

Redescription of *Echinoderes filispinosus* Adrianov, 1989 - the Brackish Water Mud Dragon (Kinorhyncha) from the Extreme Environment in the Sea of Japan, with Discussion of Transoceanic Distribution Estuarine Species

Andrey V. Adrianov^{1,2,§}, Anastassya S. Maiorova^{1,§,*}, Anastasia P. Grigorenko³, and Irina Yu. Adrianova³

¹A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch of Russian Academy of Sciences, 690041, Vladivostok, Russia. *Correspondence: E-mail: anastasia.maiorova@gmail.com (Maiorova).
E-mail: avadr@mail.ru (Adrianov)

²M.V. Lomonosov Moscow State University, Faculty of Biology, 119991, 1-12 Leninskie Gory, Moscow, Russia

³Vavilov Institute of General Genetics Russian Academy of Sciences, 119333, Moscow, Russia. E-mail: anast1998@mail.ru (Grigorenko);
i-yi-saz@mail.ru (Adrianova)

urn:lsid:zoobank.org:pub:C70FE572-A113-4AA2-84F2-5DB804F693C0

[§]AVA and ASM contributed equally to this work.

Received 21 May 2025 / Accepted 4 April 2026 / Published 2 July 2026

Communicated by Benny K.K. Chan

A brackish water mud dragon species *Echinoderes filispinosus* is redescribed from the type locality in the Sea of Japan. The species should be considered part of the *Echinoderes coulli* species group. This species is characterized by presence of a single minute middorsal spine on trunk segment 4, minute lateroventral spines on trunk segments 6–7, long lateroventral tubes on trunk segments 5 and 8, sexually dimorphic laterodorsal tubes on trunk segment 10, numerous glandular cell outlets type 2 modified into minute fringed tubes, large elongated sieve plates with posterior pore, and strongly reduced lateral terminal accessory spines. The paper documents newly found morphological characters of *E. filispinosus*, suggesting an emended classification of *Echinoderes ohtsukai* as junior synonym of *E. filispinosus*. DNA sequence also reveals that *E. ohtsukai* is completely conspecific with *E. filispinosus*. This estuarine species demonstrates outstanding ability to survive under the record seasonal variations of temperature and salinity. Transoceanic distribution of this species in the North Pacific is also discussed.

Keywords: Brackish water, *Echinoderes*, Estuary, Kinorhynchs, Transoceanic

BACKGROUND

Kinorhynchs are meiobenthic free-living segmented worms from 0.2 to 1.2 mm in length. They are distributed worldwide, usually inhabiting the upper few centimeters of various marine and estuarine sediments from littoral zone to the hadal depth up

to 9538 m (see Neuhaus 2013; Sørensen et al. 2018; Adrianov and Maiorova 2019). About 350 species of kinorhynchs have been described to date (see Sørensen and Yamasaki 2024).

Echinoderes is the most species-rich genus of kinorhynchs and already accommodates more than 150 species. Due to the progress in description of numerous

Citation: Adrianov AV, Maiorova AS, Grigorenko AP, Adrianova IY. 2026. Redescription of *Echinoderes filispinosus* Adrianov, 1989 - the brackish water mud dragon (Kinorhyncha) from the extreme environment in the Sea of Japan, with discussion of transoceanic distribution estuarine species. Zool Stud 65:25. doi:10.6620/ZS.2026.65-25.

new species of *Echinoderes* and thorough redescrptions of many old species, several putative monophyletic groups were progressively introduced within this genus (see Herranz et al. 2023). One of the most well-reasoned group is *Echinoderes coulli* group (see Randsø et al. 2019; Sørensen 2023) which currently accommodates about 25 species of *Echinoderes*.

Despite of the current progress in kinorhynch's taxonomy, new descriptions are faced with some problems when comparing some taxonomic characters to differentiate new nominal species from already described similar congeners (Grzelak et al. 2023). About half of all *Echinoderes* species were described in the last century and some currently important characters were overlooked, especially some minute characters hidden under dense cuticular hairs or confused with these hairs. Re-examinations of insufficiently described species are necessary to get a correct identification of newly collected species and also to update existing species descriptions for correct morphological comparisons and phylogenetic conclusions.

Currently, descriptions of new species are mainly relied on unique sets of main morphological characters (spines, tubes, papillae, sensory spots, glandular outlets, tergal extensions etc.) and morphometric data. However, some close species show very similar sets of diagnostic characters or even exhibit identity of these characters, being distinct genetically. In this case, integrating DNA sequences can be very helpful to reveal hidden diversity and distinguish cryptic species within kinorhynchs (Herranz et al. 2024).

The present contribution redescrbes the potential *Echinoderes coulli*-group species *E. filispinosus* from the extreme type locality characterized by the record seasonal fluctuations of temperature and salinity. This species appears the first representative of the *E. coulli*-group in the Russian water areas.

MATERIALS AND METHODS

Study site

The Vostok Bay is the most investigated water area in the Russian part of the Sea of Japan. It is characterized with the regular spatial-temporal monitoring of main hydrometeorological parameters monitored daily, monthly, and annually, with an analysis of seasonal and interannual variabilities for at least last 50 years (see Gayko 2017). The climate in this area is dominated by the monsoon, with very cold winter and warm and wet summer. Because of the outstanding seasonal variations of temperature and salinity, in the wintertime this bay is similar to typical arctic waters

whereas in the summer time its environments are similar to subtropical ones (Gayko 2017). The sampling area is situated in the most inner part of the Vostok Bay (named Vostok Harbor), in the estuary near the old and the current river mouths (Fig. 1).

Specimens sampling and preparation

Sediment samples were taken by hand and with a shovel at low tide at the depth 0.5 m. Kinorhynchs were extracted from the samples by using the bubbling and blot method (see Higgins 1988). Further, the sediment was washed with a filtered sea water, passed through a 32 µm sieve "Mermaid Bra". In the laboratory at the Biological Station "Vostok" located near the river mouth, living kinorhynchs were picked up from the washed samples and sorted under a stereomicroscope. Specimens for solely morphological observation were fixed in 4% buffered formaldehyde. Specimens selected for DNA extraction were fixed with 96% ethanol.

Among the morphological-observation specimens, individuals selected for light microscopy (LM) were transferred into a 70% ethanol-5% glycerol-25% deionized water solution. Once ethanol and water evaporated, specimens were preserved in anhydrous glycerol. All specimens were mounted individually in VECTASHIELD® mounting medium for fluorescence between two cover glasses 22 and 18 mm in length respectively. The cover glasses were positioned on Higgins-Shirayama plastic slide frames for further examination using differential interference contrast microscopy (DIC). These specimens were studied with a Zeiss® Axio Imager. Z2 microscope equipped with an AxioCamHRc camera.

Specimens selected for scanning electron microscopy (SEM) were transferred to 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, coated with gold, and observed using a Zeiss® Sigma 300VP scanning electron microscope.

In the examination procedure, the measurement protocol recently suggested by González-Casarrubios et al. (2023) is followed. Morphological measurements of *Echinoderes filispinosus* are summarized in table 1. The position of cuticular structures throughout the trunk segments are summarized in table 2. Holotype of this species Jc274 deposited in the Zoological Museum of Moscow State University was additionally observed. All specimens newly collected from the type locality are deposited to the Museum of the National Scientific Center of Marine Biology of the Far Eastern Branch of

the Russian Academy of Sciences (NSCMB FEB RAS) (MIMB 52676-52691).

DNA extraction, amplification and sequencing

A total of ten morphologically identical specimens of *Echinoderes filispinosus* from the Vostok Bay, preserved in 96% ethanol, were pooled and treated as a single sample for total DNA extraction. Extraction, amplification and sequencing of DNA were conducted in the Laboratory of Evolutionary Genomics, Vavilov Institute of General Genetics RAS. Total DNA extraction was performed using MagAttract HMW DNA Kit (Quiagen, USA) following the protocol provided by the manufacturer. After the completion of

DNA extraction the empty cuticulars were recovered from the lysis buffer and mounted in VECTASHIELD® mounting medium between two cover glasses 22 and 18 mm in length respectively, positioned on Higgins-Shirayama plastic slide frame. The slide is deposited to the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology FEB RAS under catalog number MIMB52691. Extracted DNA was used to amplify and sequence of the mitochondrial cytochrome *c* oxidase subunit 1 (*COI*) gene. Polymerase chain reaction (PCR) was performed using the Q5 high fidelity DNA polymerase (New England Biolabs, USA) and the following primers: LCO1490 (5'-GGTCAACA AATCATAAAGATATTGG-3') and HCO2198 (5'-TAA ACTTCAGGGTGACCAAAAAATCA-3') (Folmer et



Fig. 1. A, map of the Northwestern Pacific. B–D, closer view map; E–F, drone image of the sample site, October and March, 2024. White quadrant frame indicates area of closer view. Yellow spot indicates sampling area of *Echinoderes filispinosus*. White arrowhead indicates “Vostok”, Marine Biological Station. (Map from Google Earth, <https://earth.google.com/>).

