RAFFLES BULLETIN OF ZOOLOGY **64**: 3–27
Date of publication: 29 January 2016
http://zoobank.org/urn:lsid:zoobank.org:pub:819AC644-37BC-43DB-8E11-984D77804AFE

First report of kinorhynchs from Singapore, with the description of three new species

Martin V. Sørensen[1*], Ludwik Gąsiorowski[1], Phillip V. Randsø[1], Nuria Sánchez[2] & Ricardo C. Neves[3]

Abstract. The kinorhynch fauna of Singapore, or from any locality close by, has never been explored. For the present study, samples of Kinorhyncha were collected at seven localities around Singapore. This revealed the presence of at least nine different species distributed across four genera. Two species, *Echinoderes tchefouensis* and *Condyloderes paradoxus*, are known from other localities in Asia, whereas the remaining seven species are new to science. Three of them, *Centroderes impurus* sp. nov., *Echinoderes annae* sp. nov., and *Leiocanthus nagini* sp. nov., are described, whereas materials representing the remaining, potentially new, species were too limited to allow complete descriptions.

Key words. *Centroderes*, *Condyloderes*, *Echinoderes*, *Leiocanthus*, Kinorhyncha, meiofauna, *Pycnophyes*, taxonomy

INTRODUCTION

Information on Kinorhyncha from Asia has always been rather sporadic, or at least, focused on certain areas that have been explored in more detail. Through the 1950s to 1970s, surveys to document Kinorhyncha in the Indian Territory of the Bay of Bengal and Andaman Sea were carried out (Timm, 1958; Rao & Ganapati, 1968; Higgins, 1968, 1969a, b; Higgins & Rao, 1979; Sarma & Mohan, 1981) and more recently, relatively detailed information about the kinorhynch fauna in Japan and along the Korean and eastern Russian coastlines is now available (Adrianov, 1989; Higgins & Shirayama, 1990; Adrianov & Malakhov, 1999; Song & Chang, 2001; Adrianov et al., 2002a–c; Chang & Song, 2002; Sørensen et al., 2010a–c, 2012a, b, 2013; Lundbye et al., 2011; Yamasaki & Kajihara, 2012; Yamasaki et al., 2012, 2014; Sánchez et al., 2013; Thomsen et al., 2013; Yamasaki & Fujimoto, 2014; Altenburger et al., 2015). Apart from these areas, information on kinorhynchs is extremely limited, and very little is known about the kinorhynch fauna of the Malay Peninsula, Indonesia, and the Malayan Archipelago. From the Malay Peninsula we have not been able to find records of kinorhynchs identified any further than to phylum level, and only two species, *Echinoderes applicitus* Ostmann et al., 2012 and *Echinoderes tchefouensis* Lou, 1934 have been reported from, respectively, Indonesia and Malaysian Borneo (see Ostmann et al., 2012; Sørensen et al., 2012a). Kinorhynchs have never previously been reported from Singapore.

In the present study, we show results from the first exploration of the kinorhynch fauna of Singapore. Our findings are offshoots from a general meiofaunal survey that were carried out in 2014 by the last author and collaborators. Preliminary results of this survey are described by Neves et al. (in press). Seven of the localities sampled by Neves et al. (in press), yielded specimens of kinorhynchs, and in the following we will give notes on two species already known to science, and additionally provide formal taxonomic descriptions for three species new to science.

MATERIALS AND METHODS

Samples were taken during May 2014 (see Neves et al. (in press) for more detailed information on the sampling and the general meiofauna). Intertidal samples were taken by hand, whereas subtidal samples were collected with a rectangular or a triangular dredge from the research vessel *Galaxea*, of the Tropical Marine Science Institute, National University of Singapore. Information for samples yielding kinorhynchs is summarised in Table 1, and localities are illustrated on Fig. 1. Kinorhynchs were extracted from the samples using the 'Bubbling and Blot'-method (Higgins, 1964) following the procedure described by Sørensen & Pardos (2008). The specimens were subsequently picked up under a dissecting microscope, fixed overnight in 4% paraformaldehyde (PFA), and then rinsed in a 0.1 mol l^{-1} phosphate buffer solution (PBS). Unfortunately, either the PFA or the PBS formed some unwanted precipitation that stuck to the specimens and formed a rather solid coating over them. Although this did not cause major problems with specimens mounted for light microscopy (LM), many of the specimens mounted for scanning electron microscopy (SEM) were unfortunately nearly useless for morphological examination.

[1]Section for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; Email: mvsorensen@snm.ku.dk (*corresponding author)

[2]Department of Zoology and Anthropology, Universidad Complutense de Madrid, Madrid, Spain

[3]Biozentrum, University of Basel, Klingelbergstrasse 50, CH-4056 Basel, Switzerland

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

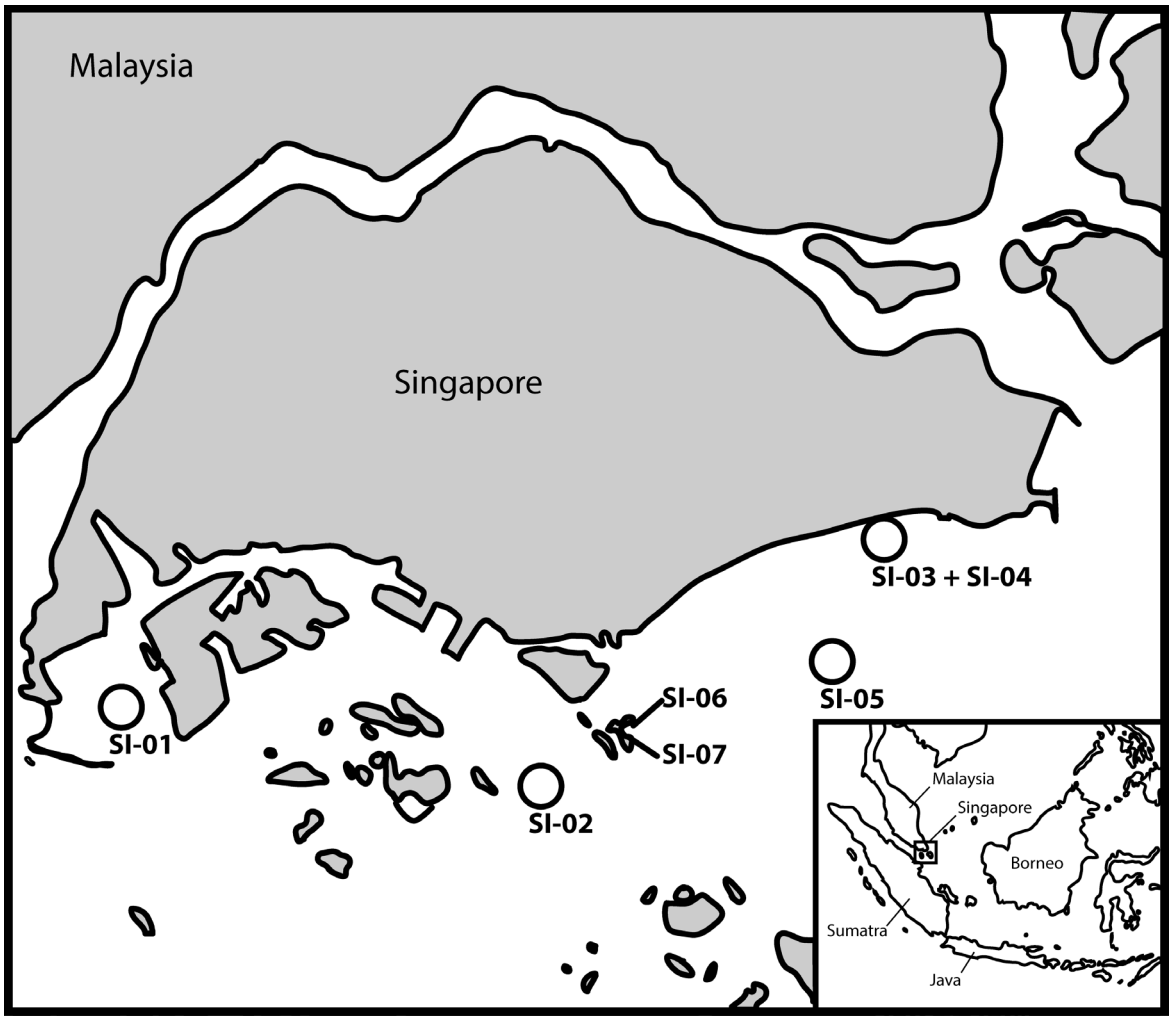

Fig. 1. Map showing the sampling localities south of Singapore Island. Inset to the lower right shows the Malaya Peninsula and Indonesian Archipelago, with Singapore indicated in the square.

Table 1. Summary of data on stations and taxa identified.

Date	Station	Location	Position	Depth (m)	Substrate	Taxa
15 May 2014	SI-01	West of Jurong Island	01°14.495'N 103°39.248'E	17	Mud	*Echinoderes tchefouensis* *Pycnophyes* sp. 1
15 May 2014	SI-02	Near Sister's Island	01°12.494'N 103°48.501'E	26	Shell gravel with mud	Kinorhyncha – specimen lost before preparation
16 May 2014	SI-03+04	Between Bedok Jetty & Sungei Bedok	01°18.387'N 103°57.591'E	9	Sand with mud	*Echinoderes tchefouensis* *Echinoderes* sp. 1 *Echinoderes* sp. 2 *Centroderes impurus* sp. nov. *Condyloderes paradoxus* *Leiocanthus nagini* sp. nov. *Pycnophyes* sp. 1 *Pycnophyes* sp. 2
16 May 2014	SI-05	Eastern fairway	01°15.589'N 103°56.680'E	52	Sand with mud	*Leiocanthus nagini* sp. nov.
19 May 2014	SI-06	Seringat Island	01°13.531'N 103°51.299'E	Intertidal	Seagrass beds	*Echinoderes tchefouensis* *Echinoderes annae* sp. nov. *Pycnophyes* sp. 1
20 May 2014	SI-07	Seringat Island	01°13.531'N 103°51.299'E	Intertidal	Seagrass beds	*Pycnophyes* sp. 1

Specimens for LM were dehydrated through a graded series of glycerine, mounted in Fluoromount G between two cover slips attached to a plastic H-S slide, and examined and photographed with an Olympus BX51 microscope, equipped with an Olympus DP20, DP27 or DP70 camera and a drawing tube. Line art illustrations made from camera lucida drafts of mounted specimens were scanned and drawn in Adobe Illustrator CS6. Measurements were made with Cell^A or Cell^D software. All dimensions reported in the tables are based on LM measurements.

Specimens for SEM were dehydrated through a series of alcohols, critical point dried, mounted on aluminium stubs, sputter coated with a platinum/palladium mix and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

Terminology follows Sørensen & Pardos (2008), Neuhaus et al. (2014) and Sánchez et al. (2013, 2014a, b). General kinorhynch classification follows Sørensen et al. (2015) and classification of Pycnophyidae follows Sánchez et al. (in press).

TAXONOMY

Class Cyclorhagida (Zelinka, 1896) Sørensen et al., 2015

Order Kentrorhagata Sørensen et al., 2015

Family Centroderidae (Zelinka, 1896) Sørensen et al., 2015

Genus *Centroderes* Zelinka, 1907

Centroderes impurus sp. nov.

(Figs. 2–5)

Material examined. Holotype adult stage-2 male, collected from sand with mud on 16 May 2014, at station SI-03 (Fig. 1, Table 1), at 9 m depth, between Bedok Jetty and Sungei Bedok in the southeast part of Singapore Island (01°18.387'N, 103°57.591'E), mounted in Fluoromount G, deposited at the Lee Kong Chian Natural History Museum, under catalogue number ZRC.MIS.0001. Paratypes include two specimens of uncertain sex, probably either adult stage-1 male or female, or eventually preadult stages (J6), collected at same locality as holotype, mounted in Fluoromount G, and deposited at the Natural History Museum of Denmark, under catalogue numbers ZMUC KIN-846 and KIN-847. Additional, non-type material, includes one adult stage-2 male and two putatively stage-1 specimens of uncertain sex, collected at same locality as holotype, and mounted for SEM. The SEM specimens are very dirty, and contributed only with limited information.

Diagnosis. *Centroderes* with middorsal acicular spines on segments 1–9 and 11; long, flexible, ventromedial acicular spines on segment 1; rigid lateroventral acicular spines on segments 8 and 9, with spine on segment 9 being conspicuously stout and robust. Male stage-2 with middorsal and midlateral crenulated spines on segment 10. Putative adult stage-1 specimens, or alternatively preadults, with middorsal and midlateral acicular spines on segment 10, and with minute tubes present in ventrolateral positions on segment 2 and lateroventral positions on segment 5. Sensory spots present paradorsally on segments 2–6 and 8–9, subdorsally on segment 1 (in male stage-2 only) and segment 11 (two pairs), laterodorsally on segments 1 (in putative J6 or stage-1 specimen only) and 3–10, midlaterally on segment 2, in a lateral accessory position on segments 1, 3–4 and 6–9 and ventromedially on segments 3–4 and 6–10.

Etymology. The species is named after the Latin word "*impurus*", meaning "unclean" or "covered with dirt", referring to the severe dirt problems that were experienced during the examination of the specimens.

Description. Adult with head, neck and eleven trunk segments (Figs. 2, 3A, B, 4A, B). For measurements and dimensions, see Table 2. Distribution of cuticular structures (spines, tubes and sensory spots) is summarised in Table 3.

The head consists of a retractable mouth cone and an introvert. The mouth cone is equipped with nine outer oral styles, each consisting of two joined units, arranged as one style anterior to each introvert sector, except at the middorsal sector 6. A double fringe consisting of numerous tips is located basally to each style. Scalid arrangement could not be examined in detail.

The neck has 16 placids that dorsally and laterally alternate in size width between broader (15–16 µm width) and narrower (6–8 µm width) ones; all placids measure 15–17 µm length. The midventral placid is broader and flanked by two narrower placids on each side.

Segment 1 consists of one complete cuticular ring with middorsal acicular spine, being short and stout in male stage-2 (Fig. 3A), and two slender, elongated spines in ventromedial positions, which extend over two following segments (Figs. 2, 5B). All spines on this and following segments are at least partly covered with minute cuticular hairs, however, frequently the proximal 1/3 of the surface is smooth. At least until segment 6 or 7, the middorsal spines appear stout in male stage-2, whereas they are more slender and acicular in the putative J6 or stage-1 specimens (compare Fig. 3A with 3B). A midventral process is present between the two ventromedial spines (Figs. 2, 4B). Sensory spots are located medially on the segment in either subdorsal (male stage-2) or laterodorsal (putative J6 or stage-1 adults) positions, and always in lateral accessory position (Fig. 4C). Sensory spots in subdorsal/laterodorsal positions are circular and composed of micropapillae arranged around a central pore (Fig. 4C); all sensory spots on all the following segments show the same appearance. The sensory spots in the lateral accessory positions differ though, and are more oval with cuticular

Table 2. Measurements from light microscopy of adult *Centroderes impurus* sp. nov. (in µm) from station SI-03, Singapore, including individual measures, mean and standard deviation (SD). Abbreviations: LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral spine or tube; MD, middorsal spine; ML: midlateral spine; MSW-6: maximum sternal width, measured on segment 6 in this species; MTS: midterminal spine; S: segment lengths; SW-10, standard width, always measured on segment 10; TL: trunk length; VM: ventromedial spine.

