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出版情報：Zoologischer Anzeiger. 282, pp.64-87, 2019-09. Elsevier
バージョン：

Zoologischer Anzeiger 282 (2019) 64–87

Contents lists available at ScienceDirect

Zoologischer Anzeiger

journal homepage: www.elsevier.com/locate/jcz

Research paper

# Echinoderid mud dragons (Cyclorhagida: Kinorhyncha) from Senghor Seamount (NE Atlantic Ocean) including general discussion of faunistic characters and distribution patterns of seamount kinorhynchs☆

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ARTICLE INFO

*Article history:*
Received 25 February 2019
Received in revised form
21 May 2019
Accepted 23 May 2019
Available online 6 June 2019

*Keywords:*
Biogeography
Description
Distribution
Meiofauna
Stepping stone
Taxonomy

ABSTRACT

Investigation of Kinorhyncha from Senghor Seamount (tropical northeastern Atlantic Ocean) and the adjacent deep-sea floor revealed seven species of *Echinoderes*. Of these, *Echinoderes kaempfae* sp. nov. and *Echinoderes schwieringae* sp. nov. are described as new species. *Echinoderes multiporus* originally found on Eratosthenes Seamount, Mediterranean Sea, and *Echinoderes* cf. *adrianovi* originally found off Florida, northwestern Atlantic Ocean, were also recovered. In addition, three additional species, which possibly represent undescribed species, occurred on Senghor Seamount. Because of the low number of available specimens or necessity of further observations of closely related congeners for these three undescribed species, we provide only a brief description of them without naming them as new species. The comparison of each species with morphologically similar congeners is also provided. Based on all records of kinorhynchs from seamounts and the adjacent deep-sea floor in the Northeastern Atlantic Ocean, Mediterranean Sea, and Arctic Sea, it is suggested that (1) the kinorhynch fauna on seamounts is partly unique, (2) seamount kinorhynchs originate both from shallow waters and the deep sea, and (3) a few kinorhynch species diversified on seamounts.



## 1. Introduction

With 125 out of ca. 290 species, *Echinoderes* Claparède, 1863 is the species-richest genus within the phylum Kinorhyncha. *Echinoderes* is cosmopolitan at the genus level and occurs in various environments, like brackish water, tidal flats, shallow sublittoral water, submarine caves, seamounts, and the deep-sea floor (e.g., Sørensen et al. 2000, 2018; Yamasaki & Kajihara 2012; Herranz et al. 2018; Sørensen 2018; Yamasaki et al. 2018a, b, c). Nonetheless at the species level, each species has been found in more restricted regions and specific environments (e.g., Sánchez et al. 2012; Neuhaus 2013; Dal Zotto & Todaro 2016; Yamasaki 2017). The echinoderid fauna of the Atlantic Ocean has been relatively well investigated in shallow waters, especially in the northeastern American coast (e.g., Higgins 1964; 1977b; Sørensen et al. 2005, 2016; Herranz et al. 2014; Landers & Sørensen 2018), the coastline of the Iberian Peninsula (Pardos et al. 1998; GaOrdóñez et al. 2008; Sánchez et al. 2012), the waters around Disko Island, West Greenland and Svalbard (Higgins & Kristensen 1988; Grzelak & Sørensen 2018, 2019). However, most of the other areas in the ocean, including the deep-sea floor and seamounts located between the shallow continental shelves, have been scarcely studied, and the species known so far might account only for a small part of the actual species diversity of *Echinoderes* in the Atlantic Ocean.

The study of echinoderid kinorhynchs on seamounts started recently. Until now, six species of the genus have been recorded from seamounts: *Echinoderes apex* Yamasaki et al., 2018, *Echinoderes meteorensis* Yamasaki et al., 2018, *Echinoderes multiporus* Yamasaki et al., 2018, *Echinoderes peterseni* Higgins & Kristensen, 1988, *Echinoderes pterus* Yamasaki et al., 2018, and one undescribed species reported in Yamasaki et al. (2018b) (Kristensen

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☆ This article is a part of the Fifth International Scalidophora Workshop special issue published in Zoologischer Anzeiger 282C, 2019.

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https://doi.org/10.1016/j.jcz.2019.05.018

2005; Yamasaki et al. 2018a, b, c). Of these, all except for the following two species have been found on one or two seamounts: *E. peterseni* has been recorded from Greenland, off Svalbard Island, and the Faroe Bank in the Atlantic Ocean and the Arctic Sea, at 9–927 m depth, and *E. pterus* from Karasik Seamount, Anaximenes Seamount, Sedlo Seamount, off North Svalbard, and in the deep Mediterranean Sea, at 675–4403 m depth. While the numbers of *Echinoderes* species reported from seamounts recently have increased, many seamounts are still uninvestigated, meaning that more species might be found as more seamounts will be investigated. Also further investigations will help elucidating the distribution range and pattern of each species.

This study deals with *Echinoderes* specimens from Senghor Seamount, located near to the Cape Verde Archipelago in the northeast Atlantic Ocean (Fig. 1). This is the first investigation of Kinorhyncha from Senghor Seamount. Two new species are described, and one species, which has previously been recorded from another seamount, as well as one species that has been recorded from the west coast of the United States, and three undescribed species are reported. Finally, the potential role of seamounts for the dispersal of kinorhynch species in general is discussed.

## 2. Material and methods

Kinorhynchs were obtained from meiofauna samples collected on Senghor Seamount and at a deep-sea station adjacent to Senghor Seamount by R/V METEOR during the expedition M79/3 in 2009 (Christiansen et al. 2011) (Fig. 1, Table 1). All sediment samples were taken with a multicorer and fixed in 4–8% formaldehyde. The samples were washed with tap water through a 40 μm mesh sieve in the laboratory. Subsequently, the meiofauna was extracted from the sediment by centrifuging with a colloidal silica polymer (H.C. Stark, Levasil 200/40%, density 1.17 g/cm$^3$) and Kaolin. After the extraction, the meiofauna was rinsed with tap water, stained with Rose Bengal, sorted under a stereomicroscope, and subsequently preserved in 75% ethanol.

Specimens for light microscopy (LM) were dehydrated in glycerol and mounted as glycerol-paraffin slides on Cobb aluminum frames and observed with a Zeiss Axioskop 50 microscope. A camera lucida equipped with the microscope was used to make drafts for line art illustrations. Final line art illustrations were drawn with Adobe Illustrator CS6 based on the drafts. Measurements were made through a camera lucida. Specimens were photographed with a Zeiss AxioCam MRc5 mounted on a Zeiss Axioplan 2 mot.

Specimens for scanning electron microscopy (SEM) were transferred from ethanol to distilled water through a graded series of ethanol, postfixed with $OsO_4$ in 0.05 M phosphate buffer (pH = 7.3) with 0.3 M sodium chloride and 0.05% sodium azide for 2.5 h, dehydrated through a graded series of ethanol, critical-point dried with a BalTec CPD 030, mounted on aluminum stubs, sputter-coated with gold-palladium with a Polaron SC 7640, and observed with a Zeiss EVO LS 10 scanning electron microscope.

The terminology follows Neuhaus & Higgins (2002), Sørensen & Pardos (2008) and Neuhaus (2013). All specimens have been deposited in the Museum für Naturkunde Berlin (= ZMB, former Zoological Museum Berlin), Germany and catalogued in the collection “Vermes” in the “Generalkatalog Freilebende Würmer”.

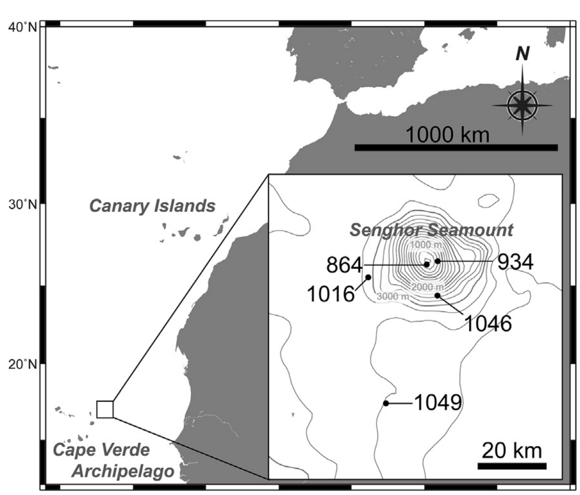



**Fig. 1.** Map of the northeastern Atlantic Ocean and Senghor Seamount, inset showing the sampling stations.

## 3. Results and discussions

Class Cyclorhagida Zelinka, 1896
Order Echinorhagata Sørensen et al., 2015
Family Echinoderidae Zelinka, 1894
Genus *Echinoderes* Claparède, 1863

### 3.1. *Echinoderes kaempfae sp. nov.*

(Figs. 2 and 3, Tables 2 and 3)
http://zoobank.org/urn:lsid:zoobank.org:act:1FE3571E-2D88-4563-A669-766465084930

#### 3.1.1. Diagnosis

*Echinoderes* with middorsal acicular spines on segments 4–8 and lateroventral acicular spines on segments 6–9; tubes only lateroventrally on segment 5 and laterodorsally on segment 10; tergal extensions long and gradually tapering towards pointed tips; without any type-2 gland cell outlets.

#### 3.1.2. Etymology

This species is named after Kristine Kämpf, a technician at the Museum für Naturkunde Berlin who technically supported this study.

#### 3.1.3. Type locality

At the foot of Senghor Seamount, northeastern Atlantic Ocean (17° 9′48″N, 22° 9′38″W), 3110 m depth (Fig. 1, Table 1).

#### 3.1.4. Material examined

Holotype: one female (ZMB 11943), collected at station 1016 at foot of Senghor Seamount, northeastern Atlantic Ocean (17° 9′48″N, 22° 9′38″W), 3110 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

Paratype: one male (ZMB 11944), collected at same locality as holotype; one male (ZMB 11945), collected at station 1046 at slope of Senghor Seamount, northeastern Atlantic Ocean (17° 7′30″N, 21°55′30″W), 1545 m depth. Both specimens mounted as glycerol-paraffin slides on Cobb aluminum frames.

#### 3.1.5. Description

Adult with head, neck, and eleven trunk segments (Figs. 2A, B, and 3A). See Table 2 for measurements. Table 3 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Head consisting of retractable mouth cone and introvert. Detailed arrangement of mouth cone and introvert characters not observed.

**Table 1**
Data of sampling stations.

| Station | seamount | date | depth (m) | latitude | longitude | Species |
|---|---|---|---|---|---|---|
| 864 | Senghor Seamount (summit) | 04/10/2009 | 132 | 17°12′17″N | 21°57′41″W | *Echinoderes* cf. *adrianovi; Echinoderes schwieringae* sp. nov. |
| 934 | Senghor Seamount (slope) | 09/10/2009 | 565 | 17°12′56″N | 21°56′22″W | *Echinoderes multiporus; Echinoderes* sp. 1; *Echinoderes* sp. 2 |
| 1016 | Senghor Seamount (foot) | 16/10/2009 | 3110 | 17° 9′48″N | 22° 9′38″W | *Echinoderes kaempfae* sp. nov. |
| 1046 | Senghor Seamount (slope) | 18/10/2009 | 1545 | 17° 7′30″N | 21°55′30″W | *Echinoderes kaempfae* sp. nov.; *Echinoderes* sp. 1 |
| 1049 | Deep-sea floor close to Senghor Seamount | 19/10/2009 | 3376 | 16°45′0″N | 22° 6′0″W | *Echinoderes* sp. 3 |

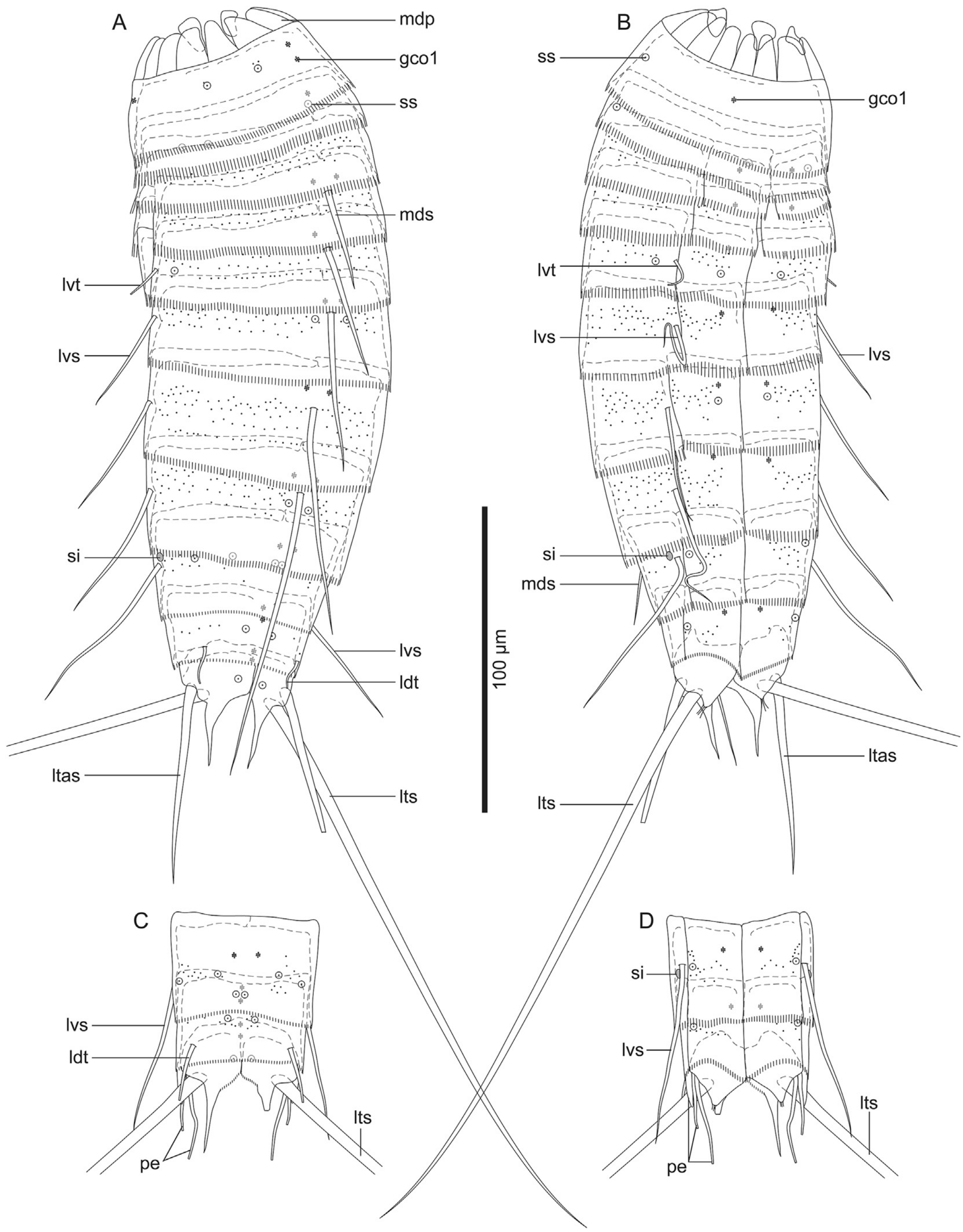



**Fig. 2.** *Echinoderes kaempfae* sp. nov., camera lucida drawings. A, B, holotype, female (ZMB 11943), whole animal, dorsal and ventral view, respectively; C, D, paratype male (ZMB 11944), segments 9–11, dorsal and ventral view, respectively. Abbreviations: gco1, type-1 gland cell outlet; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mdp, middorsal placid; mds, middorsal acicular spine; pe, penile spine; si, sieve plate; ss, sensory spot.