Table 1. Measurements (μm) and proportions (%) of adults of *Echinoderes filispinosus*

	Average ♀	Average ♂	Average all	n	Range ♀	Range ♂
TL	371	371	371	9 ♀/6 ♂	345–418	367–393
MSW–7	74	72	73	9 ♀/6 ♂	72–75	67–75
MSW–7/TL	20	19	20	9 ♀/6 ♂	19–21%	18–21%
SW	66	62	64	9 ♀/6 ♂	57–72	57–65
SW/TL	18	17	17	9 ♀/6 ♂	16–19%	15–17%
S1	33	32	33	9 ♀/6 ♂	29–44	29–37
S2	30	30	30	9 ♀/6 ♂	20–37	27–35
S3	31	31	31	9 ♀/6 ♂	27–37	24–37
S4	34	34	34	9 ♀/6 ♂	31–40	32–39
S5	36	38	37	9 ♀/6 ♂	34–43	36–44
S6	41	39	40	9 ♀/6 ♂	37–48	36–41
S7	46	45	46	9 ♀/6 ♂	38–52	42–53
S8	54	54	54	9 ♀/6 ♂	51–39	50–60
S9	56	53	55	9 ♀/6 ♂	52–62	49–56
S10	46	48	46	9 ♀/6 ♂	40–50	46–50
S11	44	42	43	9 ♀/6 ♂	42–46	39–45
TE	28	25	27	9 ♀/6 ♂	23–31	22–26
TE/TL	8	7	7	9 ♀/6 ♂	6–9%	6–7%
MD4	8	8	8	9 ♀/6 ♂	5–12	7–10
LVT5	17	18	17	9 ♀/6 ♂	13–23	15–21
LVT8	18	19	18	9 ♀/6 ♂	15–23	15–21
LTAS	16	–	16	9 ♀/6 ♂	12–21	–
LTS	191	180	187	9 ♀/6 ♂	175–203	168–189
LTS/TL	52	49	51	9 ♀/6 ♂	43–59%	46–53%
PS1	–	32	32	9 ♀/5 ♂	–	26–35
PS2	–	21	21	9 ♀/6 ♂	–	18–26
PS3	–	42	42	9 ♀/6 ♂	–	36–47

Abbreviations: LTS, lateral terminal spine; LTAS, lateral terminal acicular spine; LVS, lateroventral spine; LVT, lateroventral tube; MD, middorsal spine; MSW, maximum sternal width; PS, penile spine; S, segment length; SW, standard width; TE, tergal extension; TL, trunk length. Number after abbreviation indicates number of trunk segment.

Table 2. Summary of nature and location of sensory spots, glandular cell outlets, tubes, excretory sieve plates and spines arranged by series in *Echinoderes filispinosus*

Position trunk segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss				gcol		ss
2	gcol, ss		ft	ft, ss, ss					ft	gcol, ss
3	gcol		ss		ss		ft			gcol
4	ac	gcol	ft				ft			gcol
5		gcol	ss	ss	ft			tu		gcol, ss
6		gcol	ss	ft, ss				ac		gcol, ss
7		gcol	ss	ss		ft		ac		gcol, ss
8	ft	gcol	ss	ft		ft		tu		gcol
9		gcol	ss, ss	ss		si			ss	gcol
10	gcol, gcol	gcol	ss	tu					ss	gcol
11	gcol	gcol	ss, ms		pe (♂)		ltas (♀)	lts		ss

Abbreviations: LA: lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac, acicular spine; ft, fringed tube (glandular cell outlet type 2); gcol, glandular cell outlet type 1; ltas, lateral terminal accessory spine; lts, lateral terminal spine; ms, muscular scar; pe, penile spines; si, sieve plate; ss, sensory spot; tu, tube; (♂), male condition of sexually dimorphic character; (♀) female condition of sexually dimorphic character.

al. 1994). PCR thermal cycling conditions were: 98°C for 30s; 35 cycles of (98°C for 10 s, 55°C for 30 s, 72°C for 1 min); and 72°C for 3 min. The amplified fragments were purified using the MinElute PCR Purification Kit (Qiagen, USA), loaded on 2% SYBR Safe E-gel (Invitrogen by Thermo Fisher Scientific, USA) for electrophoresis. The desired PCR fragment ca.700 bp was cutten out of the gel and purified using MinElute Gel Extraction Kit (Qiagen, USA). Nucleotide sequences were determined by Sanger sequencing using BigDye Terminator v 3.1 (ThermoFisher Sciientiific, USA) and a 3730xl DNA Analyzer (Life Technologies, USA). The sequencing chromatogram was manually checked using the IGV program (Integrative Genomics Viewer) (Robinson et al. 2011). The cuticles of ten specimens remained from the lysis buffer after the DNA extraction were deposited at the Museum of the NCMB FEB RAS under catalog number MIMB 52691.

Genetic diversity analyses

Fragments of *COI* sequences were assembled using Mega v. 11 software (Tamura et al. 2021) and aligned to the available sequences of the other species of *Echinoderes* from NCBI database. The list of these species with the GenBank accession numbers of the sequences is represented in figure 9. The assembled sequence was deposited to GenBank (NCBI) under accession number PV053103. The maximum likelihood tree (ML tree) based on the GTR+ G nucleotide substitutions model was constructed in Mega v. 11. The bootstrap method was used for assessing the reliability of branching, with 1000 iterations.

Material examined: Holotype: To facilitate a morphological comparison with the newly collected specimens, the holotype of *Echinoderes filispinosus* was also examined. The specimen was loaned from the Zoological Museum of Moscow State University (Slide # Jc274).

Additional material: MIMB 52676-52690 (9 ♀/6 ♂) (Table 1).

In addition to the specimens listed in ‘Systematic part, table 1’ below, ten specimens (catalogue number of the exoskeletons MIMB52691) were used for DNA extraction, more than 20 specimens were mounted for SEM, and about 60 specimens (30 males and 30 females) were additionally examined for the purpose of comparison for LM.

RESULTS

Taxonomic account

Family Echinoderidae Zelinka, 1894

Genus Echinoderes Claparede, 1863

***Echinoderes filispinosus* Adrianov, 1989**

(Figs. 2–8)

Emended diagnosis: *Echinoderes* with a single minute middorsal spine on trunk segment 4; minute lateroventral spines on trunk segments 6–7; long, thin and flexible lateroventral tubes on trunk segments 5 and 8, and sexually dimorphic laterodorsal tubes on trunk segment 10. Glandular cell outlets type 2 modified into minute fringed tubes, present in middorsal position on trunk segment 8, subdorsal position on trunk segments 2 and 4, in laterodorsal position on trunk segments 2,6 and 8, in midlateral position on trunk segment 5, in sublateral position on trunk segments 7–8, in lateroventral position on trunk segments 3–4, in ventrolateral position on trunk segment 2. Large, elongated sieve plates in sublateral position on trunk segment 9. Tergal extensions long and pointed. Males with three pairs of penile spines and long laterodorsal tubes on trunk segment 10. Females with strongly reduced lateral terminal accessory spines and minute laterodorsal tubes on trunk segment 10.

Description: Measurements and dimensions are given in table 1. A summary of cuticular structures positions (spines, tubes, sensory spots, glandular cell outlets) is given in table 2. Mouth cone armament consists of 9 articulated oral styles. The introvert bears seven rings of spinoscalids and one ring of six trichoscalids associated with pear-like cuticular plates with rounded edges. The neck consists of 16 trapezoid placids numbering clockwise from midventral one. Trichoscalid plates are situated ventrally on placids 2 and 16, and dorsally on placids 6, 8, 10, 12 (Fig. 2A–B).

Trunk segment 1 consists of a complete cuticular ring. Sensory spots are located in subdorsal, laterodorsal and ventromedial positions; subdorsal and laterodorsal ones are located near the anterior segment margin; ventromedial ones are located more centrally (Figs. 2A–B; 3E; 5C; 6A). Sensory spots are large and rounded in shape (4 µm), with a single central pore (Fig. 5C). Glandular cell outlets type 1 are located in middorsal (single) and lateroventral (one pair) positions near the anterior segment margin (Fig. 2A–B). Cuticular hairs are abundant, cover most of the dorsal surface of the segment, except for a narrow hairless zone at the anterior segment margin (Fig. 2A). On the ventral surface this hairless zone extends more posteriorly, towards the ventromedial sensory spots (Fig. 2B).

Cuticular hairs emerging from rounded perforations, thus giving in DIC characteristic small-dotted drawing on this and nine following segments (Figs. 2–3). The posterior segment margin with ventral convex extension. Pectinate fringe with alternating areas of short and longer acicular tips (Fig. 2A).

Trunk segment 2 consists of a completed cuticular

ring. Sensory spots are located in middorsal (single spot), laterodorsal (twin-pair) and ventromedial (one pair) positions (Figs. 2A–B; 5D; 6A). Sensory spots are large and elongated (7 μm) (Figs. 5D; 6A). Glandular call outlets type 1 are located in middorsal (single) and ventromedial (one pair) positions (Figs. 2A–B; 3E). Fringed tubes (8–9 μm), or fringed glandular cell