Character	ZRC.MIS.0001 ♂ Holotype	KIN-846 Paratype	KIN-847 Paratype	Mean	SD
TL	376	264	255	298	67.41
MSW-6	64	62	57	61	3.61
MSW-6/TL	17.0%	23.5%	22.4%	21%	3.45%
SW-10	45	–	19	32	18.38
SW-10/TL	12.0%	–	7.5%	9.7%	3.19%
S1	36	29	28	32	6.08
S2	40	24	24	28	7.51
S3	42	25	24	30	8.96
S4	47	27	27	32	8.66
S5	50	27	27	34	11.55
S6	52	32	28	35	9.45
S7	55	28	27	34	10.69
S8	58	32	28	37	11.72
S9	58	28	24	34	13.43
S10	39	24	20	28	10.58
S11	28	21	17	22	5.57
MD1	16	17	15	16	1.00
MD2	16	16	17	16	0.58
MD3	16	21	18	18	2.52
MD4	16	20	21	19	2.65
MD5	19	23	23	22	2.31
MD6	19	28	26	24	4.73
MD7	23	32	28	28	4.51
MD8	30	37	33	33	3.51
MD9	33	37	36	35	2.08
MD10	28	48	47	41	11.27
MD11	34	41	50	42	8.02
VM1	62	53	52	56	5.51
LV2	–	8	–	8	–
LV5	–	9	10	10	0.71
LV8	18	17	17	17	0,58
LV9	39	28	27	31	6.66
ML10	24	24	23	24	0.58
LTAS	(>42)	59	60	60	0.71
LTS	44	44	45	44	0.58
LTS/LTAS	–	74.6%	75.0%	74.8%	0.30%
MD11/LTAS	–	69.5%	83.3%	76.4%	9.79%
MTS	(>85)	120	93	107	19.09
MTS/TL	–	45.5%	36.5%	41.0%	6.35%

papillae arranged in three rows and adhering to the cuticle surface (Fig. 4D). Minute, densely distributed cuticular hairs are present on the posterior half of the segment.

Segment 2 and all remaining segments consist of one tergal and two sternal plates. A middorsal spine is present in all specimens. Furthermore, minute ventrolateral tubes were observed in the putative J6 or stage-1 specimens (Fig. 5B). In male stage-2 no such structure was observed neither in LM nor in SEM; in the single specimen examined with SEM it was evident that the position where the tube would attach was filled with densely arranged prominent hairs. Similar hairs were spotted on other segments as well (Fig. 4F). Sensory spots are present in paradorsal and midlateral position. The paradorsal sensory spots are located very close to the posterior segment margin, next to the base of the middorsal spine. Secondary pectinate fringe consisting of minute cuticular hairs present on anterior part of segment; the fringe may be partially covered by the posterior margin of preceding segment. Additional hairs are densely and evenly distributed over the posterior half of the segment. Hairs in the tergosternal junction region are distinctly longer, especially anteriorly. A similar arrangement of hairs is present on segments 3–10 (Figs. 2, 4E).

Segments 3 and 4 with middorsal acicular spine. Sensory spots are present in paradorsal, laterodorsal, lateral accessory and ventromedial positions (Figs. 2, 5A). Cuticular hairs as on preceding segment.

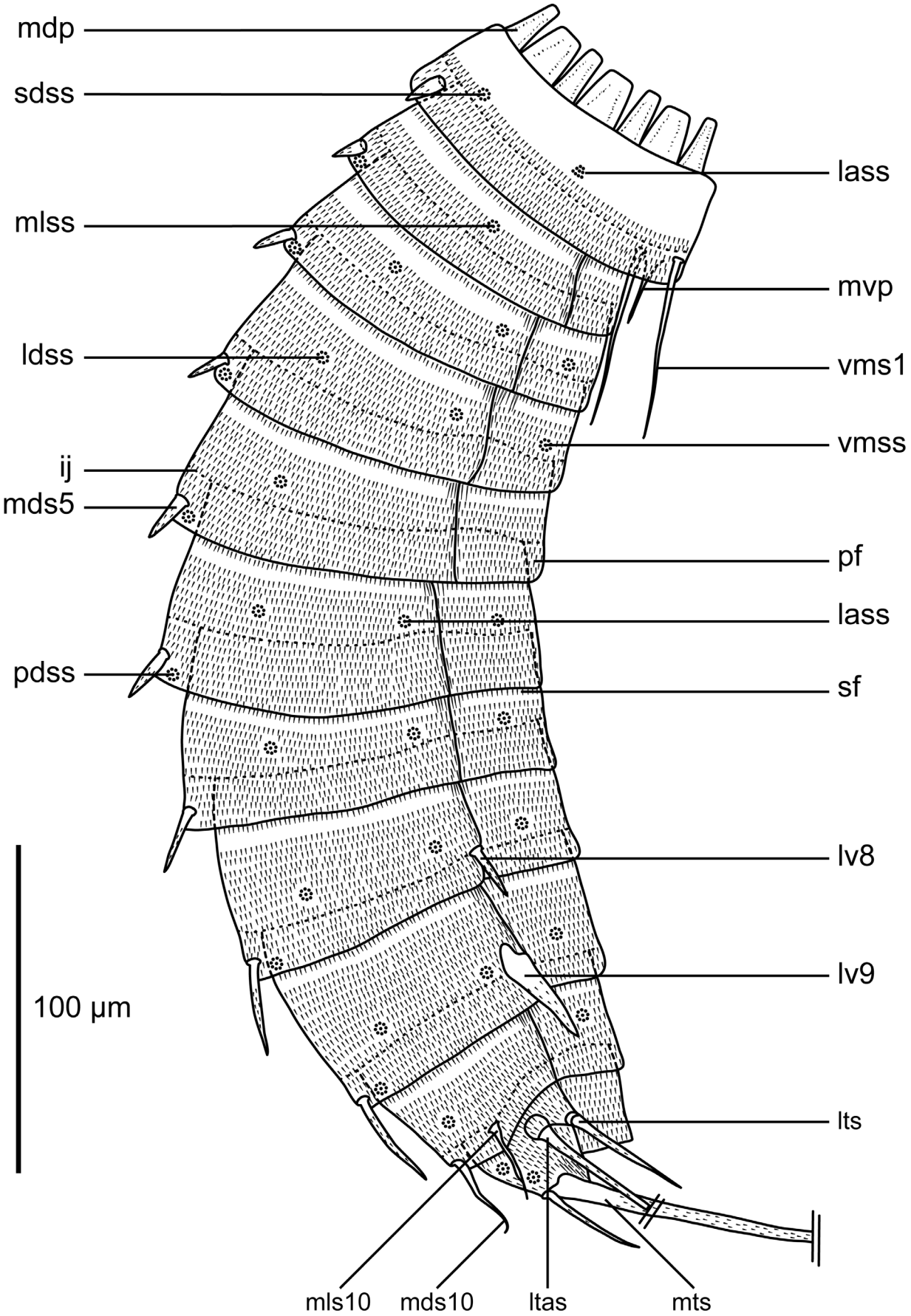

Fig. 2. Line art illustration of *Centroderes impurus* sp. nov. male stage-2, lateral view. Abbreviations: ij, intersegmentary joint line; lass, lateral accessory sensory spot; ldss, laterodorsal sensory spot; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; mdp, middorsal placid; mds, middorsal spine; mls, midlateral spine; mlss, midlateral sensory spot; mts, midterminal spine; mvp, midventral process; pdss, paradorsal sensory spot; pf, pectinate fringe; sdss, subdorsal sensory spot; sf, secondary fringe; vms, ventromedial spine; vmss, ventromedial sensory spot. Digits following labels refer to segment numbers.

Table 3. Summary of nature and location of spines, tubes and sensory spots arranged by series in *Centroderes impurus* sp. nov. Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; VL: ventrolateral; VM: ventromedial; a1, condition of character in the putative J6 preadult or adult stage-1; ac, acicular spine; cr, crenulated spines; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mts, midterminal spine; ss, sensory spot; tu, tube; ♂2, condition of character in the male stage-2; -, no structure present.

Position Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	ac		ss(♂2)	ss(a1)		ss			ac
2	ac	ss			ss			tu(a1); - (♂2)	
3	ac	ss		ss		ss			ss
4	ac	ss		ss		ss			ss
5	ac	ss		ss			tu(a1); - (♂2)		
6	ac	ss		ss		ss			ss
7	ac			ss		ss			ss
8	ac	ss		ss		ss	ac		ss
9	ac	ss		ss		ss	robust ac		ss
10	ac(a1); cr(♂2)			ss	ac(a1); cr(♂2)				ss
11	ac, mts		ss, ss			ltas	lts		

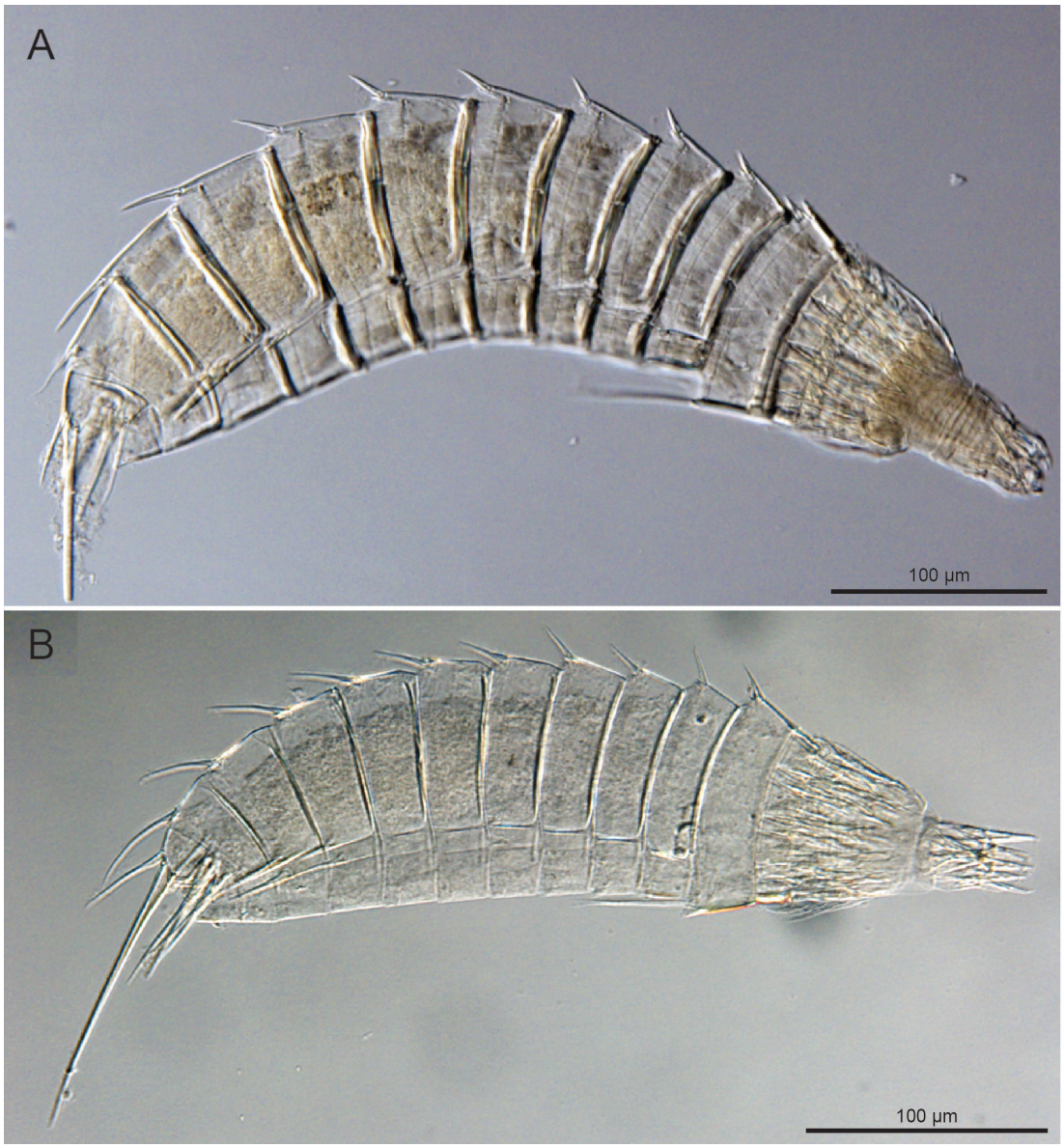

Fig. 3. Light micrographs showing lateral overviews of *Centroderes impurus* sp. nov. A, holotype, ZRC.MIS.0001, male stage-2. B, paratype, KIN-846, putative J6 or adult stage-1 of unknown gender.

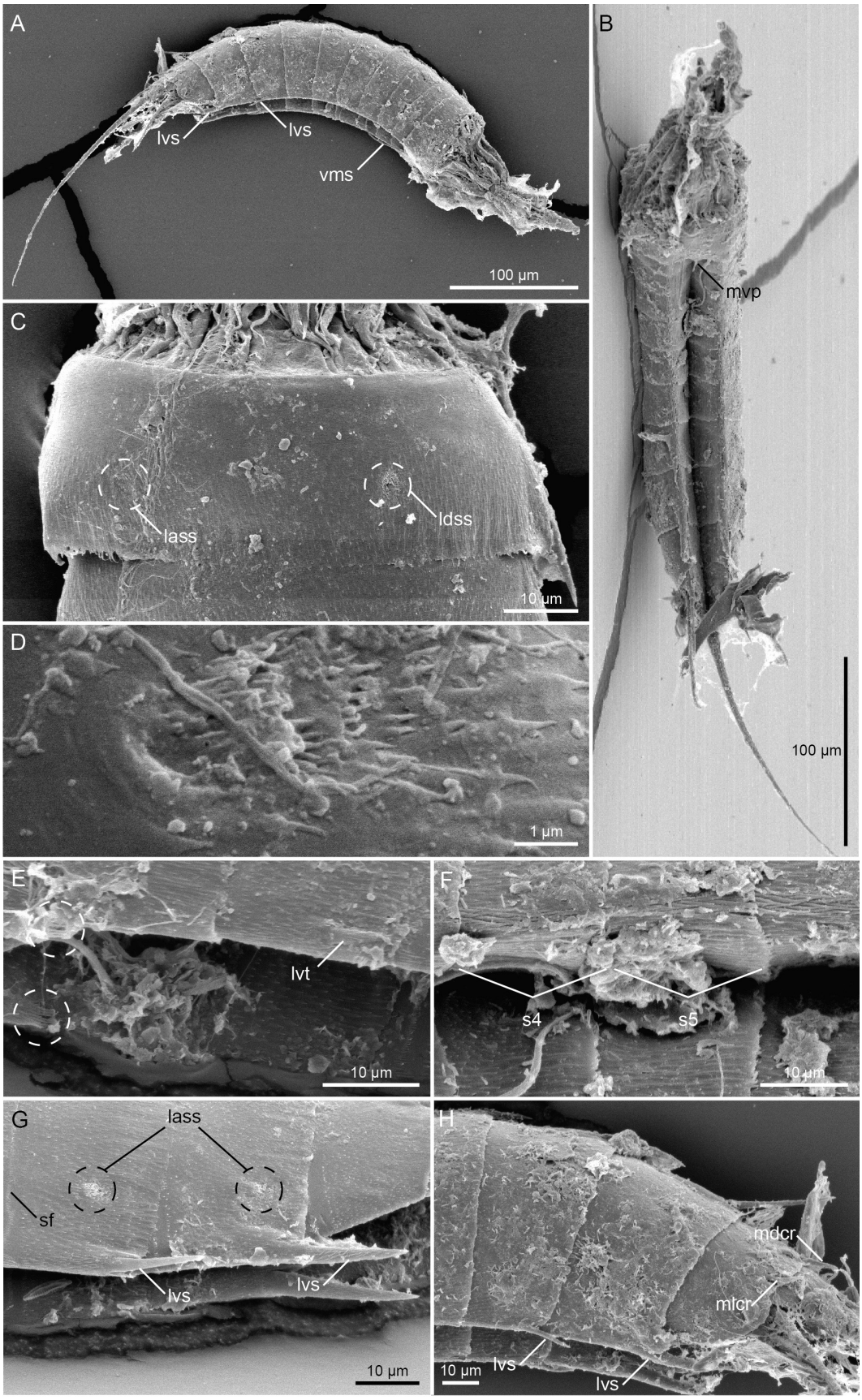

Fig. 4. Scanning electron micrographs of male stage-2 (A, B, F, H) and putative J6 or adult stage-1 of unknown gender (C–E, G) of *Centroderes impurus* sp. nov. A, lateral overview. B, ventral overview. C, Lateral view of segment 1. D, Detail showing lateral accessory sensory spot on segment 1. E, Region of tergosternal junctions of segments 4 and 5; dashed circles outline extended cuticular hairs on posterior margin of segment 3. F, Region of tergosternal junction of segments 4 and 5. G, lateroventral view of segments 8 and 9. H, Lateral view of segments 8–10 in male stage-2. Abbreviations: lvs, lateroventral spine; lvt, lateroventral tube; lass, lateral accessory sensory spot; ldss, laterodorsal sensory spot; mdcr, middorsal crenulated spine; mlcr, midlateral crenulated spine; mvp, midventral process; s, segment followed by segment number; sf, secondary fringe; vms, ventromedial spine on segment 1.