**Fig. 3.** *Echinoderes kaempfae* sp. nov., Nomarski photomicrographs. A–G, holotype, female (ZMB 11943); H, paratype, male (ZMB 11944). A, neck and segments 1–11, ventral view; B, neck and segments 1–7, dorsal view; C, neck and segments 1–7, ventral view; D, segments 4–9, dorsal view; E, segments 7–10, ventrolateral view; F, segments 10 and 11, dorsal view; G, segments 10 and 11, dorsal view, focal plane slightly different from 3F; H, segments 11, ventral view. Black arrows and white arrowheads indicate sensory spots and type-1 gland cell outlets, respectively. Abbreviations: ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine; si, sieve plate; te, tergal extension.

**Table 2**
Measurements for adult *Echinoderes kaempfae* sp. nov. (in micrometers or as percentage).

| Character | ZMB catalogue number | | |
|---|---|---|---|
| | 11943 | 11944 | 11945 |
| tl | 229 | 215 | 267 |
| msw-8 | 49 | 42 | n.a. |
| msw-8/tl | 21% | 19% | n.a. |
| sw-10 | 41 | 38 | n.a. |
| sw-10/tl | 18% | 17% | n.a. |
| s1 | 33 | 34 | n.a. |
| s2 | 26 | 26 | n.a. |
| s3 | 21 | 23 | n.a. |
| s4 | 22 | 26 | n.a. |
| s5 | 25 | 26 | n.a. |
| s6 | 29 | 28 | n.a. |
| s7 | 31 | 30 | n.a. |
| s8 | 32 | 38 | n.a. |
| s9 | 32 | 34 | n.a. |
| s10 | 36 | 38 | n.a. |
| s11 | 33 | 35 | n.a. |
| md4 (ac) | 33 | 35 | 32 |
| md5 (ac) | 42 | 39 | 44 |
| md6 (ac) | 51 | 51 | 49 |
| md7 (ac) | 72 | 79 | 76 |
| md8 (ac) | 97 | 114 | 123 |
| lv5 (tu) | 10 | 13 | 13 |
| lv6 (ac) | 33 | 38 | 34 |
| lv7 (ac) | 44 | 44 | 43 |
| lv8 (ac) | 49 | 53 | 58 |
| lv9 (ac) | 57 | 59 | 62 |
| ld10 (tu) | 12 | 19 | 19 |
| lts | 200 | 205 | 215 |
| ltas | 69 | n.a. | n.a. |
| lts/tl | 88% | 96% | 80% |
| ltas/tl | 30% | n.a. | n.a. |

Abbreviations: (ac), acicular spine; ld, length of laterodorsal tube; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; msw, maximum sternal width; n.a., character not available; s, segment length; sw, standard width; tl, trunk length; (tu), tube. Digits after abbreviation refer to segment.

Neck with 16 placids (Fig. 2A, B). Midventral placid broadest. Remaining placids similar in size. Two trichoscalid plates present ventrally and four dorsally, each associated with ventromedial, subdorsal, and laterodorsal placid, respectively (Fig. 2A, B).

Segment 1 consisting of complete cuticular ring (Fig. 2A, B). Sensory spots present in subdorsal and laterodorsal position (Figs. 2A, B, and 3B). Two type-1 gland cell outlets situated in tandem in middorsal position and paired in lateroventral position (Figs. 2A, B, and 3C). Cuticular hairs arising from perforation sites present beside sensory spots. Posterior part of this and following nine segments with primary pectinate fringe (Fig. 2). Pectinate fringe teeth of primary pectinate fringe homogeneously thin in width and relatively short in length.

Segment 2 with complete cuticular ring as segment 1 (Fig. 2A, B). This and following eight segments with pachycyclus at anterior margin of each segment. Sensory spots in middorsal and ventromedial position, and two pairs in laterodorsal position (Figs. 2A, B). Type-1 gland cell outlet located in middorsal position (Fig. 2A). Cuticular hairs arising from perforation sites on this and following eight segments. Perforation sites in anterior and central part of a segment, with hairs covering whole segment, except for ventromedial area.

Segment 3 and following eight segments consisting of one tergal and two sternal plates (Fig. 2A, B). Sensory spots absent. Type-1 gland cell outlets situated in middorsal and ventromedial position (Fig. 2A, B).

Segment 4 with middorsal acicular spine (Figs. 2A, 3B, and D). Sensory spot absent. Type-1 gland cell outlets in paradorsal and ventromedial position (Figs. 2A, B, 3B, and D).

Segment 5 with middorsal acicular spine and lateroventral tubes (Figs. 2A, B, and 3A–D). Sensory spots in sublateral and ventromedial position (Figs 2A, B, and 3C). Type-1 gland cell outlets present in paradorsal and ventromedial position (Figs. 2A, B, 3B, and D).

Segment 6 with middorsal and lateroventral acicular spines (Figs. 2A, B, and 3B–D). Sensory spots present in paradorsal position (Figs. 2A, 3B and D). Type-1 gland cell outlets present paradorsally and ventromedially (Figs. 2A, B, 3B, and D).

Segment 7 with middorsal and lateroventral acicular spines (Figs. 2A, B, 3D, and E). Sensory spots present in ventromedial position (Fig. 2B). Type-1 gland cell outlets present paradorsally and ventromedially (Figs. 2A, B, 3B, and D).

Segment 8 with acicular spines in middorsal and lateroventral position (Figs. 2A, B, 3D, and E). Sensory spots present paradorsally (Figs. 2A and 3D). Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 2A and B).

Segment 9 with lateroventral acicular spines (Figs. 2A–D, and 3E). Paradorsal, laterodorsal, midlateral and ventrolateral sensory spots present (Figs. 2A–D and 3E). Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 2A–D). Small rounded sieve plates present in lateral accessory position (Fig. 2A, B, D, and 3E).

Segment 10 with laterodorsal tubes (Fig. 2A, C, and 3F). Subdorsal and ventrolateral sensory spots present (Fig. 2A–D). Two type-1 gland cell outlets aligned middorsally (Fig. 2A and C). Additional pair of type-1 gland cell outlets present in ventromedial position (Fig. 2B and D).

**Table 3**
Summary of locations of cuticular structures and appendages in *Echinoderes kaempfae* sp. nov.

| Position Segment | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | gco1, gco1 | | ss | ss | | | | gco1 | | |
| 2 | gco1, ss | | | ss, ss | | | | | | ss |
| 3 | gco1 | | | | | | | | | gco1 |
| 4 | ac | gco1 | | | | | | | | gco1 |
| 5 | ac | gco1 | | | | ss | | tu | | gco1, ss |
| 6 | ac | gco1, ss | | | | | | ac | | gco1 |
| 7 | ac | gco1 | | | | | | ac | | gco1, ss |
| 8 | ac | gco1, ss | | | | | | ac | | gco1 |
| 9 | | gco1, ss | | ss | ss | | si | ac | ss | gco1 |
| 10 | gco1, gco1 | | ss | tu | | | | | ss | gco1 |
| 11 | gco1, gco1 | | ss | | | | pe × 3 (m), ltas (f) | lts | | |

Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

Segment 11 with lateral terminal spines (Figs. 2A–D, 3A, F–H). Three pairs of penile spines present in males, with two pairs being long tube-like and one pair thick and relatively short (Figs. 2C, D, and 3H). Lateral terminal accessory spines present in female (Figs. 2A, B, 3A, F, and G). Subdorsal sensory spots present (Fig. 2A and C). Two type-1 gland cell outlets present middorsally (Fig. 2A and C). Tergal extensions long and gradually tapering towards pointed tips and sternal extensions triangular with hairy extensions at posterior tip (Figs. 2A–D and 3G). Tergal extension divided deeply in middorsal position (Fig. 2A, C). Tergal plate separated into two plates at least in posterior part of segment not covered by segment 10; separation of posterior part of segment 11 may or may not continue anteriorly, but this was not observable through overlapping segment 10.

### 3.1.6. Taxonomic remarks

The presence of the middorsal acicular spines on segments 4–8 and lateral acicular spines/tubes on segments 5–9 of *E. kaempfae* sp. nov. is shared with a considerable number of species of *Echinoderes*, viz, 50 out of 125 species have these spines/tubes (with lateral spines/tubes varying in position, viz, midlaterally, sublaterally, lateral accessorily or lateroventrally). *Echinoderes*

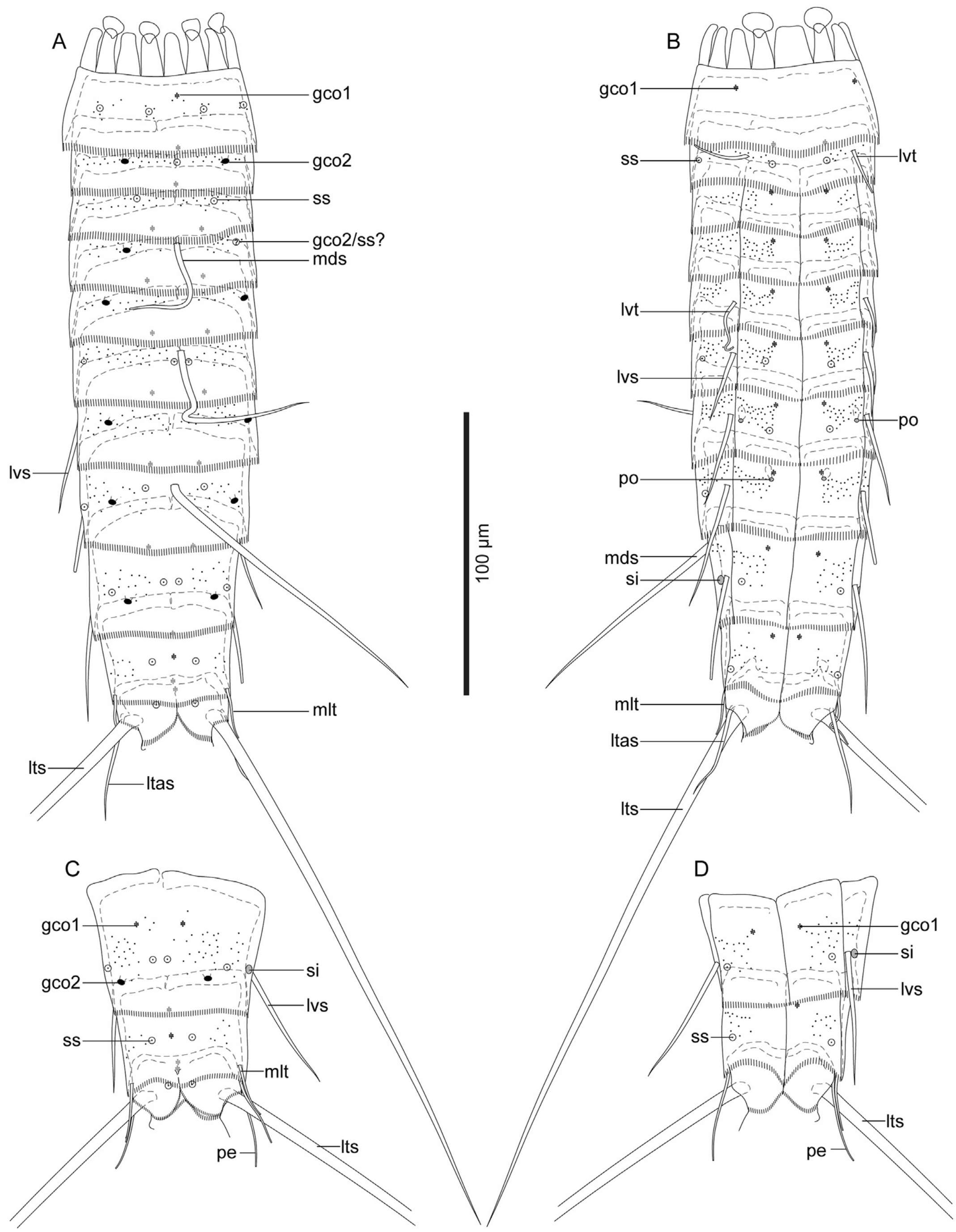



**Fig. 4.** *Echinoderes schwieringae* sp. nov., camera lucida drawings. A, B, holotype, female (ZMB 11946), whole animal, dorsal and ventral view, respectively; C, D, paratype, male (ZMB 11948), segments 9–11, dorsal and ventral view, respectively. Abbreviations: gco1/2, type-1/2 gland cell outlet; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; mlt, midlateral tube; pe, penile spine; po, pore; si, sieve plate; ss, sensory spot.


**Fig. 5.** *Echinoderes schwieringae* sp. nov., holotype, female (ZMB 11946), Nomarski photomicrographs. A, neck and segments 1–11, ventral view; B, neck and segments 1–6, dorsal view; C, neck and segments 1–6, ventral view; D, segments 5–9, ventral view; E, segments 6–9, dorsal view; F, segments 8–10, dorsal view; G, segment 11, dorsal view. Black arrows point to sensory spots, white arrowheads mark type-1 gland cell outlets, and black arrowheads indicate type-2 gland cell outlets. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; mlt, midlateral tube; po, pore.

