Helgol Mar Res (2014) 68:59–87
DOI 10.1007/s10152-013-0369-9

ORIGINAL ARTICLE

New Kinorhyncha from Florida coastal waters

María Herranz · Nuria Sánchez · Fernando Pardos · Robert P. Higgins

Received: 4 May 2013 / Revised: 8 August 2013 / Accepted: 11 September 2013 / Published online: 2 October 2013

Abstract Four new species of Kinorhynchs are described from the West Atlantic coast off Fort Pierce, Florida, USA. They are the following: *Antygomonas gwenae* n. sp., *Echinoderes riceae* n. sp., *Echinoderes adrianovi* n. sp. and *Pycnophyes norenburgi* n. sp. All species were collected at the same locality called "20 miles station." Samples were processed for standard granulometric data, yielding an estimated average particle diameter of 250 μm. The diagnostic characters and the general morphology of the new species are discussed in depth as well as the diversity and distribution of Kinorhyncha in the area.

Keywords Kinorhyncha · Meiofauna · Florida · *Echinoderes* · *Antygomonas* · *Pycnophyes*

Introduction

The kinorhynch fauna reported from the East coast of the USA includes currently 14 species. The first three kinorhynch species recorded and described in the area were *Echinoderes remanei* Blake 1930; *Pycnophyes frequens* Blake 1930; and *Kinorhynchus mainensis* Blake 1930. These three species were found to form a common assemblage from Maine to Massachusetts (Wieser 1960; Higgins 1964a, 1965). Two additional species, *Campyloderes* sp. reported as *Campyloderes macquariae* Johnston 1938 by Higgins (1980) and posteriorly assigned to *Campyloderes* cf. *vanhoeffeni* by Neuhaus and Sørensen (2013); and *Centroderes spinosus* Reinhard 1881 recognized as a new species of *Centroderes* by Neuhaus, Pardos, Sørensen and Higgins (in preparation), were found later by Higgins (1982) in the same area. The latter species was not identified correctly, and his recording represents a yet undescribed species. Blake's three species are replaced by three similar species in the area stretching from Beaufort, North Carolina to Florida. They include *Pycnophyes beaufortensis* Higgins 1964; *Kinorhynchus langi* Higgins 1964; and *Echinoderes bookhouti* Higgins 1964 (see Higgins 1964b). The kinorhynch fauna of Bermuda reported by Higgins (1982) includes *Echinoderes bispinosus* Higgins 1982; *Echinoderes bermudensis* Higgins 1982; *Kinorhynchus fimbriatus* Higgins 1982; and a new species of *Centroderes*. All of the above species were collected subtidally, but in 1977, two new cyclorhagid kinorhynchs were found in intertidal habitats. *Echinoderes sublicarum* Higgins 1977 was found in bryozoan colonies on pilings in a tidal stream in the North River Inlet, South Carolina, and *Echinoderes coulli* Higgins 1977 and was found in the mud of this same intertidal creek area. This latter species was the first kinorhynch published with a complete series of juvenile developmental stages (see Higgins 1977).

The knowledge of the marine fauna in Atlantic Florida waters has been improved along many years by the research activities developed through the Smithsonian Marine Station at Fort Pierce, FL. It became well known among researchers that these waters constitute a kind of hot spot for meiobenthic communities. Accordingly, study sites were established in 5-mile increments seaward from Fort Pierce, Florida, between 1975 and 1995 by R. P Higgins, a

Communicated by H.-D. Franke.

M. Herranz (✉) · N. Sánchez · F. Pardos
Dpto. Zoología y Antropología Física, Facultad de Biología, Universidad Complutense de Madrid, C/José Antonio Novais 2, 28040 Madrid, Spain
e-mail: mariaherranz@bio.ucm.es

R. P. Higgins
122 Strawbridge Court, Asheville, NC 28803, USA

research effort that focused mainly on the phylum Kinorhyncha. Several new species appeared but only *Zelinkaderes floridensis* Higgins 1990 was described formally. *Z. floridensis* is a cyclorhagid kinorhynch, which represented a new family, the Zelinkaderidae (see Higgins 1990). This species occurs primarily at depths around 140 m in the muddy sand found 20 miles offshore. More recently, M. V. Sørensen collected at different localities off Fort Pierce and described four new species including a new genus: *Echinoderes spinifurca* Sørensen et al. 2005, *Zelinkaderes brightae* Sørensen et al. 2007, *Antygomonas paulae* Sørensen 2007 and *Tubulideres seminoli* Sørensen et al. 2007 (see Sørensen et al. 2007).

The purpose of this paper is to describe the remaining species from Bob Higgins' old samplings from the deepest and richest of the stations hereafter referred to as "20 miles station" combining his results with new records from recent samplings.

Materials and methods

Sediment samples were taken in August 1993 from one single station: the "20 miles site," 27°30′N, 79°56′W at 140-m depth (Fig. 1) from sandy mud using a Higgins anchor dredge (Higgins and Thiel 1988) from the R/V Sunburst (Smithsonian Marine Station at Fort Pierce). The anchor dredge was designed to sample only the upper few centimeters of sediment, thereby eliminating the need for processing large volumes of otherwise uninhabited sediment. Additional material was collected in August 2011, at the same station from the same R/V and using the same dredge.

Sediment samples for granulometric studies were wet-sieved using fresh water to remove salt through a series of geological sieves with 0.5-phi (φ) intervals. Phi (φ) = $-\log_2$ of mesh size in mm (1,000, 500, 250, 125 and 63 µm mesh). A mechanical shaker was used for a period of 15 min. The material retained on each sieve was placed in disposable aluminum weighing pans and dried in an oven at 80 °C for 24 h. After drying, each fraction of the material was weighted. The sediment weight fractions (calculated in percent of the total sample) (Fig. 2a) were transformed into a cumulative frequency series and then plotted as a cumulative frequency curve (Fig. 2b). In the latter, the medium particle diameter, i.e., the φ value corresponding to the 50 % point of the cumulative scale (Md φ or φ 50), is estimated. The "quartile deviation" (QD) expresses the number of phi (φ) units lying between the upper and lower quartile diameters Q1 and Q3 (Fig. 2b). Thus, sediment with a small spread between the quartiles, i.e., a small QD φ, is regarded as being "well sorted" (Higgins and Thiel 1988).

In the samples from 1993, kinorhynchs were sorted under a stereomicroscope, fixed in 10 % formalin and, after 24 h, transferred to 20 % Carosafe ® (Carolina Biological Supply, Co.). Selected specimens were later transferred to 2 % glycerin in 70 % ethanol, which was allowed to evaporate over a period of about 5 days, thereby leaving the specimens in glycerin only. From the glycerin, each specimen was transferred to a drop of Hoyer's 150 mounting medium (Higgins and Thiel 1988) on the base coverslip of an H–S slide mount (Higgins and Thiel 1988; Shirayama et al. 1993). A 12-mm-diameter, circle cover glass was placed on the mounting medium and manipulated to orient the specimen.

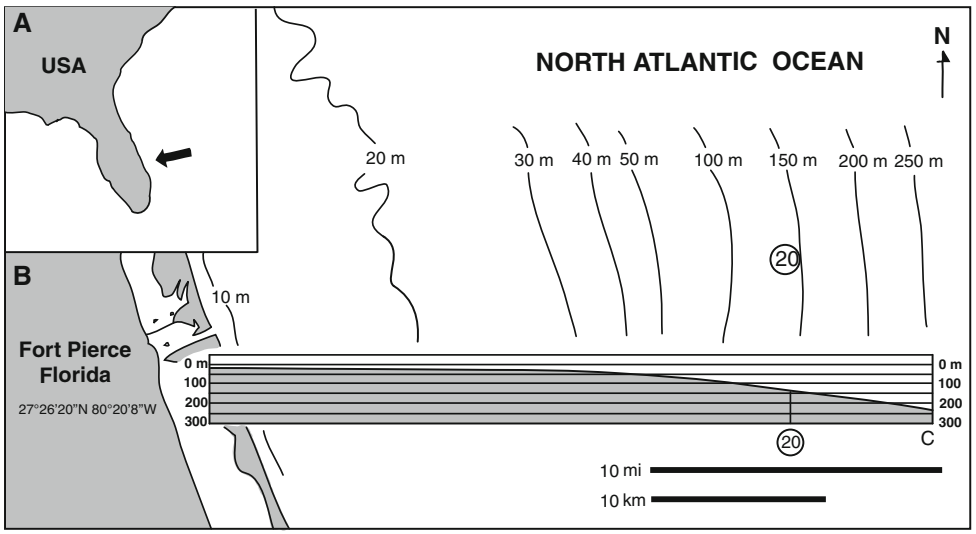

Fig. 1 Map showing **a** Florida (inset), western North Atlantic Ocean. **b** Locality of the study off Fort Pierce Station corresponding to miles off shore indicated by numbers in oval. **c** Transect showing depths from 0 to 300 m with *vertical line* corresponding to the 20 miles station

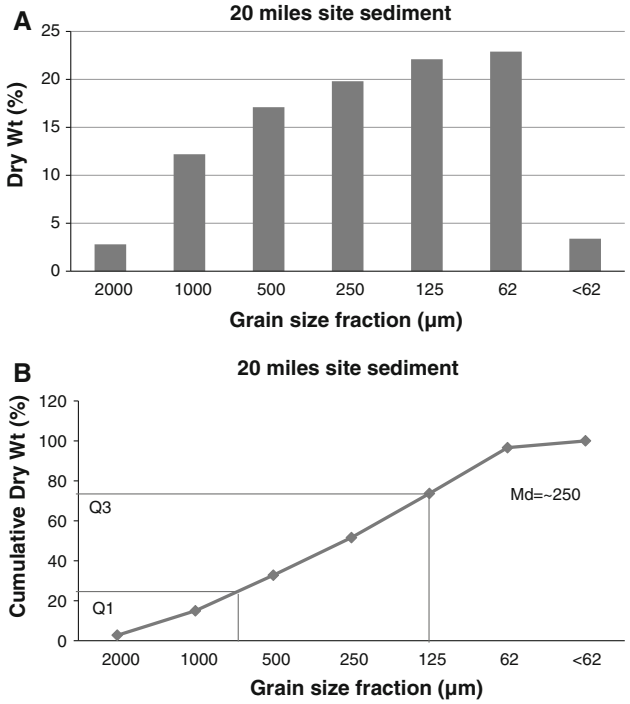

Fig. 2 Grain size fractions plotted: **a** against dry weight (%) **b** against cumulative dry weight (%). *Md* medium particle diameter. *Q1,3* quartile diameters

Specimens collected in 2011 were fixed in 10 % formalin. For light microscopy (LM) selected specimens were later dehydrated through a graded series of ethanol and transferred to glycerin prior to mounting in Fluoromount G®. All specimens were examined and photographed using an Olympus BX51 microscope with differential interference contrast optics equipped with an Olympus Colorview DP70 camera. Measurements were made using Olympus Cell A software (Olympus, Europe).

Not all species described yielded specimens suitable for scanning electron microscopy (SEM) studies. The available specimens for SEM were dehydrated through a graded series of ethanol and critical point dried. The dried specimens were mounted on aluminum stubs, sputter coated with gold and examined with a JEOL JSM-6335F field emission scanning electron microscope.

Terminology for head, neck and trunk morphology follows Neuhaus and Higgins (2002), Sørensen and Pardos (2008) for cyclorhagids and Sánchez et al. (2011) for homalorhagids. The number and distribution of introvert appendages has been studied both by rings and sectors using polar diagrams following Sørensen and Pardos (2008). The terminology used to describe the different kinds of scalids follows both Brown (1989) and Higgins (1990), recently revised and unified by Neuhaus (2012).

Results

Granulometry

Results of the sediment analyses (Fig. 2) show that a high percentage of the dry weight of the sediment is represented by grain size fractions ranging from 500 to 62 µm, with 62 µm occurring as the most frequent grain size constituting 23 % of the sediment, followed by 125 µm with 22 % and 250 µm with 17 %. Grain fractions from 250 to 62 µm constitute around 64 % of the total sediment. Cumulative dry weight graphic shows a higher slope in between 250 and 62 µm as well, showing a mean particle size around 250 µm. The grain size fractions less represented are the smallest <62 µm and the biggest 2,000 µm with a 2.8 and 3.4 %, respectively. However, the amount of the fraction smaller than 62 µm is not totally reliable due to the use of 63-µm mesh to take the samples. That means that part of the finest fraction could have been washed out during the collection in the periphery of the dredge.

Taxonomic account

Antygomonas gwenae n. sp. (Figs. 3, 4; Tables 1, 2)

Order Cyclorhagida (Zelinka 1896) Higgins 1964
Family Antygomonidae Adrianov and Malakhov 1994
Genus *Antygomonas* Nebelsick 1990

Diagnosis

Antygomonas with a very sclerotized cuticle. Anterior edge of the first trunk segment with a conspicuous notch in middorsal and midventral positions extending half of the segment length. Trunk segments 2–10 with distinct tergosternal junctions. Middorsal spines from segments 1–4 and 10 are flexible and thin, while those from segments 5–9 and 11 are conical, robust and stout. Segment 2 with a pair of lateroventral cuspidate spines located close to a pair of much smaller, flexible and hairy acicular spines. Segments 3 through 9 with lateroventral acicular spines; segments 5, 8 and 9 additionally with pair of lateroventral, lateral accessory or ventrolateral cuspidate spines. Acicular spines become very robust and stout from segment 5 in advance especially in segments 8 and 9. Cuspidate spines in lateroventral position on segments 5 and 9; cuspidate spines on segment 8 in lateral accessory position. Segment 10 with laterodorsal acicular spines flexible in males and stout and straight in females. Lateral terminal spines much shorter than lateral terminal accessory spines. Females with minute midventral conical projection of segment 9. Males differing from females by the presence of crenulated posterior half of middorsal and subdorsal spines of segment 10

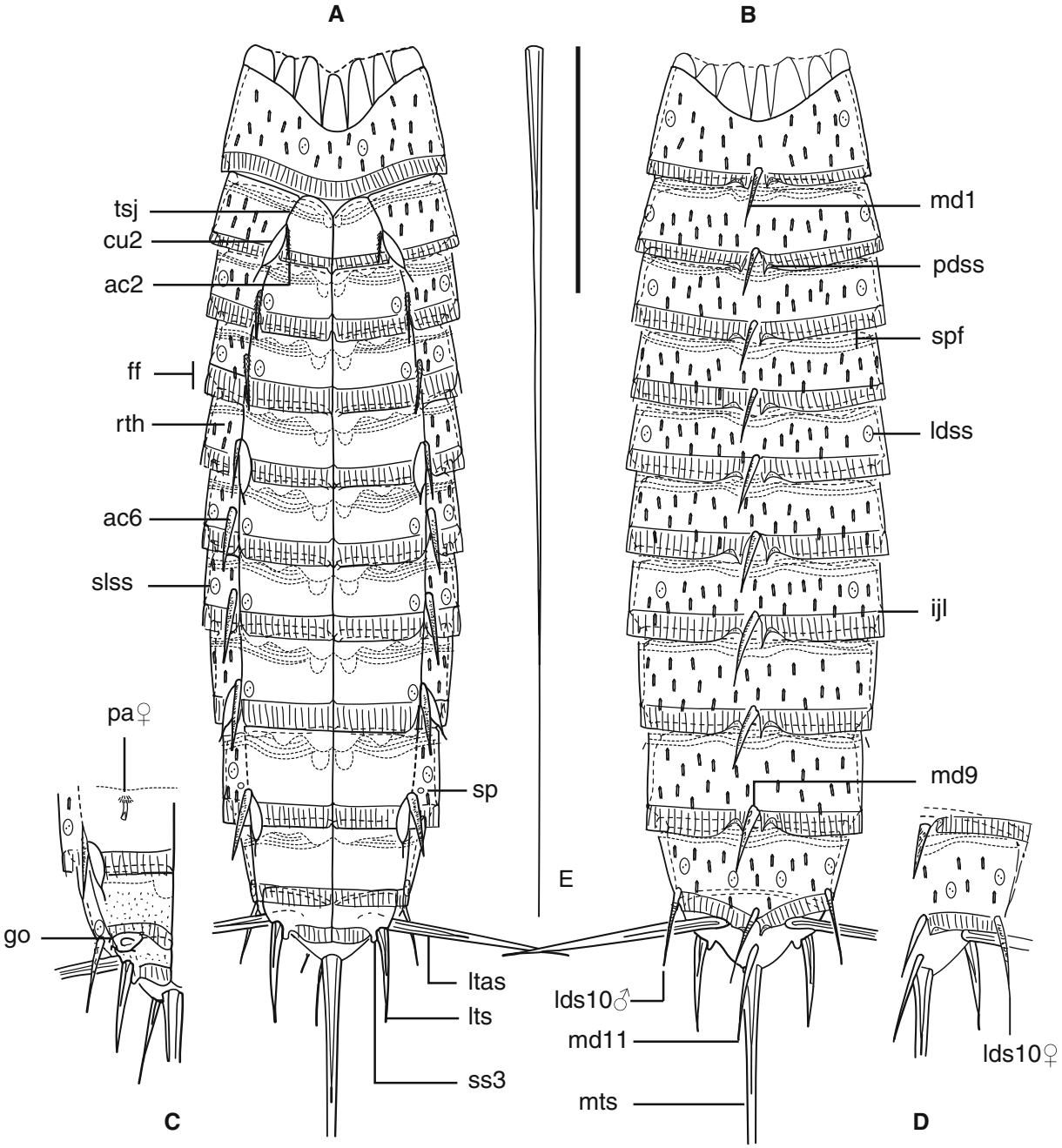

Fig. 3 *Antygomonas gwenae* n. sp. *line art* illustration. **a** Male ventral view. **b** Male dorsal view. **c** Female ventral detail of segments 10–11. **d** Female dorsal detail of segments 10–11. **e** Midterminal spine full length. *ac* acicular spine, *cu* cuspidate spine, *ff* free flap, *go* gonopore, *ijl* intersegmentary joint line, *lds* laterodorsal spine, *ldss* laterodorsal sensory spot, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *md* middorsal spine, *mts* midterminal spine, *pa* papillae, *pdss* paradorsal sensory spot, *rth* roof tile hairs, *ss3* sensory spot type 3, *slss* sublateral sensory spot, *sp* sieve plate, *spf* secondary pectinate fringe, *tsj* tergosternal junctions. Digits refer to the segment number. *Scale bar* 100 μm

and the lack of a pair of strongly sclerotized gonopores on segment 10.

