

# A new kinorhynch genus from the Antarctic deep sea and a new species of *Cephalorhyncha* from Hawaii (Kinorhyncha: Cyclorhagida: Echinoderidae)

Martin V. Sørensen

Ancient DNA and Evolution Group, Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

Received 23 July 2007; accepted 14 November 2007

## Abstract

A new species of a new kinorhynch genus with affinities to the Echinoderidae and a new species of *Cephalorhyncha* are described. *Polacanthoderes martinezi* gen. et sp. nov. was collected during the German ANDEEP-1 cruise at 2290 m depth north of the South Shetland Islands in the Southern Atlantic Ocean, approximately 170 km north of the Antarctic Peninsula. *Polacanthoderes* is characterized by the presence of a first trunk segment consisting of a complete cuticular ring, and by each of the following ten segments consisting of one tergal and two sternal plates. Cuticular hairs and perforation sites are absent, but spines are present in middorsal, subdorsal, laterodorsal, midlateral, lateral accessory, lateroventral, ventrolateral and ventromedial series on segments 4–10. The ventral side of segment 1 has a very strong and conspicuous pectinate fringe, whereas fringes are indistinct or absent on posterior segment margins of the following segments. Due to segment 1 being composed of a closed ring and the following segments of a tergal and two sternal plates, as well as to the presence of aligned middorsal spines and lateral terminal spines but absence of a midterminal spine, *Polacanthoderes* is assigned to the family Echinoderidae.

*Cephalorhyncha liticola* sp. nov. was collected in the intertidal zone of a high energy beach on the northeast coast of Oahu, Hawaii. The species is characterized by the sternal plate of segment 2 being incompletely separated anteriorly by a midventral fissure. Middorsal spines are present on segments 4–8, ventrolateral spines on segment 2, lateroventral spines on segments 5–9, lateral accessory spines on segment 8, and laterodorsal spines on segment 10. In addition, there are special sensory spots with conspicuous marginal cuticular hairs on segments 1–3, and very long pectinate fringes on the sternal plates of segments 3–10. The partly subdivided sternal plates on segment 2 show the species to belong to the echinoderid genus *Cephalorhyncha*.

© 2008 Gesellschaft für Biologische Systematik. Published by Elsevier GmbH. All rights reserved.

**Keywords:** ANDEEP; Antarctica; New genus; *Cephalorhyncha liticola* sp. nov.; *Polacanthoderes martinezi* gen. et sp. nov.; Taxonomy

## Introduction

Kinorhyncha is a phylum of microscopic, marine animals that live in muddy or sandy sediments, or

occasionally in the associated fauna of calcareous algae or in kelp holdfasts (Zelinka 1928; Moore 1973; Higgins 1983; Higgins and Kristensen 1988; Neuhaus and Higgins 2002; Neuhaus 2004). They are characterized by a retractable head with numerous appendages, termed scalids, with locomotory and sensorial functions,

E-mail address: [mvsorensen@bi.ku.dk](mailto:mvsorensen@bi.ku.dk).

by a neck with closing plates, the so-called placids, and by a trunk consisting of 11 segments. The trunk may be equipped with various cuticular structures, e.g. spines, tubules, sensory spots, gland outlets and hairs (Kristensen and Higgins 1991; Nebelsick 1992; G<sup>a</sup>Ordóñez et al. 2000; Sørensen 2006). The first kinorhynch was recorded more than 150 years ago (Dujardin 1851); today the number of species based on descriptions of adult specimens exceeds 150.

Even though kinorhynchs are known to occur in the deep sea and even may be rather common at abyssal depths, the vast majority of reports originate from the subtidal zone down to a few hundred metres depth. Kinorhynchs recorded below a depth of 500 m include species of the genera *Antygomonas* (see Bauer-Nebelsick 1996), *Campyloderes* (see Neuhaus 2004), and *Fissuroderes* (see Neuhaus and Blasche 2006). According to the literature, the deepest kinorhynch collecting location is at 7800 m in the Atacama Trench (Danovaro et al. 2002), but unfortunately the material was reported as “Kinorhyncha sp.” only. However, preliminary examinations of material from the German DIVA2 Expedition in the Angola Basin have revealed species of *Echinoderes* from a depth of 5649 m (Sørensen, pers. obs.).

The present contribution includes the descriptions of new kinorhynchs from two extremes of the group’s habitat spectrum: the Antarctic deep sea and the intertidal zone of a Hawaiian high energy beach. The specimens from Antarctica represent a new genus and species of the family Echinoderidae, whereas the Hawaiian species can be assigned to the echinoderid genus *Cephalorhyncha*. The exact phylogenetic positions of the new taxa are addressed in a second contribution in this ODE issue (Sørensen 2008).

## Material and methods

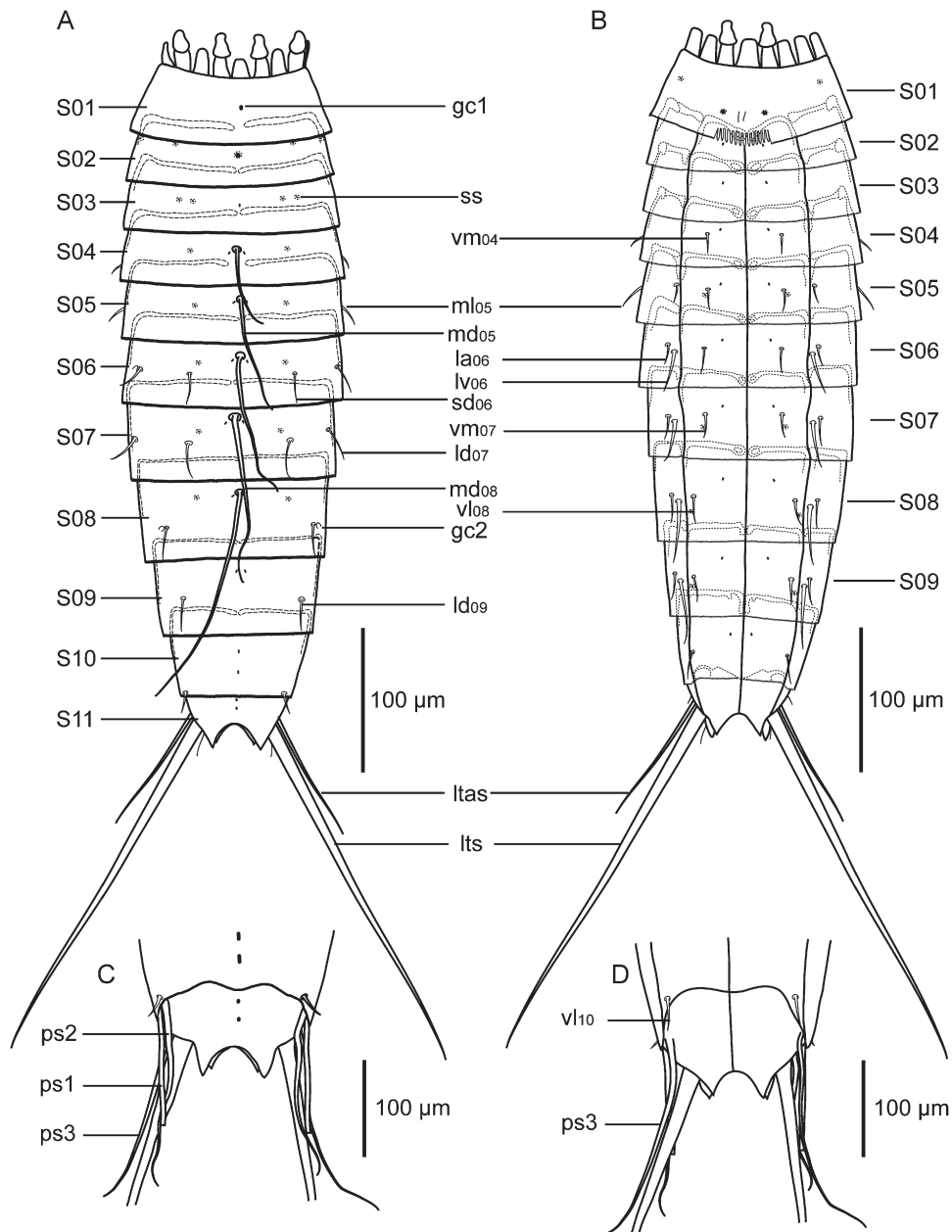
Specimens for the description of *Polacanthoderes martinezi* gen. et sp. nov. were kindly provided by the Senckenberg Institute in Wilhelmshaven, Germany. The specimens were part of the large material of meiofaunal organisms collected during the German ANDEEP-1 cruise ANT-XIX/3 of the research vessel RV Polarstern (see Gutzmann et al. 2004 for further information). The samples that yielded specimens for the present study were taken with a multiple corer at two stations on 14 February 2002, north of the South Shetland Islands in the Southern Atlantic Ocean, approximately 170 km north of the Antarctic Peninsula. Station data: PS 61/105-2: position: 61°24.14’S, 058°51.15’W, 2290 m depth; PS 61/105-6: position: 61°23.73’S, 058°50.26’W, 2274 m depth. The upper 10 cm of each sediment core were fixed in 4% buffered formalin immediately after the

samples were collected. In a laboratory the meiofauna was extracted using centrifugation with Levasil (see Neuhaus and Blasche 2006 for further details on the extraction method). Subsequently, the extracted meiofauna was sorted to main groups and stored in 4% buffered formalin at the Senckenberg Institute in Wilhelmshaven.

Specimens for the description of *Cephalorhyncha liticola* sp. nov. were collected by the author on 19 February 2006, between Kaluanui Beach and Kapaka Beach on the Northeast coast of Oahu, Hawaii, position: 21°36.369’N, 157°54.369’W. The species had been recorded at this locality one year earlier by R.M. Kristensen and A. Hejnol. Sediment was collected in the upper part of the tidal zone by digging ca. 70 cm down in the sand until ground water started to appear on the bottom. The sample was taken from the soaked sand on the bottom of the hole and was transported to the Kewalo Marine Laboratory. Specimens were extracted by adding an isotonic solution of magnesium chloride to the sediment to anaesthetize the meiofaunal organisms. After shaking the sediment and magnesium chloride solution vigorously, the supernatant was poured through a net with 30 µm mesh width. Specimens retained in the net were sorted under an Olympus ZX12 dissecting microscope and fixed in 4% borax-buffered formalin.

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 were transferred to distilled water, dehydrated through a graded series of glycerin and mounted in Fluoromount G<sup>®</sup>. The mounted specimens were examined and photographed using Nomarski differential interference contrast with an Olympus BX60 microscope equipped with a Color-View I digital camera. Measurements were made with Cell<sup>^</sup>D software for analysis of light microscopical photos. Line art illustrations were made from drafts of specimens made with a camera lucida. The pencil drafts were scanned to Adobe Illustrator, and the final line art was prepared using a Wacom drawing tablet and the digital inking method described by Coleman (2003).

