



Hadal Mud Dragons: First Insight Into the Diversity of Kinorhyncha From the Atacama Trench

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Deep-sea trenches are one of the last frontiers for deep-sea exploration and represent a large reservoir of undiscovered biodiversity. This applies in particular to organisms belonging to smaller-size classes, such as meiofauna. Among different meiofauna taxa, kinorhynchs represent a large gap in our knowledge about global marine biodiversity in general, but primarily in extreme deep-sea environments. Out of the more than 300 known mud dragon species, only a single species has ever been described from hadal depths (> 6000 m), i.e., *Echinoderes ultraabyssalis* from the Kuril-Kamchatka Trench. The results presented in this paper are based on material collected during a research expedition in 2018 investigating the Atacama Trench environment. We provide a first overview and comparison of the diversity and abundance of mud dragons in the Atacama Trench, the adjacent abyssal plain and continental slope off Chile. The study revealed six species of *Echinoderes*. Of these, *Echinoderes mamaqucha* sp. nov. is described as a new species and morphological data of three undescribed species are given. Because of the low number of available specimens, we provide only a brief description of these three species and comparison with their morphologically closest congeners, but formal descriptions are not given. Moreover, *Echinoderes juliae* and *Echinoderes pterus* were also recovered. *Echinoderes juliae* was described from the abyssal plain off Oregon and along the continental rise off California, at 2702 to 3679 m depth. *Echinoderes pterus* is known from the high Arctic, the North Atlantic, and the Mediterranean Sea, and has also been reported to show a wide bathymetric distribution, from 675 to 4403 m. Interestingly, *E. mamaqucha* sp. nov. dominated at the trench stations and it reached its highest abundance at the deepest station, at 8085 m water depth. The only other single individual that was found in the Atacama Trench was *Echinoderes* sp.1. The remaining four species were all found at the abyssal and slope stations. The obtained results seem to confirm previous hypotheses about geographic isolation of deep-sea trenches and relatively low connectivity with other habitats, reflected by limited diversity of sediment dwelling fauna, particularly in the deepest parts of trenches.

Keywords: deep-sea, meiofauna, *Echinoderes mamaqucha*, new species, taxonomy

INTRODUCTION

Kinorhynchs, small meiobenthic organisms with retractable, scald-covered head and segmented trunk, also known as mud dragons, are exclusively marine invertebrates that occur mostly in muddy or fine-grained sandy sediments, from the shallow waters to the hadal depths (Neuhaus, 2013). A clearer picture of kinorhynch fauna, diversity and community structure at shallower depths is emerging (Sørensen et al., 2012; Yamasaki et al., 2012; Dal Zotto and Todaro, 2016; Landers et al., 2018, 2020; Cepeda et al., 2019a,b; Grzelak and Sørensen, 2019a,b), but knowledge about mud dragons at abyssal (3000–6000 m) and hadal depths (>6000 m) [for definition of depth zone see Harris et al. (2014) and Jamieson et al. (2010)] is still extremely limited. This is mostly due to the remoteness of the deep-sea ecosystem, technical difficulties in obtaining reliable samples and scarcity of taxonomic expertise.

Deep-sea trenches can reach depths of 11000 m and their geomorphological features (funnel-like topography, very steep walls, and high hydrostatic pressure) constitute a challenge for logistics and equipment, and thus a serious constrain for biodiversity studies of these habitats (Jamieson et al., 2010). However, information from trenches is essential not only to understand bathymetric patterns in diversity and their regulatory mechanisms in deep-sea environments, but also overall of marine biodiversity and biogeography. These habitats may provide new insights into the factors shaping distribution patterns at the deep-sea floor and modify existing ecological paradigms. Trenches are separated from each other by remoteness spaces at abyssal depths, what might support high level of species endemism (Belyaev, 1989). In terms of meiofauna taxa, this statement still needs to be verified.

Hadal trenches remain the least studied and their kinorhynch fauna is almost completely unexplored, as we so far only know about a single identified hadal species, *Echinoderes ultraabyssalis* Adrianov and Maiorova (2019), described from 9411–9540 m water depth in the Kuril-Kamchatka Trench (Adrianov and Maiorova, 2019). The only other known records of kinorhynchs from hadal depths are the finding of an unidentified specimen of *Echinoderes* from 9000 m in the Kermadec Trench (unpublished finding by D. Leduc, see Zeppilli et al., 2018) and unidentified kinorhynchs from 7200 m in the Atacama Trench, reported by Danovaro et al. (2002).

The first kinorhynch identified from abyssal depth was *Fissuroderes rangi* Neuhaus and Blasche (2006) described from the Hikurangi Plateau east of New Zealand at 3202 m water depth by Neuhaus and Blasche (2006). A few years later Neuhaus and Sørensen (2013) reported *Campyloderes* cf. *vanhoeffeni* Zelinka (1913) in the Guinea Basin at 5064 m and in the southeastern deep-sea region of Canary Island at depths between 5055 m and 5118 m. Sánchez et al. (2014a,b) described three additional species, i.e., *Mixtophyes abyssalis* Sánchez et al. (2014a,b), *Cristaphyes nubilis* (Sánchez et al., 2014a,b), and *Krakenella farinelli* (Sánchez et al., 2014a,b), from the Guinea Basin, at depths between 5100–5175 m. The remaining and more recent reports of identified abyssal

kinorhynchs are restricted to five areas: (1) abyssal plains, 3100–3300 m, around North Atlantic seamounts, from where Yamasaki et al. (2019) describe *Echinoderes kaempfae* Yamasaki et al., 2019; (2) the East Mediterranean, 675–4403 m, from where Yamasaki et al. (2018a) describe *Echinoderes pterus* Yamasaki et al., 2018a,b; (3) abyssal plains, 3351–5766, in the vicinity of the Kuril-Kamchatka Trench, from where Adrianov and Maiorova (2015, 2016, 2018a,b) describe *Cristaphyes abyssorum* (Adrianov and Maiorova, 2015), *Condyloderes kurilensis* Adrianov and Maiorova (2016), *Meristoderes okhotensis* Adrianov and Maiorova (2018a), and *Parasemnoderes intermedius* Adrianov and Maiorova (2018b); (4) the abyssal plains, 3250–3853 m, off the Northwest American continental slope, from where Sørensen et al. (2018) describe *E. anniae*, *E. dubiosus*, *E. hamiltonorum*, *E. juliae*, *E. lupherorum*, *E. hviidarum*, *E. yamasakii*, and Sørensen et al. (2018, 2019) report three additional known kinorhynch species, *E. cf. unispinosus* Yamasaki et al. (2018a,b), *Fissuroderes higginsi* Neuhaus and Blasche (2006), and *C. kurilensis*; (5) the Clarion-Clipperton Fracture Zone, 4319–5012 m, in the tropical East Pacific, from where Sánchez et al. (2019) describe *Cephalorhyncha polunga*, *Echinoderes shenlong*, and *Meristoderes taro*.

The present contribution is the result of studies of kinorhynchs found in samples collected during Cruise SO261, which took place in 2018, in the Atacama Trench region, as part of the multidisciplinary HADES European Research Council (HADES-ERC) study of deep trench systems. Previous studies conducted in the Atacama Trench established the presence of abundant metazoan meiofauna community (Danovaro et al., 2002, 2003) and protozoan Foraminifera (Sabbatini et al., 2002). Despite the fact, that meiobenthos is a key component of benthic fauna inhabiting the Atacama Trench, biodiversity studies have been conducted only for nematodes (Gambi et al., 2003). The main purpose of this study is to provide the first assessment of the species richness and distribution of Kinorhyncha in the Atacama Trench and the adjacent abyssal plain. Here, we contribute with the description of a new species of *Echinoderes*, the second deepest kinorhynch species described so far. Furthermore, we provide detailed morphological data of three additional undescribed species and report two known species.

MATERIALS AND METHODS

Study Area

The study area is located in the Atacama Trench, part of the Peru-Chile Trench system, which is the longest trench of the Pacific Ocean, stretching for almost 6000 km along the coast of Peru and Chile (Figure 1). The Atacama Trench is narrower than other Pacific trenches (64 km in width), and with a maximum depth of 8065 m it is the deepest trench of the East Pacific and tenth deepest trench in the world (Jamieson et al., 2010). The Atacama Trench was formed by the subduction of the Nazca and Antarctic plates beneath the continental South American Plate. It is a seismically active area, resulting in occasional gravity-driven sediment slides

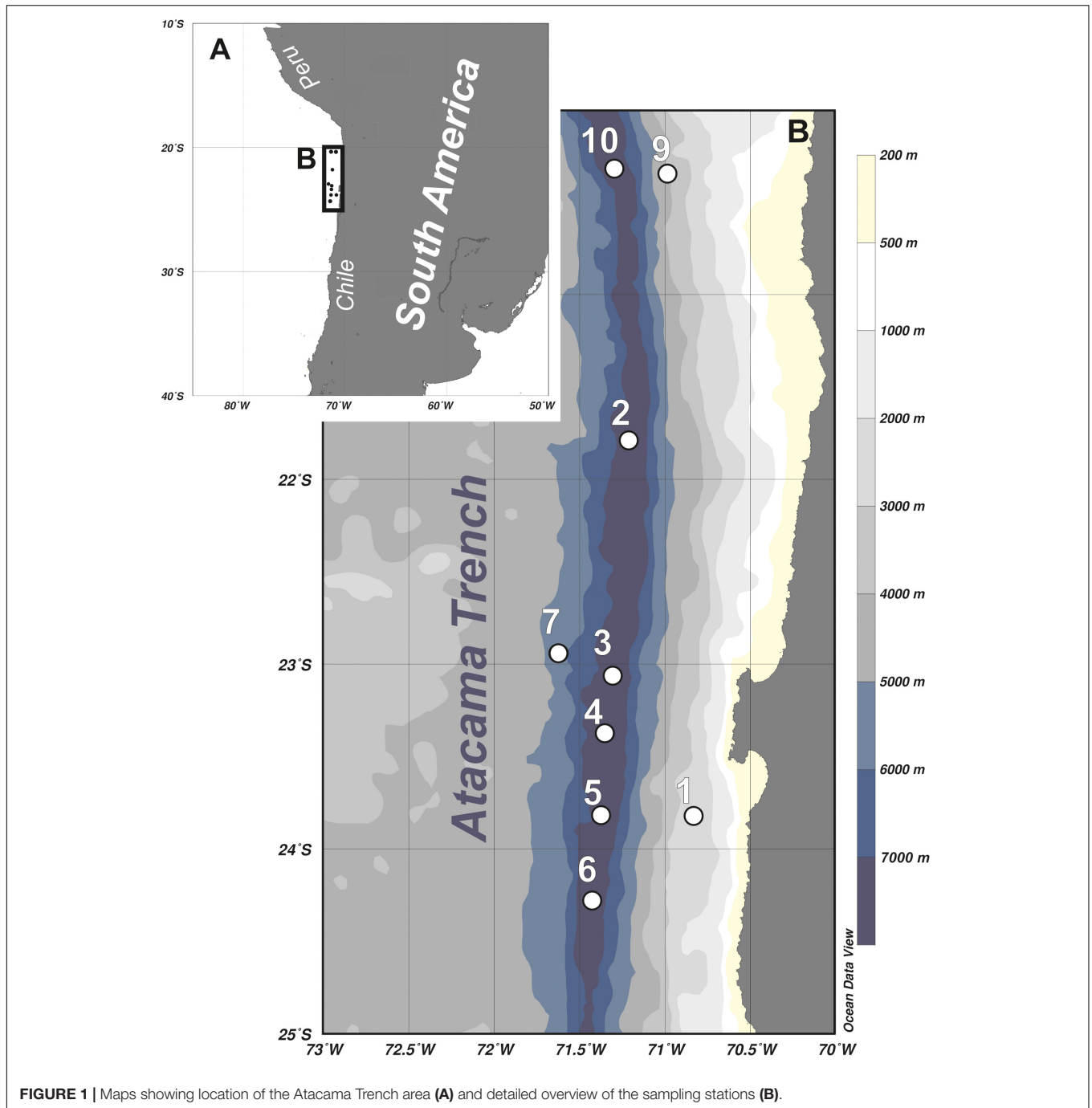


FIGURE 1 | Maps showing location of the Atacama Trench area (A) and detailed overview of the sampling stations (B).

(Lemenkova, 2019). The Atacama Trench is located in an area with significant upwelling events that lead to high primary production (Fossing et al., 1995).

Sample Collection and Preparation

The sampling was undertaken in March 2018, during the cruise (SO261) with German research vessel RV ‘Sonne,’ within a framework of the multidisciplinary HADES European Research Council (HADES-ERC) study of deep trench systems. A multicorer with tubes of 9 cm internal diameter was used to

retrieve bottom sediment from six stations arranged along the 450-km transect in the Atacama Trench (stations 2 to 6, and 10) and three stations located at the abyssal plain (7) and continental slope (1 and 9) off the Atacama Trench (Table 1 and Figure 1). From each deployment, three cores were taken from the MUC and subsampled for meiofauna analysis (5 cm in length and 2.9 cm in diameter). The samples were fixed with 4% buffered formaldehyde. In the laboratory samples were washed with freshwater in a 20 μ m sieve and meiofauna organisms were extracted using centrifugation

TABLE 1 | Coordinates and basic data of sampling stations and *Echinoderes* species identities; total no of kino.- total number of processed kinorhynchs (adults and juveniles), species- species identity, together with number of recorded *Echinoderes* adult specimens, LM-light microscopy, SEM-scanning electron microscopy, NHMD-no – Natural History Museum of Denmark catalog number.