Etymology

This species is named in honor Gwen L. Higgins, Bob Higgins' wife of through 50 years.

Type material

Holotype: adult male collected in August 1993 at the 20 miles station, Fort Pierce, off the Floridian West coast (Fig. 1) from sandy mud, mounted in Hoyer's medium. Allotype: adult female, same collecting data as holotype, mounted in Hoyer's medium. Paratype: adult female, same

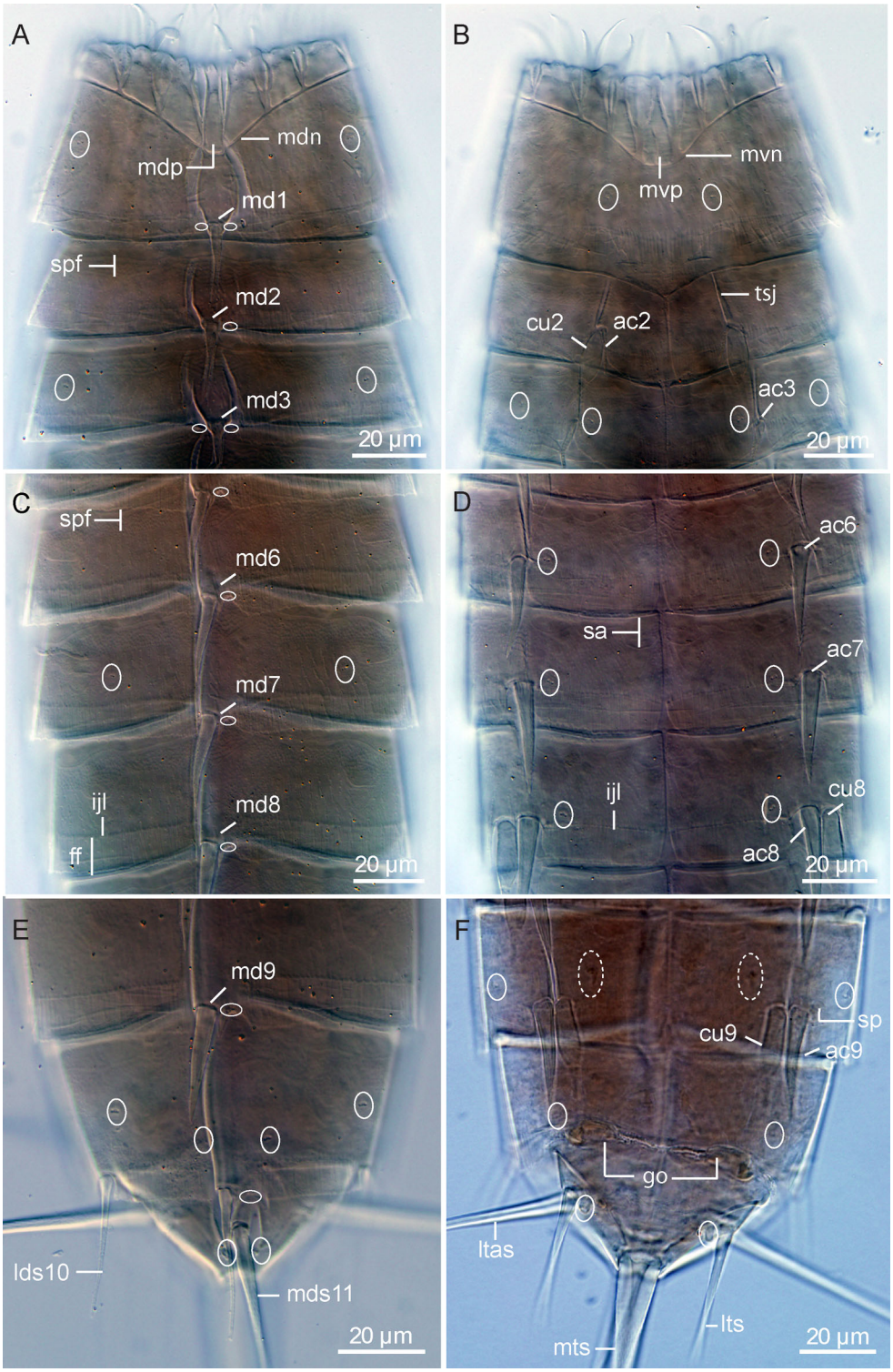

Fig. 4 Light micrographs showing details in neck and trunk morphology of *Antygomonas gwenae* n. sp. holotypic male USNM 1196402 (**a**–**e**) and allotypic female USNM 1196402 (**f**). **a** Neck and segments 1–3, dorsal view. **b** Neck and segments 1–3 ventral view. **c** Segments 6–8, dorsal view. **d** Segments 6–8 ventral view**. e** Segments 9–11, dorsal view. **f** Segments 9–11 ventral view. *ac* acicular spine, *cu* cuspidate spine, *ff* free flap, *go* gonopore, *ijl* intersegmentary joint line, *lds* laterodorsal spine, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *md* middorsal spine, *mdn* middorsal notch, *mdp* middorsal placid, *mts* midterminal spine, *mvn* midventral notch, *mvp* midventral placid, *sa* smooth area, *sp* sieve plate, *spf* secondary pectinate fringe, *tsj* tergosternal junctions. Digits after abbreviations refer to segment number. *White circles* indicate sensory spots (*solid line*) and papillae in females (*dotted line*)

Table 1 Measurements of adult *Antygomonas gwenae* n. sp. (in μm)

	Holotype male	Paratype male	Allotype female		Holotype male	Paratype male	Allotype female
TL	356	372	264	MD5	24	23	25
SW	40	62	62	MD6	24	26	27
SW/TL (%)	11.2	16.7	23.5	MD7	30	22	28
MSW-8	76.8	78.8	78.0	MD8	28	23	28
MSW/TL (%)	21.6	21.1	29.5	MD9	28	25	30
MTS	352	200	288	MD10	32	25	35
MTS/TL (%)	98.8	53.2	109.0	LDS10	33	35	28
S1	42	38	40	MD11	40	31	49
S2	31	28	26	LVS2 (cu)	24	22	18
S3	32	31	29	LVS2 (ac)	13	11	13
S4	34	34	32	LVS3	22	18	20
S5	37	35	35	LVS4	24	21	22
S6	38	38	35	VLS5 (cu)	28	22	24
S7	38	42	36	LVS5 (ac)	23	24	26
S8	41	42	40	LVS6	28	26	28
S9	42	44	42	LVS7	31	30	30
S10	44	43	40	LVS8 (ac)	32	30	30
S11	30	32	42	LAS8 (cu)	25	28	28
MD1	23	22	24	VLS9 (cu)	28	32	31
MD2	21	23	23	LVS9 (ac)	30	23	24
MD3	23	23	24	LTS11	40	41	41
MD4	24	25	25	LTAS11	89	80	80

Numbers, where inserted, indicates segment number

ac Acicular spine, *cu* cuspidate spine, *las* lateral accessory spine, *lds* laterodorsal spine, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *md* middorsal spine, *msw* maximum sternal width, *mts* midterminal spine, *sw* standard width, *s1–s11* segment lengths of trunk segments 1–11, *tl* trunk length, *vls* ventrolateral spine. Holotypic male in boldface

Table 2 Summary of nature and location of sensory spots, spines and papillae arranged by series in *Antygomonas gwenae* n. sp

Segments	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	ac	ss		ss						ss
2	ac	ss			ss			cu, ac		
3	ac	ss		ss		ss		ac	ss	
4	ac	ss				ss		ac	ss	
5	ac	ss		ss				ac	cu	
6	ac	ss				ss		ac	ss	
7	ac	ss		ss		ss		ac	ss	
8	ac	ss					cu	ac	ss	
9	ac	ss				ss		ac	cu	pa♀
10	ac	ss	ss	ac, ss				ss		
11	ac, mts	ss, ss					ltas	lts	ss	

ac Acicular spine, *cu* cuspidate spine, *la* lateral accessory, *ld* laterodorsal, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lv* lateroventral, *md* middorsal, *ml* midlateral, *mts* midterminal spine, *pa* papilla, *pd* paradorsal, *sd* subdorsal, *sl* sublateral, *ss* sensory spot, *vl* ventrolateral, *vm* ventromedial, ♀ female condition of sexually dimorphic character

collecting data as holotype and allotype, mounted in Hoyer's medium. Holotype and allotype were deposited at the National Museum of Natural History (Smithsonian Institution) under accession numbers USNM 1196402 and USNM 1196403, respectively. The single paratype is stored in the Meiofauna Laboratory collection at the Facultad de Biología, Universidad Complutense de Madrid under accession number K15/31.

Description

Adult specimens consisting of a head, a neck and eleven trunk segments (Figs. 3, 4) Measurements and dimensions are given in Table 1. A summary of cuticular characters (spines, tubules, gland outlets and sensory spots) locations is given in Table 2.

Mouth cone and introvert armature could not be examined in detail in any of the prepared specimens.

Neck with 16 placids of unequal shape, width and length. Midventral and middorsal placids are triangular and elongated measuring 6 µm wide at their bases and 22 µm long, narrower than all others (Figs. 3a, b, 4a, b). Laterally adjacent placids in the dorsal side still triangular being 14 µm wide, longer mesially than laterally but overall slightly longer than middorsal and midventral placids. Ventral placids narrower measuring 8 µm in width and 20 µm in length. Remaining placids more rectangular, nearly equal in size, 10 µm wide and 12 to 16 µm long. The cuticle between adjacent placids is more flexible, folding inwards and giving the false appearance of interstitial placids. No trichoscalid plates could be observed.

Segment 1, 42 µm long at lateral margins, 26 µm long middorsally and midventrally, forming an anterior broad notch (Figs. 3a, b, 4a, b). The cuticle in this and the following segments seems to be thicker and stronger than in other *Antygomonas* species. Middorsal spine short, hairy and flexible originating near the posterior edge of the segment in a notched margin and flanked by paradorsal sensory spots in this and the following segments. Paired sensory spots are furthermore present in laterodorsal and ventromedial positions (Figs 3a, b, 4a, b). Sensory spots in this and the following segments are rounded with short papillae and two pores, appearing very distinct in light microscopy; paradorsal sensory spots with a semicircular outline (Fig. 3b). It was not possible to identify the sensory spot type. Hence, more detailed examination through scanning electron microscopy is required to provide an exact map of these structures. Cuticular hairs are scattered over the segment. The hairs seem to have a roof tile or elongated leaf-like appearance with a perforation site, and are scattered around the segment. Wide striated free flap delimited anteriorly by a conspicuous ij-line in this and the following segments (Figs. 3a, b,4c). Pectinate fringe not apparent through LM.

Segment 2, 31 µm long at lateral margin of tergal plate, narrowing to 25 µm long at tergosternal junction. Sternal plates with arch-shaped anterior margins, each being ca. 16 µm wide anteriorly and 23 µm wide posteriorly (Figs. 3a, 4b). A pair of lateroventral cuspidate spines present, each with an associated hairy, thin and flexible acicular spine (Figs. 3a, 4b). Middorsal spine similar to that of previous segment. Paired sensory spots in paradorsal and midlateral positions. The anterior part of the tergal plate has at least four secondary pectinate fringes arranged into parallel rows on this and the following segments (Figs. 3b, 4a). All of them consist of a wavy line of minute, cuticular, spine-like scales; the last row is enlarged middorsally forming a conspicuous fringe behind the middorsal spine of each segment. Anterior to the secondary fringes a narrow smooth area without any scales occurs; this area is usually covered by the free posterior edge of the preceding segment (Fig. 4a–c). Secondary pectinate fringes on the sternal plates made by similar scales arranged into a wavy lines making out a conspicuous smooth area (Figs. 3a, 4d). Cuticular hairs with the same structure as on preceding segment but present on tergal plate only. Free flap striated and without a marked pectinate fringe as on previous segment. Middorsal and lateroventral spines on this and the following segments are associated with a conspicuous notch of the free flap (Figs. 3b, 4a, c, d).

Segment 3. Sternal plates slightly trapezoid, narrowest at anterior margins. (Figs. 3a, 4b). Flexible and hairy lateroventral spines present. Middorsal spine similar to that of previous segment. Paired sensory spots in paradorsal, laterodorsal, sublateral and ventrolateral positions. Cuticular hairs, fringes and free flap as on preceding segment.

Segment 4. Sternal plates nearly squarish. Middorsal spine slightly longer and more robust than spine on previous segments. Lateroventral acicular spines with the same appearance as those from segment 3. Paired sensory spots in paradorsal, sublateral and ventrolateral positions. Cuticular hairs, fringes and free flap as on previous segments.

Segment 5 with a middorsal spine slightly longer and stronger than the one of the previous segment (Fig. 4c). A pair of ventrolateral cuspidate spines longer than those of segment 2 closely associated with a pair of lateroventral and stout acicular spines both present with the same length (Fig. 3a). Both the middorsal and the lateral accessory acicular spines with a thick-walled cuticle around a central cavity. Paired sensory spots in paradorsal and laterodorsal positions. Cuticular hairs, fringes and free flap as on previous segment.

Segment 6 with a stout middorsal spine with the same length as the one in previous segment. A pair of wide and stout lateroventral acicular spines is present (Figs. 3a, 4d). Both the middorsal and lateroventral spines with a thick-walled cuticle around a central cavity, in this and the following segments. Paired sensory spots situated on paradorsal, sublateral and ventrolateral positions. Cuticular hairs, fringes and free flap as on previous segments.

Segment 7 with a stout middorsal spine (Figs. 3b, 4c). A pair of robust lateroventral spines is present (Figs. 3a, 4d). Sternal plates similar to those of segment 6, slightly narrowing at posterior edges. Sensory spots located in

paradorsal, laterodorsal, sublateral and ventrolateral positions. Cuticular hairs, fringes and free flap as in previous segments.

Segment 8 with a very robust middorsal spine (Fig. 3b). Lateroventral acicular spines also very stout (Fig. 3a). Both middorsal and lateroventral acicular spines with the same appearance as described in previous segments. A pair of lateral accessory cuspidate spines is present. Paired sensory spots situated in paradorsal and ventrolateral positions. Cuticular hairs, fringes and free flap as in previous segments.

Segment 9 with a stout middorsal spine (Figs. 3b, 4e). Paired ventrolateral cuspidate spines and conspicuously robust lateroventral acicular spines present (Figs. 3a, 4f). Paired sensory spots in paradorsal and sublateral positions. Female with a pair of ventromedial conical protuberances or papillae (modified gland cell outlets) (Figs. 3c, 4f). Small oval sieve plate near lateroventral tergal margin, long axis about 6 µm (Figs. 3a, 4f). Cuticular hairs, fringes and free flap as on previous segments.

Segment 10 showing either a thin and crenulated middorsal spine in males or a stout middorsal spine in females (Figs. 3b, d, 4e, f). Additionally, a pair of laterodorsal spines crenulated in males and robust in females with the same length of the middorsal spine is present. Paired sensory spots in paradorsal, subdorsal laterodorsal and lateroventral positions. The posterior margin of the tergal plate free flap has deep notches around the middorsal and laterodorsal spines. Female's free flap of the sternal plates with two ventrolateral rounded notches around the gonopores of segment 11; this free flap is straight in males (Figs. 3a, c, 4f). Cuticular hairs and pectinate fringes as on previous segments.

Segment 11 triangular, tapering posteriorly. Tergal plate slightly longer than sternal plates without tergal extensions. Segment appendages consist of a middorsal spine, a midterminal spine nearly the same length as the trunk and paired lateral terminal and lateral terminal accessory spines (Figs. 3a, b, e, 4e, f). The lateral accessory spines are twice as long as the lateral terminal spines. Paired modified sensory spots (type 3) are present at the base of the middorsal, midterminal and lateral terminal spines (Figs. 3a, b, 4e, f). These sensory spots consist of an area with densely set papillae, with a long and slender tubule protruding from the center. Female gonopores are easily recognized in LM as two strongly cuticularized areas at the intersegmental junction between segments 10 and 11 (Figs. 3c, 4f). Cuticular leaf-like hairs are lacking in this segment, instead the surface is covered by small scale-like hairs without perforation sites. A wide and striated free flap is present only in the sternal plates, lacking in tergal ones. Secondary fringes could not be examined in detail.

Remarks

The new species has sixteen placids, a first trunk segment being ring-shaped showing middorsal and midventral anterior notches, both presence of acicular and cuspidate spines, cuticular structures such as hairs and secondary fringes, and characteristic notches in the posterior margins of the trunk segments. All those characters are only shared by species of *Antygomonas.* However, there are some other important features of the new species that do not fit that well within this genus such as the high sclerotization of the trunk cuticle, the depth of the notches on segment 1 (around 50 % of the segment length), very short and robust middorsal and lateroventral spines, middorsal and laterodorsal spines of segment 10, being crenulated only in males, and the presence of distinct tergosternal junctions in segments 2–11. Based on the last difference solely, one would have to reject the assignment of the new species to the genus *Antygomonas* as originally described by Nebelsick (1990). However, and regarding this feature, Sørensen (2007) reported the presence of hardly recognizable tergosternal divisions in *A. paulae* and re-examined specimens of *Antygomonas oreas* Bauer-Nebelsick 1996, indicating that all segments from 2 to 11 consist of one tergal and two sternal plates. Subsequently, Sørensen et al. (2009) confirmed this trait also for *Antygomonas incomitata.* Thus, with the emended diagnosis based on these examinations, we can consider the genus *Antygomonas* to have segments 2–11 weakly divided into one tergal and two sternal plates; therefore, the new species can be still considered as belonging to *Antygomonas*.

