

Research Article

Cite this article: González-Casarrubios A, Sánchez N, Cepeda D, Pardos F (2024). *Meristoderes zmaj* sp. n., a new species of Kinorhyncha (Cyclorhagida: Echinoderidae) from the Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom* **104**, e1, 1–10. <https://doi.org/10.1017/S0025315423000875>

Received: 7 July 2023

Revised: 23 October 2023

Accepted: 3 November 2023

Keywords:

Istrian Peninsula; kinorhynchs; Mediterranean Sea; meiofauna; taxonomy


Corresponding author:

Alberto González-Casarrubios;
Email: albert23@ucm.es

© The Author(s), 2024. Published by Cambridge University Press on behalf of Marine Biological Association of the United Kingdom. This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial licence (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original article is properly cited. The written permission of Cambridge University Press must be obtained prior to any commercial use.



Meristoderes zmaj sp. n., a new species of Kinorhyncha (Cyclorhagida: Echinoderidae) from the Adriatic Sea

Alberto González-Casarrubios¹ , Nuria Sánchez¹, Diego Cepeda²
and Fernando Pardos¹

¹Faculty of Biological Sciences, Department of Biodiversity, Ecology and Evolution, Universidad Complutense de Madrid (UCM), 28040 Madrid, Spain and ²Faculty of Sciences, Department of Biology, Universidad Autónoma de Madrid (UAM), 28049 Madrid, Spain

Abstract

A new species of the cyclorhagid genus *Meristoderes* is described. *Meristoderes zmaj* sp. n. is distinguished from its congeners by its unique arrangement of spines and tubes. It possesses acicular spines on segments 4, 6 and 8 in middorsal position and on segments 6–9 in lateroventral position; and tubes on segment 2 in subdorsal, midlateral and ventrolateral position, on segment 5 in lateroventral position and on segment 10 in laterodorsal position. With the formal description of *M. zmaj* sp. n., the number of species within the genus is increased to 10. In addition, the appearance of a new species and its accompanying fauna within the North-Eastern Adriatic Sea fauna, extensively studied by Kinorhyncha taxonomists, is discussed.

Introduction

The Mediterranean Sea has historically been one of the best-known marine areas in terms of Kinorhyncha fauna (Neuhaus, 2013). Since the original works of Karl Zelinka, one of the most important researchers in the phylum during the late 19th and early 20th century (Zelinka, 1928), numerous taxonomic contributions have focused on describing the mud dragons inhabiting the Mediterranean waters (e.g. Higgins, 1978; Sánchez *et al.*, 2011; Dal Zotto, 2015). However, it is not uncommon to find new Mediterranean kinorhynchs still in recent days, especially in less explored regions (e.g. Yildiz *et al.*, 2016; Sánchez *et al.*, 2018; Yamasaki *et al.*, 2018; Dal Zotto *et al.*, 2019).

During a survey off the coast of Rovinj (Croatia, northern Adriatic Sea), a yet undescribed species of *Meristoderes* Herranz *et al.*, 2012 was discovered in shallow waters. This echinoderid genus is characterised by partial cuticular divisions in lateroventral or ventrolateral position (corresponding to the tergo-sternal junction) on segment 2, so that the corresponding cuticular plate is not entirely complete (Herranz *et al.*, 2012). Kinorhynch species previously known from the coasts of Rovinj are *Antygomonas incommutata* Nebelsick, 1990, *Centroderes spinosus* (Reinhard, 1881), *Condyloderes agnetis* Dal Zotto *et al.*, 2019, *Co. multispinosus* (McIntyre, 1962), *Echinoderes capitatus* (Zelinka, 1912) and presumably *E. gerardi* Higgins, 1978 (Zelinka, 1928; Nebelsick, 1990, 1992a, 1992b, 1993; Neuhaus *et al.*, 2013; Dal Zotto *et al.*, 2019). The latter species was reported by Zelinka (1928) as *Echinoderes dujardinii* Claparède, 1863, however, a recent review of both species by Sørensen *et al.* (2020) suggested that reports of *E. dujardinii* from the Mediterranean Sea are likely to correspond to *E. gerardi*.

Meristoderes is a moderately diverse genus of Kinorhyncha, currently numbering nine species. Since its monophyly is controversial (Sørensen *et al.*, 2015; Herranz *et al.*, 2022), further phylogenetic analyses are still needed to determine its taxonomic validity. Nevertheless, this contribution sticks to the genus' defining morphology, assigning the newly discovered species to *Meristoderes*.

The present work highlights the need for additional meiofaunal samplings, even in areas relatively well known in terms of kinorhynch fauna, to determine the species inhabiting a given geographical area and to increase the knowledge of frequently overlooked animal groups, such as the mud dragons.

Material and Methods

Sandy sediment samples were collected on 20–21 June 2022 from a shallow subtidal depth of 12 m near Rovinj, northern Adriatic Sea, (Figure 1; Table 1) using a Higgins' meiobenthic dredge. Meiofauna were extracted from the sediment with the bubble-and-blot method (Higgins and Thiel, 1988; Sørensen and Pardos, 2008, 2020) and preserved in 96% ethanol.

After extracting the meiofauna, remaining sediment samples were preserved in 96% ethanol and air-dried to remove debris. Sediment granulometry was then determined following the methods given in Guitián and Carballas (1976).

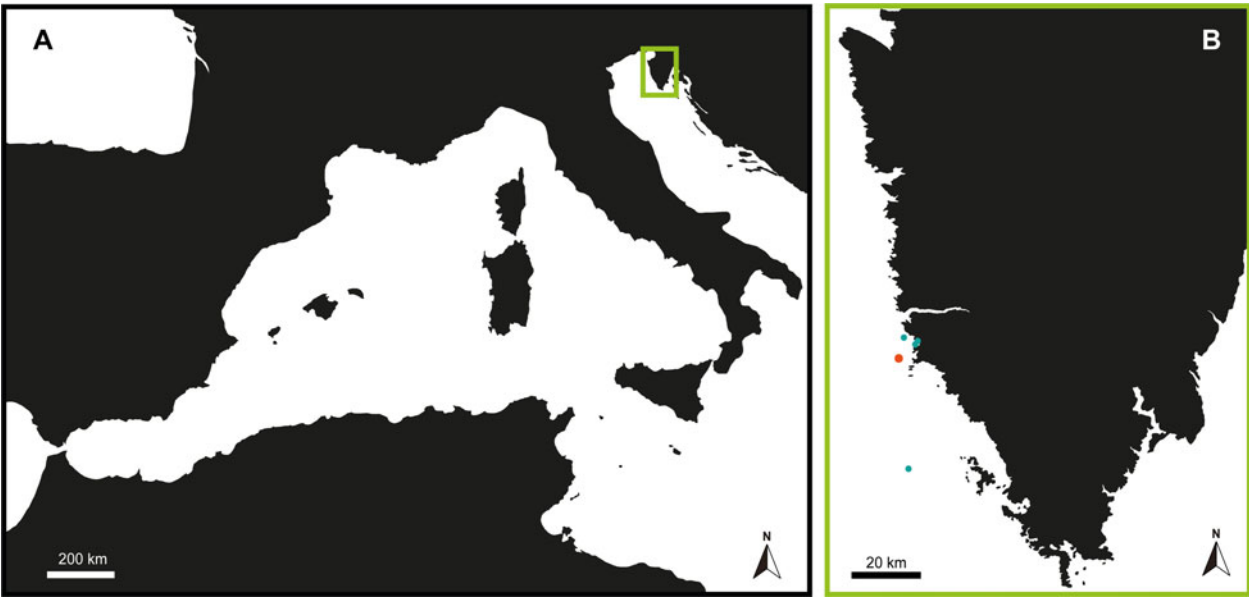


Figure 1. Map showing the sampling area. (A) General map of the Western Mediterranean Sea. The green box shows the specific sampling area. (B) Detailed map of the Istrian Peninsula; blue dots show additional samples (see Table 1); orange dot shows the sample where the new species was found.