Segment 5 with middorsal acicular spine. Minute lateroventral tubes are present in putative J6 or stage-1 specimens (Figs. 4E, 5D). Stage-2 specimens without such tubes, and instead with densely arranged prominent hairs in the areas where the tubes would attach (Fig. 4F). Sensory spots are present in paradorsal and laterodorsal positions (Figs. 2, 5A). Cuticular hairs as on preceding segment.

Segment 6 with middorsal acicular spine. Sensory spots present in paradorsal, laterodorsal, lateral accessory and ventromedial positions (Figs. 2, 5A). Cuticular hairs as on preceding segment.

Segment 7 with middorsal acicular spine. Sensory spots present in laterodorsal, lateral accessory and ventromedial positions. On this and the following segments, the laterodorsal sensory spots are located slightly closer to the midlateral position. Putative J6 or stage-1 specimens show no indication of female specific glands, as observed in other *Centroderes* (see Neuhaus et al., 2014). Cuticular hairs as on preceding segment.

Segment 8 with prominent, long middorsal acicular spine (Figs. 2, 3A). Small acicular spines present in lateroventral positions (Figs. 4G, 5E, F). Sensory spots present in paradorsal, laterodorsal, lateral accessory and ventromedial position. Putative J6 or stage-1 specimens show no indication of female specific glands. Cuticular hairs as on preceding segment.

Segment 9 with prominent, long middorsal acicular spine (Figs. 2, 3A). Conspicuously robust acicular spines are present in lateroventral positions; these spines can be twice as long as the corresponding spines on segment 8 (Figs. 4G, 5E, F, see also Table 2), especially in the male stage-2. Sensory spots present in paradorsal, laterodorsal, lateral accessory and ventromedial position. Cuticular hairs as on preceding segment.

Segment 10 with middorsal and midlateral acicular spines in putative J6 or stage-1 specimens (Figs. 3B, 5F) and with middorsal and midlateral crenulated spines in stage-2 males (Figs. 2, 3A, 4H, 5C, E). Sensory spots present in laterodorsal and ventromedial positions. Cuticular hairs as on preceding segment.

Segment 11 with middorsal, lateral terminal, lateral terminal accessory, and midterminal spines (Figs. 2, 3, 4A, B, 5F). The midterminal spine is considerably longer than the other spines on this segment (Table 2). Two pairs of subdorsal sensory spots, one pair being more anterior than the other, are present. The whole cuticular surface is covered with minute cuticular hairs which turn slightly longer and denser in the terminal part of the segment.

Notes on diagnostic features of *Centroderes impurus* sp. nov. To date, *Centroderes* accommodates five known species, namely *Centroderes spinosus* (Reinhard, 1881) from Europe (Reinhard, 1881; redescribed by Neuhaus et al., 2013) and four North American/Caribbean species: *Centroderes barbanigra* Neuhaus et al., 2014, *Centroderes bonnyae* Neuhaus et al., 2014, *Centroderes drakei* Neuhaus et al., 2014 and *Centroderes readae* Neuhaus et al., 2014. The most prominent character that enables to distinguish *Centroderes impurus* sp. nov. from other *Centroderes* species is the relative dimensions of the lateroventral spines on segments 8 and 9. Lateroventral spines on segments 8 and 9 are present in all known *Centroderes* species, however, *Centroderes impurus* sp. nov. is unique because the spines on segment 9 are much bigger and conspicuously more robust than the more regular spines on segment 8 (Figs. 2, 4G, 5E, F; Table 2). In *C. drakei* the lateroventral spines on segment 9 are also prominent and bigger than those on the preceding segment, however, in *Centroderes impurus* sp. nov., the lengths of the spines on segment 9 are nearly twice as long as those on segment 8, whereas the lateroventral segment 9 spines in *C. drakei* are only slightly longer (Neuhaus et al., 2014). Another less conspicuous feature that differentiates *Centroderes impurus* sp. nov. from the other congeneric species is the presence of sensory spots in lateral accessory positions on segment 1. Moreover, the external morphology of this sensory spot is somewhat peculiar (see Fig. 4D and detailed description above) and differs from other sensory spots.

Distinctive negative characters include the lack of sensory spots on segment 1 in ventromedial position and on segment 7 in paradorsal position. Sensory spots are present in these positions in all other known species of *Centroderes*. Furthermore, stage-2 males of *Centroderes impurus* sp. nov. lack tubes on segments 2 and 5, which are otherwise present in all other known species of *Centroderes*.

It was recently shown that in the known species of *Centroderes*, adult specimens continue moulting, and that two different adult stages can be distinguished (Neuhaus et al., 2013, 2014). In all species, except *C. bonnyae*, the different stages show differences in the arrangement and nature of spines on segment 10. However, the exact differences vary between the species (see Table 9 in Neuhaus et al., 2014). In the examined specimens of *Centroderes impurus* sp. nov. two specimens (the holotype and one other specimen mounted for SEM) were clearly identified as a stage-2 male, whereas three additional specimens (one mounted for SEM and two for light microscopy) exhibit typical stage-1 characters (i.e., thinner and more transparent cuticle, and relatively longer middorsal spines). Unfortunately, no obvious primary sexual characters could be observed, which makes it impossible to determine the sex of these specimens. Furthermore, the lack of apparent primary sexual characters (i.e., mature ovary or testis) also opens the possibility that these specimens could represent preadult stages. Therefore, it is impossible to state any clear differences between stage-1 and stage-2 specimens. This is unfortunate, especially because it would have been interesting to obtain more information about the presence/absence of the extremely minute ventrolateral or lateroventral tubes that were observed on segments 2 and 5 potential preadults or stage-1 adults. As mentioned above, such tubes are lacking in stage-2 males of *Centroderes impurus* sp. nov., whereas they are present in all the other adult stages of other *Centroderes* species. It would have been

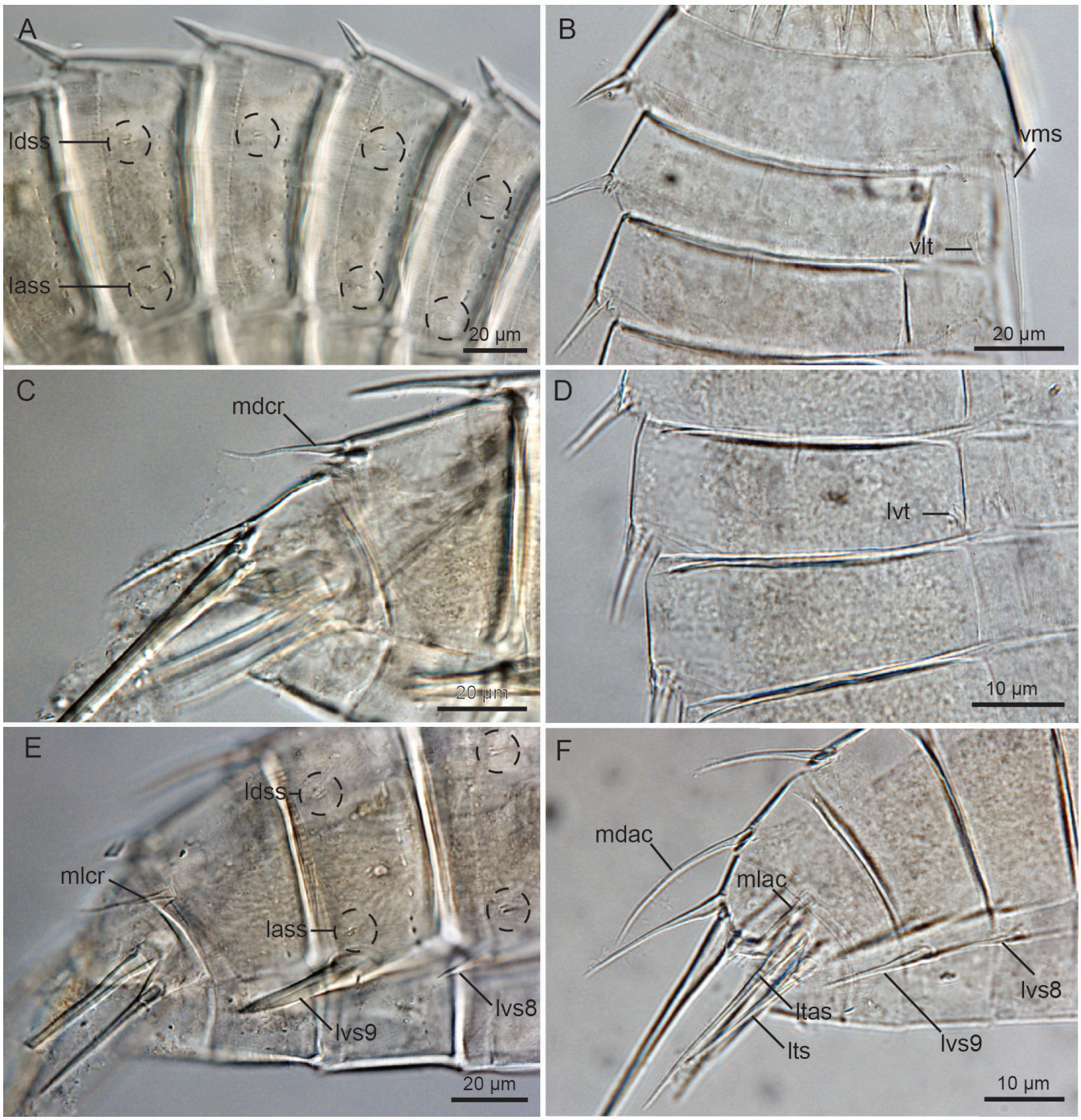

Fig. 5. Light micrographs showing details of trunk morphology in *Centroderes impurus* sp. nov. A, C, E: holotype, ZRC.MIS.0001, male stage-2; B, D, F: paratype, KIN-846, putative J6 or adult stage-1 of unknown gender. A, Segments 3–6, lateral view, with dashed circles indicating laterodorsal and lateral accessory sensory spots. B, Segments 1–3, lateral view, showing ventrolateral tube on segment 2, which is found only in this stage and not in male stage-2. C, Segments 10 and 11, lateral view, showing crenulated spines in middorsal position on segment 10. D, Segments 5–6, lateral view, showing indications of lateroventral tube on segment 5, which is found only in this stage and not in male stage-2. E, Segment 8–11, lateral view, showing crenulated spines in midlateral positions on segment 10; note the conspicuous difference between the lateroventral spines on segment 8 and segment 9; dashed circles indicate laterodorsal and lateral accessory sensory spots. F, Segment 8–11, lateral view, showing acicular spines in middorsal and midlateral positions on segment 10. Abbreviations: lass, lateral accessory sensory spot; ldss, laterodorsal sensory spot; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mdac, middorsal acicular spine; mdcr, middorsal crenulated spine; mlac, midlateral acicular spine; mlcr, midlateral crenulated spine; vlt, ventrolateral tube; vms, ventromedial spine.

desirable to understand the nature of these tubes better, and know whether their presence were correlated with the gender, or if they could be a juvenile trait that is absent in adults.

When comparing the sizes and dimensions of *Centroderes impurus* sp. nov. with previously described *Centroderes* species, the total trunk length (255–376 µm) is within the range of the lengths of *C. spinosus* (311–517 µm), *C. barbanigra* (341–528 µm), and *C. drakei* (255–521 µm), whereas the species is shorter than *C. bonnyae* (441–515 µm) and *C. readae* (430–539 µm). The relative lengths between lateral terminal spines and lateral terminal accessory spines in *Centroderes impurus* sp. nov. is 75% which is within the range of the ratios in *C. spinosus* (70–95%) and *C. readae* (63–78%), but different from the ranges in *C. barbanigra* (41–60%), *C. bonnyae* (48–57%) and *C. drakei* (44–61%).

Distribution of *Centroderes*. As mentioned above all known species of *Centroderes* have been reported from Europe or North America. For instance, *Centroderes spinosus* occurs along the European coasts from the Black Sea, through the Mediterranean Sea and into the North Sea and Skagerrak (Neuhaus et al., 2013). Formerly it was also reported from Bermuda, as well as from Maine and Massachusetts at the North American coast (Coull, 1970; Higgins, 1977, 1982, 1986). However, the North American specimens were later described as four different new species (cf. Neuhaus et al., 2014). Specimens of *Centroderes* collected in the North American region are all from the Northwest Atlantic, i.e., from the coast of Newfoundland, Massachusetts, New Jersey and Florida, from Bermuda, and from the Caribbean region and the Gulf of Mexico. Thus, *Centroderes impurus* sp. nov. represents the first record of *Centroderes* from Asia and also the first record of the genus outside the North Atlantic Region, or water directly connected with the North Atlantic. This confirms that *Centroderes*, like most other kinorhynch genera, potentially could be present in all world oceans, and could be considered as cosmopolitan.

Genus *Condyloderes* Higgins, 1969

Condyloderes paradoxus Higgins, 1969
(Fig. 6)

Material examined. Three adult specimens, two from station SI-03 and one from SI-04 (Fig. 1, Table 1). One specimen from SI-03 was mounted for LM, and subsequently deposited at the Natural History Museum of Denmark, under catalogue number ZMUC KIN-848. The remaining two specimens were mounted for SEM, but due to the dirt covering, they only contributed with very little information.