Within the suborder Conchorhagae, the genera *Semnoderes* and *Sphenoderes* share several notable characters with the new species such as the composition of the placids, combining different lengths and widths; segment 1 with more or less developed incisions or notches that could function similar to the clam-shell-like closing apparatus described for *Sphenoderes* and *Semnoderes* (see Higgins 1969; Sørensen et al. 2009; Sørensen et al. 2010; Zelinka 1928); the presence of short and stout spines (only shared with *Sphenoderes* species) and the presence of the conical papillae located in the center of each sternal plate of segment 9. However, there are some noteworthy variations in the closing apparatus: *Semnoderes* has a segment one composed of two lateral halves separated by deep but not complete incisions and a neck with narrow middorsal and midventral placids to fit into these incisions (Sørensen et al. 2009). *Sphenoderes* in turn has a first segment divided into single tergal and sternal plates and a pair of lateral plates (Higgins 1969), showing broader incisions with also broader middorsal and midventral placids. In case of *Sphenoderes poseidon* Sørensen and Thormar 2010, the first segment is clearly not divided, but the broader

incisions and placids are still present. The new species has a first segment not divided but showing conspicuous although not very deep anterior notches. Furthermore, in the neck, the midventral and middorsal placids are conspicuously narrower than the remaining ones. These differences exclude the new species to be assigned as either *Semnoderes* or *Sphenoderes*.

The doubtful position of the new species in between *Antygomonas*, *Semnoderes* and *Sphenoderes* is not unexpected knowing all the similarities shared by those genera previously reported by Sørensen et al. (2009), (2010).

Surprisingly, the new species shares other characters with species of the genus *Centroderes* such as the sexual dimorphism exhibited by the laterodorsal and middorsal spines of segment 10, being crenulated in males; this feature is not shared by any species of *Antygomonas* nor *Semnoderes* and *Sphenoderes.* However, other genera such as *Wollunquaderes*, *Tubulideres* (Sørensen et al. 2007); *Triodontoderes* (Sørensen and Rho 2009); and *Zelinkaderes* (Higgins 1990; Bauer-Nebelsick 1995; Sørensen et al. 2007) show the same dimorphism. The stout and robust middorsal and laterodorsal acicular spines of *A. gwenae* n. sp. resemble those showed in *Centroderes,* although species of *Semnoderes* and especially *Sphenoderes* (*S. poseidon* Sørensen et al. 2010) also share this character. Future phylogenetic analysis would hopefully clarify whether all these traits are relevant for taxonomy and phylogenetic relationships.

The combination of the traits displayed by the new species makes its generic assignment problematic and somehow resembles the situation described for *Wollunquaderes majkenae* (see Sørensen and Thormar 2010), which has characters pointing toward Semnoderidae and Centroderidae. We tentatively assign the new species to the genus *Antygomonas* despite all the differences listed above until phylogenetic analysis confirm or reject it. Another alternative could be to erect a new cyclorhagid intermediate genus to accommodate this single species, based on all the differences showed with the genus *Antygomonas* and the similarities shared with *Sphenoderes* and *Semnoderes*. The authors find it inadequate without a phylogenetic background. Thus, as stated above, the new species fits better within *Antygomonas* than in other alternative genera and therefore is here assigned provisionally to this genus.

Currently, the genus *Antygomonas* comprises three species: *Antygomonas incomitata* Nebelsick 1990; *A. oreas;* and *A. paulae*. The main differences between these species are basically their spine formula, or more precisely the position of the cuspidate spines on segments 6, 8 and 9 (see Nebelsick 1990; Bauer-Nebelsick 1996; Sørensen 2007). *Antygomonas gwenae* n. sp. is distinguished from *A. incomitata* by the lack of ventrolateral cuspidate spines on segment 9 and lateroventral cuspidate spines on segment 8. They also differ in length of the LTS and LTAS being equal in *A. incomitata* while different in *A. gwenae* n. sp. which shows much shorter LTS. *A. oreas* and *A. gwenae* n. sp. can be discriminated by the position of the cuspidate spines on segment 9, which is lateroventral in *A. gwenae* n. sp. and lateral accessory in *A. oreas.* Also the TL of *A. oreas* is around 50 µm shorter than *A. gwenae* n. sp. *A. paulae* and *A gwenae* n. sp. have exactly the same spine formula, but they can be easily discriminated by the body dimensions with *A. paulae* being 100 µm longer than *A. gwenae* n. sp. and by the overall appearance of the middorsal and lateroventral spines stout and short in *A. gwenae* n. sp. and long and flexible in *A. paulae. A. gwenae* n. sp. can furthermore be differentiated from *A. paulae* by the sensory spot pattern showing additional sensory spots in laterodorsal position on segments 3 and 5 and in sublateral positions on segments 3, 6, 7 and 9. The lack of ventral notches of segments 1, 3, 4 and 6–8 occurring in A. paulae and lacking in A. gwenae and the different length of the LTAS and LTS equal in *A. paulae* are as well important features to distinguish both species (see Sørensen 2007).

Echinoderes adrianovi n. sp. (Figs. 5, 6; Tables 3, 4)

Order Cyclorhagida (Zelinka 1896) Higgins 1964
Family Echinoderidae Zelinka 1894
Genus *Echinoderes* Claparède 1863

Diagnosis

Echinoderes with long middorsal spines on segments 4–8 increasing in length from segments 4–7, middorsal spine of segment 8 shorter than the one on segment 7; long subdorsal and ventrolateral tubules on segment 2; lateroventral tubules on segment 5; lateroventral spines on segments 6–9; lateral accessory tubule on segment 8; lateral accessory spines on segment 11 in females; lateral terminal spines on segment 11.

Etymology

This species is named in honor of Dr. Andrey V. Adrianov, Vice Director, Institute of Marine Biology, Far East Branch, Russian Academy of Science, Vladivostok, Russia, a student, mutual friend and colleague of R.P. Higgins.

Type material

Holotype: adult female collected on August 1993 at the 20 miles site, Fort Pierce, off the Floridian West coast (Fig. 1) 27°30′N, 79′56′W, 140 m depth from sandy mud, mounted in Hoyer's medium, deposited at National Museum of

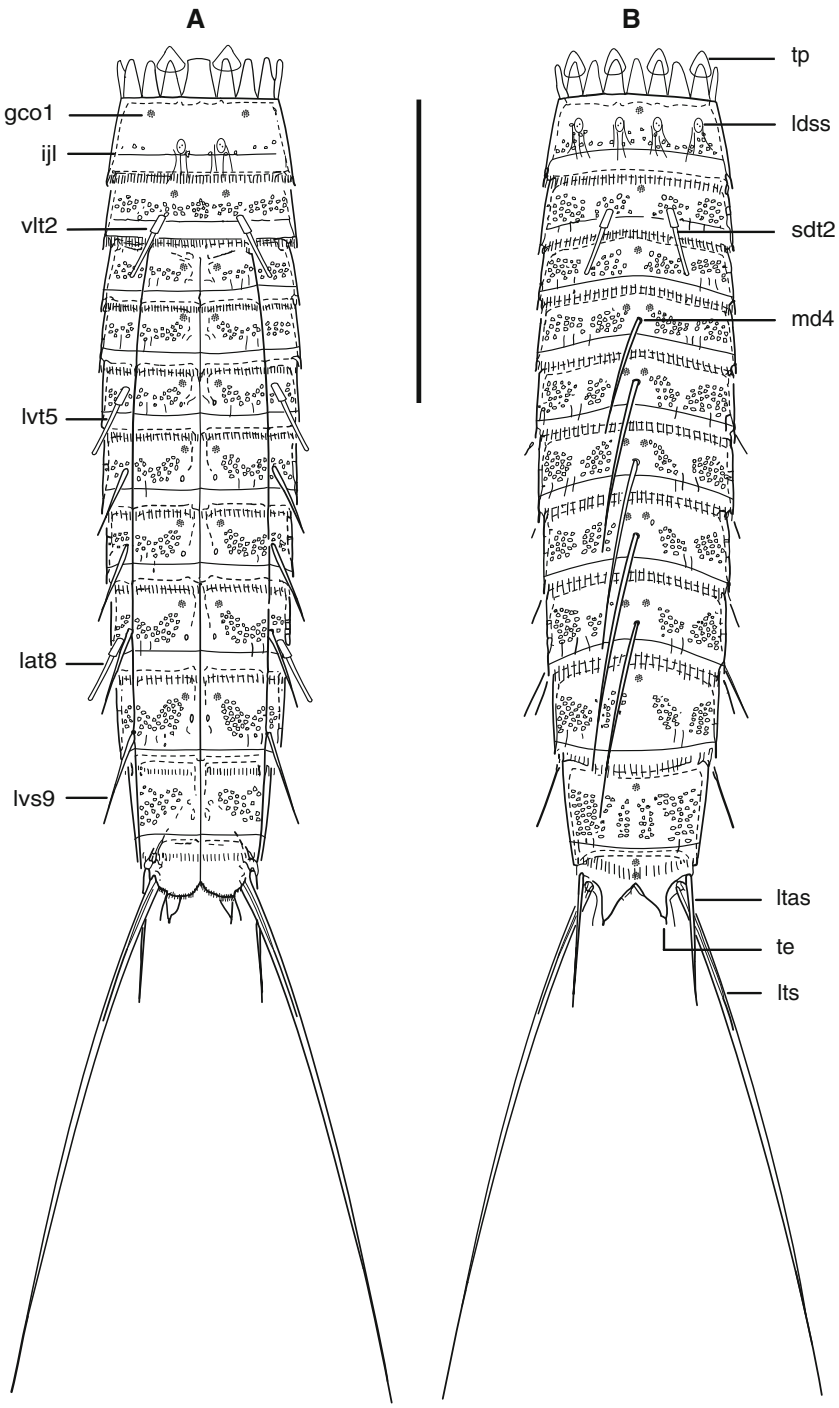

Fig. 5 *Echinoderes adrianovi* n. sp. *line art* illustration. **a** Ventral view. **b** Dorsal view. *ijl* intersegmentary joint line, *lat* lateral accessory tubule, *ldss* laterodorsal sensory spot, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *lvt* lateroventral tubule, *md* middorsal spine, *gco1* glandular cell outlet type 1, *sdt* subdorsal tubule, *te* tergal extension, *tp* trichoscalid plate, *vlt* ventrolateral tubule. Digits refer to the segment number. *Scale bar* 100 μm

Natural History (Smithsonian Institution) under accession number USNM 1196401.

Description

Holotypic female with head, neck and 11 trunk segments (Figs. 5a, b, 6a). See Table 3 for measurements and dimensions. A summary of location of cuticular characters (spines, tubules, gland outlets and sensory spots) is given in Table 4.

No specimens were available for SEM examination; thus, it was not possible to identify unambiguously all minor cuticular structures such as sensory spots and gland cell outlets. These structures are reported when apparent through LM; however, the lack of mention in the description of some segments should not be interpreted as a confirmation of their absence.

The head consists of a retractable mouth cone and an introvert. Inner and outer armature could not be examined in detail.

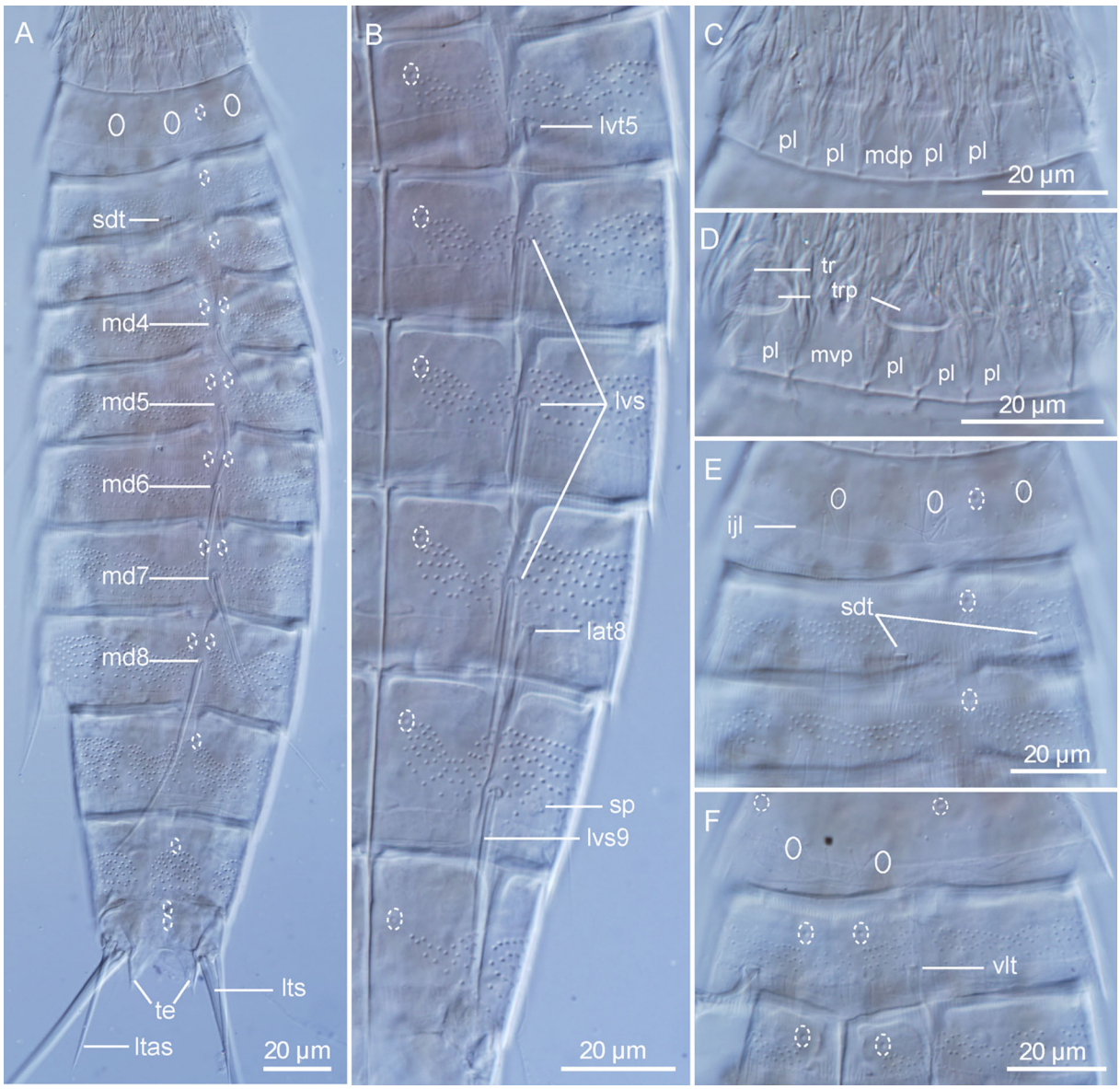

Fig. 6 Light micrographs showing details in neck and trunk morphology of *Echinoderes adrianovi* n. sp. holotypic female, USNM 1196401. **a** Dorsal view. **b** Segments 5–10 left side, ventral view. **c** Neck, dorsal view. **d** Neck lateroventral view. **e** Segments 1–3, dorsal view. **f** Segments 1–3, ventral view. *ijl* intersegmentary joint line, *lat* lateral accessory tubule, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *lvt* lateroventral tubule, *md* middorsal spine, *mdp* middorsal placid, *mvp* midventral placid, *pl* placid, *sdt* subdorsal tubule, *sp* sieve plate, *te* tergal extension, *tp* trichoscalid plate, *tr* trichoscalid, *vlt* ventrolateral tubule. *White circles* indicate glandular cell outlets type 1 (*dotted line*) and sensory spots (*solid line*). Digits after abbreviations refer to segment number

The neck consists of 16 placids all measuring 12 µm in length; midventral placid 10 µm wide at the base; and 8 µm distally where it expands laterally at its margins (Figs. 5a, 6c); remaining placids measure 6 µm at their bases and 3 µm distally. All placids articulate with the first trunk segment. Six trichoscalid plates present, 2 ventral on placids 1 and 16 and 4 dorsal on placids 6, 8, 10 and 12 (Figs. 5a, b, 6c, d). Ventral trichoscalid plates are triangular with rounded corners and wider than dorsal ones which have a triangular outline (Figs. 6c, d).

Trunk

The trunk has 11 segments, with segments 1 and 2 consisting of a closed cuticular ring, and segments 3–11 with one tergal and two sternal plates (Fig. 5a).

Table 3 Measurements (in μm) of adult *Echinoderes adrianovi* n. sp. holotype

Character	Holotype	Character	Holotype
TL	262	MD4	38
SW	42	MD5	56
SW/TL (%)	16	MD6	64
MSW-8	42	MD7	78
MSW/TL (%)	16	MD8	64
S1	28	VLT2	24
S2	28	DLT2	24
S3	24	LVS5	24
S4	24	LVS6	24
S5	26	LVS7	28
S6	29	LVS8	30
S7	30	LAT8	27
S8	34	LVS9	32
S9	36	LTS11	174
S10	40	LTAS11	44
S11	28		

Numbers, where inserted, indicates segment number

dlt Dorsolateral tubule, *lat* lateral accessory tubule, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *md* middorsal spine, *msw* maximum sternal width, *sw* standard width, *s1–s11* segment lengths of trunk segments 1–11, *tl* trunk length, *vlt* ventrolateral tubule

Table 4 Summary of nature and location of sensory spots, glandular cell outlets, spines and tubules arranged by series in *Echinoderes adrianovi* n. sp

Segments	MD	PD	SD	LD	SL	LA	LV	VL	VM
1	gco1		ss	ss			gco1		ss
2	gco1		tu					tu	gco1
3	gco1								gco1
4	ac	gco1							gco1
5	ac	gco1					tu		gco1
6	ac	gco1					ac		gco1
7	ac	gco1					ac		gco1
8	ac	gco1				tu	ac		gco1
9	gco1				sp		ac		gco1
10	gco1								gco1
11	gco1, gco1					ltas	lts		

ac Acicular spine, *gco1* glandular cell outlet type 1, *la* lateral accessory, *ld* laterodorsal, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lv* lateroventral, *md* middorsal, *pd* paradorsal, *sd* subdorsal, *sl* sublateral, *sp* sieve plate, *ss* sensory spot, *tu* tubule, *vl* ventrolateral, *vm* ventromedial

Glandular cell outlets type 1 (pore fields) are situated either at the anterior part of the segments on areas surrounded by perforation sites (ventrally) or located always anterior to the perforation site area (dorsally). Ventral pore fields are located in a lateroventral position on segment 1 and paraventrally on segments 2–10 (Figs. 5a, 6b). Dorsal pore fields are unpaired middorsally on segments 1–3, 9–10 and paradorsal pairs on segments 4–8 (Figs. 5b, 6a). Segment 11 has two unpaired middorsal pore fields above each other (Fig. 6a).

