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A New Brackish-water Species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Seto Inland Sea, Japan

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Echinoderes ohtsukai sp. nov. is described from an intertidal flat in the Seto Inland Sea, Japan, based on observations with light and scanning electron microscopy. *Echinoderes ohtsukai* is characterized by 1) a short middorsal spine on segment 4; 2) lateroventral tubules on segments 5 and 8; 3) short laterodorsal tubules on segment 10; 4) a trunk 315–395 μm long; 5) a lack of lateral terminal accessory spines in both sexes; and 6) lateral terminal spines of about 50% trunk length. The species has modified type-II glandular cell outlets, which have previously been reported among congeners only in *E. rex* Lundbye, Rho and Sørensen, 2011 from the Korea Strait.

Key Words: Kinorhyncha, Echinoderidae, meiofauna, taxonomy.

Introduction

Echinoderes Claparède, 1863, the most species-rich genus among those comprising the phylum Kinorhyncha, includes 69 valid species and has a worldwide distribution, ranging vertically from the intertidal to the abyssal zone, with the deepest record being from 5649 m (Sørensen and Pardos 2008). *Echinoderes* is characterized morphologically by having 1) 16 placids in the neck region, 2) segments 1 and 2 in the trunk region each consisting of a complete cuticular ring, 3) segments 3–11 in the trunk region comprising one tergal and two sternal plates, and 4) no midterminal spine in adults. Species of *Echinoderes* have traditionally been identified by the presence and distribution of spines and tubules. Although information on minute cuticular structures such as sensory spots, glandular cell outlets, and sieve plates observed by scanning electron microscopy (SEM) are now also important taxonomic characters, these structures have not always been consistently reported, and such data are not available for over half the species of this genus known today.

To date, there have been nine reports of kinorhynchs from Japan. The first was *Echinoderes masudai* Abe, 1930 (*q.v.*) from Gogoshima Island, but it is a *nomen dubium* because of the poor original description (Adrianov and Malakhov 1999). Tokioka (1949) reported *E. dujardini* Claparède, 1863 from Ago Bay, although this occurrence was far outside the range of the species in European waters, and thus this identification has been questioned (Higgins 1983). *Kinorhynchus yushini* Adrianov, 1989 was reported by Suzuki (1976) as *Trachydemus* sp. and later confirmed by Adrianov and Malakov (1999). The fourth was described as a new genus and species, *Dracoderes abei* Higgins and Shirayama, 1990 (*q.v.*) from Mukaisihima Island. Subsequently, four species (*E. aureus* Adrianov *et al.*, 2002c; *E. sensibilis* Adrianov *et al.*, 2002b; *Condyloderes setoensis* Adrianov *et*

al., 2002a; and *Pycnophyes tubuliferus* Adrianov, 1989) were described from Tanabe Bay (Adrianov *et al.* 2002a, b, c; Murakami *et al.* 2002). Sørensen *et al.* (2011) reported *D. abei*, *K. yushini*, and *P. tubuliferus* from five additional localities in the Seto Inland Sea.

In a faunal survey of an intertidal flat in the Seto Inland Sea, we collected specimens of species of *Echinoderes*. Here we describe this species as new, based on light and electron microscopic observations of minute cuticular structures.

Material and Methods

Sediment samples were taken from an intertidal flat near the Takehara Marine Science Station (Hiroshima University) in the Seto Inland Sea, Japan (Fig. 1A–C). The sampling area was close to the mouth of Kamogawa River (Fig. 1C,D), and the area is affected by freshwater outflow (although the salinity at the time of collecting was not recorded, see Discussion). Sediment in the area comprised mud and sand with rich detritus, and was well-oxygenated without a sulfurous smell. Thirty-two specimens were extracted from the samples by the bubbling method (Higgins 1988) and preserved in 99% ethanol. Of these, six were prepared for light microscopy, five were for SEM, 13 were kept as HY's personal collection for future molecular analysis; three were lost during preparation for SEM. For light microscopy, specimens were transferred into a solution of 95% ethanol and 5% glycerol; after evaporation of the ethanol, specimens were mounted individually in Hoyer's-125 mounting medium between two cover slips, positioned on an H-S slide (Higgins 1988), and examined with a Nomarski interference microscope. For SEM, specimens were cleaned in a 1% sodium hypochlorite solution in deionized water (DW), rinsed in DW, dehydrated in an ethanol series, dried in a CO₂ critical-point drier (Hitachi HCP-2), mounted on