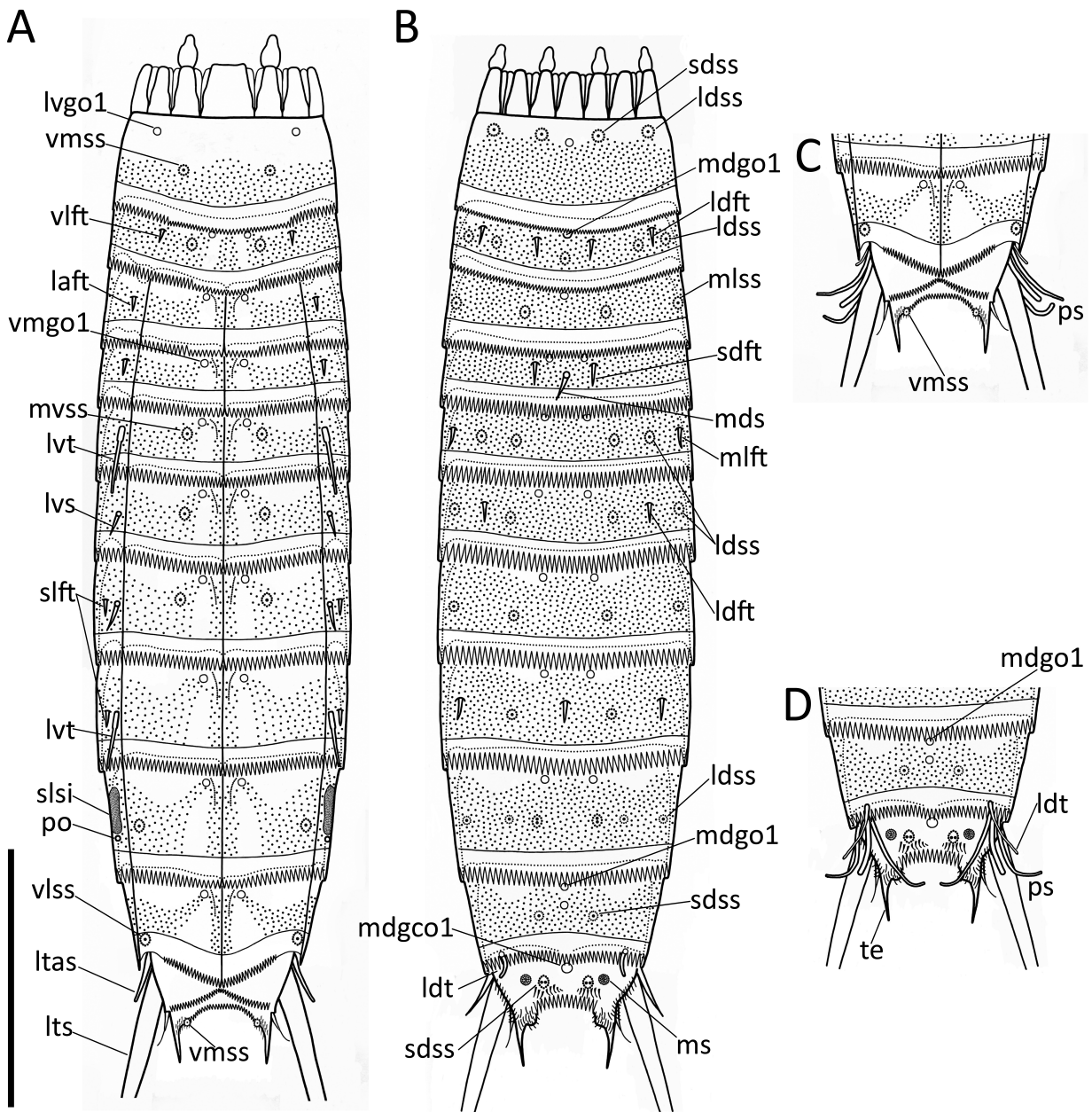


Fig. 2. Line art illustrations of *Echinoderes filispinosus*, A–B, female; C–D, male. A, C: ventral view. B, D: dorsal view. Scale bar = 100 μm . Abbreviations: laft, fringed tube in lateral accessory position; ldft, laterodorsal fringed tube; ldss, laterodorsal sensory spot; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvgo1, lateroventral glandular cell outlet type 1; lvs, lateroventral spine; lvt, lateroventral tube; mdgco1, middorsal glandular cell outlet type 1; mds, middorsal spine; mlft, midlateral fringed tube; mlss, midlateral sensory spot; ms, muscular scar; mvss, midventral sensory spot; ps, penile spine; po, pore; sdft, subdorsal fringed tube; sdss, subdorsal sensory spot; slft, sublateral fringed tube; slsi, sublateral sieve plate; slss, sublateral sensory spot; te, tergal extension; vlgo1, ventrolateral glandular cell outlet type 1; vlft, ventrolateral fringed tube; vlss, ventrolateral sensory spot; vmgo1, ventromedial glandular cell outlet type 1; vmss, ventromedial sensory spot.

outlets type 2, are located in subdorsal, laterodorsal and ventrolateral positions (Figs. 3E; 5D–E; 6A–B). Cuticular hairs are densely covering the segment surface except for narrow longitudinal hairless patches in ventromedial positions on this and eight following segments (Figs. 2A; 5A). Ventromedial area of short acutely triangular tips in the posterior pectinate fringe is narrower than on the preceding segment (Fig. 2A).

Trunk segment 3 and the following segments consist of one tergal and two sternal plates (Fig. 2A–B). Sensory spots are located in subdorsal and midlateral positions (Figs. 2B; 5D; 6A). Fringed tubes are located in lateral accessory position (Figs. 2A; 4D; 6F). There are wide hairless concave ventromedial areas and lateroventral hairless areas near the anterior segment margin (Fig. 2A). Other characters as on preceding segment.

Trunk segment 4 with minute middorsal acicular spine, usually much shorter than long cuticular hairs

(Figs. 2B; 3E; 7A). Sensory spots absent. Glandular cell outlets type 1 are located in paradorsal/subdorsal and ventromedial positions (Figs. 2A–B; 3E). Fringed tubes are located in subdorsal and lateral accessory position (Figs. 2A–B; 4D; 5C; 6F; 7A). Other characters as on preceding segment.

Trunk segment 5 with a pair of long (20 μm) and thin lateroventral tubes composed of a short and smooth basal portion and a longer distal part with minute wing-like longitudinal lateral ridges (Figs. 2A; 3C; 6C–D). Sensory spots (3–4 μm) are located in subdorsal, laterodorsal and ventromedial positions (Figs. 2A–B; 6C; 7A). Fringed tubes are located in midlateral position (Figs. 2B; 6C). Other characters as on preceding segment.

Trunk segment 6 with a pair of minute (8–9 μm) lateroventral acicular spines much shorter than neighbouring cuticular hairs (Figs. 2A; 3C; 7B). Laterodorsal sensory spots are shifted laterally as

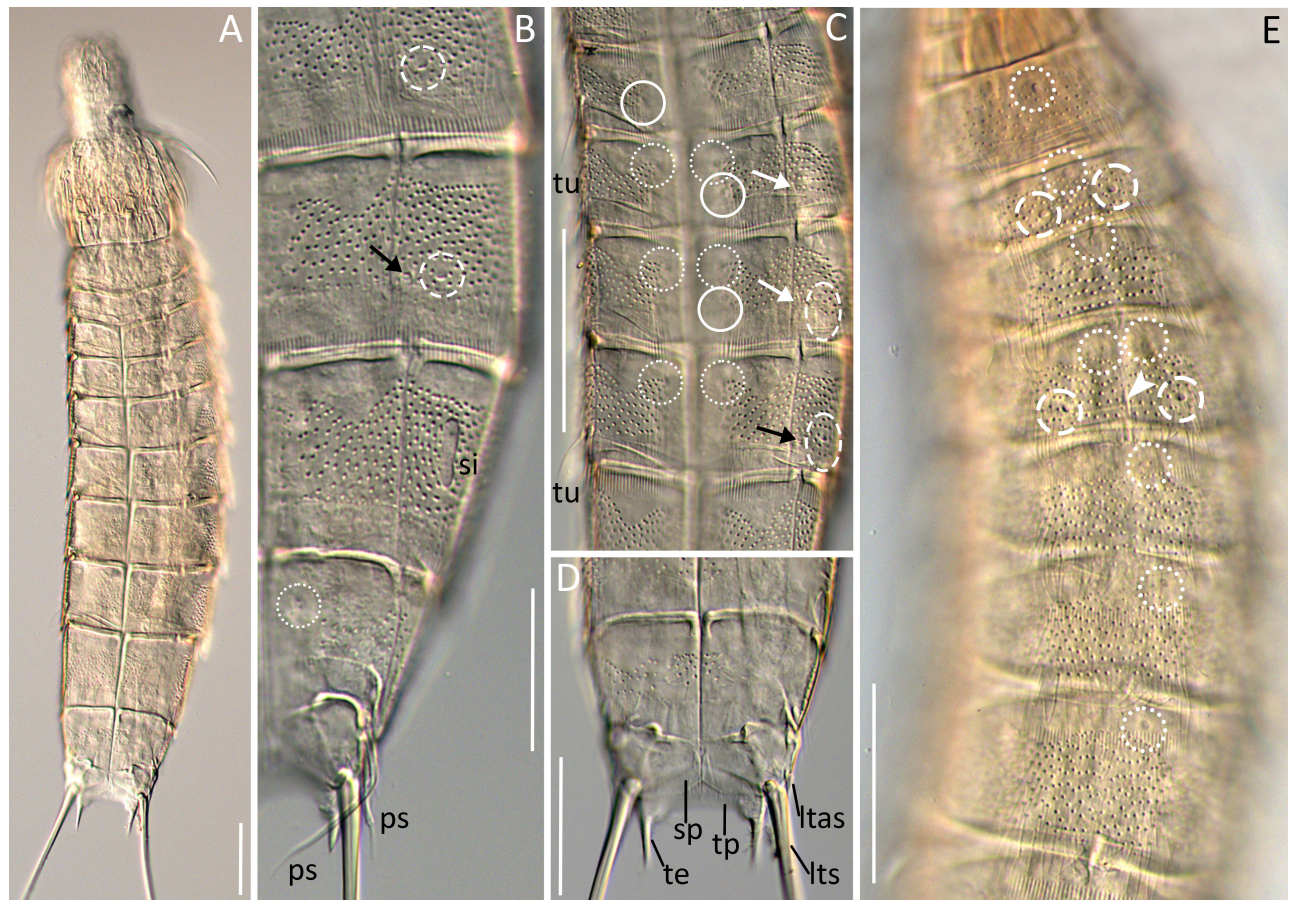


Fig. 3. Light micrographs of *Echinoderes filispinosus*. A, D–E: female; B–C: male. A–C: ventrolateral view. D: ventral view. E: dorsal view. A, total view with everted head. B, trunk segments 7–11. C, trunk segments 5–9. D, trunk segments 9–11. E, neck and trunk segments 1–8. Scale bars = 50 μm . Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spine; si, sieve plate; sp, sternal plate; te, tergal extension; tp, tergal plate; tu, tube; white continuous line circles indicate sensory spots; white dotted line circles indicate glandular cell outlets type 1; white dashed line circles indicate fringed tubes; white arrow indicates spine; black arrow indicates tube; white arrowhead indicates middorsal spine.

compared with preceding segment. Fringed tubes are located in laterodorsal position (Figs. 2B; 6C). Pectinate fringe without alternating areas of shorter and longer acicular tips. Other characters as on preceding segment.

Trunk segment 7 with a pair of minute (8–9 μm) lateroventral acicular spines (Figs. 2A; 3C). Fringed tubes are located in sublateral position (Figs. 2A; 3C). Additional concave hairless areas present in subdorsal position at the anterior segment margin (Fig. 2B). Other characters as on preceding segment.

Trunk segment 8 with a pair of lateroventral tubes similar to those on trunk segment 5 (Figs. 2A; 3B–C; 4A; 6E). Sensory spots are located in subdorsal position (Fig. 2B; Fringed tubes are in laterodorsal and sublateral positions and a single tube in middorsal position (Figs. 2A–B; 6E). Other characters as on preceding segment.