Segment 1 consists of one complete cuticular ring. Three pairs of type 1 sensory spots present in subdorsal, laterodorsal and ventromedial positions (Figs. 5a, b, 6a, f). Cuticular hair pattern distributed above the ij-line (Figs. 5a, b). Wide free flap terminates into a fine pectinate fringe.

Segment 2 consists of one complete cuticular ring. Two pairs of tubules, subdorsal and ventrolateral, are present (Figs. 5a, b, 6e, f). Cuticular perforation sites prominent and distinctly patterned forming a continuous band around the segment interrupted in laterodorsal and paraventral areas; the longest hairs are situated in the last row. Free flap and pectinated fringe as on preceding segment.

Segment 3. This and the following segments consist of one tergal and two sternal plates. Spines or tubules are not present. Cuticular hair pattern very distinct showing a dense band around the segment interrupted in laterodorsal and paraventral areas; the last row shows the longest hairs. Free flap and pectinated fringe as on preceding segment.

Segment 4 with a middorsal spine situated midway from anterior margin of tergal plate (Figs. 5b, 6a). Cuticular hair pattern as on segment 3 but also interrupted in middorsal position. Other features similar to previous segment.

Segment 5 with a middorsal spine and one pair of lateroventral tubules (Figs. 5a, 6a, b), otherwise similar to segment 4.

Segments 6 and 7 with a middorsal spine and one pair of lateroventral spines (Figs. 5a, b, 6a, b), otherwise similar to segment 4.

Segment 8 with a middorsal spine and one pair of lateroventral spines plus lateral accessory tubules (Figs. 5a, b, 6a, b), otherwise similar to segment 4.

Segment 9 with a pair of lateroventral spines, no middorsal spine is present. Paired rounded and small sieve plates are found in a sublateral position (Fig. 6b). Otherwise similar to preceding segments.

Segment 10 with a distinctive rounded perforation site patch middorsally separated from the lateral cluster (Fig. 5b, 6a); sternal pattern more uniformly clustered than on preceding segment. Oval muscle scars near posterior midline of each sternal plate. Other characters similar to previous segments.

Segment 11 smooth; tergal plate with prominent and pointed tergal extensions (Figs. 5b, 6a); sternal plates with rounded posterior margins, with minute pectinate fringe and single prominent long hair extending posteriorly, in line with tergal extensions; lateral terminal spines 66.4 % of trunk length; lateral terminal accessory spines 25 % of the lateral terminal spine length.

Remarks

Currently forty-one species of *Echinoderes* share the same middorsal spine pattern (segments 4–8). Of these, twenty-one species show ventrolateral tubules on segment 2, lateroventral tubules on segment 5 and lateroventral spines on segments 6–9. Only one species out of these twenty-one, *Echinoderes kanni* Thormar and Sørensen 2010, described from the Solomon Islands, share the pattern of spines/tubules with *E. adrianovi* n. sp. Despite the coincidence of spine/tubule formula and body proportions, both species can be differentiated by the length of these spines and tubules: *E. kanni* shows all middorsal spines increasing progressively in length, while *E. adrianovi* n. sp. shows the middorsal spine of segment 8 shorter than the one on previous segment being equal in length with the one on segment 6. The middorsal spines of segments 4–7 in *E. adrianovi* n. sp. are around 10 µm longer than in *E. kanni,* except for the middorsal spine on segment 8 which is 20 µm shorter. The length of the ventrolateral and dorsolateral tubules of segment 2 show big differences measuring twice as much in *E. adrianovi* n. sp.; tubules of segments 5 and 8 are also longer in *E. adrianovi* n. sp. but not as long as those on segment 2. Lateroventral spines show differences as well being slightly longer in *E. adrianovi* n. sp. except for the lateroventral spine on segment 9 much longer in *E. kanni.* Lateral terminal and lateral terminal accessory spines around 15 µm longer in *E. adrianovi* n. sp.

Another species that strongly resembles *E. adrianovi* n. sp. is *Echinoderes parrai* GaOrdóñez et al. 2008, described from the North coast of Spain (GaOrdóñez et al. 2008). This is the only other species of the genus *Echinoderes* combining 5 middorsal spines, dorsal tubules on segment 2 and lateral accessory tubules on segment 8. However, it lacks ventrolateral tubules on segment 2, it has much shorter LTS and LTAS and shows a bulbous appearance of the anteriormost segments; therefore, it is very easily discriminated from *E. adrianovi* n. sp.

Two other species of the same genus, *Echinoderes spinifurca* and *Echinoderes horni* Higgins 1983, are reported from the Atlantic coast of Fort Pierce, Florida, USA (Sørensen et al. 2005). Both have been found closer to shore, from the coarser sediments of the 5 miles station. *E. horni* is otherwise known only from its type locality, Carrie Bow Cay, Belize. *E. adrianovi* n. sp. is easily differentiated from *E. spinifurca* because of the very long tergal extensions and the lack of tubules laterodorsally on segment 2 and lateral accessory on segment 8 of the latter species, and from *E. horni* because this latter lacks middorsal spines.

Echinoderes riceae n. sp. (Figs. 7, 8, 9, 10; Tables 5, 6)

Diagnosis

Echinoderes with middorsal spines on segments 4, 6 and 8 gradually increasing in length posteriorly; ventrolateral tubules on segment 2; lateroventral tubules on segment 5; lateroventral spines on segments 7, 8 9; lateral accessory tubules on segment 8.

Etymology

This species is named in honor of Dr. Mary E. Rice, Emeritus Research Zoologist at the Smithsonian Marine Station at Fort Pierce, Florida, for a whole life dedicated to the marine research.

Type material

Holotype: adult female collected on August 1993 at the 20 miles site, Fort Pierce, off the Floridian West coast (Fig. 1) 27°30′N, 79′56′W, 140 m depth from sandy mud, mounted in Hoyer's medium, deposited at the National Museum of Natural History (Smithsonian Institution) under accession number USNM 1196386. Allotype: adult male, same collecting data as holotype, mounted in Hoyer's medium, deposited at National Museum of Natural History (Smithsonian Institution) under accession number USNM 1196396. Paratypes, 9 males and 9 females same collecting data as holotype, mounted in Hoyer's medium. Thirteen paratypes were deposited at the National Museum of Natural History under accession numbers USNM 1196387-95 and USNM 1196397-99. Remaining five paratypes are preserved in the Meiofauna Laboratory collection at the Facultad de Biología, Universidad Complutense de Madrid under accession numbers K15/31-36.

Additional material

Additional material was collected in August 2011 at the 20 miles site, Fort Pierce, off the Floridian West coast 27°30,84′N 79° 54,86′W; 152 m depth from fine mud. Ten specimens were studied in LM mounted in Fluoromount G®, and 5 were prepared and examined with SEM. This material is deposited in the Meiofauna Laboratory collection at the Facultad de Biología, Universidad Complutense de Madrid under accession numbers K15/1-10.

Description

Adult specimens consist of a head, a neck and eleven trunk segments (Figs. 7a, b, 9a, b). Measurements and dimensions are given in Table 5. A summary for location of sensory spots, spines, tubules and glandular cell outlets is provided in Table 6.

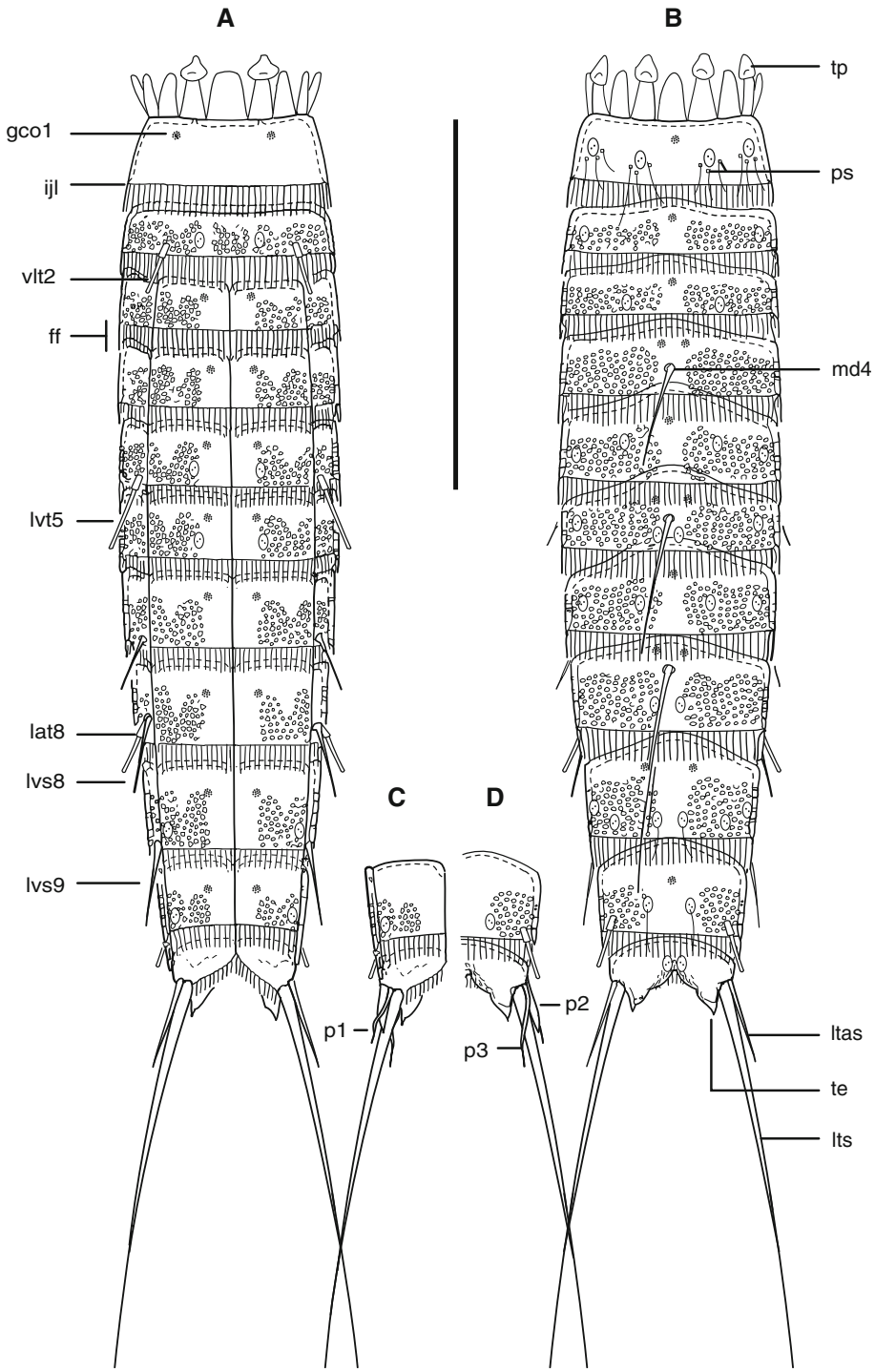

Fig. 7 *Echinoderes riceae* n. sp. line art illustration. **a** Ventral view. **b** Dorsal view. **c** Male detail segment 10–11 ventral view. **d** Male detail segments 10–11, ventral view. *ff* free flap, *ijl* intersegmentary joint line, *lat* lateral accessory tubule, *ldss* laterodorsal sensory spot, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *lvt* lateroventral tubule, *md* middorsal spine, *p1-3* penile spines, *gco1* glandular cell outlet type 1, *ps* perforation sites, *te* tergal extension, *tp* trichoscalid plate, *vlt* ventrolateral tubule. Digits refer to the segment number. *Scale bar* 100 µm

The head consists of a retractable mouth cone and an introvert (Fig. 8). The mouth cone has nine, long and pointed outer oral styles divided into two segments. The bases have a conspicuous long fringe composed of at least five fringe tips flanked by a pair of spikes (Fig. 10a); the inner armature of the mouth cone could not be examined in detail. The introvert has seven rings of spinoscalids and one additional ring of trichoscalids (Fig. 8). Ring 01 has ten primary spinoscalids consisting of a short basal sheath, equipped with two rows of long fringes and a long end piece. Ring 02 is formed by 10 laterally compressed spinoscalids, all formed by a basal part covered with a long (more than half of the length of the scalid) and smooth sheath that terminates into a short fringe with wide fringe tips (Fig. 10b). Ring 03 with 20 spinoscalids all with conspicuous sheaths around their bases and a

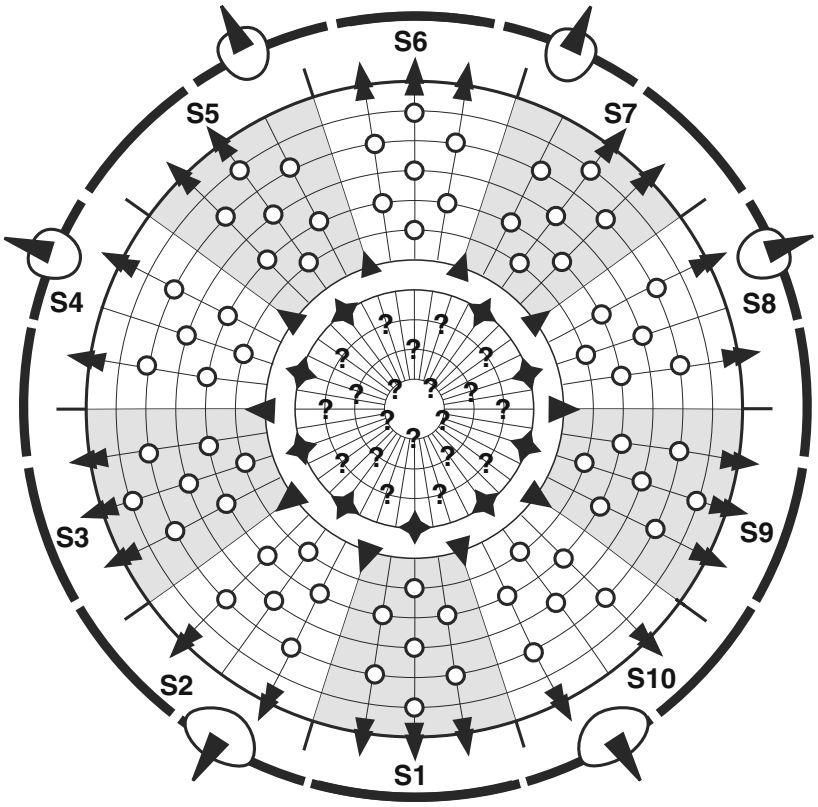

Fig. 8 Diagram of mouth cone, introvert and placids showing distribution of oral styles and scalids in *Echinoderes riceae* n. sp. "*Double diamonds*" are marked in the table with *double lines,* and quincunxes are marked with *dotted lines*. *ls* leaf-like scalid, *oos* outer oral style, *psp* primary spinoscalid, *S1-10* sectors, *sps* spinoscalid, *tr* trichoscalid

Scalid and style arrangement

Ring/Sector	1	2	3	4	5	6	7	8	9	10	Total
00 oos ✦	1	1	1	1	1	0	1	1	1	1	9
01 psp ▼	1	1	1	1	1	1	1	1	1	1	10
02 sps ○	1	1	1	1	1	1	1	1	1	1	10
03 sps ○	2	2	2	2	2	2	2	2	2	2	20
04 sps ○	1	1	1	1	1	1	1	1	1	1	10
05 sps ○	2	2	2	2	2	2	2	2	2	2	20
06 sps ○	1	0	1	0	1	1	1	0	1	0	6
07 ls	3	2	3	2	2	3	2	2	3	2	24
08 tr	0	1	0	1	1	0	1	1	0	1	6
Total scalids	10	9	10	9	10	10	10	9	10	9	115

distal fringe. These sheaths have rounded edges with a characteristic flexible spine in the middle (Fig. 10b). Rings 04 and 05 consist of 10 and 20 spinoscalids, respectively (Fig. 8); all resemble those of ring 03 but without the conspicuous sheaths. Ring 06 is formed by 6 spinoscalids, shorter than those in preceding rings and also showing shorter sheaths. Ring 07 has 20 leaf-like scalids with a wide and hairy base from where several flexible elongations arise (Fig. 10b). Six trichoscalids are present on their respective trichoscalid plates (Figs. 8, 9a, b, 10b). The introvert can also be described as divided into ten sectors defined by radii drawn through primary spinoscalids, so each sector is delimited by two consecutive primary spinoscalids (Fig. 8). The midventral sector is numbered as 1, followed clockwise by sectors 2–10. All sectors, except the middorsal sector 6, contain one oral style in the mouth cone. Even sectors contain 8 spinoscalids (other than primary ones) except for sector 6 with 10 spinoscalids. Uneven sectors contain 10 spinoscalids except for sectors 5 and 7, which also contain a trichoscalid that prevents the presence of one of the leaf-like scalids. The arrangement of the spinoscalids shows double diamonds in uneven sectors and sector 6 and quincunxes in the remaining even sectors formed by spinoscalids of rows 03–05 (Fig. 8). Trichoscalid plates with trichoscalids are situated on sectors 2, 4, 5, 7, 8 and 10. See Fig. 8 for a complete summary of oral styles, scalids and placid locations.

