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Echinoderes rex n. sp. (Kinorhyncha: Cyclorhagida), the largest *Echinoderes* species found so far

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SUMMARY: A new kinorhynch species, *Echinoderes rex* n. sp., is described from the Korea Strait. The new species is characterized by a pair of diminutive lateral terminal spines (19-23 μm) and a trunk length of 482-528 μm, making it the largest *Echinoderes* described so far. Unique for the new species is also the presence of a type of putative glandular cell outlets that have not been described previously. This paper presents light and scanning electron micrographs of the new structure. In addition, *E. rex* n. sp. is characterized by having a single middorsal spine on segment 4, lateroventral tubules on segment 5 and 8 and lateroventral acicular spines on segments 6 and 7. A pair of distinct and conspicuously large sieve plates, only described from two other species of the genus, is present on segment 9 in *E. rex* n. sp. A comparison is made with other species of *Echinoderes* and the similarities are discussed.

Keywords: Echinoderidae, Korea Strait, meiofauna, morphology, new species.

RESUMEN: *Echinoderes rex* n. sp. (Kinorhyncha: Cyclorhagida), la especie de *Echinoderes* más grande encontrada hasta el momento. – Se describe una nueva especie de kinorrinco, *Echinoderes rex* n. sp., del estrecho de Corea. La nueva especie se caracteriza por un par de diminutas espinas laterotерminales (19-23 μm) y una longitud total del tronco de 482-528 μm, lo que la convierte en el mayor *Echinoderes* conocido. Además, la nueva especie presenta como carácter exclusivo un nuevo tipo de posible poro glandular que no ha sido descrito previamente, y que se describe en este trabajo con microscopía óptica y de barrido. *E. rex* presenta una única espina mediodorsal en el segmento 4, túbulos lateroventrales en los segmentos 5 y 8, y espinas aciculares lateroventrales en los segmentos 6 y 7. En el segmento 9 aparecen un par de grandes y conspicuas placas cribadas, semejantes a las descritas únicamente en otras dos especies del género. Se compara la nueva especie con otros *Echinoderes* y se discuten sus semejanzas.

Palabras clave: Echinoderidae, estrecho de Korea, meiofauna, morfología, nueva especie.

INTRODUCTION

Echinoderes Claparède, 1863 is with its 67 valid species the most diverse kinorhynch genus. The genus is characterized by the presence of 16 placids in the neck region (midventral placid usually the broadest), the first two segments always consisting of closed cuticular rings and the following nine segments consisting of one tergal and two sternal plates. Middorsal spines are present in some species, usually restricted to segments 4 to 8; lateral terminal spines are present in all species; and lateral terminal accessory spines are—if present in the species—restricted to females. A midterminal spine is never present in adults (Higgins, 1990; Sørensen and Pardos, 2008).

Among species of *Echinoderes* the sexes are usually distinguished by the presence of lateral terminal accessory spines in females only, and pairs of short penile spines in males. However, females of some species deviate from this pattern as they lack lateral terminal

accessory spines. These species include *Echinoderes coulli* Higgins, 1977, *E. isabelae* G[a]Ordóñez *et al.*, 2007, *E. capitatus* Zelinka, 1928, *E. maxwelli* Omer-Cooper, 1957 and *E. teretis* Brown, 1985 (See Zelinka, 1928; Omer-Cooper, 1957; Higgins, 1977; Brown, 1985; Nebelsick, 1992; G[a]Ordóñez *et al.*, 2007). All of these species, except *E. coulli* but including *E. cantabricus* Pardos *et al*., 1998, also share another feature that is unusual for the genus: the presence of only one middorsal spine located on segment 4.

Sieve plates in species of *Echinoderes* are often—if observed—described as circular, small clusters of pores, often visible in scanning electron microscope only (Kristensen and Higgins, 1991; Pardos *et al.*, 1998). Large and distinctive sieve plates consisting of an elongated pore field and a posteriorly located nonporous plate with one single pore centred was described for the first time from *E. coulli* (see Kristensen and Higgins, 1991). Similar sieve plates have only been observed in one other species, *E. teretis* (see Brown, 1985).

In the present study we describe a new species of *Echinoderes*, *E. rex* n. sp., from the western Pacific Ocean, based on light and scanning electron microscopical examinations. It is the largest species in the genus known so far, with an average trunk length of 505 μm. The common sexual dimorphism found in *Echinoderes* is not present in this new species because paired lateral terminal accessory spines are lacking in females. Presence of middorsal spines is restricted to segment 4 and—for the first time since the description of *E. coulli* and *E. teretis*—a pair of similar distinctive sieve plates is observed.

MATERIALS AND METHODS

Echinoderes rex n. sp. was detected during sampling of meiobenthic animals under the KORDI (Korea Ocean Research and Development Institute) cruise of the research vessel RV *Onnuri* within the framework of the research programme POSEIDON (Pacific Ocean Study on Environmental and Interactions between Deep Ocean and National seas). Sediment samples were taken with a Smith McIntyre Grab from the subtidal zone of the Korea Strait. Specimens of *Echinoderes rex* n. sp. were collected at one station (34°34′43″N, 127°45′52″E) at 13 m depth on May 26, 2008. The sediment consisted of mud with tiny shell particles. Meiofauna was freshwater shocked (Kristensen and Higgins, 1984; Sørensen and Pardos, 2008) and extracted in the field through a 63 μm mesh sieve. The concentrated sample was fixed in 4% formalin mixed with sea water, and the meiofauna was subsequently extracted by flotation in Ludox® (DuPont) HS 40 (Burgess, 2001). The kinorhynch specimens were sorted out from the mixed meiobenthos under a high-magnification LEICA MZ 8 stereomicroscope. Specimens for scanning electron microscopy (SEM) were dehydrated through a graded series of ethanol, transferred to acetone and critical-point dried. The dried specimens were mounted on aluminum stubs, sputter coated and examined with a JEOL JSM-6335F field emission scanning electron microscope. Specimens for light microscopy (LM) were transferred to distilled water, dehydrated through a graded series of glycerin and mounted in Fluoromount G®. The mounted specimens were examined and photographed using Nomarski differential interference contrast with an Olympus BX60 microscope equipped with an Olympus DP20 camera. Measurements were made with Cell^D software for analysis of light microscopical photos.

