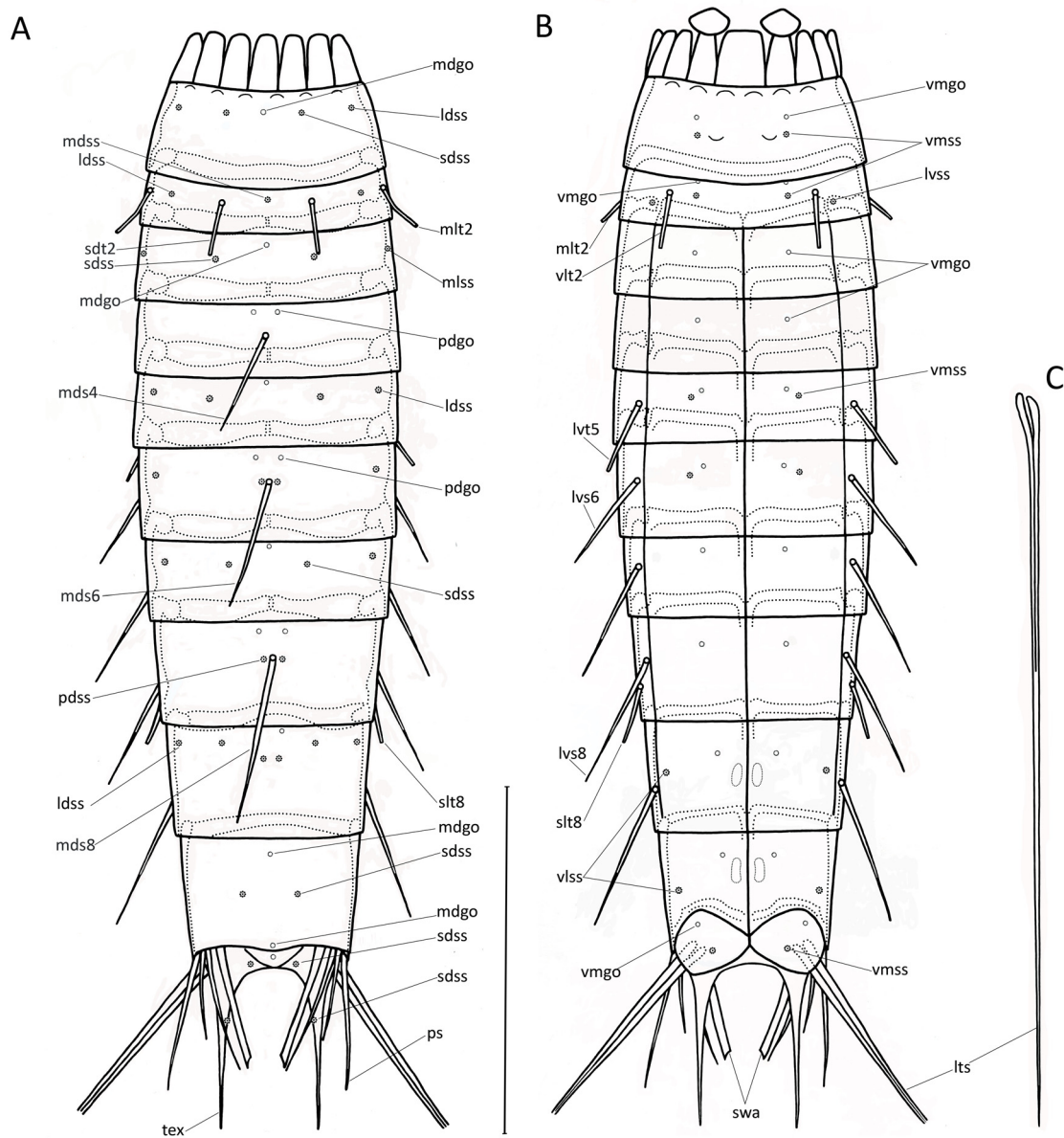


Fig. 1. *Echinoderes xiphophorus* sp. nov., ♂. **A.** Whole animal, dorsal view. **B.** Whole animal, ventral view. **C.** Lateral terminal spine. Abbreviations: ldss = laterodorsal sensory spot; lts = lateral terminal spine; lvs = lateroventral spine; lvss = lateroventral sensory spot; lvt = lateroventral tube; mdgo = middorsal glandular cell outlet type 1; mds = middorsal spine; mdss = middorsal sensory spot; mlss = midlateral sensory spot; mlt = midlateral tube; pdgo = paradorsal glandular cell outlet type 1; pdss = paradorsal sensory spot; ps = penile spine; sdss = subdorsal sensory spot; sdt = subdorsal tube; slt = sublateral tube; swa = sword-like appendage; tex = tergal extension; vlss = ventrolateral sensory spot; vlt = ventrolateral tube; vmgo = ventromedial glandular cell outlet type 1; vmss = ventromedial sensory spot. Numbers indicate the number of the trunk segment. Scale bar = 50 μ m.