Notes on taxonomy and distribution. *Condyloderes paradoxus* (Fig. 6A) and its four congeners can be discriminated by the segmental distributions of minute cuspidate spines in the lateroventral positions. In *C. paradoxus*, lateroventral cuspidate spines are present on segments 2, 4, 5, 8 and 9 (Higgins, 1969a). This distribution corresponds to the cuspidate spine distribution in the recorded specimens from Singapore (Fig. 6B, C). Other characters

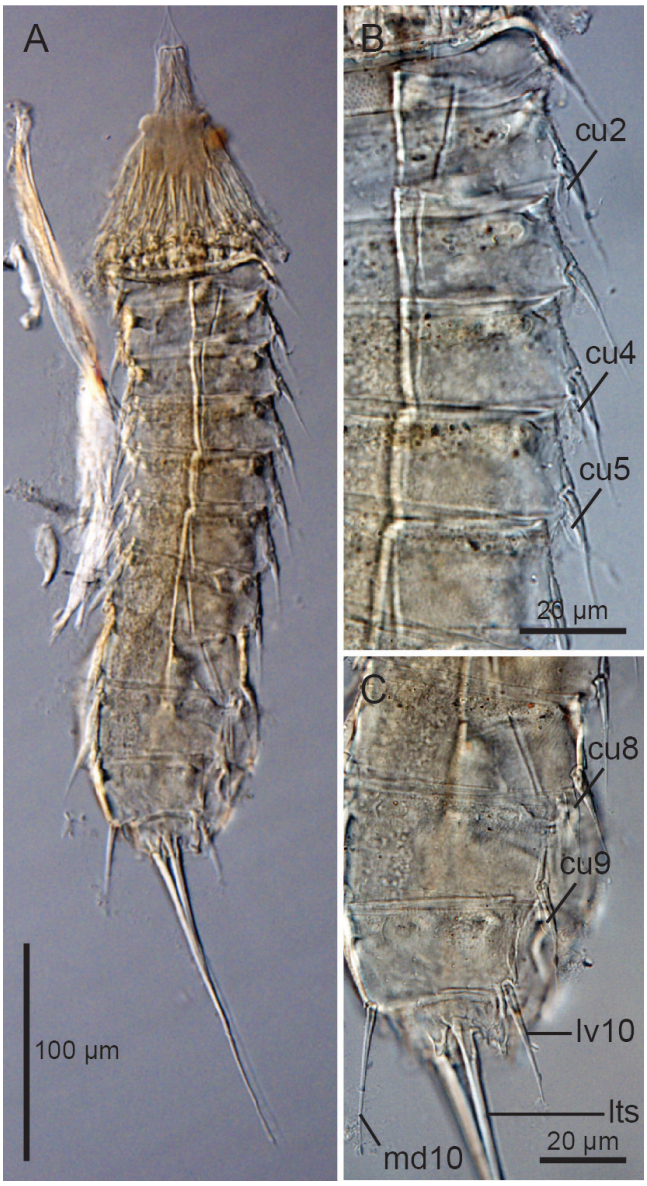

Fig. 6. Light micrographs showing overviews and details of trunk morphology in *Condyloderes paradoxus*, KIN-848. A, lateral overview. B, lateroventral spines on segments 1–6. C, terminal spines, and lateroventral spines on segments 8–11. Abbreviations: cu, cuspidate spine; lts, lateral terminal spine; lv, lateroventral acicular spine; md, middorsal acicular spine. All spines labels are followed by respective segment number.

in the examined specimens from Singapore, including the general spine distribution and dimensions, correspond with the data in the original description provided by Higgins (1969a), hence, we feel confident to identify the recorded species as *C. paradoxus*.

Condyloderes paradoxus was originally described from two localities in the Bay of Bengal, off the Indian coast near Visakhapatnam (Higgins, 1969a). Collecting the species in Singapore also suggests that *C. paradoxus* might be distributed throughout the coastal waters of the Bay of Bengal, Andaman Sea and Malacca Strait. Besides the occurrence of this species at its type locality in India, and its presence in Singapore, no other records of *C. paradoxus* appear in the literature. However, during the extensive

work on the kinorhynch fauna of the Korean Peninsula and the East China Sea, carried out by the first author and Dr H. S. Rho (see Sørensen et al., 2010a–c, 2012a, b, 2013; Lundbye et al., 2011; Thomsen et al., 2013; Sánchez et al., 2013; Altenburger et al., 2015) some specimens were actually identified as *Condyloderes* cf. *paradoxus* (Sørensen, unpubl.). The specimens occurred in samples taken at 132 m depth in the Korea Strait and between 79–103 m depth in the central part of the East China Sea, but by the time of the examinations, the identity of the specimens were considered doubtful, due to the distance between these sampling localities and the Bay of Bengal. However, with the current record of *C. paradoxus* from Singapore, which represents a biogeographic transitional point between the Indian Ocean and the West Pacific, it becomes more likely that the species has a wide distribution that ranges from the Bay of Bengal to the Korean Peninsula.

Order Echinorhagata Sørensen et al., 2015

Family Echinoderidae Zelinka, 1894

Genus *Echinoderes* Claparède, 1863

***Echinoderes annae* sp. nov.**
(Figs. 7–9)

Material examined. Holotype adult female, collected from muddy, intertidal seagrass aggregations on 19 May 2014, at station SI-06 (Fig. 1, Table 1), on Saringat Island, just south of Singapore Island (01°13.531'N 103°51.299'E), mounted in Fluoromount G, deposited at the Lee Kong Chian Natural History Museum, under catalogue number ZRC.MIS.0002. Paratypes, all mounted in Fluoromount G, were collected at same locality as holotype and include one male, deposited at the Lee Kong Chian Natural History Museum, under catalogue number ZRC.MIS.0003, and two additional males, one female, and one juvenile deposited at the Natural History Museum of Denmark under catalogue numbers ZMUC KIN-851 to KIN-854. Additional, non-type material includes six specimens, from same locality as the holotype, mounted for SEM. The SEM specimens were extremely dirty, and contributed with very limited information.

Diagnosis. *Echinoderes* with short middorsal spine on segment 4, and without any lateroventral acicular spines; tubes present in lateroventral positions on segments 5 and 8, midlateral positions on segment 9, and, in laterodorsal positions on segment 10. Glandular cell outlets type 2 present in subdorsal positions on segments 2 and 4, in laterodorsal positions on segments 2, 6 and 8, in sublateral positions on segments 5 and 7, and in lateroventral positions on segment 2. Sensory spots of type 1 and very small. Large, but narrow and elongated sieve plates present in sublateral positions on segment 9. Males with three pairs of penile spines; females with conspicuously short and stout lateral terminal accessory spines.

Etymology. The new species, *Echinoderes annae*, is named after Anna – the girlfriend of the author PVR.

Description. Adult with head, neck and eleven trunk segments (Figs. 7A, B, 8A, 9G). For measurements and dimensions see Table 4. Distribution of cuticular structures (spines, tubes, glandular cell outlets and sensory spots) is summarised in Table 5. Since all specimens mounted for SEM were covered with dirt to different degrees, the species may have additional sensory spots that were not observed and hence are not reported in the present description.

The head consists of a retractable mouth cone and an introvert. Arrangement of styles and scalids could not be examined. The neck bears 16 placids (Figs. 8B, 9A, B, G), measuring 18 µm in length.

Midventral placid broadest, measuring 19 µm in width. Trichoscalid plates present ventrally on placids 2 and 16 and dorsally on placids 6, 8, 10 and 12 (Figs. 7A, B, 8B). Ventral trichoscalid plates much broader than dorsal ones.

Segment 1 consists of a complete cuticular ring with sensory spots located near the anterior segment margin in subdorsal and laterodorsal positions (Fig. 9A), and medially in ventromedial positions (Figs. 9B). Sensory spots on this and following segments are small and rounded with seven to eight short cuticular papillae surrounding two small pores (Fig. 9D). Glandular cell outlets type 1 are present in sublateral positions. Cuticular hairs emerge through rounded perforation sites and are distributed evenly around the segment except in the anterior part of segment and around the sensory spots. The segment terminates into a pectinate fringe. Fringe with very short tips along the dorsal and lateral parts of segment margins, whereas the margins of the ventral parts have significantly longer fringe tips. Ventromedial fringe tips longest.

Segment 2 consists of a complete cuticular ring with sensory spots at least in middorsal (Fig. 9E), subdorsal and ventromedial positions (Fig. 9B). Glandular cell outlets type 1 present in middorsal and ventromedial positions; glandular cell outlets type 2 present in subdorsal, laterodorsal and lateroventral positions (Figs. 8B, C). Cuticular hairs and pectinate fringe as on segment 1. Pectinate fringe of segments 1 and 2 considerably shorter than on following segments.

Segment 3, and all following segments, consists of one tergal plate and two sternal plates. Glandular cell outlets type 1 present in middorsal and ventromedial positions. Cuticular hairs as on segment 2. Pectinate fringe of this segment with considerably longer tips than that of preceding segments. Midlateral parts of segment margin with slightly shorter fringe tips. Sensory spots not observed.

Segment 4 with very short middorsal acicular spine (Figs. 7A, 8E), and sensory spots at least, in laterodorsal positions. Glandular cell outlets type 1 present only ventromedially; glandular cell outlets type 2 present in subdorsal positions (Fig. 8E). Cuticular hairs and pectinate fringe as on segment 3.

Segment 5 with relatively long lateroventral tubes (Figs. 8D, 9C). Sensory spots present at least, in subdorsal, midlateral

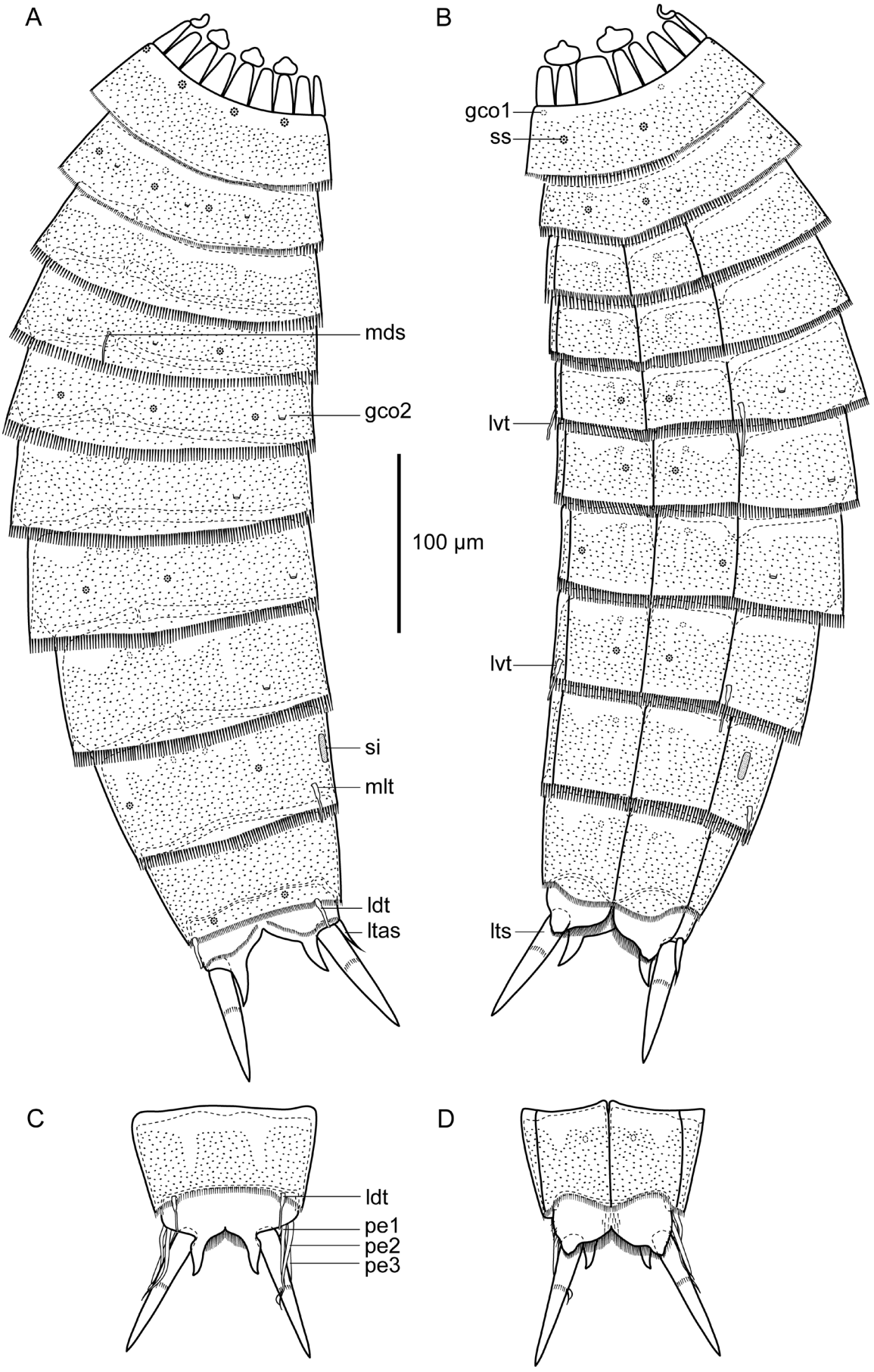

Fig. 7. Line art illustration of *Echinoderes annae* sp. nov. A, female, dorsal view. B, female, ventral view. C, male, dorsal view, segments 10–11. D, male, ventral view, segments 10–11. Abbreviations: gco1/2, glandular cell outlet type 1 or 2; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvt, lateroventral tube; mds, middorsal spine; mlt, midlateral tube; pe, penile spine; si, sieve plate; ss sensory spot.

and ventromedial positions (Fig. 9C). Glandular cell outlets type 1 present only ventromedially; glandular cell outlets type 2 present in sublateral positions (Fig. 8D). Cuticular hairs and pectinate fringe as on segment 4, but without variations in tip length around the segment.

Segment 6 with sensory spots at least in ventromedial positions (Fig. 9C). Glandular cell outlets type 1 present in paradorsal and ventromedial positions; glandular cell outlets type 2 present in laterodorsal positions (Fig. 8D, G). Cuticular hairs and pectinate fringe as on preceding segment.

Segment 7 with sensory spots present, at least in subdorsal and ventrolateral positions (Fig. 9F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions; glandular cell outlets type 2 present in sublateral positions

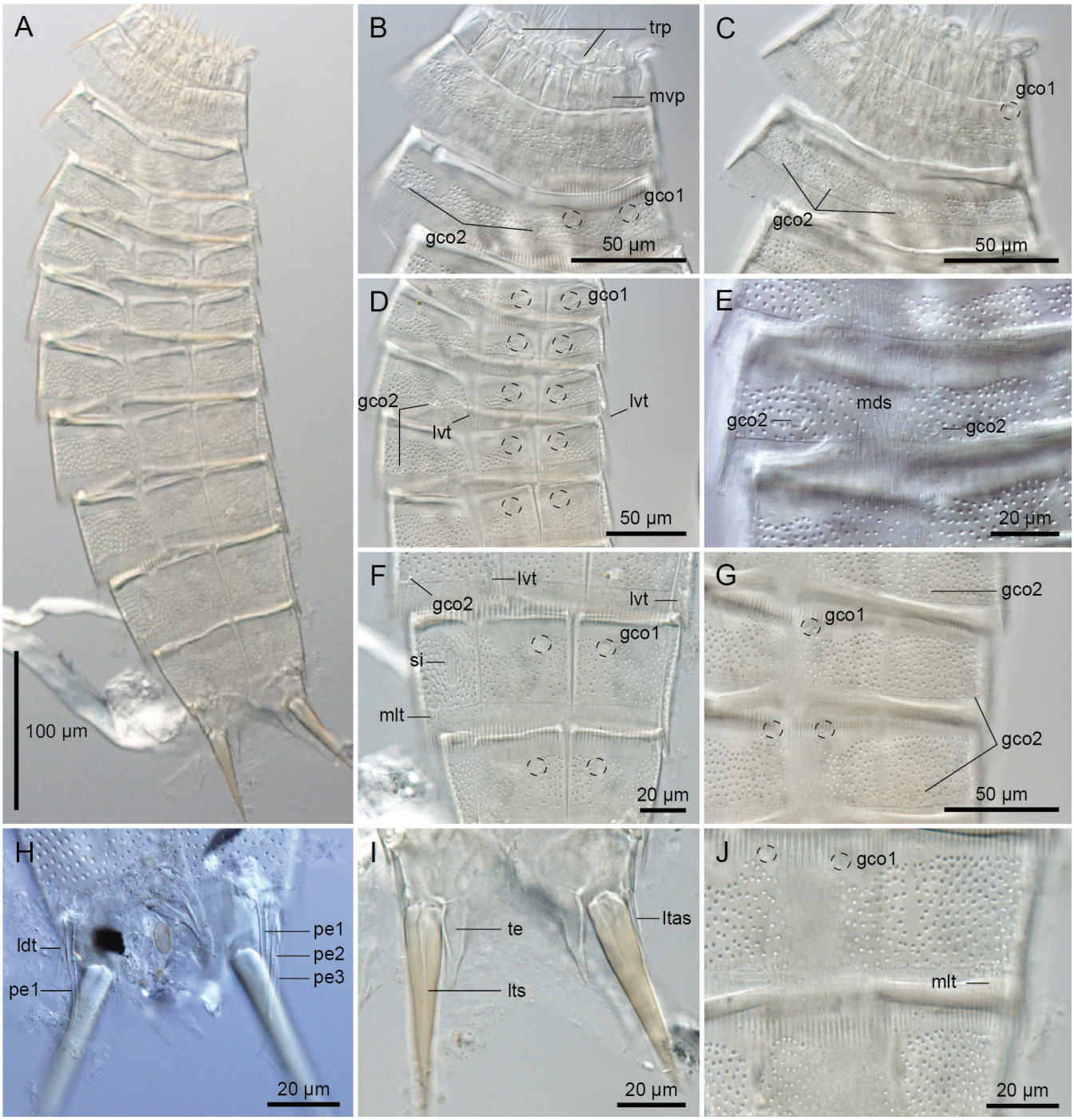

Fig. 8. Light micrographs showing overviews and details of neck and trunk morphology in female holotype, ZRC.MIS.0002 and male paratype, KIN-851, of *Echinoderes annae* sp. nov. A, lateroventral overview. B, neck and segments 1–2, lateroventral view. C, neck and segments 1–2, laterodorsal view. D, segments 3–7, lateroventral view. E, segment 4, middorsal. F, segments 8–10, lateroventral view. G, segments 6–8, dorsal view. H, segments 10–11, dorsal view, showing male morphology. I, segment 11, ventral view, showing female morphology. J, segments 9, laterodorsal view. Abbreviations: gco1/2, glandular cell outlet type 1 or 2; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvt, lateroventral tube; mds, middorsal spine; mlt, midlateral tube; mvp, midventral placid; pe1–3, penile spines; si, sieve plate; te, tergal extensions; trp, trichoscalid plate. Dashed circles mark glandular cell outlet type 1.