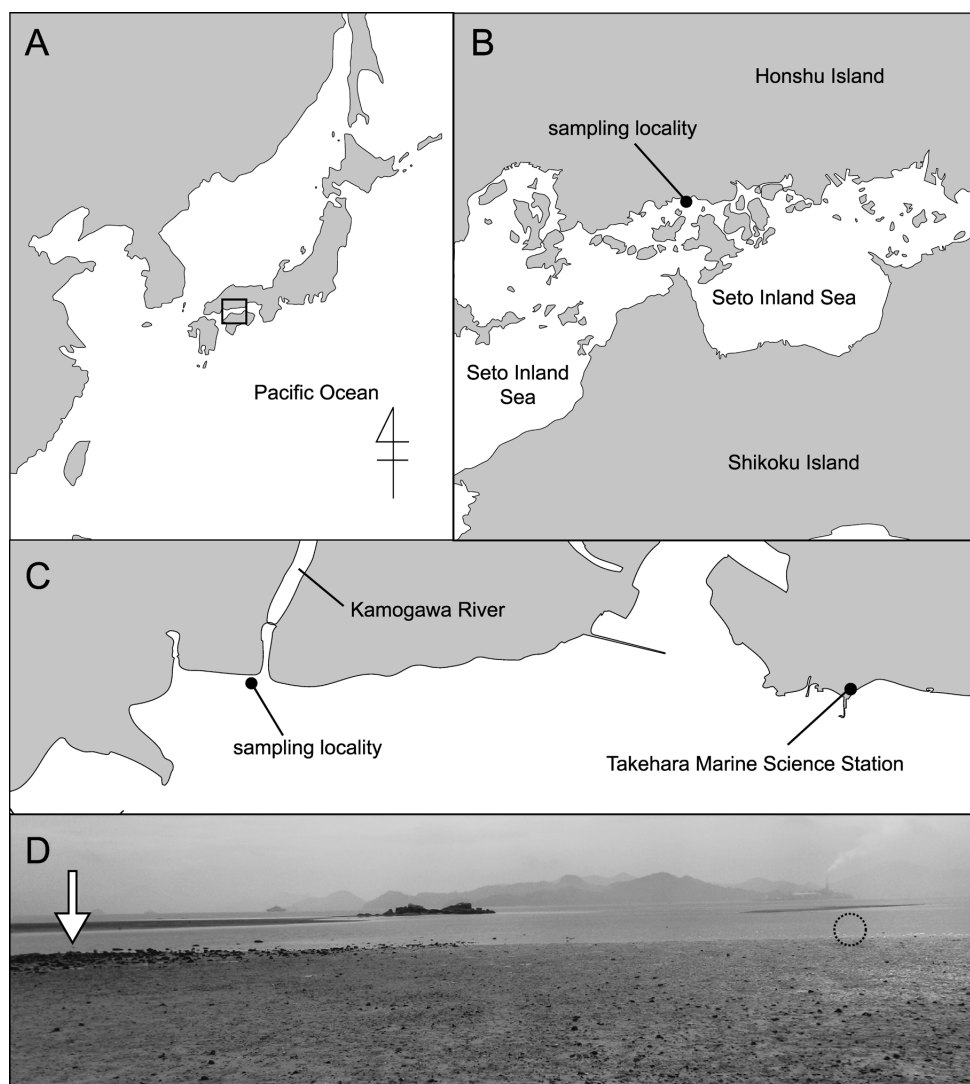


Fig. 1. Maps and photograph showing the sampling locality for *Echinoderes ohtsukai* sp. nov. A, Map of eastern Asia; B, enlargement of the rectangle in A; C, enlargement of the area indicated by the black circle in B; D, photograph of the sampling locality; white arrow indicates the Kamogawa River and dotted circle indicates the sampling site.

stubs, coated with gold in an ion sputter coater (JEOL JFC-1100), and observed by a scanning electron microscope (Hitachi S-3000N) at 30 kV accelerating voltage.

The numbering of trunk segments follows Neuhaus and Higgins (2002) and Sørensen and Pardos (2008). The terminology of trunk positions follows Pardos *et al.* (1998) and Sørensen and Pardos (2008). The type series has been deposited in the invertebrate collection of the Hokkaido University Museum (formerly the Zoological Institute), Hokkaido University (ZIHU), Sapporo, Japan.

Taxonomy

Echinoderes ohtsukai sp. nov.

[New Japanese name: Ohtsuka togekawa]
(Figs 2–8)

Material examined. Holotype, ZIHU 3976, adult male, mounted in Hoyer's-125; collected by H. Yamasaki from an

intertidal flat (34°19'32.16"N, 132°53'49.45"E), Seto Inland Sea, Japan, on 10 October 2008. Allotype, ZIHU 3977, adult female, mounted in Hoyer's-125; collection data as for the holotype. Paratypes: one male (ZIHU 3978) and three females (ZIHU 3979–3981), adults, each mounted on separate slide in Hoyer's-125; one male (ZIHU 3982) and four females (ZIHU 3983–3986), adults, each mounted on separate SEM stub; collection data as for the holotype.

Diagnosis. *Echinoderes* with trunk 315–395 μ m long; short middorsal spine present on segment 4; lateroventral tubules present on segments 5 and 8; short laterodorsal tubules present on segment 10; both sexes without lateral terminal accessory spines; lateral terminal spines about 50% of trunk length; modified type-II glandular cell outlets located in various positions on segments 2–8; large sieve plates present sublaterally on segment 9.

Description. Adults consisting of head, neck, and 11 trunk segments (Fig 2A, B, 3A). Table 1 summarizes measurements; Table 2 summarizes arrangement of spines, tubules, and cuticular structures on each segment.