Table 1. Records of *Meristoderes zmaj* sp. n. accompanying fauna collected in the vicinity of Rovinj, with sediment granulometry data. Bold font indicates the new species

Region	Locality	Date	Sample	Coordinates	Depth (m)	%Sand	%Silt	%Clay	Species
Adriatic Sea, Mediterranean Sea	Rovinj	20.06.2022	1	45°04'30.1"N 13°36'39.5"E	12	91	3	7	<i>Echinoderes ferrugineus</i> <i>Echinoderes gerardi</i> <i>Meristoderes zmaj</i> sp. n.
			2	45°05'38.3"N 13°37'06.9"E	14.7	90	4	6	<i>Echinoderes gerardi</i>
			3	45°05'39.5"N 13°38'16.5"E	12.3	42	52	6	<i>Cristaphyes carinatus</i> <i>Echinoderes capitatus</i> <i>Echinoderes ferrugineus</i> <i>Echinoderes gerardi</i> <i>Echinoderes hispanicus</i> <i>Pycnophyes communis</i>
			4	45°05'31.9"N 13°38'13.4"E	15.9	35	60	5	<i>Echinoderes capitatus</i> <i>Echinoderes gerardi</i> <i>Pycnophyes communis</i>
	–	21.06.2022	1	44°56'26.2"N 13°34'43.4"E	40	92	4	5	<i>Echinoderes capitatus</i> <i>Echinoderes ferrugineus</i> <i>Echinoderes gerardi</i> <i>Echinoderes hispanicus</i> <i>Pycnophyes robustus</i> <i>Pycnophyes zelinkaei</i> <i>Semnoderes armiger</i>

Kinorhyncha specimens were sorted under a ZEISS Stemi SV6 stereomicroscope. For light microscopy, kinorhynchs were dehydrated through a series of glycerine and were kept in 100% glycerine for 24 h. Subsequently, they were mounted on glass slides with dimethyl hydantoin formaldehyde resin (DMHF). Specimens were studied and photographed with an Olympus BX51 microscope with differential interference contrast optics equipped with an Olympus DP70 camera. For scanning electron microscopy (SEM), the animals were transferred to 100% ethanol and then chemically dried through a gradient of hexamethyldisilazane (HMDS) and ethanol. For their observation, specimens were mounted on stubs, sputter coated with gold and examined with a JEOL Ltd. JSM-6335F at CNME (National Centre for Electron Microscopy, Complutense University of Madrid). Line art illustrations and image compositions were done with Adobe Photoshop and Illustrator 2022.

Identification to genus level was done following the keys provided in Sørensen and Pardos (2020). Taxonomic measurements were done following the procedures provided in González-Casarrubios *et al.* (2023). Measurements can be consulted in the Kinorhyncha Measurement Database (González-Casarrubios and Yamasaki, 2022) and in the additional material of the present contribution (see Supplementary Table S1). The type material of the new species is deposited at the Natural History Museum of Denmark (NHMD).

Results

Ten Kinorhyncha species were found in the soft sediment samples taken in the northern Adriatic Sea (Table 1), namely *Cristaphyes carinatus* (Zelinka, 1912), *E. capitatus*, *E. ferrugineus* Zelinka, 1928, *E. gerardi*, *E. hispanicus* Pardos *et al.*, 1998, *Pycnophyes*