The terminology for head, neck and trunk morphology follows Neuhaus and Higgins (2002), Sørensen (2007) and Sørensen et al. (2007). Hence, the first trunk segment is named segment 1, followed by the second trunk segment (segment 2) and so on down to the terminal trunk segment (segment 11). This more logical terminology is gradually being adopted by most kinorhynch taxonomists, and is preferred as a replacement for the earlier interpretation of the head as segment 1, the neck as segment 2, and the trunk



**Fig. 1.** *Polacanthoderes martinezi* gen. et sp. nov. (A) Female, dorsal view. (B) Female, ventral view. (C) Male, terminal segments and penile spines, dorsal view. (D) Male, terminal segments and penile spines, ventral view. Abbreviations: gc1/2 = gland cell type 1/2; la = lateral accessory spine; ld = laterodorsal spine; ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; ml = midlateral spine; ps1/2/3 = penile spine 1/2/3; S = segment; sd = subdorsal spine; ss = sensory spot; vl = ventrolateral spine; vm = ventromedial spine. Double digits denote respective segment number.

comprising segments 3–13. For additional arguments in favour of the new terminology see Neuhaus and Higgins (2002).

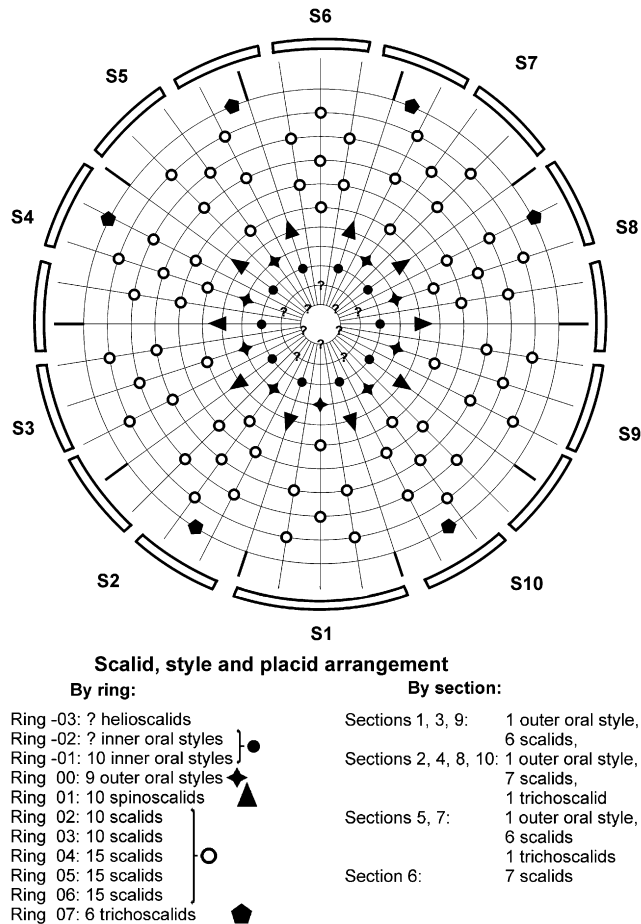
### Taxonomic section

Order Cyclorhagida Zelinka, 1896  
 Suborder Cyclorhagae Zelinka, 1896  
 Family Echinoderidae Bütschli, 1876

### Genus *Polacanthoderes* gen. nov.

#### Etymology

Incorporation of the Greek-derived “*Polacantho-*” was inspired by the dinosaur genus *Polacanthus* that also, like the new genus, is characterized by the presence of multiple serial rows of spines or spikes. The suffix “*-deres*” (derived from the Ancient Greek *δέρη* = neck) is commonly used in generic names of cyclorhagid kinorhynchs. Gender of genus name: masculine.



**Fig. 2.** Diagram of mouth cone, introvert and placids in *Polacanthoderes martinezi* gen. et sp. nov. indicating distribution of oral styles, scalids, and placids (curved bars around introvert diagram).

### Type species

*Polacanthoderes martinezi* sp. nov.

### Diagnosis

Cuticle of first trunk segment forms complete ring; cuticle of segments 2–11 with midventral and lateroventral articulations resulting in one tergal and two sternal plates. Cuticular hairs and perforation sites absent from all segments. Ventral side of segment 1 with very strong and conspicuous pectinate fringe; fringes on posterior segment margins indistinct or absent.

Strong, acicular, middorsal spines on segments 4–8. Shorter acicular spines present in following pattern: Subdorsal spines on segments 6 and 7, laterodorsal spines on segments 6–10, midlateral spines on segments 4 and 5, lateral accessory spines on segments 6–9, lateroventral spines on segments 5–9, ventrolateral spines on segments 8–10, ventromedial spines on segments 4–7.

### *Polacanthoderes martinezi* sp. nov.

(Figs. 1–5; Tables 1, 2)

### Synonymy

New genus 1 new species 1 (Sørensen and Pardos 2008).

### Etymology

The species is named after Prof. Dr. Pedro Martinez Arbizu who invited me to visit the Senckenberg Institute to work on the kinorhynch material from the ANDEEP and DIVA expeditions.

### Material examined

Southern Atlantic Ocean north of South Shetland Islands; RV Polarstern, Andeep-1 cruise; 14 February 2002: 61°24.14'S, 058°51.15'W, 2290 m depth (sample PS105-2); 61°23.73'S, 058°50.26'W, 2274 m depth (sample PS105-6). Deposited at Museum für Naturkunde of Humboldt University, Berlin, Germany.

Holotype: Adult female from PS105-6, mounted in Fluoromount G<sup>®</sup> (accession number: ZMB Vermes Generalkatalog Freilebende Würmer No. 11237). Paratypes: allotype adult male from PS105-2, mounted in Fluoromount G<sup>®</sup> four adult females and one adult male from PS105-2 and PS105-6, mounted in Fluoromount G<sup>®</sup> (accession numbers: ZMB Vermes Generalkatalog Freilebende Würmer Nos. 11238a–f).

Eight additional specimens were collected at the same localities; five of them were mounted in Fluoromount G<sup>®</sup> for LM examinations, three for SEM examinations (accession numbers: ZMB Vermes Generalkatalog Freilebende Würmer Nos. 11238g–n).

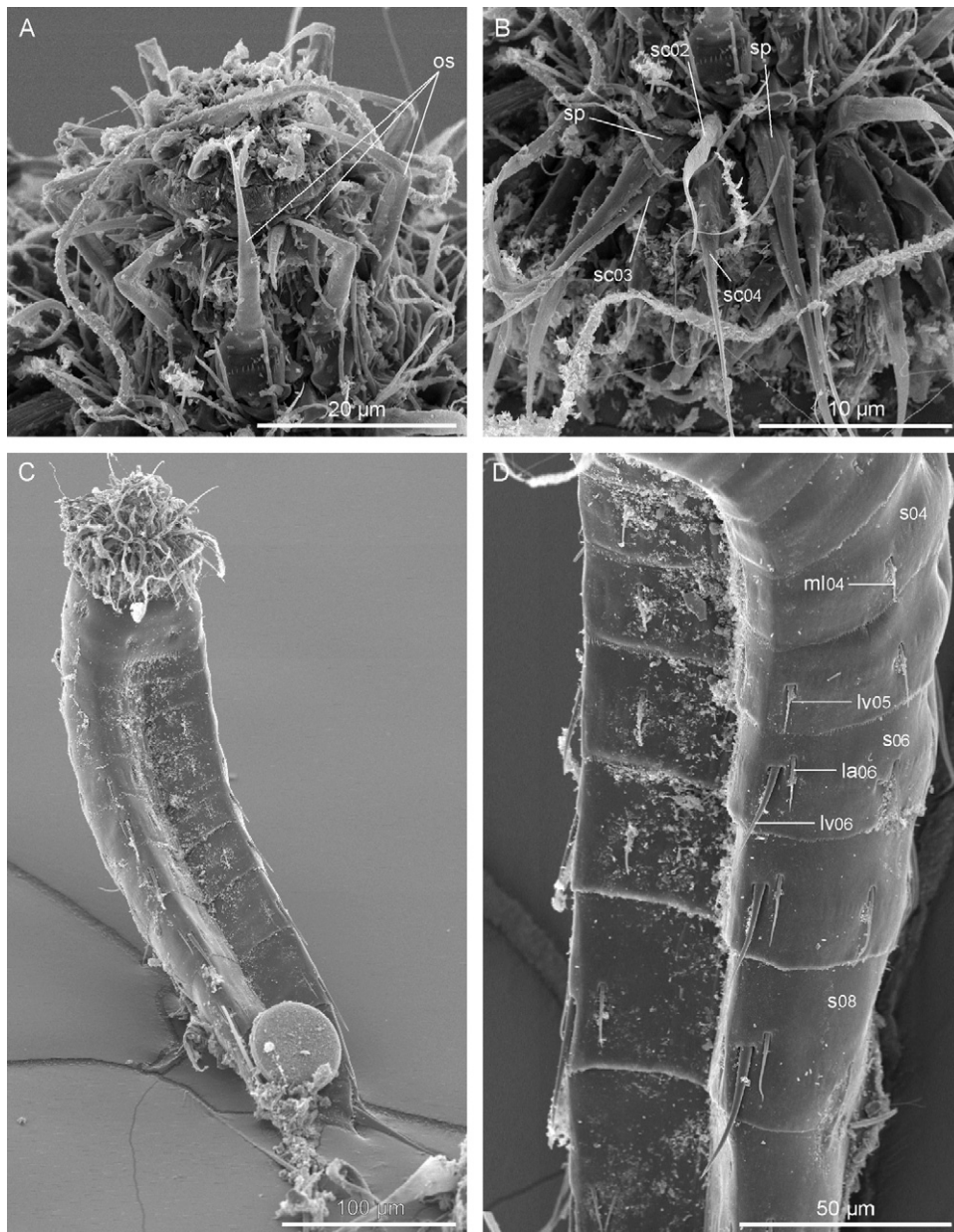
### Diagnosis

Same as genus diagnosis.

### Description

Adult with head, neck and 11 trunk segments (Figs. 1A and B, 2–5). For measurements and dimensions see Table 1; for summary of spine, sensory spot and gland outlet locations see Table 2.