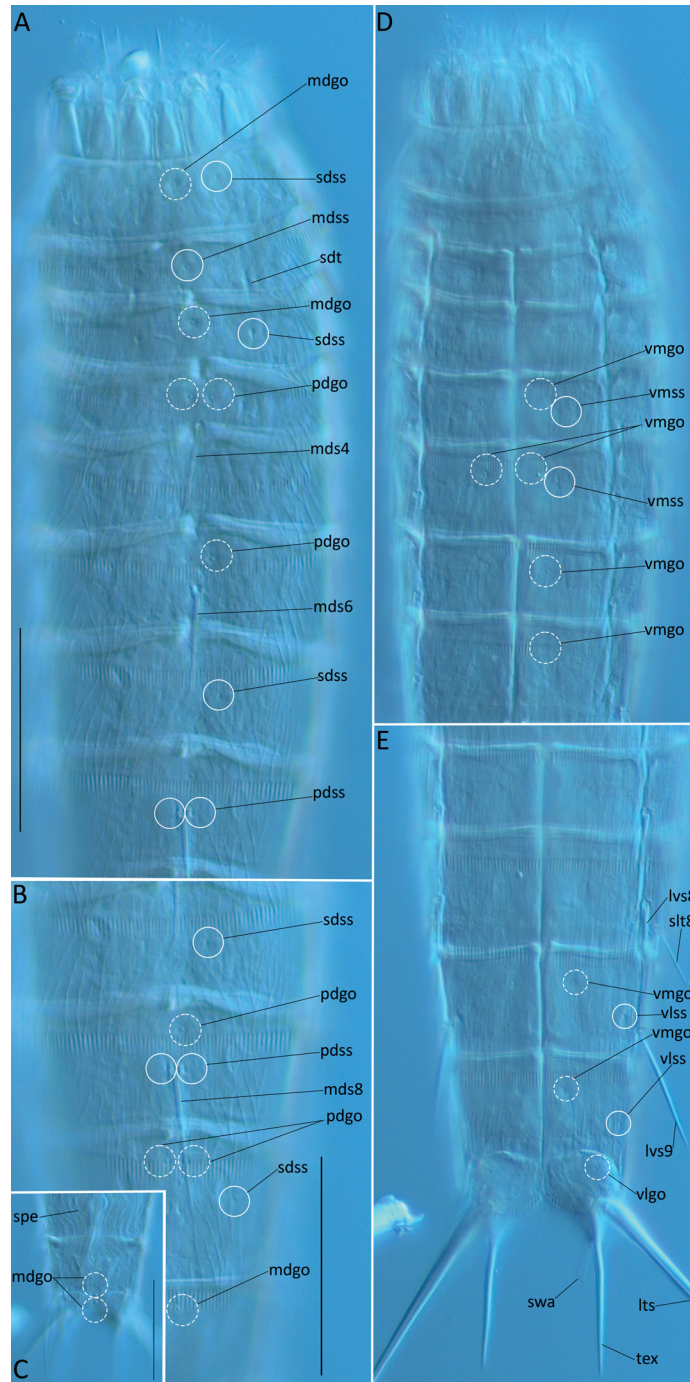


Fig. 2. *Echinoderes xiphophorus* sp. nov., holotype, ♂ (MIMB 41347), light micrographs. **A–C.** Dorsal view. **D–E.** Ventral view. **A.** Trunk segments 1–8. **B.** Trunk segments 7–10. **C.** Trunk segments 10–11. **D.** Trunk segments 1–8. **E.** Trunk segments 7–11. Abbreviations: lts = lateral terminal spine; lvs = lateroventral spine; mdgo = middorsal glandular cell outlet type 1; mds = middorsal spine; mdss = middorsal sensory spot; pdgo = paradorsal glandular cell outlet type 1; pdss = paradorsal sensory spot; sdss = subdorsal sensory spot; sdt = subdorsal tube; slt = sublateral tube; spe = spermatozoa; swa = sword-like appendage; tex = tergal extension; vlgo = ventrolateral glandular cell outlet type 1; vls = ventrolateral spine; vlss = ventrolateral sensory spot; vmgo = ventromedial glandular cell outlet type 1; vmss = ventromedial sensory spot. White circles indicate sensory spots, dotted white circles indicate glandular cell outlets. Numbers indicate the number of the trunk segment. Scale bars = 50 μ m.

TRUNK SEGMENT 3. One tergal and two sternal plates, with distinct tergo-sternal and midventral articulations, as in all remaining trunk segments; with two pairs of sensory spots in subdorsal and midlateral position (Figs 1A–B, 2A, 3B, 6B); single glandular cell outlet of type 1 in middorsal position located close to the anterior segment margin and hidden under preceding segment; with a pair of glandular cell outlets in ventromedial position; long cuticular hairs absent in ventromedial position, being replaced by much shorter cuticular hairs (Fig. 7B); other cuticular hairs and pectinate fringe as in the preceding segment.