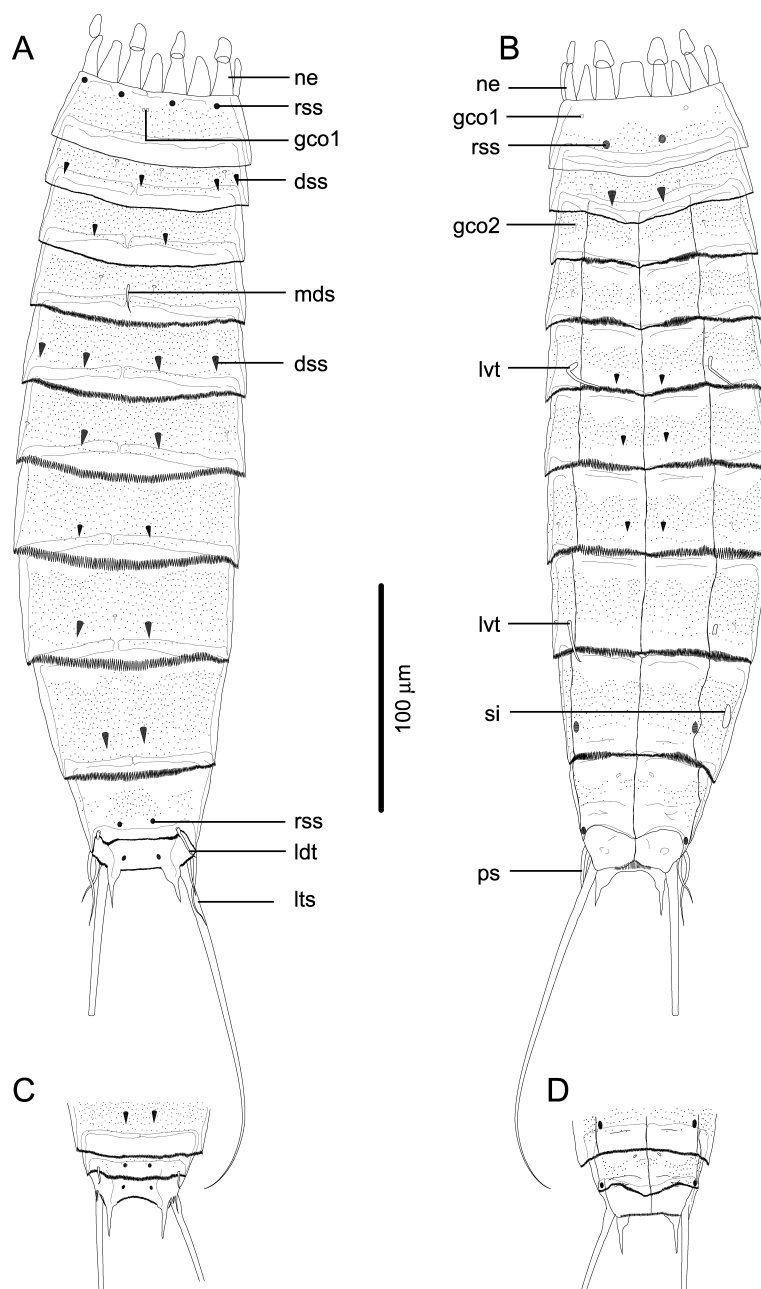


Fig. 2. *Echinoderes ohtsukai* sp. nov., camera lucida drawings. A, B, Holotype, male (ZIHU 3976), entire animal, dorsal and ventral view, respectively; C, D, allotype, female (ZIHU 3977), segments 9–11, dorsal and ventral view, respectively. Abbreviations: dss, droplet-shaped sensory spot; gco1, glandular cell outlet type I; gco2, modified glandular cell outlet type II; ldt, laterodorsal tubule; lts, lateral terminal spine; lvt, lateroventral tubule; mds, middorsal spine; ne, neck; ps, penile spine; rss, rounded sensory spot; si, sieve plate.

Head consisting of mouth cone and introvert (Figs 3A, 4A,B). Inner armature of mouth cone not observed. Outer armature consisting of nine outer oral styles covered with sets of spinous structures at their bases (Fig. 4A). Introvert comprising one ring of spinoscalids, six rings of regular scalids, and one ring of trichoscalids (Fig. 4B); spinoscalids, scalids, and trichoscalids not counted.

Neck consisting of 16 placids (Fig. 2A,B), all narrowing anteriorly. Midventral placid broadest, 14–16 μm wide at posterior margin; other placids 7–10 μm wide at posterior margin (Fig. 2A,B). Every second placid, *i.e.*, eight placids in all, with trichoscalid plates, these lacking on middorsal,

laterodorsal, lateral, lateroventral, and midventral placids (Fig. 2A,B).

Segment 1 consisting of complete cuticular ring. Pachycyclus thick along anterior margin (Figs 2A, B, 5A, 6A). Pairs of rounded sensory spots in subdorsal, laterodorsal, and ventrolateral positions (Figs 2A, B, 3B, 5A, 6A). Pairs of type-I glandular cell outlets in paradorsal and lateroventral positions (Figs 2A, B, 5A, 6A). Posterior edge with pectinate fringe composed of fine fringe tips (Figs 2A, B, 3B). Anterior part of ventral side without hairs but posterior part of both ventral and dorsal sides with acicular bracteate cuticular hairs arising from densely distributed perforation sites

Table 1. Measurements of adult *Echinoderes ohtsukai* sp. nov. from the Seto Inland Sea, Japan. Abbreviations: N, number of specimens measured; S.D., standard deviation. Abbreviations for characters: LD, laterodorsal; LTS, lateral terminal spine; LV, lateroventral; MD, mid-dorsal spine; MSW-8, maximum sternal width of segment 8; S, segment length; SW-10, standard width, always measured on segment 10; TL, trunk length; (tu), tubules.

Character	N	Range (μm)	Mean (μm)	S.D. (μm)
TL	6	315–395	369.2	28.7
MSW-8	6	63–73	67.4	3.8
SW-10	6	18–22	61.7	2.1
S 1	6	36–38	37.5	1.0
S 2	6	31–36	34.0	1.7
S 3	6	27–31	28.5	1.6
S 4	6	31–33	32.2	0.9
S 5	6	34–36	34.6	0.5
S 6	6	37–39	38.1	1.1
S 7	6	42–46	42.8	1.4
S 8	6	47–52	49.8	1.7
S 9	6	46–52	50.0	2.4
S 10	6	36–43	40.0	2.9
S 11	6	37–47	42.8	4.2
MD 4	6	12–17	14.6	2.0
LV 5 (tu)	5	22–25	22.9	1.1
LV 8 (tu)	5	15–21	18.2	2.4
LD 10 (tu)	5	18–22	19.7	1.5
LTS	5	163–190	178.8	12
LTS/TL	5	43–60%	49%	6.7%

Table 2. Summary of the positions of spines, tubules, and cuticular structures in adult *Echinoderes ohtsukai* sp. nov. Abbreviations: LA, lateral accessory; LD, laterodorsal; LV, lateroventral; MD, middorsal; ML, midlateral; PD, paradorsal; SD, subdorsal; SL, sublateral; VL, ventrolateral; VM, ventromedial; dss, droplet-shaped sensory spot; gco1, glandular cell outlet type I; gco2, modified glandular cell outlet type II (Lundbye *et al.* 2011); lts, lateral terminal spine; rss, rounded sensory spot; si, sieve plate; sp, spine; tu, tubule.

Segment	Position									
	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	—	gco1	rss	rss	—	—	—	gco1	—	rss
2	dss	—	gco2	dss, dss, gco2	—	—	—	—	gco2	dss
3	—	—	dss	—	dss	—	—	gco2	—	—
4	sp	—	gco2	—	—	—	—	gco2	—	—
5	—	—	dss	dss	gco2	—	—	tu	—	dss
6	—	—	dss	gco2	dss	—	—	—	—	dss
7	—	—	dss	—	dss	gco2	—	—	—	dss
8	gco2	—	dss	—	gco2	gco2	—	tu	—	—
9	—	—	dss	—	dss	si	—	—	dss	—
10	—	—	rss	tu	—	—	—	—	dss	—
11	—	—	rss	—	—	—	—	lts	—	—

(Figs 2A, B, 3B).

Segment 2 consisting of complete cuticular ring. Pachycycli thick along anterior margin of segment (Figs 2A, B, 5A, 6A). Droplet-shaped sensory spot in middorsal position. Two pairs of laterodorsal droplet-shaped sensory spots and one pair of ventromedial droplet-shaped sensory spots (Fig. 3B). Pairs of modified type-II glandular cell outlets (*sensu* Lundbye *et al.* 2011) in subdorsal, laterodorsal, and ventrolateral positions (Figs 2A, B, 3B, C, 5A, 6A). Acicular bracteate cuticular hairs arising from perforation sites which distribute throughout segment. Pectinate fringe as on pre-

ceding segment.