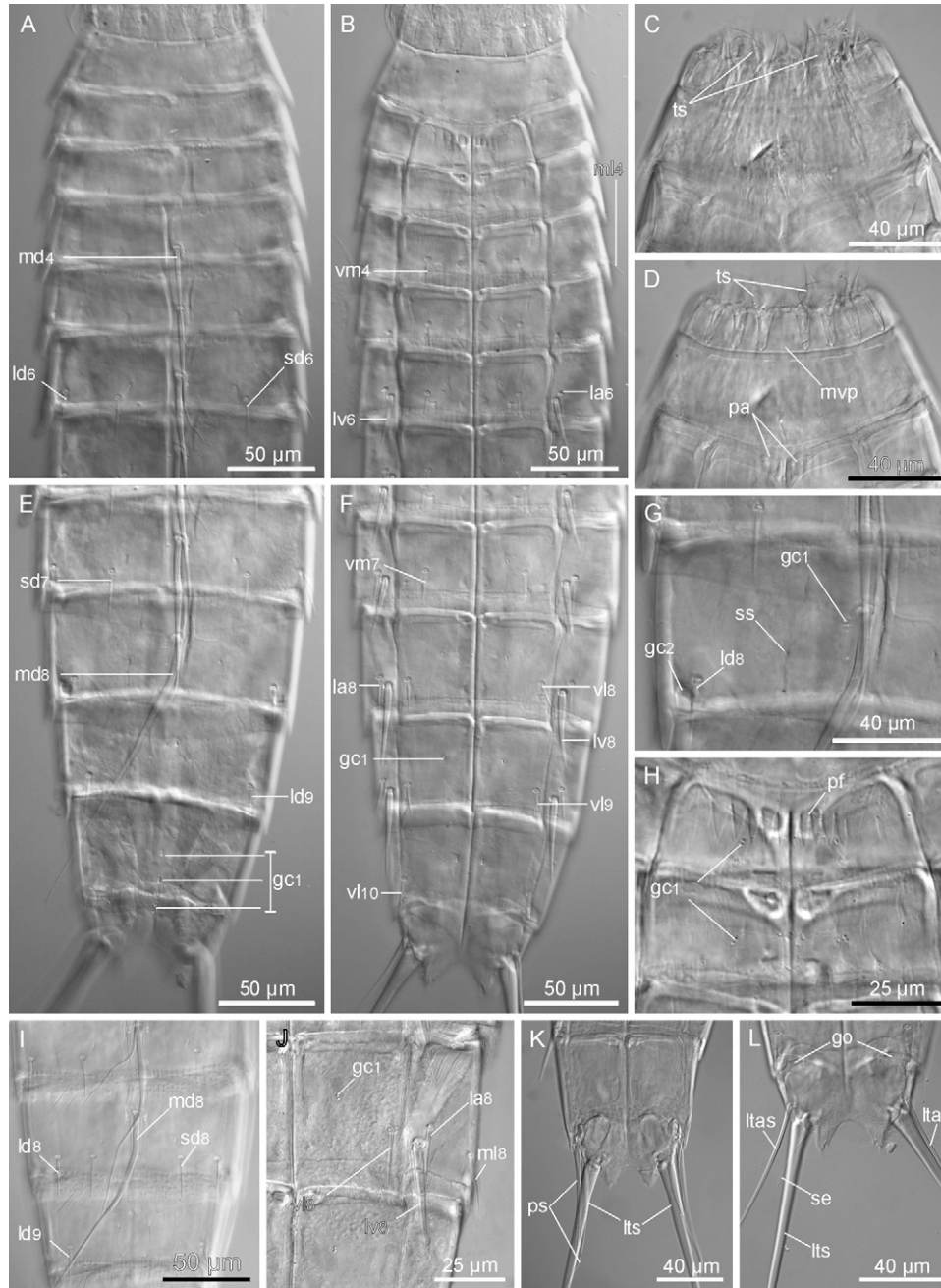
Head consisting of a retractable mouth cone and an introvert (Figs. 2, 4A–C). Outermost ring in mouth cone (ring -01) of 10 inner oral styles. Dirt on terminal parts of mouth cones in all observed specimens prevented further examination of helioscalids and inner oral styles. Nine two-segmented outer oral styles with pointed tips, situated around base of mouth cone (Figs. 2, 3A). Ring 01 of introvert consists of 10 spinoscalids (Fig. 2) that are triangular in cross-section, with pointed tips, equipped with a sheath with dense fringes on its base (Fig. 3B). Ring 02 carries 10 laterally flattened scalids that are conspicuously thin compared to spinoscalids and scalids in following rings (Fig. 3B). Rings 01 and 02 situated



**Fig. 3.** Scanning electron micrographs of *Polacanthoderes martinezi* gen. et sp. nov. (A) Mouth cone and outer oral styles. (B) Introvert section 6 (middorsal). (C) Female, ventrolateral view. (D) Segments 3–9, lateroventral view. Abbreviations: la = lateral accessory spine; lv = lateroventral spine; ml = midlateral spine; os = outer oral styles; s = segment; sc = scalid; sp = spinoscalid. Double digits denote respective introvert ring number (in Fig. 4B) or segment number (in Fig. 4D).

very closely together; scalids of ring 02 appear located almost in between spinoscalids rather than slightly below them. Ring 03 with 10 scalids that are thin and distally pointed, rounded in cross-section, equipped with fringed sheaths at their bases. Ring 03 scalids located pairwise in even-numbered introvert sections (2, 4, 6, 8, 10), missing in odd-numbered sections (Fig. 2). Ring 04 with 15 scalids resembling those in preceding ring. Ring 04 scalids located pairwise in odd-numbered introvert sections; even-numbered sections with single scalid each

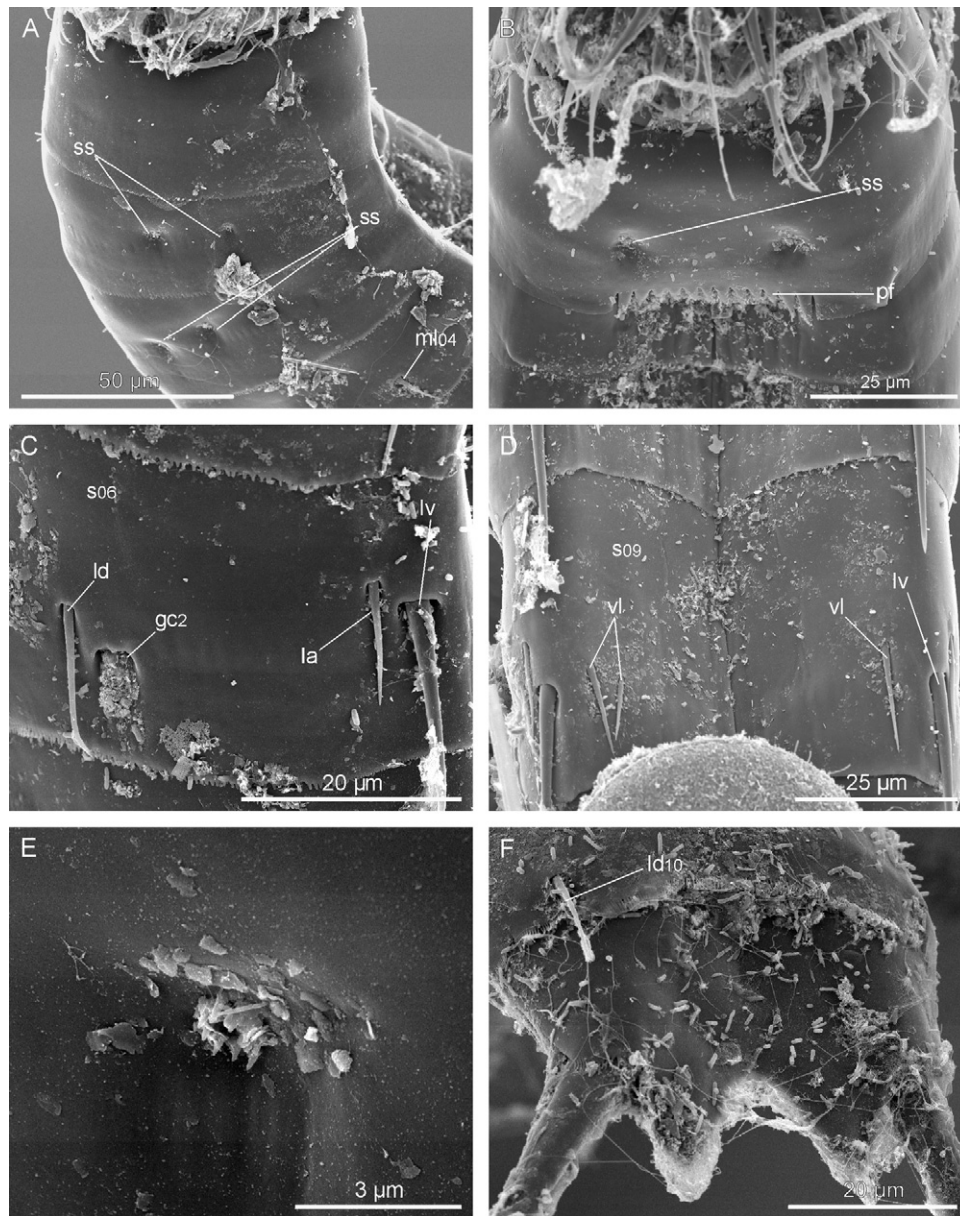
(Fig. 2). Ring 05 with 15 scalids that are shorter and more trichoscalid-like compared to those in preceding rings. Scalids in arrangement opposite to that in ring 04, i.e. pairwise in even-numbered sections, as single scalids in odd-numbered ones. Ring 06 with 15 short scalids arranged as in ring 04 (Fig. 2). Ring 07 with 6 trichoscalids, 1 each in sections 2, 4, 5, 7, 8, 10. All trichoscalids associated with a large trichoscalid plate (Fig. 1A and B). See Fig. 2 for a complete summary of oral style and scalid locations.



**Fig. 4.** Light microscope photos of *Polacanthoderes martinezi* gen. et sp. nov. (A) Segments 1–7, dorsal view. (B) Segments 1–7, ventral view. (C) Neck and first trunk segment, dorsal view. (D) Neck and first segment, ventral view. (E) Segments 7–11, dorsal view. (F) Segments 7–11, ventral view. (G) Segment 8, Detail of tergal plate. (H) Segments 2 and 3, detail of sternal plates. (I) Segments 7–9, dorsal view; note presence of subdorsal spines on segment 8, observed in few specimens only. (J) Segment 8, detail of sternal plate segment; note presence of midlateral spine, observed in this single specimen only. (K) Segments 10 and 11 in male, ventral view. (L) Segment 11 in female, ventral view. Abbreviations: gc1/2 = gland cell opening type 1/2; go = gonopore; la = lateral accessory spine; ld = laterodorsal spine; ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; ml = midlateral spine; mvp = midventral placid; pa = pachycycli; pf = pectinate fringe; ps = penile spine; sd = subdorsal spine; se = seta; ss = sensory spot; ts = trichoscalid; vl = ventrolateral spine; vm = ventromedial spine. Digits following abbreviations denote respective segment numbers.

Neck consisting of 16 placids (Figs. 1A and B, 2, 4C and D). Most placids of equal size, 17–18  $\mu\text{m}$  long, 10–11  $\mu\text{m}$  wide; midventral placid 15–17  $\mu\text{m}$  wide. All placids articulated with trunk segment 1.