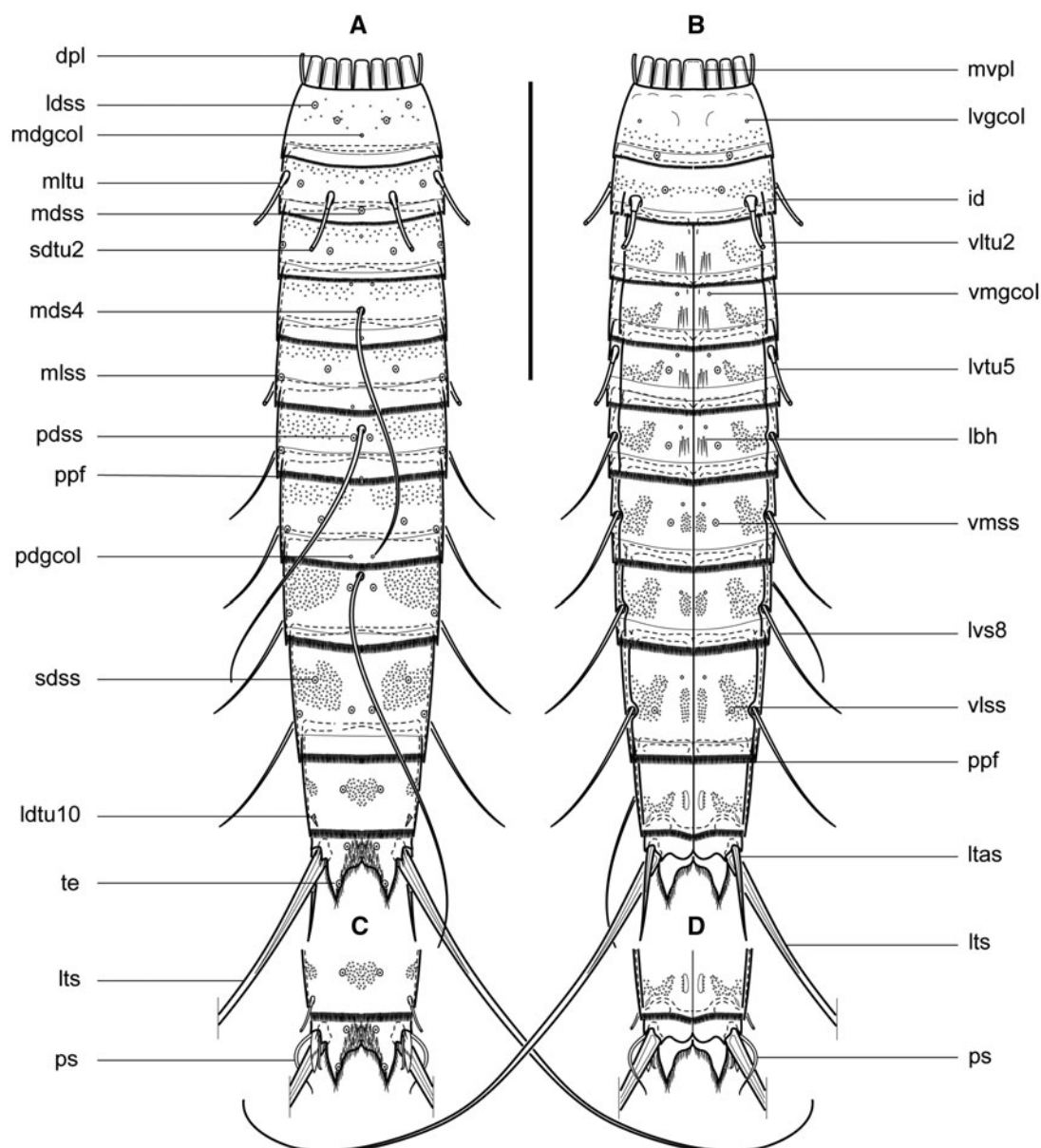


Figure 2. Line art drawing of adults of *Meristoderes zmaj* sp. n. (A) Female, dorsal overview. (B) Female, ventral overview. (C) Male, dorsal view of segments 10–11. (D) Male, ventral view of segments 10–11. dpl, dorsal placid; id, incomplete division; lbh, long bracteate hairs; ldss, laterodorsal sensory spots; ldtu, laterodorsal tube; lts, lateral terminal accessory spines; lts, lateral terminal spines; lvgcol, lateroventral type 1 glandular cell outlets; lvtu, lateroventral tube; mdgcol, middorsal type 1 glandular cell outlet; mds, middorsal spine; mdss, middorsal sensory spot; mlss, midlateral sensory spot; mltu, midlateral tube; mvpl, midventral placid; pdgcol, paradorsal type 1 glandular cell outlet; pdss, paradorsal sensory spot; ppf, primary pectinate fringe; ps, penile spines; sdss, subdorsal sensory spots; sdtu, subdorsal tube; te, tergal extensions; vlss, ventrolateral sensory spots; vltu, ventrolateral tube; vmgcol, ventromedial type 1 glandular cell outlet; vmss, ventromedial sensory spots. Number after abbreviations indicate the corresponding segment. Scalebar: 100 μ m.

communis Zelinka, 1908, *P. robustus* Zelinka, 1928, *P. zelinkaei* Southern, 1914 and *Semnoderes armiger* Zelinka, 1928, plus the new species of *Meristoderes* which is herein formally described.

Description of the new species

Class Cyclorhagida (Zelinka, 1896)

Family Echinoderidae Carus, 1885

Genus *Meristoderes* Herranz *et al.*, 2012

Meristoderes zmaj sp. n.

urn:lsid:zoobank.org:act:111E50DB-0478-46C3-A23A-77479A294289

(Figures 2–6 and Tables 2 & 3)

Material examined

Holotype. Adult female, collected on 20 June 2022 at Rovinj (Croatia, northern Adriatic Sea): 45°04'30.1"N 13°36'39.5"E at

12 m depth; mounted in DMHF, deposited at NHMD under accession number: NHMD – 1699747.

Paratype. Adult male, same collection data as holotype, deposited at NHMD under accession number: NHMD – 1699748.

Additional material. Adult female, same collection data as holotype, mounted for SEM, stored at the UCM meiofauna collection.

Diagnosis

Meristoderes with middorsal acicular spines on segments 4, 6 and 8 and lateroventral acicular spines on segments 6–9, progressively increasing in length towards the posterior segments. Long tubes in subdorsal, midlateral and ventrolateral positions of segment 2 and in lateroventral position of segment 5, and short tubes in laterodorsal position on segment 10. Tubes on segment 10 express sexual dimorphism in length, being longer

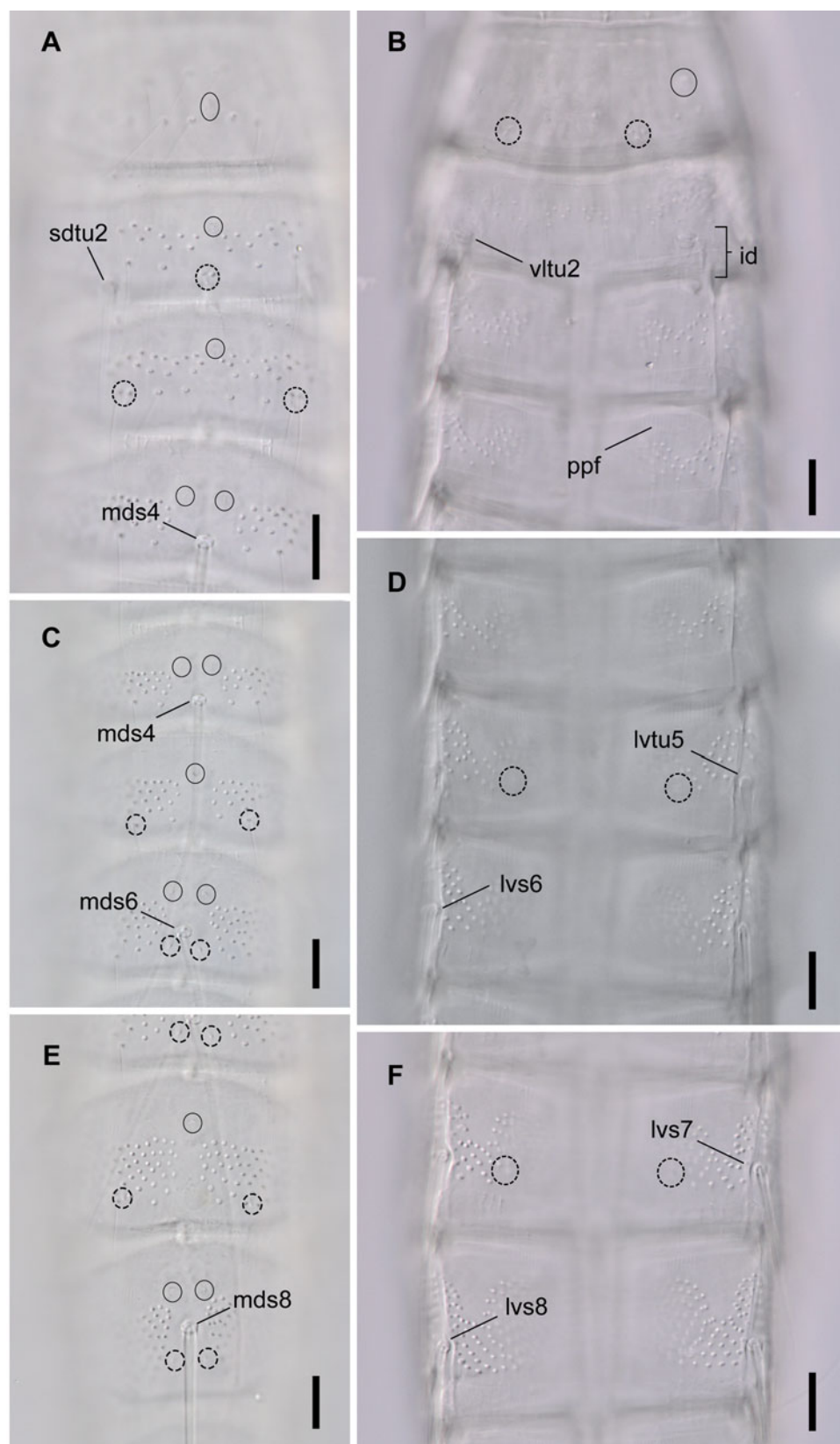


Figure 3. Light micrographs of the holotype of *Meristoderes zmaj* sp. n. the main trunk characters. (A) Dorsal view of segments 1–4. (B) Ventral view of segments 1–4. (C) Dorsal view of segments 4–6. (D) Ventral view of segments 4–6. (E) Dorsal view of segments 7–8. (F) Ventral view of segments 7–8. id, incomplete division; ltas, lateral terminal accessory spines; lts, lateral terminal spines; lvs, lateroventral spine; lvtu, lateroventral tube; mds, middorsal spine; ppf, primary pectinate fringe; sdtu, subdorsal tube; vltu, ventrolateral tube. Number after abbreviations indicates the number of the corresponding segment. Sensory spots marked as dashed circles; type 1 glandular cell outlets marked as continuous circles. Scalebars: A–F: 10 μ m.

in males. Type 2 glandular cell outlets and female papillae absent. Lateral terminal spines long and slender (LTS/TL ratio of ca. 75–78%).