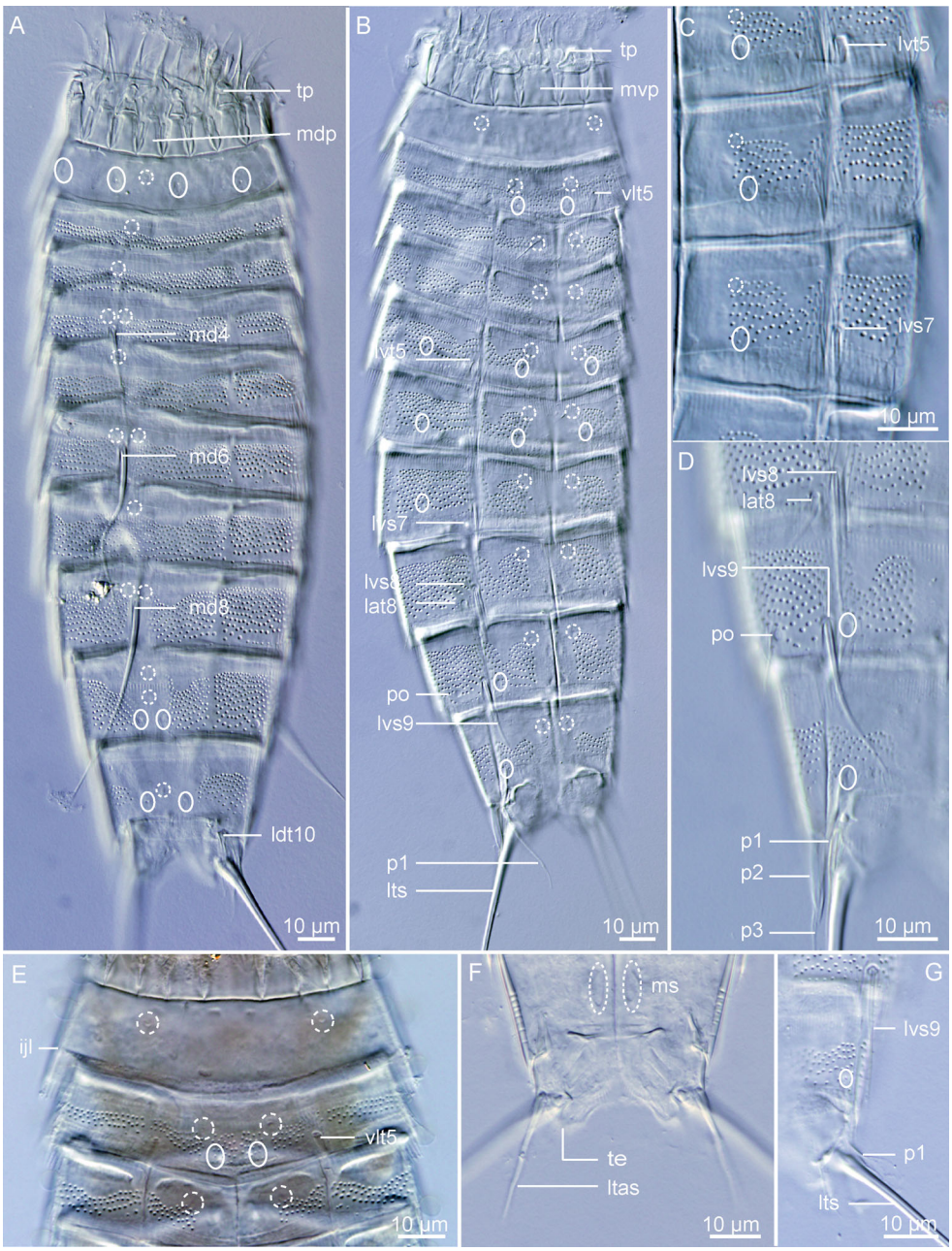

Fig. 9 Light micrographs showing details in neck and trunk morphology of *Echinoderes riceae* n. sp. Non-types. **a** Male dorsal view. **b** Male ventral view. **c** Detail of segments 5–7, ventral view, left side. **d** Male, detail of segments 8–11, ventral view, right side. **e** Detail segments 1–3, ventral view. **f** Female details segments 10–11, ventral view, focus is on the ltas. **g** Male detail of segments 10–11 ventral view, left side. *ijl* intersegmentary joint line, *lat* lateral accessory tubule, *ldt* laterodorsal tubule, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *lvt* lateroventral tubule, *md* middorsal spine, *mdp* middorsal placid, *ms* muscular scar, *mvp* midventral placid, *po* protonephridial opening, *p1-3* penile spines, *te* tergal extension, *tp* trichoscalid plate, *vlt* ventrolateral tubule. *White circles* indicate glandular cell outlets type 1 and (*dotted line*) and sensory spots (*solid line*). Digits after abbreviations refer to segment number

Neck with 16 placids, 13 µm long, conventionally numbered clockwise from the midventral one at sector 1. Midventral placid 10 µm wide at base, distal margin of placid nearly the same width. Lateral placids, 6 µm wide at base, 3 µm wide at distal margin. All placids articulate with the first trunk segment. Trichoscalid plates appear on dorsal placids 6, 8, 10, 12 and on ventral placids 2 and 16. Dorsal trichoscalid plates are rounded and small (6 µm), while ventral plates are larger and triangular, with enlarged bases (9 µm).

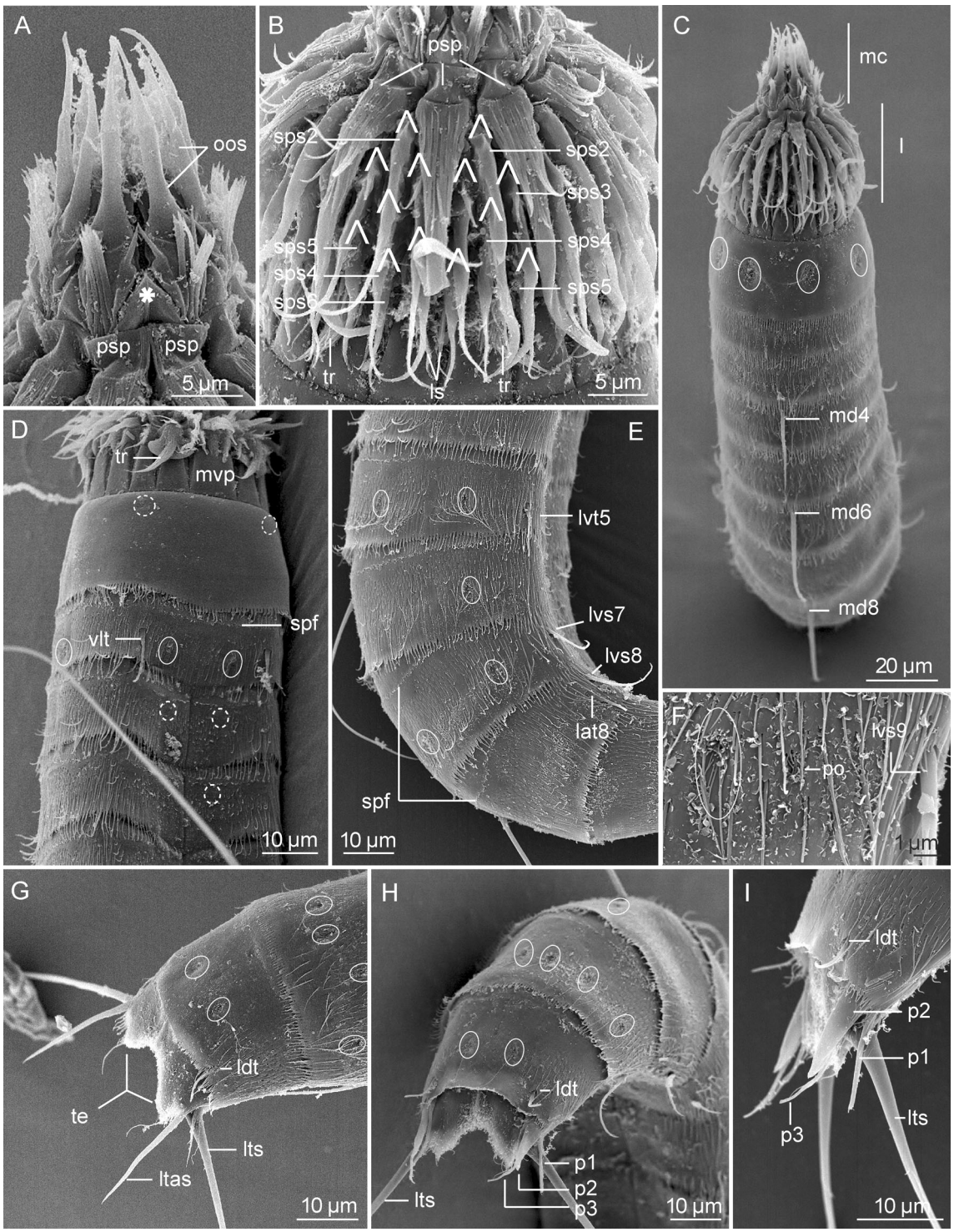

Fig. 10 Scanning electron micrographs showing trunk morphology and cuticular details in *Echinoderes riceae* n. sp. **a** Detail of mouth cone, *asterisk marks* middorsal position. **b** Detail introvert, sectors 4–5. **c** Introvert, neck and segments 1–8, dorsal view. **d** Detail of neck and trunk segments 1–4, ventral view. **e**. Detail of trunk segments 5–8, lateral view. **f** Detail of protonephridial opening on segment 9, lateral view. **g**. Female detail of trunk segments 9–11, dorsal view. **h**. Male detail of trunk segments 8–11, laterodorsal view. **i**. Male detail of penile spines on segment 11, lateral view. *I* introvert, *lat* lateral accessory tubule, *ldt* laterodorsal tubule, *ls* leaf-like scalid, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *mc* mouth cone, *md* middorsal spine, *mvp* midventral placid, *po* protonephridial opening, *oos* outer oral style, *p1-3* penile spines, *psp* primary spinoscalid, *sps* spinoscalid, *spf* secondary pectinate fringe, *te* tergal extension, *tr* trichoscalid, *vlt* ventrolateral tubule. *White circles* indicate glandular cell outlets type 1 (*dotted line*) and sensory spots (*solid line*). Digits after abbreviations refer to segment number or introvert ring number. *Lambda* symbols (Λ) mark attachment points of scalids

Trunk

Type 1 glandular cell outlets (pore fields) are ventrally situated at the anterior part of the segments, or dorsally located always anterior to the perforation sites (Figs. 7a, b, 9a, b). Ventral pore fields are located in a ventrolateral position on segment 1, paraventral position on segments 2–10. Dorsal pore fields are unpaired middorsally on segments 1, 2, 3, 5, 7, 10 and paired in a paradorsal position on segments 4, 6, 8, 9.

Secondary pectinate fringe present in the anterior margin of segments 2–11 as a continuous belt of short fringe tips (Figs. 10d, e).

Segment 1 consists of one complete cuticular ring. Pairs of subdorsal and laterodorsal sensory spots flanked by two or three long cuticular hairs emerging from rounded perforation sites present. Those are the only cuticular hairs noted both dorsally or ventrally in the segment (Figs. 7a, b, 9a, e, 10c, d) giving the cuticle a smooth appearance. Sensory spots on this segment are big, rounded with numerous papillae and two pores. Posterior margin with a short and well-developed pectinate fringe.

Segment 2 consists in one complete cuticular ring. A pair of ventrolateral tubules present. Each tubule consists of a short and smooth basal part, and a longer distal part with two small longitudinal, wing-like lateral projections (Figs. 7a, 9e, 10d). Paired sensory spots present in ventromedial and laterodorsal positions. Sensory spots in this and the following segments are smaller and more oval showing less papillae. These papillae increase in length at

Table 5 Measurements (in μm) for adults of *Echinoderes riceae,* n. sp

Character	Type		*n*		Range		Average		SD	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
TL	240	222	9	10	206–240	196–248	226	224	10.9	16.0
SW (%)	28	32	8	8	26–38	29–37	30	33	4.3	3.4
SW/TL (%)	11.7	14.4	8	8	12–17	12–18	13	15	1.9	1.8
MSW-10	44	42	7	8	40–48	38–45	44	41	2.4	2.3
MSW/TL	18.3	18.9	7	8	18–22	17–21	19	18	1.2	1.4
S1	23	24	8	8	23–26	23–28	24	25	1.3	1.6
S2	23	22	8	8	21–24	20–26	23	23	1.3	1.8
S3	22	24	8	8	21–27	22–26	24	24	2.1	1.4
S4	24	24	8	8	23–28	22–28	25	24	2.3	1.3
S5	25	26	8	8	25–30	24–32	27	28	2.2	1.4
S6	28	26	8	8	26–33	26–34	28	30	2.7	2.3
S7	32	32	8	8	27–34	28–34	31	32	2.6	2.3
S8	31	34	8	8	30–34	30–34	33	30	1.5	1.6
S9	32	34	8	8	31–34	30–33	32	21	1.2	1.4
S10	28	32	8	8	27–30	29–22	28	32	1.5	1.4
S11	18	22	8	8	18–20	19–38	19	33	0.7	0.9
MD4	24	24	9	9	17–26	20–34	23	26	3.4	5.1
MD6	50	48	9	9	32–56	38	46	49	7.6	5.2
MD8	64	60	7	10	60–70	57–44	63	62	3.6	2.9
VLT2	11	l6	9	10	10–16	10–15	12	15	2.4	2.1
LVS5	16	16	9	10	12–21	10	16	15	2.9	1.9
LVS7	20	20	9	10	18–28	20–26	21	21	3.0	1.4
LVS8	24	24	9	10	21–30	22–26	24	24	3.0	1.4
LAT8	16	19	7	10	16–21	14–32	18	20	2.0	2.5
LVS9	28	27	8	10	24–30	30–64	27	27	2.0	2.0
LTS11	108	130	7	10	100–114	92–105	109	121	4.0	9.6
LTAS11	26	N/A	9	N/A	25–30	49	27	N/A	1.7	N/A

Numbers, where inserted, indicates segment number

lat Lateral accessory tubule, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lvs* lateroventral spine, *md* middorsal spine, *msw* maximum sternal width, *n* number of measured specimens, *s1–s11* segment lengths of trunk segments 1–11, *sd* standard derivation, *sw* standard width, *tl* trunk length, *vlt* ventrolateral tubule

Table 6 Summary of nature and location of sensory spots, glandular cell outlets, spines and tubules arranged by series in *Echinoderes riceae* n. sp

Segments	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss					gco1	
2	gco1			ss					tu	ss, gco1
3	gco1		ss							gco1
4	ac	gco1								gco1
5	gco1		ss		ss			tu		ss, gco1
6	ac	gco1, ss			ss					ss, gco1
7	gco1		ss		ss			ac		gco1
8	ac	gco1, ss					tu	ac		gco1
9		gco1, ss	ss	ss		sp		ac	ss	gco1
10	gco1		ss	tu					ss	gco1
11		ss					ltas	lts		

ac Acicular spine, *gco1* glandular cell outlet type 1, *la* lateral accessory, *ld* laterodorsal, *ltas* lateral terminal accessory spine, *lts* lateral terminal spine, *lv* lateroventral, *md* middorsal, *ml* midlateral, *pd* paradorsal, *sd* subdorsal, *sl* sublateral, *sp* sieve plate, *ss* sensory spot, *tu* tubule, *vl* ventrolateral, *vm* ventromedial

the posterior side of the sensory spot, with usually one very long seta or spine pointing backwards and reaching far beyond the sensory spot limit (Fig. 10f). Cuticular hairs on this and the following segments quite long, emerging from bracteated perforation sites. Cuticular hair pattern extending from the midventral area toward the tergal–sternal junctions; a small area of cuticular hairs without perforation sites is present paraventrally (Fig. 10d). Tergal plates with a median belt of perforation sites (Fig. 7b). Pectinate fringe slightly longer than on previous segment.

Segment 3 consists of one tergal and two sternal plates as do the remaining segments to the 11th. (Figs. 7a, 9b). Spines or tubules are not present. A pair of sensory spots is present in a subdorsal position. Cuticular hair pattern and pectinate fringe as on previous segment.

Segment 4 with a middorsal spine (Figs. 7b, 9a, 10c), no sensory spots present, cuticular hair pattern similar to that of previous segments. Pectinate fringe well developed.

Segment 5 with one pair of lateroventral tubules (Figs. 7a, 9b, c, 10e). Paired sensory spots in ventromedial, subdorsal and midlateral positions. Cuticular hair patterns and pectinate fringe are similar to the preceding segments.

Segment 6 with a middorsal spine (Figs. 7b, 9a, 10c). No lateroventral spines or tubules present (Figs. 7a, 9c, 10e). Paired ventromedial, paradorsal and midlateral sensory spots. Cuticular hair pattern and pectinate fringe as in segment 5.

Segment 7 with one pair of lateroventral spines (Figs. 7a, 9c, 10e). Paired subdorsal and midlateral sensory spots. Cuticular hair patterns and pectinate fringe as in preceding segments.

Segment 8 with a middorsal spine (Figs. 7b, 9a), one pair of lateroventral spines, and lateral accessory tubules slightly separated from the lateroventral spines (Figs. 7a, 9d, 10e). A pair of paradorsal sensory spots present. Cuticular hair pattern and pectinate fringe similar to that of previous segments.

Segment 9 with one pair of lateroventral spines (Figs. 7a, 9b, d). Paired sensory spots present in ventrolateral, laterodorsal, subdorsal and paradorsal positions. Paired protonephridial openings present in sublateral positions; those openings are not sieve-plate-like, but are formed by a small opening surrounded by few pores and several papillae (Figs. 9d, 10f). Cuticular hair pattern and pectinate fringe similar to that of previous segments.