Segment 1 consisting of one complete ring (Figs. 1A and B, 3C, 4A–D). Pachycycli simple, inconspicuous. Posterior segment margin on dorsal and lateral sides almost smooth or with inconspicuous serration, on



**Fig. 5.** Scanning electron micrographs of *Polacanthoderes martinezi* gen. et sp. nov. (A) Segments 1–4, lateral view. (B) Segments 1 and 2, ventral view. (C) Segment 6, midlateral part of tergal plate. (D) Segment 9, sternal plates. (E) Middorsal sensory spot on segment 2. (F) Segment 11, dorsal view. Abbreviations: gc2 = gland cell opening type 2; la = lateral accessory spine; ld = lateroventral spine; lv = lateroventral spine; ml = midlateral spine; pf = pectinate fringe; s = segment; ss = sensory spot; vl = ventrolateral spine. Double digits denote respective segment number.

ventral side with very prominent fringe (Figs. 1B, 4H, 5B). Surface of this and the following 10 segments smooth, without cuticular hairs or perforation sites (Fig. 3C and D). Paired sensory spots present in a sublateral and a ventrolateral position (Figs. 1B, 5B), located inside cuticular depressions (see Fig. 5E for corresponding sensory spot on segment 2); each spot consisting of a rounded group of a few relatively thick cuticular papillae. Number of pores could not be observed. Type 1 gland outlets in middorsal position; on this and the following segments appearing as

small, rounded cuticle areas with numerous minute perforations.

Segment 2 and following segments consist of one tergal and two sternal plates (Figs. 1A and B, 3C and D, 4A–H). Lateroventral articulations between tergal and sternal plates, as well as midventral articulation between sternal plates, distinct and complete (Fig. 4H). Anterior and outer lateral pachycycli in sternal plates well-developed, forming prominent loop near antero-medial plate margins (Fig. 4H). Posterior margin of segment with very weakly developed pectinate fringe.

**Table 1.** Measurements of adult *Polacanthoderes martinezi* gen. et sp. nov.

Character	Range	Mean	S.D.	<i>n</i>
TL	447–500 µm	469 µm	20.3 µm	10
SW-10	70–78 µm	75 µm	2.6 µm	12
SW/TL	15–17%	16%	0.6%	10
MSW-6	88–93 µm	91 µm	2.1 µm	11
MSW/TL	18–20%	19%	0.7%	10
S1	41–48 µm	46 µm	2.4 µm	12
S2	41–48 µm	45 µm	2.2 µm	12
S3	45–53 µm	49 µm	2.6 µm	12
S4	50–62 µm	54 µm	3.8 µm	12
S5	50–63 µm	55 µm	3.9 µm	12
S6	56–69 µm	61 µm	4.0 µm	12
S7	57–73 µm	63 µm	4.9 µm	12
S8	67–76 µm	71 µm	3.3 µm	12
S9	62–71 µm	65 µm	2.7 µm	12
S10	60–70 µm	65 µm	3.9 µm	12
S11	43–49 µm	47 µm	2.1 µm	12
MD 4	58–66 µm	62 µm	2.9 µm	10
MD 5	71–81 µm	77 µm	3.5 µm	10
MD 6	93–106 µm	102 µm	4.1 µm	9
MD 7	112–124 µm	118 µm	4.3 µm	11
MD 8	142–154 µm	149 µm	4.0 µm	9
SD 6	20–26 µm	23 µm	2.0 µm	12
SD 7	22–28 µm	25 µm	1.8 µm	12
LD 6	19–23 µm	21 µm	1.2 µm	12
LD 7	20–26 µm	23 µm	1.7 µm	12
LD 8	20–23 µm	22 µm	1.1 µm	11
LD 9	18–24 µm	22 µm	2.0 µm	12
LD 10	13–21 µm	16 µm	2.8 µm	7
ML 4	12–17 µm	14 µm	2.0 µm	9
ML 5	17–23 µm	19 µm	1.9 µm	11
LA 5	13–15 µm	14 µm	0.7 µm	11
LA 6	12–17 µm	15 µm	1.3 µm	12
LA 7	14–19 µm	18 µm	1.6 µm	12
LA 8	16–21 µm	19 µm	1.6 µm	12
LA 9	17–20 µm	18 µm	1.0 µm	12
LV 6	26–39 µm	29 µm	2.3 µm	12
LV 7	29–32 µm	31 µm	1.0 µm	12
LV 8	41–43 µm	42 µm	0.7 µm	12
LV 9	39–49 µm	43 µm	2.6 µm	12
VL 8	16–20 µm	18 µm	1.5 µm	12
VL 9	16–21 µm	19 µm	1.5 µm	12
VL 10	13–23 µm	17 µm	2.6 µm	12
VM 4	12–14 µm	14 µm	0.7 µm	12
VM 5	13–15 µm	14 µm	0.6 µm	12
VM 6	13–16 µm	14 µm	0.8 µm	12
VM 7	15–17 µm	17 µm	0.7 µm	12
PS2 (m)	72–91 µm	80 µm	10.0 µm	3
PS3 (m)	82–97 µm	91 µm	8.1 µm	3
LTS	228–264 µm	248 µm	9.9 µm	12
LTAS (f)	85–97 µm	91 µm	3.1 µm	9
LTS/TL	46–57%	53%	3.8%	10
LTAS/TL	17–22%	20%	1.4%	8
LTAS/LTS	34–39%	36%	1.7%	9

S.D. = standard deviation, *n* = number of specimens measured.

Abbreviations: LA = lateral accessory, LD = laterodorsal, LTAS = lateral terminal accessory spine, LTS = lateral terminal spine, LV = lateroventral, MD = middorsal, ML = midlateral, MSW-6 = maximum sternal width at segment 6, PS1/2 = penile spine 1/2, SD = subdorsal, SW-10 = standard width of segment 10, S1–11 = segment lengths of trunk segments 1–11, TL = trunk length, VL = ventrolateral, VM = ventromedial.

No secondary fringe present on this or any following segment. Sensory spots present in middorsal, subdorsal and laterodorsal positions (Fig. 5A and E); all spots located inside cuticular depressions (Fig. 5E), consist of a ring of cuticular papillae with a central pore. Type 1 gland outlets located in ventromedial position (Fig. 4H).

Segment 3 with one middorsal type 1 gland cell outlet marked by a cuticular depression and consisting of three small pores. One additional pair of type 1 gland cell outlets in ventromedial position (Fig. 4H). Two pairs of sensory spots, resembling those on preceding segment, in somewhat subdorsal position (Fig. 5A); one pair of sensory spots in midlateral position.

Segment 4 with one long, rigid middorsal spine and pair of much shorter midlateral and ventromedial spines (Figs. 1A and B, 3C and D, 4A and B). A pair of sensory spots, similar to those on preceding segment, in subdorsal position. Type 1 gland outlets in paradorsal and ventromedial positions.

Segment 5 with one long, rigid middorsal spine and pairs of much shorter midlateral, lateroventral and ventromedial spines (Figs. 1A and B, 3D, 4A and B). Sensory spots, similar to those on preceding segment, in subdorsal, midlateral and ventromedial positions; midlateral and ventromedial sensory spots very close to bases of spines in corresponding positions. Type 1 gland outlets in paradorsal and ventromedial positions. Antero-medial loops of sternal pachycycli less prominent than those on preceding segments.

Segment 6 with one long, rigid middorsal spine and pair of much shorter subdorsal, laterodorsal, lateral accessory, lateroventral and ventromedial spines (Figs. 1A and B, 3D, 4A and B, 5C). Midlateral spines absent. Subdorsal, laterodorsal, lateral accessory, and ventromedial spines very short, barely reaching posterior segment margin; lateroventral spines clearly longer and stronger, reaching beyond segment margin (Fig. 3D). A pair of sensory spots present in subdorsal position. Laterodorsal sensory spots absent, but a large type 2 gland cell outlet present in corresponding position (Fig. 5C). Type 2 gland cell outlets on this and the following segments are large openings with strong, folded anterior and anterolateral edges. Type 1 gland outlets in paradorsal and ventromedial positions.

Segment 7 spine pattern similar to that on segment 6 (Figs. 1A and B, 3D, 4E and F). Sensory spots in subdorsal, laterodorsal and ventromedial positions; ventromedial sensory spot slightly posterior to ventromedial spine. Type 1 gland outlets in paradorsal and ventromedial positions.

Segment 8 with one long, rigid middorsal spine and pairs of shorter laterodorsal, lateral accessory, lateroventral and ventrolateral spines (Figs. 1A and B, 3D, 4E–G). Subdorsal and ventromedial spines apparently absent in most specimens, but segment shows some intraspecific variation: three specimens (two females, one



**Table 2.** Summary of nature and location of sensory spots, pores, spines and tubules arranged by series in *Polacanthoderes martinezi* gen. et sp. nov.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gc1					ss			ss	
2	ss		ss	ss						gc1
3	gc1		ss, ss		ss					gc1
4	ac	gc1	ss		ac					ac, gc1
5	ac	gc1	ss		ac, ss			ac		ac, ss, gc1
6	ac	gc1	ac, ss	ac, gc2			ac	ac		ac, gc1
7	ac	gc1	ac, ss	ac, ss			ac	ac		ac, ss, gc1
8	ac	gc1	ss	ac, gc2			ac	ac	ac, ss	gc1
9		gc1		ac			ac	ac	ac, ss	gc1
10	gc1 gc1			ac					ac	gc1
11	gc1 gc1						ltas (f)	lts		se

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 sexually dimorphic character, gc1/2 = gland cell type 1/2, ltas = lateral terminal accessory spine, lts = lateral terminal spine, se = seta, ss = sensory spot.

male) have also one pair of subdorsal spines (Fig. 4I); another female has one pair of midlateral spines (Fig. 4J). Furthermore, one female carries one additional laterodorsal spine on right body side. Paired sensory spots in the subdorsal (Fig. 4G) and ventrolateral positions; pair of large type 2 gland outlets in the laterodorsal position (Fig. 4G). Type 1 gland outlets in paradorsal (Fig. 4G) and ventromedial positions. Anterior pachycycli of sternal plates well-developed; lateral pachycycli on this and the following segments much more indistinct.

Segment 9 and the remaining two segments without middorsal spine (Figs. 1A, 4E). Other, shorter spines present in laterodorsal, lateral accessory, lateroventral and ventrolateral positions (Figs. 1A and B, 4E, F and I). One specimen with one additional laterodorsal spine on left body side; another specimen with one additional ventrolateral spine on right body side (Fig. 5D). Sensory spots found in a ventrolateral position only. Type 1 gland outlets in paradorsal and ventromedial positions. No sieve plate or traces of protonephridial openings detected.

Segment 10 with one pair of minute laterodorsal and ventrolateral spines (Figs. 1A and B, 4F, 5F). Lateral accessory and lateroventral spines absent. Sensory spots not observed. Posterior fringes on sternal plates slightly stronger than on preceding segments. Two type 1 gland outlets in a middorsal position (Fig. 4E), one pair in a ventromedial position close to midventral line.