Trunk segment 9 without tubes and acicular spines. There are a pair of large, very elongated subdorsal sensory spots (up to 7–8 μm) in subdorsal position, with two longitudinally arranged pores marked by secret droplets (Figs. 6D; 7C). Other sensory spots are about twice smaller (4 μm), with only one pore,

located in subdorsal, laterodorsal and ventrolateral positions (Figs. 2A–B; 6D; 7C). Fringed tubes absent. With large, elongated sieve plates and nephridial pores in sublateral position (Fig. 7D). Other characters as on preceding segment.

Trunk segment 10 with sexually dimorphic tubes in laterodorsal position at the posterior segment margin (Fig. 2B–D). Male tubes are long (up to 20 μm) and slender, similar of those described on trunk segments 5 and 8 (Fig. 8B); female tubes are short (5–6 μm), usually curved and without the basal part (Fig. 7C). Elongated sensory spots are located in subdorsal and ventrolateral positions (Figs. 7C; 8A–B). Glandular cell outlets type 1 are located in middorsal (two outlets) and ventrolateral position (Figs. 2A–D; 3B; 4C). Without fringed tubes, sieve plates and pores. There are hairless concave midventral and wide ventromedial areas near the anterior margin of tergal plate (Figs. 2A–D; 3D; 4C). Sternal plates with large concave hairless areas near the anterior margin and wide hairless areas in ventromedial position (Figs. 3D; 4A). Tips of posterior pectinate fringe are smaller than those on the previous segment. Sternal plates extend posteriorly near the midventral

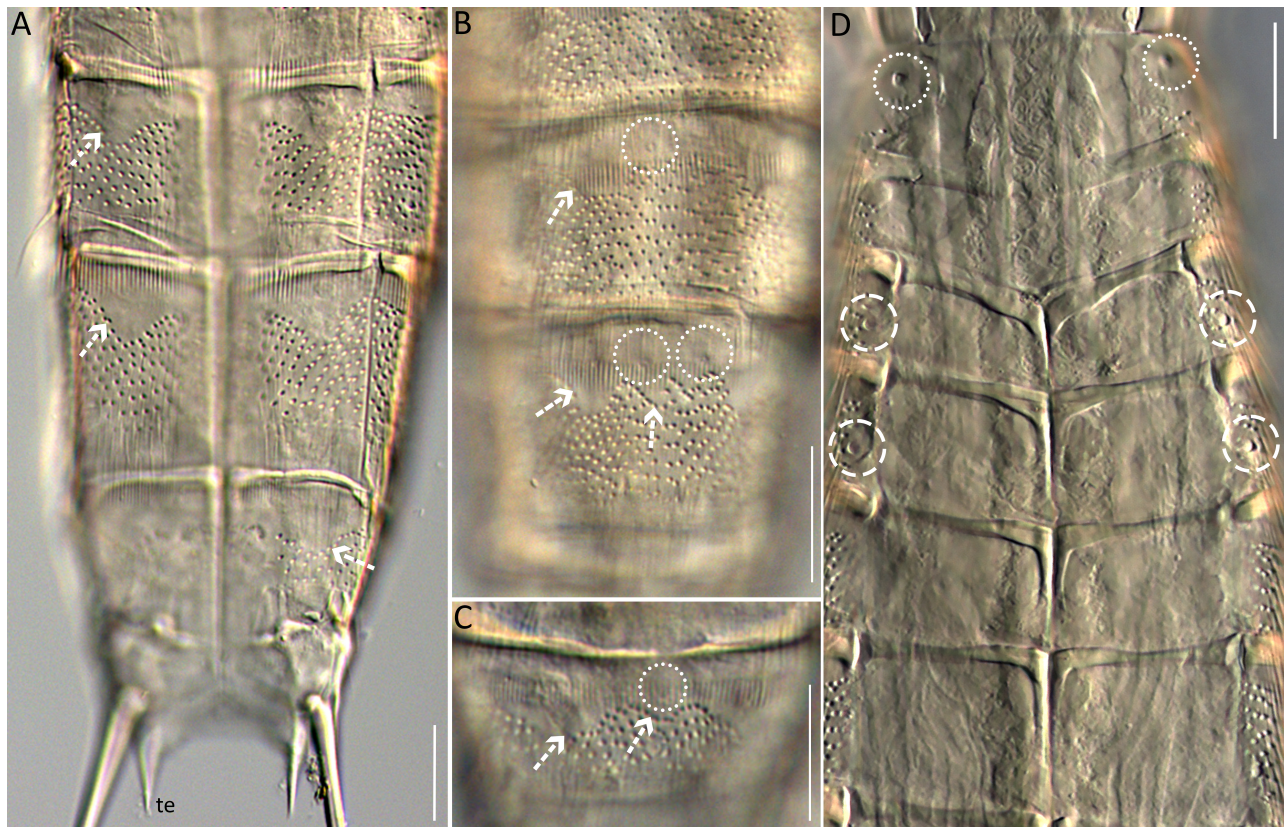


Fig. 4. Light micrographs of *Echinoderes filispinosus*. A–C: female. D: male. A, D: ventral view. B–C, dorsal view. A, trunk segments 7–11; B, trunk segments 8–9; C, trunk segment 10; D, trunk segments 1–6. Scale bars = 20 μm . Abbreviations: te, tergal extension; white dotted line circle indicates glandular cell outlets type 1; white dashed line circle indicates fringed tubes; white dashed line arrow indicates concave margin of hairless area.

junction (Fig. 8A). The segment can be partly retracted into preceding segment (Fig. 8B).

Trunk segment 11 with lateral terminal spines (Fig. 2A). Males with three pairs of penile spines; two of them very long (about 30 μm) and flexible, one rather short and stout (Figs. 2C–D; 3B; 8A–B). Females with reduced lateral terminal accessory spines (12–13 μm) (Figs. 2A–B; 3D). One pair of very large elongated sensory spots (7 μm), each with two pores, is located in subdorsal position (Figs. 7C, E; 8B). A pair of smaller (3 μm) round sensory spots is present in ventromedial position at the posterior edge of the segment (Fig. 8A, C). Relatively large (4 μm) glandular cell outlet type 1 is situated in middorsal position (Fig. 7E). There are two large muscular scars in subdorsal position (Fig. 7E). Cuticular hairs is very rare, situated laterally to subdorsal sensory spots (Fig. 8B). There are fringed

areas with long cuticular hairs in lateroventral position (Fig. 8C). Pectinate fringe is well-developed, with very narrow tips. Tergal extensions are long and pointed (Figs. 7C; 8A–C).

DISCUSSION

Notes on diagnostic features

In the original description of *E. filispinosus*, many currently important characters were overlooked, especially minute characters hidden under dense cuticular hairs (*e.g.*, very short middorsal spine on trunk segment 4, minute lateroventral spines, glandular cell outlets types 1, fringed tubes and sensory spots) (see Adrianov 1989). The first re-examination of this

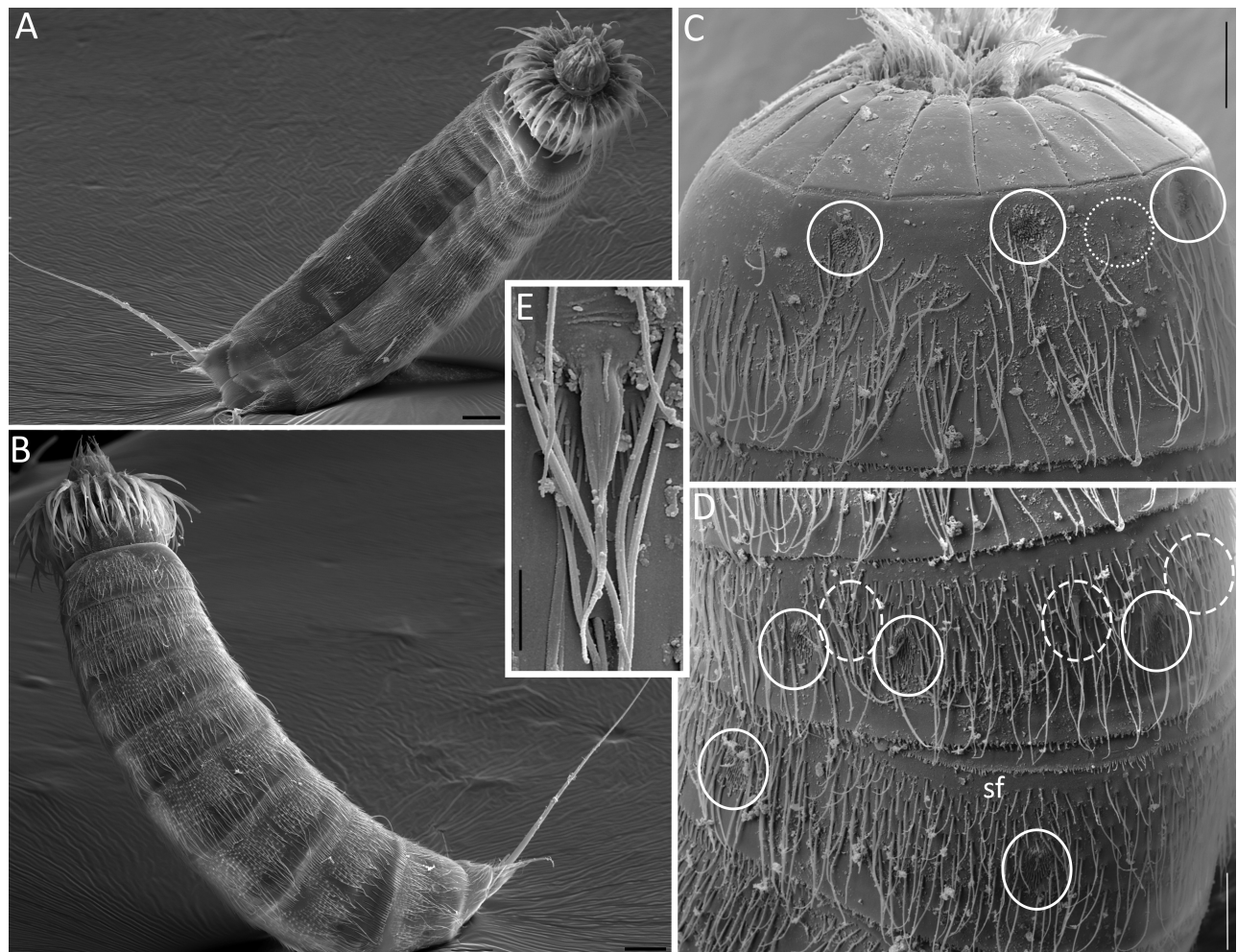


Fig. 5. Scanning electron micrographs of *Echinoderes filispinosus*, male. A, total with everted head, ventral view. B, total with everted head, dorsolateral view. C, trunk segment 1, dorsal view. D, trunk segments 2–3, dorsal view. E, trunk segment 2, fringed tube. Scale bars: A–B = 20 μm ; C–D = 10 μm ; E = 2 μm . Abbreviations: sf, secondary cuticular pectinate fringe; white continuous line circle indicates sensory spot; white dotted line circle indicates glandular cell outlet type 1; white dashed line circle indicates fringed tube.