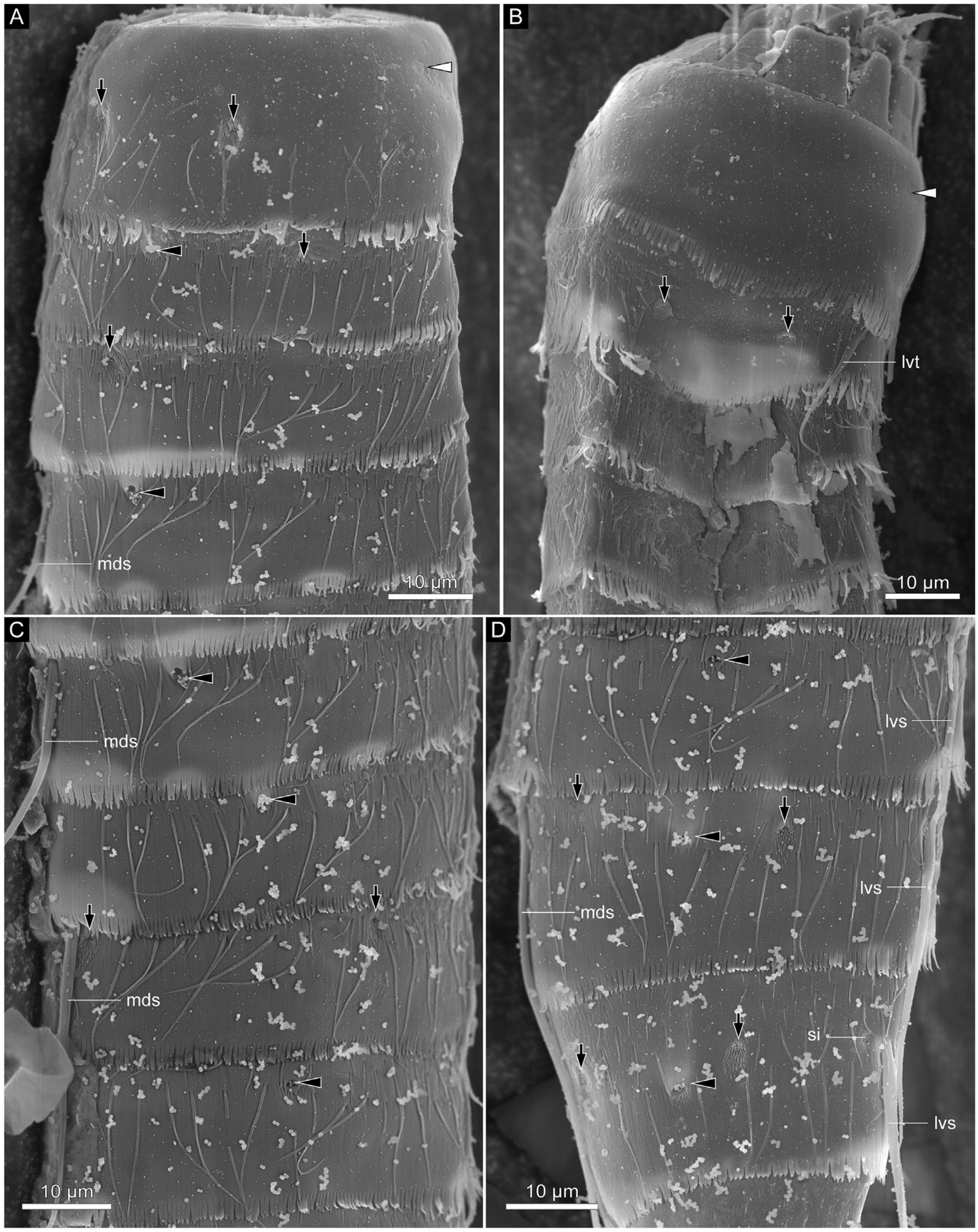



**Fig. 6.** *Echinoderes schwieringae* sp. nov., male (A, C, D) and female (B) scanning electron micrographs. A, segments 1–4, lateral view (right side); B, neck and segments 1–4, ventral view; C, segments 4–7, laterodorsal view (right side); D, segments 7–9, lateral view (right side). Black arrows point to sensory spots, white arrowheads mark type-1 gland cell outlets, and black arrowheads indicate type-2 gland cell outlets. Abbreviations: lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine.

*kaempfae* sp. nov. can be distinguished from all species, except for *Echinoderes bookhouti* Higgins, 1964 and *Echinoderes cernunnos* Sørensen et al., 2012, by the presence of laterodorsal tubes on segment 10 and the complete absence of other tubes (Higgins 1964; Sørensen et al. 2012, 2016). In comparison with *E. bookhouti* and *E. cernunnos*, *E. kaempfae* sp. nov. can be discriminated by the complete absence of any type-2 gland cell outlets, which are present in subdorsal and lateroventral position on segment 2 and in midlateral position on segment 8 in *E. bookhouti* and present in subdorsal, laterodorsal, sublateral, and ventrolateral position on segment 2, in midlateral position on segments 5 and 7, and in sublateral position on segment 8 in *E. cernunnos* (see Sørensen et al. 2012, 2016).

*Echinoderes kaempfae* sp. nov. shows additional similarities to *E. cernunnos* in having long tergal extensions gradually tapering towards pointed tips, and possibly two tergal plates with a middorsal junction. Both characters do not occur in any other species of *Echinoderes*. Therefore, these characters may indicate a closer relationship of the two species. At the same time, apart from the presence or absence of the type-2 gland cell outlets, the two species are conspicuously different in the sensory-spot pattern (*E. kaempfae* sp. nov. has fewer sensory spots than *E. cernunnos*), the

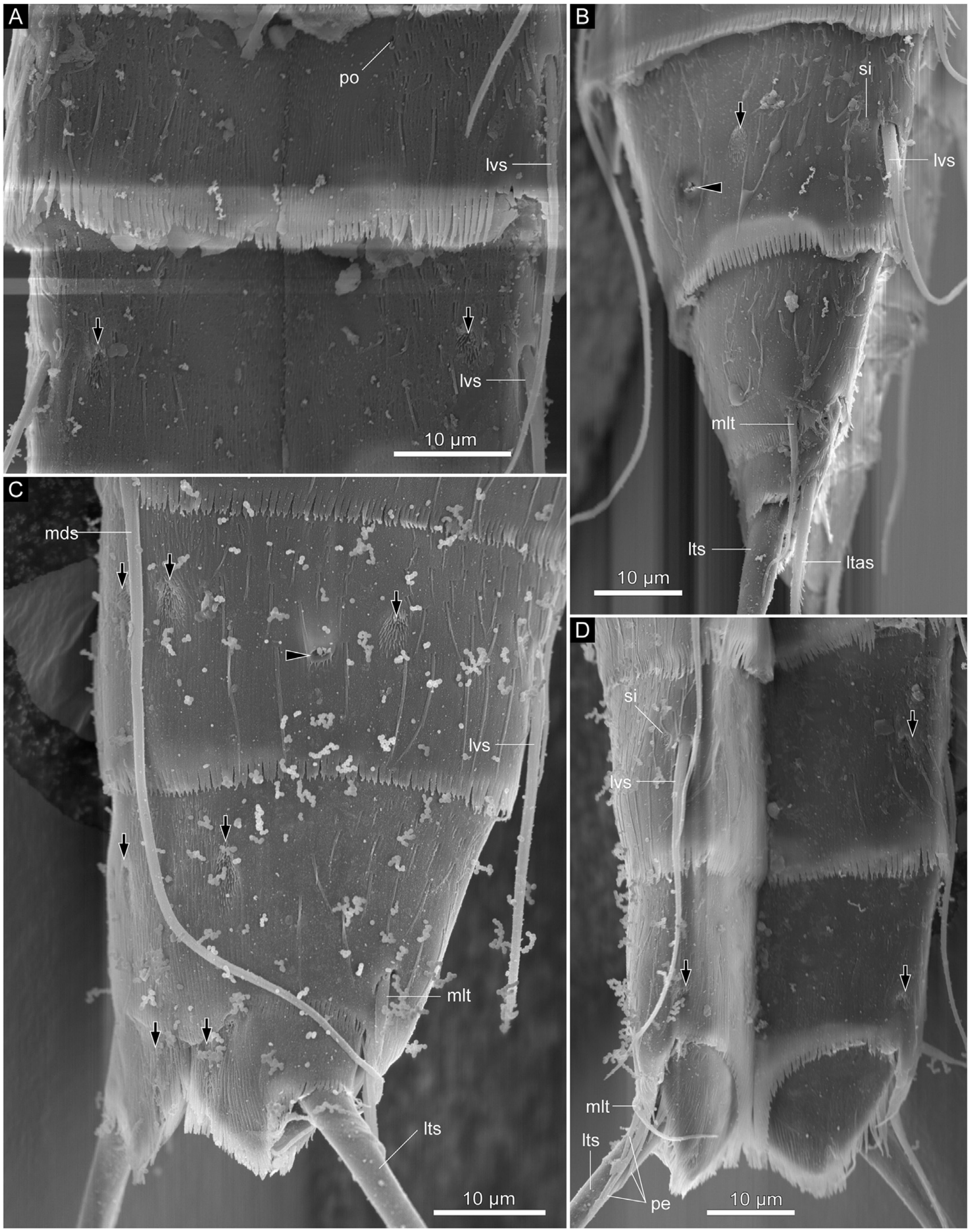



**Fig. 7.** *Echinoderes schwieringae* sp. nov., male (C, D) and female (A, B), scanning electron micrographs. A, segments 8 and 9, ventral view; B, segments 9–11, lateral view (right side); C, segments 9–11, laterodorsal view (right side); D, segments 9–11, ventral view. Black arrows and black arrowheads indicate sensory spots and type-2 gland cell outlet, respectively. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; mds, middorsal acicular spine; mlt, midlateral tube; pe, penile spine; po, pore; si, sieve plate.

abundance of cuticular hairs on segment 1 (they are present only beside the sensory spots in *E. kaempfae* sp. nov., while they are scattered around the segment in *E. cernunnos*), and the length of the lateral terminal spine (200–215 μm representing 80–96% of trunk length in *E. kaempfae* sp. nov., whereas 66–73 μm representing 22.1–26.2% of trunk length in *E. cernunnos*) (Sørensen et al. 2012).

### 3.2. *Echinoderes schwieringae* sp. nov.

(Figs. 4–7, Tables 4 and 5)

http://zoobank.org/urn:lsid:zoobank.org:act:1CA6DDFB-FD55-44BE-9092-02D37C9EE5E8

#### 3.2.1. Diagnosis

*Echinoderes* with middorsal acicular spines on segments 4, 6, and 8; lateroventral acicular spines on segments 6–9; lateroventral tubes on segments 2 and 5; midlateral tubes on segment 10; type-2 gland cell outlets in subdorsal position on segments 2 and 4 and in laterodorsal position on segments 5 and 7–9.

#### 3.2.2. Etymology

This species is named after Antje Schwiering, a technician at the Museum für Naturkunde Berlin who technically supported this study.

**Table 4**
Measurements for adult *Echinoderes schwieringae* sp. nov. (in micrometers or as percentage).

| Character | N | Range | Mean | SD |
|---|---|---|---|---|
| tl | 5 | 222–281 | 244.2 | 22.3 |
| msw-7 | 4 | 42–47 | 45.4 | 2.3 |
| msw-7/tl | 4 | 19–20% | 19.3% | 0.6% |
| sw-10 | 4 | 37–42 | 40.3 | 2.2 |
| sw-10/tl | 4 | 17–18% | 17.1% | 0.4% |
| s1 | 4 | 31–35 | 33.1 | 2.2 |
| s2 | 4 | 21–29 | 25.7 | 3.5 |
| s3 | 4 | 23–25 | 24.1 | 1.0 |
| s4 | 4 | 24–27 | 25.1 | 1.5 |
| s5 | 4 | 23–27 | 25.0 | 2.2 |
| s6 | 4 | 24–30 | 26.7 | 2.7 |
| s7 | 4 | 31 | 31.0 | 0.5 |
| s8 | 4 | 34–37 | 35.0 | 1.2 |
| s9 | 4 | 35–39 | 37.7 | 2.0 |
| s10 | 4 | 40–43 | 41.8 | 1.3 |
| s11 | 4 | 19–25 | 22.7 | 2.7 |
| md4 (ac) | 5 | 46–54 | 51.2 | 3.2 |
| md6 (ac) | 5 | 63–75 | 68.5 | 4.5 |
| md8 (ac) | 4 | 110–119 | 113.7 | 3.6 |
| lv2 (tu) | 5 | 19–23 | 21.0 | 1.6 |
| lv5 (tu) | 4 | 23–25 | 24.2 | 1.1 |
| lv6 (ac) | 5 | 25–28 | 26.4 | 1.2 |
| lv7 (ac) | 5 | 31–36 | 33.6 | 2.2 |
| lv8 (ac) | 5 | 44–47 | 45.7 | 1.0 |
| lv9 (ac) | 5 | 45–50 | 47.2 | 1.8 |
| ml10 (tu) | 5 | 15–21 | 19.2 | 2.2 |
| lts | 5 | 153–239 | 208.9 | 32.9 |
| ltas | 2 | 38–41 | 39.6 | 1.6 |
| lts/tl | 5 | 64–97% | 87.8% | 13.1% |
| ltas/tl | 2 | 14–17% | 15.2% | 2.2% |

Abbreviations: (ac), acicular spine; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; ml, length of midlateral tube; msw, maximum sternal width; N, number of specimens measured; s, segment length; SD, standard deviation; sw, standard width; tl, trunk length; (tu), tube.

### 3.2.3. Type locality

On summit of Senghor Seamount, northeastern Atlantic Ocean (17°12′17″N, 21°57′41″W), 132 m depth (Fig. 1, Table 1).

### 3.2.4. Material examined

Holotype: one female (ZMB 11946), collected at station 864 on summit of Senghor Seamount, northeastern Atlantic Ocean (17°12′17″N, 21°57′41″W), 132 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

Paratype: three males and one female (ZMB 11947–11950), collected together with holotype, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

Non-type: one female and one male (ZMB 11960–11961), collected together with holotype, mounted on an aluminum stub for SEM observations.

### 3.2.5. Description

Adult with head, neck, and eleven trunk segments (Figs. 4A, B, and 5A). See Table 4 for measurements. Table 5 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Head consisting of retractable mouth cone and introvert. Mouth cone with inner and nine outer oral styles. Introvert composed of one ring of primary scalids, several rings of spinoscalids, and one ring of trichoscalids. Detailed arrangement of inner oral styles and spinoscalids not observed. Trichoscalids arising from trichoscalid plates.

Neck with 16 placids (Fig. 4A, B). Midventral placid broadest. Remaining placids similar in size. Two trichoscalid plates present ventrally and four dorsally, each associated with ventromedial, subdorsal, and laterodorsal placid, respectively (Fig. 4A, B).

Segment 1 consisting of complete cuticular ring (Fig. 4A, B). Sensory spots present in subdorsal and laterodorsal position (Figs. 4A, 5B and 6A). Each sensory spot on this and following segments rounded or droplet-shaped, consisting of single central pore surrounded by micropapillae (Figs. 6 and 7). Type-1 gland cell outlets situated in middorsal and lateroventral position (Figs. 4A, B, 5B, C, and 6A, B). Cuticular hairs arising from round perforation sites sporadically present on dorsal side and completely absent on ventral side (Figs. 4A, B, and 6A, B). Posterior edge of this and following ten segments with primary pectinate fringe (Figs. 4, 6 and 7). Pectinate fringe teeth of primary pectinate fringe thin.

Segment 2 consisting of complete cuticular ring as segment 1 (Fig. 4A, B). This and following eight segments with pachycyclus at anterior margin of each segment. Tubes present in lateroventral position (Figs. 4B, 5C and 6B). Sensory spots in middorsal, midlateral, and ventromedial position (Figs. 4A, B, 5A, C, and 6A, B). Type-1 gland cell outlets located in middorsal and ventromedial position (Figs. 4A, B, and 5B, C). Type-2 gland cell outlets in subdorsal position (Figs. 4A, 5B and 6A). Opening of each type-2 gland cell outlet of this and following segments large, oval shape, and conspicuous both in LM and SEM observations (Figs. 5B, 6A, C, D, 7B and C). Bracteated cuticular hairs arising from perforation sites on this and following eight segments. Perforation sites in anterior and central part of a segment, with hairs covering whole segment, except for ventromedial area (Figs. 4, 6 and 7).