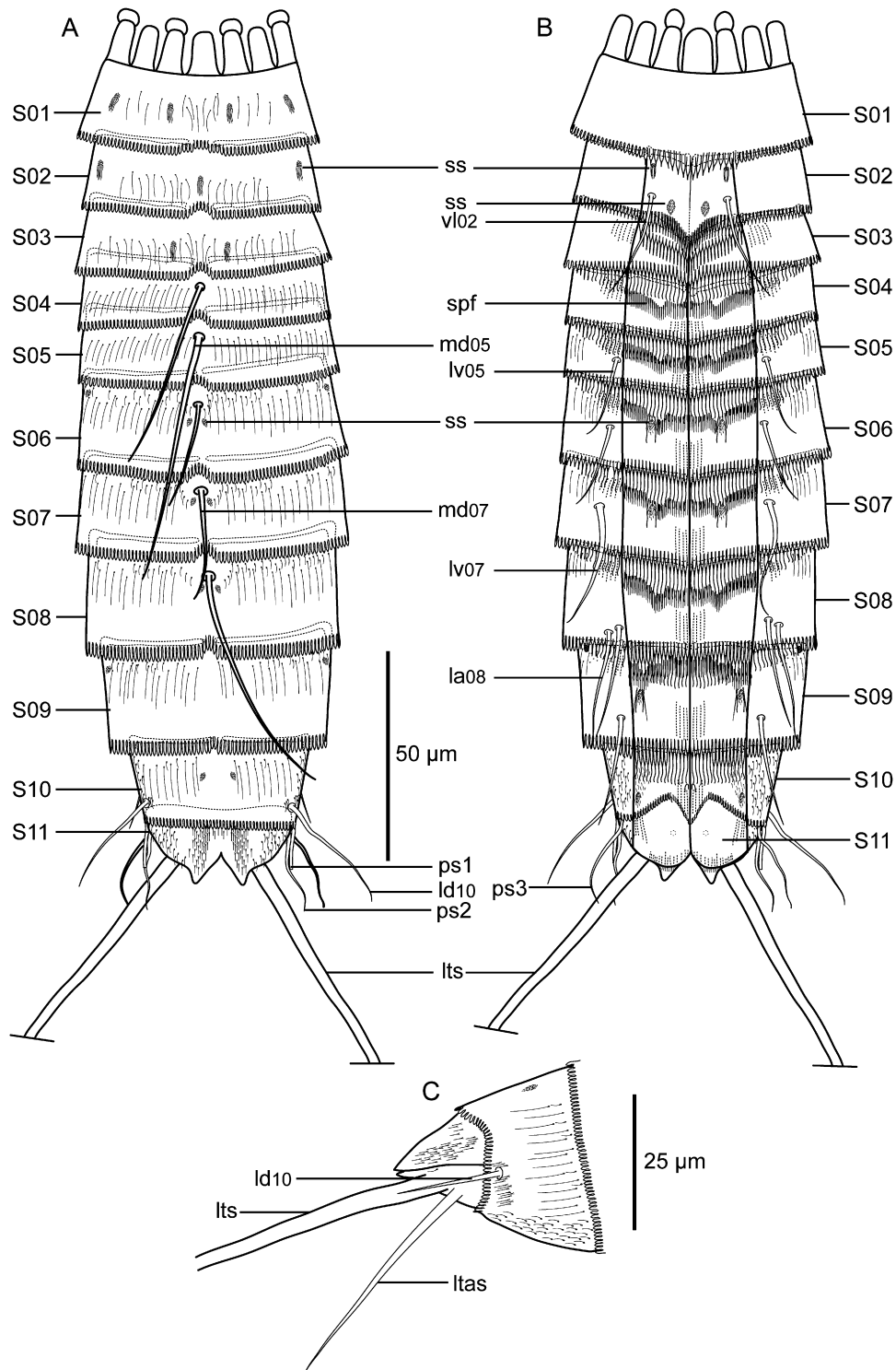
Segment 11 with weakly developed pachycycli. Tergal and sternal posterior extensions triangular or cone-shaped, resemble each other (Figs. 1, 4F–L, 5F). Tergal extensions slightly longer, extending beyond sternal extensions. Two closely set type 1 gland outlets in a middorsal position (Fig. 4E). No sensory spots found.

One pair of lateral terminal spines present in both sexes. In addition, females with one pair of lateral terminal accessory spines (Figs. 1A and B, 4L). Some females also with pair of thin, long setae (ca. 35 µm) originating near outer bases of sternal extensions (Fig. 4L); these setae break off easily, thus their presence/absence in males could not be evaluated conclusively. Males without lateral terminal accessory spines, but with two long, flexible penile spines (Figs. 1C and D, 4K).

#### Notes on diagnostic features

The combination of segment 1 forming a closed ring, the following segments being composed of a tergal and two sternal plates, presence of aligned middorsal spines and lateral terminal spines, and absence of a midterminal spine suggests close relations with the echinoderid genera *Cephalorhyncha*, *Fissuroderes* and *Echinoderes*. Hence, the new genus and species can be assigned to the family Echinoderidae. Its exact position in the family is addressed in a separate phylogenetic analysis (Sørensen 2008, this issue).

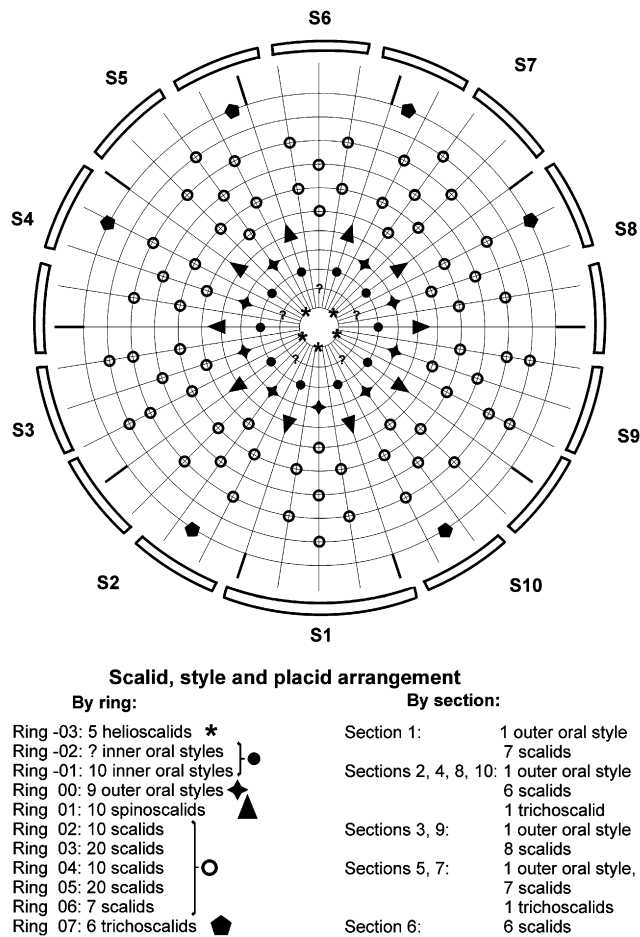
Within Echinoderidae, *Polacanthoderes martinezi* gen. et sp. nov. shares the complete division of the sternal plates of segment 2 with species of *Fissuroderes* only (see Neuhaus and Blasche 2006). However, *P. martinezi* is easily discriminated from species of *Fissuroderes* and any other known kinorhynch genus by the presence of serial spines in various unusual positions. Paired spines in the subdorsal and/or laterodorsal positions are found in some species of *Echinoderes* – e.g. in *E. cantabricus* Pardos et al., 1998; *E. hispanicus* Pardos et al., 1998; *E. intermedius* Sørensen, 2006; *E. newcaledoniensis* Higgins, 1967; *E. peterseni* Higgins & Kristensen, 1988; and *Fissuroderes higginsii* Neuhaus & Blasche, 2006 (Higgins 1967; Higgins and Kristensen 1988; Pardos et al. 1998; Neuhaus and Blasche 2006;



**Fig. 6.** *Cephalorhyncha liticola* sp. nov. (A) Male, dorsal view. (B) Male, ventral view. (C) Female, trunk segments 10 and 11, lateral view. Abbreviations: la = lateral accessory spine; ld = laterodorsal spine; ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; ps<sub>1/2/3</sub> = penile spine 1/2/3; S = segment; spf = secondary pectinate fringe; ss = sensory spots; vl = ventrolateral spine. Double digits denote respective segment number.

Sørensen 2006) – but in these species such spines are always restricted to the second trunk segment. Only *E. capitatus* (Zelinka, 1928) possesses sublateral spines

elsewhere, i.e. on segments 6, 7 and 9 (Zelinka 1928; Nebelsick 1992), but since this species otherwise fits well within *Echinoderes*, its spine pattern must be considered



**Fig. 7.** Diagram of mouth cone, introvert and placids in *Cephalorhyncha liticola* sp. nov. indicating distribution of oral styles, scalids and placids (curved bars around introvert diagram).

as a result of convergent evolution. To the present author's knowledge, midlateral and ventrolateral spines on any segment other than the second have not been found in any other echinoderid kinorhynch, and ventromedial spines have been reported only from segment 8 in *E. capitatus*. In contrast, *Polacanthoderes martinezi* gen. et sp. nov. has ventromedial spines on segments 4–7.

## Genus *Cephalorhyncha* Adrianov, 1999

### *Cephalorhyncha liticola* sp. nov.

(Figs. 6–11; Tables 3, 4)

### Etymology

The species name is derived from Latin “*litus*” = beach and “*-cola*” = dweller, thus is to be treated as a noun in apposition for the purposes of nomenclature.

### Material examined

USA, Hawaii, northeast coast of Oahu, upper part of tidal zone between Kaluanui Beach and Kapaka Beach, 21°36.369'N, 157°54.369'W; 19 February 2006. Deposited at Zoological Museum, University of Copenhagen, Denmark.

Holotype: Adult male, mounted in Fluoromount G<sup>®</sup> (ZMUC KIN-205). Paratypes: allotype adult female, mounted in lateral aspect in Fluoromount G<sup>®</sup> (ZMUC KIN-206); adult male, mounted in Fluoromount G<sup>®</sup> (ZMUC KIN-207).

Additional material: Two adult males mounted for SEM.

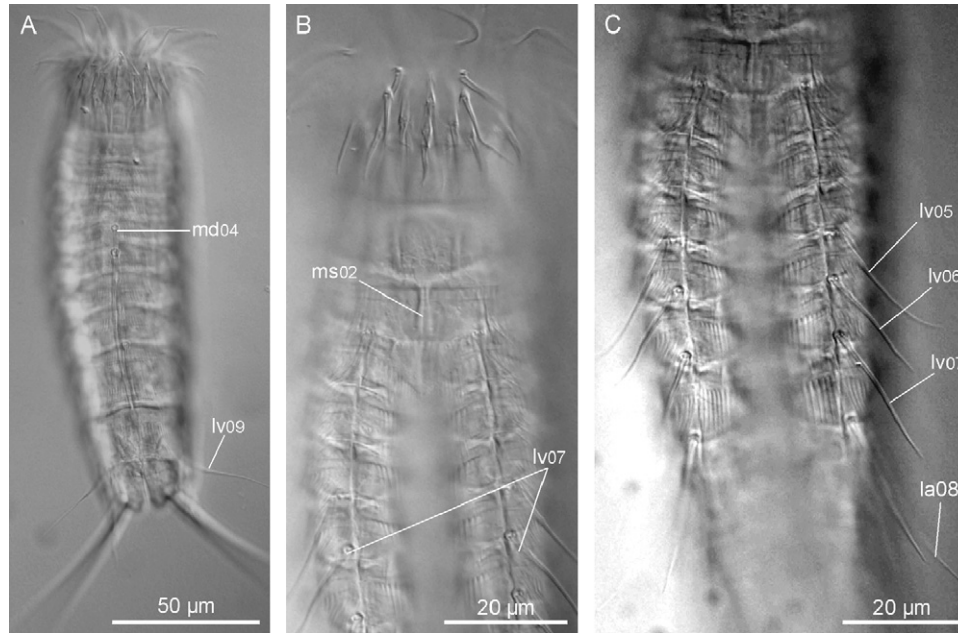
### Diagnosis

Cuticle of first trunk segment forming complete ring. Cuticle of segment 2 forming one tergal and one sternal plate, the latter incompletely separated anteriorly by a midventral fissure. Cuticle of segments 3–11 with midventral and lateroventral articulations resulting in one tergal and two sternal plates per segment. Mid-dorsal spines present on segments 4–8; ventrolateral spines on segment 2; lateroventral spines on segments 5–9; lateral accessory spines on segment 8; laterodorsal spines on segment 10; lateral terminal spines (in both sexes) and lateral terminal accessory spines (in females only) on segment 11. Sensory spots with conspicuous marginal cuticular hairs in subdorsal and laterodorsal positions on segment 1, middorsal and laterodorsal positions on segment 2, and in a subdorsal position on segment 3. Cuticular hairs and perforation sites mostly present on tergal plates on segments 1–9. Sternal plates on segments 3–10 with conspicuously long pectinate fringes.