species has been made after ten years, including the use of SEM facilities (see Adrianov and Malakhov 1999, figs. 5.32–5.33). Some additional characters used in kinorhynch taxonomy at that time have been more carefully described (laterodorsal and lateroventral tubes,

some sensory spots, tergal extensions, arrangement of cuticular hairs). Nevertheless, some abovementioned minute characters were also overlooked because these characters were still not used in the kinorhynch taxonomy (see Adrianov and Malakhov 1999, figs.

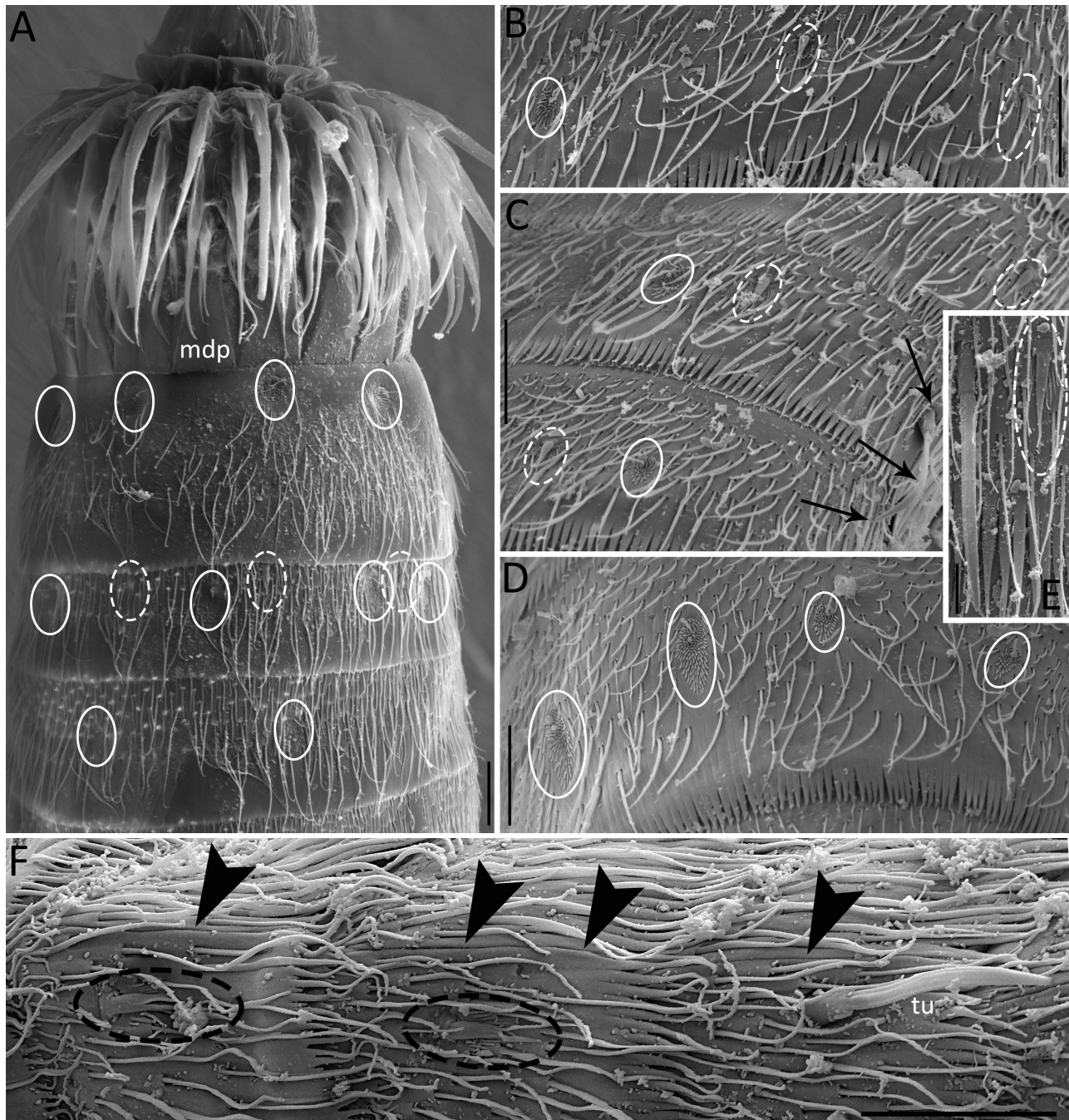


Fig. 6. Scanning electron micrographs of *Echinoderes filispinosus*, male. A, head, neck and trunk segments 1–3 dorsal view. B, trunk segment 8, lateral (right) view. C, trunk segments 4–6, dorsolateral (right) view. D, trunk segment 9, dorsolateral view. E, lateroventral tube and fringed tube, trunk segment 8. F, trunk segments 3–5, lateral view. Scale bars: A–D, F = 10 μ m; E = 4 μ m. Abbreviations: mdp, middorsal placid; tu, tube; white continuous line circle indicates sensory spot; white and black dashed line circles indicates fringed tubes; black arrow indicates lateroventral tube; black arrowhead indicates tergo-sternal articulation.

5.32–5.33). This re-examination provides all necessary data for the current approaches in kinorhynch taxonomy mainly relied on unique sets and arrangements of main morphological characters (spines, tubes, sensory spots, glandular outlets etc.) and morphometry.

This re-examination of *E. filispinosus* confirmed its placement within the *E. coulli*-group. Firstly, considered as a group highly adapted to variable salinities in the estuarine environments (Ostmann A. et al. 2012) this *E. coulli*-group is currently thought to be a monophyletic clade of kinorhynchs with worldwide distribution (Randsø et al. 2019; Sørensen 2023). Key morphological characters of this group include absence of middorsal spines or presence of minute middorsal spine only on trunk segment 4; absence of lateroventral spines or presence of minute lateroventral spines only on trunk segments 6–7; presence of lateroventral tubes on trunk segments 5 and 8; absence or reducing of

lateral terminal accessory spines; and enlarged sieve plates with posterior pore (Randsø et al. 2019).

The newly found morphological characters of *E. filispinosus* coincide with those of *E. ohtsukai*, firstly described from the Seto Inland Sea (Yamasaki and Kajihara 2012) and later redescribed from the British Columbia coastline (Herranz and Leander 2016). The DNA sequence from the mitochondrial *COI* gene generated from *E. filispinosus* from the type locality in the Vostok Bay and specimens of *E. ohtsukai* from both, the type locality in Japan and new locality in the Northeastern Pacific, are also identical based on comparison of 649 nucleotides, and *E. ohtsukai* is thus a junior synonym of *E. filispinosus*.

Very careful description of all morphological details of *E. ohtsukai* and its comparison with other congeners from the *E. coulli*-group are provided by Herranz and Leander (2016).