Segment 3 and following eight segments consisting of one tergal and two sternal plates (Fig. 4A, B). Sensory spots present in

**Table 5**
Summary of locations of cuticular structures and appendages in *Echinoderes schwieringae* sp. nov.

| Position segment | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | gco1 | | ss | ss | | | | gco1 | | |
| 2 | gco1, ss | | gco2 | | ss | | | tu | | gco1, ss |
| 3 | gco1 | | ss | | | | | | | gco1 |
| 4 | ac | | gco1, gco2* | | | | | | | gco1 |
| 5 | | | gco1 | gco2 | | | | tu | | gco1 |
| 6 | ac | ss | gco1 | | ss | | | ac | | gco1, ss |
| 7 | | | gco1 | gco2 | | | | ac | po (f) | gco1, ss |
| 8 | ac | | gco1, ss | gco2 | ss | | | ac | | gco1, po (f) |
| 9 | | ss | gco1 | gco2, ss | | | si | ac | ss | gco1 |
| 10 | gco1, gco1 | | ss | | tu | | | | ss | gco1 |
| 11 | gco1, gco1 | | ss | | | | pe × 3 (m), ltas (f) | lts | | |

Asterisk means one side of this type-2 gland cell outlet looks like either poorly developed type-2 gland cell outlet or sensory spot only in one specimen (ZMB 11946). Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 gland cell outlet; gco2, type-2 gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pe, penile spine; pd, paradorsal; po, pore; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

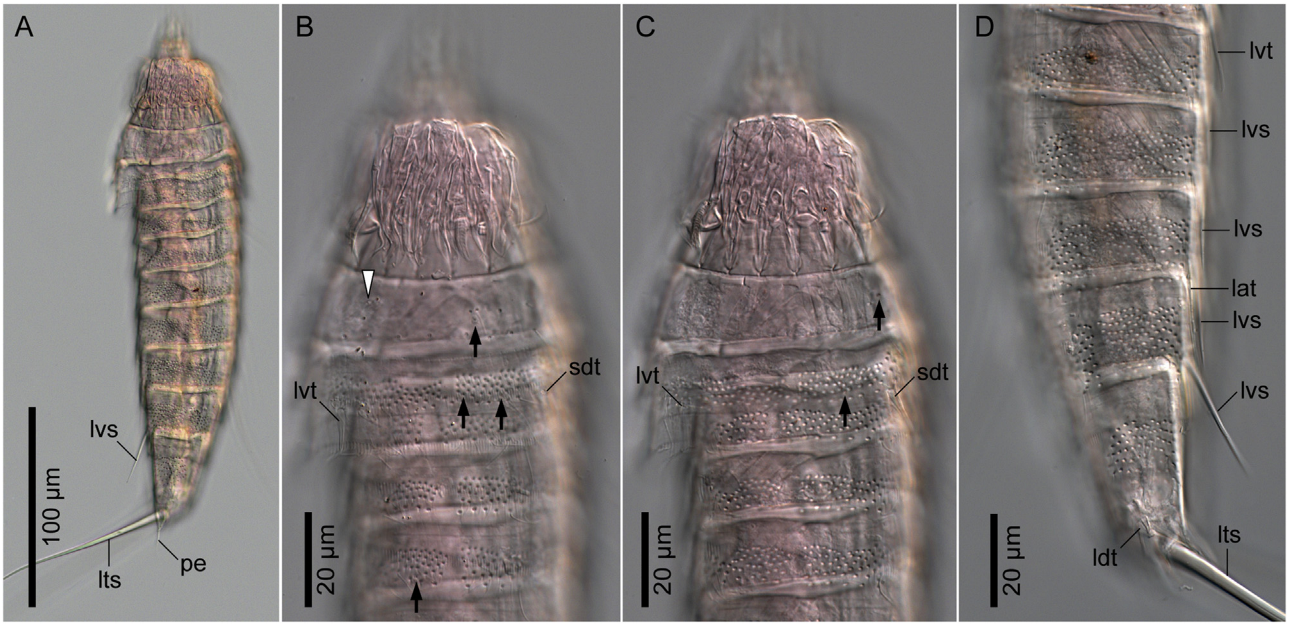



**Fig. 8.** *Echinoderes* cf. *adrianovi*, male, Nomarski photomicrographs. A, head, neck, and segments 1–11, lateral view (left side); B, head, neck, and segments 1–4, lateral view (left side); C, head, neck, and segments 1–4, lateral view (left side), slightly different focal plane to Fig. 10B; D, segments 6–11, lateral view (right side). Black arrows and white arrowhead indicate sensory spots and type-1 gland cell outlet, respectively. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; pe, penile spine; sdt, subdorsal tube.

subdorsal position (Figs. 4A, 5B and 6A). Type-1 gland cell outlets situated in middorsal and ventromedial position (Figs. 4A, B, and 5B).

Segment 4 with middorsal acicular spine (Figs. 4A, 5B and 6A, and C). Type-1 gland cell outlets in subdorsal and ventromedial position (Figs. 4A, B, and 5B). Type-2 gland cell outlets in subdorsal position (Figs. 4A, B, 5B, 6A, and C). Only one female specimen (ZMB 11946) clearly possessing one subdorsal type-2 gland cell outlet on one side, while a structure on the other side giving the impression of a poorly developed type-2 gland cell outlet or sensory spot (Fig. 4A; Table 5).

Segment 5 with lateroventral tubes (Figs. 4B, 5C, and D). Sensory spot absent. Type-1 gland cell outlets present in subdorsal and ventromedial position (Figs. 4A, B, and 5B). Type-2 gland cell outlets in laterodorsal position (Figs. 4A, 6C).

Segment 6 with middorsal and lateroventral acicular spines (Figs. 4A, B, 5B–E, and 6C). Sensory spots present in paradorsal, midlateral, and ventromedial position (Figs. 4A, B, 5B, E, and 6C). Type-1 gland cell outlets present subdorsally and ventromedially (Figs. 4A, B, 5B, and E).

Segment 7 with lateroventral acicular spines (Figs. 4A, B, 5A, D, and 6D). Sensory spots present in ventromedial position (Fig. 4B). Type-1 gland cell outlets present subdorsally and ventromedially (Figs. 4A, B, and 5E). Type-2 gland cell outlets in laterodorsal position (Figs. 4A, 6C, and D). Small pores present ventrolaterally only in females (Figs. 4B and 5D).

Segment 8 with acicular spines in middorsal and lateroventral position (Figs. 4A, B, 5A, D, E, 6D, 7A, and C). Sensory spots present subdorsally and midlaterally (Figs. 4A, B, 5E, and 6D). Type-1 gland cell outlets present in subdorsal and ventromedial position (Figs. 4A, B, and 5E). Type-2 gland cell outlets in laterodorsal position (Figs. 4A, 5F and 6D). Small pores present in ventromedial position only in females (Figs. 4B and 7A).

Segment 9 with lateroventral acicular spines (Figs. 4B–D, 5A, 6D, and 7A–D). Paradorsal, laterodorsal and ventrolateral sensory spots present (Figs. 4A–D, 5E, 6D, and 7A–D). Type-1 gland cell outlets present in subdorsal and ventromedial position (Figs. 4A–D and 5E). Type-2 gland cell outlets in laterodorsal position (Figs. 4A, C, 5F, 6D, 7B, and C). Small rounded sieve plates present in lateral accessory position (Figs. 4B–D, 6D, 7B, and D).

Segment 10 with midlateral tubes (Figs. 4A–C, 5G, and 7B–D). Subdorsal and ventrolateral sensory spots present (Figs. 4A–D, 5F, 7C, and D). Two type-1 gland cell outlets aligned middorsally (Figs. 4A, C, and 5F). Additional pair of type-1 gland cell outlets present in ventromedial position (Fig. 4B, D).

Segment 11 with lateral terminal spines (Figs. 4A–D, 5G, and 7B–D). Three pairs of penile spines present in male, all being long and tube-like (Figs. 4C, D, and 7D). Lateral terminal accessory spines present in females (Figs. 4A, B, 5G, and 7B). Subdorsal sensory spots present (Fig. 4A, C, and 7C). Two type-1 gland cell outlets present middorsally (Fig. 4A and C). Tergal extensions short and only slightly extending beyond rounded sternal extensions (Figs. 4A–D, 7C, and D). A couple of long fringe teeth on lateral posterior end of segment longer than others, often forming tufts which look like setae in LM (Fig. 4).

### 3.2.6. Taxonomic remarks

The spine and tube pattern of *Echinoderes schwieringae* sp. nov., having middorsal acicular spines only on segments 4, 6, and 8, lateroventral acicular spines on segments 6–9, lateroventral/ventrolateral tubes on segments 2 and 5, and lacking lateral accessory/sublateral tubes on segment 8, is similarly found in *E. apex*, *Echinoderes bermudensis* Higgins, 1982, *Echinoderes hamiltonorum* Sørensen et al., 2018, *Echinoderes joyceae* Landers & Sørensen, 2016, and *E. multiporus* (Higgins 1982; Landers & Sørensen 2016; Sørensen et al. 2018; Yamasaki et al. 2018b, c).

Nonetheless, *E. schwieringae* sp. nov. is unique in its pattern of the type-2 gland cell outlets, being present subdorsally on segments 2 and 4, laterodorsally on segments 5 and 7–9. The pattern is useful for the distinction of the new species from the above

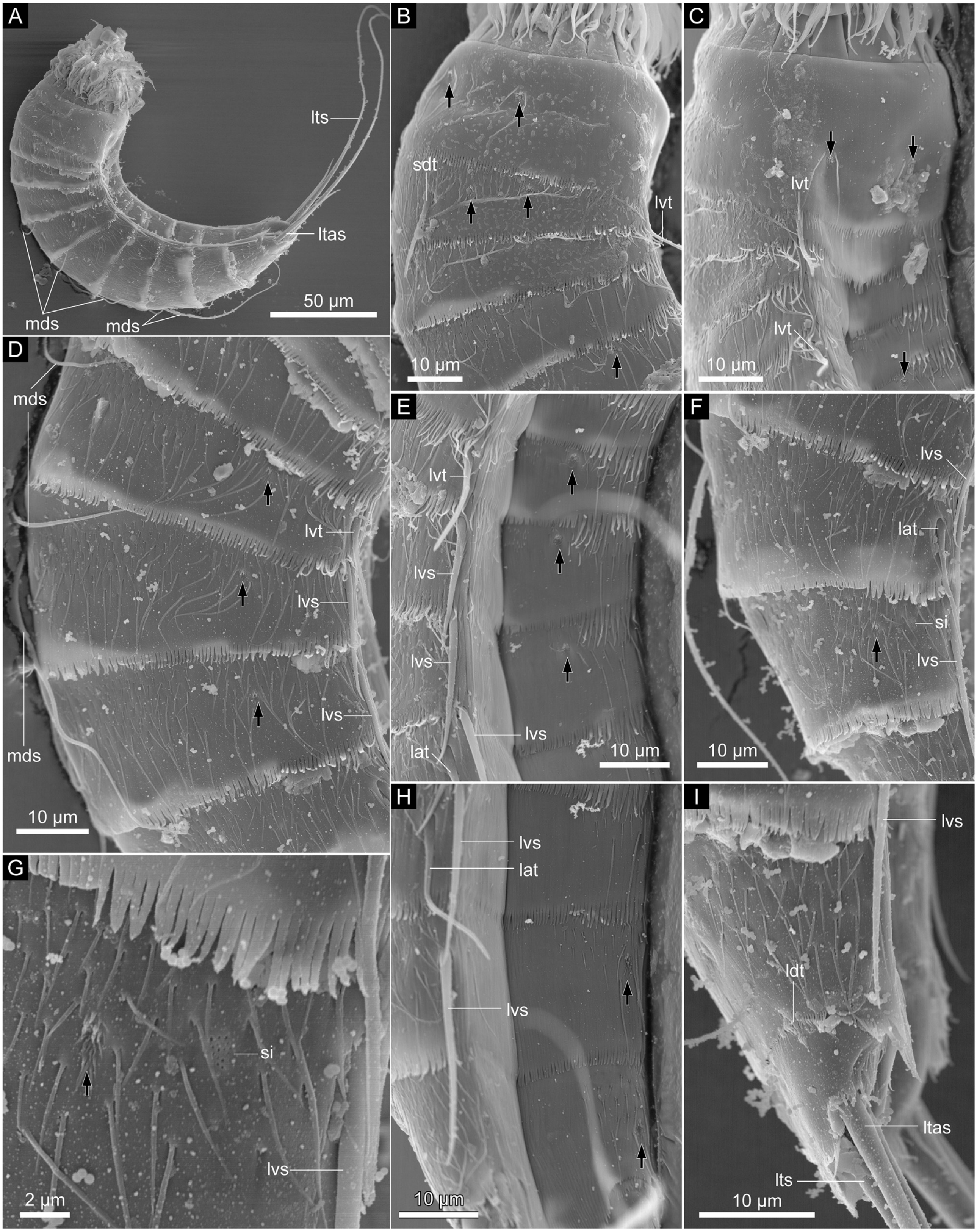



**Fig. 9.** *Echinoderes* cf. *adrianovi*, females, scanning electron micrographs. A, head, neck, and segments 1–11, lateral view (right side); B, neck and segments 1–5, lateral view (right side); C, neck and segments 1–5, ventral view; D, segments 4–8, lateral view (right side); E, segments 4–8, ventral view; F, segments 7–9, lateral view (right side); G, segment 9, midlateral to lateroventral area (right side); H, segments 8–10, ventral view; I, segments 10 and 11, lateral view (right side). Black arrows indicate sensory spots. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; sdt, subdorsal tube; si, sieve plate.

**Table 6**
Measurements for adult *Echinoderes* cf. *adrianovi* (in micrometers or as percentage).

| Character | ZMB 11951 |
|---|---|
| tl | 200 |
| md4 (ac) | 43 |
| md5 (ac) | 36 |
| md6 (ac) | 62 |
| md7 (ac) | 63 |
| md8 (ac) | 85 |
| sd2 (tu) | 14 |
| lv2 (tu) | 18 |
| lv5 (tu) | 19 |
| lv6 (ac) | 21 |
| lv7 (ac) | 25 |
| lv8 (ac) | 28 |
| lv9 (ac) | 30 |
| ld10 (tu) | 14 |
| lts | 186 |
| lts/tl | 93% |

Abbreviations: (ac), acicular spine; ld, length of laterodorsal tube; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; sd, length of subdorsal tube; tl, trunk length; (tu), tube.

mentioned five species: *E. apex* with the type-2 gland cell outlets subdorsally on segment 2, sublaterally on segment 6, and lateral accessory on segment 8; *E. bermudensis* without any type-2 gland cell outlet; *E. hamiltonorum* with the type-2 outlets subdorsally on segment 2, laterodorsally on segment 2, and sublaterally on segments 1, 2, and 8; *E. joyceae* with the outlets subdorsally on segment 2, midlaterally on segment 6, sublaterally on segment 8; and *E. multiporus* with the outlets subdorsally on segment 2 and laterodorsally on segments 4–9 (Higgins 1982; Landers & Sørensen 2016; Sørensen et al. 2018; Yamasaki et al. 2018b, c).

Among them, *E. multiporus* is similar to *E. schwieringae* sp. nov. in having dorsal type-2 gland cell outlets on most of the segments, tubes on segment 10 midlaterally, and sexual dimorphic papillae/pores on the ventral side in females. Having one or two pairs of dorsal type-2 gland cell outlets is not rare in *Echinoderes* species, however, the two species possess a considerably higher number of the type-2 gland cell outlets, viz, 6 and 7 pairs in *E. schwieringae* sp. nov. and *E. multiporus*, respectively. Among the *Echinoderes* species, the presence of sexual dimorphic papillae/pores has been confirmed so far in *E. schwieringae* sp. nov. and *E. multiporus* plus *Echinoderes collinae* Sørensen, 2006, *Echinoderes gerardi* Higgins, 1978, *Echinoderes gizoensis* Thormar & Sørensen, 2010, *Echinoderes kozloffi* Higgins, 1977, and the *Echinoderes spinifurca*-species group (Thormar & Sørensen 2010; Herranz & Leander 2016; Sørensen et al. 2018; Yamasaki et al. 2018b). Indeed, the presence of female papillae/pores may be more common in *Echinoderes* but just overlooked in some species (Herranz & Leander 2016). Nonetheless, the similarities of the pattern in spines, tubes, type-2 gland cell outlets and sexual dimorphic papillae/pores between the two species may or may not stem from a close phylogenetic relationship. The species also co-occurred on the Senghor Seamount, however, can be easily distinguished by the pattern of the type-2 gland cell outlet as mentioned above, as well as the shape of the tergal extensions (short tergal extensions in *E. schwieringae* sp. nov., whereas long and pointed tergal extensions in *E. multiporus*) (Yamasaki et al. 2018b).