### Description

Adult with head, neck and 11 trunk segments (Figs. 5–11). For measurements and dimensions see Table 3; for summary of spine and sensory spot locations see Table 4.

Head consisting of a mouth cone and an introvert with seven rings of scalids (Figs. 7, 8A and B, 9A and B, 11A). Innermost ring (ring-03) of mouth cone consisting of 5 helioscalids, outermost ring (ring-01) with 10 inner oral styles (Fig. 7). Inner oral styles of ring-02 could not be examined in any prepared specimen. Ring 00 consisting of 9 two-segmented outer oral styles with pointed tips. Ring 01 consists of 10 spinoscalids (Fig. 7), each equipped with a basal fringe with 7 short spines, followed by two lateral, much longer spines and a median group with another 4 spines (Fig. 11A). Ring 02 with 10 scalids; ring very close to the preceding one, thus ring 02 scalids appear as if located in between spinoscalids rather than slightly below them (Fig. 11A). All scalids in ring 02 with a sheath wrapped around their proximal halves; sheath terminating in a distal



**Fig. 8.** Light microscope photos of *Cephalorhyncha liticola* sp. nov. (A) Overview of male, dorsal view. (B) Segments 1–7, ventral view. (C) Segments 2–9, ventral view. Abbreviations: la = lateral accessory spine; lv = lateroventral spine; md = middorsal spine; ms = midsternal articulation. Double digits denote respective segment number.

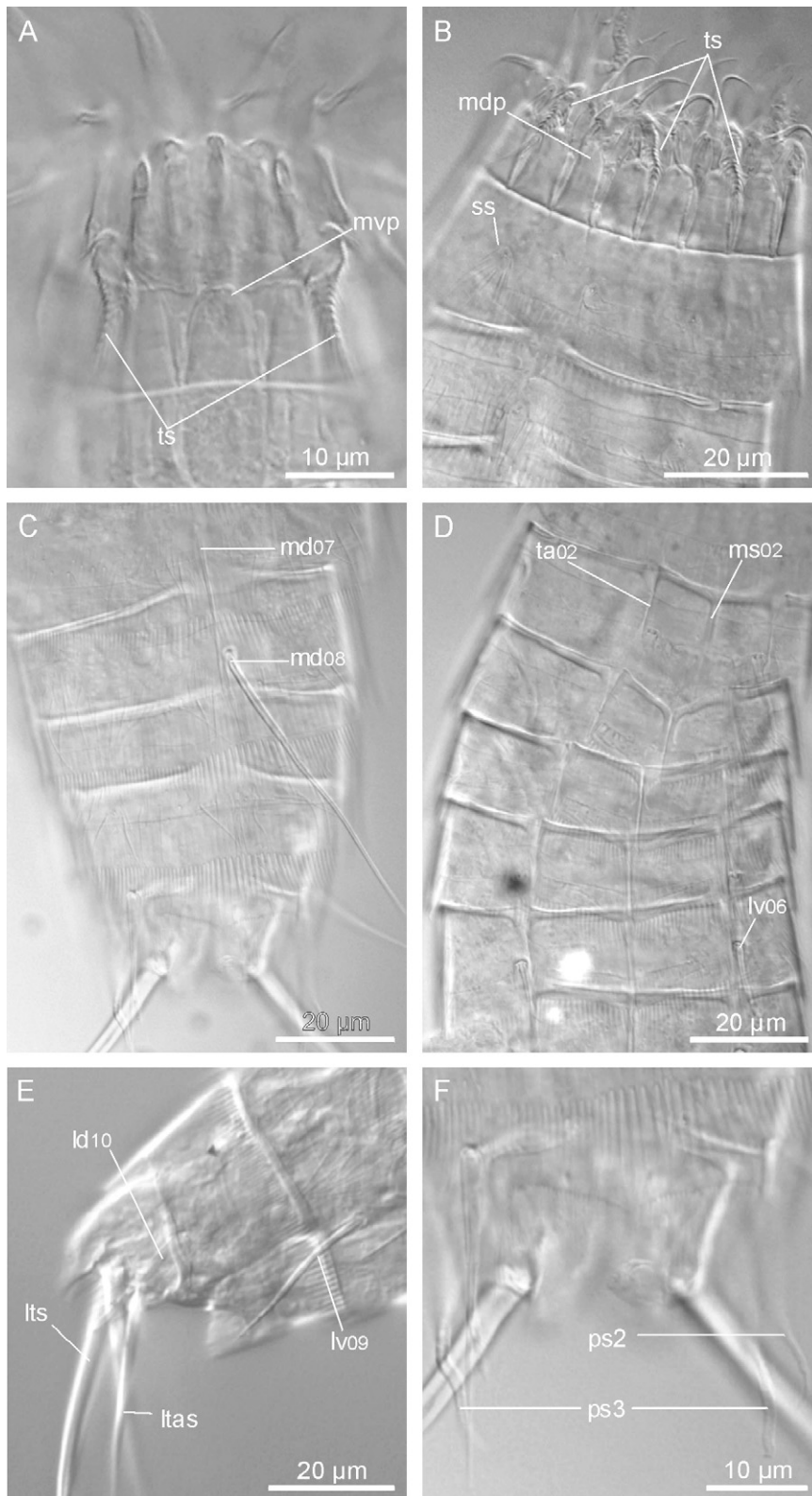
fringe. Rings 03, 04 and 05 with 20, 10 and 20 scalids, respectively; hence each introvert section has 2 ring 03 scalids, 2 ring 05 scalids, and 1 ring 04 scalid (Fig. 7). All scalids in rings 03–05 resembling those of ring 02. Ring 06 with 7 scalids only: 1 each in sections 1, 5, 7, and 2 each in sections 3 and 9 (Fig. 7). Scalids of ring 06 shorter than those of preceding rings; sheath covers only most basal part of each scalid. Ring 07 with 6 trichoscalids in sections 2, 4, 5, 7, 8 and 10 (Figs. 7, 9A and B, 11A); trichoscalids absent from sections 6, 1, 3 and 9, but presence of small fringed plates in the latter three sections may indicate positions of secondarily reduced trichoscalids; orientation of investigated specimens did not allow examination of section 6 for presence of such fringed plates. See Fig. 7 for a complete summary of oral style, scalid and placid locations.

Neck consisting of 16 distinct, well defined placids with conspicuously rounded distal corners (Figs. 6A and B, 7, 9A and B, 11B). Most placids of uniform size, 8–9 µm long, 5 µm wide at their bases; midventral placid slightly wider: 7 µm at its base. Proximally, placids articulated with first trunk segment through well defined joins (Fig. 11B).

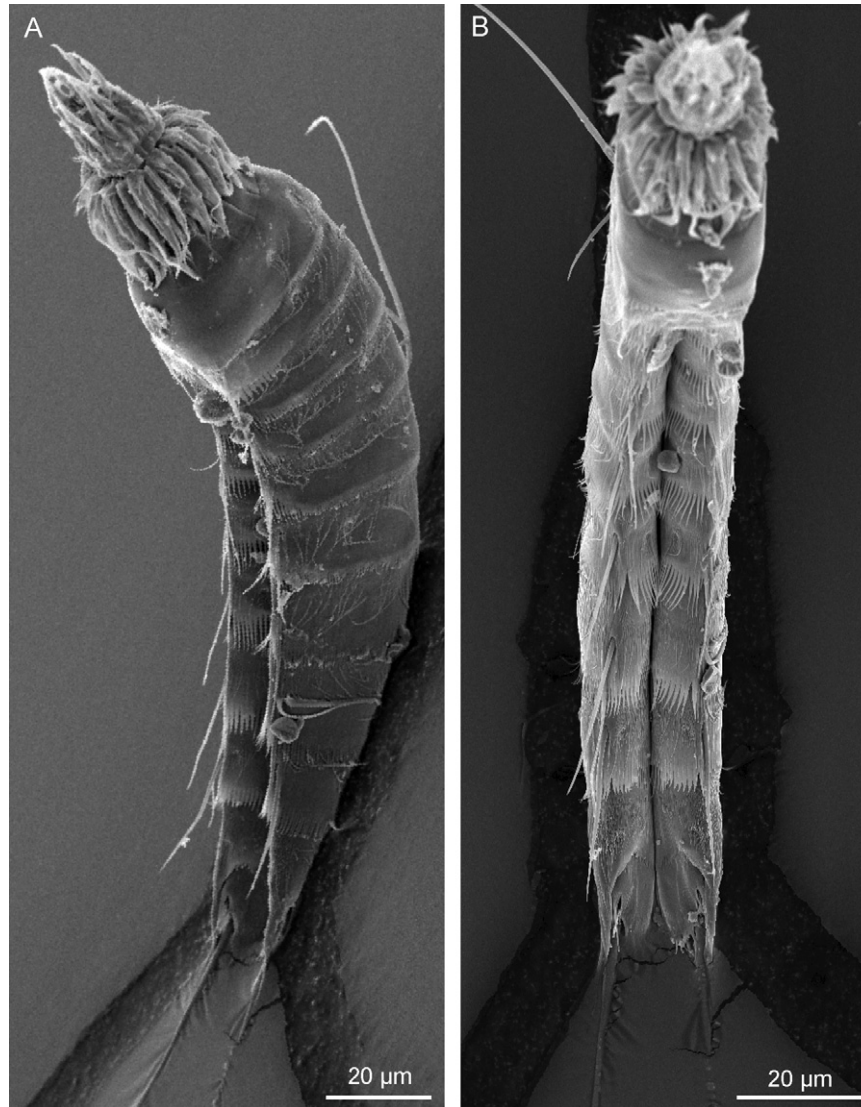
Segment 1 consisting of one complete ring. This and the following nine segments laterally compressed, generally higher than wide (Fig. 10). Posterior segment margin with well-defined pectinate fringe (Fig. 11B and C). A few cuticular hairs present on dorsal and laterodorsal parts of segment only; hairs relatively long, flexible in appearance, extending through rounded

perforation sites. A pair of subdorsal and laterodorsal sensory spots present (Figs. 6A, 9B, 11B); spots relatively large, roundish or slightly oval, consisting of numerous cuticular papillae; number of pores could not be determined; margin of posterior half of each sensory spot always flanked by a group of long cuticular hairs (Figs. 9B, 11B).