Station	Location	Date	Latitude (S)	Longitude (W)	Depth (m)	Total no of kino.	Species	Mounting	NHMD-no
1	continental slope	06.03.2018	23° 48.72'	70° 50.04'	2560	4	<i>E. juliae</i> (1), <i>Echinoderes</i> sp. 3 (1)	LM LM	NHMD-872652 NHMD-872651
2	trench	23.03.2018	21° 46.86'	71° 12.48'	7994	12	<i>E. mamaqucha</i> sp. nov. (3)	LM + SEM	NHMD-872645-46
3	trench	17.03.2018	23° 02.94'	71° 18.12'	7915	11	<i>E. mamaqucha</i> sp. nov. (2)	LM + SEM	NHMD-872647
4	trench	14.03.2018	23° 21.78'	71° 20.60'	8085	26	<i>E. mamaqucha</i> sp. nov. (10)	LM + SEM	NHMD-872636-43
5	trench	11.03.2018	23° 49.02'	71° 22.32'	7770	14	<i>E. mamaqucha</i> sp. nov. (2)	LM	NHMD-872648-49
6	trench	08.03.2018	24° 15.96'	71° 25.38'	7720	12	<i>E. mamaqucha</i> sp. nov. (2) <i>Echinoderes</i> sp.1 (1)	LM + SEM LM	NHMD-872635 NHMD-872653
7	abyssal plain	20.03.2018	22° 56.22'	71° 37.08'	5500	5	<i>E. mamaqucha</i> sp. nov. (1) <i>Echinoderes</i> sp. 2 (1)	LM LM	NHMD-872650 NHMD-872654
9	continental slope	28.03.2018	20° 19.97'	70° 58.70'	4050	5	<i>E. pterus</i> (1)	SEM	
10	trench	26.03.2018	20° 19.14'	71° 17.46'	7770	7	<i>E. mamaqucha</i> sp. nov. (1)	LM	NHMD-872644

with LUDOX solution, following the standard protocol (Vincx, 1996). Kinorhynchs were picked up and stored in a 4% formaldehyde solution. For preparation of light microscopy (LM) slides, specimens were dehydrated through a graded series of glycerine and mounted in Fluoromount-G. The specimens were examined with an Olympus BX51 microscope with differential interference contrast, and photographed with an Olympus DP27 camera. Measurements were made with Cell^D software. Line art figures were made with Adobe Illustrator CS6. Specimens for scanning electron microscopy (SEM) were dehydrated through a graded alcohol-acetone series and critical point dried. Dried specimens were mounted on aluminum stubs, sputter coated with a platinum/palladium mix and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

All specimens were identified to species level, except for the juveniles. Identification of kinorhynchs to species level was based on the relevant taxonomic literature (Herranz et al., 2018; Sørensen et al., 2018; Yamasaki et al., 2018b, 2020; Adrianov and Maiorova, 2019).

RESULTS

Systematics

Class Cyclorhagida Zelinka (1896) *sensu* Sørensen et al. (2015)
 Order Echinorhagata Sørensen et al. (2015)
 Family Echinoderidae Carus (1885)
 Genus *Echinoderes* Claparède (1863)
Echinoderes mamaqucha sp. nov.
 ZooBank.org lsid: zoobank.org:pub:1A9867FF-1C58-4F17-A869-F7534B262518.

Material Examined

Holotype

Adult female, collected on March 8, 2018 at station 6 (Figure 1 and Table 1), from 7720 m depth, in the Atacama Trench (24° 15.96'S 71° 25.38'W), mounted in Fluoromount-G, deposited

at the Natural History Museum of Denmark, under catalog number NHMD-872635.

Paratypes

Eleven females and four males collected at stations (station 2, 3, 4, 5, 7, 10) located along the Atacama Trench axis (Figure 1 and Table 1), mounted in Fluoromount-G, deposited at the Natural History Museum of Denmark (NHMD-872636 to NHMD-872650).

Additional Material

Four females and one male mounted for SEM and stored in the personal collection of MVS.

Etymology

The species name refers to Mama Qucha, sea- and fish goddess in Inca Mythology, protectress of sailors, and Sea Mother.

Diagnosis

Echinoderes with middorsal acicular spines on segments 4 to 8, and in lateroventral positions on segments 6 to 9. Tubes present in subdorsal and ventrolateral positions on segment 2, lateroventral positions on segment 5, lateral accessory positions on segment 8 and laterodorsal positions on segment 10; tubes on segment 2 very short and truncate.

Description

Adults with head, neck and eleven trunk segments (Figures 2A,B, 3A, 4A). Overview of measures and dimensions are given in Table 2. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, is summarized in Table 3.

The head consists of a retractable mouth cone and an introvert (Figure 4B). The external mouth cone armature consists of nine outer oral styles, each composed of two joined units, arranged as one style anterior to each introvert sector, except the middorsal sector 6; each outer oral style with basal fringe consisting of six spinous tips. The introvert was partly retracted in one specimen, and otherwise fully retracted in remaining ones; hence information was only available for the anteriormost scaldid

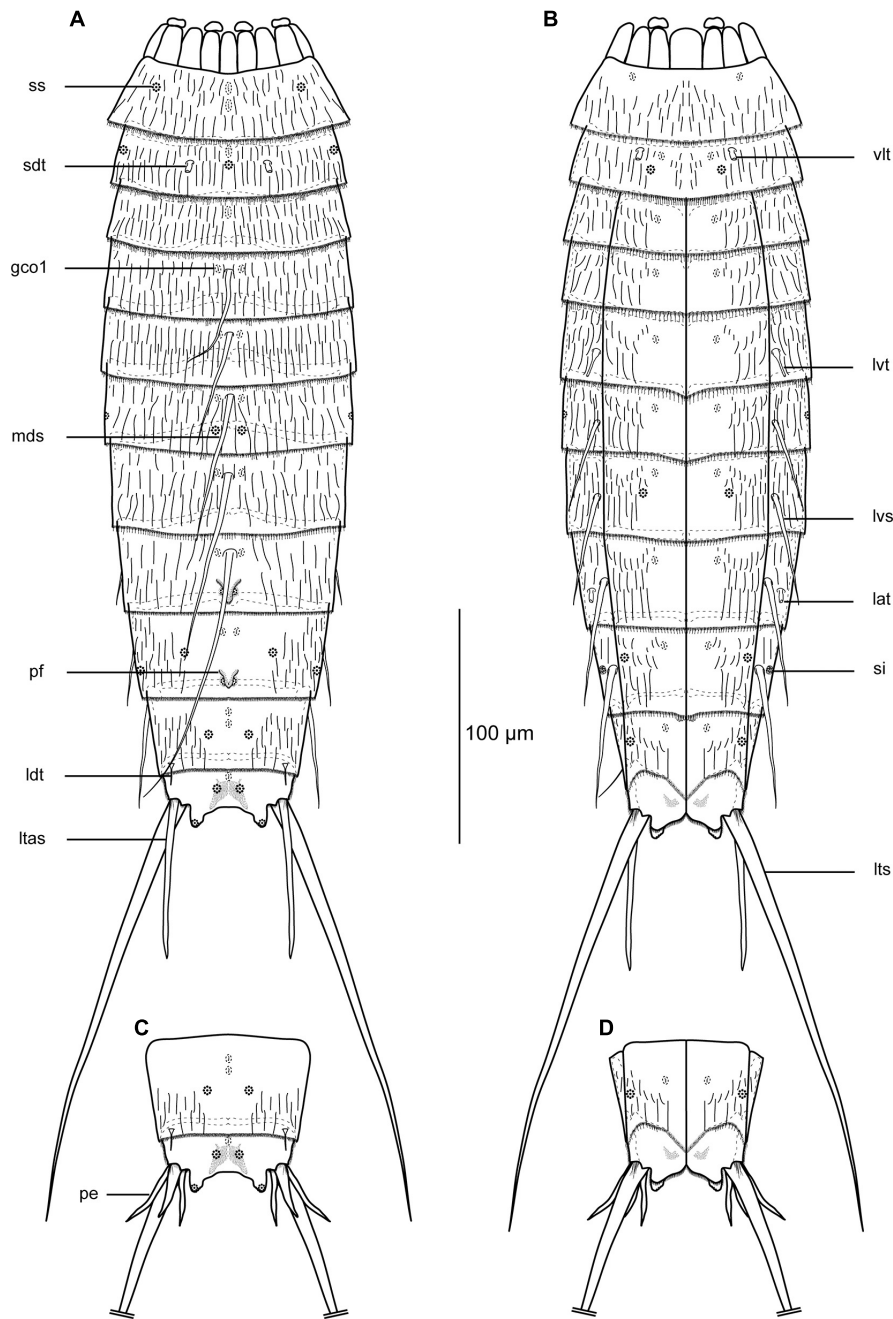


FIGURE 2 | Line art illustrations of *Echinoderes mamaqucha* sp. nov. **(A)** female, dorsal view; **(B)** female ventral view; **(C)** male, segments 10–11, dorsal view; **(D)** male, segments 10–11, ventral view. *gco1*, glandular cell outlet type 1; *lat*, lateral accessory tube; *ldt*, laterodorsal tube; *ltas*, lateral terminal accessory spine; *lts*, lateral terminal spine; *lvs*, lateroventral spine; *lvt*, lateroventral tube; *mds*, middorsal spine; *pe*, penile spines; *pf*, papillary flap; *sdt*, subdorsal tube; *si*, sieve plate; *ss*, sensory spot; *vit*, ventrolateral tube.

rings. Ten primary spinoscalids present, each consisting of a basal sheath and a distal end piece with a blunt tip. The sheaths have two distinctively differentiated transverse fringes: a most basal fringe with fringe tips attaching to the surface of the scalid, and a slightly more distal fringe where the fringe tips emerge from a transverse furrow; distal to this second fringe, the sheath has a dense hair cover. End pieces are smooth and flexible. Ring

02 has 10 spinoscalids, and Ring 03 has 20. All spinoscalids in these rings are well-developed, and consist of a basal sheath and a pointed end piece; the basal sheaths of spinoscalids in both rings terminate into fine, fringed margins, whereas those of Ring 03 have in addition a strong, basal median spike (**Figure 4B**). The number of spinoscalids and their exact morphology could not be determined posterior to Ring 3.

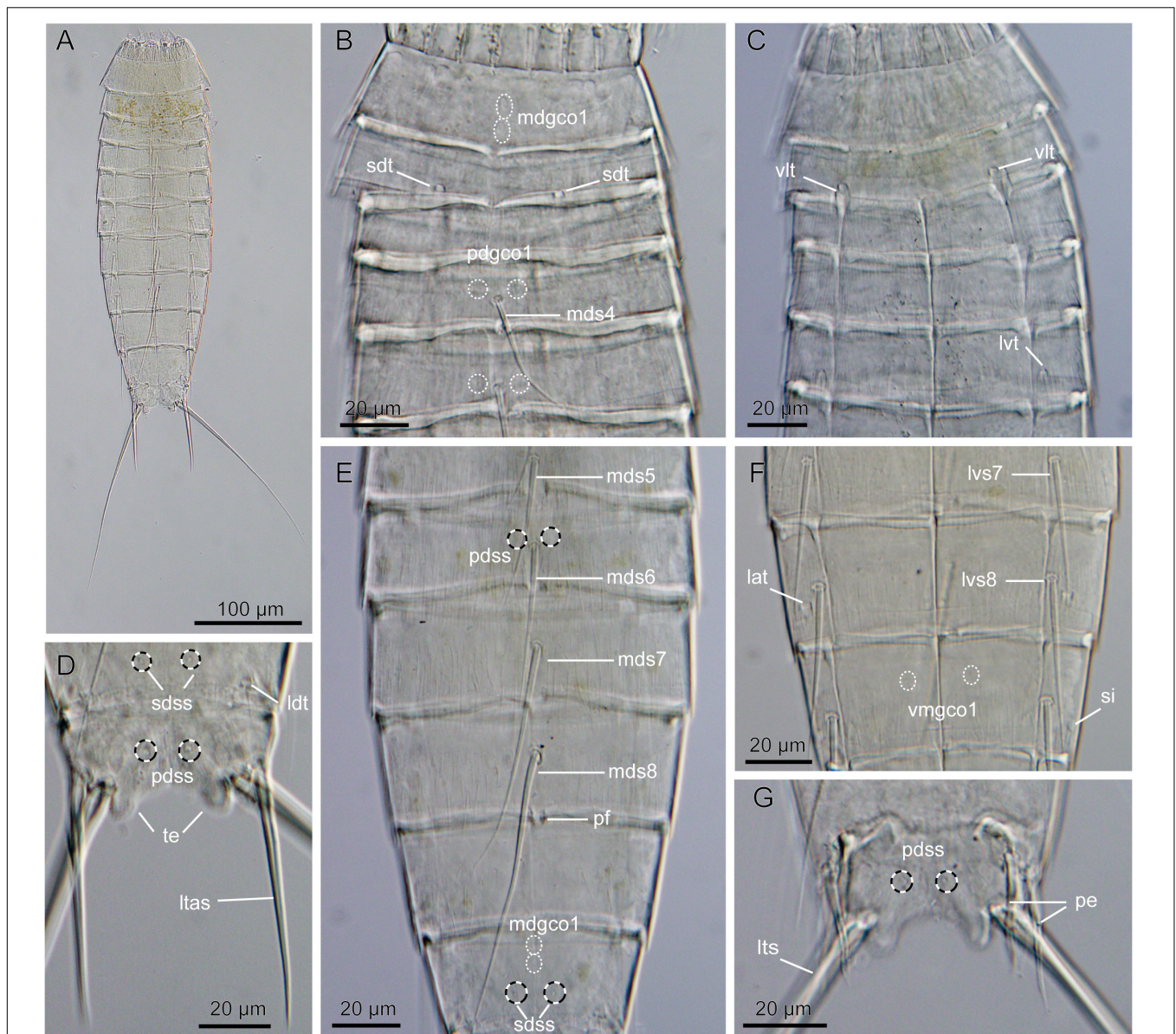


FIGURE 3 | Light micrographs showing overview and details of *Echinoderes mamaqucha* sp. nov. **(A,D–F)** Female holotype (NHMD-872635). **(B,G)** Male paratype (NHMD-872636). **(C)** Female paratype (NHMD-872641). **(A)** Ventral overview. **(B)** Segments 1 to 5, dorsal view. **(C)** Segments 1 to 5, ventral view. **(D)** Segments 10 to 11, dorsal view. **(E)** Segments 5 to 10, dorsal view. **(F)** Segments 7 to 9, ventral view. **(G)** Segments 10–11, dorsal view. *lat*, lateral accessory tube; *ldt*, laterodorsal tube; *lts*, lateral terminal spine; *ltas*, lateral terminal accessory spine; *lvs*, lateroventral spine, followed by segment number; *lvt*, lateroventral tube; *mdgco1*, middorsal glandular cell outlet type 1; *mgs*, middorsal spine, followed by segment number; *pdgco1*, paradorsal glandular cell outlet type 1; *pdss*, paradorsal sensory spot; *pe*, penile spine; *pf*, papillary flap; *sdss*, subdorsal sensory spot; *sdt*, subdorsal tube; *si*, sieve plate; *te*, tergal extension; *vlt*, ventrolateral tube; *vmgco1*, ventromedial glandular cell outlet type 1.