Table 4. Measurements from light microscopy of adult *Echinoderes annae* sp. nov. (in µm) from intertidal station SI-06, Singapore, including number of measured specimens (*n*), mean and standard deviations (SD). Abbreviations: ac: acicular spine; LD: laterodorsal; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; ML: midlateral; MSW: maximum sternal width, measured on segments 6 or 9*; MVP: midventral placid; pe: penile spine; S: segment lengths; SW-10: standard width, always measured on segment 10; TL: trunk length; tu: tube. *Maximum sternal width measured on segment 9 in female holotype, but on segment 6 in male paratypes.

Character	n	Range	Mean	SD
TL	4	204–448	363.25	109.15
MSW-6*	3	75–79	77.33	2.08
MSW-6/TL	3	18.8–36.8%	25.34	9.93
MSW-9*	1	81	N/A	N/A
MSW-9/TL	1	18.1	N/A	N/A
SW-10	4	68–79	71	5.35
SW/TL	4	16.62–33-3%	21.3	8.03
S1	5	36–37	36.6	0.55
S2	4	38–42	40.25	1.71
S3	5	39–53	45.8	5.89
S4	5	43–57	51.6	5.37
S5	5	52–65	56.6	5.13
S6	5	51–69	60.8	6.57
S7	5	63–71	65.6	3.29
S8	5	61–75	66.6	5.32
S9	5	60–75	65.8	5.93
S10	5	48–55	52.2	2.95
S11	5	36–48	40.8	5.45
MD4 (ac)	2	13	13	0.00
LV5 (tu)	3	16–24	21.33	4.62
LV8 (tu)	3	21–23	22	1.00
ML9 (tu)	2	16	16	0.00
LD10 (tu)	1	21	N/A	N/A
LTAS (ac)	2	20	20	0.00
LTS (ac)	5	61–66	63	2.12
LTAS/LTS	2	31.6–32.8%	32.27	0.74
LTS/TL	4	14.1–29.9%	19.11	7.27
Pe1	1	47	N/A	N/A
Pe2	1	53	N/A	N/A
MVP length	5	17–19	17.8	0.84
MVP width	5	17–19	18.2	0.84

Table 5. Summary of nature and location of spines, tubes, glandular cell outlets and sensory spots arranged by segment in *Echinoderes annae* sp. nov. Abbreviations: LA: Lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD, subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac, acicular spine; gco1/2, glandular cell outlet type 1 or 2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; pe, penile spines; si, sieve plate; ss, sensory spot; tu, tube; ♀, female condition of sexually dimorphic character; ♂, male condition of sexually dimorphic character.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1			ss	ss		gco1				ss
2	gco1, ss		gco2, ss	gco2				gco2		gco1, ss
3	gco1									gco1
4	ac		gco2	ss						gco1
5			ss		ss	gco2		tu		gco1, ss
6		gco1		gco2						gco1, ss
7		gco1	ss			gco2			ss	gco1
8		gco1		gco2				tu		gco1, ss
9		gco1		ss	tu	si				gco1
10		gco1	ss	tu						gco1
11					pe(♂)		ltas(♀)	lts		

(Fig. 8G), as on segment 5. Fringe tips of pectinate fringe slightly longer on middorsal margin than those on preceding segments. Cuticular hairs as on preceding segment.

Segment 8 with lateroventral tubes (Figs. 8F, 9F). Sensory spots present at least in ventromedial positions (Fig. 9F). Glandular cell outlets type 1 present in paradorsal (Fig. 8G) and ventromedial positions; glandular cell outlets type 2 present in laterodorsal positions (Fig. 8F, G), as on segment 6.

Segment 9 with midlateral tubes (Figs. 8F, J, 9I), and a pair of large, elongated sieve plates in sublateral positions (Fig. 8F). Sensory spots present at least in laterodorsal positions. Glandular cell outlets type 1 present in paradorsal and

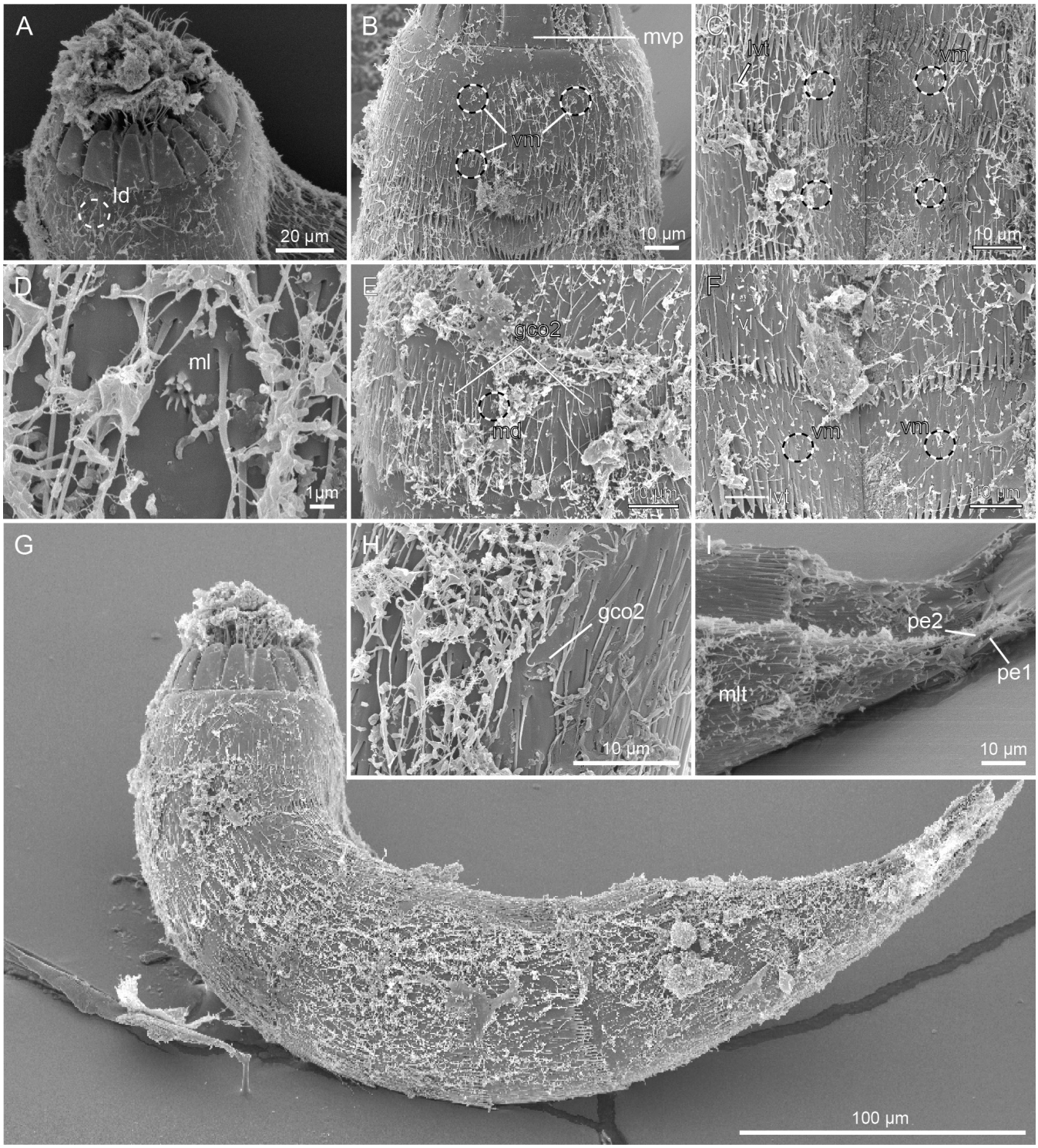

Fig. 9. Scanning electron micrographs of male specimen, showing overviews and details of neck and trunk morphology in *Echinoderes annae* sp. nov. A, neck and segment 1, lateral view. B, neck and segments 1–3, midventral view. C, segments 5–6, midventral view. D, detail showing midlateral sensory spot on segment 5. E, segment 2, middorsal. F, segments 7–8, midventral view. G, lateral overview. H, segment 7, sublateral view. I, segments 9–11, lateral view. Abbreviations: gco2, glandular cell outlet type 2; ld, laterodorsal sensory spot; lvt, lateroventral tube; md, middorsal sensory spot; ml, midlateral sensory spot; mlt, midlateral tube; mvp, midventral placid; pe1–2, penile spines; vm, ventromedial sensory spot.

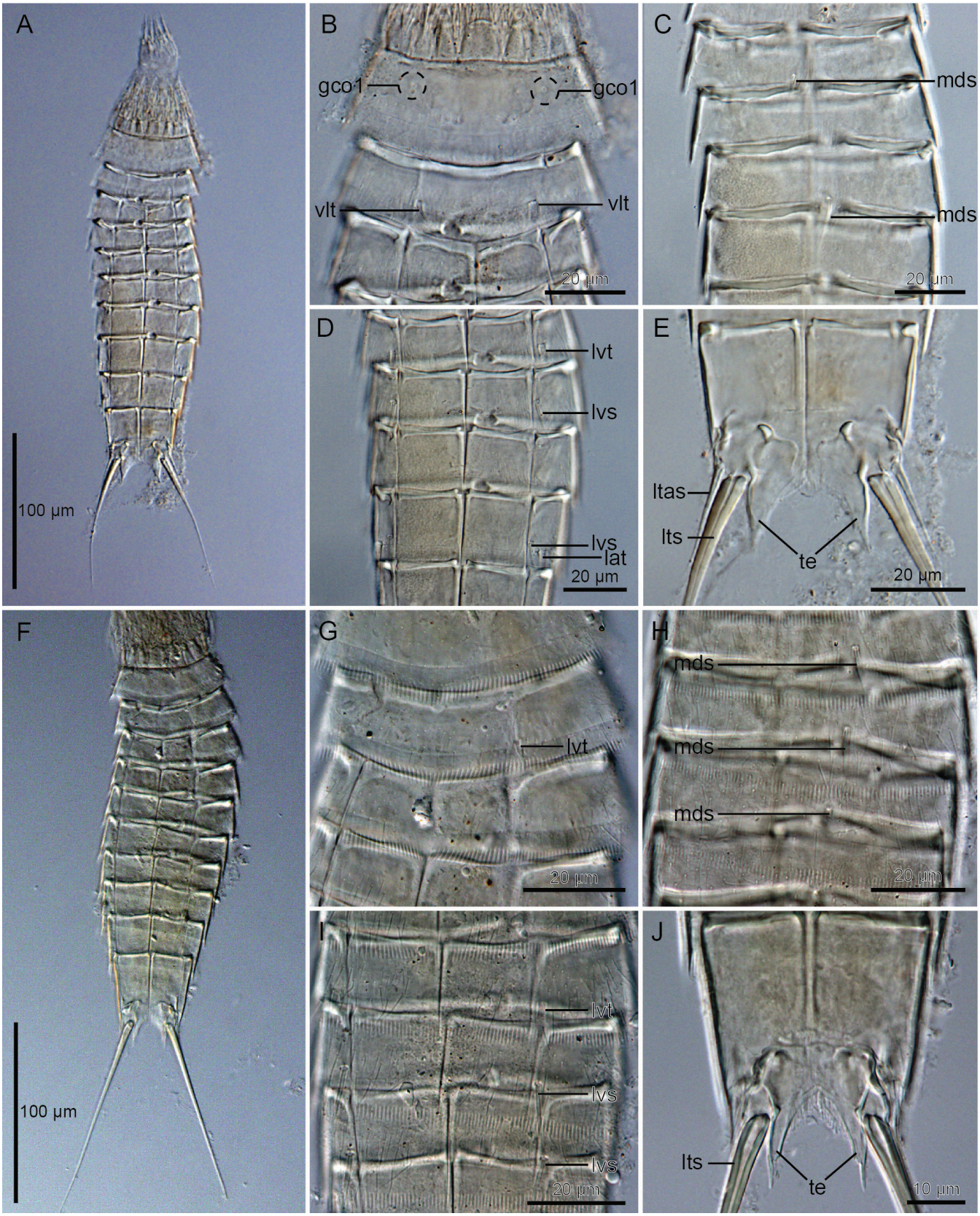

Fig. 10. Light micrographs showing overviews and details of trunk morphology in female *Echinoderes* sp. 1, KIN-855 (A–E) and male *Echinoderes* sp. 2, KIN-856 (F–J). A, ventral overview. B, Neck region and segments 1–3, ventral view. C, segments 4–7, dorsal view. D, segments 5–8, ventral view. E, segments 10–11, ventral view. F, ventral overview. G, Segments 1–3, ventral view. H, segments 4–7, dorsal view. I, segments 5–7, ventral view. J, segments 10–11, ventral view. Abbreviations: gco1, glandular cell outlet type 1; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; te, tergal extensions; vlt, ventrolateral tube.

ventromedial positions (Figs. 8F, J). Pectinate fringe and cuticular hairs as on preceding segment.

Segment 10 with sexually dimorphic laterodorsal tubes near the posterior segment margin (Fig. 8H). Tubes are apparently similar in length but differ in width of both the proximal shaft and the distal tip. In males, the distal parts of the tubes are much thinner, and the proximal shaft is slightly longer than those in females (Figs. 7A, C, 8H). Sensory spots present at least in subdorsal positions. Glandular cell outlets type 1 present in paradorsal and ventromedial positions (Fig. 8F). Cuticular hairs as on preceding segments. Pectinate fringe of posterior margin with shorter and thinner tips than those on preceding segments.