The terminology in the taxonomic account follows Pardos *et al.* (1998), Neuhaus and Higgins (2002), and Sørensen and Pardos (2008). For comparison, type specimens of *Echinoderes coulli* were loaned from the Smithsonian Institution: paratypic females type I, ranging from accession number USNM 54385–200.1 to 54385–200.5 and USNM 54385–200.7 to 54385–200.10; paratypic females type II, ranging from accession number USNM 54388–200.11 to USNM 54388–200.21 and from USNM 54388–200.23 to 54388–200.30; and paratypic males accession numbers USNM 54391–200.31, 54391–200.33 to 54391–200.36 and 54391–200.37 to 54391–200.40. *Echinoderes maxwelli*: holotypic male, accession number 1957:12:22:1 and allotypic female, accession number 1957:12:22:2 were loaned from the British Museum of Natural History. Furthermore, specimens of *Echinoderes teretis* were used for comparison. The specimens were collected in Candlagan Creek, 247 km south of Sydney, Australia, and were used in a previous study by Nicholas and Sørensen (2009). The specimens are stored in the collection of the Natural History Museum of Denmark under accession numbers ZMUC KIN-454 to KIN-456.

RESULTS

Family ECHINODERIDAE Bütschli, 1876
Genus *Echinoderes* Claparède, 1863

Echinoderes rex n. sp.
(Figs 1, 2A, F, 3, 4A, 5)

Material examined. Holotype, adult female, mounted in Fluoromount G®, deposited at the Zoological Museum, Natural History Museum of Denmark, under accession number ZMUC KIN-384. Additional material mounted for light microscopy includes four female paratypes, deposited at the Zoological Museum, Natural History Museum of Denmark, under accession numbers: ZMUC KIN-385, to KIN-388.

Allotype, adult male, mounted for SEM, deposited at the Zoological Museum, Natural History Museum of Denmark, under accession number ZMUC KIN-389. Additional material mounted for SEM includes three female paratypes, deposited at the Zoological Museum, Natural History Museum of Denmark, under accession numbers ZMUC KIN-390 to KIN-392.

Diagnosis. Trunk large, 482-528 μm, but lateral terminal spines very short, 19-23 μm. Short, feebly visible

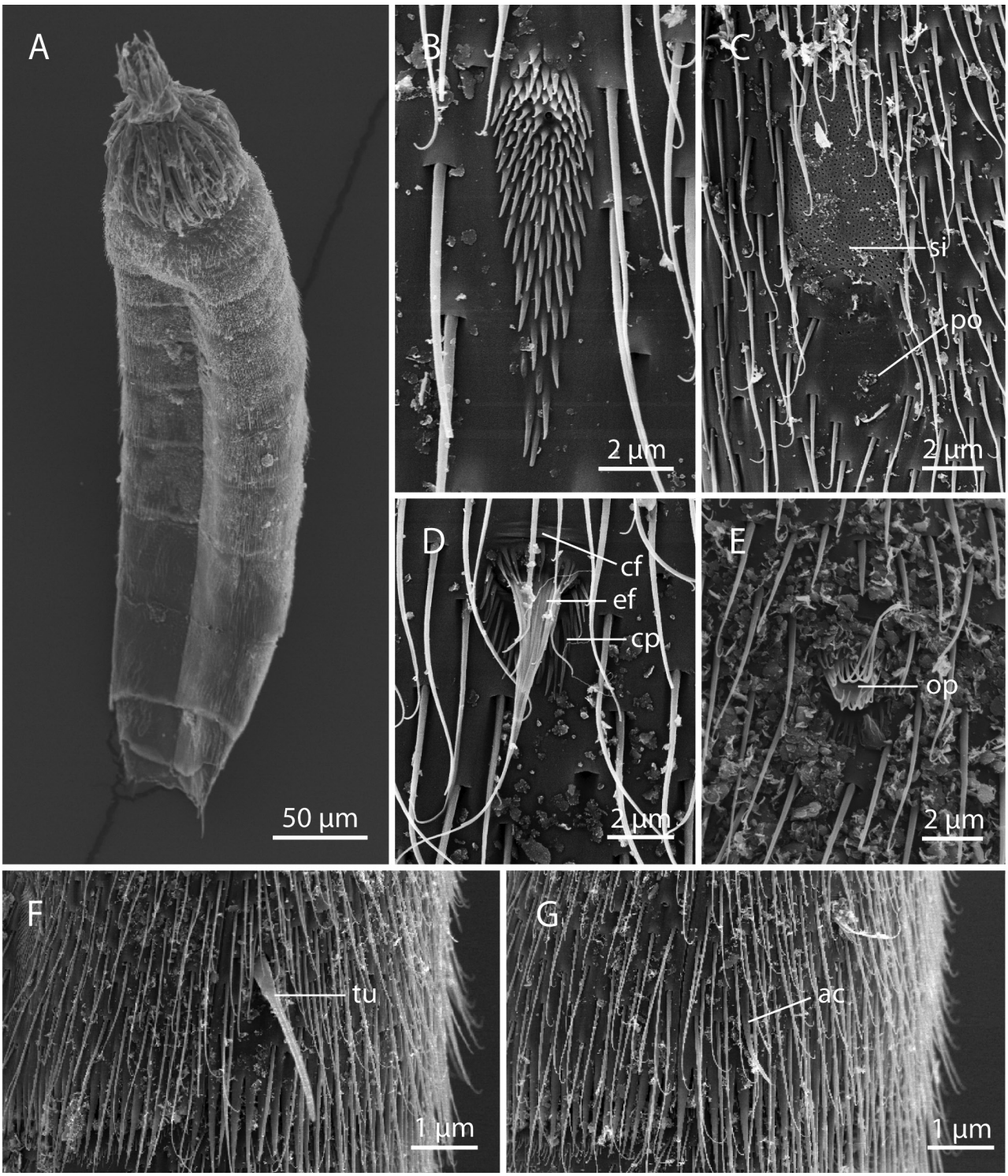

FIG. 1. – Scanning electron micrographs of *Echinoderes rex* n. sp. A**,** ventrolateral view; B, detail from segment 7 showing droplet shaped sensory spot as it appears in the ventrolateral positions; C, detail from segment 9 showing sieve plate consisting of an elongated porous plate and a single pore posteriorly; D, detail from midlateral position on segment 8 showing modified glandular cell outlet type II; E, detail from ventrolateral position on segment 2 showing modified glandular cell outlet type II; F, detail from segment 5 showing lateroventral tubule; G, detail from segment 6 showing lateroventral acicular spine. Abbreviations: ac, acicular spines; cf, cuticular furrows; cp, cuticular papillae; ef, elongated fringes; op, opening; po, pore; si, sieve plate; tu, tubule.