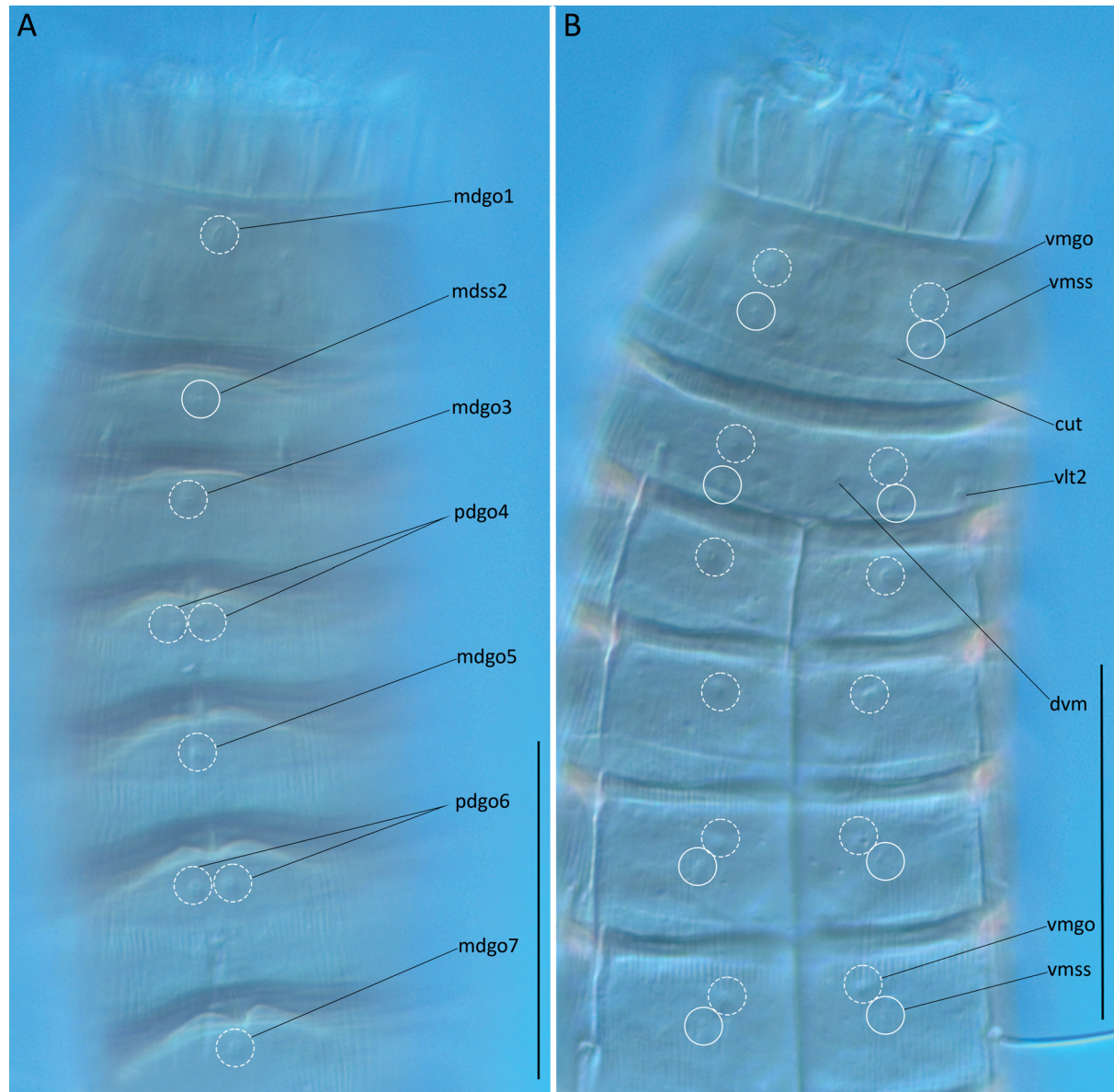


Fig. 3. *Echinoderes xiphophorus* sp. nov., paratype ♂ (MIMB 41348), trunk segments 1–6, light micrographs. **A.** Dorsal view. **B.** Ventral view. Abbreviations: cut = cuticular scars; dvm = dorsoventral muscle attachment site; mdgo = middorsal glandular cell outlet of type 1; mdss = middorsal sensory spot; pdgo = paradorsal glandular cell outlet of type 1; vlt = ventrolateral tube; vmgo = ventromedial glandular cell outlet type 1; vmss = ventromedial sensory spot. White circles indicate sensory spots. Dotted white circles indicate glandular cell outlets. Numbers indicate the number of the trunk segment. Scale bars = 50 µm.

TRUNK SEGMENT 4. With acicular spine in middorsal position (Figs 2A, 4A); with two pairs of glandular cell outlet of type 1 in paradorsal and ventromedial positions, paradorsal outlets usually hidden under previous segment (Figs 2A, D, 3); long cuticular hairs absent in middorsal position beneath acicular spine; other cuticular hairs and pectinate fringe as in the preceding segment.

TRUNK SEGMENT 5. No acicular spine in middorsal position; one pair of tubes in lateroventral position (Figs 4C, 7B); three pairs of sensory spots in subdorsal, laterodorsal and ventromedial position; single glandular cell outlet of type 1 in middorsal position located close to the anterior segment margin and usually hidden under previous segment; with one pair of glandular cell outlets of type 1 in ventromedial positions; pectinate fringe and cuticular hairs as in the trunk segment 3.

TRUNK SEGMENT 6. With acicular spine in middorsal position (Figs 2A, 4A, 6D); with a pair of acicular spines in lateroventral position (Fig. 4B); with three pairs of sensory spots in paradorsal, laterodorsal and ventromedial position; with two pairs of glandular cell outlets of type 1 in paradorsal and ventromedial position, paradorsal outlets usually hidden under previous segment; pectinate fringe and cuticular hairs as in the trunk segment 4.