Neck with 16 placids. Midventral placid broadest, 12 µm in width and 18 µm in length. Remaining placids narrower, 9 µm in width and 17 µm in length, similar in size. Four dorsal and two ventral trichoscalid plates are present, each carrying a thick and bushy trichoscalid.

Segment 1 consists of a complete cuticular ring (Figures 2A,B, 3B,C, 4A,C,D). One pair of sensory spots is located in laterodorsal positions, anterior on the segment, but not at anterior margin. Sensory spots on this and following

segments small and rounded, with numerous micropapillae surrounding a central pore (Figures 4C,D,F–H). Two longitudinally arranged glandular cell outlets type 1 present in middorsal position, and one additional pair present in lateroventral positions (Figures 4C,D). Cuticular hairs relatively well-spaced, distributed evenly around the segment, except in hairless ventromedial areas on anterior segment half (Figures 4C,D). Posterior segment margin almost straight, forming a pectinate fringe; pectinate fringe tips

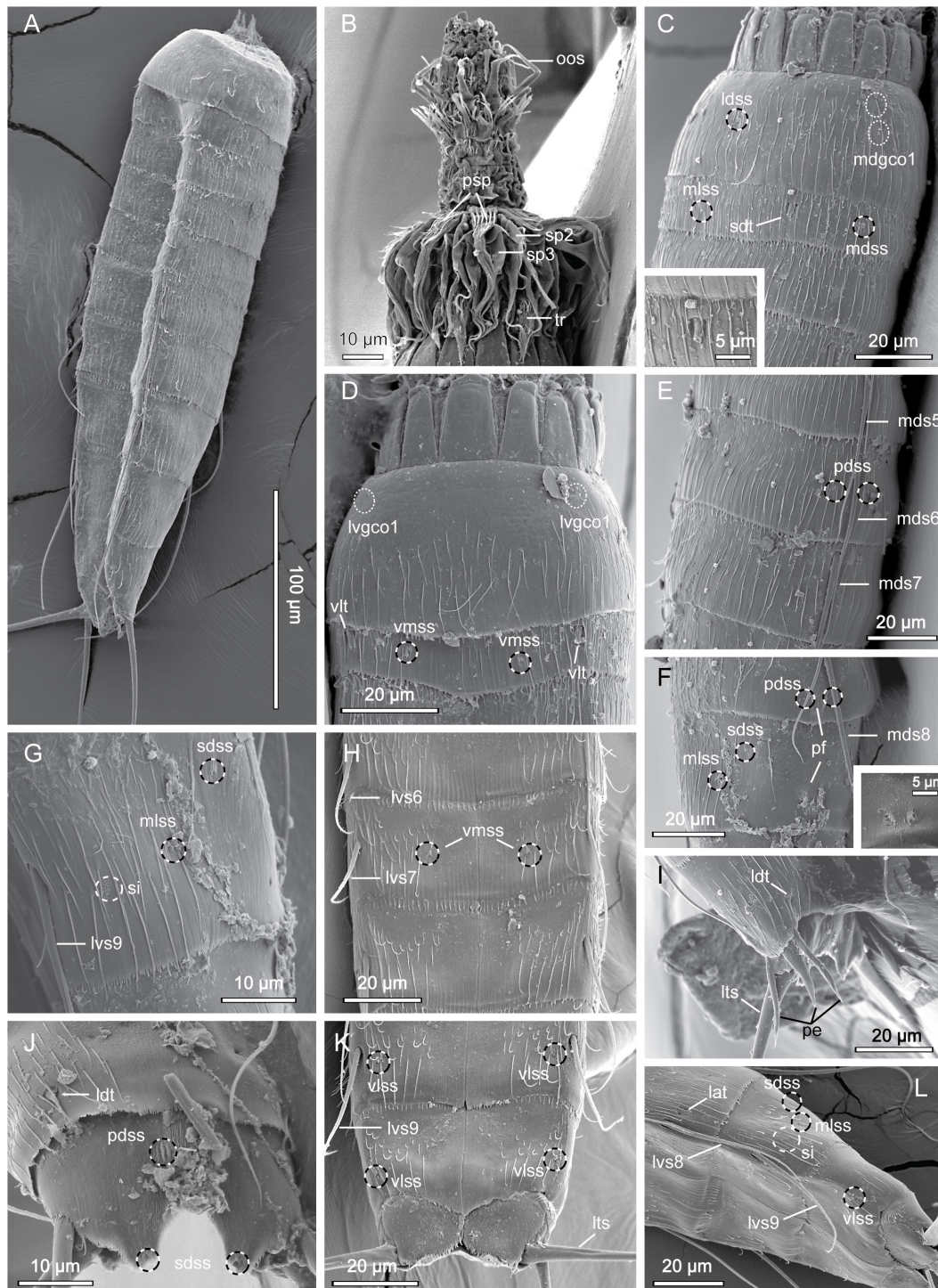


FIGURE 4 | Scanning electron micrographs showing overviews and details of *Echinoderes mamaqucha* sp. nov. **(A)** Lateroventral overview. **(B)** Mouth cone and introvert sectors 8 to 7. **(C)** Segments 1 to 3, dorsolateral view, with close-up showing subdorsal tube on segment 2. **(D)** Segments 1 to 2, ventral view. **(E)** Segments 5 to 7, dorsolateral view. **(F)** Segments 8 to 9, dorsolateral view, with close-up showing papillary flap on segment 9. **(G)** Segment 9, lateral view. **(H)** Segments 6 to 8, ventral view. **(I)** Segments 10 to 11 of male, lateral view. **(J)** Segments 10 to 11 of female, dorsal view. **(K)** Segments 9 to 11 of female, ventral view. **(L)** Segments 8 to 11, lateroventral view. *lat*, lateral accessory tube; *ldss*, laterodorsal sensory spot; *ldt*, laterodorsal tube; *lts*, lateral terminal spine; *lvgco1*, lateroventral glandular cell outlet type 1; *lvs*, lateroventral spine, followed by segment number; *mdgco1*, middorsal glandular cell outlet type 1; *mds*, middorsal spine, followed by segment number; *mdss*, middorsal sensory spot; *mlss*, midlateral sensory spot; *oos*, outer oral style; *pdss*, paradorsal sensory spot; *pe*, penile spine; *pf*, papillary flap; *psp*, primary spinoscalid; *sdss*, subdorsal sensory spot; *sdt*, subdorsal tube; *si*, sieve plate; *sp*, spinoscalid followed by introvert ring number; *tr*, trichoscalid; *vlt*, ventrolateral tube; *vmss*, ventromedial sensory spot.

TABLE 2 | Measurements from light microscopy of *Echinoderes mamaqucha* sp. nov. (in μm) from the Atacama Trench, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	16	252–325	296	20.8
MSW-6	16	63–69	67	1.7
MSW-6/TL	16	20.8–26.7%	22.9%	1.8%
SW-10	16	53–56	54	0.9
SW-10/TL	16	16.8–21.6%	18.4%	1.4%
S1	16	28–35	31	1.8
S2	16	24–30	26	1.6
S3	16	24–31	27	1.7
S4	16	28–35	30	1.9
S5	16	29–36	32	1.8
S6	16	34–40	36	1.9
S7	16	34–42	38	1.8
S8	16	39–45	42	1.6
S9	16	39–44	41	1.7
S10	16	33–43	36	3.2
S11	16	25–32	28	2.0
MD4 (ac)	16	35–43	40	2.4
MD5 (ac)	15	43–53	47	3.1
MD6 (ac)	15	47–57	52	3.5
MD7 (ac)	16	63–80	72	4.6
MD8 (ac)	16	96–120	109	7.5
LV6 (ac)	16	34–42	38	2.4
LV7 (ac)	16	40–49	45	2.9
LV8 (ac)	16	49–57	54	2.1
LV9 (ac)	16	58–69	64	3.3
LTS	16	170–206	187	9.7
LTS/TL	16	54.4–75.8%	63.5%	6.7%
LTAS	12	58–72	68	3.9

(ac), acicular spine; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral; MD, middorsal; MSW-6, maximum sternal width, measured on segment 6 in this species; S, segment lengths; SW-10, standard width, always measured on segment 10; TL, trunk length.

thin, weakly developed, well-spaced with even shorter and finer tips in between.

Segment 2 consists of a complete cuticular ring, with minute ($<5 \mu\text{m}$) tubes located in subdorsal and ventrolateral positions (**Figures 3B,C, 4C,D**); tubes are not differentiated into thick proximal part and thinner distal tubular part with lateral wings, but are merely short tubular, truncate tips. Sensory spots present in middorsal, midlateral and ventromedial positions. Glandular cell outlets type 1 present in middorsal and ventromedial positions. Pachycyclus of anterior segment margin interrupted in middorsal position. Secondary pectinate fringe present near anterior segment margin of this and following segments, but usually covered by the preceding segment. Cuticular bracteate hairs lightly scattered on ventral side and more densely in dorsal and lateral areas. Pectinate fringe tips slightly longer than on preceding segment, but still very flexible; margin between tips very finely serrated.

Segment 3, and remaining segments, consists of one tergal and two sternal plates; pachycycli of anterior segment

margins with interruption in middorsal positions and around tergo-sternal and midsternal junctions. Segment with glandular cell outlets type 1, located in middorsal and ventromedial positions. On this and following seven segments, cuticular hairs arranged in two to three rows across the tergal plate, except for hairless midlateral areas, and on the lateral halves of the sternal plates; paraventral and ventromedial areas devoid of hairs. Pectinate fringe as on preceding segment.

Segment 4 with flexible acicular spine in middorsal position and pairs of glandular cell outlets type 1 located in paradorsal and ventromedial positions (**Figures 2A,B, 3B**). Cuticular hairs, and pectinate fringe of posterior margin as on preceding segment.

Segment 5 with acicular spine in middorsal position and relatively short ($10 \mu\text{m}$) tubes in lateroventral positions (**Figures 2A,B, 3C,E**); tubes are longer and more slender than those on segment 2, but without the common differentiation into thick bases and end piece with lateral wings. Pectinate fringe tips of posterior margin slightly longer; glandular cell outlets type 1, and cuticular hairs otherwise as on preceding segments.

Segment 6 with acicular spines in middorsal and lateroventral positions (**Figures 2A,B, 3E, 4E,H**). Sensory spots present in paradorsal and midlateral positions. Glandular cell outlets type 1, and pectinate fringe of posterior margin as on preceding segment.

Segment 7 with acicular spines in middorsal and lateroventral positions (**Figures 2A,B, 3E,F, 4E,H**). One pair of sensory spots located ventromedially. One specimen (out of five examined under SEM) lacked this character and one showed only one sensory spot on the right sternal plate; for some specimens examined under LM presence/absence of ventromedial sensory spots could not be confirmed. Other structures as on preceding segment.

Segment 8 with acicular spines in middorsal and lateroventral positions (**Figures 2A,B, 3E,F, 4L**). Middorsal spine long, reaching posterior part of segment 11, but never exceeding its margin (**Figure 3G**). Short tubes ($<10 \mu\text{m}$) present in lateral accessory positions (**Figures 3F, 4L**); tubes resemble those on segment 2. Sensory spots located in paradorsal positions only, hardly visible due to the presence of a papillary flap - a V-shaped structure present middorsally at the posterior part of the segment (**Figures 2A, 3E, 4F**). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Cuticular hairs on sternal plates as on preceding segment; hairs on tergal plate scarcer with hairless middorsal and paradorsal patches (**Figure 4H**). Pectinate fringe of posterior margin with shorter tips, on dorsal side much less developed in comparison to preceding segment.