middorsal spine present on segment 4, lateroventral tubules present on segments 5 and 8, short, flexible lateroventral spines present on segments 6 and 7, and very short and hook-shaped laterodorsal tubules present

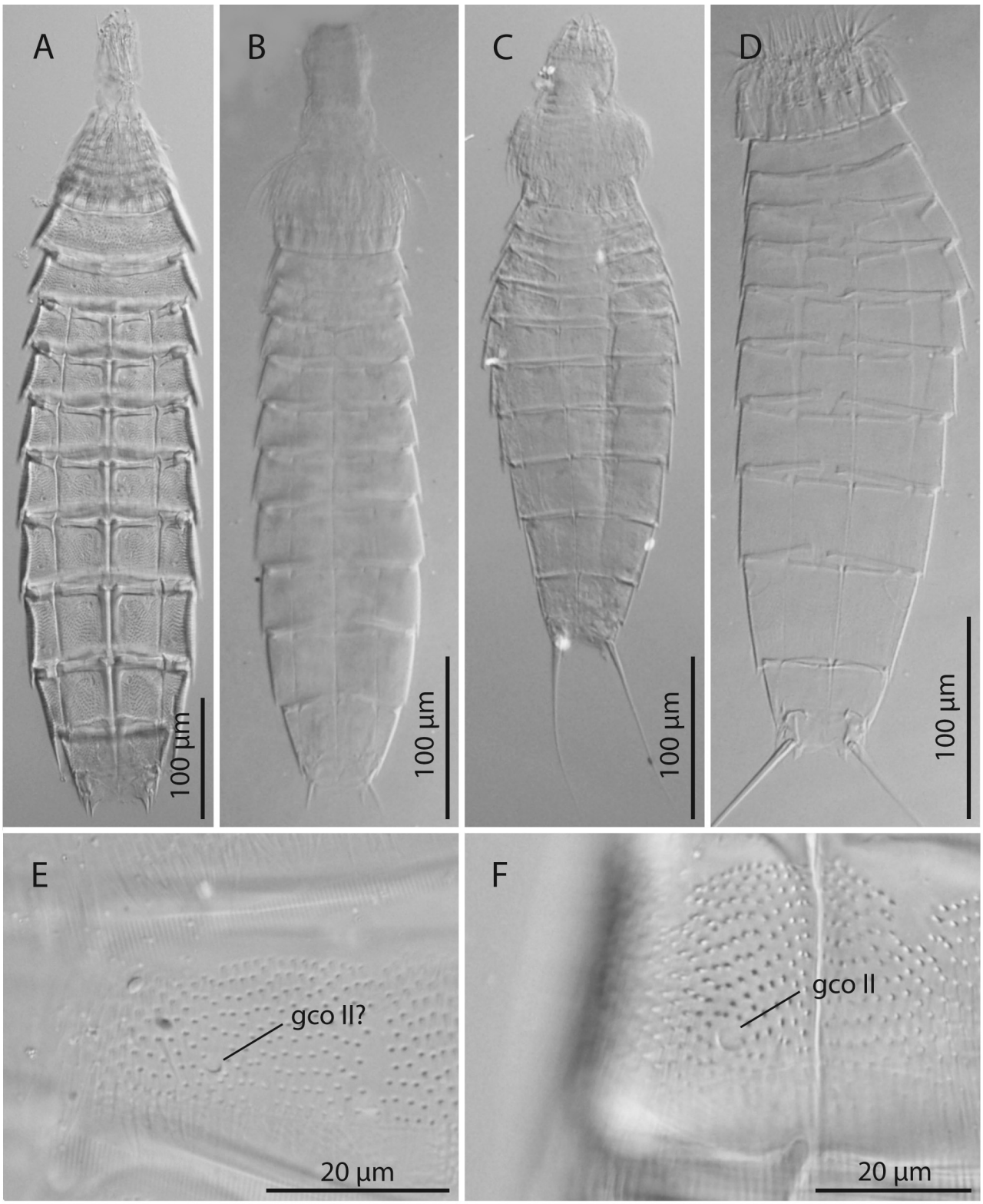

FIG. 2. – Light microscope photos showing selected species of *Echinoderes*. A, *Echinoderes rex* n. sp. holotypic female, ventral view; B, *E. coulli*, USNM 54388, paratypic female type II, ventral view; C, *E. teretis*, ZMUC KIN-454, female, ventral view; D, *E. maxwelli*, 12.22.1., holotypic male, ventral view; E, *E. maxwelli*, 12.22.2., allotypic female, detail from segment 6, showing putative modified type II glandular cell outlet; F, *E. rex* n. sp., holotypic female, detail from segment 6, showing modified type II glandular cell outlet. Abbreviations: gco II, modified glandular cell outlet type II.

TABLE 1. – Measurements of adult *Echinoderes rex* n. sp. from the western Pacific Ocean, the Korea Strait, including number of measured specimens (n) and standard deviation (SD). Abbreviations: LTS: lateral terminal spine; LV: lateroventral; MD: middorsal spine; MSW-8: Maximum sternal width, measured on segment 8 in this species; S: segment lengths; SI: sieve plate length; SW-10, standard width, always measured on segment 10; TL: trunk length; (tu): tubules.

Character	n	Range	Mean	S.D.
TL	5	482-528 µm	505 µm	18.99 µm
MSW-8	5	88-95 µm	92 µm	2.90 µm
SW-10	5	77-86 µm	83 µm	3.64 µm
S1	5	44-46 µm	45 µm	0.58 µm
S2	5	39-44 µm	41 µm	1.63 µm
S3	5	37-48 µm	42 µm	4.36 µm
S4	5	41-46 µm	43 µm	1.76 µm
S5	5	43-50 µm	48 µm	2.51 µm
S6	5	47-55 µm	53 µm	3.51 µm
S7	5	54-63 µm	60 µm	3.34 µm
S8	5	65-74 µm	70 µm	3.63 µm
S9	5	70-79 µm	74 µm	3.29 µm
S10	5	48-60 µm	55 µm	5.61 µm
S11	5	26-30 µm	27 µm	1.88 µm
MD 4	5	12-17 µm	14 µm	2.05 µm
LV 5 (tu)	5	15-21 µm	17 µm	2.64 µm
LV 8 (tu)	5	12-14 µm	13 µm	0.91 µm
LTS	5	20-24 µm	21 µm	1.48 µm
LTS/TL	5	3.8-4.8%	4.2%	0.36%
SI 9	5	15-21 µm	18 µm	2.45 µm

on segment 10. Males with two lateral penile spines, females without lateral terminal accessory spines. Putative type II glandular cell outlets with conspicuous tuft of cuticular extensions present in various positions. Segment 9 with large, elongated sieve plate, located in a sublateral position, anterior to distinct pore.