Etymology

The species is named after Zmaj (змaj), a medieval representation of a dragon-like, giant reptilian creature from the Slavic folklore.

In the Croatian mythology, Zmaj were powerful beings forces of good who protected mankind from evil.

Description

Adult with head, neck and 11 trunk segments. See Table 2 for measurements and dimensions, and Table 3 for summary of

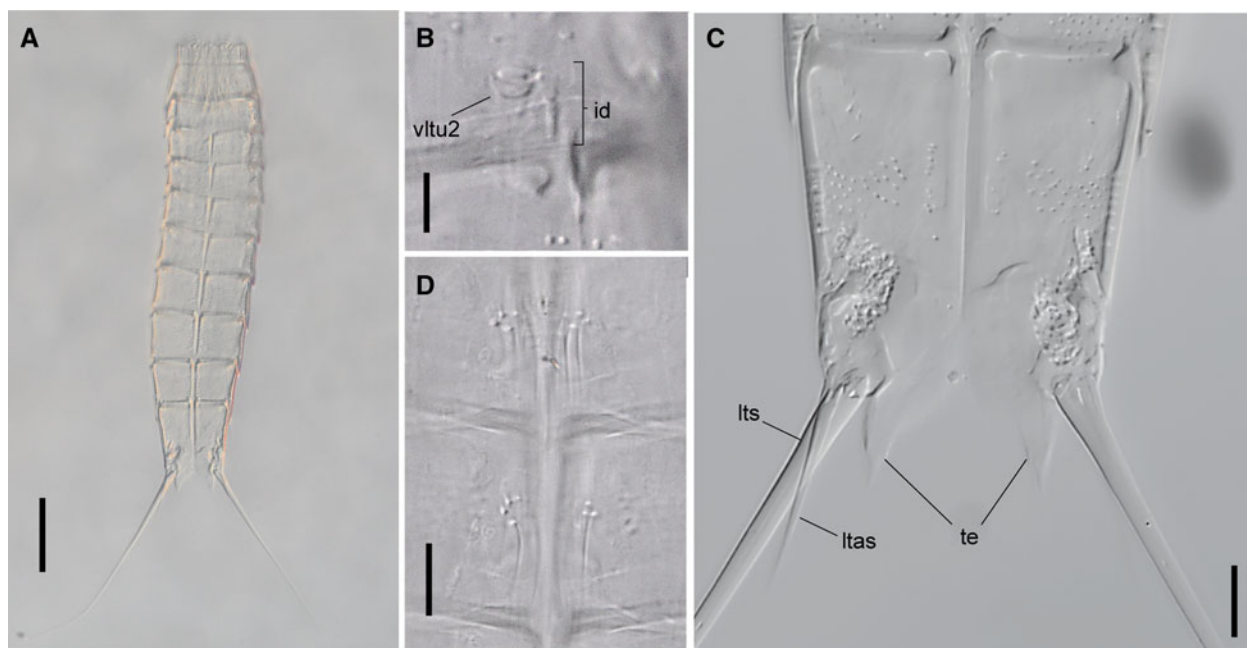


Figure 4. Light micrographs of the holotype (A–C, E) and paratype (D) of *Meristoderes zmaj* sp. n. showing overviews and detailed trunk characters. (A) Ventral overview. (B) Close-up of the incomplete division and ventrolateral tube of segment 2. (C) Ventral view of segments 10–11. (D) Detail of the midventral long bracteate hairs. id, incomplete division; ltas, lateral terminal accessory spines; lts, lateral terminal spines; te, tergal extensions; vltu, ventrolateral tube. Scalebars: A: 50 μ m; B–D: 10 μ m.

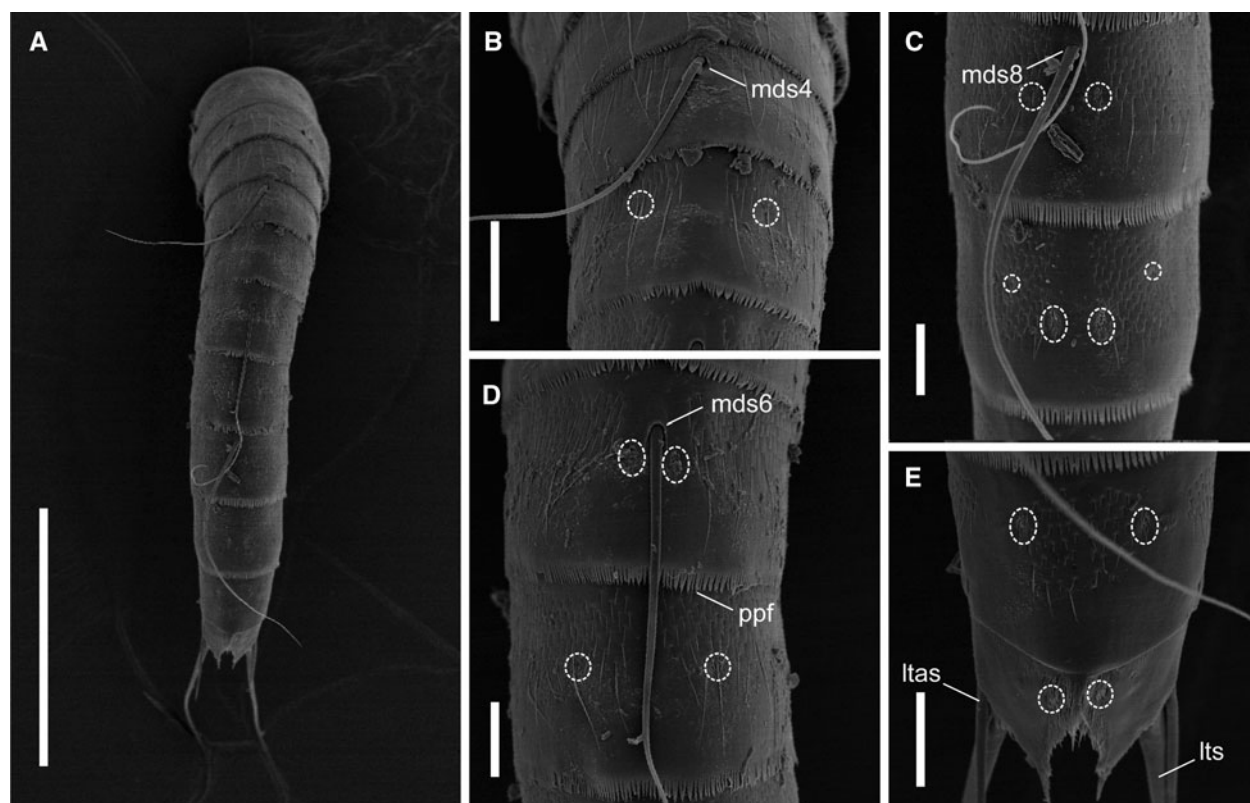


Figure 5. Scanning electron micrographs of additional female of *Meristoderes zmaj* sp. n. showing overviews and detailed trunk characters. (A) Dorsal overview. (B) Dorsal view of segments 4–5. (C) Dorsal view of segments 8–9. (D) Dorsal view of segments 6–7. (E) Dorsal view of segments 10–11. ltas, lateral terminal accessory spines; lts, lateral terminal spines; mds, middorsal spine; ppf, primary pectinate fringe. Number after abbreviations indicate the number of the corresponding segment. Sensory spots marked as dashed circles; type 1 glandular cell outlets marked as continuous circles. Scalebars: A: 100 μ m; B–E: 10 μ m.

spine, tube, nephridiopore, glandular cell outlet and sensory spot locations.