Segment 10 without spines. Males and females with a pair of laterodorsal tubules (Figs. 7b, d, 9a). Paired ventrolateral and subdorsal sensory spots present, the latter with a long conspicuous hair emerging (Fig. 10h). The posterior margin of the segment has a free flap with a midventral extension covering partially segment 11. The primary pectinate fringe is very short ventrolaterally, but increases in length toward the midventral position. Cuticular hair pattern more widely separated dorsally, and restricted to slightly smaller area ventrally.

Segment 11 with one pair of long and flexible lateral terminal spines (Figs 7a, b, 10g). Paradorsal sensory spots are present adjacent to the middorsal fringed area of the tergal plates. No cuticular hairs with perforation sites noted; short pectinate fringe present. Tergal extensions are pointed and with a small notch on the medial side (Figs. 7a, b, 9f, 10g, h). Their margins have cuticular hair-like extensions and fringes that are very long midlaterally and anterior to the insertion of the lateral terminal spines (Fig. 10g, h). Sternal plates short and triangular with fringed margins. Females with paired lateral terminal accessory spines (Figs. 7a, b, 9f, 10g); males with three pairs of

penile spines (P1–P3) instead. P1 and P3 longer than P2 which is shorter and many times thicker (Figs. 7c, d, 9d, g, 10h, i).

Remarks

Echinoderes riceae n. sp. is one of 12 species in the genus having middorsal spines on segments 4, 6 and 8. From these, 6 species (*Echinoderes abbreviatus* Higgins 1983; *Echinoderes higginsi* Huys and Coomans 1989; *Echinoderes hispanicus* Pardos et al. 1998; *Echinoderes kristenseni* Higgins 1985; *Echinoderes riedli* Higgins 1978; and *Echinoderes wallaceae* Higgins 1983) share the presence of lateroventral tubules on segment 2 and lateroventral spines on segments 6–9 with a lateral accessory tubule on segment 8 (see Higgins 1978, 1983, 1985; Huys and Coomans 1989; Pardos et al. 1998). However, *E. riceae* n. sp. shows a unique spine formula lacking the lateroventral spine on segment 6; thus, it is easily discriminated from all other similar species. Another relevant feature is the nearly complete absence of cuticular hairs on segment 1. Except for the cuticular hairs associated with the dorsal sensory spots, the surface of this segment is ventrally smooth giving it a special appearance only shared by few echinoderid species such as *Echinoderes coulli* Higgins 1977. This species show great differences in spine/tubule formula with *E. riceae* lacking middorsal or lateroventral spines and only showing lateroventral tubules on segments 5 and 8 (see Higgins 1977); therefore, there is no way to confuse them. However, the presence of cuticular hairs is a feature that has to be used with caution because not all species described (mostly old descriptions) contain this information in detail.

Three other kinorhynchs of this genus are known from the area, *E. adrianovi* n. sp., *E. horni* and *E. spinifurca*. As noted earlier, *E. adrianovi* n. sp. have middorsal spines on segments 4–8, lateroventral spines on segments 6–9, subdorsal and ventrolateral tubules on segment 2 and lateral accessory tubules on segment 8. *E. horni* has no middorsal spines, and *E. spinifurca*, although sharing its spine formula with 11 other species, has remarkably long terminal tergal extensions.

Introvert

Echinoderes is the most diverse genus within the phylum Kinorhyncha containing to date 77 species (Neuhaus 2012); unfortunately, only 6 of them have a detailed description of the introvert: *Echinoderes applicitus* Ostmann et al. 2012; *Echinoderes capitatus* Zelinka 1928; *Echinoderes cernunnos* Sørensen et al. 2012; *Echinoderes microaperturus* Sørensen et al. 2012, *E. spinifurca* and *E. tchefouensis* Lou 1934 (Nebelsick 1993; Ostmann et al. 2012; Sørensen and Pardos 2008; Sørensen et al. 2012b). Regarding the introvert structure, the echinoderid species with the greatest resemblance with *E. riceae* n. sp is *E. applicitus* showing identical uneven sectors and even sectors 4 and 8. The only differences are the number and distribution of leaf-like scalids in sectors 2 and 10 and the lack of a spinoscalid in ring 06 of sector 6. Despite the similarities showed by the introvert characters in *E. riceae* n. sp and *E. applicitus*, trunk features are completely different. Another species, but from a different genus, showing a similar scalid arrangement to *E. riceae* n. sp is *Meristoderes macracanthus* Herranz et al. 2012 (see Herranz et al. 2012); differences occur with respect to the number of scalids in the posteriormost rings and in *M. macracanthus*, its lack of leaf-like lateral scalids on sectors where trichoscalids are present (2, 4, 5, 7, 10). This feature makes the arrangement of scalids within the sector asymmetrical; a trait which is also shared by *E. riceae* n. sp, *E. applicitus, E. microaperturus*, *E. cernunnos*, *E. tchefouensis* in sectors 5 and 7 as well as *Meristoderes herranzae* Sørensen et al. 2012 (see Sørensen et al. 2012a) in sectors 2, 4, 8, 10, although the last four species have less spinoscalids in even sectors.

The scalid pattern of *E. riceae* n. sp. is unique. However, the arrangement of scalids by sectors with "double diamonds" in uneven sectors and "quincunxes" in the even ones (Fig. 8) seems to be rather common in the echinoderid genera *Echinoderes, Cephalorhyncha* and *Meristoderes*, and also in other genera such as *Antygomonas*, *Dracoderes*, *Centroderes* or *Pycnophyes*. The number of scalids of *E. riceae* n. sp (115) seems to be the highest ever reported, showing more scalids in the uneven numbered sectors. The presence of more scalids in the uneven sectors was previously reported by Sørensen et al. (2012b) as a common feature in the majority of species among Kinorhyncha. Nevertheless, the taxonomic and phylogenetic significance of the introvert characters, mainly type, number and arrangement of scalids, need to be tested and evaluated thoroughly, and thus, the resemblances reported should be used with caution.

Pycnophyes norenburgi n. sp. (Figs. 11, 12, 13; Tables 7, 8)

Order Homalorhagida (Zelinka 1896) Higgins 1964
Family Pycnophyidae Zelinka 1896
Genus *Pycnophyes* Zelinka 1907

Diagnosis

Pycnophyes with middorsal elevations on segments 1–9 flanked by paradorsal sensory spots. These sensory spots are associated with butterfly-like intracuticular atria on

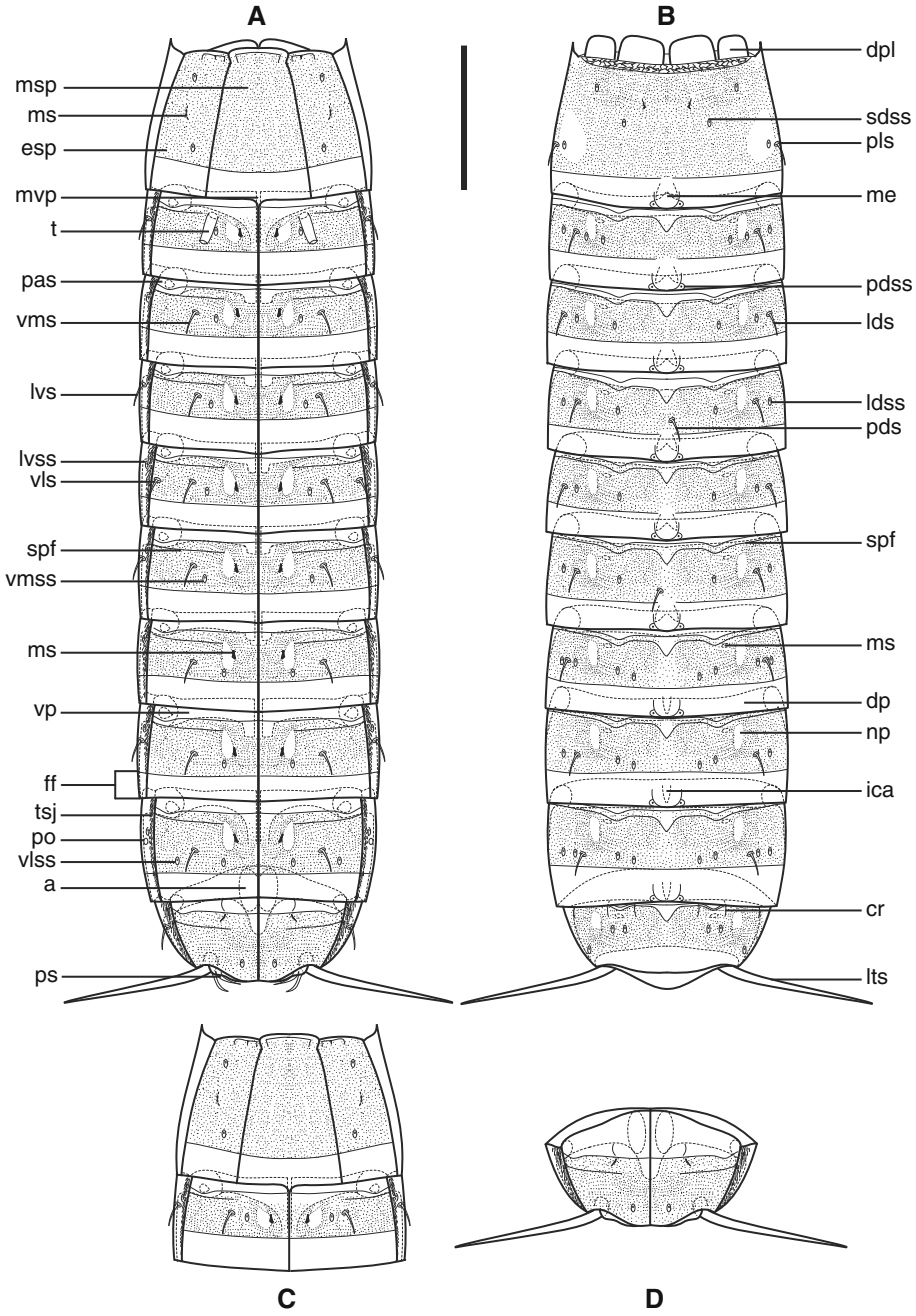

Fig. 11 Line art illustrations of *Pycnophyes norenburgi* n. sp. **a** Male, ventral view. **b** Male, dorsal view. **c** Female, segments 1–2, ventral view. **d** Female, segments 10–11, ventral view. *a* apodeme, anteromesial thickenings of ventral pachycyclus, *cr* cuticular ridge, *dp* dorsal pachycycli, *dpl* dorsal placid, *esp* episternal plate, *ff* free flap, *ica* intracuticular atria of sensory spot, *lds* laterodorsal seta, *ldss* laterodorsal sensory spot, *lts* lateroterminal spine, *lvs* lateroventral seta, *lvss* lateroventral sensory spot, *me* middorsal elevation, *ms* muscular scar, *msp* midsternal plate, *mvp* midventral process, *np* naked patch, *pas* peg and socket joint, *pds* paradorsal seta, *pdss* paradorsal sensory spot, *pls* paralateral seta, *po* protonephridial opening, *ps* penile spine, *sdss* subdorsal sensory spot, *spf* secondary pectinate fringe, *t* tube, *tsj* tergosternal junction, *vms* ventromedial seta, *vmss* ventromedial sensory spot, *vls* ventrolateral seta, *vlss* ventrolateral sensory spot, *vp* ventral pachycyclus. *Scale bar* 100 μm

segments 1–6 and with middorsal intracuticular atria on segments 7–9. Middorsal elevations less conspicuous on segments 7–9. Unpaired paradorsal seta on segments 4 and 6. Laterodorsal setae on segments 2–9, paralateral ones on segment 1, lateroventral ones on segments 2, 4, 6, 8 and 10 (the latter only in males), ventrolateral ones on segment 5 and ventromedial ones on segments 2–9 (absent on segment 2 in males). Conspicuous elongated paraventral muscular scars on segments 2–10, only visible with LM. Type 1 sensory spots in paradorsal positions on segments 1–9; any other sensory spot belongs to type 2. Trunk surface appears finely perforated in LM.

Etymology

This species is named in honor of Dr. Jon Norenburg, head of Zoology Department at the National Museum of Natural History, Smithsonian Institution, Washington DC, for his continuous contribution and support of meiofauna research worldwide.

Type material

Thirteen specimens (4 males and 9 females) mounted in Fluoromount G® were studied with LM, and 4 specimens

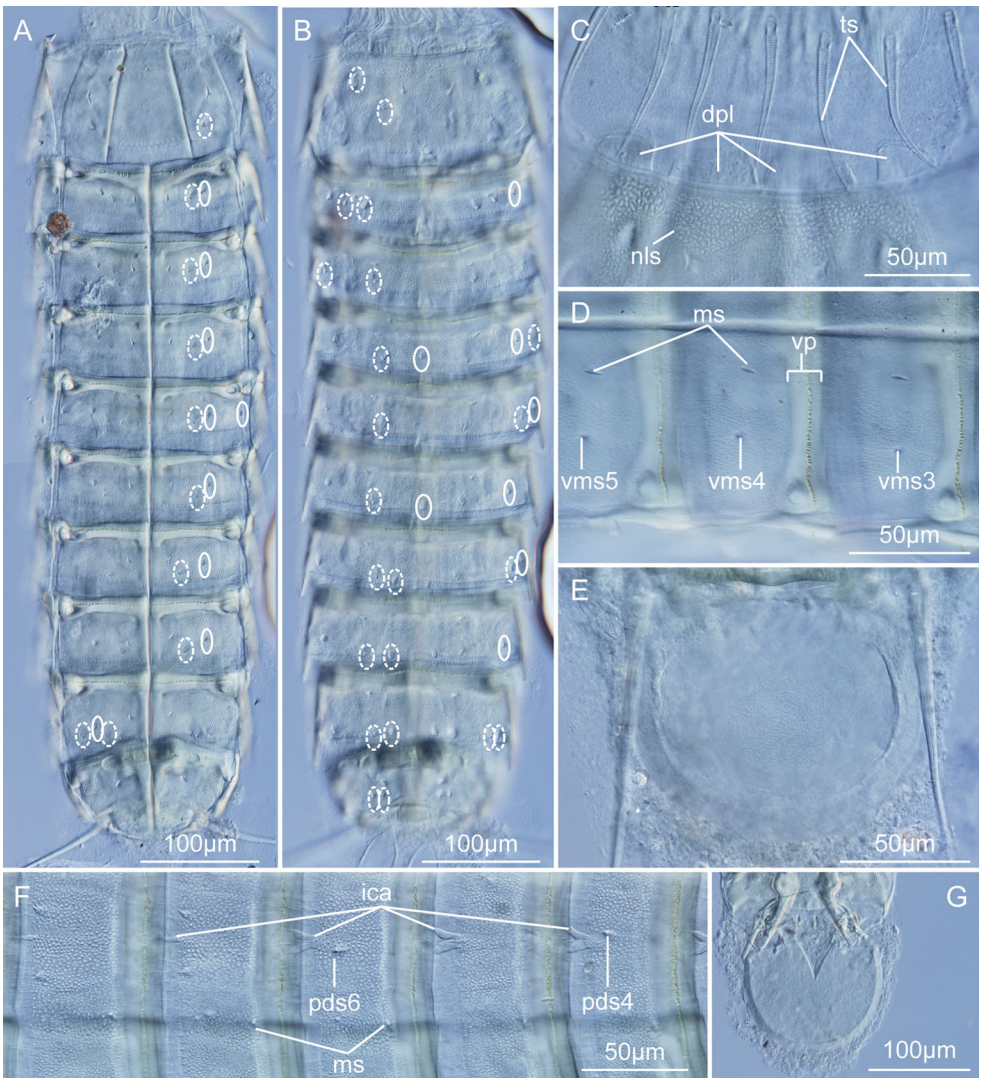

Fig. 12 Light micrographs showing details in neck and trunk morphology of *Pycnophyes norenburgi* n. sp. **a** Allotypic female, USNM 1207884, ventral view. **b** Allotypic female, USNM 1207884, dorsal view. **c** Male, dorsal placids. **d** Male, sternal plates of segments 3–5. **e** Female, spermatophore with a tangled ball of sperm inside. **f** Holotypic male, USNM X, dorsal view of segments 4–8. **g** Female, spermatophore overview attached to the last segment of the trunk between the two laterotermINAL spines. Sensory spots are marked with dotted circlets. Setae are marked with *circlets*. *dpl* dorsal placids, *ica* intracuticular atria of sensory spot, *ms* muscular scar, *nls* net-like structure, *pds* paradorsal seta, *ts* trichoscalid, *vms* ventromedial seta, *vp* ventral pachycyclus. Digits after abbreviations refer to segment numbers

(3 males and 1 female) were studied with SEM. Holotype: adult male collected on August 2011 at the 20 miles station, Fort Pierce, off the Floridian West coast (Fig. 1) 27°30,84′N 79°54,86′ W; 152 m depth from fine mud, deposited at the National Museum of Natural History (Smithsonian Institution) under accession number USNM 1207950. Allotype: adult female, same collecting data as holotype, deposited at the National Museum of Natural History under accession number USNM 1207884. Paratypes: 1 male and 4 females, same collecting data as holotype, deposited at the National Museum of Natural History under accession numbers USNM 1207885–1207889. The remaining material is deposited in the Meiofauna Laboratory collection at the Facultad de Biología, Universidad Complutense de Madrid, accession numbers K15/37-43.