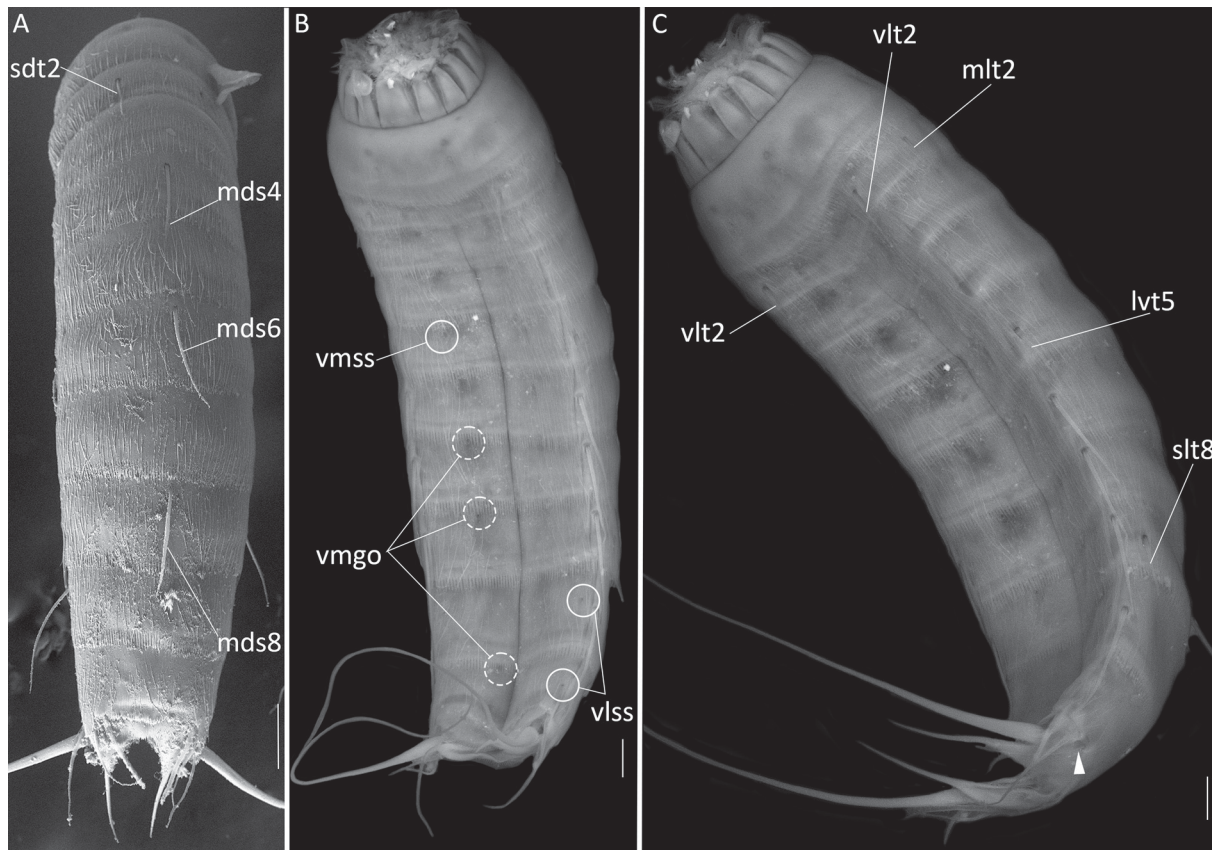


Fig. 4. *Echinoderes xiphophorus* sp. nov., ♂, SEM micrographs. **A.** Dorsal view. **B–C.** Ventral view, uncoated SEM specimens. Abbreviations: lvt = lateroventral tube; mds = middorsal spine; mlt = midlateral tube; sdt = subdorsal tube; slt = sublateral tube; vlss = ventrolateral sensory spot; vlt = ventrolateral tube; vmgo = ventromedial glandular cell outlet type 1; vmss = ventromedial sensory spot. White circles indicate sensory spots. Dotted white circles indicate glandular cell outlets. White arrowhead indicates cuticular hole of broken sword-like appendage. Numbers indicate the number of the trunk segment. Scale bars: A = 20 μ m; B–C = 10 μ m.

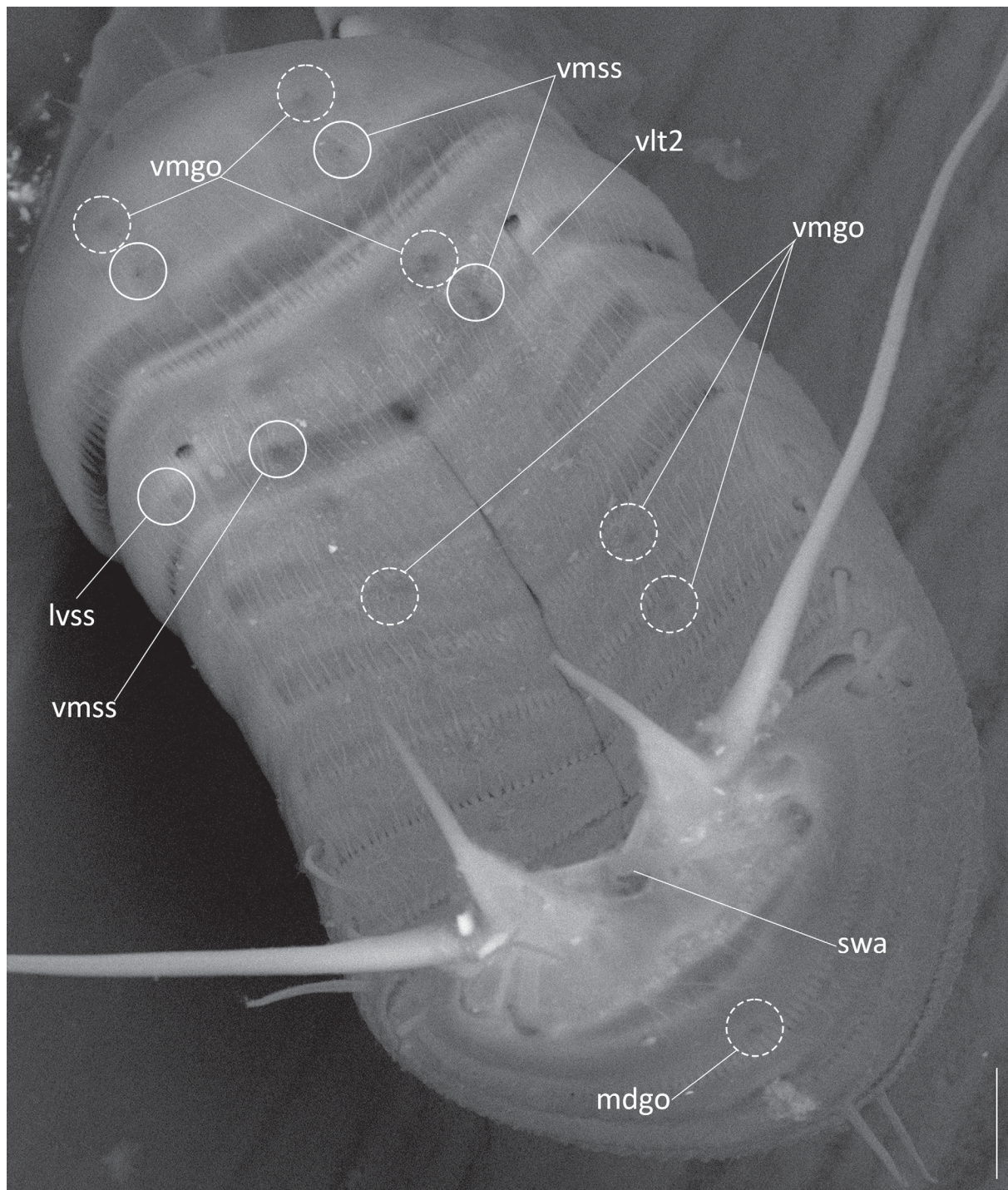


Fig. 5. *Echinoderes xiphophorus* sp. nov., ♂, SEM micrograph of uncoated specimen, ventral view. Abbreviations: lvss = lateroventral sensory spot; mdgo = middorsal glandular cell outlet type 1; swa = sword-like appendage; vlt = ventrolateral tube; vmgo = ventromedial glandular cell outlet type 1; vmss = ventromedial sensory spot. White circles indicate sensory spots. Dotted white circles indicate glandular cell outlets. Number after vlt indicates the number of the trunk segment. Scale bar = 10 μ m.

TRUNK SEGMENT 7. No acicular middorsal spine; with two pairs of sensory spots in subdorsal and laterodorsal position; with single glandular cell outlets of type 1 in middorsal position (usually hidden under previous segment) and one pair of outlets in ventromedial position; other spines, pectinate fringe and cuticular hairs as in the preceding segment.