Segment 9 with a pair of lateroventral spines. Rounded and very small sieve plates present in sublateral positions (**Figures 2B, 3F, 4G**). Sensory spots present in paradorsal, subdorsal, midlateral and ventrolateral positions (**Figures 2A,B, 4F,G,K,L**). Paradorsal pair difficult to detect due to the presence of a papillary middorsal flap, which however is smaller than on preceding segment (**Figure 4F**). Cuticular hair covering less dense than on preceding segment; central part of the tergal plate devoid of hairs. Pectinate fringe tips slightly shorter on lateral

TABLE 3 | Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes mamaqucha* sp. nov.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1,gco1			ss				gco1		
2	gco1,ss		tu		ss				tu	gco1,ss
3	gco1									gco1
4	ac	gco1								gco1
5	ac	gco1						tu		gco1
6	ac	gco1,ss			ss			ac		gco1
7	ac	gco1						ac		gco1,ss*
8	ac	gco1,ss					tu	ac		gco1
9		gco1,ss	ss		ss	si		ac	ss	gco1
10	gco1,gco1		ss	tu					ss	gco1
11	gco1	ss	ss		pe x3 (♂)		ltas(♀)	lts		gco1

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, glandular cell outlet type 1; ltas, lateral terminal accessory spine; lts, lateral terminal spine; si, sieve plate; ss, sensory spot (*not present in all specimens); tu, tube; (♀), female condition of sexually dimorphic characters; (♂), male condition of sexually dimorphic characters.

sides, otherwise as on preceding segment. Glandular cell outlets type 1 as on preceding segments.

Segment 10 with minute, very slender laterodorsal tubes near posterior segment margin (Figures 2A,C, 3D, 4I,J); appearance of the tubes similar in both sexes. Sensory spots present in subdorsal and ventrolateral positions. Subdorsal pair located in the middle of the segment, but in a few cases, one sensory spot is shifted posteriorly to a position very close to posterior segment margin. Glandular cell outlets type 1 present as two middorsal ones and one pair in ventromedial position. Cuticular hairs scarcer than on preceding segment. Anterior part of the tergal plate devoid of hairs; hairs on the sternal plates short and present mostly on the lateral halves and near posterior segment margin. Margins of the sternal plates extend midventrally (Figure 4K). Pectinate fringe with very short tips.

Segment 11 with a pair of long lateral terminal spines (Figures 2A,B, 3A). Females with strong, stout lateral terminal accessory spines (Figures 2A,B, 3A,D). Males with three pairs of penile spines; median penile spine stouter than dorsal and ventral ones, but all three pairs generally stout and rigid, gradually tapering in distal 1/4 (Figures 2C,D, 3G, 4I). Sensory spots present in paradorsal and subdorsal positions. The latter ones located at the posterior margin of the tergal extensions (Figure 4J). One middorsal glandular cell outlet type 1 present. Tergal extensions short and rounded (Figures 2, 3D,G). The posterior margin of the sternal plates also rounded, not exceeding beyond, but nearly as long as tergal extensions. Pectinate fringe of posterior margin with short tips, except in lateral positions where longer and more flexible fringe tips are present. The segment completely devoid of cuticular hairs, but has a relatively dense covering of hair-like extensions in the mid- and paradorsal positions, as well as small patches present in paraventral and ventromedial areas.

Differential Diagnosis

The spine and tube distribution in the middorsal and lateroventral series of *E. mamaqucha* sp. nov., with middorsal spines on segments 4 to 8, and tubes/spines in lateroventral

positions of segments 5 to 9 is the most common pattern observed among species of *Echinoderes* and is shared by 44 congeners (Yamasaki et al., 2020). However, when we combine these characters with the presence of subdorsal and ventrolateral tubes on segment 2 we shorten the list to only 3 species, i.e., *E. adrianovi* Herranz et al. (2014), *E. levanderi* Karling (1954), *E. kanni* Thormar and Sørensen (2010) (Karling, 1954; Thormar and Sørensen, 2010; Herranz et al., 2014; Sørensen, 2018). Despite the coincidence of spine/tube formula *E. mamaqucha* sp. nov. can still be easily distinguished from the abovementioned species based on other traits, e.g., very short tubules, dimensions of acicular spines, shape of tergal extension, and general appearance of primary pectinate fringe. *Echinoderes levanderi* cannot in any way be confused with *E. mamaqucha* sp. nov. since the morphometrics of both species differ significantly. *Echinoderes levanderi* is conspicuously larger, has markedly longer lateral terminal spines, and consequently, shows a larger proportion of lateral terminal spine to trunk length (90.5%) than *E. mamaqucha* sp. nov. (63.5%). Most importantly, however, *E. levanderi* possesses sublateral tubes on segments 5 and 8, very characteristic large sieve plates, pointed tergal extension and extremely well-developed pectinate fringes with very long tips throughout the body (Sørensen, 2018). *Echinoderes mamaqucha* sp. nov. is more similar to *E. kanni* and *E. adrianovi*, and shares the presence of lateral accessory tubes on segment 8, dorsal tubes on segment 10 and the absence of glandular cell outlet types 2 (Thormar and Sørensen, 2010; Herranz et al., 2014). Nevertheless, both species can be distinguished from *E. mamaqucha* sp. nov. by their markedly longer (up to 2–4 times) tubes, much shorter and thinner lateral accessory terminal spines, and pointed tergal extensions (Thormar and Sørensen, 2010; Herranz et al., 2014; Yamasaki et al., 2019). Both species also have very prominent cuticular perforation sites which are missing in *E. mamaqucha* sp. nov.

Interestingly, *E. mamaqucha* sp. nov. shows a much closer general resemblance with *E. bathyalis* Yamasaki et al. (2018a,b) and *E. dubiosus* Sørensen et al. (2018). Both are deep-water

species, described from East Atlantic (> 2500 m water depth) and North-Eastern Pacific (> 3500 m water depth), respectively (Sørensen et al., 2018; Yamasaki et al., 2018b). *Echinoderes mamaqucha* sp. nov. and these two species share identical spine patterns and are characterized by having a long middorsal spine on segment 8 and long lateroventral spines on segment 9. The spines easily reach and even extend beyond the posterior margin of segment 10. However, in *E. mamaqucha* sp. nov. none of them extends beyond the posterior margin of segment 11, whereas in the two latter species the middorsal spine on segment 8 and lateroventral spines on segment 9 always extent beyond the terminal segment (Sørensen et al., 2018; Yamasaki et al., 2018a,b). *Echinoderes mamaqucha* sp. nov. also resemble the two species in terms of trunk shape and length, and in possessing short tergal extension. Nevertheless, the posterior edge of the tergal plate is more pointed in *E. bathyalis* and *E. dubiosus*. In addition, *E. mamaqucha* sp. nov. has uncommon middorsal structures on segments 8 and 9 that resemble those reported for the first time from *E. dubiosus* and described as papillary flap (Sørensen et al., 2018). This trait is present on segment 9 only in *E. dubiosus*, but its similarity with the structures found on segments 8 and 9 in *E. mamaqucha* sp. nov. is striking. Sørensen et al. (2018) described the structure as “papillary flap or tuft of papillae, flanked by a pair of paradorsal sensory spots,” which is exactly what can be observed for *E. mamaqucha* sp. nov. Furthermore, similar to *E. dubiosus*, *E. mamaqucha* has laterodorsal tubes on segment 10 and lateral tubes on segment 8. In the latter species, tubes are located in lateral accessory position, whereas they are sublateral in *E. dubiosus*. The most striking difference between *E. mamaqucha* sp. nov. and two other species is, however, the tube arrangement on segment 2. While *E. mamaqucha* sp. nov. is characterized by the presence of subdorsal and ventrolateral tubes on this segment, both *E. dubiosus* and *E. bathyalis* lack this character, and have instead one pair of glandular cell outlet type 2 in midlateral position. Even though the tubes in the new species are extremely short and sometimes difficult to visualize in LM, and that the attachments of tubes might sometimes resemble glandular cell outlets type 2, the structures still appear in different positions. Therefore, presence of tubes on segment 2 makes *E. mamaqucha* sp. nov. easily distinguishable from its two other deep-sea, and potentially closely related, congeners.

Other Species of *Echinoderes*

Besides *E. mamaqucha* sp. nov. five additional species of *Echinoderes*, represented by one specimen each, were identified in the investigated material. One specimen was identified as *Echinoderes juliae* Sørensen et al. (2018) and one as *Echinoderes pterus* Yamasaki et al. (2018a,b), whereas the three remaining ones could not be identified with certainty. All three unidentified species share several characters with already described species, but they also showed character traits that made exact identification uncertain. Although they might represent undescribed species, formal descriptions will not be provided since all specimens occurred only as singletons.

Echinoderes juliae Sørensen et al. (2018) (Figure 5 and Table 4)

Material examined: adult female, collected on March 6, 2018, at station 1, at 2560 m depth, on abyssal plain, east of the Atacama Trench (23°49'S 70°50'W) (Figure 1 and Table 1), mounted in Fluoromount-G, deposited at the Natural History Museum of Denmark, under catalog number NHMD-872652.

Brief Description

Echinoderes with middorsal spines on segments 4 to 8 and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral position on segment 5 only. Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, in sublateral positions on segments 3, 4 and 8, and in midlateral positions on segment 5 (Figures 5B–D). Tergal extensions conspicuous long and slender, with long, flexible tips (Figure 5E).

Remarks

Echinoderes juliae belongs to one of the deep-sea species originally found on the abyssal plain off Oregon and along the continental rise off California, the Northeast Pacific at 2702 to 3679 m depth (Sørensen et al., 2018). Despite significant geographical distance (ca. 7000 km) between the type locality and the Atacama Trench region, the morphology and morphometrics of the examined specimen are completely in line with the original description of *E. juliae* in Sørensen et al. (2018) (Figure 5 and Table 4). Differences were detected neither in sensory spots positions nor in glandular cell outlets types 1 and 2.

Echinoderes pterus Yamasaki et al. (2018a,b) (Figure 6)

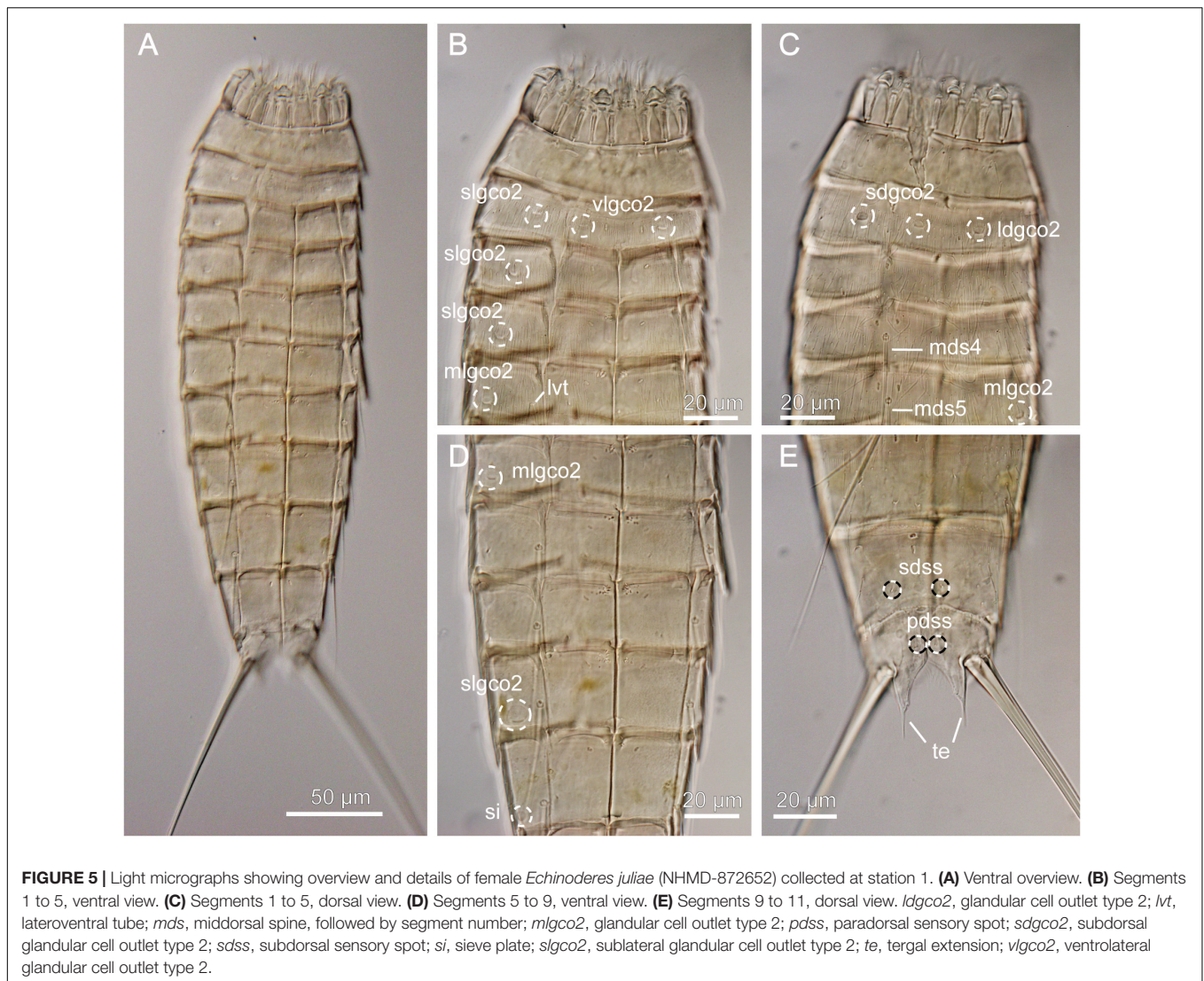
Material examined: adult female, collected on March 28, 2018, at station 9, at 4050 m depth, on abyssal plain, east of the Atacama Trench (20°20'S 70°59'W) (Figure 1 and Table 1), mounted in aluminum stub for SEM and stored in the personal collection of MVS.