Additional material

Because of the close resemblance of the new species with *Pycnophyes frequens*, topotype specimens of this latter species were loaned from the Smithsonian Institution and checked with LM. This material includes two males and two females collected by R. P. Higgins on June 13, 1962, in Salisbury Cove, Mount Desert Island, Maine, position 44°26′N, 68°17′W; 15 m depth, gray mud, deposited in the

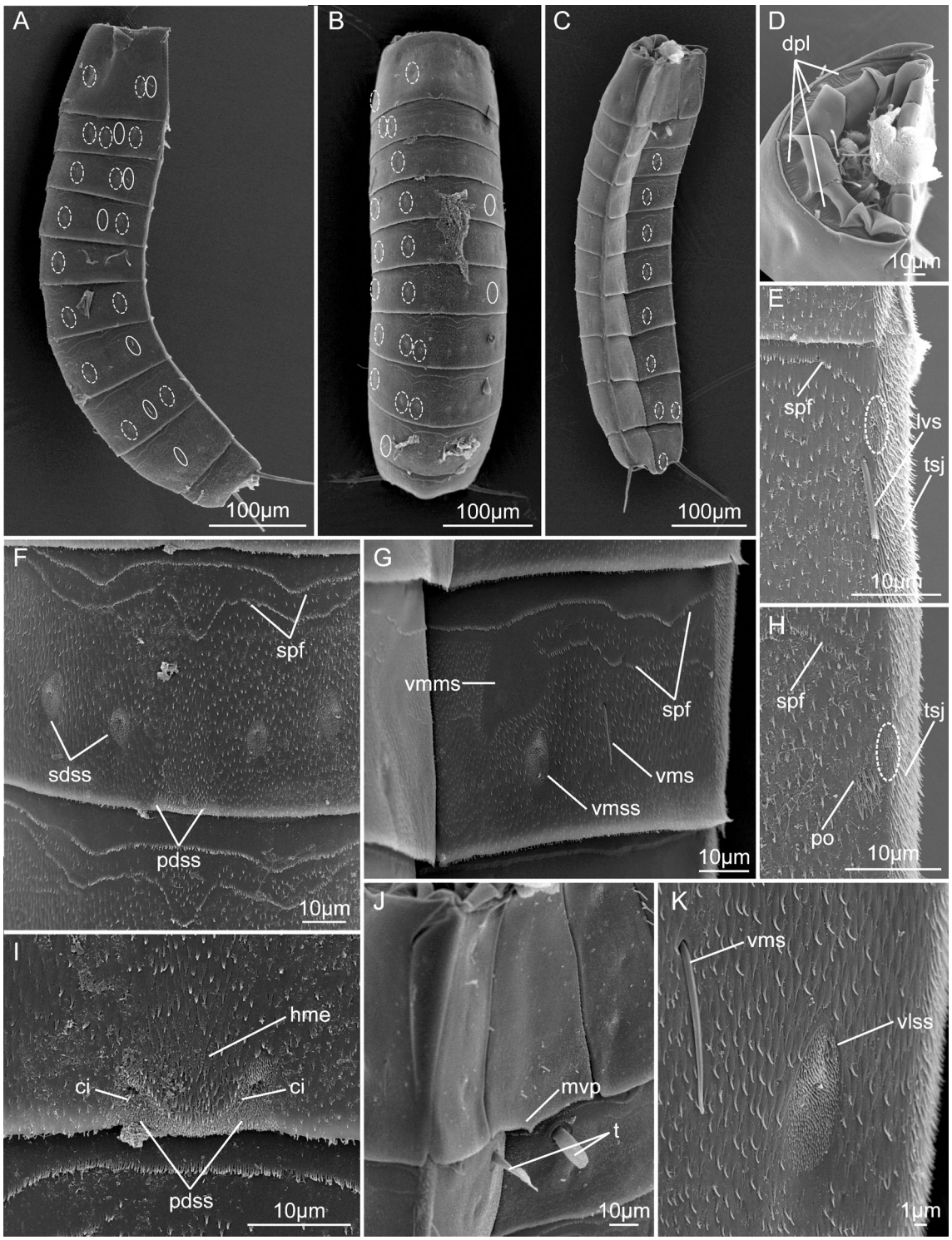

Fig. 13 Scanning electron micrographs showing trunk morphology and cuticular details in *Pycnophyes norenburgi* n. sp. **a** Male, lateral view. **b** Male, dorsal view. **c** Male, lateroventral view. **d** Male, dorsal placids. **e** Male, lateral view of segment 4. **f** Male, dorsal view of segment 7. **g** Male, ventral view of segment 7. **h** Male, lateral view of segment 9, protonephridial opening. **i** Male, dorsal view of segment 6. **j** Male, lateroventral view of segments 1–2. **k** Male, ventral view of segment 9. *ci* cilium, *dpl* dorsal placid, *hme* hairy middorsal elevation, *lvs* lateroventral seta, *mvp* midventral process, *pdss* paradorsal sensory spot, *po* protonephridial opening, *sdss* subdorsal sensory spot, *spf* secondary pectinate fringe, *t* tube, *tsj* tergosternal junction, *vmms* ventromedial muscular scar, *vms* ventromedial seta, *vmss* ventromedial sensory spot, *vlss* ventrolateral sensory spot. Sensory spots are marked with *dotted circlets*. Setae are marked with *circles*

Table 7 Measurements (in µm) for adults of *Pycnophyes norenburgi* n. sp

Character	*n*		Range		Average		SD	
	♀	♂	♀	♂	♀	♂	♀	♂
TL	5	4	601–669	646–738	635	710	28.1	42.9
SW10	3	1	129–141	129	135	–	8.9	–
SW/TL (%)	3	1	19–23	0.18	0.21	–	0.03	–
MSW-8	3	1	151–152	155	152	–	0.03	–
MSW/TL (%)	3	1	0.23–0.25	0.21	0.24	–	0.02	–
LTS/TL	3	2	0.16–0.19	0.17	0.17	0.17	0.02	0.01
S1	3	1	103–109	104	107	–	4.1	–
S2	3	1	62–67	68	64	–	3.1	–
S3	3	1	64—69	63	66	–	3.8	–
S4	3	1	58–70	70	64	–	8.7	–
S5	3	1	59–68	69	63	–	5.9	–
S6	3	1	63–71	74	67	–	5.9	–
S7	3	1	69–70	78	69	–	1.3	–
S8	3	1	74–77	81	76	–	2.5	–
S9	3	1	67–73	80	70	–	4.1	–
S10	3	1	70–78	86	74	–	5.8	–
S11	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
LTS11	4	2	108–122	120–133	115	125	7.2	0.04
SPL	5	0	97–125	–	108	–	13.3	–
SPW	5	0	103–136	–	121	–	13.3	–
SWT	5	0	8–13	–	11	–	1.7	–

lts Lateral terminal spine, *msw* maximum sternal width, *n* number of measured specimens, *sd* standard deviation, *spl* spermatophore length, *spw* spermatophore width, *sw* standard width, *s1–s11* segment lengths of trunk segments 1–11, *swt* spermatophore wall thickness, *tl* trunk length

marine invertebrate collection of US National Museum, under accession numbers W30973–W30974 and 1185888–1185889. Loaned specimens were in poor condition and were subsequently remounted in glycerin–paraffin (two specimens) and Fluoromount G® (two specimens). The specimen under accession number 1185888, male, was assigned as neotype. Moreover, seven specimens of *P. frequens* collected from Woods Hole (Massachusetts) loaned for examination from the Natural History Museum of Denmark (accession numbers ZMUC KIN-00667 to KIN 00673).

Description

Measurements and dimensions of the examined specimens are summarized in Table 7. The distribution of cuticular setae and sensory spots is summarized in Table 8.

Mouth cone and introvert armature could not be examined in detail in any of the prepared specimens.

Neck with 4 dorsal and 2 ventral placids. All placids seem robust with a concave surface. Medial two dorsal placids wide and rectangular, whereas the lateral two dorsal placids are narrower, with a square profile (Figs. 11b, 12c, 13d). Ventral placids smaller than dorsal ones. Ventral placids widely rectangular, extending from the midventral line to the middle region of the episternal plates. All placids without trichoscalid plates, joined and articulated with the anterior edge of the first trunk segment. Placids continue anteriorly and merge with the thin and flexible cuticle of the introvert.

Trunk with 11 segments (Figs. 11a, b, 12a, b, 13a, c). First segment with one tergal and three ventral plates. Remaining segments with one tergal and two sternal plates. The segment width is fairly constant, with the maximum width at segment 8, turning narrower posteriorly. Cuticle appears thick, pachycycli and peg and socket joints appear well developed on all segments, the latter less conspicuous on segment 10. Most trunk surface, except pairs of naked oval patches located laterodorsally and ventromedially, covered by short, scale-like cuticular hairs without perforation sites (Figs. 11a, b). These cuticular hairs are longer on the middorsal elevation and on the first half of the segment than on the posterior one. In LM, the cuticle appears finely punctuated (Fig. 12f), probably perforated by numerous intracuticular pores. However, these do not reach the surface that appears smooth with SEM, except for the scale-like hairs referred to above (Figs. 13f, g). Tergal plates of segments 1–6 with paradorsal sensory spots

Table 8 Summary of nature and location of cuticular features arranged by series for adults of *Pycnophyes norenburgi* n. sp

f female condition of sexually dimorphic character, *ld* laterodorsal, *lts* lateroterminal spine, *lv* lateroventral, *m* male condition of sexually dimorphic character, *p* penile spine, *pd* paradorsal, *pl* paralateral, *sd* subdorsal, *se* setae, *ss* sensory spot, *t* tube, *vl* ventrolateral, *vm* ventromedial, *1* unpaired cuticular structure

Segments	PD	SD	LD	PL	LV	VL	VM
1	ss	ss	ss, ss	se			ss, ss
2	ss	ss	ss, se, ss		se, ss		ss, se(f), t(m)
3	ss	ss	ss, se		ss		ss, se
4	se(1), ss	ss	se, ss		se, ss		ss, se
5	ss	ss	ss, se		ss	se	ss, se
6	se(1), ss	ss	se, ss		se, ss		ss, se
7	ss	ss, ss	ss, se, ss		ss		ss, se
8	ss	ss, ss	se, ss		se, ss		ss, se
9	ss	ss, ss	se(m), ss, ss		ss	ss	ss, se
10		ss, ss	ss		se(m)		ss
11					lts		

associated with conspicuous butterfly-like intracuticular atria; middorsal elevations never surpasses the posterior edge of the segment (Figs. 12f, 13f, i). Tergal plates of segments 7–9 with inconspicuous middorsal elevations and middorsal unpaired intracuticular atria, not butterfly-like (Figs. 11b, 12f, 13f). Two pairs of muscular scars, one conspicuous and elongated in paraventral position and one more rounded, oblique and less clear, in subdorsal position (Fig. 12d). Free flaps striated longitudinally, only visible with LM. Minute pectinate fringe, only visible with SEM. Secondary pectinate fringes located in the anteriormost region of the segments.

Segment 1 with lateral margins of tergal plate projecting anteriorly into horn-like extensions. Tergal anterior edge of segment smooth, not denticulated, followed by a net-like area, not always well developed (Fig. 12c). Tergal plate with middorsal elevation flanked by one pair of paradorsal sensory spots associated with intracuticular atria. One pair of paralateral setae and three additional pairs of sensory spots, one subdorsal and two laterodorsal. From these latter, one is located near the anterior margin of the segment, and the other is very close to the already mentioned paralateral setae. All sensory spots on this and the following segments (except the paradorsal ones), belong to type 2. They are oval and elongated, with two pores, median and anterior, surrounded by numerous cuticular papillae. A cilium emerges from the median pore, while the anterior pore opens on a short elevated tube. The paradorsal sensory spots share an elongated area of cuticular papillae. Their cuticular papillae are smaller, surrounding a single pore through which a cilium emerges (Fig. 13i). Ventral side with one trapezoidal midsternal plate and two episternal plates, all of them with an inconspicuous cuticular ornamentation in its anterior region, weakly concave. Posterior margin of midsternal plate with a pointed midventral process (Fig. 13j). Each episternal plate with a curved, crescentic muscular scar in the middle region of the plate and two ventromedial sensory spots, one located at the anterior third of the segment, and one at the posterior third. Pectinate fringe on the posterior edge of the segment reduced, only detectable with SEM.

Segment 2 showing a tergal plate with a middorsal elevation flanked by one pair of paradorsal sensory spots with conspicuous intracuticular atria. One pair of laterodorsal and lateroventral setae. Four additional pairs of sensory spots located in the middle region of the tergal plate: one subdorsal, two laterodorsal and one lateroventral. One of the laterodorsal sensory spots appears mesial to the laterodorsal seta and the other one laterally, close to the paralateral line (Fig. 11b). Lateroventral sensory spots are smaller and narrower than others and appear located adjacent to the tergosternal junctions (Fig. 13e, h). One pair of subdorsal oval muscular scars, inconspicuous and only visible with LM, located anterior to the subdorsal sensory spots, between this sensory spot and one laterodorsal-naked oval patch. Two secondary pectinate fringes run parallel and close to the anterior edge of the segment (Fig. 13f). The anteriormost one shows two subdorsal indentations pointing backwards, while the posterior one has three similar indentations, two subdorsal and one middorsal, this latter deeper and pointed (Figs. 11b, 13f). Sternal plates with a pair of ventromedial sensory spots and a pair of paraventral elongated muscular scars. A pair of ventromedial naked oval patches appears adjacent to the muscular scars. Females furthermore with a pair of ventromedial setae (Fig. 11c). Males with one pair of ventromedial tubes, big and short (Figs. 11a, 13j). Longitudinal band of densely packed cuticular hairs along the tergosternal junctions (Figs. 13e, h). Two secondary fringes near and parallel to the anterior margin of the segment. The anteriormost extends along the whole ventral margin of the segment and shows ventrolateral indentations. The posteriormost without indentations and running from the tergosternal junctions to the ventromedial naked patches. Pectinate fringe as on previous segment.

Segment 3 showing a tergal plate with middorsal elevation, one pair of paradorsal sensory spots associated with intracuticular atria similar to those on previous segments. One pair of laterodorsal setae located more laterally than the same on previous segment. Three additional pairs of sensory spots, one subdorsal, one laterodorsal and one lateroventral. The laterodorsal pair of sensory spots appears in the same position as the laterodorsal setae of segment 2 (Figs. 11b, 12b, 13a). Lateroventral sensory spots at the same position as those on the previous segment. One pair of subdorsal muscular scars located anterior to the subdorsal sensory spots and one pair of laterodorsal-naked oval patches. Sternal plates with one pair of ventromedial setae located slightly anterior to the sensory spots (Fig. 11a).

Segment 4 showing a tergal plate with a middorsal elevation, one pair of paradorsal sensory spots associated with intracuticular atria similar to those on previous segments. A single, unpaired paradorsal seta on the right side of the middorsal elevation (Figs. 11b, 12f). One pair of laterodorsal and lateroventral setae, the former appears in the same position as the laterodorsal sensory spots of segment 3 (Figs. 11b, 12b, 13a). Three pairs of sensory spots, one subdorsal, one laterodorsal and one lateroventral, the latter same as on previous segments (Fig. 13e). Laterodorsal sensory spots appear in the same position as the laterodorsal setae of segment 3 (Fig. 13a). One pair of subdorsal muscular scars and one pair of laterodorsal-naked oval patches as those on segment 3. Sternal plates as on segment 3 (Figs. 11a, 12d).

Segment 5 with tergal and sternal plates as those on segment 3 but with a pair of ventrolateral setae.

Segment 6 with a tergal plate similar to that on segment 4 but with the single, unpaired paradorsal seta on the left side of the middorsal elevation (Figs. 11b, 12f, 13i). Sternal plates as those on segment 4.

Segment 7 showing a tergal plate with middorsal elevation less conspicuous than those on previous segments. Middorsal intracuticular atria pointed, not butterfly-like (Fig. 12f). One pair of laterodorsal setae. Six pairs of tergal sensory spots, one paradorsal, two subdorsal (Fig. 11b, 13f), two laterodorsal, on both sides of the laterodorsal seta; and one lateroventral same as on previous segments. Sternal plates similar to those on segment 3, with the ventromedial sensory spots mesially displaced (Figs. 11a, 12a, 13b, g).

Segment 8 showing a tergal plate with middorsal elevation, intracuticular atria and paradorsal sensory spots similar to those on segment 7. Without paradorsal setae (Fig. 12f). Pairs of laterodorsal and lateroventral setae, the former located in the same position as the mesial laterodorsal sensory spots of segment 7 (Figs. 11b, 12b, 13a). Four additional pairs of sensory spots: two subdorsal, one laterodorsal in the same position as the laterodorsal setae of segment 7, and one lateroventral same as on previous segments (Figs. 12b, 13a). Sternal plates as on segment 7.

Segment 9 with tergal plate same as on segment 8 but with an additional pair of laterodorsal sensory spots. Laterodorsal setae present in males only. Protonephridial opening located paralaterally, not sieve-like but formed by several minute tubes with bevelled endings and surrounded by few short cuticular hairs (Fig. 13h). Sternal plates similar to those on segment 7 but with one pair of ventrolateral sensory spots (Figs. 11a, 13c, k).

Segment 10 showing a tergal plate without middorsal elevation or intracuticular atria. One pair of lateroventral setae present in males only (Figs 11a, d). With one pair of subdorsal muscular scars and three pairs of sensory spots: two subdorsal and one laterodorsal, the latter near the posterior margin of the segment (Fig. 12b). Three pairs of longitudinal cuticular ridges near anterior margin of the segment, two subdorsal and one laterodorsal. Sternal plates with one pair of ventromedial sensory spot near the posterior margin of the segment (Fig. 13c) and one pair of elongated ventromedial muscular scars similar to those on previous segments but reversed and more oblique. One pair of anteromedial apodemes near anterior margin. Females with the apodemes displaced. One pair of ventromedial cuticular ridges. Posterior margin of the segment rounded and moderately projecting ventromedially (Fig. 13c).