Etymology. The species name "*rex*" is from Latin, meaning "king", and refers to the species' distinct and prominent appearance in light microscopy, as well as its considerable trunk length, making it the largest of all known species of *Echinoderes*.

Description. The adult specimen consists of a head, a neck and eleven trunk segments (Figs 1A, 2A,3). Measurements and dimensions are given in Table 1. A summary of sensory spot, spine and tubule positions is provided in Table 2. Scalid distribution could not be observed.

The neck consists of 16 placids, all about 16-20 µm in length. The midventral placid is the broadest (21 µm); remaining placids 12-14 µm and all narrow anteriorly.

Segment 1 consists of one complete cuticular ring. The cuticle on this, and the following segments, appears to be relatively thick. Pachycycli are well-developed along the anterior margin of this and the second segment (Fig. 2A). Pairs of laterodorsal and midlateral rounded sensory spots are present near the anterior margin of the segment. A pair of ventrolateral rounded sensory spots is located halfway down the segment. These sensory spots, and all other found on this species, belong to type 1 and consist of a droplet-shaped field of several small, pointed cuticular papillae and two pores (Fig. 1B). A type I glandular cell outlet is present in the middorsal position. Cuticular hairs on this and all following segments emerge through slit-like perforation sites that are typical for bracteate hairs. However, an actual bractea is not present on the margin of the slit (see Fig. 1B-D for corresponding hairs on other segments). Perforation sites are densely scattered over the surface of the segment without any characteristic pattern. On this and the following nine segments, the posterior segment margin terminates into a pectinate fringe with slender, pointed and relatively long fringe tips.

Segment 2 consists of one complete cuticular ring. The cuticular structures found in the middorsal to sublateral positions on the tergal plate show sexual dimorphism. Females have a middorsal, droplet-shaped sensory spot and a pair of laterodorsal and midlateral droplet-shaped sensory spots. A pair of "modified type II glandular cell outlets" (Fig. 2F) is located subdorsally. These structures consist of a large opening surrounded by a tuft of cuticular extensions (Fig. 1D,E). Numerous minute cuticular papillae are located in a circle around the elongated fringes. The cuticle has fur-

TABLE 2. – Summary of nature and location of sensory spots, glandular cell outlets and spines arranged by series in *Echinoderes rex* n. sp. from the Korea Strait. 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; f, female condition of sexual dimorphic character; gco1, glandular cell outlet type I; gco2, modified glandular cell outlet type II; lts, lateral terminal spine; m, male condition of sexual dimorphic character; si, sieve plate; ss1, sensory spot type 1 (for some sensory spots it was not possible to determine their types); tu, tubule; (!) only observed in one individual; (!!) observed in some, but not all of the examined animals.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1			ss1	ss1				ss1	
2	gco1,ss1(f)	ss1(m)	gco2	ss1(f),gco2(m)	ss1				gco2	gco1,ss1
3			ss1		ss1		gco2(f)			gco1
4	ac		gco1,gco2	ss1			gco2			gco1
5			gco1,ss1		ss1			tu		gco1,ss1
6			gco1,ss1		ss1		gco2	ac		gco1,ss1
7			gco1,ss1		ss1		gco2	ac		gco1,ss1
8	gco2(!)		gco1,ss1		gco2		gco2	tu		gco1
9			gco1,ss1	ss1(!)	ss1	si			ss1	gco1
10	gco1(!)		gco1,ss1(!!)	tu					ss1	gco1
11			ss1(!!)					lts		