Head. With retractable mouth and introvert. None of the examined specimens had the introvert everted, hence no details

on number, arrangement and morphology of the oral styles and scalds can be provided.

Neck. With 16 trapezoidal placids. Midventral placid widest (ca. 12 μ m wide at base, 12–13 μ m long), remaining ones

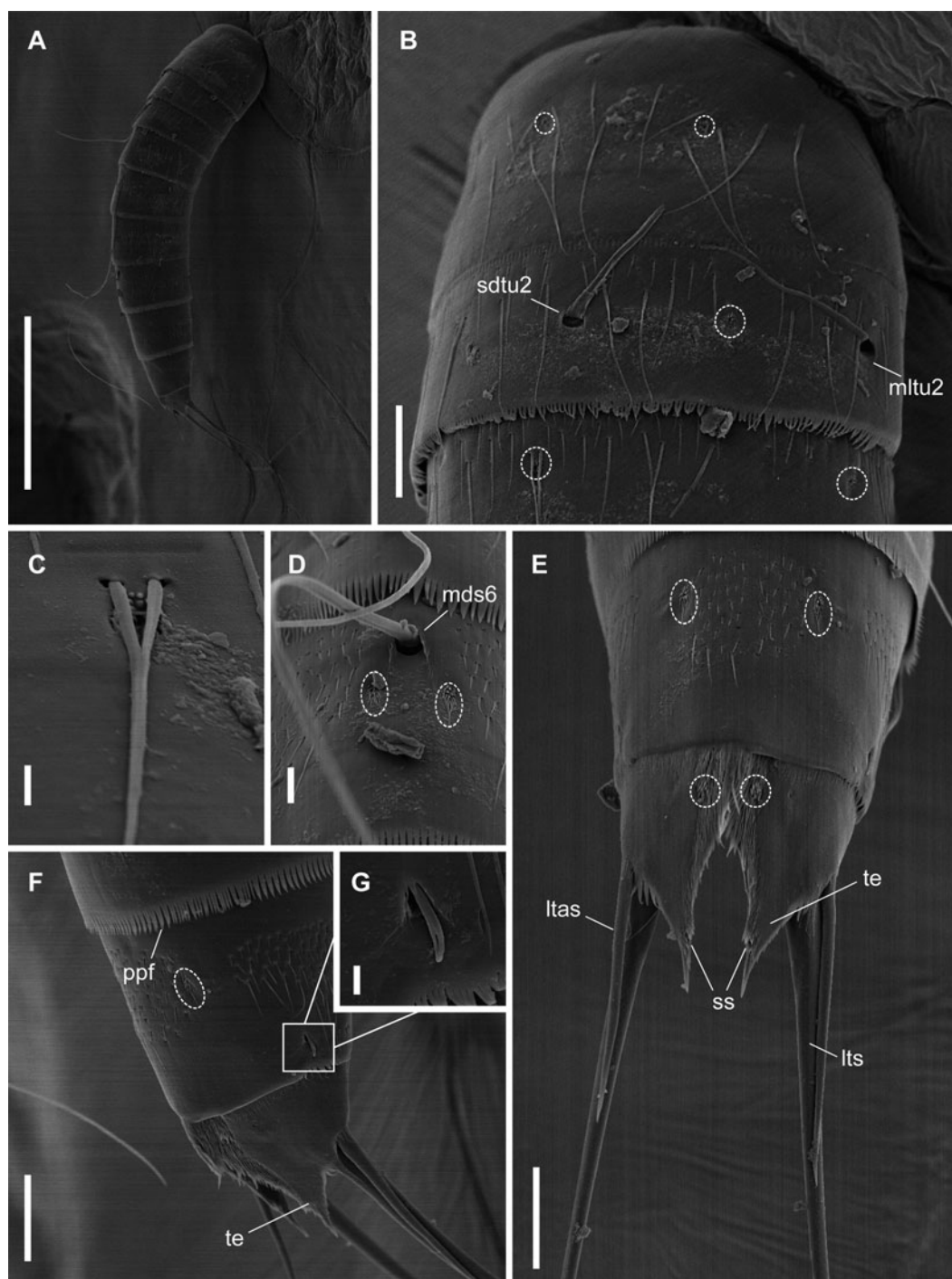


Figure 6. Scanning electron micrographs of additional female of *Meristoderes zmaj* sp. n. showing overviews and detailed trunk characters. (A) Lateral overview. (B) Lateral view of segments 1–2. (C) Detail on the middorsal sensory spot of segment 2. (D) Detail on the acicular spine and paradorsal sensory spots of segment 6. (E) Dorsal view of segments 10–11. (F) Lateral view of segments 10–11. (G) Close-up on the laterodorsal tube of segment 10. ltas, lateral terminal accessory spines; lts, lateral terminal spines; mds, middorsal spine; mltu, middlateral tube; ppf, primary pectinate fringe; sdtu, subdorsal tube; ss, sensory spot; te, tergal extension. Number after abbreviations indicate the number of the corresponding segment. Sensory spots marked as dashed circles; type 1 glandular cell outlets marked as continuous circles. Scalebars: A: 100 μm ; B, E–F: 10 μm ; C, G: 1 μm ; D: 3 μm .

narrower (ca. 6–8 μm wide at base, 12–13 μm long) (Figures 2A, B). Four dorsal and two ventral trichoscalid plates associated with trichoscalids; dorsal trichoscalid plates rounded, small; ventral ones larger, rhomboidal.

Trunk. With 11 cuticular segments (Figures 2A, B, 4A, 5A, 6A). Segment 1 as a closed cuticular ring; segment 2 as a cuticular ring with incomplete tergosternal divisions in lateroventral/ventrolateral position and a midventral fold; segments 3–11 with one tergal and two sternal plates (Figures 2A, B, 3A, B,

4B). Sternal plates reach their maximum width at segment 8, tapering towards the posterior segments; sternal plates narrow compared to the total trunk length (MSW8/TL ratio ca. 22%), giving the animal a slender outline (Figures 2A, B, 4A, 5A, 6A). Cuticular hairs acicular, bracteate (except for those of segment 1), emerging from rounded to oval perforation sites (Figures 5B–E, 6B, E, F). Cuticular hairs distributed in 1–2 straight, transverse rows on segment 1; in 2–3 straight, transverse rows on segment 2 and in 3–9 rows becoming wavy in ventrolateral and

Table 2. Measurements of female holotype (NHMD – 1699747) and male paratype (NHMD – 1699748) of *Meristoderes zmaj* sp. n. ac, acicular spine; CL, cumulative length; LD, laterodorsal; LTAS, lateral terminal accessory spines; LTS, lateral terminal spines; LV, lateroventral; MD, middorsal; ML, midlateral; MSW, maximum external width; S, segment; SD, subdorsal; SW, standard sternal width (measured at segment 10); TL, total length; tu, tube; VL, ventrolateral. Number after abbreviations indicate the corresponding segment. All measurements are taken in microns (μm) unless is specified