### 3.3. *Echinoderes* cf. *adrianovi* Herranz et al., 2014

(Figs. 8 and 9, Tables 6 and 7)

#### 3.3.1. Material examined

Non-type: one male (ZMB 11951), collected at station 864 on summit of Senghor Seamount, northeastern Atlantic Ocean (17°12′17″N, 21°57′41″W), 132 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame. Two females (ZMB 11962–11963), same location data as for male, mounted on an aluminum stub for SEM observations.

#### 3.3.2. Brief description

Since the general morphology of the examined specimens agrees widely with the original description of *Echinoderes adrianovi* in Herranz et al. (2014), the following description mainly focuses on taxonomically important characters and characters which are different or were not mentioned in Herranz et al. (2014). See Table 6 for measurements. Table 7 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Segment 1 with sensory spots in subdorsal, laterodorsal, and ventromedial position (Figs. 8B, C, 9B, and C). Each sensory spot of this and following segments rounded, small, consisting of one central pore surrounded by micropapillae (Fig. 9B–H). Type-1 gland cell outlets situated at least in lateral accessory position (Fig. 8B). Posterior edge of this and following nine segments with primary pectinate fringe. Pectinate fringe teeth of primary pectinate fringe on this and following segment short and thin (Fig. 9B, C).

Segment 2 with tubes present on subdorsal and ventrolateral position (Figs. 8B, C, 9B, and C). Two pairs of sensory spots in laterodorsal position (Figs. 8B, C, and 9B). Additional sensory spot in middorsal position.

**Table 7**
Summary of locations of cuticular structures and appendages in *Echinoderes* cf. *adrianovi*.

| Position segment | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | gco1 | | ss | ss | | | gco1 | | | ss |
| 2 | gco1, **ss** | | tu | **ss, ss** | | | | tu | | gco1 |
| 3 | gco1 | | **ss** | | | | | | | gco1 |
| 4 | ac | gco1 | | | | | | | | gco1 |
| 5 | ac | gco1 | | | **ss** | | | tu | | gco1, **ss** |
| 6 | ac | gco1, **ss** | | | **ss** | | | ac | | gco1, **ss** |
| 7 | ac | gco1, **ss** | | | **ss** | | | ac | | gco1, **ss** |
| 8 | ac | gco1, **ss** | | | | | tu | ac | | gco1 |
| 9 | gco1 | **ss** | **ss** | | **ss** | si | | ac | ss | gco1 |
| 10 | gco1 | | **ss** | **tu** | | | | | ss | gco1 |
| 11 | gco1, gco1 | | **ss** | | | | **pe × 3 (m)**, ltas (f) | lts | | |

Underlines indicate the structures only reported in Herranz et al. (2014) but not confirmed in the specimens from Senghor Seamount. Bold characters are the newly found structures in the specimens from Senghor Seamount. Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

**Table 8**
Measurements for adult *Echinoderes multiporus* and comparison of them between two populations. Columns N and SD indicate sample size and standard deviation, respectively.

| Character | Specimens from Senghor Seamount | | | | Specimens from Eratosthenes Seamount (data obtained from Yamasaki et al. 2018b) | | | | Total | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | Range | Mean | SD | N | Range | Mean | SD | N | Range | Mean | SD |
| tl | 3 | 241–267 | 257.6 | 14.5 | 9 | 198–229 | 210.0 | 11 | 12 | 198–267 | 221.9 | 24.3 |
| msw-7 | 1 | 50 | n.a. | n.a. | 5 | 43–51 | 46.8 | 3.3 | 6 | 43–51 | 47.2 | 3.2 |
| msw-7/tl | 1 | 21% | n.a. | n.a. | 5 | 21–24% | 22.2% | 1.5% | 6 | 21–24% | 21.9% | 1.5% |
| sw-10 | 1 | 39 | n.a. | n.a. | 5 | 35–39 | 37.5 | 1.6 | 6 | 35–39 | 37.7 | 1.6 |
| sw-10/tl | 1 | 16% | n.a. | n.a. | 5 | 16–19% | 17.8% | 1.3% | 6 | 16–19% | 17.6% | 1.3% |
| s1 | 1 | 34 | n.a. | n.a. | 5 | 30–34 | 31.8 | 1.6 | 6 | 30–34 | 32.1 | 1.7 |
| s2 | 1 | 26 | n.a. | n.a. | 5 | 23–26 | 24.4 | 1.3 | 6 | 23–26 | 24.7 | 1.3 |
| s3 | 1 | 23 | n.a. | n.a. | 5 | 20–21 | 20.6 | 0.6 | 6 | 20–23 | 20.9 | 1.0 |
| s4 | 1 | 24 | n.a. | n.a. | 5 | 20–23 | 21.8 | 0.9 | 6 | 20–24 | 22.1 | 1.1 |
| s5 | 1 | 25 | n.a. | n.a. | 5 | 21–22 | 21.9 | 0.7 | 6 | 21–25 | 22.5 | 1.6 |
| s6 | 1 | 29 | n.a. | n.a. | 5 | 21–24 | 23.0 | 0.9 | 6 | 21–29 | 24.0 | 2.5 |
| s7 | 1 | 31 | n.a. | n.a. | 5 | 26–27 | 26.3 | 0.5 | 6 | 26–31 | 27.0 | 1.8 |
| s8 | 1 | 32 | n.a. | n.a. | 5 | 28–30 | 29.3 | 0.9 | 6 | 28–32 | 29.8 | 1.5 |
| s9 | 1 | 39 | n.a. | n.a. | 5 | 29–33 | 31.1 | 1.8 | 6 | 29–39 | 32.4 | 3.6 |
| s10 | 1 | 43 | n.a. | n.a. | 5 | 36–41 | 38.2 | 2.1 | 6 | 36–43 | 39.0 | 2.7 |
| s11 | 1 | 31 | n.a. | n.a. | 5 | 26–33 | 30.8 | 2.7 | 6 | 26–33 | 30.9 | 2.4 |
| md4 (ac) | 2 | 34–37 | 35.4 | 1.6 | 5 | 32–40 | 36.0 | 3.2 | 7 | 32–40 | 35.8 | 2.7 |
| md6 (ac) | 3 | 63–69 | 66.1 | 3.3 | 6 | 63–68 | 65.6 | 2.0 | 9 | 63–69 | 65.7 | 2.3 |
| md8 (ac) | 3 | 82–94 | 88.7 | 6.2 | 6 | 79–86 | 82.1 | 2.9 | 9 | 79–94 | 84.3 | 5.1 |
| vl2 (tu) | 3 | 17 | 17.0 | 0.3 | 8 | 11–17 | 14.6 | 2.1 | 11 | 11–17 | 15.3 | 2.1 |
| lv5 (tu) | 2 | 16–21 | 18.5 | 3.9 | 6 | 14–19 | 16.0 | 2.5 | 8 | 14–21 | 16.6 | 2.9 |
| lv6 (ac) | 3 | 28–35 | 32.1 | 3.5 | 9 | 31–36 | 33.0 | 1.6 | 12 | 28–36 | 32.8 | 2.1 |
| lv7 (ac) | 3 | 38–46 | 43.2 | 4.2 | 9 | 39–44 | 41.8 | 1.7 | 12 | 38–46 | 42.1 | 2.4 |
| lv8 (ac) | 3 | 52–56 | 54.3 | 1.9 | 9 | 49–57 | 52.3 | 2.5 | 12 | 49–57 | 52.8 | 2.4 |
| lv9 (ac) | 3 | 56–58 | 57.1 | 1.1 | 9 | 51–60 | 55.4 | 3.0 | 12 | 51–60 | 55.8 | 2.7 |
| ml10 (tu) | 3 | 16–17 | 16.7 | 0.5 | 9 | 14–18 | 16.3 | 1.5 | 12 | 14–18 | 16.4 | 1.3 |
| lts | 3 | 162–167 | 164.6 | 2.4 | 8 | 130–165 | 143.8 | 11.3 | 11 | 130–167 | 149.5 | 13.6 |
| ltas | 2 | 49–52 | 50.2 | 2.3 | 5 | 41–49 | 45.8 | 3.0 | 7 | 41–52 | 47.0 | 3.4 |
| lts/tl | 3 | 62–67% | 64.0% | 3.0% | 8 | 64–72% | 68.5% | 2.9% | 11 | 62–72% | 67.3% | 3.5% |
| ltas/tl | 2 | 18–19% | 18.9% | 0.7% | 5 | 21–23% | 21.8% | 1.0% | 7 | 18–23% | 21.0% | 1.7% |

Abbreviations: (ac), acicular spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; ml, length of midlateral tube; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube; vl, length of ventrolateral tube.

Segment 3 with sensory spots present in subdorsal position. Pectinate fringe teeth of primary pectinate fringe on this and following five segments thin and long from sublaterally to lateroventrally, and short in other positions (Fig. 9B–H).

Segment 4 with middorsal acicular spine (Fig. 9A and D).

Segment 5 with middorsal acicular spine and lateroventral tubes (Figs. 8D, and 9A, C–E). Sensory spots in midlateral and ventromedial position (Figs. 8B and 9B–E).

Segment 6 with middorsal and lateroventral acicular spines (Figs. 8D, and 9D, E). Sensory spots present in paradorsal, midlateral, and ventromedial position (Fig. 9D, E).

Segment 7 as segment 6 (Figs. 8D and 9D–F).

Segment 8 with acicular spines in middorsal and lateroventral position (Figs. 8D, 9E and H). Lateral accessory tubes present (Figs. 8D, 9E, F, and H). Sensory spots present paradorsally.

Segment 9 with lateroventral acicular spines (Figs. 8A, D, and 9F–I). Paradorsal, subdorsal, midlateral, and ventrolateral sensory spots present (Fig. 9F–H). Small rounded sieve plates in sublateral position (Fig. 9F and G).

Segment 10 with laterodorsal tubes, being shorter in females than those in males (Figs. 8D and 9I). Subdorsal and ventrolateral sensory spots present (Fig. 9H). Type-1 gland cell outlets middorsally.

Segment 11 with lateral terminal spines (Figs. 8A, D, 9A, and I). Three pairs of penile spines present in male (Fig. 8A), and lateral terminal accessory spines in females (Fig. 9A and I). Subdorsal sensory spots present.

### 3.3.3. Taxonomic remarks

The laterally mounted LM specimen as well as the low number of available specimens from Senghor Seamount only allow a partial observation of characters, and some information in the description, especially about the type-1 gland cell outlets of the specimens, may be lacking. Thus, the information of the type-1 gland cell outlet is not used for the identification of the species here.

The specimens from Senghor Seamount are similar to only two *Echinoderes* species, *Echinoderes kanni* Thormar & Sørensen, 2010 and *E. adrianovi* Herranz et al., 2014, in possessing middorsal acicular spines on segments 4–8, lateroventral acicular spines on segments 6–9, subdorsal tubes on segment 2, lateroventral/ventrolateral tubes on segments 2 and 5 (Thormar & Sørensen 2010; Herranz et al. 2014). Of the two species, *E. kanni* differs from the specimens observed in this study by the pectinate fringe teeth of the primary pectinate fringe on segments 3–8 being similar in length, whereas fringes of the specimens from Senghor Seamount are obviously longer in sublateral to lateroventral areas (Thormar & Sørensen 2010). Morphometrics of the LM specimen from Senghor Seamount also differ from those of *E. kanni*, e.g., the former has a smaller trunk length than the latter (200 µm in the specimen from Senghor Seamount, whereas 222–283 µm in *E. kanni*) and longer lateral terminal spines (186 µm in the former, whereas 141–157 µm in the latter), consequently the former shows a larger proportion of lateral terminal spine to trunk length (93%) than the latter (53–67%).

*Echinoderes adrianovi* was originally found off the Floridian West coast, northwestern Atlantic Ocean at 140 m depth (Herranz et al. 2014). Several differences between the original description of *E. adrianovi* and the specimens from Senghor Seamount are detected. The first difference is that *E. adrianovi* lacks the laterodorsal tubes on segment 10 (Herranz et al. 2014), whereas the specimens from Senghor Seamount possesses it. However, the tubes on segment 10 are very short in females of the Senghor

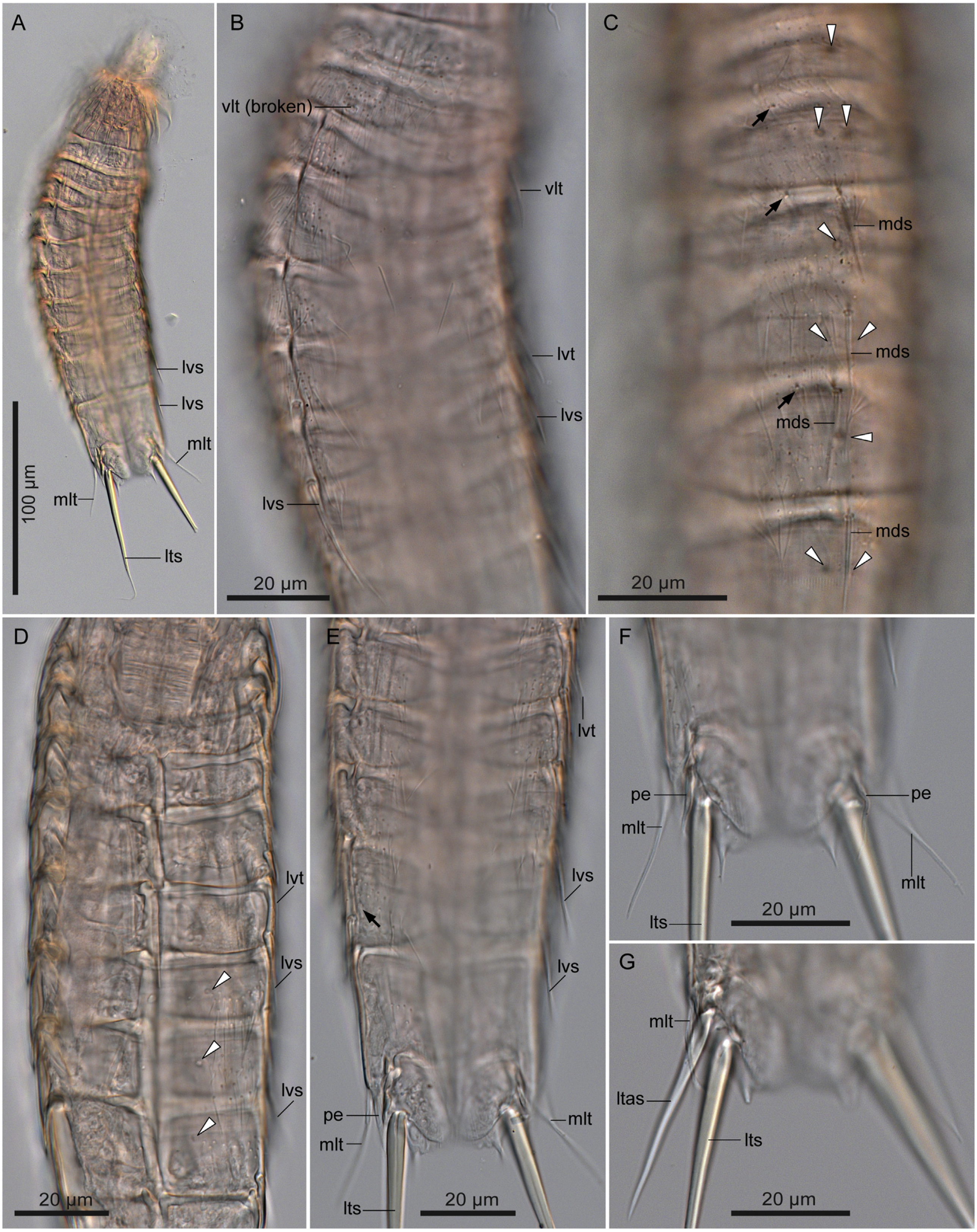



**Fig. 10.** *Echinoderes* sp. 1, male (ZMB 11956) (A, B, E, F) and female (ZMB 11955) (C, D, G), Nomarski photomicrographs. A, head, neck, and segments 1–11, ventral view; B, segments 1–8, ventral view; C, segments 3–8, dorsal view; D, segments 1–9, ventral view; E, segments 5–11, ventral view; F, segments 10 and 11, ventral view; G, segment 11, ventral view. Black arrows and white arrowheads indicate sensory spots and type-1 gland cell outlets, respectively. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; mlt, midlateral tube; pe, penile spine; vlt, ventrolateral tube.