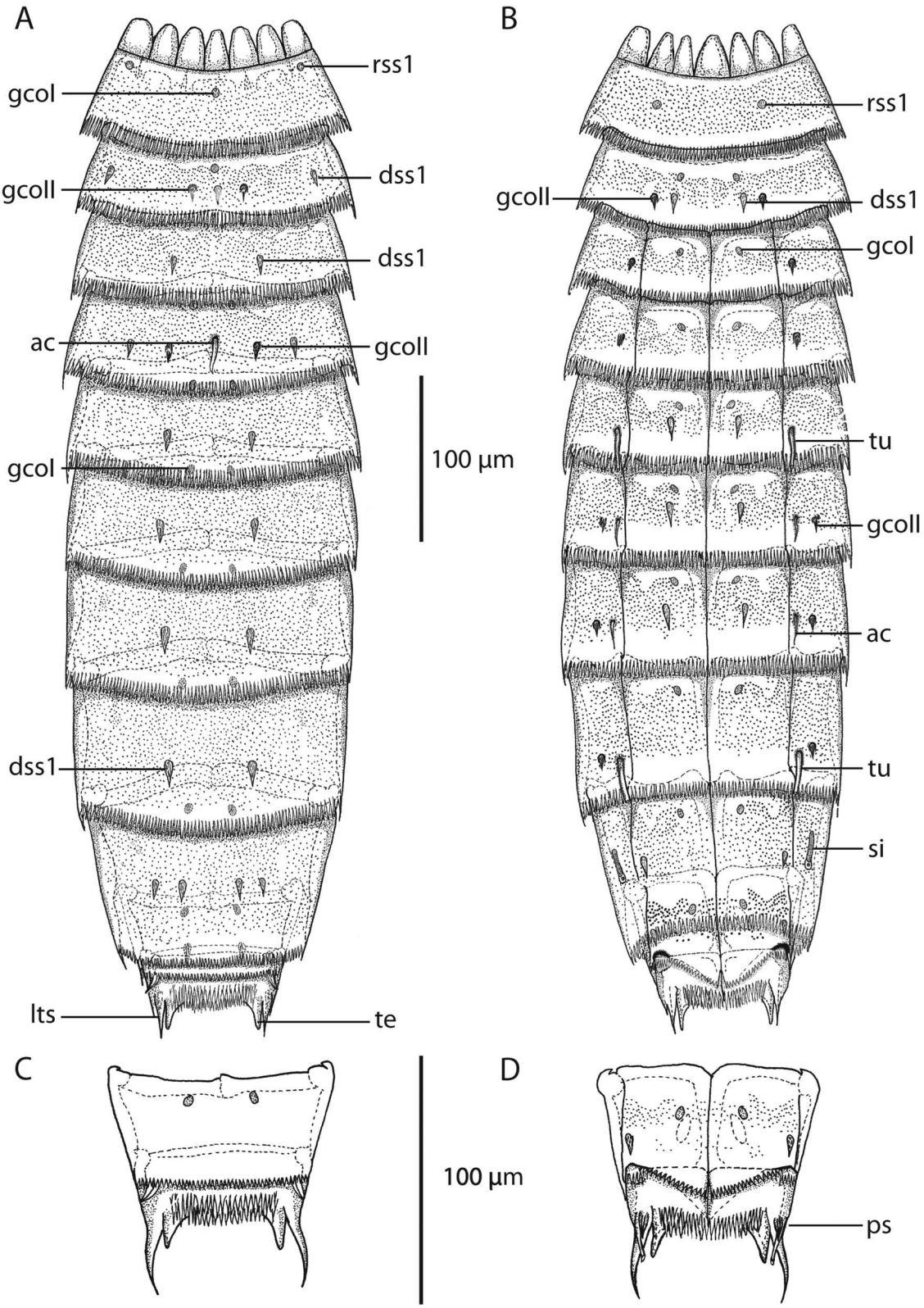

FIG. 3. – Line art illustrations of *Echinoderes rex* n. sp. A, female, dorsal view; B, female, ventral view; C, male, segments 10 and 11, dorsal view; D, male, segments 10 and 11, ventral view. Abbreviations: ac, acicular spine; dss1, droplet shaped sensory spot type 1; gcoI, glandular cell outlet type I; gcoII, modified glandular cell outlet type II; lts, lateral terminal spine; ps, penile spines; rss1, rounded sensory spots type 1; si, sieve plate; te, tergal extension; tu, tubule.

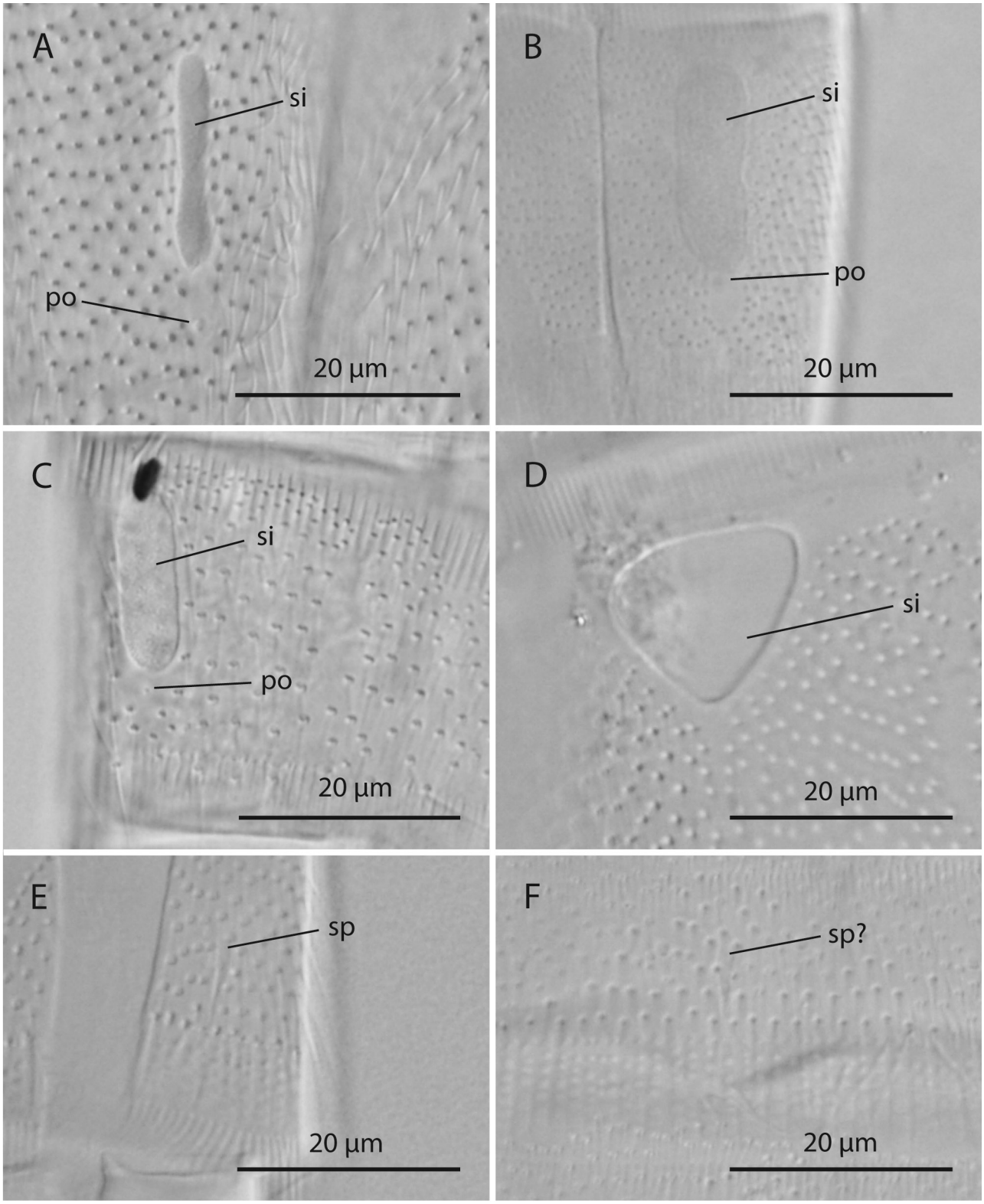

FIG. 4. – Light microscope photos showing cuticular details in selected species of *Echinoderes*. A, sieve plate in *Echinoderes rex* n. sp. female, segment 9, lateral view; B, sieve plate in female *E. coulli* type II, USNM 54388, segment 9, lateral view; C, sieve plate in female *E. teretis*, ZMUC KIN-454, segment 9, lateral view; D, sieve plate in female *E. maxwelli*, 12.22.2., segment 9, lateral view; E, male *E. maxwelli*, 12.22.1., segment 6, lateroventral spine; F, male *E. maxwelli,* 12.22.1., detail from middorsal position of segment 4, showing weak indications of a feebly visible spine. Abbreviations: po, pore; si, sieve plate; sp, spine.