Character	Holotype (♀)	Paratype (♂)
TL	285	292
CL	369	393
CL/TL (%)	129.47	134.59
MSW-8	62	56
MSW-8/TL (%)	21.75	19.18
SW	45	53
SW/TL (%)	15.79	14.73
S1	32	36
S2	32	33
S3	30	29
S4	31	33
S5	33	34
S6	36	35
S7	38	36
S8	40	42
S9	43	43
S10	36	43
S11	18	29
MD4 (ac)	95	89
MD6 (ac)	–	–
MD8 (ac)	132	109
SD2 (tu)	21	–
ML2 (tu)	–	–
VL2 (tu)	16	–
LV5 (tu)	20	24
LV6 (ac)	21	26
LV7 (ac)	36	34
LV8 (ac)	40	35
LV9 (ac)	36	35
LD10 (tu)	–	–
LTS	222	220
LTS/TL (%)	77.89	75.34
LTAS	37	–
LTAS/TL (%)	12.98	–
LTAS/LTS (%)	16.67	–

subdorsal positions on segments 3–10; sternal plates of segments 3–6 with a patch of 3–4 long bracteated hairs in paraventral position and those of segments 7–10 with a paraventral patch of regular-sized hairs (Figures 2A, B, 4D). Primary pectinate fringe long, straight, serrated, with equal length tips (Figures 2A, B, 3B, 5D, 6F). Secondary pectinate fringe not observed.

Segment 1. Without spines and tubes. Type 1 glandular cell outlets in middorsal and lateroventral positions. Sensory spots

in subdorsal, laterodorsal and ventromedial positions. Sensory spots on this and following segments oval, with one or two central pores surrounded by 3–5 concentric rings of micropapillae, sometimes flanked by a pair of long hairs (Figures 2A, B, 3A, B, 6B).

Segment 2. With long tubes in subdorsal, midlateral and ventrolateral positions. Type 1 glandular cell outlet in middorsal position. Sensory spots in middorsal (posterior to the glandular cell outlet), laterodorsal and ventromedial positions (Figures 2A, B, 3A, B, 4B, 6B).

Segment 3. Without spines and tubes. Type 1 glandular cell outlet in middorsal position. Sensory spots in subdorsal and midlateral positions (Figures 2A, B, 3A, B).

Segment 4. With long middorsal acicular spine surpassing the posterior margin of the following two to three segments. Type 1 glandular cell outlets in paradorsal and ventromedial positions (Figures 2A, B, 3A, D, 5B).

Segment 5. With long tubes in lateroventral position. Type 1 glandular cell outlets in middorsal and ventromedial positions. Sensory spots in subdorsal, midlateral and ventromedial positions (Figures 2A, B, 3C, D, 5B).

Segment 6. With long middorsal acicular spine surpassing the posterior margin of the two following segments, longer than that of segment 4, and also with long acicular spines in lateroventral position. Type 1 glandular cell outlets in paradorsal and ventromedial positions. Sensory spots in paradorsal, midlateral and ventromedial positions (Figures 2A, B, 3C, D, 5D, 6D).

Segment 7. With long acicular spines in lateroventral position. Type 1 glandular cell outlet in middorsal and ventromedial positions. Sensory spots in subdorsal, midlateral and ventromedial positions (Figures 2A, B, 3E, F, 5D).

Segment 8. With long middorsal acicular spine surpassing the posterior margin of the tergal extensions, longer than that of segment 6, and also with long acicular spines in lateroventral position. Type 1 glandular cell outlets in paradorsal and ventromedial positions. Sensory spots in paradorsal and midlateral positions (Figures 2A, B, 3E, B, 5C).

Segment 9. With long acicular spines in lateroventral position. Type 1 glandular cell outlets in paradorsal and ventromedial positions. Sensory spots in paradorsal, subdorsal, midlateral and ventrolateral positions (Figures 2A, B, 5C). Nephridiopore in sublateral position.

Segment 10. With laterodorsal tubes differing in length among sexes (those of males slightly longer). Two type 1 glandular cell outlets in middorsal position, longitudinally aligned. Sensory spots in subdorsal position (Figures 2A–D, 4C, 5E, 6E–G).

Segment 11. With long, slender lateral terminal spines (LTS/TL ratio ca. 75–78%). Females with paired, relatively short lateral terminal accessory spines (LTAS/LTS ca. 17%). Males with three pairs of penile spines, first and third pairs longer and filiform, second pair shorter and thicker. Type 1 glandular cell outlet in middorsal position. Two pairs of sensory spots in subdorsal position, one on central position of the segment and the other one on the tip of the tergal extensions. Hairly middorsal protuberance conspicuous in SEM observation. Tergal extensions triangular, long, distally pointed (Figures 2A–D, 4C, 5E, 6E, F).

Discussion

Taxonomic remarks of the new species

The new species belongs to the genus *Meristoderes* as it fulfils all the diagnostic characters of Echinoderidae and, in addition, has a single cuticular plate on segment 2 with incomplete subcuticular divisions

Table 3. Summary of nature and arrangement of cuticular characters of *Meristoderes zmaj* sp. n. ac, acicular spine; gcol, type 1 glandular cell outlet; LA, lateral accessory; LD, laterodorsal; ltas, lateral terminal accessory spines; lts, lateral terminal spines; LV, lateroventral; MD, middorsal; ML, midlateral; ne, nephridiopore; PD, paradorsal; ps, penile spines; SD, subdorsal; SL, sublateral; ss, sensory spot; tu, tube; VL, ventrolateral; VM, ventromedial. ♂ and ♀ shows dimorphic characters

Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss				gcol		ss
2	gcol, ss		tu	ss	tu				tu	ss
3	gcol		ss		ss					
4	ac	gcol								gcol
5	gcol		ss		ss			tu		gcol, ss
6	ac	gcol, ss			ss			ac		gcol, ss
7	gcol		ss		ss			ac		gcol, ss
8	ac	gcol, ss			ss			ac		gcol
9		gcol, ss	ss		ss	ne		ac	ss	gcol
10	gcol x2		ss	tu						
11	gcol		ss x2		ps x3 (♂)		ltas (♀)	lts		

in a lateroventral/ventrolateral position, which allows it to be differentiated from other echinoderid genera (Herranz *et al.*, 2012; Sørensen and Pardos, 2020). Given that the partial ventral fissures characteristic of *Meristoderes* as well as that the existence of the genus is questioned according to phylogenetic analyses, the new species is then compared with all members of the Echinoderidae.

Regarding *Meristoderes*, the new species can be distinguished from its congeners by its spine and tube pattern. *Meristoderes zmaj* sp. n. has middorsal spines on segments 4, 6 and 8 and lateroventral spines on segments 6–9. This spine distribution is shared with four species: *Meristoderes boylei* Herranz and Pardos, 2013, *M. elleae* Sørensen *et al.*, 2013, *M. herranzae* Sørensen *et al.*, 2013 and *M. macracanthus* Herranz *et al.*, 2012 (Herranz *et al.*, 2012; Herranz and Pardos, 2013; Sørensen *et al.*, 2013). The remaining congeners have middorsal spines on more (segments 4–8 in *M. taro* Sánchez *et al.*, 2019) or fewer segments (segments 6 and 8 in *M. okhotensis* Adrianov and Maiorova, 2018 and only on segment 4 in *M. galathea* Herranz *et al.*, 2012), or lack lateroventral spines on segments 6 and 7 (*M. glaber* Sørensen *et al.*, 2013 and *M. imugi* Sørensen *et al.*, 2013) (Sørensen *et al.*, 2013; Adrianov and Maiorova, 2018; Sánchez *et al.*, 2019).