Segment 11 with conspicuously short and stout lateral terminal spines (Fig. 8H, I), with a ring of fine trichoids or cuticular markings around each spine, about 1/3 from its proximal end. Males with three pairs of penile spines (Fig. 8H); females with short lateral terminal accessory spines (Fig. 8I). Segment with few cuticular hairs only. Sensory spots not observed. Glandular cell outlets absent. Tergal extensions elongate and triangular (Figs. 7, 8I).

Notes on diagnostic features of *Echinoderes annae* sp. nov. The presence of midlateral tubes on segment 9 and lateral terminal accessory spines on segment 11 in females, combined with a very short middorsal spine on segment 4, makes *Echinoderes annae* sp. nov. unique among all known kinorhynchs. The new species is furthermore recognised by its dense layer of cuticular hairs and enlarged sieve plates. The presence of enlarged sieve plates is shared with nine other *Echinoderes* species, belonging to the so-called *Echinoderes coulli* group (see Ostmann et al., 2012; Sørensen, 2014; Yamasaki & Fujimoto, 2014). Attention to the group has increased in the recent years with new species being described almost every year. Currently, the group contains nine species: *Echinoderes applicitus* Ostmann et al., 2012, *Echinoderes coulli* Higgins, 1977, *Echinoderes hwiizaa* Yamasaki & Fujimoto, 2014, *Echinoderes komatsui* Yamasaki & Fujimoto, 2014, *Echinoderes marthae* Sørensen, 2014, *Echinoderes maxwelli* Omer-Cooper, 1957, *Echinoderes ohtsukai* Yamasaki & Kajihara, 2012, *Echinoderes rex* Lundbye et al., 2011, and *Echinoderes teretis* Brown, 1999 in Adrianov & Malakhov, 1999 (see also Brown, 1985).

The group is suggested to be monophyletic with the following morphological features supporting this hypothesis: (1) middorsal spines absent, or if present reduced to a short spine on segment 4 only; (2) lateroventral spines either absent, or present simultaneously on segments 6 and 7; (3) lateral tubes present at least and always simultaneously on segments 5 and 8; (4) lateral terminal accessory spines either absent or strongly reduced; (5) an enlarged sieve plate with a large posterior pore present laterally on segment 9 (Sørensen, 2014; Yamasaki & Fujimoto, 2014). The morphology and habitat of *Echinoderes annae* sp. nov. fit perfectly with the traits that characterise species of the *Echinoderes coulli* group, and hence the species must be considered a member of this group.

Other recorded species of *Echinoderes*

Besides *Echinoderes annae* sp. nov., three additional species of *Echinoderes* were recorded from the investigated area. One species could readily be identified as *Echinoderes tchefouensis* Lou, 1934; one could not be identified with certainty, and one obviously represents an undescribed species, but a formal description will not be provided because we only had a single specimen available for examination. Short notes on diagnostic characters and distribution follow here.

***Echinoderes tchefouensis* Lou, 1934**

Material examined. *Echinoderes tchefouensis* appeared on stations SI-01, SI-03, and SI-06, and was hence the most ubiquitous species in the area. A total of six adult specimens were mounted for LM, and deposited at the Natural History Museum of Denmark, under catalogue numbers ZMUC KIN-857 to KIN-862.

Notes on taxonomy and distribution. The species was originally described from the Yantai area on the Chinese Northeast Coast (Lou, 1934). The original description was rather poor, and would in itself fit dozens of *Echinoderes* species. However, R. P. Higgins later collected specimens of *Echinoderes* in the area, and considered these to be conspecific with *E. tchefouensis*. Later, Higgins & Kristensen (1988) provided a note about the unusual lateral spine pattern in these specimens, with lateroventral spines/tubes on segments 5, 8 and 9 only. This enabled Sørensen et al. (2012a) to identify numerous specimens from adjacent waters as *E. tchefouensis*, and, based on these, provide a redescription that met present days' requirements. The species is easily recognised because it lacks lateroventral spines on segments 6 and 7, combined with the presence of regular-sized glandular cell outlets type 2 in subdorsal position on segment 2, and a pair of extraordinary large outlets in laterodorsal positions on segment 8 (see Sørensen et al., 2012a for additional characters).

The record of *E. tchefouensis* in Singapore increases the known distributional range of the species, and makes it one of the apparently most widely distributed species of *Echinoderes*. According to the collectings of Sørensen et al. (2012a) the species covers an area from the Korean Peninsula in northeast, to an easternmost occurrence near Saipan Islands in the West Pacific, and south through the East China Sea and the Philippines, to Sipadan in Malaysian Borneo that until now has marked its southernmost point of distribution. However, the record of the species in Singapore, suggests that it not only has a wide West Pacific distribution, but also could be widespread in the Indonesian Archipelago, and perhaps even could extent into the Indian Ocean. With such a wide distribution, the species would be ideal for population genetic studies, where haplotypes from geographically very distant populations could be compared.

Another interesting finding is the appearance of *E. tchefouensis* at the intertidal station SI-06. Until now, the

species has mostly been recorded from subtidal stations (9–140 m according to Sørensen et al., 2012a). The only other intertidal record of the species is from Saipan in the Northern Mariana Islands (Sørensen et al., 2012a). Apparently the species is not only widely distributed, but also highly opportunistic and able to adapt to different habitats.

Echinoderes sp. 1

Material examined. Two specimens of an unknown species, *Echinoderes* sp. 1, were collected at station SI-03. One specimen was mounted for SEM, but was useless for examination. The other was mounted for LM (Fig. 10A–E), and deposited at the Natural History Museum of Denmark, under catalogue number ZMUC KIN-855.

Descriptive notes. Female *Echinoderes* (Fig. 10A) with middorsal spines on segments 4 and 6 (Fig. 10C), and laterodorsal tubes on segment 10. Ventral side with ventrolateral tubes on segment 2 (Fig. 10B), lateroventral tubes on segment 5, lateroventral spines on segments 6, 8 and 9, but not on 7, and lateral accessory tubes on segment 8 (Fig. 10D). Tergal extensions, triangular, with curved external margins, and almost straight, serrated/hairy inferior margins (Fig. 10E). Glandular cell outlets of type 2 are not present.

The observed spine pattern quite clearly reveals that the species is new to science. Only two other species, namely, *Echinoderes bispinosus* Higgins, 1982 and *Echinoderes astridae* Sørensen, 2014, have their middorsal spines restricted to segments 4 and 6, but both species have lateroventral spines on segments 6 to 9, segment 7 included (see Higgins, 1982; Sørensen, 2014). *Echinoderes bispinosus* furthermore lacks tubes in any position on segment 8, whereas the tubes on segment 8 in *E. astridae* are located in sublateral position. Also the lateral spine pattern in *Echinoderes* sp. 1, with lateroventral spines on segments 6, 8 and 9, but not on 7, is unique among all species of *Echinoderes*.

With the shared presence of middorsal spines on segments 4 and 6, and a similarity in general habitus, it is not unlikely that *Echinoderes* sp. 1 represents a Southeast Asian relative to *E. bispinosus* and *E. astridae*. *Echinoderes astridae* is known from São Sebastião in Brazil only (Sørensen, 2014), whereas *E. bispinosus* is described from Bermuda (Higgins, 1982). A species very similar to *E. bispinosus* was furthermore quite recently reported from Turkey (Sönmez et al., in press), but the geographic distance between Bermuda and the East Mediterranean suggests that the Turkish record represents a similar, but yet new species.

Echinoderes sp. 2

Material examined. Two specimens of another unknown species, *Echinoderes* sp. 2, were collected at station SI-03. One specimen mounted for SEM did not provide any information, whereas the other one mounted for LM (Fig. 10F–J) provided fragmentary information. The LM specimen was deposited at the Natural History Museum of Denmark, under catalogue number ZMUC KIN-856.

Notes on diagnostic characters. Male *Echinoderes* (Fig. 10F) with quite short middorsal spines at least on segments 4, 5 and 6 (Fig. 10H). Round middorsal scars on segments 7 and 8 indicate that spines could have been present here as well, although this is uncertain. This also prevents the opportunities for further identification or description. Additional characteristics include laterodorsal tubes on segment 10, lateroventral tubes on segments 2 and 5 (Fig. 10G, I), and short lateroventral spines on segments 6 to 9 (Fig. 10I). Tergal extensions, with curved external margins, and pointed offset tips at exterior margins (Fig. 10J). Glandular cell outlets of type 2 are not present.

The fragmented information about the dorsal spine patterns makes further attempts to identify the species meaningless. The lateral spine pattern, with spine/tubes on segments 5 to 9, is shared with 56 described congeners, and 33 of these also show lateroventral or ventrolateral tubes on segment 2. The very short middorsal spines, combined with the lateral spine pattern show some resemblance with species such as *Echinoderes ehlersi* Zelinka, 1913, *Echinoderes gerardi* Higgins, 1978, *Echinoderes imperforatus* Higgins, 1983, and *Echinoderes sensibilis* Adrianov et al., 2002 (see Adrianov et al., 2002c), but the long and pointed tergal extensions in the Singapore species (Fig. 10J) differ completely from the rather short and well-spaced ones present in these species. Hence, for now, we would expect *Echinoderes* sp. 2 to represent a new species, but that a formal description would have to wait until more and better material is available.

Class Allomalorhagida Sørensen et al., 2015

Family Pycnophyidae (Zelinka, 1896) Sánchez et al. (in press)

Genus *Leiocanthus* Sánchez et al. (in press)

Leiocanthus nagini sp. nov.

(Figs. 11–13)

Material examined. Holotype adult male, collected from sand with mud on 16 May 2014, at station SI-05 (Fig. 1, Table 1), at 52 m depth, at the locality "Eastern Fairway" southeast of Singapore Island (01°15.589'N 103°56.680'E), mounted in Fluoromount G, deposited at the Lee Kong Chian Natural History Museum, under catalogue number ZRC. MIS.0004. Additional, non-type material, includes one adult female, collected from sand with mud on 16 May 2014, at station SI-03 (Fig. 1, Table 1), at 9 m depth, between Bedok Jetty and Sungei Bedok in the southeast part of Singapore Island (01°18.387'N 103°57.591'E), and mounted for SEM.

Diagnosis. *Leiocanthus* without middorsal elevations. Paradorsal setae present on segments 2–9, paired ones on segment 4. Tergal anterior margin of segment 1 strongly denticulated and followed by a broad, ornamented area. Dorsal and ventral sides on segment 10 with longitudinal cuticular thickenings, visible with LM and SEM. Type 1 sensory spots present on segments 1–10, but not detectable on segment 11.

Etymology. The species name, *nagini*, is the female version of Nāgá – the Sanskrit word for a group of divine dragons or serpent deities known from Hindu and Buddhist mythology. Nagini is furthermore Lord Voldemort's serpent, known from J. K. Rowling's Harry Potter novels.

Description. The single specimen available for SEM was not suitable for introvert examinations, and detailed information on number and arrangement of scalids and oral teeth was thus not possible to obtain.

Neck with four dorsal and two ventral placids (Figs. 11A, B, 13A, B). All placids are thick and hard, with a depressed surface, and articulating with the anterior edge of the first trunk segment. Dorsal placids are rectangular and of similar size, whereas the ventral ones are broader and curve towards the lateral sides. Cuticular folds appear between dorsal and ventral placids. Trichoscalid plates are absent.

Trunk consisting of 11 segments (Figs. 11A, B, 12A, B). First segment with one tergal and three sternal plates (Figs. 11A, B, 13A, B); segments 2–11 with one tergal and two sternal plates (Figs. 11A, B, 12B). Dimensions and measurements of holotype are summarised in Table 6, and distribution of spines, sensory spots and setae in Table 7. The segment width is nearly constant along the trunk, reaching the maximum width at segment 5 and tapering slightly from this segment towards the posterior ones. Pachycycli of tergal and sternal plates are well-developed, with regular sized peg-and-socket joints from segments 2–10. Hairy tergosternal junctions, with numerous short cuticular hairs present on segments 2–10. Conspicuous, oval glandular cell outlets present in laterodorsal and ventromedial positions on segments 2–10 (Fig. 11A, B). Indistinct, rounded muscular scars present in laterodorsal and ventromedial positions on segments 2–10. One pair of laterodorsal and ventrolateral cuticular ridges present on segments 2–10. One pair of apodemes near the anterior margins of segments 9 and 10 (Fig. 11A).

Segment 1 with anterolateral margins of tergal plate projecting into horn-like extensions. Tergal, anterior margin of the segment strongly denticulated, followed by a broad, longitudinal cuticular ornamentation (Figs. 11B, 12E, 13A). Posterior margin of dorsal plate smooth, without middorsal structure specialisation (middorsal process or elevation) or intracuticular atria. Tergal plate with one pair of subdorsal glandular cell outlets, one pair of paralateral setae (Fig. 13B) and three pairs of sensory spots: one pair in subdorsal and two pairs in laterodorsal positions. Sensory spots on this and all following segments belong to type 1, which are rounded and small, consisting of several small cuticular papillae around a central collar of wider papillae. Ventral side with two episternal plates and one trapezoidal midsternal plate, the latter one overhanging the anterior edge of the segment (Figs. 11A, C, 13B). Anterior margin of each sternal plate is ornamented and followed by a contiguous depressed area (Fig. 13B). Each episternal plate with a glandular cell outlet in the medial region and two ventromedial sensory spots. Pectinate fringe on both dorsal and ventral sides thin, only visible with SEM. Conspicuous parallel, cuticular wrinkles present in the posterior parts of tergal and episternal plates, but absent in the midsternal one.

Table 6. Measurements from light microscopy of male holotype of *Leiocanthus nagini* sp. nov. (in µm) from station SI-05, Singapore. Abbreviations: LTS: lateral terminal spine; MSW: maximum sternal width, measured on segment 5 in this species; S: segment lengths; StW, sternal widths, followed by segment number; TL: trunk length.

Character	KIN-867 ♂ Holotype
TL	579
S1	85
S2	56
S3	61
S4	67
S5	69
S6	63
S7	66
S8	73
S9	73
S10	72
S11	37
StW1	122
StW2	138
StW3	139
StW4	139
StW5	140
StW6	137
StW7	129
StW8	128
StW9	123
StW10	116
StW11	–
MSW/TL	24.2%
LTS	139
LTS/TL	24.0%

Segment 2 without middorsal elevation or intracuticular atria at the posterior margin of the dorsal plate. Tergal plate with a single paradorsal seta, and paired setae in laterodorsal and lateroventral positions. Paired sensory spots present in subdorsal and laterodorsal positions. Dorsal side with short secondary pectinate fringes in the anterior part of the segment, present from the tergosternal junction to the laterodorsal longitudinal ridge. Sternal plates with one pair of ventromedial sensory spots. Males with a pair of thick ventromedial tubes (Fig. 11A). Females instead with a pair of ventrolateral setae (Figs. 11C, 12F). Ventral side with secondary pectinate fringe similar to that on the dorsal side, stretching from the tergosternal junction to the ventromedial cuticular ridge. Posterior margin of tergal and sternal plates with conspicuous parallel, cuticular wrinkles. Tergosternal junctions with numerous short cuticular hairs. Muscular scars and glandular cell outlets present in laterodorsal and ventromedial positions. Pachycycli of tergal and sternal plates well-developed, with regular sized peg-and-socket joints. Pectinate fringe as on the preceding segment.