**Table 9**
Measurements for adult *Echinoderes* sp. 1 (in micrometers or as percentage).

| Character | ZMB catalogue number | | |
|---|---|---|---|
| | 11956 | 11955 | 11957 |
| tl | 181 | 191 | 215 |
| msw-8 | 44 | 45 | n.a. |
| msw-8/tl | 25% | 24% | n.a. |
| sw-10 | 40 | 40 | 41 |
| sw-10/tl | 22% | 21% | 19% |
| s1 | 25 | 26 | 29 |
| s2 | 21 | 20 | 20 |
| s3 | 19 | 19 | 20 |
| s4 | 20 | 22 | 21 |
| s5 | 22 | 21 | 23 |
| s6 | 23 | 24 | 24 |
| s7 | 25 | 25 | 26 |
| s8 | 28 | 27 | 29 |
| s9 | 28 | 27 | 31 |
| s10 | 38 | 39 | 43 |
| s11 | 26 | 23 | 28 |
| md4 (ac) | n.a. | 16 | 15 |
| md5 (ac) | 15 | 16 | 15 |
| md6 (ac) | 16 | 17 | 17 |
| md7 (ac) | n.a. | 18 | 19 |
| md8 (ac) | 18 | 17 | 19 |
| vl2 (tu) | 20 | 19 | 18 |
| lv5 (tu) | 19 | n.a. | 23 |
| lv6 (ac) | 21 | 21 | 22 |
| lv7 (ac) | 26 | 22 | 26 |
| lv8 (ac) | 26 | 22 | 26 |
| lv9 (ac) | 25 | 27 | 29 |
| ml10 (tu) | 32 | 24 | 22 |
| lts | 72 | 84 | 105 |
| ltas | n.a. | 40.3 | n.a. |
| lts/tl | 39% | 44% | 49% |
| ltas/tl | n.a. | 21% | n.a. |

Abbreviations: (ac), acicular spine; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; ml, length of midlateral tube; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube; vl, length of ventrolateral tube.

Seamount specimens (Fig. 9I), and probably difficult or impossible to detect in females with LM. Since *E. adrianovi* was described based on a single female specimen for LM (Herranz et al. 2014), the tubes on segment 10 of the specimen may have been overlooked. Herranz et al. (2014) did not provide details about sensory spots on segments 2 to 11, and a comparison of sensory spot pattern between the two species is therefore not possible. The last difference is the length of middorsal acicular spines: the middorsal acicular spine on segment 8 is shorter than that on segment 7 in *E. adrianovi*, while the spine on segment 8 is longer than that on segment 7 in the specimens from Senghor Seamount. Because the measurements are based on a single individual for both *E. adrianovi* from Florida and the specimen of the Senghor Seamount, it is difficult to conclude whether the difference of length of the middorsal spines represents intra- or interspecific variation at present.

The other characters, including complete absence of the type-2 gland cell outlets as well as other morphometrics do not show any clear difference between *E. adrianovi* and the specimens from Senghor Seamount. Thus in this paper, we regard the specimens from Senghor Seamounts as *E.* cf. *adrianovi* stressing the necessity of further observation of more specimens from both populations in Florida and Senghor Seamount.

### 3.4. *Echinoderes multiporus* Yamasaki et al., 2018a, b, c

(Table 8)

#### 3.4.1. *Material examined*

Non-type: one male and two females (ZMB 11952–11954), collected at station 934 at slope of Senghor Seamount, northeastern Atlantic Ocean (17°12′56″N, 21°56′22″W), 565 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

#### 3.4.2. *Remarks*

The specimens from Senghor Seamount are identical with the original description of *E. multiporus*, hence, only morphometric data of the specimens for Senghor Seamount together with those of the original description in Yamasaki et al. (2018b) is provided in Table 8. The new finding of *E. multiporus* from Senghor Seamount expands the distribution pattern of the species: from the Mediterranean Sea to the northeastern Atlantic Ocean, from seamount slope to seamount summit, 565–991 m depth.

### 3.5. *Echinoderes sp. 1*

(Fig. 10, Tables 9 and 10)

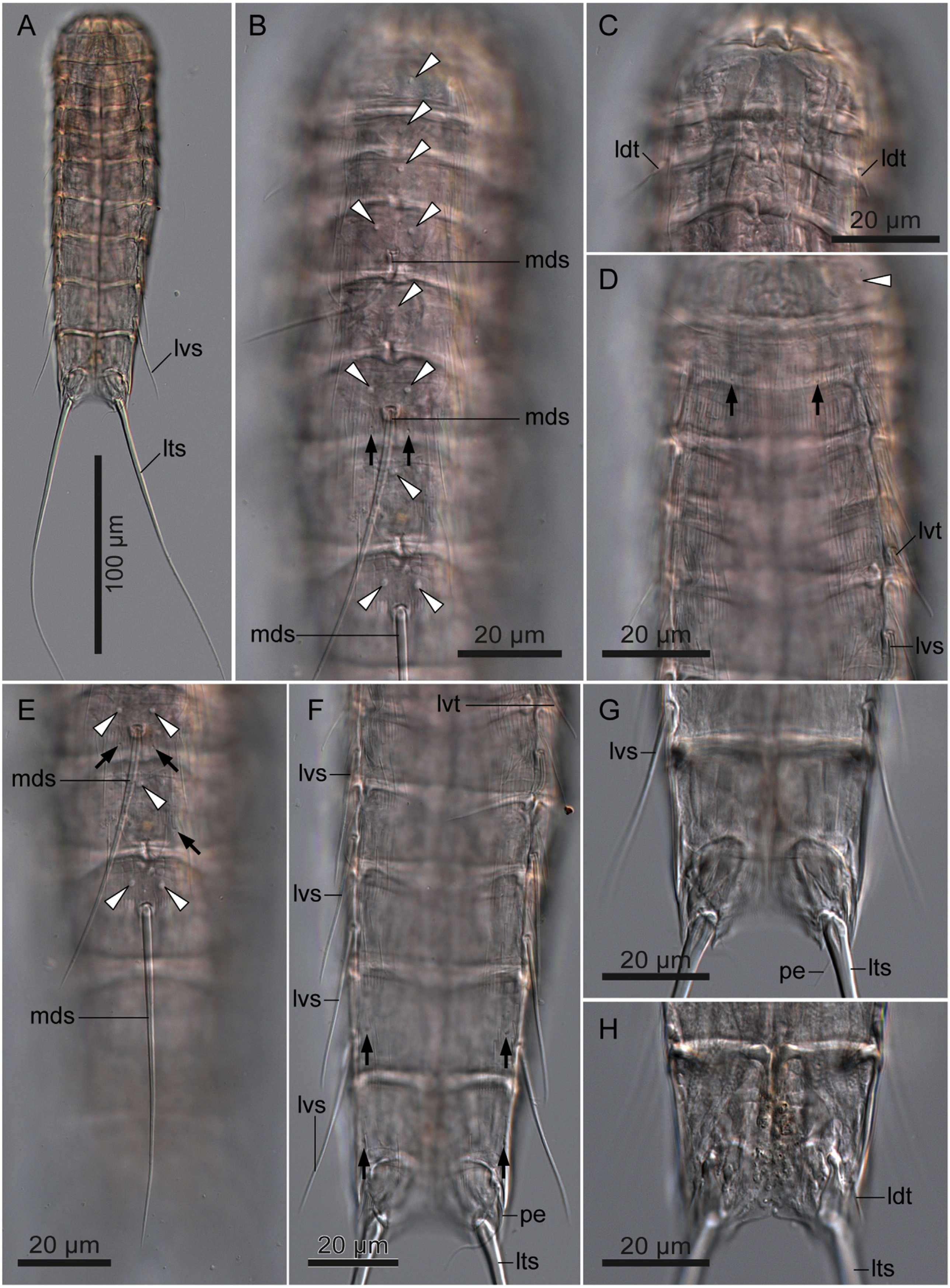
#### 3.5.1. *Material examined*

One male (ZMB 11956) and one female (ZMB 11955), collected at station 934 at slope of Senghor Seamount, northeastern Atlantic Ocean (17°12′56″N, 21°56′22″W), 565 m depth; one female (ZMB 11957), collected at station 1046 at slope of Senghor Seamount, northeastern Atlantic Ocean (17° 7′30″N, 21°55′30″W), 1545 m depth. All specimens mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

**Table 10**
Summary of locations of cuticular structures and appendages in *Echinoderes* sp. 1.

| Position segment | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | gco1 | | ss | ss | | | | | gco1 | |
| 2 | gco1, ss | | ss | | ss | | | | tu | ss |
| 3 | gco1 | | ss | | | | | | | gco1 |
| 4 | ac | gco1 | ss | | | | | | | gco1 |
| 5 | ac, gco1 | | | ss | | | | tu | | gco1 |
| 6 | ac | gco1 | ss | | | | | ac | | gco1 |
| 7 | ac, gco1 | | | ss | | | | ac | pa (f) | gco1 |
| 8 | ac | gco1 | | ss | | | | ac | | gco1, pa (f) |
| 9 | | gco1 | ss | | | ss | si | ac | ss | gco1 |
| 10 | gco1, gco1 | | ss | | tu | | | | | gco1 |
| 11 | gco1, gco1 | | ss | | | | pe × 3 (m), ltas (f) | lts | | |

Abbreviations: ac, acicular spine; (f), female condition of sexually dimorphic character; gco1, type-1 gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral; (m), male condition of sexually dimorphic character; md, middorsal; ml, midlateral; pa, papilla; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.


A
lvs
lts
100 μm
B
mds
mds
mds
20 μm
C
ldt
ldt
20 μm
D
lvt
lvs
20 μm
E
mds
mds
20 μm
F
lvt
lvs
lvs
lvs
lvs
pe
lts
20 μm
G
lvs
pe
lts
20 μm
H
ldt
lts
20 μm

### 3.5.2. *Brief description*

Adult with head, neck, and eleven trunk segments (Fig. 10A). See Table 9 for measurements. Table 10 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

Head with retractable mouth cone and introvert. Detailed arrangement of mouth cone and introvert characters not observed.

Neck with 16 placids, midventral one being broadest and remaining ones similar in size. Two trichoscalid plates present ventrally and four dorsally.

Segment 1 consisting of complete cuticular ring. Sensory spots present in subdorsal and laterodorsal position. Type-1 gland cell outlets situated in middorsal and lateroventral position. Cuticular hairs arising from perforation sites covering whole segment except for anterior quarter area of ventral side. Posterior edge of this and following nine segments with primary pectinate fringe. Pectinate fringe teeth of primary pectinate fringe short and thin.

Segment 2 composed of complete cuticular ring as segment 1. This and following eight segments with pachycyclus at anterior margin of each segment. Tubes present in ventrolateral position (Fig. 10B). Sensory spots in middorsal, subdorsal, midlateral, and ventromedial position. Type-1 gland cell outlet located in middorsal position. Cuticular hairs arising from perforation sites cover whole segment.

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Sensory spots present in subdorsal position. Type-1 gland cell outlets situated in middorsal and ventromedial position (Fig. 10C). Cuticular hairs arising from perforation sites on this and following seven segments covering whole segment except for ventromedial area.

Segment 4 with middorsal acicular spine (Fig. 10C). Sensory spots present in subdorsal position (Fig. 10C). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 10C).

Segment 5 with middorsal acicular spine and lateroventral tubes (Fig. 10B–E). Sensory spots in laterodorsal position. Type-1 gland cell outlets present in middorsal and ventromedial position (Fig. 10C).

Segment 6 with middorsal and lateroventral acicular spines (Fig. 10B–D). Sensory spots present in subdorsal position (Fig. 10C). Type-1 gland cell outlets present paradorsally and ventromedially (Fig. 10C).

Segment 7 with middorsal and lateroventral acicular spines (Fig. 10B, C). Sensory spots present in laterodorsal position. Ventrolateral papillae present only in female. Type-1 gland cell outlets present middorsally and ventromedially (Fig. 10C, D).

Segment 8 with acicular spines in middorsal and lateroventral position (Fig. 10A, D, and E). Sensory spots present laterodorsally. Ventromedial papillae present only in female. Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 10C, D).

Segment 9 with lateroventral acicular spines (Fig. 10A, E). Subdorsal, sublateral and ventrolateral sensory spots present (Fig. 10E). Type-1 gland cell outlets present in paradorsal and ventromedial position (Fig. 10D). Small rounded sieve plates present in lateral accessory position.

Segment 10 with relatively long midlateral tubes in both sexes (Fig. 10A, E–G). Subdorsal sensory spots present. Two type-1 gland cell outlets aligned middorsally. Additional pair of type-1 gland cell outlets present in ventromedial position.

**Table 11**
Measurements for adult *Echinoderes* sp. 2 (in micrometers or as percentage).

| Character | ZMB 11958 |
|---|---|
| tl | 191 |
| msw-7 | 41 |
| msw/tl | 21% |
| sw-10 | 36 |
| sw/tl | 19% |
| s1 | 28 |
| s2 | 23 |
| s3 | 20 |
| s4 | 22 |
| s5 | 23 |
| s6 | 26 |
| s7 | 27 |
| s8 | 30 |
| s9 | 30 |
| s10 | 29 |
| s11 | 18 |
| md4 (ac) | 37 |
| md6 (ac) | 62 |
| md8 (ac) | 80 |
| ld2 (tu) | 14 |
| lv5 (tu) | 15 |
| lv6 (ac) | 31 |
| lv7 (ac) | 36 |
| lv8 (ac) | 39 |
| lv9 (ac) | 44 |
| ld10 (tu) | 12 |
| lts | 179 |
| lts/tl | 94% |

Abbreviations: (ac), acicular spine; ld, length of laterodorsal tube; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube.