Additionally, the new species has three pairs of long tubes on segment 2 in subdorsal, midlateral and ventrolateral positions. Only *M. glaber*, *M. herranzae*, *M. imugi* and *M. okhotensis* have similar tubes on segment 2 (Sørensen *et al.*, 2013; Adrianov and Maiorova, 2018). However, *M. glaber* and *M. imugi* lack tubes in lateral position, *M. okhotensis* has an extra pair in laterodorsal position and the dorsal ones of *M. herranzae* are located in laterodorsal instead of subdorsal position and it also lacks the lateral ones. Taking all into account, it seems that *M. herranzae* is the most similar species to *M. zmaj* sp. n., but the possession of lateral accessory tubes on segment 8 and only two pairs of these structures on segment 2 in the former allows their differentiation (Sørensen *et al.*, 2013).

Finally, *M. boylei*, *M. elleae*, *M. herranzae*, *M. imugi* and *M. macracanthus* (Herranz *et al.*, 2012; Herranz and Pardos, 2013; Sørensen *et al.*, 2013) have conspicuous extra tubes in the lateral series besides the lateroventral spines. All of them have these tubes in lateral accessory position, except for *M. imugi* and *M. okhotensis* in which tubes are located sublaterally and midlaterally, respectively (Herranz *et al.*, 2012; Herranz and Pardos, 2013; Sørensen *et al.*, 2013; Adrianov and Maiorova, 2018). Therefore, *M. zmaj* sp. n. follows a general arrangement of cuticular appendages, but the combination of spine and tube pattern is a unique within the genus.

Compared to other species of Echinoderidae, the new species can also be distinguished by its unique pattern of tubes and spines. The presence of middorsal spines on segments 4, 6 and 8, lateroventral tubes on segment 5 and lateroventral spines on segments 6–9 is the second most common pattern within the family, shared by 28 species. Nevertheless, 20 of them also possess tubes in the lateral series on segment 8, a feature absent in the new species. Only eight species share with *M. zmaj* sp. n. the referred distribution of spines and the absence of lateral tubes in segment 8, namely *E. apex* Yamasaki *et al.*, 2018, *E. bermudensis* Higgins, 1982, *E. hamiltonorum* Sørensen *et al.*, 2018, *E. joyceae* Landers and Sørensen, 2016, *E. legolasi* Grzelak and Sørensen, 2022, *E. multiporus* Yamasaki *et al.*, 2018, *E. schwieringae* Yamasaki *et al.*, 2019 and *E. shenlong* Sánchez *et al.*, 2019. However, all these species have only one pair of tubes on segment 2 (in lateroventral or ventrolateral position), except for *E. abbreviatus* Higgins, 1983 (subdorsal and lateroventral tubes), *E. legolasi* (no tubes) and *E. shenlong* (no tubes), whereas *M. zmaj* sp. n. has three pairs of tubes on this segment. Several species with the same spine pattern resemble the new species by also having three tubes on segment 2, namely *E. belenae* Pardos *et al.*, 2016, *E. hispanicus*, *E. newcaledoniensis* Higgins, 1967, *E. peterseni* Higgins and Kristensen, 1988, *E. xiphophorus* Adrianov and Maiorova, 2021; but, as referred above, all of them possess tubes on segment 8, among other differences. Therefore, the pattern of spines and tubes of *M. zmaj* sp. n. is also unique within the whole family.

Kinorhyncha community

Among the six kinorhynch species previously reported from Rovinj, named *A. incomitata*, *C. spinosus*, *C. agnetis*, *C. multispinosus*, *E. capitatus* and *E. gerardi* (Zelinka, 1928; Nebelsick, 1990, 1992a, 1992b, 1993; Higgins, 1969; Neuhaus *et al.*, 2013; Dal Zotto *et al.*, 2019), only the two Echinoderes were also found in the present survey (Table 1). Most of the remaining species collected in the samples represented new reports for Croatia, but their presence is not an exceptional finding, as they were already known from the nearby waters of Trieste (less than 100 km away, northeast Italy). That is the case of *C. carinatus*, *E. capitatus*, *E. ferrugineus*, *P. communis*, *P. robustus* and *S. armiger* (Zelinka, 1928; Nebelsick, 1992b; Yamasaki and Dal Zotto, 2019).

It is noteworthy that four of the local species were not found in our study (Zelinka, 1928; Nebelsick, 1990, 1992a, 1992b, 1993;

Higgins, 1969; Neuhaus *et al.*, 2013; Dal Zotto *et al.*, 2019). This fact could be partly explained by the depth of the samples, most of them collected in very shallow waters, whereas *C. agnetis* was discovered from relatively deep areas off Rovinj (Dal Zotto *et al.*, 2019) and *C. spinosus* and *Condyloderes multispinosus* are commonly collected in deeper sediment samples (Neuhaus *et al.*, 2013). All this suggests that future samplings around Croatia could provide numerous novel reports and even hidden species of kinorhynchs that are still waiting to be discovered.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000875>.

Acknowledgements. This contribution was partially funded by the project Fauna Ibérica XII: Escaladóforos de la Península Ibérica y Baleares (PGC-2018 095851-B-C62), of the MICINN (Ministerio de Ciencia, Innovación y Universidades), Spain.

Author contributions. N. S. and F. P. designed the sampling. A. G.-C., N. S., D. C. and F. P. participated in the sampling campaign to collect the specimens. A. G.-C. separated, mounted, identified and photographed the specimens. A. G.-C., D. C. and N. S. wrote the manuscript. A. G.-C. and F. P. made the image compositions. All authors reviewed and accepted the latest version of the manuscript.

Competing interests. None.