Brief Description

Echinoderes with middorsal spines on segments 4 to 8 and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral position on segment 5 and in laterodorsal position on segment 10. Characteristic tufts of long hairs present in laterodorsal positions on segment 9. Glandular cell outlets type 2 absent.

Remarks

Echinoderes pterus is a species with a wide geographic distribution, ranging from the high Arctic, the North Atlantic, and into the Mediterranean Sea (Yamasaki et al., 2018a), and it has also been reported to show a wide bathymetric distribution, from 675 to 4403 m. Besides having this unusually wide range, *E. pterus* possesses a set of traits that easily distinguishes it from other congeners. The most characteristic is the presence of tufts of hairs on segment 9 - a structure unique for *E. pterus*. The second feature is the conspicuously thick and long lateroventral



spines on segment 9, however this character is observed only in the male representatives of the Arctic and North Atlantic populations (Yamasaki et al., 2018a). In the examined material we found only one female specimen, thus lateroventral spines on segment 9 could not be used as a diagnostic character. Exact morphometric details of our specimen are also unavailable because it was mounted for SEM. Nevertheless, the examined specimen possesses the diagnostic key features of *E. pterus*, i.e., the spine and tube pattern and the presence of the tufts of hairs on segment 9 (Figures 6D,G). Moreover, we were able to confirm the presence of almost all sensory spots, according to the original description provided by Yamasaki et al. (2018a); the only exception were sensory spots in paraventral positions on segment 8 and in subdorsal positions on segment 10 that could not be observed due to the mounting position of the examined specimen. In addition to this, our specimen, similar to *E. pterus*, has long, rather thin cuticular hairs distributed along the body (except segment 1), and a primary pectinate fringe with long, thin tips, characteristically curved in the paraventral

sectors of segment 1 and 2 (Figure 6, see also Figure 6C in Yamasaki et al., 2018a). Segment 1 is completely hairless, except for hairs associated with the relatively large sensory spots present in subdorsal and laterodorsal positions (Figures 6A,B,E,F), which is also characteristic for the type specimens of *E. pterus*. Therefore, the identity of the examined specimens seems to be unquestionable.

***Echinoderes* sp. 1 (Figure 7 and Table 4)**

Material examined: one female, collected on March 8, 2018, at station 6, at 7720 m depth in the Atacama Trench (24°16'S 71°25'W) (Figure 1 and Table 1), mounted in Fluoromount-G, deposited at the Natural History Museum of Denmark, under catalog number NHMD-872653.

Brief Description

Echinoderes with middorsal spines on segments 6 and 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in ventrolateral positions on segment 2, lateroventral

TABLE 4 | Measurements from light microscopy of *Echinoderes* species from the Atacama Trench with comparison of measurements for the closely related species.

Character	<i>E. juliae</i> present study	<i>E. juliae</i> Sørensen et al., 2018	<i>Echinoderes</i> sp. 1	<i>E. ultraabyssalis</i> Adrianov and Maiorova, 2019	<i>Echinoderes</i> sp. 2	<i>E. dubiosus</i> Sørensen et al., 2018	<i>Echinoderes</i> sp. 3	<i>E. hakaensis</i> Herranz et al., 2018
TL	300	285–327	257	255–340	278	238–281	211	266–382
MSW	56	51–54	59	53–60	60	60–70	47	62
MSW/TL	18.7%	15.6–18.6%	23.0%	16–22%	21.7%	22–25%	22.3%	16–23%
SW-10	44	41–47	46	42–49	51	51–57	39	46–47
SW-10/TL	14.7%	12.8–15.4%	17.9%	13–17%	18.6%	19–22%	18.5%	12–17%
MD4 (ac)	48	31–44			51	30–52	55	40
MD5 (ac)	55	42–56			56	41–78		
MD6 (ac)	broken	59–70	59	42–51	69	64–87	85	60
MD7 (ac)	80	67–78			113	68–93		
MD8 (ac)	97	71–98	70	65–76	193	96–136	81	75–80
LV6 (ac)	47	33–43	35	31–40	45	28–56	26	30–31
LV7 (ac)	50	41–48	39	38–42	58	32–68	30	30–34
LV8 (ac)	55	44–61	45	39–49	74	39–91	30	25–34
LV9 (ac)	62	40–60	46	47–60	94	79–120	30	27–33
LTS	222	205–248	234	181–205	337	186–323	145	128
LTS/TL	74.0%	68.8–78.8%	91.1%	59–73%	121%	75–118%	69%	48–33%
LTAS	126	128–133	50	42–47	70	61–78	49	35–38

(ac), acicular spine; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral; MD, middorsal; MSW, maximum sternal width; S, segment lengths; SW-10, standard width, always measured on segment 10; TL, trunk length.

positions on segment 5, lateral accessory positions on segment 8 and laterodorsal positions on segments 9 and 10.

Adults with head, neck and eleven trunk segments (Figures 7A,D). Overview of measures and dimensions are given in Table 4.

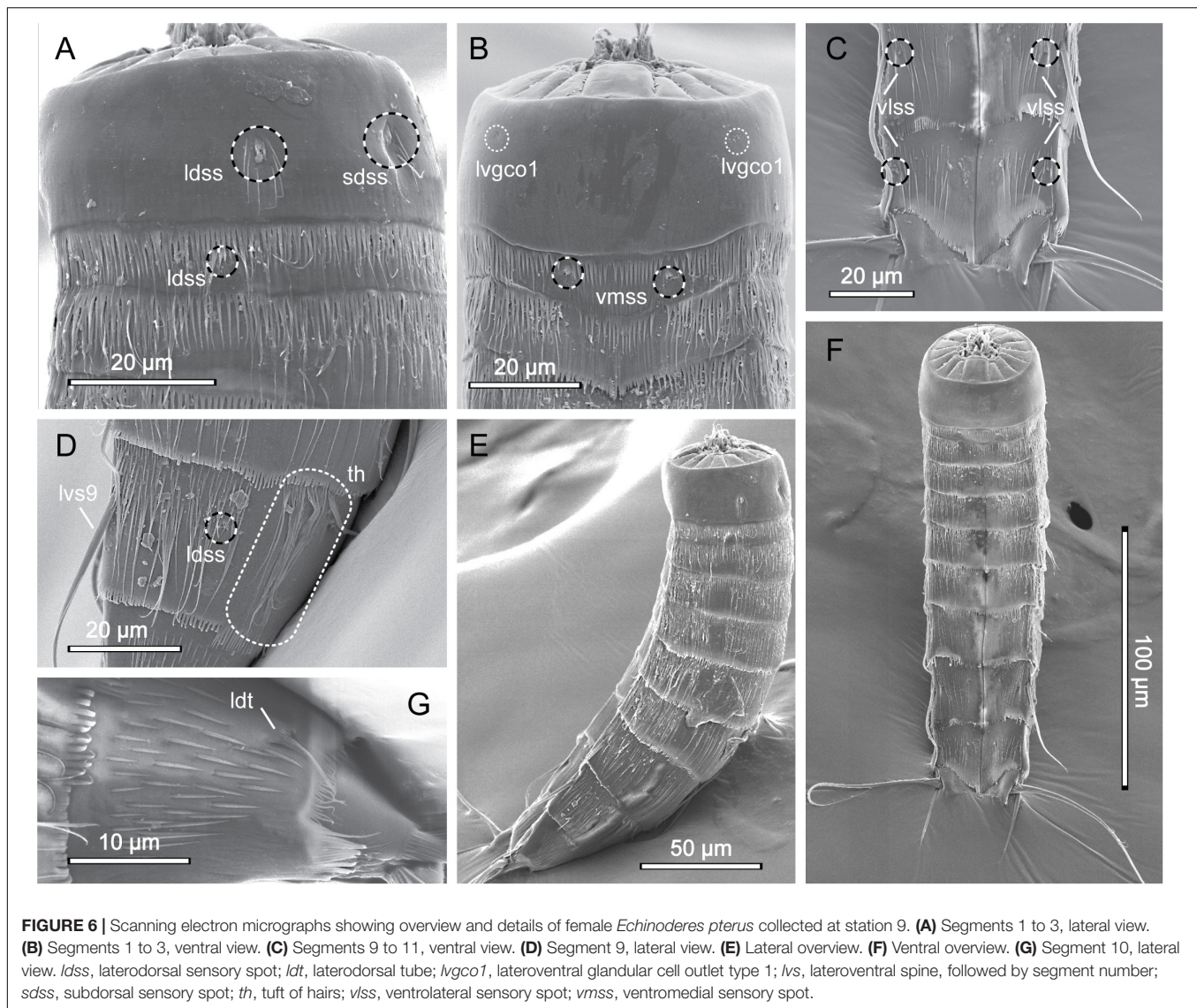
Segments 1 and 2 composed of complete cuticular rings. Segment 1 with glandular cell outlet type 1 in middorsal position and sensory spots in subdorsal and ventrolateral positions (Figure 7C). Posterior margin of this and following nine segments with primary pectinate fringe. Segment 2 with ventrolateral tubes and pair of ventromedial glandular cell outlets type 1 (Figure 7B). No structures observed on the tergal plate. Cuticular hairs on both segments relatively long, distributed around the segments, but covering only the posterior parts. Segments 3 to 11 consist of one tergal and two sternal plates. Pachycycli of anterior segments margins with clear interruptions in middorsal positions and around tergo-sternal and midsternal junctions (Figures 7A,D). Segments 3 and 4 with ventromedial glandular cell outlet type 1 only; no sensory spots or other traits observed. Segment 5 with lateroventral tube, a pair of sensory spots located midlaterally, and ventromedial glandular cell outlets type 1; similar outlets present at following four segments as well (Figure 7E). Segment 6 with middorsal acicular spine, lateroventral spines, paradorsal, midlateral and ventromedial sensory spots and glandular cell outlets type 1 in paradorsal position (Figures 7D,E). Segment 7 with lateroventral spines, pair of paradorsal and midlateral sensory spots and paradorsal glandular cell outlets type 1 present. Segment 8 with spines in middorsal and lateroventral positions, lateral accessory tubes, paradorsal sensory spots and paradorsal glandular cell outlets type 1 (Figures 7D,E). Segment 9 with lateroventral spines, distinct, long laterodorsal tubes and three pairs of

sensory spots, located in paradorsal, subdorsal and ventrolateral positions; small sieve plate located in lateral accessory positions (Figure 7F). Segment 10 with laterodorsal tubes, sensory spot and two glandular cell outlets type 1 located middorsally, and a pair of sensory spots in ventrolateral position. Segment 11 with a pair of very long lateral terminal spines (Figure 7A), nearly reaching trunk length (Table 4). Female with relatively strong and long lateral terminal accessory spines. Sensory spots present in paradorsal positions. A protuberance-like structure emerges between segments 10 and 11 in middorsal position (Figure 7F).

Remarks

The spine pattern with middorsal acicular spines on segment 6 and 8 is extremely rare among *Echinoderes* species. This trait is shared only with three species, i.e., *E. daenerysae* Grzelak and Sørensen (2018) in Grzelak and Sørensen (2018), *E. hviidarum* Sørensen et al. (2018) and *E. ultraabyssalis* Adrianov and Maiorova (2019) (Grzelak and Sørensen, 2018; Sørensen et al., 2018; Adrianov and Maiorova, 2019). The latter two are typical deep-water species, described from the Northeast Pacific (ca. 2700 m water depth) and Northwest Pacific (< 9000 m water depth), respectively, while *E. daenerysae* is known from shallower waters of the Arctic Ocean (100–250 m water depth).

A second very rare feature of *Echinoderes* sp. 1 is the presence of laterodorsal tubes on segment 9. Interestingly, all three abovementioned species have laterodorsal tubes on this segment, which suggests that these four species might be closely related. The only other species with tubes in this position on the tergal plate is *Echinoderes belenae* Pardos et al. (2016), but this species cannot in any way be confused with *Echinoderes* sp. 1 due to the presence of 3 middorsal spines, on segment 4, 6 and 8,



numerous tubes in various positions and short lateral terminal spines (Pardos et al., 2016).