Segment 3 and following eight segments consisting of one tergal and two sternal plates (Fig. 2A, B). Pachycycli thick along anterior margin and along tergo-sternal and midsternal junctions (Fig. 2A, B). Tergal plate with pairs of droplet-shaped sensory spots in subdorsal and midlateral positions (Figs 2A, 3B). Pair of modified type-II glandular cell outlets in lateroventral position. Cuticular hairs and pectinate fringe as on preceding segment.

Segment 4 with short aciculate middorsal spine (17 μm long in holotype, 12–15 μm long in allo- and paratypes) nev-

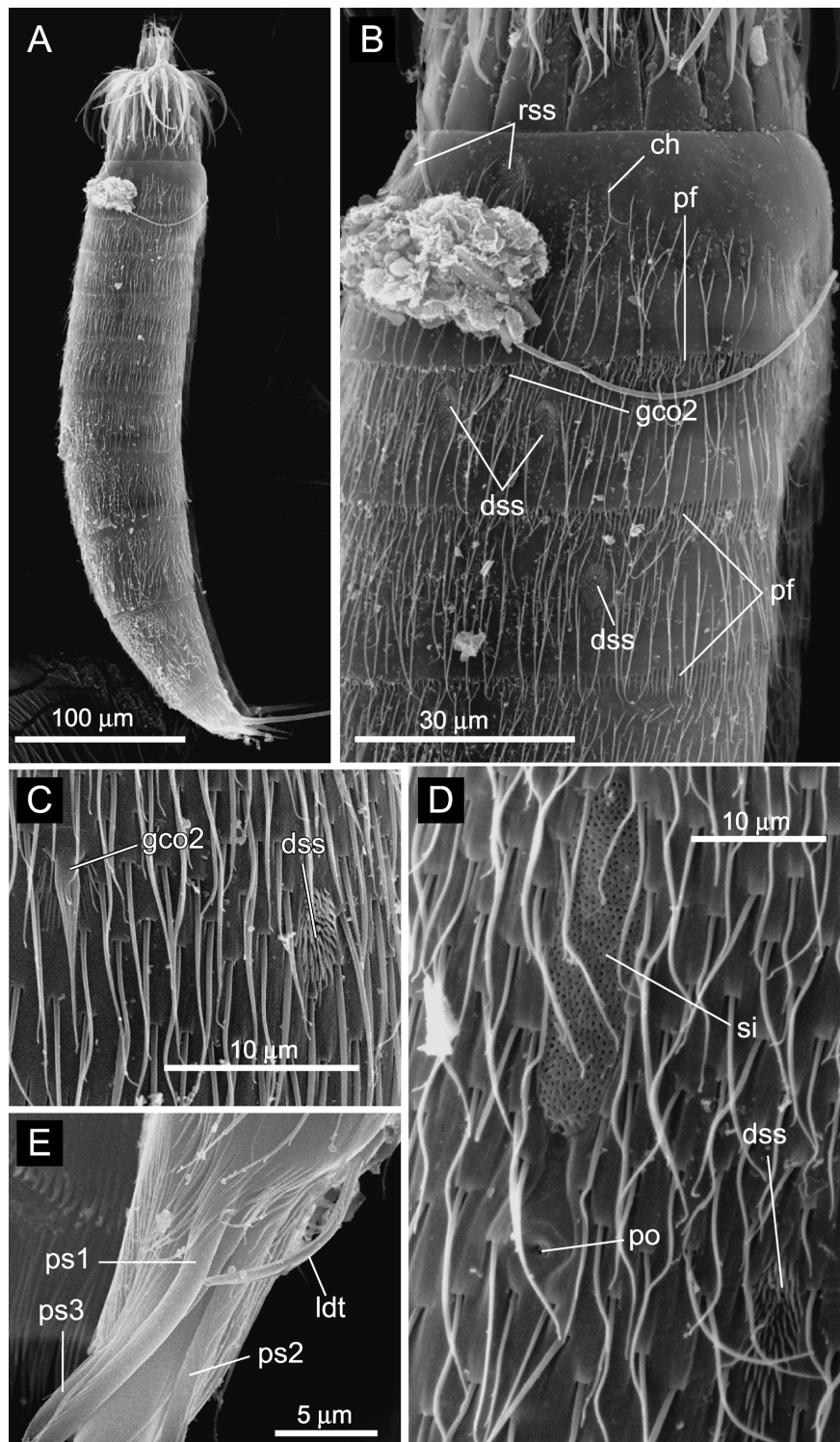


Fig. 3. *Echinoderes ohtsukai* sp. nov., scanning electron micrographs. A, B, Paratype, female (ZIHU 3983); C–E, paratype, male (ZIHU 3982). A, General habitus, lateral view; B, neck and segments 1–4, lateral view; C, enlargement of segment 7, lateral view; D, enlargement of segment 9, lateral view; E, enlargement of segments 10 and 11, lateroventral view. Abbreviations: ch, cuticular hair; dss, droplet-shaped sensory spot; gco2, modified glandular cell outlet type II; ldt, laterodorsal tubule; pf, pectinate fringe; po, pore; ps1, penile spine 1; ps2, penile spine 2; ps3, penile spine 3; rss, rounded sensory spot; si, sieve plate; ss, sensory spot.

er reaching the segment edge (Figs 2A, 5B). Sensory spots absent. Pairs of modified type-II glandular cell outlets in subdorsal and lateroventral positions. Pachycycli, cuticular hairs, and pectinate fringes of this and following six segments as on segment 3 (Figs 5B, 6B).