Segment 11 showing tergal and sternal plates without any remarkable cuticular features, only a pair of lateroterminal cuticular processes on the tergal plate and one pair of robust lateroterminal spines. Males with two pairs of flexible penile spines of equal size. Some of the studied female specimens bear spermatophores, they are spherical capsules covered by debris, tightly held at the posterior end of the trunk, between the two lateroterminal spines that appear to embrace it (Figs. 12e, g). These spermatophores show a thick wall slightly wider in the middle region than in the lateral areas (Fig. 12e). Measurement data on these spermatophores are included in Table 7. In all cases, the capsules contained a tangled ball of sperm inside without any recognizable arrangement.

Remarks

The new species shares the presence of paradorsal setae exclusively on segments 4 and 6 with only two species: *Pycnophyes cryopygus* Higgins and Kristensen 1988 and *Pycnophyes emarginatus* Higgins 1983. However, *P. cryopygus* presents laterodorsal setae on segments 2, 4, 6–9, whereas the new species has this kind of setae on segments 2–9. Moreover, *P. cryopygus* differs from the new species by the presence of middorsal processes and lateroventral setae on segments 2–4, 6, 8 and 10. Although *P. cryopygus* and the new species have

ventromedial setae on segments 3–9, *P. cryopygus* has these setae on segment 3–6 lined-up and the setae on segment 7–9 are mesially displaced, whereas the new species shows always all of them lined-up, exactly in the same point on each segment. Finally, the distribution of sensory spots and muscular scars in both dorsal and ventral sides is different in both species (Higgins and Kristensen 1988).

Pycnophyes emarginatus and *Pycnophyes norenburgi* n. sp. share the presence of middorsal setae on segments 4 and 6, laterodorsally on segments 2–8 and ventromedially on segments 3–9 (Higgins 1983). However, *P. emarginatus* lacks laterodorsal setae on segment 9 and ventrolateral ones on segment 5, and it also differs from the new species regarding the position of the ventromedial setae with relative to the sensory spots (these setae appear mesial to sensory spots) and the distribution of lateroventral setae and sensory spots (Higgins 1983).

Nevertheless, *P. norenburgi* n. sp. shows most resemblance with *P. frequens*, described from the East coast of USA and redescribed by Higgins (1965). From the information provided in the original description (Blake 1930) and the redescription (Higgins 1965), the distribution pattern of sensory spots and setae cannot be stated reliably. Consequently, the authors requested both topotype material and recently collected specimens from Woods Hole (Massachusetts). Examination of this material allowed a proper identification of the relevant cuticular structures and their position. The protuberances identified by Higgins (1965) as "sensory hair" on segment 5 in ventrolateral position as well as the middorsal ones on segments 4, 6 and 8 correspond to setae (the latter are actually located in paradorsal position, not middorsally). Contrarily, the protuberances observed ventrolaterally on the episternal plates and along the tergal plate of segment 10 are actually sensory spots and not setae. *P. frequens* and the new species described herein share many similarities: the finely perforated trunk surface; the ventral cuticular ornamentation on segment 1; shape and position of paraventral muscular scars (segments 2–10); the naked oval patches next to these paraventral muscular scars, the appearance of pachycycli, peg and socket joints and anteromesial apodemes; the middorsal elevations on segments 1–9 associated with intracuticular atria, the unpaired paradorsal setae, laterodorsal setae on segments 2–9, lateroventral ones on segments 2, 4, 6, 8 and 10 (the latter only in males), ventrolateral ones on segment 5 and ventromedial ones on segments 3–9 (males also with a pair of setae on segment 2). Nevertheless, *P. frequens* bears paradorsal setae on segments 4, 6 and 8, lateroventral ones on segment 9 and laterodorsal ones on segment 9 in both sexes, whereas *P. norenburgi* n. sp. lacks paradorsal setae on segment 8 and lateroventral ones on segment 9, as well as laterodorsal ones on segment 9 in females. Moreover, despite both species show laterodorsal sensory spots not aligned (sensory spots of segments 3, 5 and 7 appear slightly mesially displaced), all the specimens of *P. norenburgi* n. sp. have alternation as to the position between laterodorsal setae and sensory spots of these three segments, so neither laterodorsal setae nor sensory spots appear aligned, while *P. frequens* has the laterodorsal setae lined-up. Furthermore, the tergal anterior ornamentation of the first segment with a net-like pattern in *P. norenburgi* n. sp. lacking it in *P. frequens*, the number and shape of secondary pectinate fringes, and the distribution of longitudinal cuticular ridges are different in both species. All these characters were consistently found in all the specimens studied from Florida and support the erection of the new species *P. norenburgi* n. sp.

The presence of specimens bearing a spherical capsule with sperm inside attached to the segment 11 is not new; such structure, identified as spermatophore, was observed by several authors in different kinorhynch species, most of them homalorhagids: *Centroderes spinosus*, *Kinorhynchus ilyocryptus* (Higgins 1961), *K. langi*, *Kinorhynchus phyllotropis* Brown and Higgins 1983, *Pycnophyes dentatus* (Reinhard 1881), *Pycnophyes flaveolatus* Zelinka 1928, *P. frequens*, *Pycnophyes greenlandicus* Higgins and Kristensen 1988 and *Pycnophyes kielensis* Zelinka 1928 (see Nyholm 1947; Higgins 1965, 1974; Brown 1983; Kristensen and Higgins 1991; Adrianov and Malakhov 1999; Neuhaus 2012). Data on number of individuals bearing such capsules is available only for *K. phyllotropis* (see Brown 1983), *P. dentatus* and *P. kielensis* (see Neuhaus 2012). The incidence detected was similar for these three species, 1 of 88 females, while in the present work, about 50 out of 100 collected specimens had this structure. However, only few specimens kept it attached after the fixing process, perhaps explaining the low incidence reported in the literature. In all cases, the spermatophores were observed attached to females, with sperm inside as a tangled ball suggesting that the sperm could have started the migration into the female body through the gonopores (Brown 1983).

However, the knowledge about these spermatophores and their function in reproduction is still limited, as well as how males produce the spermatophores, how these are transferred from males to females and how and where the fertilization occurs (Neuhaus 1999). Also, the role of the so-called penile spines of males and their special tubes of segment 2 is to be determined, as well as the female oviposition (Nyholm 1947; Lang 1963; Brown 1983; Kristensen and Higgins 1991; Neuhaus and Higgins 2002). Future studies, probably through culturing techniques, would shed light into the reproductive processes of kinorhynchs.

Conclusion

To date, studies in the Atlantic Floridian waters have reported a total of 7 species of kinorhynchs belonging to 4 different genera: *A. paulae*, *E. bookhouti*, *E. horni*, *E. spinifurca*, *T. seminoli*, *Z. brightae* and *Z. floridensis.* From these only *E. bookhouti* was not found in Fort Pierce. The present contribution adds four new species to the area: *A. gwenae* n. sp*, E. adrianovi* n. sp.*, E. riceae* n. sp. and *P. norenburgi* n. sp. Very recent samplings in the region have revealed additional, yet undescribed kinorhynch species (Herranz pers. obs.), showing that the area still holds a high diversity of Kinorhyncha to unveil.

The 20 miles station seems to be a special locality; its particular type of sediment called "green/gray mud" shows a highly diverse kinorhynch fauna with 5 different genera and 6 different species: *Z. floridensis*, *Centroderes* sp. 1, *E. adrianovi* n. sp. *E. riceae* n. sp. *A. gwenae* n. sp. and *P. norenburgi* n. sp. All these species were found on this locality exclusively and are not present in nearby localities with different sediments. It should be noted that *Z. floridensis*, *E. riceae* and *P. norenburgi* n. sp. were also very abundant.

Acknowledgments The authors are grateful for the assistance of Dr. Mary Rice and Dr. Jon Norenburg, Smithsonian Institution, who acted as scientific advisors to M. Herranz during her research visit to the Smithsonian Marine Station at Fort Pierce (SMSFP) and have been colleagues and friends of R. P. Higgins for many years. Dr. Valerie Paul (Head Scientist) and the staff of the SMSFP provided us with excellent working facilities and technical support. The loan of topotype material of *Pycnophyes frequens* by the Smithsonian Institution is greatly acknowledged. Dr. B. Neuhaus, Museum für Naturkunde, Berlin, kindly remounted two loaned specimens of *P. frequens.* The generous contribution of Dr. M. V. Sørensen, Natural History Museum of Denmark, for his loan of specimens of *P. frequens* from Woods Hole, Massachusetts, is deeply appreciated. The staff of the Centro Nacional de Microscopía Electrónica is acknowledged for the use of the SEM. This work was financed by the research project CGL 2009-08928 (Ministerio de Ciencia y Tecnología, Government of Spain) to FP and a Link Foundation grant to MH. This publication is Smithsonian Marine Station no. 926.

References

Adrianov AV, Malakhov VV (1999) Kinorhyncha. In: Jamieson BGM (ed) Reproductive biology of invertebrates. Vol. IX, Part A. Wiley, Chichester, pp 193–211

Bauer-Nebelsick M (1995) *Zelinkaderes klepali* sp.n. from shallow water sands of the Red Sea. Ann Nat Mus Wien 97B:57–74

Bauer-Nebelsick M (1996) *Antygomonas oreas* sp. n., a new deep sea kinorhynch from the Pacific Ocean (Kinorhyncha: Cyclorhagida). Ann Nat Mus Wien 98B:5–22

Blake CH (1930) Three new species of worms belonging to the order Echinodera. Biol Surv Mt Desert Reg 4:3–10

Brown R (1983) Spermatophore transfer and subsequent sperm development in a homalorhagid Kinorhynch. Zool Scr 12:257–266

Brown R (1989) Morphology and ultrastructure of the sensory appendages of a kinorhynch introvert. Zool Scr 18(4):471–482

Brown R, Higgins RP (1983) A new species of Kinorhynchus (Homalorhagida, Pycnophyidae) from Australia with a redescription and range extension of other Kinorhyncha from the South Pacific. Zool Scr 12:161–169

Ga Ordóñez D, Pardos F, Benito J (2008) Three new Echinoderes (Kinorhyncha, Cyclorhagida) from North Spain, with new evolutionary aspects in the genus. Zool Anz 247:95–111

Herranz M, Thormar J, Benito J, Sánchez N, Pardos F (2012) *Meristoderes* gen. nov., a new kinorhynch genus, with the description of two new species and their implications for echinoderid phylogeny (Kinorhyncha: Cyclorhagida, Echinoderidae). Zool Anz 251:161–179

Higgins RP (1961) Three new homalorhagid kinorhynchs from the San Juan Archipelago Washington. J Elisha Mitchell Sci Soc 77:81–88

Higgins RP (1964a) Redescription of the kinorhynch *Echinoderes remanei* (Blake, 1930) Karling 1954. Trans Am Microsc Soc 83:243–247

Higgins RP (1964b) Three new Kinorhyncha from the North Carolina coast. Bull Mar Sci Gulf Caribb 14(3):479–493

Higgins RP (1965) The homalorhagid Kinorhyncha of northeastern U.S. coastal waters. Trans Am Microsc Soc 84:65–72

Higgins RP (1969) Indian Ocean Kinorhyncha: 1. *Condyloderes* and *Sphenoderes*, new cyclorhagid genera. Smithson Contrib Zool 14:1–13

Higgins RP (1974) Kinorhyncha. In: Giese AG, Pearse JS (eds) Reproduction of marine invertebrates, Vol. 1: acoelomate and pseudocoelomate metazoans. Academic Press, New York, pp 507–518

Higgins RP (1977) Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. Trans Am Microsc Soc 96:340–354

Higgins RP (1978) *Echinoderes gerardi* n. sp. and *E. riedli* (Kinorhyncha) from the Gulf of Tunis. Trans Am Microsc Soc 97(2):171–180

Higgins RP (1982) Three new species of Kinorhyncha from Bermuda. Trans Am Microsc Soc 104:305–316

Higgins RP (1983) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, Il. Kinorhyncha. Smithson Contrib Mar Sci 18:1–131

Higgins RP (1985) The genus Echinoderes (Kinorhyncha: Cyclorhagida) from the English Channel. J Mar Biol Assoc UK 65:785–800

Higgins RP (1990) Zelinkaderidae, a new family of cyclorhagid Kinorhyncha. Smithson Contrib Zool 500:1–26

Higgins RP, Kristensen RM (1988) Kinorhyncha from Disko Island, West Greenland. Smithson Contr Zool 458:1–56

Higgins RP, Thiel L (1988) Introduction to the study of Meiofauna. Smithsonian Institution Press, Washington DC

Huys R, Coomans A (1989) *Echinoderes higginsi* sp. n. (Kinorhyncha, Cyclorhagida) from the southern North Sea with a key to the genus Echinoderes Claparède. Zool Scr 18:211–221

Kristensen RM, Higgins RP (1991) Kinorhyncha. In: Harrison FW, Ruppert EE (eds) Microscopic anatomy of invertebrates, Vol. 4: Aschelminthes. Wiley-Liss, New York, pp 377–404

Lang K (1963) The relations between the Kinorhyncha and Priapulida and their connection with the Aschelminthes. In: Dougherty EC (ed) The Lower Metazoa comparative biology and phylogeny. University of California Press, Berkeley, pp 256–262

Nebelsick M (1990) *Antygomonas incomitata* gen. et sp.n. (Cyclorhagida, Kinorhyncha) and its phylogenetic relationships. Zool Scr 19:143–152

Nebelsick M (1993) Introvert, mouth cone, and nervous system of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida) and implications for the phylogenetic relationships of Kinorhyncha. Zoomorphology 113:211–232

Neuhaus B (1999) Kinorhyncha. In: Knobil E, Neill JD (eds) Encyclopedia of reproduction, vol 2. Academic Press, San Diego, pp 933–937

Neuhaus B (2012) Kinorhyncha (=Echinodera). In: Schmidt-Rhaesa A (ed) Handbook of Zoology, Gastrotricha, Cycloneuralia and Gnathifera, volume 1: Nematomorpha, Priapulida, Kinorhyncha, Loricifera. Walter de Gruyter, Berlin, pp 181–348

Neuhaus B, Higgins RP (2002) Ultrastructure, biology and phylogenetic relationships of Kinorhyncha. Integ Comp Biol 42:619–632

Neuhaus B, Sørensen MV (2013) Populations of *Campyloderes* sp. (Kinorhyncha, Cyclorhagida): One global species with significant morphological variation? Zool Anz 252:48–75

Nyholm KG (1947) Studies in Echinoderida. Arkiv Zool 39A(14):1–36

Ostmann A, Nordhaus I, Sørensen MV (2012) First recording of kinorhynchs from Java, with the description of a new brackish water species from a mangrove-fringed lagoon. Mar Biodiversity 42:79–91

Pardos F, Higgins RP, Benito J (1998) Two new Echinoderes (Kinorhyncha, Cyclorhagida) from Spain, including a reevaluation of kinorhynch taxonomic characters. Zool Anz 237:195–208

Reinhard W (1881) Über *Echinoderes* und *Desmoscolex* der Umgegend von Odessa. Zool Anz 4:588–592

Sánchez N, Pardos F, Herranz M, Benito J (2011) *Pycnophyes dolichurus* sp. nov. and *P. aulacodes* sp. nov. (Kinorhyncha, Homalorhagida, Pycnophyidae), two new kinorhynchs from Spain with a reevaluation of homalorhagid taxonomic characters. Helgol Mar Res 65:319–334

Shirayama Y, Kaku T, Higgins RP (1993) Double-sided microscopic observation of meiofauna using an H-S-slide. Benthos Res 44:41–44

Sørensen MV (2007) A new species of *Antygomonas* (Kinorhyncha: Cyclorhagida) from the Atlantic coast of Florida, USA. Cah Biol Mar 48:155–168

Sørensen MV, 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 MV, Rho HS (2009) *Triodontoderes anulap* gen. et sp. nov.—a new cyclorhagid kinorhynch genus and species from Micronesia, UK. J Mar Biol Assoc 89(6):1269–1279

Sørensen MV, Thormar J (2010) *Wollunquaderes majkenae* gen. et sp nov.—a new cyclorhagid kinorhynch genus and species from the Coral Sea, Australia. Mar Biodiv 40:261–275

Sørensen MV, Heiner I, Ziemer O (2005) A new species of *Echinoderes* from Florida (Kinorhyncha: Cyclorhagida). Proc Biol Soc Wash 118:499–508

Sørensen MV, Heiner I, Ziemer O, Neuhaus B (2007) *Tubulideres seminoli* gen. et n. sp. and *Zelinkaderes brightae* n. sp. (Kinorhyncha, Cyclorhagida) from Florida. Helgol Mar Res 61:247–265

Sørensen MV, Heiner I, Hansen JG (2009) A comparative morphological study of the kinorhynch genera *Antygomonas* and *Semnoderes* (Kinorhyncha: Cyclorhagida). J Morphol 63:129–147

Sørensen MV, Rho HS, Kim D (2010) A new species of the rare genus *Sphenoderes* (Cyclorhagida, Kinorhyncha), with differential notes on *S. indicus* Higgins, 1969. Mar Biol Res 6:472–484

Sørensen MV, Rho HS, Min WG, Kim D, Chang CY (2012a) Occurrence of the newly described kinorhynch genus *Meristoderes* (Cyclorhagida: Echinoderidae) in Korea, with the description of four new species. Helgol Mar Res 67:291–319

Sørensen MV, Rho HS, Min WG, Kim D, Chang CY (2012b) An exploration of *Echinoderes* (Kinorhyncha: Cyclorhagida) in Korean and neighboring waters, with the description of four new species and a redescription of *E. tchefouensis* Lou, 1934. Zootaxa 3368:161–196

Thormar J, Sørensen MV (2010) Two new species of Echinoderes (Kinorhyncha: Cyclorhagida) from the Solomon Islands. Meiofauna Mar 18:67–96

Wieser W (1960) Benthic studies in Buzzards Bay, TI. The meiofauna. Limnol Oceanogr 5:121–137

Zelinka C (1896) Demonstration von Tafeln der Echinoderes-Monograhie. Verhandlungen der deutschen Zoologischen Gesselschaft 6:197–199

Zelinka C (1928) Monographie der Echinodera. Verlag Wilhelm Engelmann, Leipzig