Echinoderes sp. 1 shares different features with *E. daenerysae*, *E. hviidarum* and *E. ultraabyssalis*. These include the relatively small body size (<300 μm), presence of tubes in lateroventral positions on segment 5 and in lateral accessory positions on segment 8, as well as long lateral terminal spines and absence of glandular cell outlet type 2. *Echinoderes* sp. 1 furthermore shares the presence of a middorsal protuberance between segments 10 and 11 with the latter two species. Nevertheless, *E. hviidarum* is easily distinguished from *Echinoderes* sp. 1 by the absence of tubes on segment 2. In contrast, *E. daenerysae* and *Echinoderes* sp. 1 share the presence of ventrolateral tubes on segment 2, whereas only *E. daenerysae* has tubes in laterodorsal positions also. Among the three species, *E. ultraabyssalis* appears to be morphologically closest to *Echinoderes* sp. 1. This is the deepest kinorhynch species described so far, and similar to *Echinoderes* sp. 1, it possesses one pair of tubes, located ventrolaterally

on segment 2. Morphometrics of both species also show great resemblance (Table 4), with the exception of the proportions of the lateral terminal spines vs. trunk length. *Echinoderes* sp. 1 has longer lateral terminal spines, nearly as long as the trunk length (LTS/TL = 91%), while the lateral terminal spines in *E. ultraabyssalis* are no longer than 2/3 of the trunk length (mean LTS/TL = 59%). It appears that also the arrangement and number of sensory spots show some differences between these two species. Although only one specimen was available for examination and we cannot exclude the possibility that some sensory spots were missed, we can at least confirm their presence in subdorsal positions on segment 11 and in midlateral positions on segments 5 and 6. None of these were described for *E. ultraabyssalis*. However, the key character to distinguish *Echinoderes* sp. 1 from *E. ultraabyssalis* is the presence of laterodorsal tubes on segment 10. Although the presence of such tubes can be difficult to visualize with LM, the tubes are well visible in *Echinoderes* sp. 1, while their absence in *E. ultraabyssalis* was confirmed

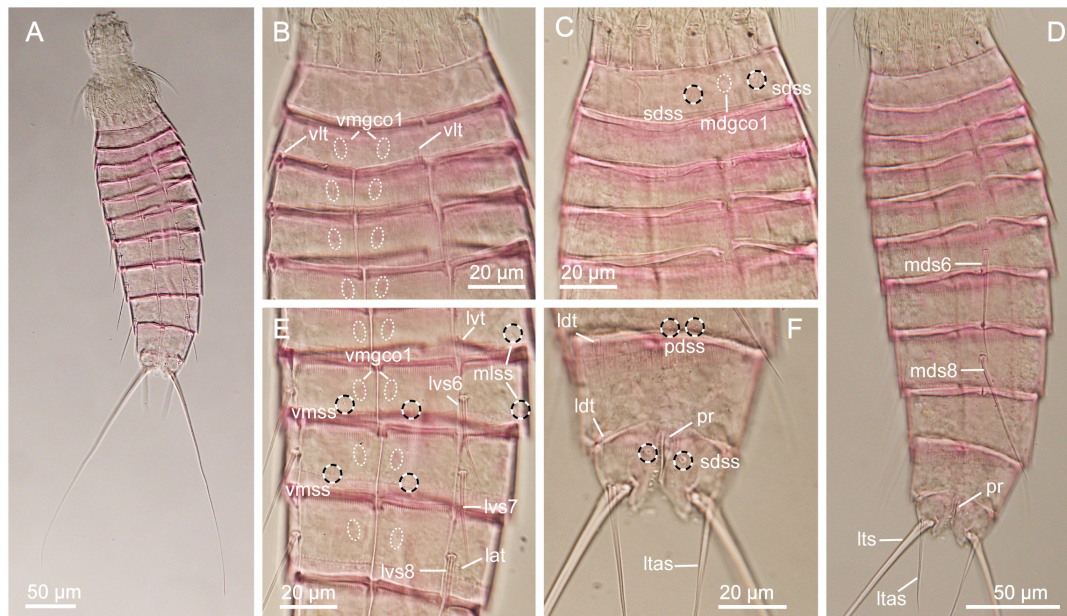


FIGURE 7 | Light micrographs showing overview and details of female *Echinoderes* sp. 1 (NHMD-872653) collected at station 6. **(A)** Ventral overview. **(B)** Segments 1 to 5, ventral view. **(C)** Segments 1 to 5, dorsal view. **(D)** Dorsal overview. **(E)** Segments 5 to 8, ventral view. **(F)** Segments 9 to 11, dorsal view. *lat*, lateral accessory tube; *ldt*, laterodorsal tube; *ltas*, lateral terminal accessory spine; *lts*, lateral terminal spine; *lvs*, lateroventral spine, followed by segment number; *lvt*, lateroventral tube; *mdgco1*, middorsal glandular cell outlet type 1; *mds*, middorsal spine, followed by segment number; *mlss*, midlateral sensory spot; *pdss*, paradorsal sensory spot; *pr*, protuberance; *sdss*, subdorsal sensory spot; *vlt*, ventrolateral tube; *vmgco1*, ventromedial glandular cell outlet type 1; *vmss*, ventromedial sensory spot.

with SEM (Adrianov and Maiorova, 2019). Therefore, we believe that, even though the differences between *Echinoderes* sp. 1 and *E. ultraabyssalis* are subtle, we should consider them as diagnostic until more material becomes available for comparison. It seems clear that the two species are closely related hadal/deep-sea trench species.

Echinoderes sp. 2 (Figure 8 and Table 4)

Material examined: one female, collected on March 20, 2018, at station 7, at 5500 m depth in the Atacama Trench (22°56'S 71°37'W) (Figure 8 and Table 1), mounted in Fluoromount-G, deposited at the Natural History Museum of Denmark, under catalog number NHMD-872654.

Brief Description

Echinoderes with middorsal spines on segments 4 to 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral positions on segment 5, lateral accessory positions on segment 8 and laterodorsal position on 10.

Adults with head, neck and eleven trunk segments (Figures 8A,D). Overview of measures and dimensions are given in Table 4.

Segments 1 and 2 composed of complete cuticular rings. Segment 1 with sensory spots in subdorsal and laterodorsal positions, two glandular cell outlets type 1 in middorsal position and pair in ventrolateral positions (Figure 8C). Posterior edge of this and following nine segments with primary pectinate fringe. Segments 2 and 3 without any conspicuous cuticular structures, except for one middorsal glandular cell outlet type 1 (Figure 8B).

Segment 4 with acicular middorsal spine; paradorsal and ventromedial glandular cell outlets types 1, present on this and following five segments (Figures 8C,F). Segment 5 with acicular spine in middorsal position and tubes in lateroventral positions (Figures 8A,C). Segment 6 with acicular spines in middorsal and lateroventral positions; sensory spots present in midlateral position. Segment 7 with acicular spines in middorsal and lateroventral positions; sensory spots present in ventromedial positions. Segment 8 with acicular spines in middorsal and lateroventral positions; middorsal spine very long, exceeding posterior part of segment 11 (Figure 8A). Tubes present in lateral accessory positions (Figure 8F). Sensory spots located in paradorsal positions only, but hardly visible due to the presence of a middorsal papillary flap on the posterior part of the segment (Figure 8E). Segment 9 with long lateroventral spines, which exceed way beyond the terminal segment (Figure 8G). Sensory spots present in paradorsal and ventrolateral positions. Papillary flap, smaller than on preceding segment, present middorsally on the posterior part of the segment (Figure 8E). Rounded, small sieve plates present in lateral accessory positions (Figure 8F). Segment 10 with well visible, relatively long laterodorsal tubes, paradorsal sensory spots and glandular cell outlets type 1 present in middorsal and ventromedial positions. Segment 11 with long lateral terminal spines. Specimen with thick lateral terminal accessory spines. Sensory spots present in subdorsal position. Two glandular cell outlets type 1 located middorsally. Tergal extensions short and pointed/triangular (Figure 8G). The posterior margins of the sternal plates rounded, much shorter than tergal extensions (Figure 8G).

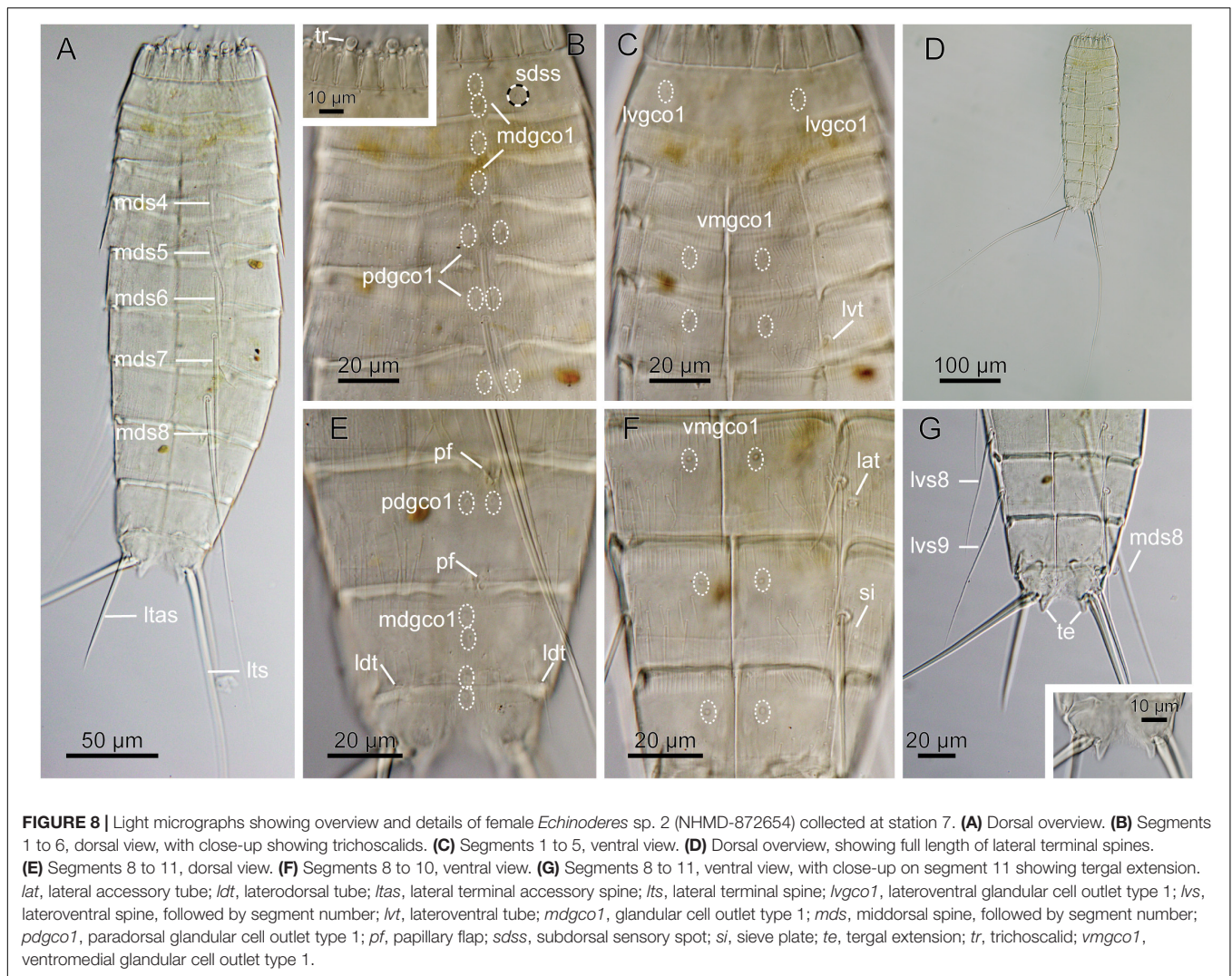


FIGURE 8 | Light micrographs showing overview and details of female *Echinoderes* sp. 2 (NHMD-872654) collected at station 7. **(A)** Dorsal overview. **(B)** Segments 1 to 6, dorsal view, with close-up showing trichoscalids. **(C)** Segments 1 to 5, ventral view. **(D)** Dorsal overview, showing full length of lateral terminal spines. **(E)** Segments 8 to 11, dorsal view, with close-up on segment 11 showing tergal extension. *lat*, lateral accessory tube; *ldt*, laterodorsal tube; *lts*, lateral terminal accessory spine; *lts*, lateral terminal spine; *lvgco1*, lateroventral glandular cell outlet type 1; *lvs*, lateroventral spine, followed by segment number; *lvt*, lateroventral tube; *mdgco1*, glandular cell outlet type 1; *mds*, middorsal spine, followed by segment number; *pdgco1*, paradorsal glandular cell outlet type 1; *pf*, papillary flap; *sdss*, subdorsal sensory spot; *si*, sieve plate; *te*, tergal extension; *tr*, trichoscalid; *vmgco1*, ventromedial glandular cell outlet type 1.

Remarks

The spine and tube pattern of *Echinoderes* sp. 2, with presence of middorsal spines on segments 4 to 8, tubes/spines in lateroventral positions of segments 5 to 8, tubes in lateral accessory position on segment 8 and in laterodorsal position on segment 10, is shared with 7 species (Yamasaki et al., 2020), i.e., *E. adrianovi*, *Echinoderes barbadensis* Cepeda et al. (2019a), *Echinoderes dujardini* Claparède (1863), *Echinoderes gerardi* Higgins (1978), *Echinoderes muricatus* Pardos et al. (2016), *Echinoderes parrai* G^aOrdóñez et al. (2008), *Echinoderes* sp. 2 in Yamasaki et al. (2018b) (Higgins, 1978; G^aOrdóñez et al., 2008; Herranz et al., 2014; Pardos et al., 2016; Yamasaki et al., 2018b; Cepeda et al., 2019a; Sørensen et al., 2020). Nevertheless, *Echinoderes* sp. 2 is unique among the congeners by its absence of tubes or glandular cell outlets type 2 on segment 2. If we do not consider the presence of tubes on segment 8 in the comparison, which sometimes might be difficult to see with LM, *Echinoderes* sp. 2 may resemble three other species, i.e., *Echinoderes kaempfae*, *E. pterus* and *Echinoderes*

stockmani Adrianov (1999) in Adrianov and Malakhov (1999) (Adrianov and Malakhov, 1999; Yamasaki et al., 2018a, 2019). Nevertheless, all species can easily be discriminated from *Echinoderes* sp. 2. *Echinoderes pterus* can be distinguished by the presence of the tufts of hairs on segment 9 - a structure unique for this species (see discussion above). *Echinoderes stockmani* possesses additional pairs of tubes on segments 7 and 9, in laterodorsal and subdorsal positions, respectively. Among the abovementioned species, *E. kaempfae* appears to be most similar to *Echinoderes* sp. 2. *Echinoderes kaempfae* is a deep-sea species, described from 3110 m depth at the foot of Senghor Seamount in the Northeast Atlantic (Yamasaki et al., 2019). Next to the spines and tubes pattern (with exception of presence/absence of lateral accessory tube on segment 8), *Echinoderes* sp. 2 and *E. kaempfae* share the presence of long and thin terminal spines and general appearance/shape of the trunk. However, the two species are conspicuously different in tergal extension shape, which appears significantly longer and more pointed in *E. kaempfae*. The latter species also

have shorter spines than *Echinoderes* sp. 2, both on dorsal and ventral sides.