Segment 2 consisting of one tergal and one sternal plate; the latter incompletely subdivided by indistinct midventral articulation (Figs. 6B, 8B, 9D); division most conspicuous in anterior part of segment, anterior pachycyclus clearly divided. Lateroventral articulations between tergal and sternal plate well-defined, but articulation sites without posteriorly extending projections. Pair of flexible ventrolateral spines present (Figs. 6B, 11C). Large, droplet-shaped sensory spot with numerous cuticular papillae in middorsal position (Fig. 11C); additional sensory spots in laterodorsal, ventrolateral and ventromedial positions; laterodorsal spots close to anterior segment margin, thus can be partly covered by preceding segment (Fig. 11B). Spots rounded to oval, with long marginal cuticular hairs. Ventrolateral sensory spots very small, long hairs almost covering papillated central parts of spots (Fig. 11C and D). Ventromedial sensory spots large, with numerous cuticular papillae but no marginal hairs (Fig. 11C). Long, flexible cuticular hairs present on tergal plate, but only close to anterior segment margin. Sternal plate with cuticular hairs around ventrolateral sensory spots only. Pectinate fringe on posterior segment margin well-developed (Fig. 11C).



**Fig. 9.** Light microscope photos of *Cephalorhyncha liticola* sp. nov. (A) Introvert and placids in male, ventral view. (B) Placids and segments 1 and 2 in male, dorsal view. (C) Segments 7–11 in male, dorsal view. (D) Segments 1–6 in male, ventral view. (E) Segments 9–11 in female, lateral view. (F) Terminal segment in male, dorsal view. Abbreviations: ld = laterodorsal spine; ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; mdp = middorsal placid; ms = midsternal articulation;.mvp = midventral placid; ps2/3 = penile spine 2/3; ss = sensory spot; ta = tergal-sternal articulation; ts = trichoscalid. Double digits denote respective segment number.



**Fig. 10.** Scanning electron micrographs of male *Cephalorhyncha liticola* sp. nov. (A) Lateroventral view. (B) Ventral view.

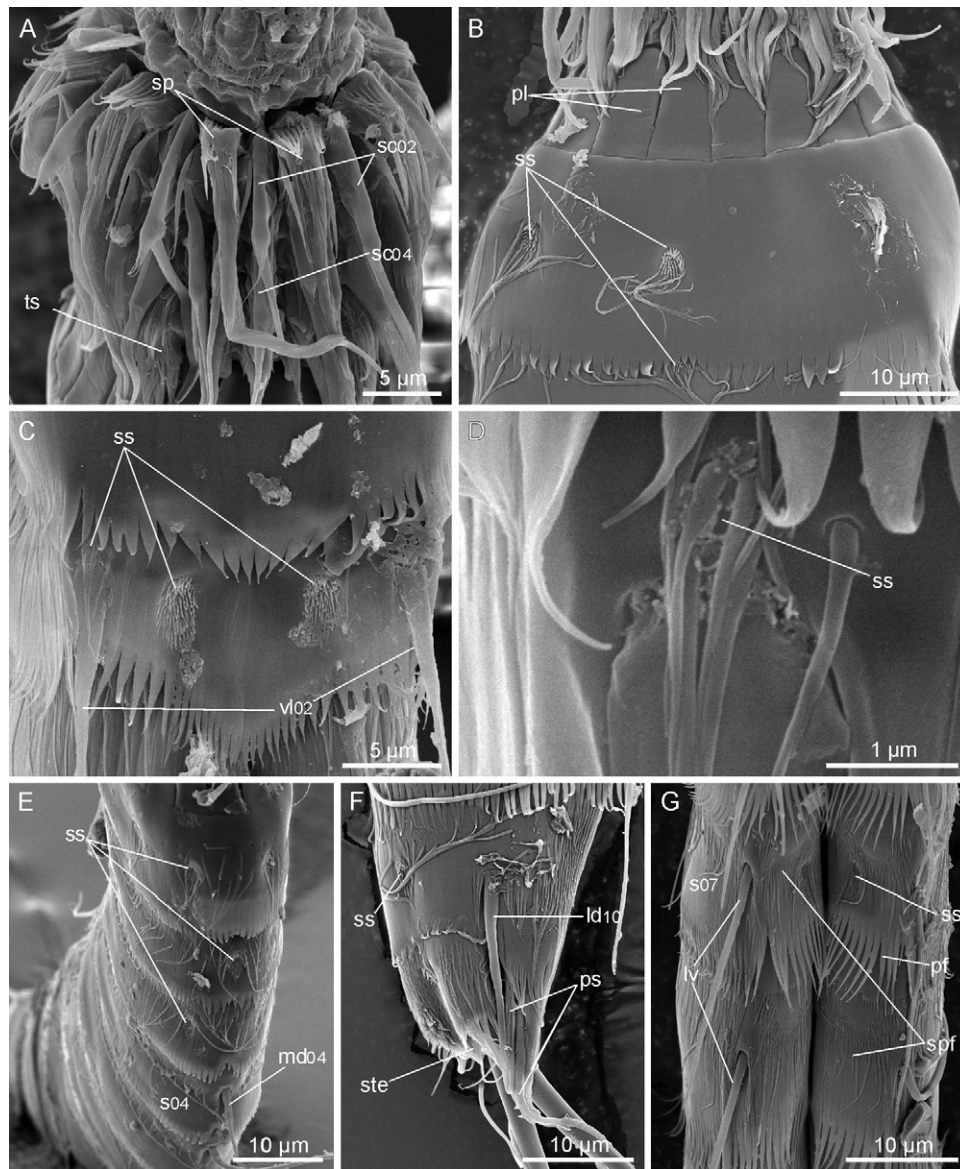
Segment 3 and following segments each consisting of one tergal and two sternal plates (Figs. 6A and B, 8A, 10). Spines absent, but pair of large, wedge-shaped sensory spots present in subdorsal position (Fig. 11E). Sensory spots with numerous long cuticular papillae and marginal hairs. Cuticular hairs present near anterior segment margin of tergal plate. Sternal plates without hairs, but with unusually strong secondary fringe on anterior halves of plates forming long, hair-like extensions (Fig. 6B; see also Fig. 11G for corresponding secondary fringes on segments 7 and 8). Posterior margin of tergal plate with regular fringe; fringes of sternal plates forming long spinous projections.

Segment 4 with one long, slightly flexible middorsal spine (Figs. 6A, 8A, 11E). Sensory spots absent. Cuticular hairs and fringes similar to those on preceding segment.

Segment 5 with one long, slightly flexible middorsal spine and pair of lateroventral flexible spines or tubules (Figs. 6B, 8C). Otherwise, segment similar to the preceding one.

Segment 6 with one middorsal spine and pair of lateroventral acicular spines (Figs. 6A and B, 8C, 9D). Sensory spots in paradorsal, midlateral and ventromedial positions. Paradorsal and midlateral sensory spots wedge-shaped, apparently without marginal cuticular hairs. Ventromedial sensory spots droplet- to wedge-shaped, with lateral marginal hairs. Cuticular hairs and fringes similar to those on preceding segment.

Segment 7 with one middorsal spine and pair of lateroventral acicular spines (Figs. 6A and B, 8B and C, 11G). Sensory spots in paradorsal and ventromedial positions (Fig. 11G), resembling those in corresponding positions on preceding segment. Cuticular hairs and fringes (Fig. 11G) similar to those on preceding segment.



**Fig. 11.** Scanning electron micrographs of male *Cephalorhyncha liticola* sp. nov. (A) Ventral view showing introvert sections 2, 1 and 10. (B) Placids and segment 1, lateral view. (C) Segment 2, ventral view. (D) Very small ventrolateral sensory spot near anterior margin of sternal plate on segment 2. (E) Segments 1–4, dorsolateral view. (F) Segments 10 and 11, lateral view. (G) Segments 7 and 8, ventral view. Abbreviations: ld = laterodorsal spine; lv = lateroventral spine; md = middorsal spine; pf = pectinate fringe; pl = placids; ps = penile spines; s = segment; sc = scapularia; sp = spinoscalid; spf = secondary pectinate fringe; ss = sensory spot; ste = sternal extensions; ts = trichoscalid; vl = ventrolateral spine. Double digits denote introvert ring number (in Fig. 10A) or segment number (in Fig. 10C–G).

Segment 8 with one middorsal spine, pair of lateroventral acicular spines, and pair of longer, more flexible lateral accessory spines (Figs. 6A and B, 8C, 9C, 11G). Sensory spots in paradorsal position only. Cuticular hairs and fringes similar to those on preceding segment.

Segment 9 and remaining two segments without middorsal spines, each with pair of lateroventral spines (Figs. 6B, 8A). Pairs of wedge-shaped sensory spots in midlateral and ventromedial positions. Pair of sieve plates covering protonephridial openings in sublateral

position near anterior margin of segment. Cuticular hairs and fringes similar to those on preceding segment.

Segment 10 with one pair of laterodorsal spines (Figs. 6A and C, 9E, 11F). Lateroventral spines absent. Wedge-shaped sensory spots in paradorsal (Fig. 11F) and ventromedial positions. Lateral sides of tergal plate covered by areas of densely set cuticular hairs. Additionally, lateral sides of laterodorsal spine attachment sites flanked by two areas with hairs (Fig. 11F). Otherwise, cuticular hairs restricted to area near anterior margin of tergal plate. Tergal plate terminating

**Table 3.** Measurements of two male and one female *Cephalorhyncha liticola* sp. nov.

Character	ZMUC KIN-205 Male holotype	ZMUC KIN-206 Female allotype	ZMUC KIN-207 Male paratype
TL	185 µm	210 µm	127 µm
SW-10	30 µm	29 µm	26 µm
SW/TL	16%	18%	20%
MSW-8	37 µm	31 µm	26 µm
MSW/TL	20%	15%	20%
S1	20 µm	19 µm	11 µm
S2	19 µm	19 µm	14 µm
S3	17 µm	22 µm	13 µm
S4	17 µm	22 µm	13 µm
S5	17 µm	27 µm	12 µm
S6	23 µm	28 µm	13 µm
S7	20 µm	29 µm	14 µm
S8	28 µm	31 µm	17 µm
S9	31 µm	32 µm	23 µm
S10	23 µm	27 µm	21 µm
S11	20 µm	23 µm	20 µm
MD 4	–	45 µm	33 µm
MD 5	–	77 µm	56 µm
MD 6	24 µm	–	–
MD 7	29 µm	–	–
MD 8	57 µm	–	52 µm
VL 2	26 µm	–	–
LV 5	–	–	26 µm
LV 6	20 µm	18 µm	21 µm
LV 7	27 µm	26 µm	26 µm
LV 8	32 µm	27 µm	27 µm
LV 9	30 µm	28 µm	26 µm
LA 8	29 µm	33 µm	34 µm
LD 10	32 µm	20 µm	32 µm
PS1 (m)	16 µm	n/a	11 µm
PS2 (m)	23 µm	n/a	22 µm
PS3 (m)	28 µm	n/a	34 µm
LTS	–	149 µm	131 µm
LTAS (f)	n/a	45 µm	n/a
LTS/TL	–	71%	103%
LTAS/TL	n/a	21%	n/a
LTAS/LTS	n/a	30%	n/a

Abbreviations: LA = lateral accessory spine, LD = laterodorsal spine, LTAS = lateral terminal accessory spine, LTS = lateral terminal spine, LV = lateroventral, MD = middorsal, MSW = maximum sternal width at segment 8, PS1–3 = penile spines 1–3, SW-10 = standard width of segment 10, S1–11 = segment lengths of trunk segments 1–11, TL = trunk length, VL = ventrolateral; (f) = female, (m) = male condition of sexually dimorphic characters; n/a = not applicable; – = could not be measured.

in posterior fringe as on preceding segments. Sternal plates also with posterior fringes, but the latter much less developed than on preceding segments.