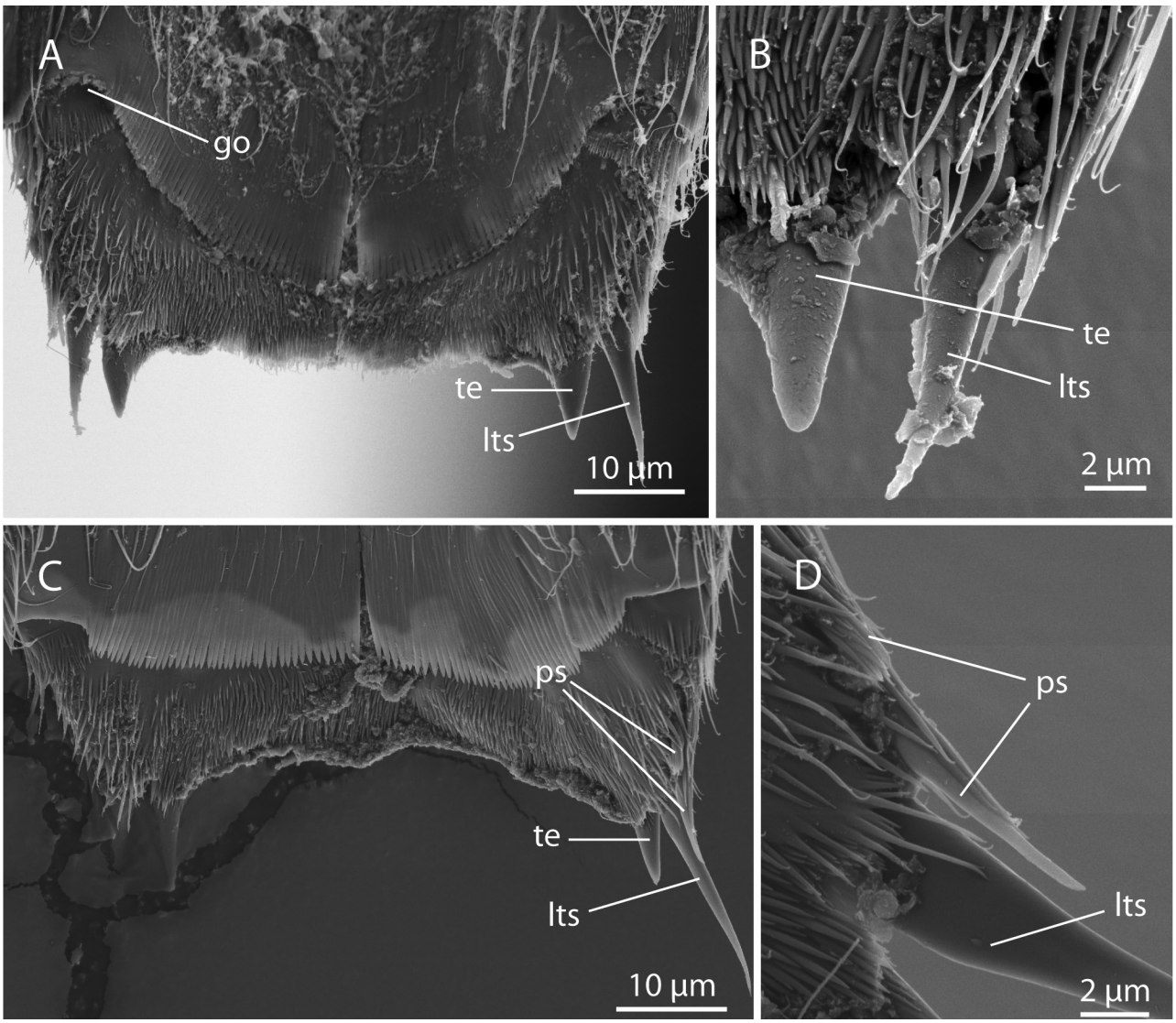

FIG. 5. – Scanning electron micrographs of terminal segments in *Echinoderes rex* n. sp. A: Segments 10 to 11 in female, ventral view. B: Detail from segment 11 in female. C: Segments 10 to 11 in male, ventral view. D: Detail from segment 11 in male. Abbreviations: go, gonopore opening; lts, lateral terminal spine; ps, penile spine; te, tergal extension.

rows just above the extension of the glandular cell outlet (Fig. 1D). Due to the opening's resemblance to type II glandular cell outlets, it will tentatively be referred to as a modified type II glandular cell outlet. Males have a pair of droplet-shaped paradorsal and midlateral sensory spots, and a pair of sub- and laterodorsal modified type II glandular cell outlets. Otherwise, both sexes have one pair of ventromedial, droplet-shaped sensory spots, one pair of ventromedial type I glandular cell outlets and one pair of ventrolateral modified type II glandular cell outlets. Perforation sites are distributed in a characteristic band around the segment, being narrow on the ventral side and broad on the dorsal side (Fig. 3A,B). Patches, completely devoid of cuticular hairs, are elongate and extend posterior to the sensory spots on both tergal and sternal plates. These patches are found on this and the following segments.

Segment 3 and following 8 segments consist of one tergal and two sternal plates (Figs. 2A, 3B). Pachycycli are well-developed along the anterior margins of the tegumental plates and along the tergosternal, and midsternal junctions (Fig. 2A). Tergal plates with droplet-shaped sensory spots in subdorsal and midlateral positions. Type I glandular cell outlets are present in the ventromedial position. Females also have a pair of lateral accessory modified type II glandular cell outlets. Perforation sites are distributed in a band around the segment, being narrow on the ventral side and broad on the dorsal side. The anterior end of the perforation site band forms a characteristic pattern on this and the following segments (Figs. 2A, 3B).

Segment 4 possesses a short, soft middorsal acicular spine (12-17 µm) (Fig. 3A). A pair of droplet-shaped sensory spots is found in the laterodorsal position. Pairs

of type I and modified type II glandular cell outlets are located in a subdorsal position. Furthermore, a pair of type I glandular cell outlets is found ventromedially and modified type II glandular cell outlets are located in the lateral accessory position. Perforation sites as on previous segments (Fig. 3A). These patches are found from segment 4 to 10.