Segment 5 with pair of lateroventral tubules ($23\mu\text{m}$ long in holotype, broken in allotype, $22\text{--}25\mu\text{m}$ long in paratypes) (Figs 2B, 6B, 7A). Pairs of droplet-shaped sensory spots in subdorsal, laterodorsal, and ventromedial positions. Pair of modified type-II glandular cell outlets in midlateral position

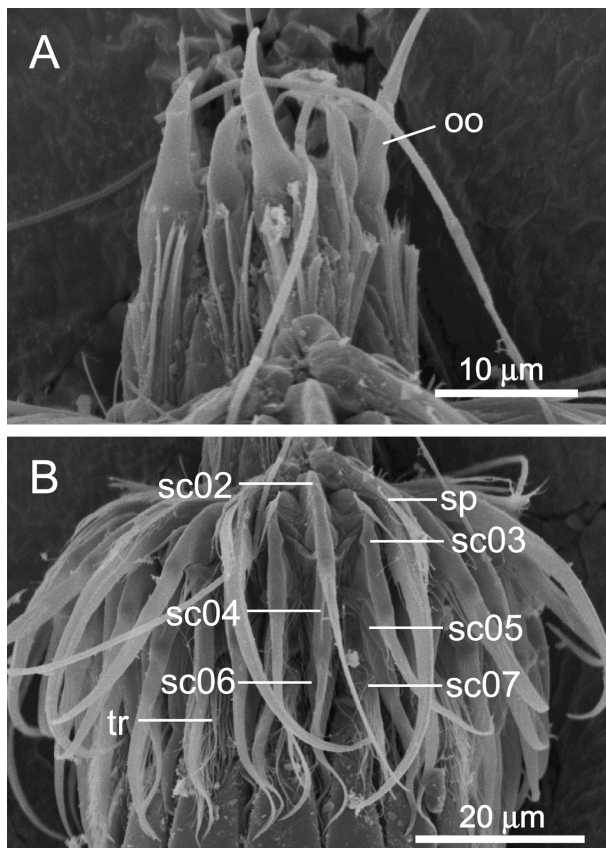


Fig. 4. *Echinoderes ohtsukai* sp. nov., paratype, female (ZIHU 3983), scanning electron micrographs. A, Mouth cone, lateral view; B, introvert, lateral view. Abbreviations: oo, outer oral styles; sc, scalids; sp, spinoscalids; tr, trichoscalids. Digits after the labels refer to introvert ring numbers.

(Fig. 7A).

Segment 6 without spines or tubules. Pairs of droplet-shaped sensory spots in subdorsal, midlateral, and ventromedial positions. Pair of modified type-II glandular cell outlets in laterodorsal position.

Segment 7 similar to segment 6 except for presence of pair of modified type-II glandular cell outlets in sublateral position, and absence of laterodorsal modified type-II glandular cell outlets (Figs 2A, B, 3C).

Segment 8 with pair of lateroventral tubules (17 µm long in holotype, broken in allotype, 15–21 µm in paratypes) (Figs 2B, 7B). Pair of droplet-shaped sensory spots in subdorsal positions. Five modified type-II glandular cell outlets, one middorsally and two pairs in midlateral and sublateral positions.

Segment 9 with three pairs of droplet-shaped sensory spots in subdorsal, midlateral, and ventrolateral positions (Figs 2B, 3D, 7B). Pair of oval sieve plates (12 µm long and 3 µm width in all specimens examined) in sublateral position (Figs 2B, 3D, 7B). Single pore about 3 µm posterior to each sieve plate (Fig. 3D).

Segment 10 with pair of rounded sensory spots in subdorsal position and pair of droplet-shaped sensory spots in ventrolateral position (Fig. 2A–D). Pair of horn-like laterodorsal tubules present (19 µm long in holo- and allotypes, 20–22 µm long in paratypes) (Figs 2A, C, 3E, 8A).

Segment 11 without perforation sites or acicular cuticular hairs. Pair of rounded sensory spots in subdorsal position (Fig. 2A, C). Pachycyclus thick along anterior margin. Pair of lateral terminal spines present, about 50% as long as trunk (163 µm long, 45% of trunk length in holotype; 190 µm, 60% in allotype; 171–190 µm, 43–49% in paratypes). Lateral terminal accessory spines absent in both sexes (Fig. 2A–D). Three pairs of penile spines present only in males (Figs 2A, B, 3E, 8B). Penile spine 1 longest (ca. 40 µm in both holotype and male paratype, ZIHU 3978); penile spine 2 second longest (ca. 30 µm in both holotype and male paratype, ZIHU 3978); penile spine 3 shortest (ca. 10 µm in both holotype and male paratype, ZIHU 3978). Tergal plate terminating in pair of pointed tergal extensions (ca. 13 µm from base of extension to tip in all specimens). Posterior margin between tergal extensions densely fringed.

Etymology. The species is named in honor of Professor Susumu Ohtsuka of Hiroshima University for his generous help in this study.

Species associations. *Echinoderes ohtsukai* co-occurred with two other kinorhynchids, *Kinorhynchus yushini* and *Pycnophyes tubuliferus*.

Remarks. Among the 69 species of *Echinoderes*, four have been reported to have a single middorsal spine on segment 4 and to lack lateral terminal accessory spines in females, as in *E. ohtsukai*. These are *E. capitatus* (Zelinka, 1928), *E. isabellae* G^aOrdóñez *et al.*, 2008, *E. rex* Lundbye *et al.*, 2011, and “*E. teretis*” (Zelinka 1928; Brown 1985; Nebelsick 1992; Adrianov and Malakhov 1999; G^aOrdóñez *et al.* 2008; Lundbye *et al.* 2011). The name “*Echinoderes teretis*”, which first appeared in Brown’s (1985) unpublished PhD thesis, is an unavailable name, which we do not intend to describe although it has been frequently used with Brown (1985) as the naming authority (e.g., Adrianov and Malakhov 1999; WoRMS 2010; Lundbye *et al.* 2011). None of these latter works has made the name available and, despite our morphological characterization of this species below, we disclaim any intention of making it available herein and assuming its authorship. In addition, four other species have lateroventral tubules only on segments 5 and 8, as in *E. ohtsukai*: *E. applicitus* Ostmann *et al.*, 2012; *E. coulli* Higgins, 1977; *E. maxwelli* (Omer-Cooper, 1957); and *E. filispinosus* Adrianov, 1989 (Omer-Cooper 1957; Higgins 1960, 1977; Adrianov 1989; Ostmann *et al.* 2012).

Echinoderes applicitus differs from *E. ohtsukai* in the form of the tergal extensions (short and conical with filiform tips in *E. applicitus* vs long with pointed tips in *E. ohtsukai*) and in the absence of the middorsal spine on segment 4 (present in *E. ohtsukai*).