TRUNK SEGMENT 8. With acicular spine in middorsal position (Figs 2A, 4A, 6E); with a pair of tubes in sublateral position (Figs 2E, 4C, 7D); with one pair of sensory spots in paradorsal position (Figs 6E, 7C); with two pairs of glandular cell outlets of type 1 in paradorsal and ventromedial position (Fig. 2B, D); other spines, pectinate fringe and cuticular hairs as in the preceding segment.

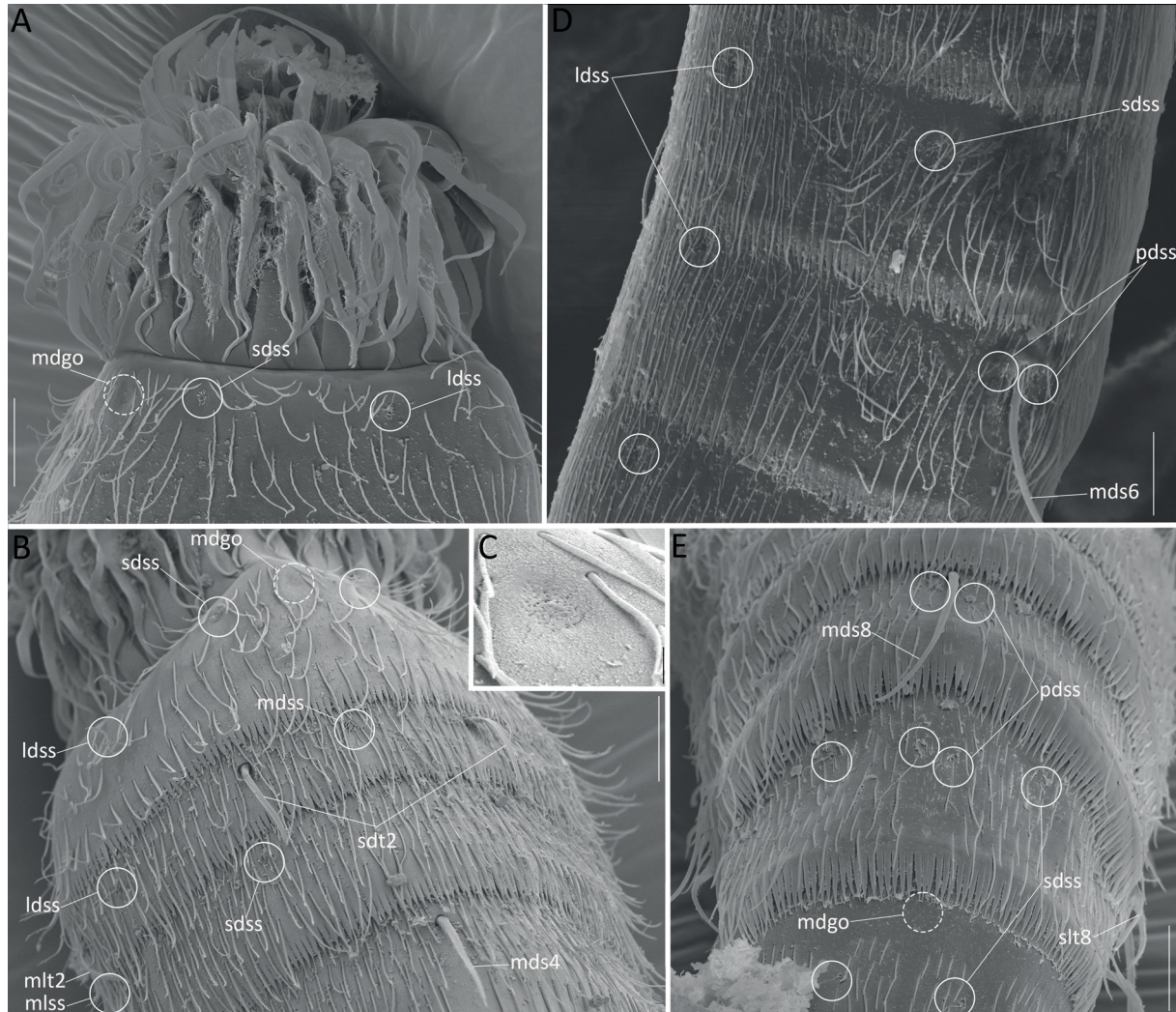


Fig. 6. *Echinoderes xiphophorus* sp. nov., ♂, SEM micrographs. **A, D.** Dorsolateral view. **B, C, E.** Dorsal view. **A.** Head, neck, and trunk segment 1. **B.** Trunk segments 1–4. **C.** Middorsal glandular cell outlet type 1 on trunk segment 1. **D.** Trunk segments 5–7. **E.** Trunk segments 8–10. Abbreviations: ldss = laterodorsal sensory spot; mdgo = middorsal glandular cell outlet type 1; mds = middorsal spine; mdss = middorsal sensory spot; mlss = midlateral sensory spot; mlt = midlateral tube; pdss = paradorsal sensory spot; sdss = subdorsal sensory spot; sdt = subdorsal tube; slt = sublateral tube. White circles indicate sensory spots. Dotted white circles indicate glandular cell outlets. Numbers indicate the number of the trunk segment. Scale bars: A–B, D–E = 10 µm; C = 1 µm.

TRUNK SEGMENT 9. No acicular middorsal spine; no tubes; with four pairs of sensory spots in paradorsal, subdorsal, laterodorsal and ventrolateral position (Figs 2E, 6E, 7C–E, 8C); with two pairs of glandular cell outlets of type 1 in paradorsal and ventromedial positions (Fig. 2B, E); pair of excretory sieve plates in lateral accessory position; other spines, pectinate fringe and cuticular hairs as in the preceding segment.