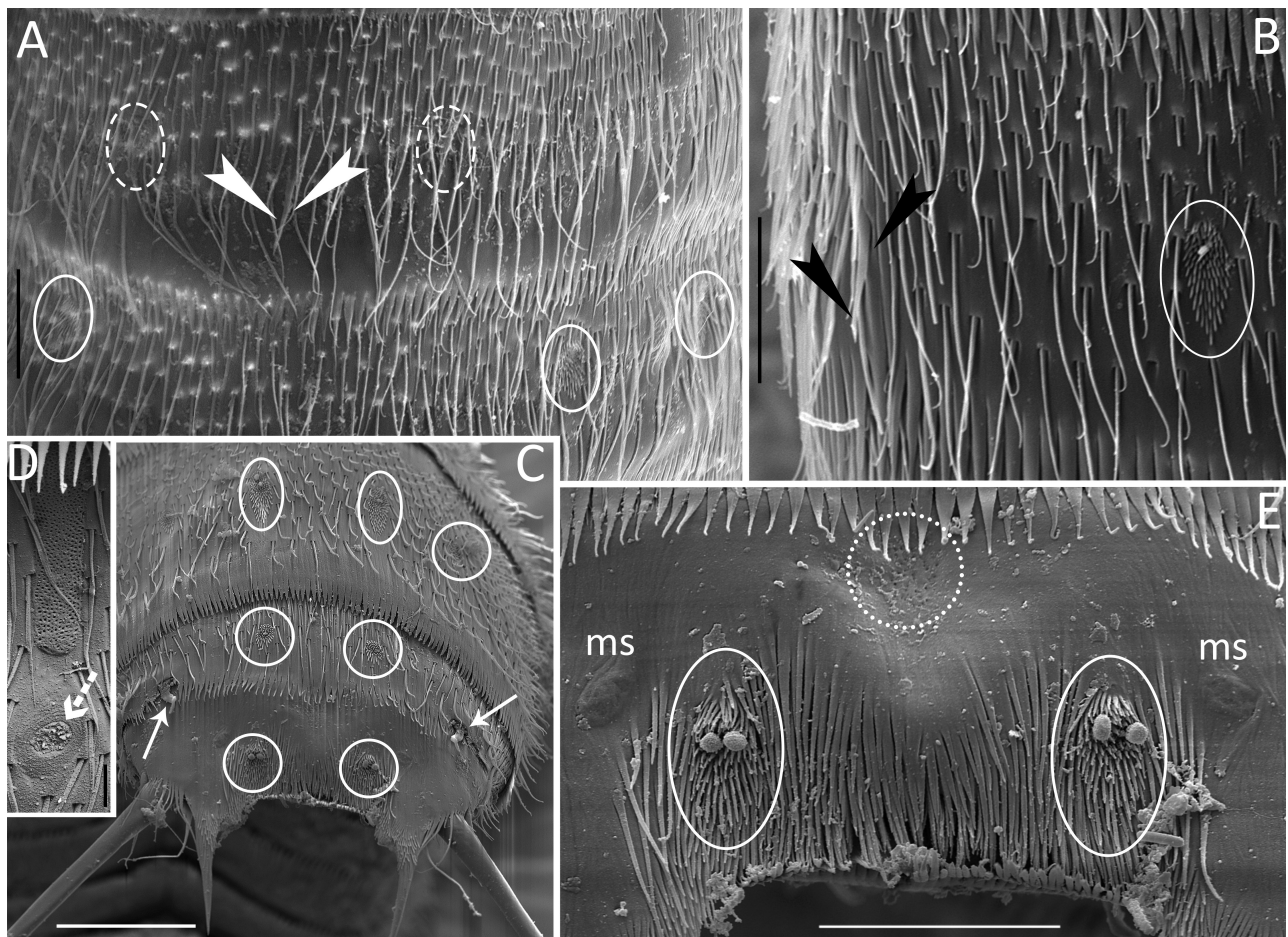


Fig. 7. Scanning electron micrographs of *Echinoderes filispinosus*, female. A, trunk segments 4–5, dorsal view. B, trunk segment 6, ventrolateral (right) view. C, trunk segments 9–11, dorsal view. D, sieve plate and pore, trunk segment 9, lateral (right) view. E, trunk segment 11, dorsal view. Scale bars: A–B, E = 10 μ m; C = 20 μ m; D = 2 μ m. Abbreviations: ms, muscular scar; white continuous circles indicate sensory spots, white dashed line circle indicates fringed tube; white arrow indicates laterodorsal tube; white dashed line arrow indicates sieve plate pore; white arrowhead indicates middorsal spine; black arrowhead indicates lateroventral spine.

The only other representative of the *E. coulli*-group in the Sea of Japan is *E. rex* Lundbye et al., 2011 found at the Oki Islands (see Yamasaki et al. 2024a). Both species, *E. rex* and *E. filispinosus*/*E. ohtsukai* share a minute middorsal spine on trunk segment 4, arrangement of spines and tubes on trunk segments 5–8 and 10, and presence of characteristic fringed tubes (modified glandular cell outlets type 2) (see Lundbye et al. 2011; Yamasaki and Kajihara 2012; Herranz and Leander 2016; present paper). Nevertheless, *E. rex* is well distinguished by much shorter lateral terminal spines in both sexes and presence of only two pairs of penile spines in males (Lundbye et al. 2011; Herranz and Leander 2016). Morphologically these fringed tubes in *E. filispinosus*/*E. ohtsukai* and *E. rex* are very similar to those in *E. maxwelli* Omer-Cooper, 1957 described from the South Africa coast (Randsø et al. 2019, fig. 2D–E, G). In all three species, these characters are

modified glandular cell outlets type 2, composed of a heavy cuticular fringe or tuft surrounding the orifice of the glandular outlet.

Notes on molecular analysis

Mitochondrial cytochrome *c* oxidase subunit 1 (*COI*) gene, which is often used for barcoding of marine organisms, was used for species identification (see Gong et al. 2018). The *COI* gene PCR fragment (649 bp) was sequenced from ten pooled morphologically identic specimens of *E. filispinosus* from the type locality.

All nucleotide positions were unambiguously determined within the pooled sample, allowing us to state that we are dealing with an absence of intraspecific polymorphism. Moreover, three sequences of *E. ohtsukai* deposited in the NCBI (LC096964.1, KU674383.1, LC096965.1), also no found any

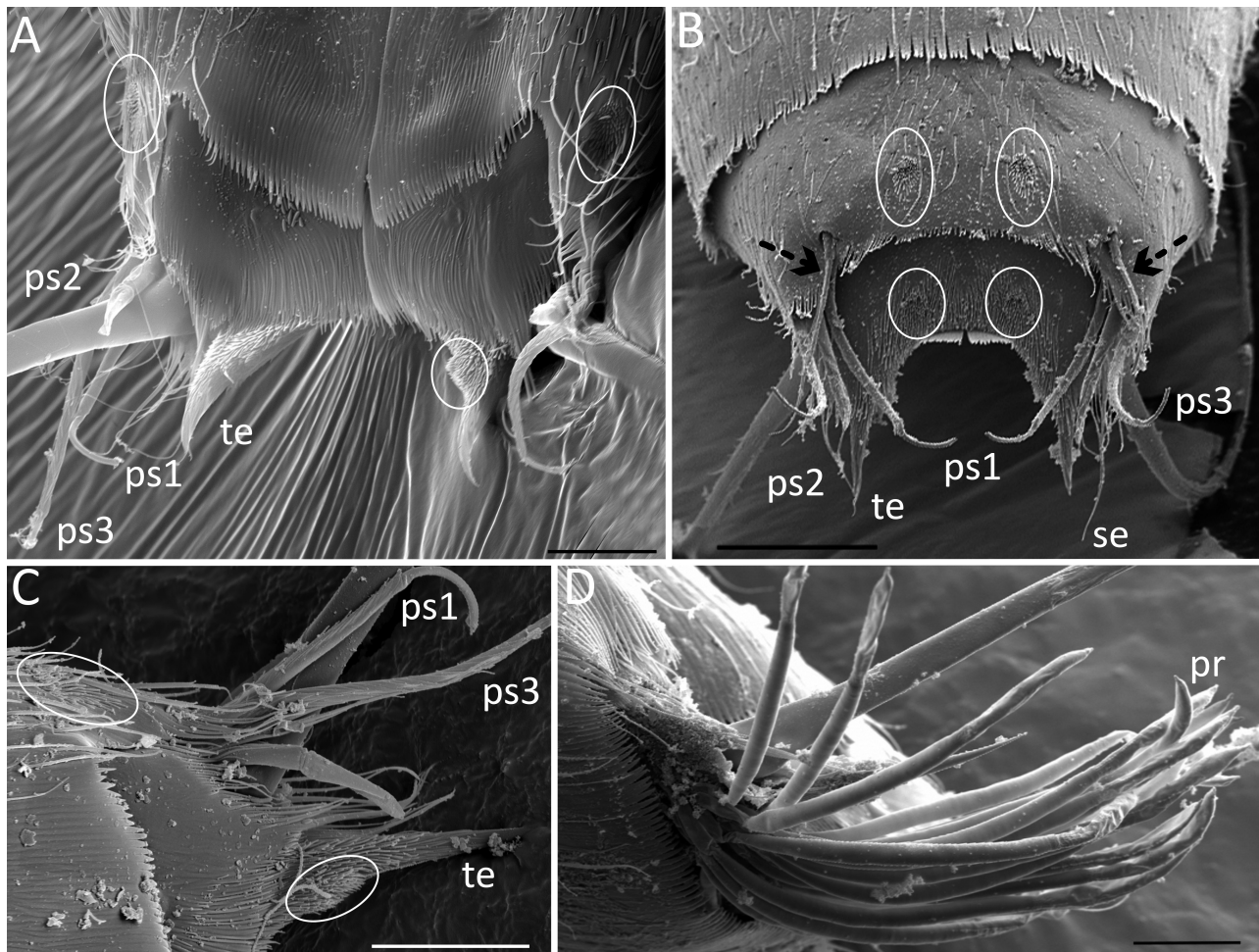


Fig. 8. Scanning electron micrographs of *Echinoderes filispinosus*. A–C: male. D: female. A, trunk segments 10–11, ventral view. B, trunk segments 9–11, dorsal view. C, trunk segments 10–11, ventral view. D, trunk segments 10–11, lateral (right) view. Scale bars: A, C–D = 10 μ m; B = 20 μ m. Abbreviations: pr, protozoans; ps, penile spine (number after abbreviation indicates corresponding pair); se, seta; te, tergal extension; white continuous circles indicate sensory spots; black dashed line arrow indicates laterodorsal tube.

differences between each other.

Comparative analysis of the *COI* gene fragment with the same fragments of other *Echinoderes* species revealed the complete identity of the sequences of *E. filispinosus* and *E. ohtsukai*. The maximum likelihood tree (ML tree) was built to visualize the comparative analysis (see Fig. 9). We demonstrated that *E. filispinosus* is clustered together with the other

three specimens of *E. ohtsukai*, deposited in the NCBI (LC096964.1, KU674383.1, LC096965.1), with 100% bootstrap support (Fig. 9). At the same time, other congeners differ significantly from *E. filispinosus* and from each other and every species has its own pattern of nucleotide substitutions in a given gene region. Thus, based on the sequence of *COI* gene, *E. filispinosus* is genetically identical to *E. ohtsukai*.