Echinoderes capitatus and *E. ohtsukai* both have a pair of lateroventral spines on segments 5 and 8, but differ in the arrangement of tubules on segments 2, 6, 7, and 9: *E. capitatus* has four pairs of tubules on segment 2 and one pair each on segments 6, 7, and 9 (Nebelsick 1992) whereas *E. ohtsukai* lacks tubules on segments 2, 6, 7, and 9.

Echinoderes coulli and *E. maxwelli* differ from *E. ohtsukai* in lacking a middorsal spine on segment 4 (present in *E. ohtsukai*); furthermore, these two species lack laterodorsal

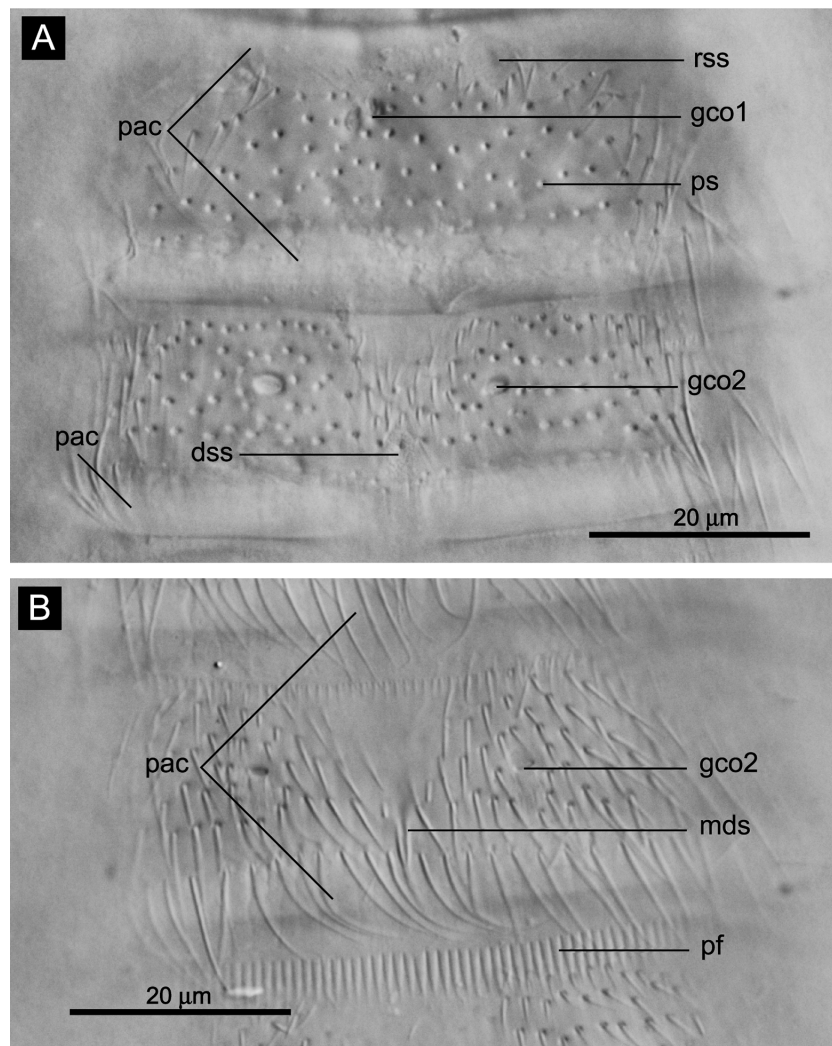


Fig. 5. *Echinoderes ohtsukai* sp. nov., holotype, male (ZIHU 3976), Nomarski photomicrographs. A, Segments 1 and 2, dorsal view; B, segment 4, dorsal view. Abbreviations: dss, droplet-shaped sensory spot; gco1, glandular cell outlet type I; gco2, modified glandular cell outlet type II; mds, middorsal spine; pac, pachycycli; pf, pectinate fringe; ps, perforation site; rss, rounded sensory spot.

tubules on segment 10 (present in *E. ohtsukai*).

Echinoderes filispinosus differs from *E. ohtsukai* in lacking a middorsal spine on segment 4 (present in *E. ohtsukai*) and in having a pair of lateral terminal accessory spines (absent in *E. ohtsukai*).

Echinoderes isabelae differs from *E. ohtsukai* in having subdorsal, laterodorsal, sublateral, and ventrolateral tubules on segment 2 (no tubules in *E. ohtsukai*); lateroventral spines on segments 6 and 7 (no spines in *E. ohtsukai*); subdorsal tubules on segment 7 (no tubules in *E. ohtsukai*); sublateral tubules and lateral accessory tubules on segment 8 (only lateroventral tubules in *E. ohtsukai*); and lateroventral spines on segment 9 (no spines in *E. ohtsukai*). *Echinoderes isabelae* lacks laterodorsal tubules on segment 10 (present in *E. ohtsukai*).

Echinoderes rex resembles *E. ohtsukai* in having pairs of lateroventral tubules on segments 5 and 8, a pair of laterodorsal tubules on segment 10, and a pair of large sieve plates on segment 9 (Lundbye *et al.* 2011). In this genus, only these two species have been reported to have modified type-II glandular cell outlets, although the position and ar-

rangement of the outlets on each segment are not identical between them. *Echinoderes rex* differs from *E. ohtsukai* in having a longer trunk (482–528 µm vs 315–395 µm in *E. ohtsukai*), very much shorter lateral terminal spines (20–24 µm vs 163–190 µm in *E. ohtsukai*), lateroventral spines on segments 6 and 7 (absent in *E. ohtsukai*), and two pairs of penile spines in males (three pairs in *E. ohtsukai*).

Echinoderes teretis differs from *E. ohtsukai* in having lateral spines on segments 6 and 7 (absent in *E. ohtsukai*). In addition, “*E. teretis*” has neither tubules nor spines on segment 10, while *E. ohtsukai* has a pair of laterodorsal tubules on this segment.