Segment 3 without middorsal elevation or associated intracuticular atria on tergal plate. A single paradorsal seta,

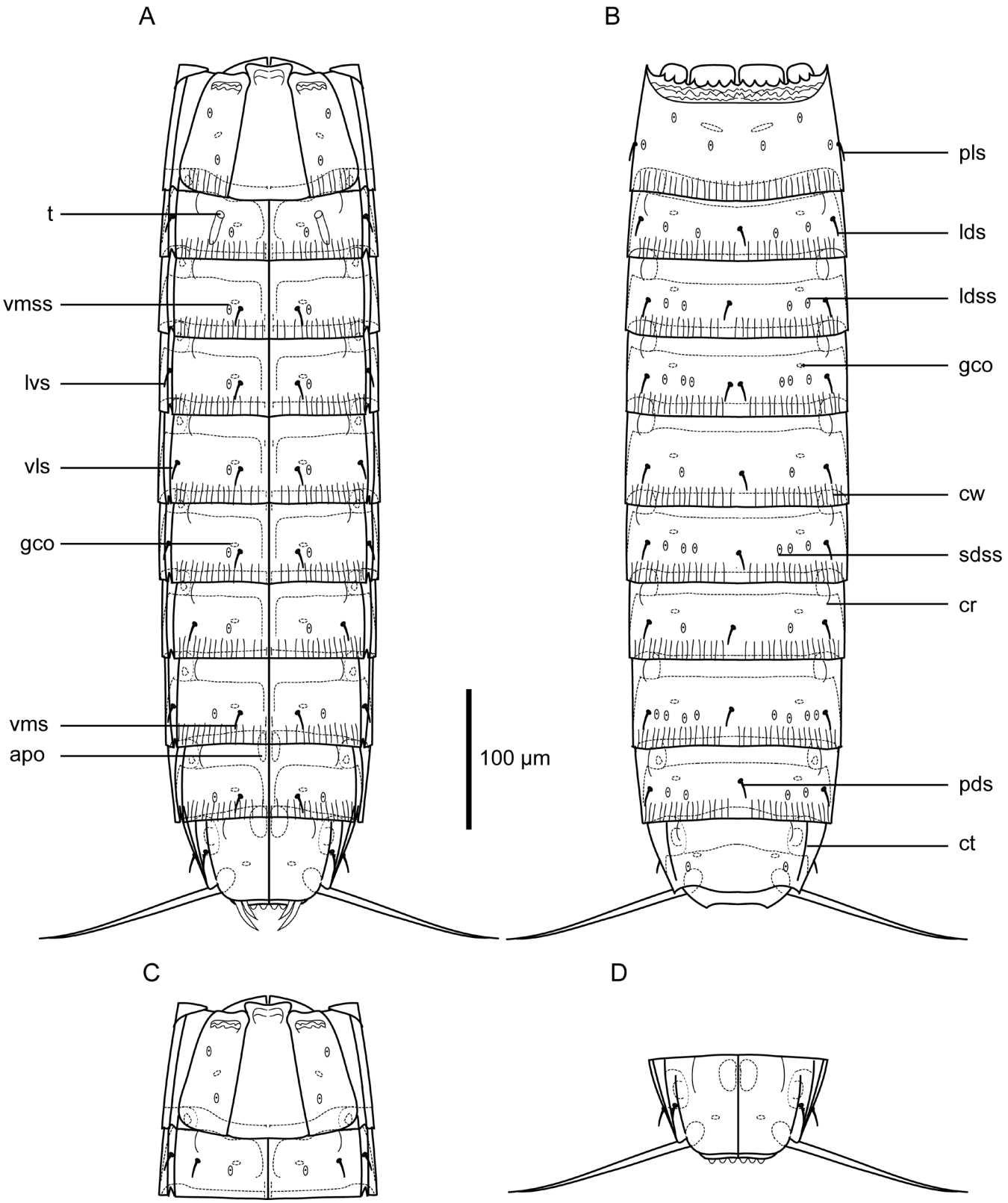

Fig. 11. Line art illustration of *Leiocanthus nagini* sp. nov. A, male, ventral view. B, male, dorsal view. C, female, ventral view, segments 1–2. D, female, ventral view, segments 10–11. Abbreviations: apo, apodemes; cr, cuticular ridge; ct, cuticular thickening; cw, cuticular wrinkles; gco, glandular cell outlets; lds, laterodorsal setae; ldss, laterodorsal sensory spot; lvs, lateroventral setae; pds, paradorsal setae; pls, paralateral setae; sdss, subdorsal sensory spot; t, tube; vls, ventrolateral setae; vms, ventromedial setae; vmss, ventromedial sensory spot.

one pair of laterodorsal setae, and two pairs of laterodorsal sensory spots are present on tergal plate. Both pairs of laterodorsal sensory spots are located mesially to the laterodorsal setae. Lateroventral setae absent. Sternal plates with one pair of ventromedial setae and sensory spots, with the sensory spots located lateral to the setae (Fig. 12F). Otherwise similar to preceding segment.

Segment 4 without middorsal elevation or associated intracuticular atria on tergal plate. Paired setae present in paradorsal, laterodorsal and lateroventral positions. Three pairs of sensory spots present, one in subdorsal and two in laterodorsal positions, all of them located mesially to the laterodorsal setae. Sternal plates as on segment 3. Otherwise similar to preceding segments.

Segment 5 with tergal plate (Fig. 13C) almost similar to that of segment 3 (Fig. 11B), but only with a single pair of laterodorsal sensory spots. Sternal plates similar to those on segment 3, except for the presence of paired ventrolateral setae. Otherwise similar to preceding segments.

Segment 6 with tergal plate (Figs. 11B, 12D, 13C) almost similar to that of segment 4, but with a single paradorsal seta. Sternal plates same as those of segment 3, but with the ventral setae in females displaced to a ventrolateral position (Figs. 11A, 13D). Otherwise similar to preceding segments.

Segment 7 with tergal and sternal plates (Figs. 11A, B, 12D, 13D) almost as those of segment 5, except for the ventral setae that are displaced to a ventrolateral position (Figs. 11A, 13D). Otherwise similar to preceding segments.

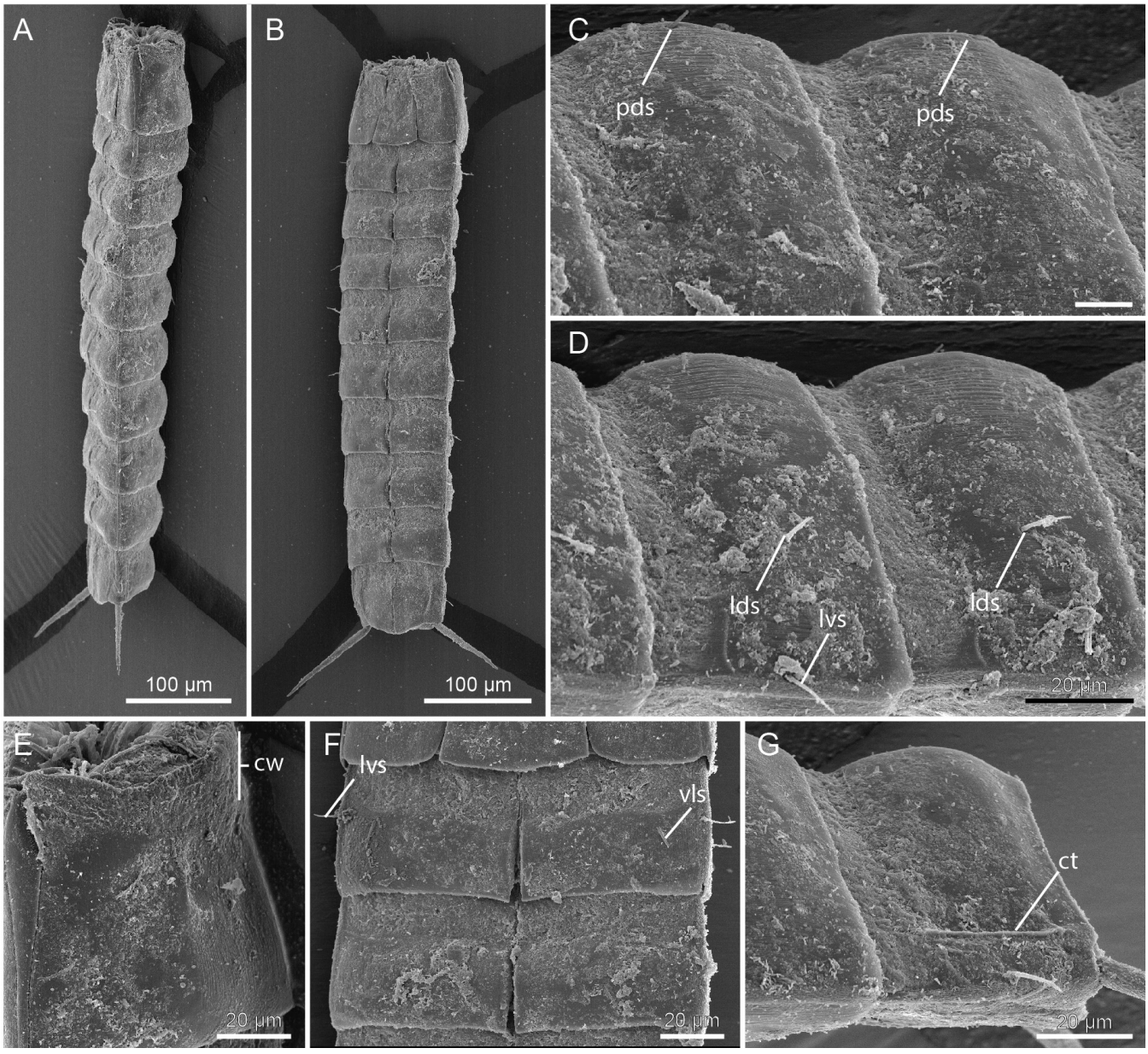

Fig. 12. Scanning electron micrographs of female *Leiocanthus nagini* sp. nov. A, ventrolateral overview. B, ventral overview. C, Middorsal regions of segments 8–9. Note the absence of middorsal structure specialisations. D, Middorsal regions of segments 6–7. Note the absence of middorsal structure specialisations. E, Lateral view of segment 1, showing cuticular wrinkles. F, Ventral view of segments 3–4. G, Lateral view of segment 10, showing the longitudinal cuticular thickening. Abbreviations: ct, cuticular thickening; cw, cuticular wrinkles; lds, laterodorsal seta; lvs, lateroventral seta; pds, paradorsal seta; vls, ventrolateral setae.

Table 7. Summary of location of spines, setae and sensory spots in *Leiocanthus nagini* sp. nov. Abbreviations: LD: laterodorsal; LV: lateroventral; PD: paradorsal; PL: paralateral; SD: subdorsal; VL: ventrolateral; VM: ventromedial; lts, lateral terminal spine; pe, penile spines; se, seta (* indicates unpaired seta); ss, sensory spot; tu, tube; ♀, female condition of sexually dimorphic character; ♂, male condition of sexually dimorphic character.

Position Segment	PD	SD	LD	PL	LV	VL	VM
1		ss	ss,ss	se			ss,ss
2	se*	ss	ss,se		se	se(♀)	ss,t(♂)
3	se*		ss,ss,se				ss,se
4	se	ss	ss,ss,se		se		ss,se
5	se*		ss,se			se	ss,se
6	se*	ss	ss,ss,se		se	se(♀)	ss,se(♂)
7	se*		ss,se			se	ss
8	se*	ss	ss,ss,ss,se		se		ss,se
9	se*		ss,ss,se				ss,se
10			ss		se	se	
11				pe,pe(♂)	lts		

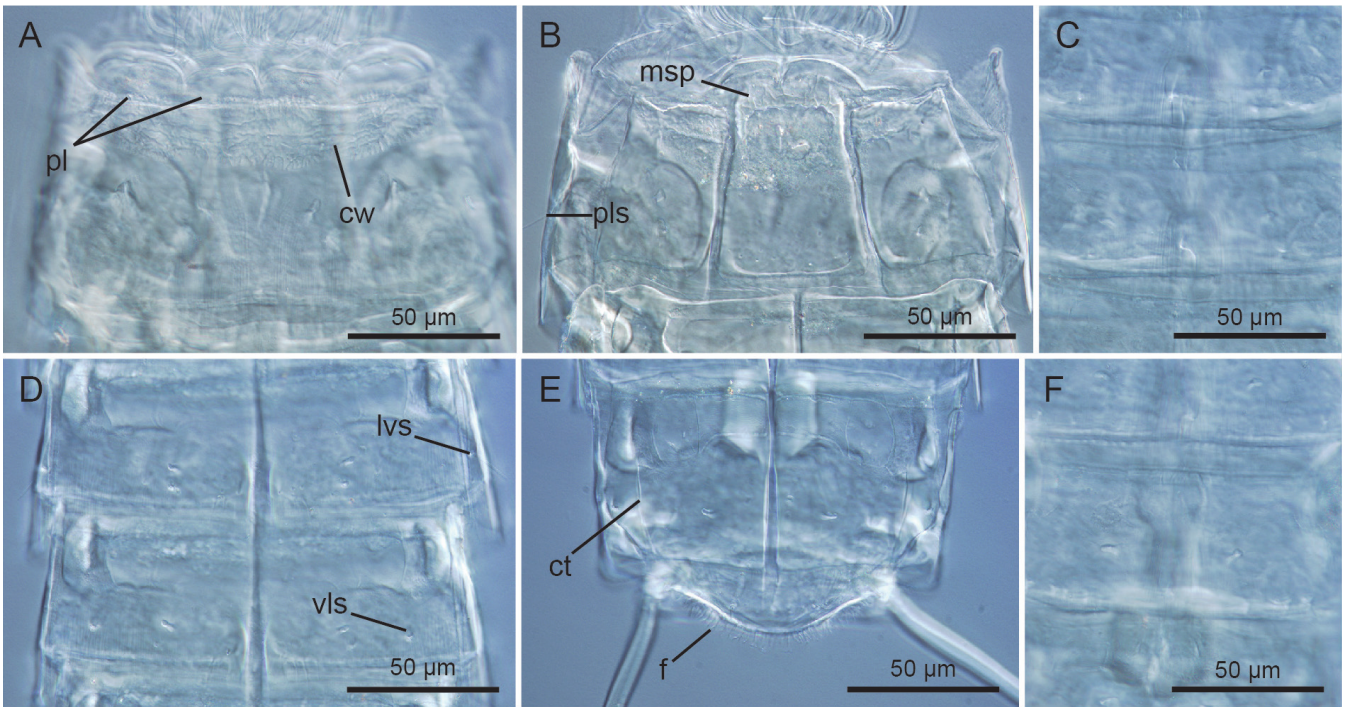

Fig. 13. Light micrographs showing details of trunk morphology in holotypic male of *Leiocanthus nagini* sp. nov., ZRC.MIS.0004. A, dorsal placids and dorsal anterior margin of segment 1. B, ventral placids and ventral anterior margin of segment 1. C, middorsal region of segments 5–6. Note the absence of middorsal structure specialisations. D, ventral view of segments 6–7. E, ventral view of segments 10–11, showing the special shape of the posterior fringe. F, middorsal region of segments 8–9. Note again the absence of middorsal structure specialisations. Abbreviations: ct, cuticular thickening; cw, cuticular wrinkles; f, irregular fringe; lvs, lateroventral seta; msp, midsternal plate; pl, placids; pls, paralateral setae; vls, ventrolateral seta.

Segment 8 with tergal plate (Figs. 11B, 12C, 13F) similar to that of segment 6, but with one additional pair of laterodorsal sensory spots, making it three laterodorsal pairs in total (Fig. 11B). Sternal plates as those on segment 3. Otherwise similar to preceding segments.

Segment 9 with tergal (Figs. 11B, 12C, 13F) and sternal plates similar to those of segment 3. Protonephridial opening in paralateral position, with the pore surrounded by a few short cuticular hairs; opening not sieve-like. Paired apodemes (or anteromesial thickenings of ventral pachycycli) present near the anterior margin of segment (Fig. 11A). Otherwise similar to preceding segment.