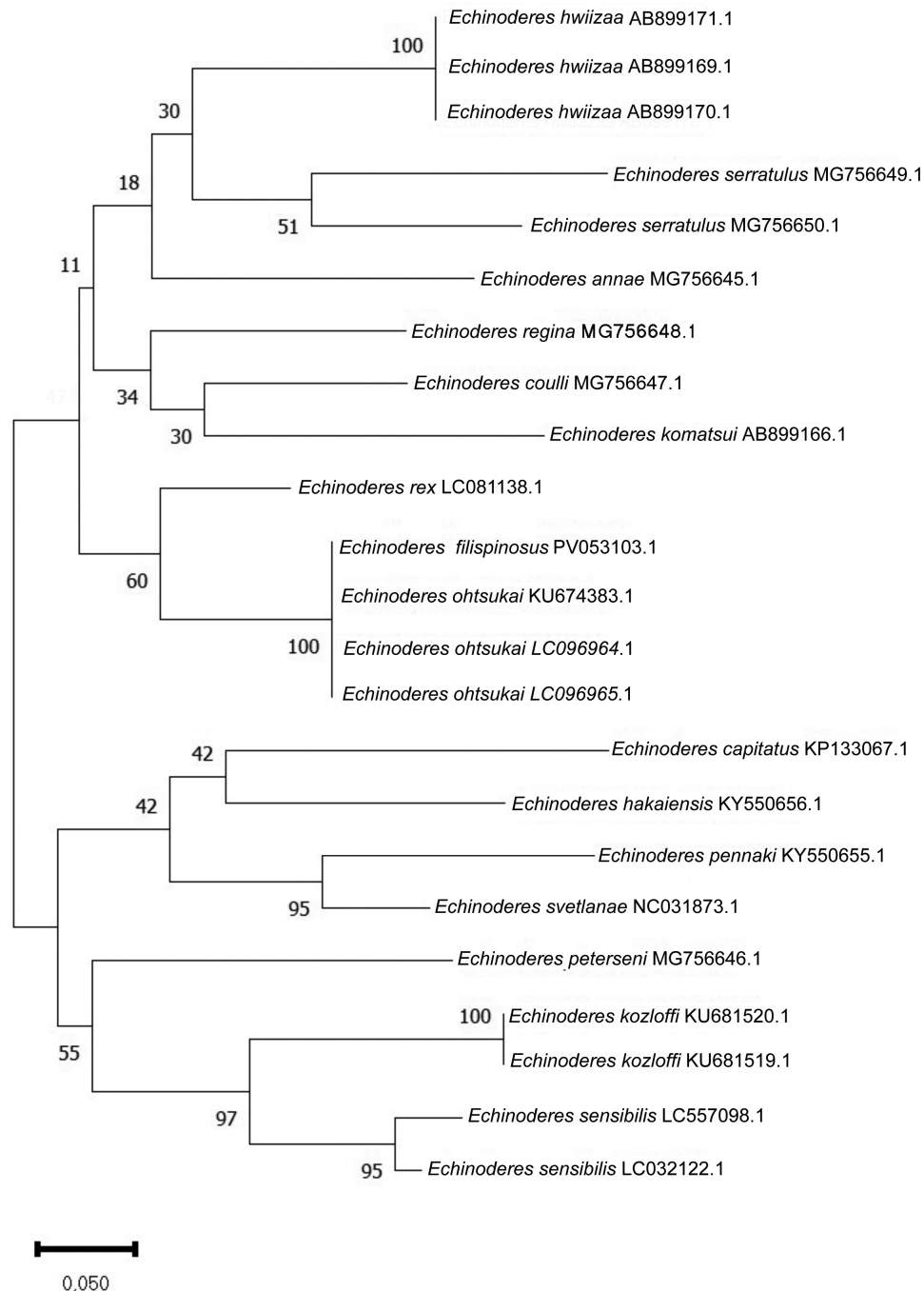


Fig. 9. Maximum likelihood phylogeny of *Echinoderes* using the GTR+G model on 590 bp fragment of *COI* gene with bootstrap support values displayed adjacent at each node. Numbers after the species name represent the GenBank accession number of the sequence.

Notes on epibionts

Both, *E. filispinosus* and *E. ohtsukai* usually have epibionts associated with various cuticular structures. As noted by Herranz and Leander (2016), epibiotic filamentous bacteria were found in almost all collected specimens of *E. ohtsukai* from British Columbia. These bacteria were mostly concentrated in the posteriormost segments and usually associated with glandular openings or sensory spots (see Herranz and Leander 2016, fig. 13C). Many specimens of *E. filispinosus* collected in the Vostok Bay have dense bunches of rod-shaped with a distal constriction protozoans (up to 50 µm long) usually associated with gonopores (Fig. 8D). Very similar, but also non-identified rod-shaped protozoans (40–60 µm long) were described on the terminal segment of *E. applicatus* Ostmann et al. 2012 from the brackish water lagoon at the coast of Java in Indonesia (Ostmann A. et al. 2012, fig. 6 E–F).

Notes on ecological patterns in sampling area

Specimens of *E. filispinosus* have been regularly collected in muddy sand in the sampling area in the Vostok Bay (Fig. 1) within the last 40 years at the depth 0.5–5 m throughout the year when the estuary is free of ice. Adult (sexually mature) individuals occurred all year round, without visible responses of their abundance to well-defined seasonal changes (own observations).

Ice firstly appears here in the late November and retains until late March. The thickness of the ice in harsh winters reaches 80–85 cm. The water in this time is uniform throughout the depth and temperature is close to freezing point (up to -1.9°C in January and February) (Stepanov 1976; Gayko 2017). Stratification in the water column is distinct only in the summertime. The maximum surface temperature in summer reaches 25–26°C in August. The temperature jump layer appears only at the depth 5–10 m (Stepanov 1976; Gayko 2017).

Average annual salinity in the Vostok Bay is about 31.5‰, with a maximum in March (up to 35‰) (Stepanov 1976; Propp and Propp 1981; Gayko 2017). Due to ice formation in wintertime, the salinity in the inner part of the bay in the Vostok Harbour is about 35‰ (in the estuary near the river mouths up to 36–37‰) (Stepanov 1976; Gayko 2017). In summertime, during heavy rains the salinity in the estuary in a 5-meter water layer can drop to 0‰.

Thus, *E. filispinosus* demonstrates outstanding adaptations to a great variability of temperature (from -1.9°C to +25–27°C) and salinity (from 37 to 0‰), and shows an amazing ability to survive in such extreme conditions.

E. ohtsukai firstly described from an intertidal

muddy flat in the Seto Inland Sea near the Kamogawa River mouth and some later found in a brackish estuary in the British Columbia on the opposite side of the Pacific, is also noted as living in habitats with remarkably fluctuating salinity (Yamasaki and Kajihara 2012; Herranz and Leander 2016). Both these habitats are not so extreme as in the Vostok Bay, but these findings also confirm the ability of *E. filispinosus*/*E. ohtsukai* to survive in a very unstable environmental condition.

Another intertidal estuarine representative of *E. coulli*-group with the greatest tolerance to high temperature and to both, low and very high salinity is *E. komatsui* Yamasaki et Fujimoto, 2014, described from subtropical tidal flat along the Oura River in Okinawajima Island, Japan (Uozumi et al. 2018). As it was shown in laboratory experiments, *E. komatsui* survived in salinity from 1 to 44‰ (but died at 0‰) and stay alive about 4.5 days at 40°C (Uozumi et al. 2018). Many other representatives of the *E. coulli*-group are also well adapted to the variable estuarine habitats, being euryhaline forms, and also can thrive in a wide range of temperature, but *E. filispinosus* appears the only known species capable to survive below 0°C and at the lowest salinity (0‰) in the summer rain season.

Notes on distributional patterns

Likely to the most meiobenthic invertebrates, kinorhynchs have no planktonic larvae and have limited for dispersal over the sea floor. Nevertheless, some species, both deep-sea and rather shallow ones, show very wide geographic distribution (Sørensen et al. 2012; Neuhaus and Sørensen 2013; Adrianov and Maiorova 2022 2024).

There are only a few representatives of *Echinoderes* with the transoceanic distribution. The species with the widest geographical distribution among this genus is *E. lupherorum* Sørensen et al. 2018. This species is characterized by the pan-oceanic distribution and has been recorded from Northwestern (Emperor Ridge), Northeastern (off California) and Southwestern (off New Zealand) Pacific (Sørensen et al. 2018; Adrianov and Maiorova 2024). *E. filispinosus*/*E. ohtsukai* recorded from Russian (north part of the Sea of Japan), Japanese (Seto Inland Sea), and Canadian (British Columbia) waters appears to be the first *Echinoderes* species with amphi-Pacific distribution (Adrianov and Malakhov 1999; Yamasaki and Kajihara 2012; Herranz and Leander 2016). *E. tchefouensis* Lou, 1934 is widely distributed in the Western and Indo-West Pacific and has been recorded from many localities from the Korea Strait and East-China Sea to Singapore and Malaysia (Herranz and Leander 2016; Sørensen et

al. 2016). Intertidal *E. sensibilis* Adrianov et al. 2002 recorded from the Pacific coast of Japan, Okinawa and Korean waters is also found in Hawaiian (Sørensen et al. 2020).

Currently, several hypotheses have been discussed to explain this phenomenon, including potential pathways with the abyssal or even rather shallow currents (Adrianov and Maiorova 2022 2024), through continental drifts (Ostmann A. et al. 2012; Randsø et al. 2019) or by human-mediated introduction with transportation of aqua cultured species (Herranz and Leander 2016). As noted by Herranz and Leander (2016), aquaculture activities can play an important role in transporting kinorhynchs from one coast of the Pacific to the other. These authors have suggested that specimens of *E. ohtsukai* could be transported to Canada together with Japanese oysters.

This assumption is well-reasoned, but one more potential explanation of transoceanic distribution of shallow-water *E. filispinosus*/*E. ohtsukai* also could be suggested.

The earthquake in Japan in 2011 generated a huge tsunami that launched an extraordinary transoceanic biological rafting. As noted by Carlton et al. (2017), about 300 living marine species were transported by oceanic currents from Japan to North America by rafting on various objects that travelled many thousand kilometers across the Pacific. Millions of objects ranging in size from plastic and wood pieces to docks and fishing vessels (including those having large bait boxes with biologically rich debris with numerous meiofaunal organisms) were carried into the ocean. Since 2012, this debris with living organisms originated from Japan has landed on coastline from Alaska to California, and also to Hawaii. About 60% of all rafting macrobenthic species (cnidarians, bryozoans, annelids, molluscs, crustaceans) were detected on the fishing vessels (Carlton et al. 2017). In addition, representatives of 33 taxa of microinvertebrates and 19 taxa of protists were also found in the debris (Carlton et al. 2017). Actually, there are considerable underestimates of the real species number. Hardly could be imagine that Japanese kinorhynchs can avoid this possibility to reach the North American waters.