Segment 5 with one pair of short lateroventral tubules located close to the posterior margin of the segment (Fig. 3B). Paired droplet-shaped sensory spots are located in the subdorsal, midlateral and ventromedial positions. Furthermore pairs of type I glandular cell outlets are found subdorsally and ventromedially.

Segments 6 and 7 with one pair of short, lateroventral acicular spines (Fig. 3B). Sensory spots and type I glandular cell outlets as on segment 5. Lateral accessory modified type II glandular cell outlets are located on the posterior part of the segment.

Segment 8 with one pair of lateroventral tubules (Fig. 3B), one pair of droplet-shaped sensory spots and type I glandular cell outlets located in the subdorsal position (Fig. 3A). Type I glandular cell outlets furthermore located ventromedially. Paired modified type II glandular cell outlets present in the lateral accessory and midlateral positions. One additional middorsal modified type II glandular cell outlet was furthermore observed in a single specimen.

Segment 9 with one pair of subdorsal, midlateral and ventrolateral droplet-shaped sensory spots. In one specimen one pair of sensory spots was also found in the laterodorsal position. Type I glandular cell outlets located subdorsally and ventromedially. A pair of well-developed, large (15-21 μm) sieve-plate openings is located sublaterally (Fig. 3B). It consists of an elongated porous plate and a posterior pore situated in a nonporous, slightly prolapsed plate that overlaps with the outermost posterior part of the big porous plate (Figs. 1C, 4A).

Segment 10 with a pair of short, but stout and slightly hook-shaped laterodorsal tubules that extend from the posteriormost part of the segment. In SEM they appear to extend from the intersegmental joint between segment 10 and 11, but LM reveals that they originate from segment 10. A pair of droplet-shaped sensory spots is present ventrolaterally. Six out of the nine examined animals furthermore have a pair of droplet-shaped sensory spots located subdorsally. Type I glandular cell outlets are located subdorsally and ventromedially. One additional middorsal type I glandular cell outlet was furthermore observed in a single specimen. The posterior margins of the sternal plates are rounded ventromedially. This feature is more distinct in females (Figs. 3B, D, 5A,C).

Segment 11 with a pair of subdorsal droplet-shaped sensory spots in some specimens, but these are lacking in others. The lateral terminal spines (LTS) are remarkably short (Figs. 2A, 3, 5A-C) ranging from 20 to 24 μm. Lateral terminal accessory spines are lacking in both sexes (Fig. 3). In females the gonopores are visible ventrolaterally as two distinct protuberances (Fig. 5A). Males with two pairs of short and inconspicuous penile spines in a lateral accessory position and with longer lateral terminal spines than found in females (Fig. 5B,D). One of the penile spines is tubule-shaped and fringed (Fig. 5C,D). The tergal plates terminate into two, paired tergal extensions. The tergal extension forms a pair of short but stout spinous projections (Fig. 3). The posterior margin in between the tergal extensions is densely fringed and more or less straight in males, but more rounded in females (Fig. 5A,C).

DISCUSSION

Notes on diagnostic features

Echinoderes rex n. sp. is easily recognized by its diminutive lateral terminal spines (19-23 μm) (Figs 1A, 2A, 3A,B) and the length of its body (482-528 μm), making it the largest *Echinoderes* species described so far. It can also be distinguished by its spine/tubule composition that includes a single middorsal spine on segment 4, lateroventral tubules on segment 5 and 8 and lateroventral acicular spines on segments 6 and 7. The characteristic fringed cuticular structures, referred to as modified type II glandular cell outlets, are unique for the species and have not, to our knowledge, been reported previously from any kinorhynch species. Furthermore, the species is characterized by its large and distinctive sieve plates and the lack of lateral terminal accessory spines in females. The latter feature is shared only with six other known species of *Echinoderes*, *E. capitatus*, *E. coulli*, *E. isabelae*, *E. maxwelli* and *E. teretis* (see Zelinka, 1928; Omer-Cooper, 1957; Higgins, 1977; Brown, 1985; Nebelsick, 1992; G^{a}Ordóñez *et al.*, 2007) in addition to a yet undescribed species of *Echinoderes* from Spain (Herranz and Pardos, pers. com.).

Of the six other species that lack lateral terminal accessory spines in the females, *E. teretis* is the species that most resembles *E. rex* n. sp. in having only one middorsal spine on segment 4, lateroventral tubules on segment 5 and 8 and lateroventral spines on segment 6 and 7. *Echinoderes teretis* differs from *E. rex* n. sp. by its remarkably smaller trunk length (207-264 μm) and overall trunk shape with conspicuously broad segments 4 to 6 (Fig. 2C).

Echinoderes rex n. sp. has only two pairs of penile spines, both located in a lateral position, whereas *E. teretis* possesses two pairs of lateral and one pair of dorsal penile spines. The length of the lateral terminal spines is furthermore considerably longer in *E. teretis*, being 106-141 μm (46-65% of trunk length) in this species, as opposed to only 20-24 μm (4% of trunk length) in *E. rex* n. sp.

Echinoderes maxwelli (Fig. 2D) has the same overall body shape as *E. rex* n. sp. although the trunk length differs (328 μm in *E. maxwelli* vs. 482-528 μm in *E. rex* n. sp.). Based on the original description of

E. maxwelli (see Omer-Cooper, 1957) and the corrections and additional notes by Higgins (1977), the two species resemble each other in having one pair of tubules lateroventrally on segments 5 and 8, and males with only two pairs of penile spines, although penile spines in *E. maxwelli* are longer (1/6 the length of the lateral terminal spines) than those in *E. rex* n. sp. The lengths of the lateral terminal spines also differ considerably, being 184-212 μm (56-66% of the trunk length) in *E. maxwelli*. Type material was loaned from British Museum of Natural History, and based on our examinations we found the following additional similarity: *E. maxwelli* has a pair of diminutive spines in the lateroventral positions of segment 6 and 7 (Fig. 4E). Furthermore, we found characters that in LM could be interpreted as the same kind of modified type II glandular cell outlets (Fig. 2E) as observed in *E. rex* n. sp. However, examination with SEM would be required to confirm this. An inconspicuous, short, flexible structure that could be interpreted as a spine was found middorsally on segment 4 (Fig. 4F) but to ensure this, further examination is required. Opposite to *E. rex* n. sp., *E. maxwelli* has no perforation sites on the ventral side of the 1st segment. The sieve-plate is remarkably large and triangular in shape extending from the lateroventral side to a more laterodorsal position (Fig. 4D). *Echinoderes capitatus* and *E. rex* n. sp. share the presence of a middorsal spine on segment 4 only, and the presence of paired ventrolateral tubules on segments 5 and 8. However, they differ regarding their distribution patterns and numbers of the tubules. Whereas *E. rex* n. sp. possesses tubules on segments 5 and 8, in the lateroventral position on both segments, *E. capitatus* has numerous tubules distributed in subdorsal to ventromedial positions between segments 2 to 9 (Nebelsick, 1992). Furthermore, the total body length of *E. capitatus* is 270-290 μm and the lateral terminal spines are long (64-88 μm) and medially curved.