TRUNK SEGMENT 10. No acicular spines; with two pairs of sensory spots in subdorsal and ventrolateral position (Figs 2E, 6E, 8C); with single glandular cell outlets of type 1 in middorsal position and one pair in ventromedial position (Figs 2B, E, 5); males possess a pair of very long and flattened sword-like

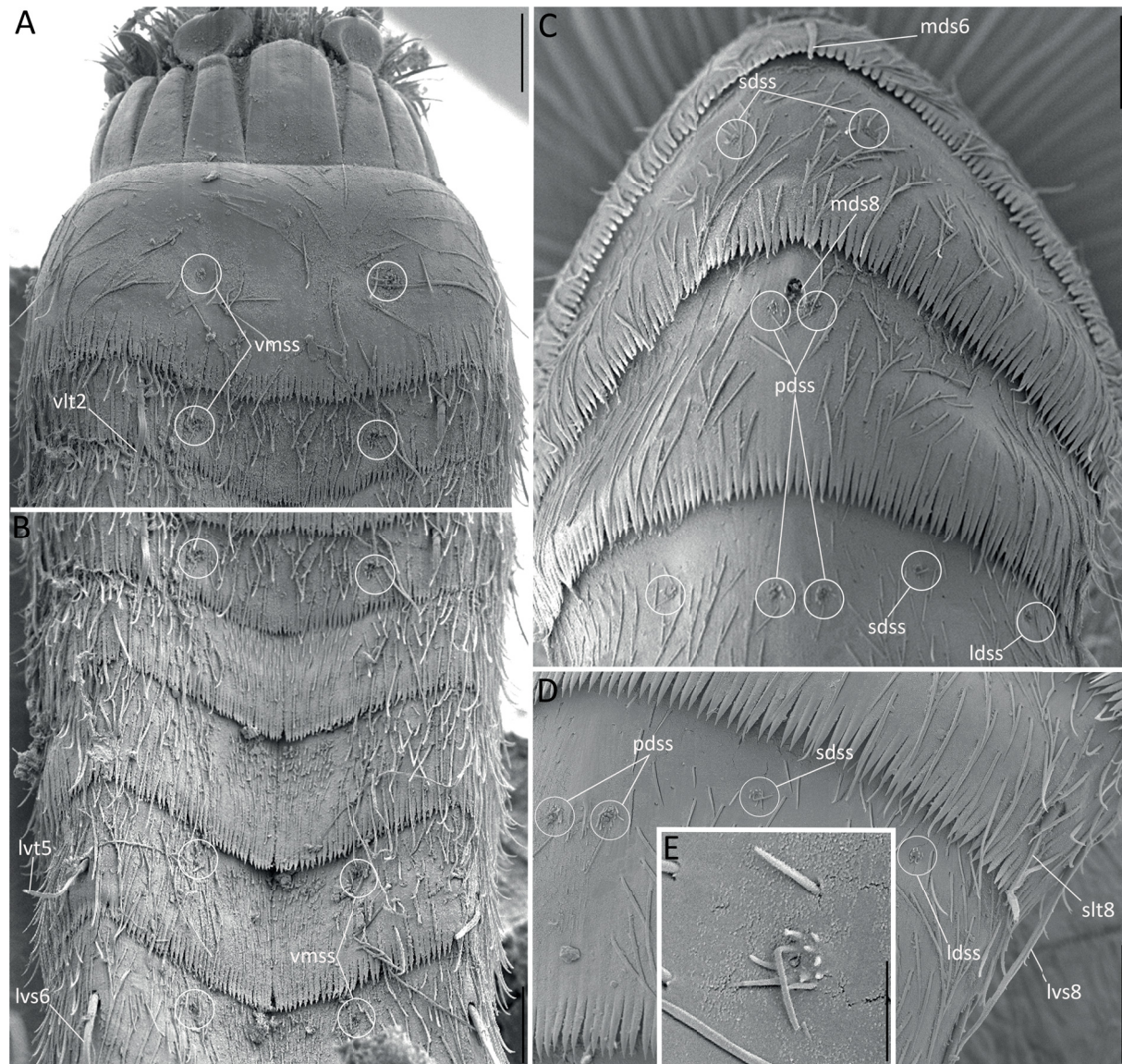


Fig. 7. *Echinoderes xiphophorus* sp. nov., SEM micrographs. **A–B.** ♂, ventral view. **A.** Trunk segments 1–2. **B.** Trunk segments 2–5. — **C–E.** ♀, dorsal view. **C.** Trunk segments 6–9. **D.** Trunk segment 9. **E.** Subdorsal sensory spot on trunk segment 9. Abbreviations: ldss = laterodorsal sensory spot; lvs = lateroventral spine; lvt = lateroventral tube; mds = middorsal spine; pdss = paradorsal sensory spot; sdss = subdorsal sensory spot; slt = sublateral tube; vlt = ventrolateral tube; vmss = ventromedial sensory spot. White circles indicate sensory spots. Numbers indicate the number of the trunk segment. Scale bars: A–D = 10 µm; E = 2 µm.