Segment 11 apparently consisting of one tergal and two sternal plates; possible subdivision of tergal plate could not be evaluated conclusively. Tergal and sternal

**Table 4.** Summary of nature and location (Pos. = position; Seg. = segment) of sensory spots, pores, spines and tubules arranged by series in *Cephalorhyncha liticola* sp. nov.

Pos. Seg.	MD	PD	SD	LD	ML	LA	LV	VL	VM
1			ss	ss					
2	ss			ss				ac, ss	ss
3			ss						
4	ac								
5	ac						ac/tu		
6	ac	ss			ss		ac		ss
7	ac	ss					ac		ss
8	ac	ss				ac	ac		
9					ss		ac		ss
10		ss		ac					ss
11						ltas (f)	lts		

Abbreviations: LA = lateral accessory, LD = laterodorsal, LV = lateroventral, MD = middorsal, ML = midlateral, PD = paradorsal, SD = subdorsal, VL = ventrolateral, VM = ventromedial; ac = acicular spine, (f) = female condition of sexually dimorphic character, ltas = lateral terminal accessory spine, lts = lateral terminal spine, ss = sensory spot, tu = tubule.

plates terminating in rounded extensions; tergal extensions slightly longer, extending beyond sternal extensions. Pair of lateral terminal spines present in both sexes; females with additional pair of lateral terminal accessory spines (Figs. 6C, 9E). Males with three pairs of penile spines (Figs. 6A and B, 9F, 11F); one pair short, rigid and stubby, the others longer, pointed, much more flexible.

#### Notes on diagnostic features

The presence of a second trunk segment consisting of one tergal plate and one sternal plate that is partly subdivided into two substernites shows the new species to belong to the echinoderid genus *Cephalorhyncha*. Currently, this genus contains only two other species: *C. asiatica* (Adrianov, 1989) and *C. nybakkeni* (Higgins, 1986) (Adrianov and Malakhov 1999; Neuhaus and Blasche 2006). *Cephalorhyncha nybakkeni* was described from a high energy beach in California and has not been recorded since. The species inhabits the same kind of habitat as *C. liticola* sp. nov., i.e. the marine pore water around the mid-tide level on sandy beaches (Higgins 1986). However, *C. nybakkeni* and *C. liticola* sp. nov. are easily separated by the lateral accessory spines on segment 8 present in *C. liticola* sp. nov. but lacking in *C. nybakkeni*.

*Cephalorhyncha asiatica* was described from estuarine mud at 8 m depth (Adrianov 1989; Adrianov and Malakhov 1999), hence its habitat differs significantly from that of *C. liticola* sp. nov. and *C. nybakkeni*. The spine formulas of *C. liticola* sp. nov. and *C. asiatica* are identical, but the two species can be discriminated by



other features. The most distinct difference concerns the lateroventral articulations between the tergal and sternal plate on segment 2. In *C. liticola* sp. nov. the plates meet in a regular articulation, whereas in *C. asiatica* the articulation zone extends posteriorly so that it forms a long, spinous caudal projection. Moreover, *Cephalorhyncha liticola* sp. nov. possesses a pair of very large and prominent sensory spots on segment 10 that are lacking in *C. asiatica*. *Cephalorhyncha asiatica*, in turn, has a pair of prominent paradorsal sensory spots on segment 9 and pairs of ventromedial type 1 gland cell outlets on segments 2–10; both features are absent in *C. liticola*. *Cephalorhyncha asiatica* also lacks conspicuous marginal cuticular hairs around the large sensory spots on the anteriormost segments. These hairs are easily observable with a light microscope; thus, their absence in *C. asiatica* can be confirmed here.

## Acknowledgements

I am indebted to Pedro Martinez Arbizu and the staff at the Senckenberg Institute in Wilhelmshaven, Germany, for inviting me to come and work on their exciting collection of Antarctic kinorhynchs from the ANDEEP-1 cruise. Mark Q. Martindale and Andreas Hejnal are highly acknowledged for offering work facilities at the Kewalo Marine Laboratory, and Reinhardt M. Kristensen and Katrine Worsaae for assistance during collecting and sorting of material on Hawaii. I thank Birger Neuhaus and Fernando Pardos for valuable discussions, and B. Neuhaus for kindly providing specimens of *Cephalorhyncha* and *Fissuroderes* from the Museum für Naturkunde in Berlin. Oliver Coleman, also from MfN, made the invaluable effort to introduce me to the digital inking techniques that enabled me to make much better habitus drawings than I usually do. The Zoological Museum, University of Copenhagen, provided access to scanning electron microscope facilities. Funding was provided by the Danish Natural Science Research Council (Grant nos. 21-04-0331 and 21-04-0047). The compound microscope, camera lucida and imaging software were funded by the Carlsberg Foundation (Grant no. 2005-1-545) and the Novo Nordisk Foundation. The project was supported by the Census of Abyssal Marine Life “CeDAMar”. This is AndEEP publication # 104.

## References

- Adrianov, A.V., 1989. First record of kinorhynchs from the Sea of Japan. *Zool. Zhur.* 68, 17–27 (in Russian).
- Adrianov, A.V., Malakhov, V.V., 1999. *Cephalorhyncha* of the World Ocean. KMK Scientific Press, Moscow (in Russian with English translation).
- Bauer-Nebelsick, M., 1996. *Antygomonas oreas* sp.n., a new deep sea kinorhynch from the Pacific Ocean. *Ann. Nat. Mus. Wien* 98B, 5–22.
- Coleman, C.O., 2003. “Digital inking”: how to make perfect line drawings on computers. *Org. Divers. Evol.* 14, 1–14.
- Danovaro, R., Gambia, C., Della Croce, N., 2002. Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. *Deep-Sea Res. I* 49, 843–857.
- Dujardin, F., 1851. Sur un petit animal marin, l’Echinodère, formant un type intermédiaire entre les Crustacés et les Vers. *Ann. Sci. Nat., Zool., Sér.* 3, 15, 158–160.
- G<sup>o</sup>Ordóñez, D., Pardos, F., Benito, J., 2000. Cuticular structures and epidermal glands of *Echinoderes cantabricus* and *E. hispanicus* (Kinorhyncha, Cyclorhagida) with special reference to their taxonomic value. *J. Morphol.* 246, 161–178.
- Gutzmann, E., Martinez Arbizu, P., Rose, A., Veit-Köhler, G., 2004. Meiofauna communities along an abyssal depth gradient in the Drake Passage. *Deep-Sea Res. II* 51, 1617–1628.
- Higgins, R.P., 1967. The Kinorhyncha of New-Caledonia. Expédition Française sur les Recifs Coralliens de la Nouvelle Calédonie 2, 75–90.
- Higgins, R.P., 1983. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. *Smithson. Contrib. Mar. Sci.* 18, 1–131.
- Higgins, R.P., 1986. A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from a coarse-sand California beach. *Trans. Am. Microsc. Soc.* 105, 266–273.
- Higgins, R.P., Kristensen, R.M., 1988. Kinorhyncha from Disko Island, West Greenland. *Smithson. Contrib. Zool.* 458, 1–56.
- Kristensen, R.M., Higgins, R.P., 1991. Kinorhyncha. In: Harrison, F.W., Ruppert, E.E. (Eds.), *Microscopic Anatomy of Invertebrates*, vol. 4. The Aschelminthes. Wiley-Liss, New York, pp. 377–404.
- Moore, P.G., 1973. *Campyloderes macquariae* Johnston, 1938 (Kinorhyncha: Cyclorhagida) from the northern hemisphere. *J. Nat. Hist.* 7, 341–354.
- Nebelsick, M., 1992. Ultrastructural investigations of three taxonomic characters in the trunk region of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida). *Zool. Scr.* 21, 335–345.
- Neuhaus, B., 2004. Description of *Campyloderes* cf. *vanhoefeni* (Kinorhyncha, Cyclorhagida) from the Central American East Pacific deep sea with a review of the genus. *Meiofauna Mar.* 13, 3–20.
- Neuhaus, B., Blasche, T., 2006. *Fissuroderes*, a new genus of Kinorhyncha (Cyclorhagida) from the deep sea and continental shelf of New Zealand and from the continental shelf of Costa Rica. *Zool. Anz.* 245, 19–52.
- Neuhaus, B., Higgins, R.P., 2002. Ultrastructure, biology, and phylogenetic relationships of Kinorhyncha. *Integ. Comp. Biol.* 42, 619–632.
- Pardos, F., Higgins, R.P., Benito, J., 1998. Two new *Echinoderes* (Kinorhyncha, Cyclorhagida) including a reevaluation of kinorhynch taxonomic characters. *Zool. Anz.* 237, 195–208.
- Sørensen, M.V., 2006. New kinorhynchs from Panama, with a discussion of some phylogenetically significant cuticular structures. *Meiofauna Mar.* 15, 51–77.

- Sørensen, M.V., 2007. A new species of *Antygomonas* (Kinorhyncha: Cyclorhagida) from the Atlantic coast of Florida, USA. *Cah. Biol. Mar.* 48, 155–168.
- Sørensen, M.V., 2008. Phylogenetic analysis of the Echinoderidae (Kinorhyncha: Cyclorhagida). *Org. Divers. Evol.* 8, 233–246.
- Sørensen, M.V., Pardos, F., 2008. Kinorhynch systematics and biology – an introduction to the study of kinorhynchs, inclusive identification keys to the genera. *Meiofauna Mar* 16, 21–73.
- Sørensen, M.V., Heiner, I., Ziemer, O., Neuhaus, B., 2007. *Tubulideres seminoli* gen. et sp. nov. and *Zelinkaderes brightae* sp. nov. (Kinorhyncha, Cyclorhagida) from Florida. *Helgoland Mar. Res.* 61, 247–265.
- Zelinka, C., 1928. *Monographie der Echinodera*. Wilhelm Engelmann, Leipzig.