Echinoderes sp. 2 shows the closest resemblance to the deep-sea species *E. dubiosus*. Although the latter possess glandular cell outlets type 2 on segment 2 that are missing in *Echinoderes* sp. 2, the two species are conspicuously similar. Both share the same spines patterns on the dorsal and ventral side, the presence of laterodorsal tubes on segment 10, presence of papillary flaps - middorsal structures previously described for only *E. dubiosus* and *E. mamaqucha* sp. nov. - and very similar sensory spot distribution patterns. Moreover, both species show great similarity in terms of morphometrics (Table 4). Very long spines, especially lateral terminal spines that are equal or sometimes longer than trunk length, characterize both species (Table 4). However, the middorsal spines on segments 7 and 8 are even longer in *Echinoderes* sp. 2 compared to those in *E. dubiosus*. Especially the middorsal spine of segment 8 extends well beyond the terminal segment in *Echinoderes* sp. 2, opposite to *E. dubiosus* where it only reaches segment 11 (Sørensen et al., 2018). *Echinoderes* sp. 2 also has tubes in lateral accessory positions on segment 8, which differs from *E. dubiosus* that very clearly has its tubes in sublateral positions, leaving a conspicuously larger gap between the tubes and the lateroventral spines. Therefore, based on all abovementioned differences we assume the examined specimen represents an undescribed species. However, since only a single specimen is available, it is too premature to provide a formal description.

***Echinoderes* sp. 3 (Figure 9 and Table 4)**

Material examined: one female, collected on March 6, 2018, at station 1, at 2560 m depth on abyssal plain, east of the Atacama Trench (23°49'S 70°50'W) (Figure 1 and Table 1), mounted in Fluoromount-G, deposited at the Natural History Museum of Denmark, under catalog number NHMD-872651.

Brief Description

Echinoderes with middorsal spines on segments 4, 6, and 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, lateroventral position on segment 5, sublateral position on segment 8 and laterodorsal position on segment 10.

Adults with head, neck and eleven trunk segments (Figure 9A). Overview of measures and dimensions are given in Table 4.

Segments 1 and 2 composed of complete cuticular rings. Segment 1 with sensory spots in subdorsal and lateroventral positions, glandular cell outlet type 1 in middorsal position and pair located ventrolaterally (Figures 9B,C). Posterior margin of this and following nine segments with primary pectinate fringe, with well-developed, thin and long fringe tips (Figures 9D-F). Segment 2 with subdorsal, laterodorsal, sublateral and ventrolateral tubes, single sensory spot and glandular cell outlet type 1 present middorsally and paired glandular cell outlets type 1 located ventromedially (Figures 9B,C). Cuticular hairs on this and following eight segments generally abundant, long, distributed continuously around the segments, except

the ventromedial sectors of the segments. Segments 3 to 11 consist of one tergal and two sternal plates. Pachycycli of anterior segments margins with clear interruptions in middorsal positions and around tergo-sternal and midsternal junctions (Figures 9B-H). Segment 3 with subdorsal sensory spots, single glandular cell outlet type 1 in middorsal position and paired ones in ventromedial positions; ventromedial outlets present at following seven segments as well (Figures 9C,K). Segment 4 with middorsal acicular spine. Glandular cell outlet type 1 observed in paradorsal positions; no sensory spots present. Segment 5 with lateroventral tubes and single middorsal glandular cell outlet type 1. Segment 6 with middorsal acicular spine, lateroventral spines, paradorsal and ventromedial sensory spots and glandular cell outlets type 1 in paradorsal position (Figures 9D,K). Segment 7 with lateroventral spines, pair of ventromedial sensory spots and single middorsal glandular cell outlet type 1. Segment 8 with spines in middorsal and lateroventral positions, sublateral tubes, paradorsal sensory spots and paradorsal glandular cell outlets type 1 (Figures 9G,H,K). Segment 9 with lateroventral spines, two pairs of sensory spots, located in paradorsal and ventrolateral positions and paradorsal glandular cell outlets type 1; small sieve plate located in lateral accessory positions. Segment 10 with laterodorsal tubes, sensory spot and glandular cell outlet type 1 located middorsally, and pair of sensory spots in subdorsal and ventrolateral positions. Segment 11 with pair of long lateral terminal spines (Figure 9A). Female with relatively strong and long lateral terminal accessory spines (Figure 9A and Table 4). Sensory spots present in subdorsal position; two glandular cell outlets type 1 located middorsally. Tergal extensions short and pointed, with two small serrations at the posterior inner margin (Figure 9J).

Remarks

Echinoderes sp. 3 resembles *Echinoderes hakaiensis* described by Herranz et al. (2018) from 88–140 m depth at Calvert Island, British Columbia, and subsequently found at markedly greater depth, 2719 m, off the United States west coast (Herranz et al., 2018; Sørensen et al., 2018). There is no other species with acicular spines in middorsal position on segments 4, 6 and 8 and four pairs of tubes on segment 2. In addition, both species share the presence of tubes on segment 8 in sublateral position, the positions of several glandular cell outlets type 1 and sensory spots, as well as shape of tergal extensions. Nevertheless, we did not assign *Echinoderes* sp. 3 to *E. hakaiensis* because of some morphological differences between two species. Considering the wide bathymetrical and geographical distance between British Columbia and the Atacama Trench region and the fact that only a single specimen was available for investigation, we cannot be sure whether observed morphological discrepancies result solely from inter-population variations or indicate two, closely related species. The major difference between *Echinoderes* sp. 3 and *E. hakaiensis* are morphometric details. *Echinoderes* sp. 3 is markedly smaller in trunk length than *E. hakaiensis* (TL: 211 μm vs. 324 μm , respectively), but has significantly longer middorsal spines on segments 4 and 6 (MDS4: 55 μm and MDS6: 85 μm in *Echinoderes* sp. 3, whereas MDS: 40 μm and MDS: 60 μm in *E. hakaiensis*) and longer lateral terminal spines (LTS: 145 μm

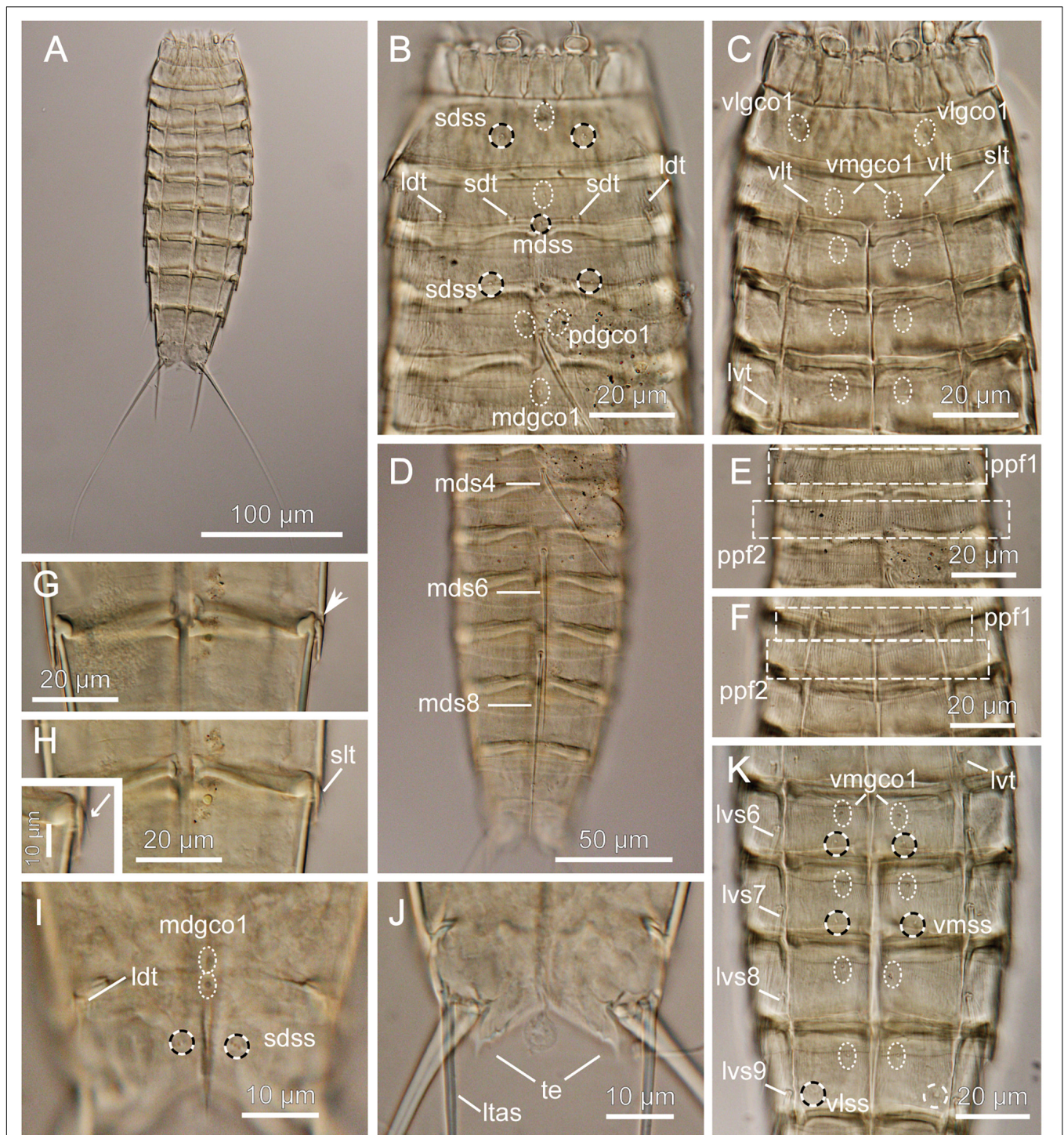


FIGURE 9 | Light micrographs showing overview and details of female *Echinoderes* sp. 3 (NHMD-872651) collected at station 1. **(A)** Ventral overview. **(B)** Segments 1 to 5, dorsal view. **(C)** Segments 1 to 5, ventral view. **(D)** Segments 4 to 11, dorsal view. **(E)** Segments 2 to 4, dorsal view. **(F)** Segments 2 to 4, ventral view. **(G)** Segments 8 to 9, ventral view. **(H)** Segments 8 to 9, ventral view with close-up showing sublateral tube. **(I)** Segments 10 to 11, dorsal view. **(J)** Segment 11, ventral view. **(K)** Segments 5 to 9, ventral view. *ldt*, laterodorsal tube; *ltas*, lateral terminal accessory spine; *lvs*, lateroventral spine, followed by segment number; *lvt*, lateroventral tube; *mdgco1*, middorsal glandular cell outlets type 1; *mds*, middorsal spine, followed by segment number; *pdgco1*, paradorsal glandular cell outlets type 1; *ppf*, primary pectinate fringe, followed by segment number; *sdss*, subdorsal sensory spot; *sdt*, subdorsal tube; *slt*, sublateral tube; *te*, tergal extension; *vlgco1*, ventrolateral glandular cell outlets type 1; *vlss*, ventrolateral sensory spot; *vlt*, ventrolateral tube; *vmgco1*, ventromedial glandular cell outlets type 1. Arrow in G shows sublateral interruption.

vs. 128 μm) (Table 4). Differences in trunk and lateral terminal spine lengths result in higher TL/LTS ratio in *Echinoderes* sp. 3 in comparison to *E. hakaiensis* (TL/LTS: 69 vs. 40%, respectively). In *Echinoderes* sp. 3 the pectinate fringe tips of the primary pectinate fringe on segments 1 and 2 are long and thin, both on the dorsal and ventral side (Figures 9E,F), whereas the pectinate fringe tips in *E. hakaiensis* are much shorter and less-developed, almost absent in the ventral sector of segment 2 (see Figure 12C in Herranz et al., 2018). Another character that makes *Echinoderes* sp. 3 differ from *E. hakaiensis* is the presence of laterodorsal tubes on segment 10 in the female. Although tubes in this position were observed in male representatives of *E. hakaiensis*, their absence in female was confirmed with SEM (Herranz et al., 2018). In the investigated specimen, the tubes are difficult to visualize, but they are certainly present (Figure 9I). Abovementioned differences leave it uncertain whether the examined specimen is identical with *E. hakaiensis*, but since only a single specimen is available, we hesitate to describe the species as a new species.