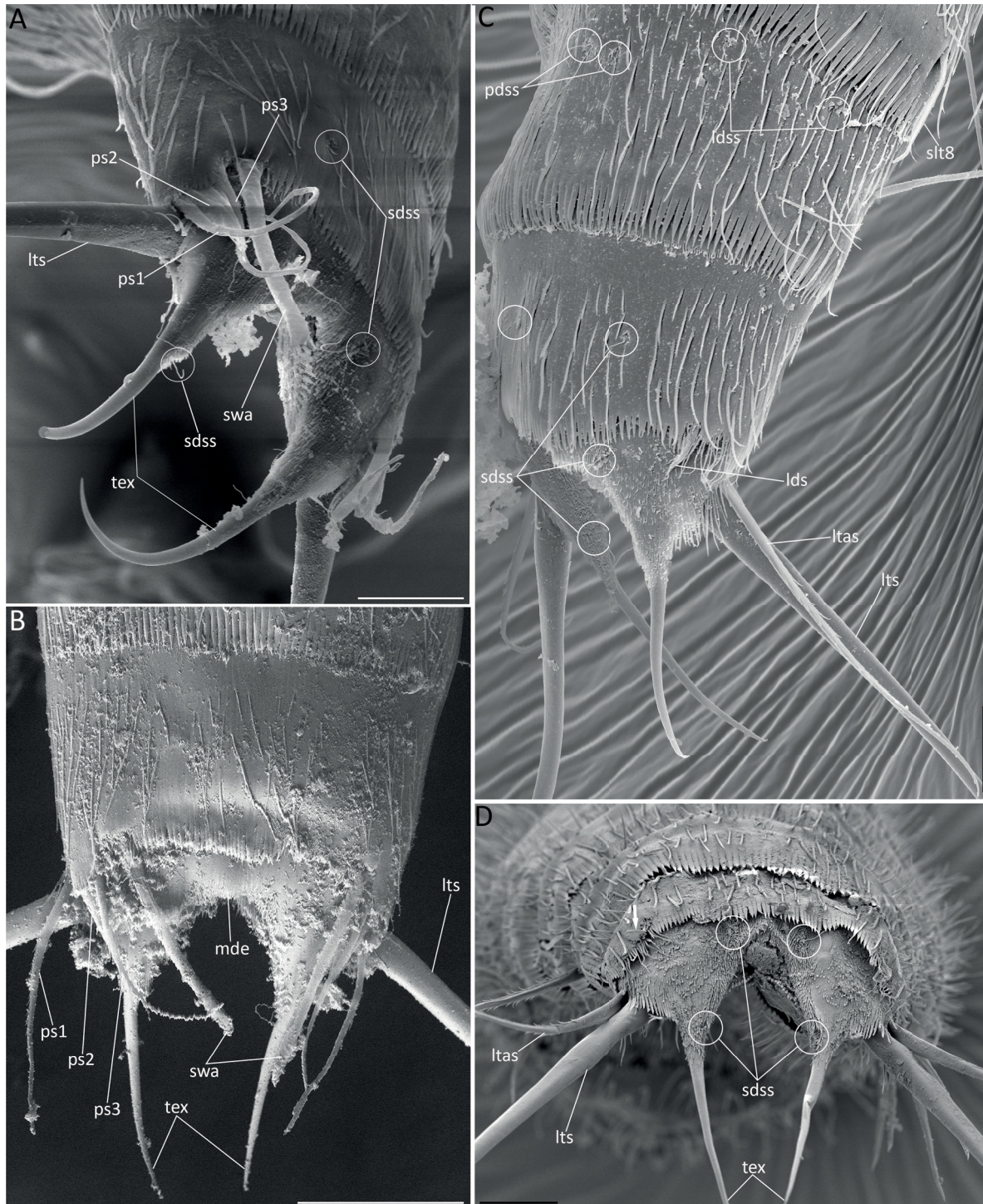


Fig. 8. *Echinoderes xiphophorus* sp. nov., SEM micrographs. **A–B.** ♂, trunk segments 10–11. **A.** Dorsolateral view. **B.** Dorsal view. — **C–D.** ♀, trunk segments 9–11. **C.** Lateral view. **D.** Posterior view. Abbreviations: lds = laterodorsal spine/tube; ldss = laterodorsal sensory spot; ltas = lateral terminal accessory spine; lts = lateral terminal spine; mde = middorsal elevation; pdss = paradorsal sensory spot; ps = penile spine; sdss = subdorsal sensory spot; slt = sublateral tube; swa = sword-like appendage; tex = tergal extension. White circlets indicate sensory spots. Numbers after ps indicate the number of the pair, the number after slt indicates the number of the trunk segment. Scale bars: A, C–D = 10 μ m; B = 20 μ m.

appendages (similar in shape to Japanese swords katana or wakizashi) in laterodorsal position, dorsally to penile spines, only slightly shorter than tergal extensions (about 80% of TE) (Fig. 8A–B); females with a pair of short tubes/spines in laterodorsal position corresponding to sword-like appendages of male (Fig. 8C–D); other characters as in the preceding segment.

TRUNK SEGMENT 11. One pair of long lateral terminal spines (Fig. 1C); tergal extensions very long, about 15–16% of TL (Figs 4–5, 8); tergal plate with nearly rounded middorsal elevation (Fig. 8B, D); with two pairs of sensory spots in subdorsal and ventromedial position, and additional pair of sensory spots present at the base of tergal extensions (Fig. 8A, C–D); with two glandular cell outlets of type 1 in middorsal position and one pair ventrolateral position (Figs 2C, E, 5); males with three pairs of penile spines, first and third pairs thin and flexible, spine of second pair shorter and cone-shaped with terminal tuft of cuticular hairs (Figs 5, 8A–B); female with a pair of long and thin lateral terminal accessory spines; sexes can be also recognized by observation of gonads.

Discussion

Taxonomic remarks

Echinoderes xiphophorus sp. nov. is well distinguished from all congeners by a unique combination of characters: three pairs of tubes on trunk segment 2 and one pair of tubes on trunk segments 5 and 8 middorsal spines on trunk segments 4, 6, 8; acicular lateroventral spines on trunk segments 6–9; extremely long tergal extensions of 11th trunk segment; very long sword-like appendages dorsal to penile spines in male and short spines at the same position in female (Fig. 1A–B).

Among the more than 130 species of the genus *Echinoderes* described so far, only five possess three pairs of tubes on trunk segment 2. Three shallow-water species, *E. newcaledoniensis* Higgins, 1967 from South-West Pacific, *E. peterseni* Higgins & Kristensen, 1988 from the Greenland Sea, North-West Atlantic, and *E. ohtsukai* Yamasaki & Kajihara, 2012 from North Pacific, possess three pairs of tubes in subdorsal, laterodorsal and ventrolateral position (see Higgins 1967; Higgins & Kristensen 1988; Adrianov & Malakhov 1999; Yamasaki & Kajihara 2012). The first two species are also characterized by having middorsal spines on trunk segments 4, 6 and 8, and additional lateral tubes on trunk segment 8, but well differ from the new species by the shape of much shorter tergal extensions. In addition, *E. peterseni* bears additional lateral tubes on trunk segment 9. *Echinoderes ohtsukai* is well distinguished by the presence of only a single minute middorsal spine on trunk segment 4. *Echinoderes belenae* Pardos, Herranz & Sanchez, 2016 from the Pacific coast of Panama possesses three pairs of tubes in subdorsal, midlateral and ventrolateral position (see Pardos *et al.* 2016). This species well differs from the new one by having very short and stubby lateral terminal spines. The fifth species, *E. hispanicus* Pardos, Higgins & Benito, 1998 from Spain, bears tubes in subdorsal, sublateral and ventrolateral position (see Pardos *et al.* 1998) and well differs from the new species by the shape and length of the terminal tergal extensions.