**Table 12**
Summary of locations of cuticular structures and appendages in *Echinoderes* sp. 2.

| Position segment | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | gco1 | | ss | | | | gco1 | | | |
| 2 | gco1 | | | tu | | | | | | ss, gco1 |
| 3 | gco1 | | ss | | | | | | | gco1 |
| 4 | ac | gco1 | | | | | | | | gco1 |
| 5 | gco1 | | | | | | | tu | | gco1 |
| 6 | ac | gco1, ss | | | | | | ac | | gco1 |
| 7 | gco1 | | ss | | | | | ac | | ss, gco1 |
| 8 | ac | gco1, ss | | | | | | ac | | gco1 |
| 9 | | gco1, ss | | | | | si | ac | ss | gco1 |
| 10 | gco1 | | | tu | | | | | ss | gco1 |
| 11 | gco1 | | | | | | pe × 3 | lts | | |

Abbreviations: ac, acicular spine; gco1, type-1 gland cell outlet; la, lateral accessory; ld, laterodorsal; lts, lateral terminal spine; lv, lateroventral; md, middorsal; ml, midlateral; pe, penile spine; pd, paradorsal; sd, subdorsal; si, sieve plate; sl, sublateral; ss, sensory spot; tu, tube; vl, ventrolateral; vm, ventromedial.

Segment 11 with lateral terminal spines (Fig. 10A, E–G). Three pairs of penile spines present in male, with two pairs being long tube and one pair thick and relatively short (Fig. 10E, F). Lateral terminal accessory spines present in females (Fig. 10G). Subdorsal sensory spots present. Two type-1 gland cell outlets present middorsally. Tergal extensions short

**Fig. 11.** *Echinoderes* sp. 2, male, Nomarski photomicrographs. A, neck and segments 1–11, ventral view; B, segments 1–8, dorsal view; C, neck and segments 1–3, dorsal view; D, segments 1–6, ventral view; E, segments 6–10, dorsal view; F, segments 6–11, ventral view; G, segments 9–11, ventral view; H, segments 10 and 11, dorsal view. Black arrows and white arrowheads indicate sensory spots and type-1 gland cell outlets, respectively. Abbreviations: ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; pe, penile spine.

and gradually tapering, and sternal extensions rounded (Fig. 10E–G).

### 3.5.3. Taxonomic remarks

The spines and tubes pattern of *Echinoderes* sp. 1, namely the presence of middorsal acicular spines on segments 4–8, lateroventral/lateral accessory acicular spines on segments 6–9, lateroventral/ventrolateral tubes on segments 2 and 5, and laterodorsal/midlateral/sublateral tubes on segment 10, and the absence of any other spine/tube is quite common in *Echinoderes* and shared by 19 species. Nevertheless, only 9 species of them have short and gradually tapering tergal extensions and lack type-2 glandular cell outlets: *Echinoderes aureus* Adrianov et al., 2002; *E. gizoensis*; *Echinoderes imperforatus* Higgins, 1983; *Echinoderes lanceolatus* Chang & Song, 2002; *Echinoderes pacificus* Schmidt, 1974; *Echinoderes pilosus* Lang, 1949; *Echinoderes sensibilis* Adrianov et al., 2002; *Echinoderes sublicarum* Higgins, 1977; *Echinoderes worthingi* Southern, 1914 (see Southern 1914; Lang 1949; Schmidt 1974; Higgins 1977b, 1983, 1986; Adrianov et al. 2002a, b; Chang & Song 2002; Thormar & Sørensen 2010).

Among the 9 congeners, the medium length of the middorsal acicular spines (each spine exceeds the posterior edge of the corresponding segment, but never exceeds that of the subsequent segment), the relatively long midlateral tubes on segment 10 (similar length or longer than the other middorsal and lateroventral acicular spines), and the pattern of the type-1 gland cell outlet on the dorsal side (middorsal position on segments 1–3, 5, 7, 10, and 11 and in paradorsal position on segments 4, 6, 8, and 9) indicates that *Echinoderes* sp. 1 is most similar to *E. aureus* and *E. lanceolatus* (see Adrianov et al. 2002a; Chang & Song 2002). Although, *Echinoderes* sp. 1 differs from *E. aureus* and *E. lanceolatus* by its small trunk length (181–215 μm in *Echinoderes* sp. 1, whereas 277–313 μm in *E. aureus* and 266–341 μm in *E. lanceolatus*) (Adrianov et al. 2002a; Chang & Song 2002), many other characters, e.g., sensory spots and primary pectinate fringe, cannot be compared because such information does not seem to be completely described for *E. aureus* and *E. lanceolatus*. Thus, we postpone naming *Echinoderes* sp. 1 as a new species until further information on *E. aureus* and *E. lanceolatus* will become available.

## 3.6. Echinoderes sp. 2

(Fig. 11, Tables 11 and 12)

### 3.6.1. Material examined

Non-type: one male (ZMB 11958), collected at station 934 at slope of Senghor Seamount, northeastern Atlantic Ocean (17°12′56″N, 21°56′22″W), 565 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

### 3.6.2. Brief description

Adult with head, neck, and eleven trunk segments (Fig. 11A). See Table 11 for measurements. Table 12 indicates positions of cuticular structures (sensory spots, gland cell outlets, spines, tubes, and sieve plates).

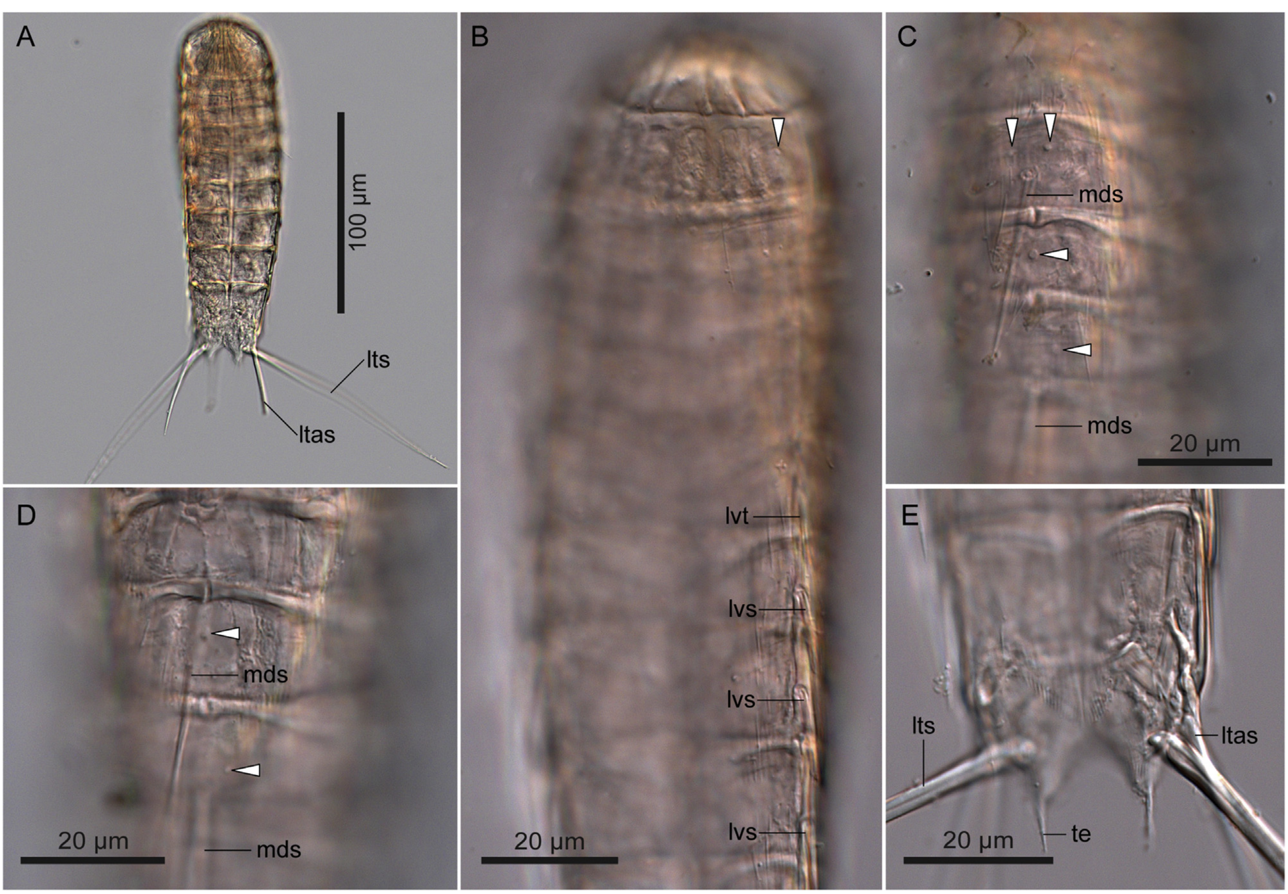



**Fig. 12.** *Echinoderes* sp. 3, female, Nomarski photomicrographs. A, neck and segments 1–11, ventral view; B, segments 1–8, ventral view; C, segments 3–6, dorsal view; D, segments 6–8, dorsal view; E, segments 10 and 11, ventral view. White arrowheads indicate type-1 gland cell outlets. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral acicular spine; lvt, lateroventral tube; mds, middorsal acicular spine; te, tergal extension.

**Table 13**
Measurements for adult *Echinoderes* sp. 3 (in micrometers or as percentage).

| Character | ZMB 11959 |
|---|---|
| tl | 167 |
| msw-7 | 38 |
| msw/tl | 23% |
| sw-10 | 35 |
| sw/tl | 21% |
| s1 | 29 |
| s2 | 20 |
| s3 | 19 |
| s4 | 19 |
| s5 | 20 |
| s6 | 21 |
| s7 | 24 |
| s8 | 24 |
| s9 | 26 |
| s10 | 29 |
| s11 | 21 |
| md4 (ac) | 32 |
| md6 (ac) | 51 |
| md8 (ac) | 84 |
| lv5 (tu) | 11 |
| lv6 (ac) | 23 |
| lv7 (ac) | 27 |
| lv8 (ac) | 32 |
| lv9 (ac) | 35 |
| ld10 (tu) | 12 |
| lts | 157 |
| ltas | 54 |
| lts/tl | 94% |
| ltas/tl | 32% |

Abbreviations: (ac), acicular spine; ld, length of laterodorsal tube; ltas, length of lateral terminal accessory spine; lts, length of lateral terminal spine; lv, length of lateroventral spine/tube; md, length of middorsal spine; msw, maximum sternal width; s, segment length; sw, standard width; tl, trunk length; (tu), tube.

**Table 14**
Summary of locations of cuticular structures and appendages in *Echinoderes* sp. 3.

| Position | md | pd | sd | ld | ml | sl | la | lv | vl | vm |
|---|---|---|---|---|---|---|---|---|---|---|
| segment | | | | | | | | | | |
| 1 | | | | | | | | | gco1 | |
| 2 | gco1 | | | | | | | | | |
| 3 | gco1 | | | | | | | | | gco1 |
| 4 | ac | gco1 | | | | | | | | gco1 |
| 5 | gco1 | | | | | | | tu | | gco1 |
| 6 | ac | gco1 | | | | | | ac | | gco1 |
| 7 | gco1 | | | | | | | ac | | gco1 |
| 8 | ac | gco1 | | | | | | ac | | gco1 |
| 9 | | gco1 | | | | | | ac | | gco1 |
| 10 | gco1 | | | | | | | | | gco1 |
| 11 | gco1 | | | | | | ltas | lts | | |

Abbreviations: ac, acicular spine; gco1, type-1 gland cell outlet; 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; tu, tube; vl, ventrolateral; vm, ventromedial.

Head with retractable mouth cone and introvert. Detailed arrangement of mouth cone and introvert characters not observed.

Neck with 16 placids, midventral one being broadest and remaining ones similar in size. Two trichoscalid plates present ventrally and four dorsally.

Segment 1 consisting of complete cuticular ring. Sensory spots present in subdorsal position. Type-1 gland cell outlets situated in middorsal and lateral accessory position (Fig. 11B, D). Posterior edge of this and following nine segments with primary pectinate fringe.

Segment 2 as complete cuticular ring. Tubes present in laterodorsal position (Fig. 11C). Sensory spots in ventromedial position (Fig. 11D). Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 11B).

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Sensory spots present in subdorsal position. Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 11B).

Segment 4 with middorsal acicular spine (Fig. 11B). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 11B).

Segment 5 with lateroventral tubes (Fig. 11D, F). Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 11B).

Segment 6 with middorsal and lateroventral acicular spines (Fig. 11B, D–F). Sensory spots present in paradorsal position (Fig. 11B, E). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 11B, E).

Segment 7 with lateroventral acicular spines (Fig. 11F). Sensory spots present in subdorsal and ventromedial position (Fig. 11E). Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 11B, E).

Segment 8 with acicular spines in middorsal and lateroventral position (Fig. 11B, E, and F). Sensory spots present paradorsally. Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 11B, E).

Segment 9 with lateroventral acicular spines (Fig. 11A, F, and G). Paradorsal and ventrolateral sensory spots present (Fig. 11F). Type-1 gland cell outlets in paradorsal and ventromedial position. Small rounded sieve plates in lateral accessory position.

Segment 10 with laterodorsal tubes (Fig. 11H). Ventrolateral sensory spots present (Fig. 11F). Type-1 gland cell outlets middorsally and ventromedially.

Segment 11 with lateral terminal spines (Fig. 11A, F–H). Three pairs of penile spines present (Fig. 11G). Type-1 gland cell outlet middorsally.

### 3.6.3. Taxonomic remarks

*Echinoderes* sp. 2 is unique among the congeners in having tubes on segment 2 only in laterodorsal position, indicating that *Echinoderes* sp. 2 represents an undescribed species. However, only one male specimen of the species was available in this study, hence, other minute characters like sensory spots and type-1 gland cell outlets might have been overlooked. The lack of additional specimens also prevented us from describing sexual dimorphism and intra-populational variation. Thus, we do not establish a new species based on this single specimen in this study, but report the species to demonstrate the biodiversity of kinorhynchs on Senghor Seamount.

## 3.7. *Echinoderes sp. 3*

(Fig. 12, Tables 13 and 14)

### 3.7.1. Material examined

Non-type: one female (ZMB 11959), collected at station 1049 on deep-sea floor close to Senghor Seamount, northeastern Atlantic Ocean (16°45′0″N, 22° 6′0″W), 3376 m depth, mounted as a glycerol-paraffin slide on a Cobb aluminum frame.

### 3.7.2. Brief description

Adult with head, neck, and eleven trunk segments (Fig. 12A). See Table 13 for measurements. Table 14 indicates positions of cuticular structures (gland cell outlets, spines, tubes, and sieve plates). Sensory spots may be present but were not checked.

Head with retractable mouth cone and introvert. Detailed arrangement of mouth cone and introvert characters not observed.