Discussion

Echinoderes ohtsukai is the sixth kinorhynch species known from intertidal or estuarine habitats with fluctuating salinities. The other five, all also species of *Echinoderes*, are *E. applicitus* (mangrove-fringed lagoon, Java Island, Indonesia) (Ostmann *et al.* 2012); *E. coulli* (intertidal mud, North

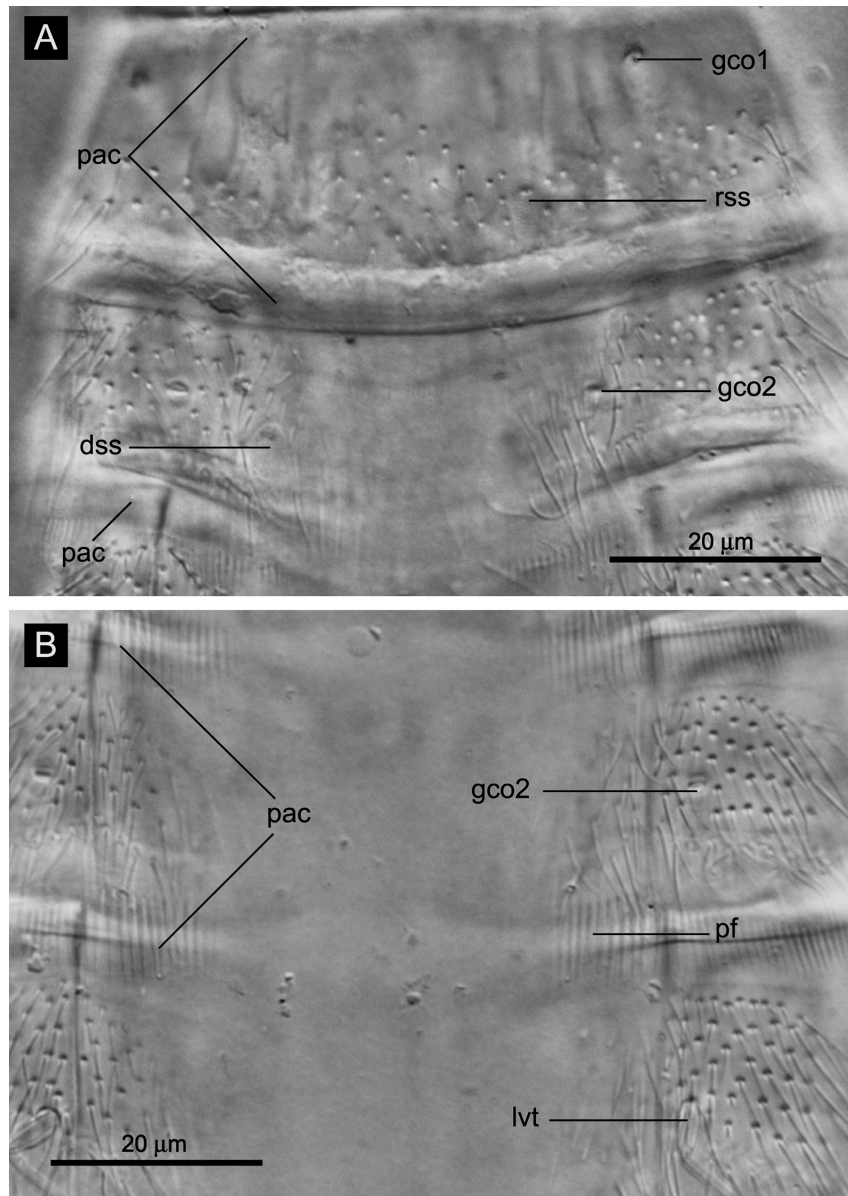


Fig. 6. *Echinoderes ohtsukai* sp. nov., holotype, male (ZIHU 3976), Nomarski photomicrographs. A, Segments 1 and 2, ventral view; B, segments 4 and 5, ventral view. Abbreviations: dss, droplet-shaped sensory spot; gco1, glandular cell outlet type I; gco2, modified glandular cell outlet type II; lvt, lateroventral tubule; pac, pachycycli; pf, pectinate fringe; rss, rounded sensory spot.

Inlet Estuary, South Carolina, USA) (Higgins 1977); *E. maxwelli* (mud and sand, estuary of the Kleinemonde River, South Africa) (Omer-Cooper 1957); *E. sublicarum* Higgins, 1977 (among hydroids, *Eudendrium* sp., North Inlet Estuary, South Carolina, USA) (Higgins 1977); and “*E. teretis*” (Australia: coarse and sandy mud; Erina Creek, Brisbane Water, Broken Bay, Hunters Hill, Cunninghams Reach, Lane Cover River, Port Jackson) (Brown 1985; Adrianov and Malakhov 1999). The type locality of *E. ohtsukai* is influenced by freshwater outflow from the Kamogawa River. Although we did not record the salinity at the time of collection, the salinity at the site at the same tidal stage (ebb tide) measured on 7 June 2011 was 30 PSU (Y. Narahara, pers. comm.).

Kristensen and Higgins (1991) speculated that the exceptionally large sieve plate, probably in combination with a posteriorly situated pore, found in *E. ohtsukai* and other

brackish-water species, functions in osmotic regulation. We tend to concur. In cyclorhagids, the protonephridium consists of terminal cells, a non-ciliated canal cell, and a nephridiopore cell (Kristensen and Hay-Schmidt 1989). In echinoderid species, the nephridiopore cell opens to the exterior via a sieve plate (e.g., Zelinka 1928; Kristensen and Hay-Schmidt 1989; Kristensen and Higgins 1991; Neuhaus and Blasche 2006; Sørensen 2008; Thormar and Sørensen 2010). In contrast to the small, rounded sieve plates in strictly marine species (e.g., 3–5 μm in diameter in *E. aquilonius* Higgins and Kristensen, 1988), those found in brackish-water species are large and elliptical: 3×15 μm in *E. applicitus* (Ostmann *et al.* 2012), 3×15 μm in *E. coulli* (Horn 1978), 3×12 μm in *E. ohtsukai*, and 6×15 μm in “*E. teretis*” (Lundbye *et al.* 2011); in *E. maxwelli*, also a brackish-water species, the sieve plate is triangular, with each edge