Segment 10 without dorsal structures (Figs. 11B, 12G). Tergal plate with one pair of lateroventral setae and a pair of laterodorsal sensory spots. Sternal plates with ventrolateral setae. Ventromedial sensory spots not found. Paired apodemes present near the anterior margin of the segment (Figs. 11A, 13E). Lateral margins of tergal and sternal plates

with conspicuous, longitudinal cuticular thickening visible with LM and SEM (Figs. 12G, 13E). Otherwise similar to preceding segment.

Segment 11 with a pair of lateral terminal spines (Fig. 11A, B, D). Males with two pairs of penile spines and genital pores surrounded by a tuft of long hairs. Posterior segment margin with characteristic, irregularly fringed shape (Fig. 13E).

Notes on diagnostic features of *Leiocanthus nagini* sp. nov. *Leiocanthus nagini* sp. nov. is easily distinguished from other pycnophyid species by its presence of paradorsal setae on segments 2–9 combined with the absence of middorsal structure specialisations. The lack of middorsal structure specialisations is characteristic for species of *Leiocanthus*. The genus currently accommodates 12 species, inclusive *Leiocanthus nagini* sp. nov., but only nine have lateral terminal spines. Six species of *Leiocanthus* share the lack of middorsal structure specialisation on all segments with *Leiocanthus nagini* sp. nov., namely *Leiocanthus lageria* (Sánchez et al., 2014), *Leiocanthus sculptus* (Lang, 1949), *Leiocanthus ecphantor* (Higgins, 1983), *Leiocanthus corrugatus* (Higgins, 1983), *Leiocanthus pardosi* (Sánchez et al., 2013) and *Leiocanthus faveolus* (Brown, 1999 in Adrianov & Malakhov, 1999) (see original descriptions, Brown, 1985, and Sánchez et al., in press). Of these species, only *L. pardosi* and *L. faveolus* have paradorsal setae on segments 2–9. However, *L. faveolus* also has paradorsal setae on segment 1. Such setae are absent in *Leiocanthus nagini* sp. nov.

Moreover, *L. pardosi* and the new species share the presence of longitudinal cuticular thickenings on segment 10, both on the dorsal and ventral sides, and a special shape of the posterior fringe on segment 11. In addition, the ventral setae on segment 7 are in these two species displaced to a more ventrolateral position, opposed to the rest of the species mentioned above, which have setae in ventromedial positions. *Leiocanthus nagini* sp. nov. also has paired paradorsal setae on segment 4, whereas *L. pardosi* has paired paradorsal setae on segment 9 and does not have neither laterodorsal setae on segment 9 nor parallel cuticular wrinkles along the trunk.

Notes on other recorded species of Pycnophyidae. Additional specimens of *Pycnophyes* were collected at all localities, except for stations SI-02 and SI-05 (see Table 1). However, the specimens were rather dirty and damaged, and hence not in a condition that allowed much further identification. Four specimens, *Pycnophyes* sp. 1, from four different localities appeared to belong to the same species, probably new to science. The specimens were mounted for LM and are deposited at the Natural History Museum of Denmark, under catalogue numbers ZMUC KIN-863 to KIN-866. One additional specimen, *Pycnophyes* sp. 2, from SI-03 differed from the other recorded *Pycnophyes* species in its distribution of setae, hence, it is considered to represent another, yet undescribed species. This single specimen was mounted for SEM and is kept in the personal collection of the first author.

ACKNOWLEDGEMENTS

We are greatly indebted to Heinrich Reichert (Basel) for his financial support during the fieldwork at Singapore. RCN is grateful to Tan Koh Siang for his support and hospitality at the Tropical Marine Science Institute (TMSI), National University of Singapore (NUS). Specimens were collected under the auspices of the Comprehensive Marine Biodiversity Survey (CMBS; 2010–2015) organised by the National Parks Board and NUS. The technical support and sampling work by the staff and students at the Marine Biology and Ecology Laboratory (TMSI), especially Gan Bin Qi, Chim Chee Kong and Teresa Stephanie Tay, are also greatly appreciated. RCN also wish to thank Jeremias Brand (Basel) for his help with sediment collection and processing.

LITERATURE CITED

Adrianov AV (1989) The first report of Kinorhyncha of the Sea of Japan. Zoologicheskii Zhurnal, 68: 17–27.

Adrianov AV & Malakhov VV (1999) Cephalorhyncha of the World Ocean. KMK Scientific Press, Moscow, 328 pp.

Adrianov AV, Murakami C & Shirayama Y (2002a) Taxonomic study of the Kinorhyncha in Japan. II. *Condyloderes setoensis*, a new species (Kinorhyncha: Cyclorhagida) from Tanabe Bay (Honshu Island) – first representative of the genus in the Pacific Ocean. Proceedings of the Biological Society of Washington, 115: 189–216.

Adrianov AV, Murakami C & Shirayama Y (2002b) *Echinoderes aureus* n. sp. (Kinorhyncha: Cyclorhagida) from Tanabe Bay (Honshu) – first representative of the genus in the Pacific Ocean. Proceedings of the Biological Society of Washington, 115: 205–216.

Adrianov AV, Murakami C & Shirayama Y (2002c) Taxonomic study of the Kinorhyncha in Japan. III. *Echinoderes sensibilis* n. sp. (Kinorhyncha: Cyclorhagida) from Tanabe Bay. Zoological Science, 19: 463–473.

Altenburger A, Rho HS, Chang CY & Sørensen MV (2015) *Zelinkaderes yong* sp. nov. from Korea – the first recording of *Zelinkaderes* (Kinorhyncha: Cyclorhagida) in Asia. Zoological Studies, 54: 24.

Brown R (1985) Developmental and taxonomic studies of Sydney Harbour Kinorhyncha. Dissertation, Macquarie University, Australia.

Chang CY & Song YH (2002) *Echinoderes lanceolatus*, a new kinorhynch from Korea (Kinorhyncha, Cyclorhagida, Echinoderidae). The Korean Journal of Systematic Zoology, 18: 203–211.

Claparède ARE (1863) Zur Kenntnis der Gattung *Echinoderes* Duj. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt. Verlag von Wilhelm Engelmann, Leipzig, pls. XVI–XVII, pp. 90–92, 119.

Coull BC (1970) Shallow water meiobenthos of the Bermuda platform. Oecologia, 4: 325−357.

Higgins RP (1964). Three new kinorhynchs from the North Carolina Coast. Bulletin of Marine Science of the Gulf and Caribbean, 14: 479–493.

Higgins RP (1968) Taxonomy and postembryonic development of the Cryptorhagae, a new suborder for the mesopsammic kinorhynch genus *Cateria*. Transactions of the American Microscopical Society, 87: 21–39.

Higgins RP (1969a) Indian Ocean Kinorhyncha, 1: *Condyloderes* and *Sphenoderes*, new cyclorhagid genera. Smithsonian Contributions to Zoology, 14: 1–13.

Higgins RP (1969b) Indian Ocean Kinorhyncha, 2: Neocentrophyidae, a new homalorhagid family. Proceedings of the Biological Society of Washington, 82: 113–128.

Higgins RP (1977) Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. Transactions of the American Microscopical Society, 96: 340–354.

Higgins RP (1978) *Echinoderes gerardi* n. sp. and *E. riedli* (Kinorhyncha) from the Gulf of Tunis. Transactions of the American Microscopical Society, 97: 171–180.

Higgins RP (1982) Three new species of Kinorhyncha from Bermuda. Transactions of the American Microscopical Society, 101: 305−316.

Higgins RP (1983) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. Smithsonian Contributions to Marine Science, 18: 1–131.

Higgins RP (1986) Kinorhyncha. In: Sterrer W & Schöpfer-Sterrer C (eds) Marine Fauna and Flora of Bermuda: A Systematic Guide to the Identification of Marine Organisms. John Wiley & Sons New York. Pp. 220−222.

Higgins RP & Kristensen RM (1988) Kinorhyncha from Disko Island, West Greenland. Smithsonian Contributions to Zoology, 458: 1–56.

Higgins RP & Rao GC (1979) Kinorhynchs from the Andaman Islands. Zoological Journal of the Linnean Society, 67: 75–85.

Higgins RP & Shirayama Y (1990) Dracoderidae, a new family of the cyclorhagid Kinorhyncha from the Inland Sea of Japan. Zoological Science, 7: 939–946.

Lang K (1949) Echinoderida. In: Odhner NH (ed.) Further zoological results of the Swedish Antartic Expedition 1901–1903. Vol. IV, No. 2, Norstedt and Söner, Stockholm. Pp. 1–22.

Lou TH (1934) Sur la presence d'un nouveau kinorhynque a Tchefou: *Echinoderes tchefouensis* sp. nov. Contributions from the Institute of Zoology, National Academy of Peiping, 1: 1–9. [In Mandarin with French translation]

Lundbye H, Rho HS & Sørensen MV (2011) *Echinoderes rex* n. sp. (Kinorhyncha: Cyclorhagida) – the largest *Echinoderes* species found so far. Scientia Marina, 75: 41–51.

Neuhaus B (2013) Kinorhyncha (=Echinodera). In: Schmidt-Rhaesa A (ed.) Handbook of Zoology. Gastrotricha, Cycloneuralia and Gnathifera. Volume 1. Nematomorpha, Priapulida, Kinorhyncha, Loricifera. De Gruyter, Berlin/Boston. Pp. 181–348.

Neuhaus B, Pardos F, Sørensen MV & Higgins RP (2013). Redescription, morphology, and biogeography of *Centroderes spinosus* (Reinhard, 1881) (Kinorhyncha, Cyclorhagida) from Europe. Cahiers de Biologie Marine, 54: 109–131.

Neuhaus B, Pardos F, Sørensen MV & Higgins RP (2014) New species of *Centroderes* (Kinorhyncha: Cyclorhagida) from the Northwest Atlantic Ocean, life cycle, and ground pattern of the genus. Zootaxa, 3901: 1–69.

Neves RC, Brand J, Gan BQ & Reichert H (in press). First time surveying meiofauna in Singapore. Raffles Bulletin of Zoology, Supplement.

Omer-Cooper J (1957) Deux nouvelle especes de Kinorhyncha en provenance de L´Afrique du Sud. Bulletin Mensuel de la Sociéte Linnéenne De Lyon, 26: 213–216.

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. Marine Biodiversity, 42: 79–91.

Rao GC & Ganapati PN (1968) The interstitial fauna inhabiting the beach sands of Waltair coast. Proceedings of the National Institute of Sciences, India, 34: 82–125.

Reinhard W (1881) Über *Echinoderes* und *Desmoscolex* der Umgegend von Odessa. Zoologischer Anzeiger, 4: 588−592.

Sánchez N, Herranz M, Benito J & Pardos F (2014a) *Pycnophyes almansae* sp. nov. and *Pycnophyes lageria* sp. nov., two new homalorhagid kinorhynchs (Kinorhyncha: Homalorhagida) from the Iberian Peninsula, with special focus on the introvert features. Marine Biology Research, 10: 17–36.

Sánchez N, Pardos F & Sørensen MV (2014b) Deep-sea Kinorhyncha: two new species from the Guinea Basin, with evaluation of an unusual male feature. Organisms Diversity and Evolution, 14: 349–361.

Sánchez N, Rho HS, Min W G, Kim D & Sørensen MV (2013) Four new species of *Pycnophyes* (Kinorhyncha: Homalorhagida) from Korea and the East China Sea. Scientia Marina, 77: 353–380.

Sánchez N, Yamasaki H, Pardos F, Sørensen MV & Martínez, A. (in press). Morphology disentangles the systematics of a ubiquitous but elusive meiofaunal group (Kinorhyncha: Pycnophyidae). Cladistics

Sarma NSR & Mohan PC (1981) On the ecology of the interstitial fauna inhabiting the Bhimilipatnam coast (Bay of Bengal). Mahasagar-Bulletin of the National Institute of Oceanography, 14: 257–263.

Song YH & Chang CY (2001) First record of *Campyloderes macquariae* Jonhston (Kinorhyncha, Cyclorhagida, Centroderidae) from the North Pacific. The Korean Journal of Systematic Zoology, 17: 207–216.

Sönmez S, Köroğlu NÖ & Karaytuğ S (in press) First record of the family Echinoderidae Zelinka, 1894 (Kinorhyncha: Cyclorhagida) from Turkish marine waters. Biharean Biologist, 10: art.151205

Sørensen MV (2014) First account of echinoderid kinorhynchs from Brazil, with the description of three new species. Marine Biodiversity, 44: 251–274.

Sørensen MV, Dal Zotto M, Rho HS, Herranz M, Sánchez N, Pardos F & Yamasaki H (2015) Phylogeny of Kinorhyncha based on morphology and two molecular loci. PLoS ONE 10(7): e0133440.

Sørensen MV, Herranz M, Rho HS, Min W, Yamasaki H, Sánchez N & Pardos F (2012b) On the genus *Dracoderes* Higgins & Shirayama, 1990 (Kinorhyncha: Cyclorhagida) with a redescription of its type species, *D. abei*, and a description of a new species from Spain. Marine Biology Research, 8: 210–232.

Sørensen MV & Pardos F (2008) Kinorhynch systematics and biology – an introduction to the study of kinorhynchs, inclusive identification keys to the genera. Meiofauna Marina, 16: 21–73.

Sørensen MV, Pardos F, Herranz M & Rho HS (2010a) New data on the genus *Paracentrophyes* (Homalorhagida, Kinorhyncha), with the description of a new species from the West Pacific. The Open Zoology Journal, 3: 42–59.

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

Sørensen MV, Rho HS & Kim D (2010c) A new species of *Condyloderes* (Cyclorhagida, Kinorhyncha) from Korea. Zoological Science, 27: 234–242.

Sørensen MV, Rho HS, Min W, Kim D & Chang CY (2012a) 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.

Sørensen MV, Rho H, Min W-G, Kim D & Chang C (2013) Occurrence of the newly described kinorhynch genus *Meristoderes* (Cyclorhagida: Echinoderidae) in Korea, with the description of four new species. Helgoland Marine Research, 67: 291–319.

Thomsen VG, Rho HS, Kim D & Sørensen MV (2013) A new species of *Dracoderes* (Kinorhyncha: Dracoderidae) from Korea provides further support for a dracoderid-homalorhagid relationship. Zootaxa, 3682: 133–142.

Timm RW (1958) Two new species of *Echinoderella* (Phylum Kinorhyncha) from the Bay of Bengal. Journal of the Bombay Natural History Society, 55: 107–109.

Yamasaki H & Fujimoto S (2014) Two new species in the *Echinoderes coulli* group (Echinoderidae, Cyclorhagida, Kinorhyncha) from the Ryukyu Islands, Japan. ZooKeys, 382: 27–52.

Yamasaki H, Hiruta SF, Kajihara H & Dick MH (2014) Two kinorhynch species (Cyclorhagida, Echinoderidae, *Echinoderes*) show different distribution patterns across Tsugaru Strait, Northern Japan. Zoological Science, 31: 421–429.

Yamasaki H & Kajihara H (2012) A new brackish-water species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Seto Inland Sea, Japan. Species Diversity, 17: 109–118.

Yamasaki H, Kajihara H & Mawatari SF (2012) First report of kinorhynchs from Hokkaido, Japan, including a new species of *Pycnophyes* (Pycnophyidae: Homalorhagida). Zootaxa, 3425: 23–41.

Zelinka K (1894) Über die Organisation von Echinoderes. Verhandlungen der Deutschen Zoologischen Gesellschaft, 4: 46–49.

Zelinka K (1896) Demonstration von Tafeln der *Echinoderes*-Monographie. Verhandlungen der Deutschen Zoologischen Gesellschaft, 6: 197–199.

Zelinka K (1907) Zur Kenntnis der Echinoderen. Zoologischer Anzeiger, 32: 130–136.

Zelinka K (1913) Der Echinoderen der Deutschen Südpolar-Expedition, 1901-1903. Band 14. Reimer, Berlin.