This hypothesis also seems to be quite appropriate to explain probable “transporting” of intertidal *E. sensibilis* from the east coast of Honshu to Hawaiian.

Findings of *E. filispinosus*/*E. ohtsukai* in the north part of the Sea of Japan, in the Seto Inland Sea and in British Columbia, and its outstanding tolerance to marginal environmental fluctuations, let us hope that future studies should be able to demonstrate the presence of this species in other areas in both Northwestern and Northeastern Pacific.

CONCLUSIONS

A very common and abundant kinorhynch *Echinoderes filispinosus* was occasionally re-examined by adding DNA sequence from the mitochondrial *COI* gene from specimens collected at its type locality in the Vostok Bay. The support of ‘old’ well-known species in this area, using molecular barcode data, reveals that *E. filispinosus* is completely genetically identical to *E. ohtsukai*. Re-examination of morphological characters of *E. filispinosus* and description of overlooked features further support the replacement of *Echinoderes ohtsukai* to a junior synonym of *E. filispinosus*.

Acknowledgments: This work has been carried out with the support of the Federal scientific and technical program in the field of environmental development of the Russian Federation and climate change for 2021–2030, Russian Federation (Project No. 123080800009-5).

Authors’ contributions: AVA, ASM contributed equally to this work. Conceptualization: AVA, ASM; Methodology: AVA, AYA, APG, ASM; Investigation: AVA, ASM; Data Curation: AVA, ASM; Writing - Original Draft: AVA, ASM; Writing - Review & Editing: AVA, AYA, APG, ASM; Project administration AVA, ASM; Funding acquisition: AVA, ASM.

Competing interests: The authors declare that there are no competing interests.

Availability of data and materials: The author confirms that the data supporting the findings of this study are available in the article and its supplementary materials. The new collected specimens from the type locality are deposited at the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology Far Eastern Branch of the Russian Academy of Sciences, Palchevskogo 17, Vladivostok, Russia. The DNA sequences obtained in this study are deposited in GenBank with respective accession numbers.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

- Adrianov AV. 1989. The first report on Kinorhyncha of the Sea of Japan. *Zool Zhurnal* 68:17–27.
- Adrianov AV, Maiorova AS. 2019. *Echinoderes ultraabyssalis* sp. nov.

- from the Kuril-Kamchatka Trench – the first hadal representative of the Kinorhyncha (Kinorhyncha: Cyclorhagida). *Prog Oceanogr* **178**:102142. doi:10.1016/j.pcean.2019.102142.
- Adrianov AV, Maiorova AS. 2022. Kinorhynchs (Kinorhyncha) from methane cold seeps in the Bering Sea, with biogeographical discussion and ecological notes. *Deep - Sea Res Part II Top Stud Oceanogr* **204**:105132. doi:10.1016/j.dsr2.2022.105132.
- Adrianov AV, Maiorova AS. 2024. The first Mud Dragons (Kinorhyncha) from the Emperor Seamount Chain (Northwestern Pacific) with notes on their biogeography and distribution patterns in the Pacific Deep-Sea. *Deep Res Part II Top Stud Oceanogr* **218**:105430. doi:10.1016/j.dsr2.2024.105430.
- Adrianov AV, Malakhov VV. 1999. Cephalorhyncha of the world ocean. KMK Scientific Press Ltd., Moscow.
- Carlton JT, Chapman JW, Geller JB et al. 2017. Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. *Science* **357**:1402–1406. doi:10.1126/science.aao1498.
- Folmer O, Black M, Hoeh W et al. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol* **3**:294–299.
- Gayko LA. 2017. Hydrometeorological regime of the Vostok Bay (Sea of Japan). POI FEB RAS, Vladivostok.
- Gong S, Ding Y, Wang Y et al. 2018. Advances in DNA barcoding of toxic marine organisms. *Int J Mol Sci* **19**:2931. doi:10.3390/ijms19102931.
- González-Casarrubios A, Cepeda D, Pardos F et al. 2023. Towards a standardisation of morphological measurements in the phylum Kinorhyncha. *Zool Anz* **302**:217–223. doi:10.1016/j.jcz.2022.11.015.
- Grzelak K, Yamasaki H, Minks S et al. 2023. Revision of an Arctic kinorhynch species: *Echinoderes svetlanae* and *E. tubilak* are junior synonyms of *E. remanei*. *Zool Anz* **302**:75–89. doi:10.1016/j.jcz.2022.11.001.
- Herranz M, Leander BS. 2016. Redescription of *Echinoderes ohtsukai* Yamasaki and Kajihara, 2012 and *E. kozloffii* Higgins, 1977 from the northeastern Pacific coast, including the first report of a potential invasive species of kinorhynch. *Zool Anz* **265**:108–126. doi:10.1016/j.jcz.2016.02.004.
- Herranz M, Leander BS, Grzelak K. 2024. First evidence of cryptic diversity in mud dragons (Kinorhyncha) and description of *Echinoderes quasae* sp. nov. from the northeastern Pacific coast. *Zool Anz* **313**:241–254. doi:10.1016/j.jcz.2024.10.010.
- Herranz M, Moreleon AD, Rho HS, Sørensen MV. 2023. Expanding the *Echinoderes coulli* group (Kinorhyncha: Cyclorhagida) with a new species from the Chuuk Islands, Micronesia. *Zool Anz* **302**:67–74. doi:10.1016/j.jcz.2022.11.010.
- Higgins RP. 1988. Kinorhyncha. In: Higgins RP, Thiel H (eds) *Introduction to the Study of Meiofauna*. Smithsonian Institution, Washington D.C. London, pp. 328–331.
- Lundbye H, Rho HS, Sørensen MV. 2011. *Echinoderes rex* n. sp. (Kinorhyncha: Cyclorhagida), the largest *Echinoderes* species found so far. *Sci Mar* **75**:41–51. doi:10.3989/scimar.2011.75n1041.
- Neuhaus B. 2013. Kinorhyncha (= Echinodera). In: Schmidt-Rhaesa A (ed) *Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera. Vol. 1: Nematomorpha, Priapulida, Kinorhyncha, Loricifera*. De Gruyter, Berlin, Boston, pp. 181–348.
- Neuhaus B, Sørensen MV. 2013. Populations of *Campyloderes* sp. (Kinorhyncha, Cyclorhagida): One global species with significant morphological variation? *Zool Anz* **252**:48–75. doi:10.1016/j.jcz.2012.03.002.
- Ostmann A, Nordhaus I, Sørensen MV. 2012. First recording of kinorhynchs from Java, with the description of a new brackish water species from a mangrove-fringed lagoon. *Mar Biodivers* **42**:79–91. doi:10.1007/s12526-011-0094-z.
- Propp MV, Propp LN. 1981. Hydrochemical background of the primary production process in the coastal waters of the Sea of Japan. *Biol Morya*, pp. 29–37.
- Randsø PV, Yamasaki H, Bownes SJ et al. 2019. Phylogeny of the *Echinoderes coulli*-group (Kinorhyncha: Cyclorhagida: Echinoderidae) – a cosmopolitan species group trapped in the intertidal. *Invertebr Reprod Dev* **33**:501–517. doi:10.1071/IS18069.
- Robinson JT, Thorvaldsdóttir H, Winckler W et al. 2011. Integrative genomics viewer. *Nat Biotechnol* **29**:24–26. doi:10.1038/nbt.1754.
- Sørensen MV. 2023. New data on the *Echinoderes coulli*-group (Kinorhyncha: Cyclorhagida: Echinoderidae): A new species from New Caledonia mangroves, and a redescription of *E. bengalensis* (Timm, 1958). *Zool Anz* **302**:90–101. doi:10.1016/j.jcz.2022.11.009.
- Sørensen MV, Gąsiorowski L, Randsø PV et al. 2016. First report of kinorhynchs from Singapore, with the description of three new species. *Raffles Bull Zool* **64**:3–27.
- Sørensen MV, Goetz FE, Herranz M et al. 2020. Description, redescription and revision of sixteen putatively closely related species of *Echinoderes* (Kinorhyncha: Cyclorhagida), with the proposition of a new species group – the *Echinoderes dujardinii* group. *Eur J Taxon* **730**:1–101. doi:10.5852/ejt.2020.730.1197.
- Sørensen MV, Rho HS, Min WG et al. 2012. An exploration of *Echinoderes* (Kinorhyncha: Cyclorhagida) in Korean and neighboring waters, with the description of four new species and a redescription of *E. tchefouensis* Lou, 1934. *Zootaxa* **196**:161–196. doi:10.11646/zootaxa.3368.1.8.
- Sørensen MV, Rohal M, Thistle D. 2018. Deep-sea Echinoderidae (Kinorhyncha: Cyclorhagida) from the Northwest Pacific. *Eur J Taxon* **456**:1–75. doi:10.5852/ejt.2018.456.
- Sørensen MV, Yamasaki H. 2024. An interactive identification key to species of the kinorhynch orders Kentrorhagata, Xenosomata, and Anomoirhaga. *Zool Anz* **311**:45–47. doi:10.1016/j.jcz.2024.06.003.
- Stepanov VV. 1976. Characteristics of temperature and salinity in the Vostok Bay, Sea of Japan. In: *Biological Studies of the Vostok Bay*. Vladivostok, pp. 12–22.
- Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Mol Biol Evol* **38**:3022–3027. doi:10.1093/molbev/msab120.
- Uozumi R, Yamasaki H, Hirose E. 2018. Mangrove forests may serve as stable environments for the meiobenthic *Echinoderes komatsui* (Kinorhyncha: Cyclorhagida): distribution patterns and population dynamics in a subtropical estuary. *Mar Biol Res* **14**:321–333. doi:10.1080/17451000.2017.1408916.
- Yamasaki H, Kajihara H. 2012. A new brackish-water species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Seto Inland Sea, Japan. *Species Divers* **17**:109–118. doi:10.12782/sd.17.1.109.
- Yamasaki H, Yoshida M, Jimi N et al. 2024. Kinorhynch fauna from Oki Islands, with the description of a new *Echinoderes* species and its phylogenetic relationships within the family Echinoderidae. *Zool Anz* **313**:87–101. doi:10.1016/j.jcz.2024.08.006.