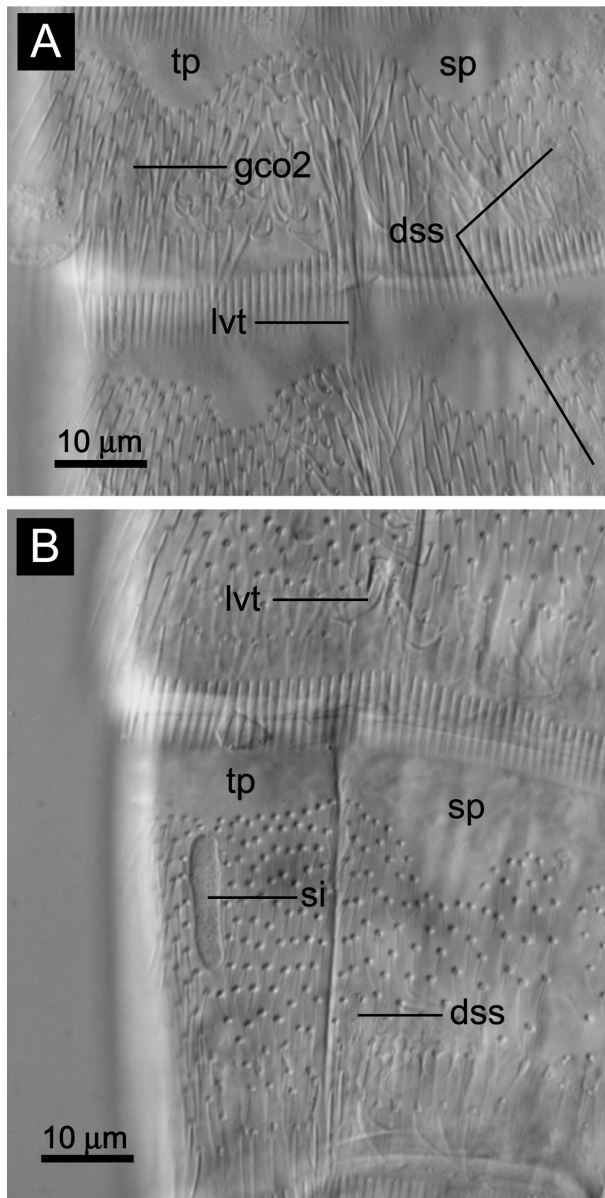


Fig. 7. *Echinoderes ohtsukai* sp. nov., paratype, female (ZIHU 3980), Nomarski photomicrographs. A, Segments 5 and 6, ventral view; B, segments 8 and 9, ventral view. Abbreviations: dss, drop-let-shaped sensory spot; gco2, modified glandular cell outlet type II; lvt, lateroventral tubule; si, sieve plate; sp, sternal plate; tp, tergal plate.

15–20 µm long. No information is available on the presence or absence of a sieve plate (or a posterior pore) in *E. sublicarum*. An isolated, single pore is situated at or near the center of a rounded, glabrous area abutting the posterior edge of the sieve plate in five brackish-water species, *E. applicitus*, *E. coulli*, *E. maxwelli*, *E. ohtsukai*, and “*E. teretis*” (Horn 1978; Lundbye *et al.* 2011; Ostmann *et al.* 2012; M. V. Sørensen, pers. comm.), and also in the marine species *E. rex*; the last is exceptional among the species of *Echinoderes* (and the rest of the phylum) in that it has a large, elliptical sieve plate (2–3 × 15–21 µm) even though it is mariculous (Lundbye *et al.* 2011).

The five species of *Echinoderes* with both a large sieve

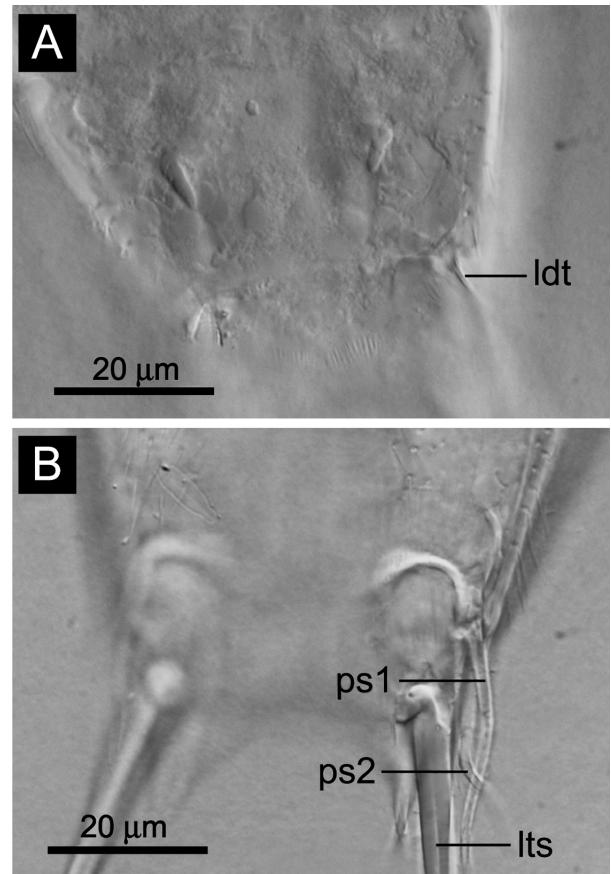


Fig. 8. *Echinoderes ohtsukai* sp. nov., holotype, male (ZIHU 3976), Nomarski photomicrographs. A, Segments 10 and 11, dorsal view; B, segments 10 and 11, ventral view. Abbreviations: ldt, laterodorsal tubule; lts, lateral terminal spine; ps1, penile spine 1; ps2, penile spine 2.

plate and a posterior pore may comprise a monophyletic group. These include four brackish-water species (*E. applicitus*, Indonesia; *E. coulli*, East Coast, USA; *E. ohtsukai*, Japan; and “*E. teretis*”, Australia) and the marine species *E. rex* (Korea). In addition to the large sieve plate and the posterior pore, these species have other characters in common, including the absence of lateral terminal accessory spines, the reduction or lack of acicular middorsal spines, and the absence of laterodorsal and subdorsal spines on segment 2. This combination of characters is not found in congeners, is not obviously associated with adaptation to brackish water, and is thus unlikely to have evolved convergently. However, whether adaptation to a brackish-water environment occurred only once or several times independently among species in *Echinoderes* remains open to question (cf. Ostmann *et al.* 2012).

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