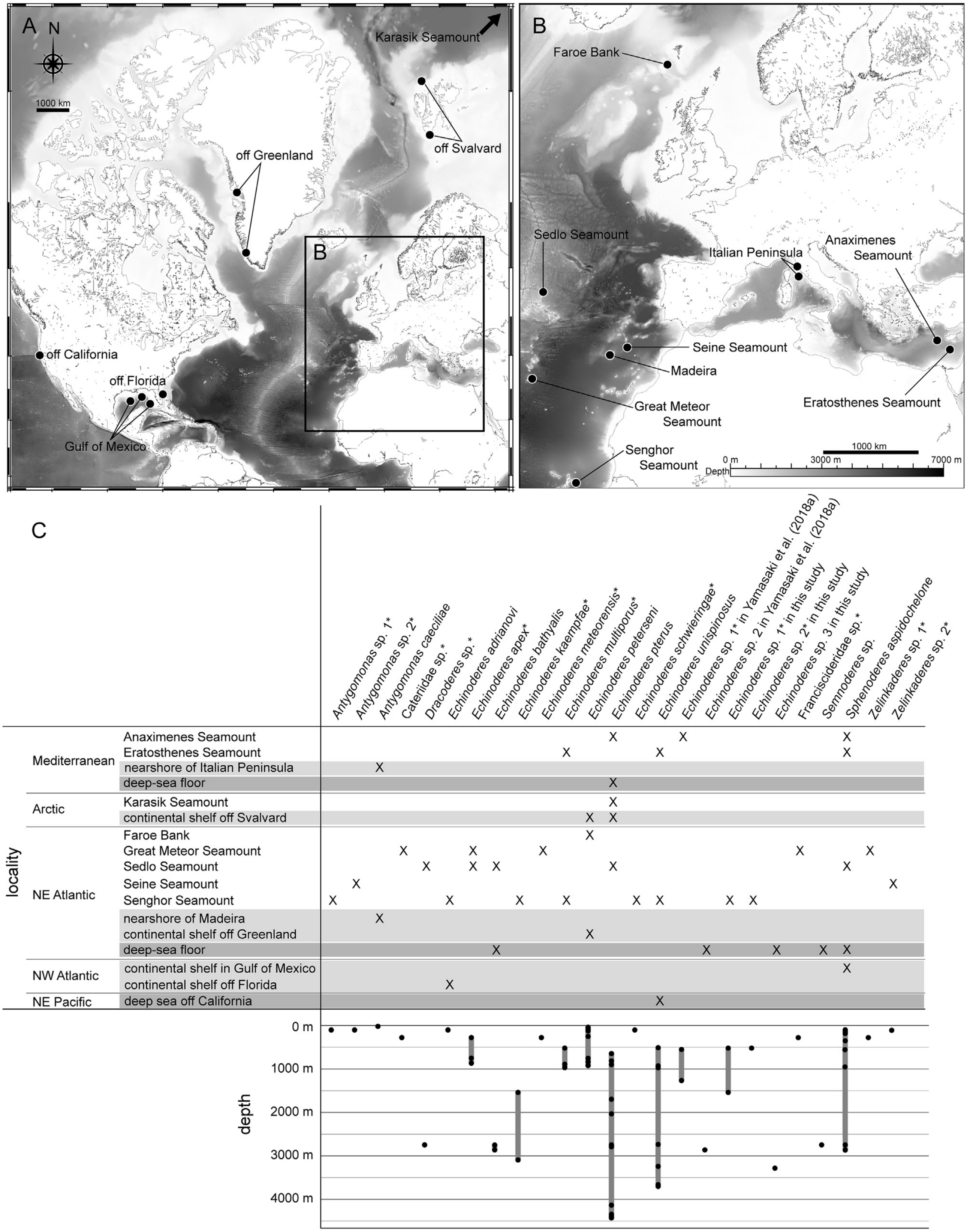



**Fig. 13.** Distribution of kinorhynchs found on seamounts and the adjacent deep-sea floor in the Northeast Atlantic Ocean, Mediterranean Sea, and Arctic Sea. A, map of the North Atlantic Ocean, Mediterranean Sea, Arctic Sea, and Northeast Pacific Ocean; B, close-up map of the Northeast Atlantic Ocean and Mediterranean Sea; C, records of each kinorhynch species found on seamounts and the adjacent deep-sea floor, and bathymetric distribution of each species. It should be noted that the record of *Echinoderes adrianovi* from Senghor Seamount is based on the identification as "*Echinoderes* cf. *adrianovi*" in this study.

Neck with 16 placids, midventral one being broadest and remaining ones similar in size. Two trichoscalid plates present ventrally and four dorsally.

Segment 1 consisting of complete cuticular ring. Type-1 gland cell outlets in ventrolateral position (Fig. 12B). Posterior edge of this and following nine segments with primary pectinate fringe.

Segment 2 as complete cuticular ring. Tubes absent. Type-1 gland cell outlets in middorsal position.

Segment 3 and following eight segments consisting of one tergal and two sternal plates. Type-1 gland cell outlets in middorsal and ventromedial position.

Segment 4 with middorsal acicular spine (Fig. 12C). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 12C).

Segment 5 with lateroventral tubes (Fig. 12B). Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 12C).

Segment 6 with middorsal and lateroventral acicular spines (Fig. 12B–D). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 12C).

Segment 7 with lateroventral acicular spines (Fig. 12B). Type-1 gland cell outlets in middorsal and ventromedial position (Fig. 12D).

Segment 8 with acicular spines in middorsal and lateroventral position (Fig. 12B, D). Type-1 gland cell outlets in paradorsal and ventromedial position (Fig. 12D).

Segment 9 with lateroventral acicular spines. Type-1 gland cell outlets in paradorsal and ventromedial position. Sieve plates not observed.

Segment 10 type-1 gland cell outlets middorsally and ventromedially.

Segment 11 with lateral terminal spines and lateral terminal accessory spines (Fig. 12A, E). Type-1 gland cell outlet middorsally. Tergal extension long and spinose (Fig. 12E).

*3.7.3. Taxonomic remarks*

Although 25 congeners possess middorsal acicular spines on segments 4, 6, and 8 and lateroventral acicular spines/tubes on segments 5–9 as *Echinoderes* sp. 3, only *E. meteorensis* and one species described by Sánchez et al. (2019) are similar to *Echinoderes* sp. 3 in lacking any tube on segment 2. Nevertheless, *Echinoderes* sp. 3 is different from *E. meteorensis* in lacking type-2 gland cell outlets. *Echinoderes* sp. 3 obviously represents a different species in comparison with the species in Sánchez et al. (2019) because the former possesses long and spinose tergal extensions whereas the latter shows rounded tergal extensions (Sánchez et al. 2019). In the single available specimen of *Echinoderes* sp. 3, structures on the lateral side were hard to observe. Although we confirmed the complete absence of any tube on segment 2 and any type-2 gland cell outlets throughout the trunk, the possibility remains that other tubes may have been overlooked on the lateral side of other segments. Thus, we regard the specimen as "*Echinoderes* sp. 3" without naming it as a new species in this study.

## 4. Discussion

Seamounts and islands have attracted attention for their faunistic uniqueness as well as their role for distribution of meiofauna (George 2013). Since 2016, we have carried out a project on seamount kinorhynchs in order to figure out the faunistic relationships between seamount summits, the bottom of seamounts, and the adjacent deep-sea floor, as well as the role of seamounts for the distribution of meiofauna. The faunistic information about seamounts and the adjacent deep-sea floor in the northeastern Atlantic Ocean, Mediterranean Sea, and Arctic Sea has drastically increased in the past years. So far, 15 *Echinoderes* species, including the six species reported in this study, have been recorded from seamounts and the adjacent deep-sea floor (Kristensen 2005; Yamasaki et al. 2018a, b, c). In addition, *Antygomonas* sp. 1, *Antygomonas* sp. 2, *Dracoderes* sp., *Sphenoderes aspidochelone* Sørensen & Landers, 2017 in Sørensen & Landers (2018), *Semnoderes* sp., *Zelinkaderes* sp. 1, *Zelinkaderes* sp. 2, Cateriidae sp., and Franciscideridae sp. were found on Anaximenes Seamount, Eratosthenes Seamount, Great Meteor Seamount, Senghor Seamount, Sedlo Seamount, Seine Seamount, and the deep-sea floor in the northeastern Atlantic Ocean (Fig. 13C; Yamasaki, Neuhaus and George., unpubl.). *Antygomonas caeciliae* Dal Zotto, 2015 was also found during the project from nearshore of Madeira, which is a volcanic island having the same origin as seamounts (Fig. 13C). Although many seamounts and large areas of the adjacent deep-sea floor in the northeastern Atlantic Ocean are still unexplored, the information recently accumulated allows us to discuss the faunistic character and distribution pattern of seamount kinorhynchs and the potential role of seamounts for their dispersal.

Out of the 25 species listed in Fig. 13C, three species were found only on the deep-sea floor adjacent to seamounts, *A. caeciliae* was from nearshore of an island or a continent, and the remaining 21 species were found on one or several seamounts. Among the 22 island and seamount kinorhynchs, 15 species (= 68%) occurred only on one or several seamounts suggesting they may be seamount-endemic species. The high ratio of seamount-endemic species indicates that there may be a unique kinorhynch fauna on seamounts, which differs from that in the surrounding area, viz, the deep-sea floor. The ratio of seamount-endemic kinorhynch species to non-seamount-endemic species is much higher than that for macro- and megafauna (29–34%), fish (11%), and general invertebrates (15%) (Wilson & Kaufmann 1987; Richer de Forges et al. 2000), while it is lower in comparison with the ratio for harpacticoid copepods (98%) and with general meiobenthic species (92%) as calculated by George (2013).

Although at least two kinorhynch species were recovered from all seamounts except for the Faroe Bank and Karasik Seamount (Fig. 13C), most species found on any given seamount are totally distinct and not closely related to each other (Yamasaki et al. 2018a, b, c; this study). Exceptions are *E. schwieringae* sp. nov. and *E. multiporus*, which are closely related and inhabit Senghor Seamount (Fig. 13C; this study). A similar result was reported for argestid harpacticoids from Great Meteor Seamount: closely related species occurred within the same summit community suggesting species radiation on the plateau (George & Schminke 2002; George 2004). However *E. schwieringae* sp. nov. and *E. multiporus* inhabit different depths and were not found at the same locality on Senghor Seamount (Fig. 13C). In addition, *E. multiporus* was also recovered from Eratosthenes Seamount but *E. schwieringae* sp. nov. was not. Considering the distributional difference of the two species, speciation of them may have happened on a seamount, followed by adaptation to a new microhabitat and settlement on another seamount – or vice versa.

Among the seamount species, eight species occurred at several disconnected localities: *E. apex* and *E. multiporus* occurred on two seamounts; *E. peterseni* and *E. adrianovi* occurred on a seamount and the continental shelf (note: the record of the species from Senghor Seamount was based on the record of "*E.* cf. *adrianovi*"); *Echinoderes bathyalis* and *Echinoderes unispinosus* occurred on seamount(s) and the deep-sea floor; and *E. pterus* and *Sp. aspidochelone* occurred in all three environments, viz, on seamounts, on the deep-sea floor, and on the continental shelf (Fig. 13A–C). It is surprising that *E. adrianovi*, *E. apex*, *E. multiporus*, and *E. peterseni* reported from shallow-waters inhabit geographically disconnected areas despite they have so far not been recorded from the in-between deep sea (Fig. 13C). It is also noteworthy that *E. joyceae*, which is probably the most closely related species to *E. apex*, has been recorded from the continental shelf of the Gulf of Mexico (Landers & Sørensen 2016), but has not been found on the deep-sea floor. Occurrence of shallow-water species both on a seamount and on the continental shelf was suggested for Halacarida by Bartsch (2003): halacarid taxa on Great Meteor Seamount would occur also at the coasts of the Azores, Europe, and North Africa. Büntzow (2011) documented that some harpacticoids inhabited more than one seamount suggesting that seamounts generally act as stepping stones for the dispersal of Harpacticoida. Similarly, some seamount kinorhynch species seem to be restricted to shallow waters, and seamounts would help them to disperse widely via seamounts as stepping stones. This might be the case for *A. caeciliae*: the species may distribute widely using islands as stepping stones. However, it should be noted that we cannot exclude the possibility that the lack of records for *E. adrianovi*, *E. apex*, *E. multiporus*, *E. peterseni*, and *A. caeciliae* from the deep sea in between the shallow waters represents a sampling artifact. Further investigations in the deep sea may find them, making them eurybathic species as the species discussed below.

*Echinoderes unispinosus E. pterus*, and *Sp. aspidochelone*, on the other hand, showed both bathymetrically and geographically a wide distribution pattern (Sørensen & Landers 2018; Sørensen et al. 2018; Yamasaki et al. 2018a, b; this study). *Echinoderes bathyalis* has been reported only from the foot of Sedlo Seamount and from the deep-sea floor adjacent to Sedlo Seamount so far. However, *Echinoderes dubiosus* Sørensen et al., 2018, which represents a closely related species of *E. bathyalis*, was described from the deep-sea floor off California (Sørensen et al. 2018), indicating that this species-group may widely inhabit the deep-sea environment. The same is the case for the *E. unispinosus* species-group. In addition to the records of *E. unispinosus*, *Echinoderes* sp. 1 in Yamasaki et al. (2018a), which is definitely closely related to *E. unispinosus* was recorded from Anaximenes Seamount, and *E. unispinosus*-like specimens were found at various localities in the deep sea of the Arctic Sea, Mediterranean Sea, central west and southeast Atlantic Ocean, and Southern Ocean (Herranz pers. comm.; Yamasaki and Neuhaus, unpubl.). Although *E. kaempfae* showed a eurybathic distribution pattern on Senghor Seamount, it has not been recorded outside of the seamount. This might be because the species may be restricted to the seamount, or the species may also inhabit the deep-sea floor but has not been found because of lack of comprehensive investigations of deep-sea kinorhynchs. An eurybathic distribution of seamount species is also known for zosimeid harpacticoids: half of the species found on Great Meteor Seamount also occurred in deep-sea environments (Koller & George 2011). The presence of such an eurybathic meiofauna on seamounts may be caused by migration from the deep-sea floor on to seamounts. Despite the fact that the kinorhynch fauna on the deep-sea floor has only been investigated sporadically, deep-sea kinorhynchs seem to disperse much more widely than previously expected. The same species as or similar species of *E. bathyalis*, *E. unispinosus*, *E. pterus*, and *E. kaempfae* plus *Echinoderes* sp. 2 in Yamasaki et al. (2018a), *Echinoderes* sp. 3 in this study, and *Semnoderes* sp. are expected to be discovered from various deep-sea regions in future studies.

In summary, the kinorhynch fauna on seamounts was partly unique but showed partly similarities to both other shallow waters and the deep-sea floor. Many kinorhynch species occurring on a seamount were probably seamount-endemic species (Fig. 13C). From the distribution pattern of seamounts species and their relatives, seamount kinorhynchs may have originated from three different environments: (1) some species probably originated from shallow waters and dispersed widely using seamounts as stepping stones (*E. adrianovi*, *E. apex*, *E. multiporus*, and *E. peterseni*), (2) some species were eurybathic occurring also on the deep-sea floor and possibly originated from the deep sea (*E. bathyalis*, *E. pterus*, *E. unispinosus*, and *Sp. aspidochelone*), and (3) few kinorhynch species may have speciated on seamounts (*E. schwieringae* sp. nov. and *E. multiporus*). Nonetheless, we still have scarce data on the kinorhynch fauna on seamounts and especially from the deep sea. Further investigations and studies are required to detect more accurately the distribution pattern of kinorhynchs and mechanisms of dispersal and speciation.

## Acknowledgements

This study was supported by a grant from the Deutsche Forschungsgemeinschaft DFG to KHG (GE 1086/20-1) and to BN (NE 931/6-1). We greatly appreciate technical support by Kristine Kämpf, Antje Schwiering, and Anke Sänger, Museum für Naturkunde Berlin. We also thank Dr Martin V. Sørensen and Dr María Herranz for reviewing the manuscript and providing helpful comments.

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