The bathyal *E. balerioni* Grzelak & Sørensen, 2019 from the Arctic Ocean, close to Spitsbergen Archipelago, also possesses three pairs of tubes on trunk segment 2 in laterodorsal, sublateral and ventrolateral position (see Grzelak & Sørensen 2019). *Echinoderes balerioni* and *E. xiphophorus* sp. nov. are characterized by similar spine/tubes formula. Nevertheless, *E. balerioni* is well distinguished from the new species by having a tube on trunk segment 8 in the lateral accessory position, opposite to the sublateral position in *E. xiphophorus* sp. nov., and the shape of the sternal plates of the posteriormost segment (see Grzelak & Sørensen 2019: fig. 2). Also, this species has no sword-like appendages dorsally to three pairs of penile spines in males.

The shallow-water Mediterranean *E. capitatus* (Zelinka, 1928) even possesses four pairs of tubes on trunk segment 2 in subdorsal, laterodorsal, midlateral and ventrolateral position, but is easily distinguished by

the single middorsal spine on trunk segment 4, a different spine formula and rather short triangular tergal extensions (see Yamasaki & Dal Zotto 2019).

Some species of *Echinoderes* are also characterized by very long dagger-like tergal extensions. For instance, *E. sylviae* Landers & Sørensen, 2018 from the Gulf of Mexico, West Atlantic, and *E. lupherorum* Sørensen *et al.*, 2018 and *E. kohni* Varney, Funch, Kocot & Sørensen, 2019 from the North-East Pacific have tergal extensions about 7 and 8% of TL, respectively (see Sørensen *et al.* 2018; Varney *et al.* 2019). In *E. higginsi* Huys & Coomans, 1989 from the North Sea and *E. spinifurca* Sørensen *et al.*, 2005 from the Gulf of Mexico these extensions constitute about 11% of TL (see Huys & Coomans 1989; Sørensen *et al.* 2005). *Echinoderes cernunnos* Sørensen *et al.*, 2012 from Korean waters, North-West Pacific, has tergal extensions about 13% of TL (see Sørensen *et al.* 2012). Very long tergal extensions are described in *E. yamasakii* Sørensen *et al.*, 2018 from the North-East Pacific, about 13–16% of TL (see Sørensen *et al.* 2018). Only two of these *Echinoderes*, *E. lupherorum* and *E. yamasakii*, are deep-sea species, while all others inhabit shallow waters. All these echinoderids well differ from the new species by the spine/tubes formula. For instance, *E. sylviae*, *E. lupherorum*, *E. kohni*, *E. spinifurca*, *E. cernunnos*, and *E. yamasakii*, are well distinguished by the presence of middorsal spines on trunk segments 4–8. *Echinoderes higginsi*, having middorsal spines on trunk segments 4, 6 and 8, differs from the new species by a different number and arrangement of the tubes on the trunk segment 2. The longest terminal extensions within *Echinoderes* are described in bathyal *E. balerioni* from the Arctic Ocean, about 18.3% of TL (see Grzelak & Sørensen 2019).

Two other representatives of echinoderids, *Meristoderes okhotensis* Adrianov & Maiorova, 2018 from the deepest depression of the Okhotsk Sea, North-West Pacific, and the deep-water *Fissuroderes rangi* Neuhaus, 2006 from the New Zealand waters, South-West Pacific, are also characterized by very long tergal extensions, 16 and 17% of TL, respectively (see Neuhaus & Blasche 2006; Adrianov & Maiorova 2016). *Fissuroderes rangi* is easily distinguished by the structure of the second trunk segment with well-developed midventral and lateral articulations resulting in tergal and two sternal plates. *Meristoderes okhotensis* possesses a second trunk segment with remarkably curved intracuticular fissures in lateroventral position, well visible with DIC only and corresponding to the tergo-sternal articulations of the following trunk segments, thus also forming an indistinct differentiation into one tergal and one sternal plate (see Adrianov & Maiorova 2018a: fig. 2b, d). The new species of *Echinoderes* is externally very similar to *Meristoderes okhotensis* by the spine/tubes formula and by presence of very long tergal extensions. The latter species also bears three pairs of tubes on trunk segment 2 in subdorsal, laterodorsal and ventrolateral position; lateroventral tubes on trunk segment 5, lateral tubes on trunk segment 8, and lateroventral acicular spines on trunk segments 6–9 (see Adrianov & Maiorova 2018a). However, *M. okhotensis* can easily be distinguished from the new species by the presence of only two middorsal spines on trunk segments 6 and 8, and by different arrangement of sensory spots and glandular cell outlets.

Similar to *M. okhotensis*, the new species is also characterized by very small sensory spots on trunk segments 3–10, just about 1 µm in length and only with a few petals around one pore. One of the remarkable characters of these sensory spots in both species is the presence of 1–2 remarkably long posterior petals, 3–4 times as long as the sensory spots themselves (see Adrianov & Maiorova 2018a: fig. 4c–h) (Fig. 7D–E).

Interestingly, *M. okhotensis* is the only other species of kinorhynchs having sword-like appendages dorsally to three pairs of penile spines in males (see Adrianov & Maiorova 2018a: fig. 4f). These appendages in *M. okhotensis* are about twice as short as the tergal extensions, and similar in shape as the Roman gladius. In *E. xiphophorus* sp. nov., these sword-like appendages are much longer, constituting about 80% of the tergal extensions, and more similar in shape to the Japanese katana or wakizashi (Fig. 8A–B). These appendages cannot be misinterpreted with ordinary penile spines usually situated

more laterally at the boundary between two posteriormost segments. In contrast to the flexible penile spines that appear round in cross-section in both species, these appendages are remarkably flattened and not flexible. Probably, these sword-like appendages can be homologized with tubes of trunk segment 10, known in many species of *Echinoderes*, but not with ordinary penile spines. Nevertheless, these structures, present only in males, are suspected to be used in copulation process, but their real function is still not understood (see Adrianov & Maiorova 2018a).

Echinoderes xiphophorus sp. nov. constitutes the second bathyal representative of the genus *Echinoderes* in the North-West Pacific, the first deep-sea representative of the Echinoderidae in the Sea of Japan and the deepest representative of the Kinorhyncha in this sea.

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