DISCUSSION

Nearly 75% of the seafloor is at abyssal and hadal depths (> 3000 m) making it the largest benthic habitat globally (Harris et al., 2014). However, our understanding of the lower-abyssal and particularly the hadal zones (> 6000 m) is still very much in its initial stage. Trench biology represents a major frontier in deep-sea studies and the fauna inhabiting these regions probably represents the least understood communities in our ocean (Blankenship-Williams and Levin, 2009). The present study provides the first overview of mud dragon species inhabiting the Atacama Trench and adjacent abyssal and bathyal depths. Our material revealed six species of *Echinoderes*. Of these, *Echinoderes mamaqucha* sp. nov. is described as a new species and morphological data of three undescribed species are given. Moreover, two already known species, i.e., *Echinoderes juliae* and *Echinoderes pterus* were recovered.

Abundance and Species Richness in Hadal Zone

It seems to be a general trend that benthic abundance decreases with increasing water depth (Rex et al., 2006; Wei et al., 2010). Nonetheless, studies conducted in hadal trenches have revealed relatively abundant benthic communities, particularly meiofauna (Danovaro et al., 2002; Schmidt and Martínez Arbizu, 2015; Leduc et al., 2016). Many hadal trenches are close to land and receive organic inputs from terrestrial and coastal sources, increasing microbial activity (Wenzhöfer et al., 2016; Glud et al., 2021) and supporting higher benthic densities than expected for greater depths (Danovaro et al., 2002; Jamieson et al., 2010). In addition, the persistent rain of particulate organic matter (POM) from the surface layers is deposited along the trench axis (von Huene and Scholl, 1991; Turnewitsch et al., 2014). Among others, the Atacama Trench underlies one of the most productive surface waters, which results in high total trench POC flux (Steward and Jamieson, 2018; Glud et al., 2021), reduced sediment grain size and exceptionally high meiofaunal abundance at hadal

depths (7800 m) (Danovaro et al., 2002). As reported by Danovaro et al. (2002), abundance of all meiofauna taxa were notably higher at hadal station in comparison with bathyal depths, and this trend also includes the kinorhynchs (0.2 ± 0.3 and 46 ± 40 ind./10 cm^2 , at 1050 and 7800 m, respectively). In our study, the abundance of kinorhynchs recorded at trench stations was not as high as reported in the previous study by Danovaro et al. (2002) (5.7 ± 2.7 ind./10 cm^2), but a clear increase in mud dragons abundance with water depth was observed (Figure 10). The highest number of individuals in the deepest station (Figure 10), is in accordance with observations for other trenches (Schmidt and Martínez Arbizu, 2015; Leduc et al., 2016). The steep slopes of the trenches create a gravity-driven downward transport and therefore elevated deposition of organic matter and intensified microbial metabolism, which support high faunal standing stocks at the greatest depth of hadal trenches (Danovaro et al., 2003; Glud et al., 2013).

Even though they are rich in terms of abundance and/or biomass, hadal benthic communities are rather poor in number of species. Moreover, a high degree of endemism is attributed to the hadal fauna as a whole and also within each trench (Wolff, 1960; Belyaev, 1989; Eustace et al., 2016), although, the selective pressures driving such picture remains unclear. Physical/geographical isolation, sufficiently different environmental conditions experienced by each trench and/or geological age of the trench habitats are considered to be major contributing factors to low species diversity and high endemism of trench bottom fauna (Jamieson et al., 2010). Interestingly, the kinorhynch community at the Atacama Trench hadal stations was dominated by a single species, namely *E. mamaqucha* sp. nov. that occurred at all six sites along the trench axis and was present almost exclusively at hadal depths (Figure 10 and Table 1). The only exception was the abyssal station at 5550 m, where a single specimen of *E. mamaqucha* sp. nov. was found. Stations at the trench floor extend across > 400 km, but the north-south alignment of the trench axis probably acts as dispersal corridor and thereby facilitates similarity among the kinorhynch fauna along a longitudinal gradient. A similar picture was obtained from an amphipod study at hadal depths in the Atacama Trench (Perrone et al., 2002), where only one undescribed species was documented. A single dominating amphipod species at hadal depths was also found in northwest Pacific trenches (Kuril-Kamchatka, Japan, Izu-Bonin, Mariana, and Philippine trenches; Kamenskaya, 1981; France, 1993) and southwest Pacific trenches (Kermadec and Tonga trenches; Blankenship et al., 2006). This could suggest that *E. mamaqucha* sp. nov. likewise represents an endemic hadal mud dragon form for the Atacama Trench. This assumption should be taken with caution though, since our knowledge of the distribution of microscopic marine animals suffers from lack of data and sampling bias (Boakes et al., 2010) and assessing true biogeographical ranges or distribution patterns is very challenging, especially for a group such as kinorhynchs.

Hadal vs. Abyssal and Bathyal Depths

It is noteworthy that the mud dragon species observed at the trench floor differed from those collected at the surrounding

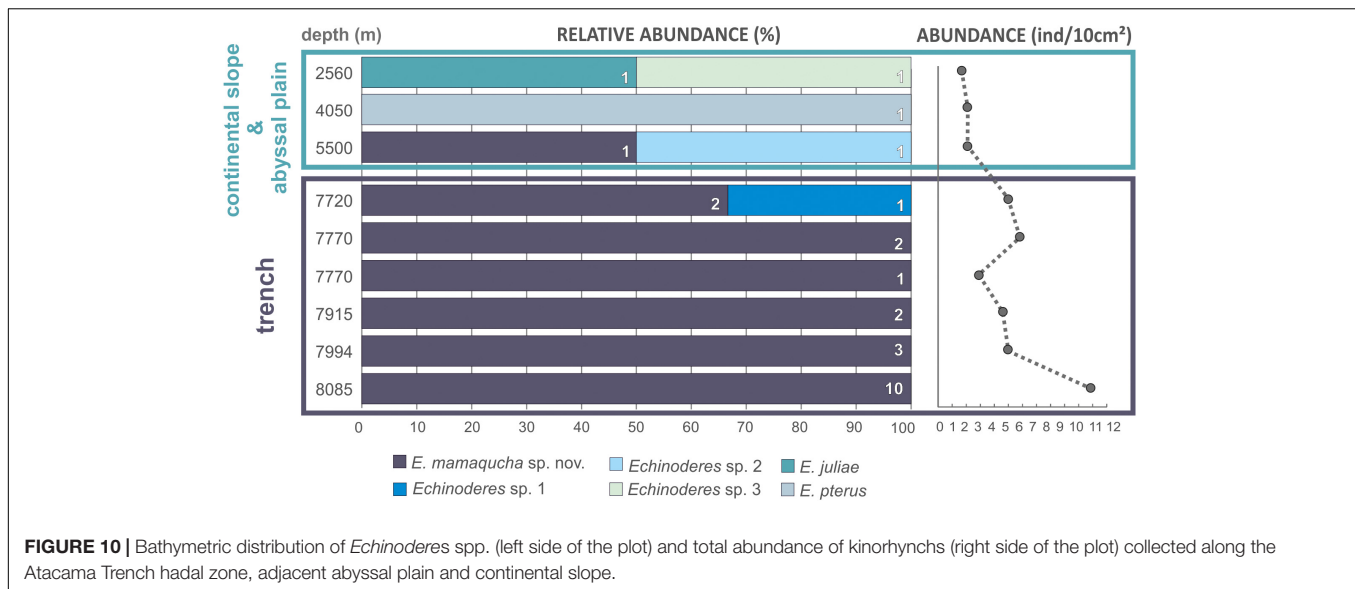


FIGURE 10 | Bathymetric distribution of *Echinoderes* spp. (left side of the plot) and total abundance of kinorhynchs (right side of the plot) collected along the Atacama Trench hadal zone, adjacent abyssal plain and continental slope.

abyssal plain and continental slope (Figure 10 and Table 1). Even though, abundance of kinorhynchs was very low and small sample size might have important implication on the assessment of kinorhynchs diversity, our results are in line with other hadal studies. It has already been documented that trenches and their adjacent abyssal plain can differ significantly in their macrobenthic (Jamieson et al., 2011; Fujii et al., 2013; Gallo et al., 2015) and meiobenthic communities (Kitahashi et al., 2013; Leduc et al., 2016; Schmidt et al., 2019), due to the combination of environmental conditions at trenches floor that are not found in any other deep-sea environment. However, these geographical and depth gradients do not act as sharp boundaries but rather as transitional zones (Jamieson et al., 2011), thus still the hadal zone can share few fauna species with abyssal communities, but less likely with bathyal ones (Eustace et al., 2016; Brandt et al., 2019). The precise depth at which this transition occurs is expected to be trench-specific (Fujii et al., 2013; Schmidt and Martínez Arbizu, 2015), and may vary within trenches. Our results seem to fit well with these previous observations, as species turnover between hadal, abyssal and bathyal depths can be clearly noted (Figure 10). Individuals of *E. mamaqucha* sp. nov. dominated at the hadal zone, sediments of abyssal stations were inhabited by *E. pterus*, *Echinoderes* sp. 2 and *E. mamaqucha* sp. nov., while *E. juliae* and *Echinoderes* sp. 3 were found at the shallower station located at the continental slope. Nevertheless, it should also be noted, that all mud dragon species of the Atacama Trench region belong to one genus *Echinoderes*. *Echinoderes* is the most common, widely distributed and species-rich mud dragon genus. However, from the currently 24 known abyssal mud dragon species, only 11 belong to *Echinoderes*, which indicates that the generic diversity of deep-sea kinorhynchs is higher than it would seem to be, given our results. On the other hand, a very extensive study performed on the northeastern Pacific clearly showed that the deep-sea kinorhynch fauna in this region is dominated by echinoderids (Sørensen et al., 2018). It is therefore

difficult to predict whether the observed diversity pattern, with representatives of only one mud dragon genus, reflects limitation in the data or low diversified kinorhynch community, distinctive for the Atacama Trench region. A lack of characterization of Kinorhyncha communities across the Pacific abyssal plain makes it difficult to assess the geographic distribution of deep-sea forms.

Community Composition and Comparison With Other Deep-Sea Species

What should be highlighted though, is that the newly described species (*E. mamaqucha* sp. nov.) as well as the other three potentially new species (*Echinoderes* sp. 1, *Echinoderes* sp. 2, and *Echinoderes* sp. 3) show a very close resemblance to other deep-water species of *Echinoderes*. *Echinoderes mamaqucha* sp. nov. and *Echinoderes* sp. 2 show a close similarity to *E. dubiosus* that was described from the North-Eastern Pacific (> 3500 m water depth) (Sørensen et al., 2018) and *E. bathyalis* described from the East Atlantic (> 2500 m water depth) (Yamasaki et al., 2018b). The second striking morphological similarity can be noted between the specimen of *Echinoderes* sp. 1 found at 7720 m and *E. ultraabyssalis* described from the deepest depression of the Kuril-Kamchatka Trench (> 9000 m; Adrianov and Maiorova, 2019). In other words, even though each trench and surrounding abyssal plains seem to host a unique fauna at the species level, there is still a close phylogenetic relationship between the species at these extreme depths. This either suggests a certain gene flow between these deep habitats, or that they originally were invaded by a few species that subsequently speciated further. The potential of gene flow of pan-oceanic scale has been already documented for some benthic deep-sea taxa (Eustace et al., 2016; LaBella et al., 2017), including meiofaunal organisms (Pawlowski et al., 2007; Bik et al., 2010;

Fontaneto, 2019 and references therein). Hence, similarities between geographically distinct species is highly possible, as a result of incomplete lineage sorting following the historical tectonic movements (e.g., formation of the Isthmus of Panama) or dispersal over large distance, e.g., through thermohaline circulation (Pawlowski et al., 2007; Ptatscheck and Traunspurger, 2020). The latter may seem even more likely, as in the material from abyssal station at 4050 m we found *E. pterus*. This species was already noted at several locations in the Arctic Ocean, in the North Atlantic and the Mediterranean, from the continental shelf to the deep-sea floor and on seamounts (Yamasaki et al., 2018a, 2019). A similar example is the presence of *E. juliae* and *Echinoderes* sp. 3 in the sediments collected from continental slope station at 2560 m. *Echinoderes juliae* is known from the abyssal plain and continental rise off California (Sørensen et al., 2018) and despite significant geographical distance (ca. 7000 km) we found considerable consistency of morphological characters between *E. juliae* at its type locality and the individual from the Atacama Trench region. In contrast, *Echinoderes* sp. 3 shows close morphological resemblance to *E. hakaiensis* – a species described from British Columbia (Herranz et al., 2018) and later found in the deep-water off California (Sørensen et al., 2018). These findings support the previous suggestions about the capability of deep-sea kinorhynch species to disperse over great distances (Neuhaus and Sørensen, 2013; Sørensen et al., 2018; Yamasaki et al., 2018a, 2019). Yet, the distribution process, the ongoing dispersal directions and migration routes are unknown.

Hadal trenches remain among the least sampled deep-sea habitats, although their unusual isolation and distribution offer exceptional opportunities to test many ecological and evolutionary theories (Blankenship-Williams and Levin, 2009). Therefore, we hope that this first evaluation of mud dragon diversity in the Atacama Trench add to other hadal studies providing new information about species diversity, which at last will enhance our understanding of biodiversity patterns in the deep-sea.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author/s.

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AUTHOR CONTRIBUTIONS

KG acquired the funding for taxonomic studies, performed morphological examinations and taxonomic work, and prepared the original draft and figures. DZ conceived the general idea of the study and acquired the funding for the deep-sea cruise. MSh processed meiofauna samples. MSø conceived the general idea of the taxonomic study, supervised morphological and taxonomic studies, and manuscript writing. All authors proof-read the manuscript prior to submission, contributed to the final version and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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