Echinoderes isabelae and *E. rex* n. sp. share the presence of a single middorsal spine on segment 4, paired lateroventral tubules on segment 5 and 8 and paired spines in the same positions on segment 6 and 7. The two species can be distinguished by several characters: Firstly, the trunk length of *E. isabelae* is 223-240 μm and its body shape is bulbous with the 1st and 2nd segment being the broadest (GªOrdóñez *et al.*, 2007). *Echinoderes isabelae* also has pairs of several paired tubules on segment 2, a pair of sublateral tubules on segment 7, and paired lateroventral spines on segments 6 to 9. Its lateral terminal spines are considerably longer than in *E. rex* n. sp., being 87-94 μm, and males have three pairs of penile spines, as opposed to only two in *E. rex* n. sp.

Echinoderes rex n. sp. and the previously mentioned yet undescribed species from Spain, *Echinoderes* nov. sp., share the presence of a single middorsal spine on segment 4 only, the lateroventral pair of tubules on segment 5 and the paired spines in the same position on segments 6 and 7. However, the undescribed species differs by its overall body shape and by being considerably shorter (270 μm) than *E. rex* n. sp. *Echinoderes* nov. sp. also has pairs of tubules in a subdorsal, laterodorsal, lateral accessory and ventrolateral position on segment 2 and pairs of tubules in a subdorsal and lateral accessory position on segment 8, together with a pair of lateroventral acicular spines on the same segment. The three pairs of penile spines are distinct and long (28μm) and the lateral terminal spines are 97 μm.

Of the 6 species that lack a lateral terminal accessory spine in the females, *E. coulli* (Fig. 2B) is the one that deviates the most from *E. rex* n. sp. Their most conspicuous similarity, apart from the lack of lateral terminal accessory spines in females, is the small, lateroventral tubules on segment 5 and 8 and the short lateral terminal spines, being 5.6% of the trunk length in the *E. coulli* female type II and 3.8-4.8% in *E. rex* n. sp. Taxonomic significant differences between them include the trunk length (348-364 μm compared to the 482-528 μm in *E. rex* n. sp.) and the complete absence of middorsal spines in *E. coulli*. Furthermore, *E. coulli* has three pairs of penile spines and characteristic thin, lanceolate extensions of cuticle flares at the base of the gonoporeal area (Higgins, 1977). Such flares are not present in *E. rex* n. sp., and the species has only two pairs of penile spines

Among the six species that are characterized by the absence of lateral terminal accessory spines in females, three species share another distinctive character: the very well developed sieve-plates on segment 9, as found in *E. rex* n. sp. (Fig. 4A). The species that share this feature are *E. rex* n. sp., *E. coulli* (Fig. 4B) and *E. teretis* (Fig. 4C). In *E. rex* (Fig. 4A) the elongated porous plate is narrower than in the two other species, and the posterior pore that is situated in a nonporous, slightly prolapsed plate is situated somewhat more posterior than in *E. coulli* and *E. teretis*. In *E. coulli* (Fig. 4B) the pore is located anteriorly and closer to the posterior end of the porous plate and in *E. teretis* (Fig. 4C) the pore is situated in the centre of the nonporous plate. The size and appearance of the elongated porous plate in *E. coulli* and *E. teretis* are similar.

Another species of *Echinoderes* that resembles *E. rex* n. sp. is *Echinoderes cantabricus* Pardos *et al.*, 1998, in having the characteristic, single, middorsal spine on segment 4. *E. cantabricus* resembles *E. rex* n. sp. in its overall body shape, though it is slightly smaller (328-408 μm). It has lateroventral tubules on segments 5 and 8 and spines in the same position on segments 6 and 7. The two species differ in the amount of tubules, *E. cantabricus* having a midlateral pair on segment 1 and four pairs, subdorsally, laterodorsally, sublaterally and ventrolaterally on segment 2, and the males having an additional subdorsal pair on segment 10. In addition to these differences, the sieve plate in *E. cantabricus* is smaller and more rounded. Females have lateral terminal accessory spines, and the two sexes show dimorphism regarding their lengths. Males

of *E. cantabricus* have three pairs of penile spines, as opposed to only two in *E. rex* n. sp.

The internal relationships of *Echinoderes* are far from clarified. A clarification would require a prober phylogenetic analysis, and include reexamination of most of the not recently described species. However, with the description of *E. rex* n. sp. we see indications that may suggest potential monophyletic clades of species within the genus. For instance, the similarities discussed above could indicate a closer relationship between the species *E. rex* n. sp., *E. capitatus*, *E. coulli*, *E. isabelae*, *E. maxwelli*, *E. teretis* and the yet undescribed species of *Echinoderes* from Spain, which all are characterized by the absence of lateral terminal accessory spines in both sexes. Lateral terminal accessory spines in females is a sexually dimorphic character trait that is found in most species of the family Echinoderidae, including species of the genera *Fissuroderes* (see Neuhaus and Blasche, 2006), *Polacanthoderes* (see Sørensen, 2008) and *Cephalorhyncha* (see Adrianov and Malakhov, 1999). This would suggest that the presence of lateral terminal accessory spines is synapomorphic for all echinoderid species; the absence of these spines in the seven particular species mentioned above would thus be due to secondary reduction, and hence could be considered synapomorphic for these species. Within this potential clade, the presence of an enlarged sieve plate on segment 9 could indicate a closer relationship between *E. rex* n. sp., *E. coulli* and *E. teretis*. These, and other hypotheses about the interrelationships between species of *Echinoderes*, will hopefully be tested in a formal, phylogenetic analysis in the near future.

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