References

- Adrianov AV and Maiorova AS (2018) *Meristoderes okhotensis* sp. nov. – the first deepwater representative of kinorhynchs in the Sea of Okhotsk (Kinorhyncha: Cyclorhagida). *Deep Sea Research Part II: Topical Studies in Oceanography* **154**, 99–105. <https://doi.org/10.1016/j.dsr2.2017.10.011>
- Adrianov AV and Maiorova AS (2021) *Echinoderes xiphophorus* sp. nov. – the first deep-water representative of Echinoderidae in the Sea of Japan (Kinorhyncha: Cyclorhagida). *European Journal of Taxonomy* **773**, 169–186. <https://doi.org/10.5852/ejt.2021.773.1523>
- Dal Zotto M (2015) *Antygomonas caeciliae*, a new kinorhynch from the Mediterranean Sea, with report of mitochondrial genetic data for the phylum. *Marine Biology Research* **11**, 689–702. <https://doi.org/10.1080/17451000.2015.1007872>
- Dal Zotto M, Neuhaus B, Yamasaki H and Todaro MA (2019) The genus *Condyloderes* (Kinorhyncha: Cyclorhagida) in the Mediterranean Sea, including the description of two new species with novel characters. *Zoologischer Anzeiger* **282**, 206–231. <https://doi.org/10.1016/j.jcz.2019.05.006>
- González-Casarrubios A, Cepeda D, Pardos F, Neuhaus B, Yamasaki H, Herranz M, Grzelak K, Maiorova A, Adrianov A, Dal Zotto M, Di Domenico M, Landers SC and Sánchez N (2023) Towards a standardisation of morphological measurements in the phylum Kinorhyncha. *Zoologischer Anzeiger* **302**, 217–223. <https://doi.org/10.1016/j.jcz.2022.11.015>
- González-Casarrubios A and Yamasaki H (2022) Kinorhyncha measurement database. Available from <https://sites.google.com/a/meiobenthos.com/laboratory/database/kinorhyncha-measurement-database> [accessed 24 May 2023].
- Grzelak K and Sørensen MV (2022). *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Hikurangi Margin, New Zealand. *European Journal of Taxonomy*, **844**, 1–108. <https://doi.org/10.5852/ejt.2022.844.1949>
- Gutián F and Carballas T (1976) *Técnicas de análisis de suelos*. Pico Sacro, Santiago de Compostela.
- Herranz M and Pardos F (2013) *Fissuroderes Sørenseni* sp. nov. and *Meristoderes boylei* sp. nov.: first Atlantic recording of two rare kinorhynch genera, with new identification keys. *Zoologischer Anzeiger – A Journal of Comparative Zoology* **253**, 93–111. <https://doi.org/10.1016/j.jcz.2013.09.005>
- Herranz M, Stiller J, Worsaae K and Sørensen MV (2022) Phylogenomic analyses of mud dragons (Kinorhyncha). *Molecular Phylogenetics and Evolution* **168**, 107375. <https://doi.org/10.1016/j.ympev.2021.107375>
- Herranz M, Thormar J, Benito J, Sánchez N and Pardos F (2012) *Meristoderes* gen. nov., a new kinorhynch genus, with the description of two new species and their implications for echinoderid phylogeny (Kinorhyncha: Cyclorhagida, Echinoderidae). *Zoologischer Anzeiger* **251**, 161–179. <https://doi.org/10.1016/j.jcz.2011.08.004>
- Higgins RP (1967) The Kinorhyncha of New-Caledonia. *Expédition Française sur les Recifs coralliens de la Nouvelle-Calédonie 2. Éditions de la Fondation Singer-Polignac, Paris*, pp. 75–90.
- Higgins RP (1969) Indian Ocean Kinorhyncha: 1. *Condyloderes* and *Sphenoderes*, new cyclorhagid genera. *Smithsonian Contributions to Zoology* **14**, 1–13. <https://doi.org/10.2307/3225748>
- Higgins RP (1978) *Echinoderes gerardi* n. sp. and *E. riedli* (Kinorhyncha) from the Gulf of Tunis. *Transactions of the American Microscopical Society* **97**, 171–180.
- Higgins RP (1982) Three new species of Kinorhyncha from Bermuda. *Transactions of the American Microscopical Society* **101**, 305–316. <https://doi.org/10.2307/3225748>
- Higgins RP (1983) The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, II. Kinorhyncha. *Smithsonian Contributions to the Marine Sciences* **1**–131. <https://doi.org/10.5479/si.01960768.18.1>
- Higgins RP and Kristensen RM (1988). Kinorhyncha from Disko Island, West Greenland. *Smithsonian Contributions to Zoology* **458**, 1–56. <https://doi.org/10.5479/si.00810282.458>
- Higgins RP and Thiel H (1988). *Introduction to the Study of Meiofauna*. Washington, D.C: Smithsonian Institution Press.
- Landers SC and Sørensen MV (2016) Two new species of *Echinoderes* (Kinorhyncha, Cyclorhagida), *E. romanoi* sp. n. and *E. joyceae* sp. n., from the Gulf of Mexico. *ZooKeys* **594**, 51–71. <https://doi.org/10.3897/zookeys.594.8623>
- Nebelsick M (1990) *Antygomonas incomitata* gen. et sp.n. (Cyclorhagida, Kinorhyncha) and its phylogenetic relationships. *Zoologica Scripta* **19**, 143–152. <https://doi.org/10.1111/j.1463-6409.1990.tb00248.x>
- Nebelsick M (1992a) Sensory spots of *Echinoderes capitatus* (Zelinka, 1928) (Kinorhyncha, Cyclorhagida). *Acta Zoologica* **73**, 185–195. <https://doi.org/10.1111/j.1463-6395.1992.tb01186.x>
- Nebelsick M (1992b) Ultrastructural investigations of three taxonomic characters in the trunk region of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida). *Zoologica Scripta* **21**, 335–345. <https://doi.org/10.1111/j.1463-6409.1992.tb00335.x>
- Nebelsick M (1993) Introvert, mouth cone, and nervous system of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida) and implications for the phylogenetic relationships of Kinorhyncha. *Zoomorphology* **113**, 211–232. <https://doi.org/10.1007/BF00403313>
- Neuhaus B (2013) Kinorhyncha (=Echinodera). In Schmidt-Rhaesa A (ed), *Handbook of Zoology, Gastrotricha, Cycloneuralia and Gnathifera, Volume 1: Nematomorpha, Priapulida, Kinorhyncha, Loricifera*. Berlin: Walter de Gruyter, pp. 181–348. <https://doi.org/10.1515/9783110272536.181>
- Neuhaus B, Pardos F, Sørensen MV and Higgins RP (2013) Redescription, morphology, and biogeography of *Centroderes spinosus* (Reinhard, 1881) (Kinorhyncha, Cyclorhagida) from Europe. *Cahiers de Biologie Marine* **54**, 109–131. <https://doi.org/10.21411/CBM.A.8E3FD0CA>
- Pardos F, Herranz M and Sánchez N (2016) Two sides of a coin: the phylum Kinorhyncha in Panama. II) Pacific Panama. *Zoologischer Anzeiger – A Journal of Comparative Zoology* **265**, 26–47. <https://doi.org/10.1016/j.jcz.2016.06.006>
- Sánchez N, García-Herrero Á, García-Gómez G and Pardos F (2018) A new species of the recently established genus *Setaphyes* (Kinorhyncha, Allomalorhagida) from the Mediterranean with an identification key. *Marine Biodiversity* **48**, 249–258. <https://doi.org/10.1007/s12526-017-0651-1>
- Sánchez N, Pardos F, Herranz M and Benito J (2011) *Pycnophyes dolichurus* sp. nov. and *P. aulacodes* sp. nov. (Kinorhyncha, Homalorhagida, Pycnophyidae), two new kinorhynchs from Spain with a reevaluation of homalorhagid taxonomic characters. *Helgoland Marine Research* **65**, 319–334. <https://doi.org/10.1007/s10152-010-0226-z>
- Sánchez N, Pardos F and Martínez Arbizu P (2019) Deep-sea Kinorhyncha diversity of the polymetallic nodule fields at the Clarion-Clipperton Fracture Zone (CCZ). *Zoologischer Anzeiger* **282**, 88–105. <https://doi.org/10.1016/j.jcz.2019.05.007>
- Sørensen MV, Dal Zotto M, Rho HS, Herranz M, Sánchez N, Pardos F and Yamasaki H (2015) Phylogeny of Kinorhyncha based on morphology and two molecular loci. *PLoS ONE* **10**, e0133440. <https://doi.org/10.1371/journal.pone.0133440>
- Sørensen MV, Goetz FE, Herranz M, Chang CY, Chatterjee T, Durucan F, Neves RC, Özlem YN, Norenburg J and Yamasaki H (2020) Description, redescription and revision of sixteen putatively closely related species of *Echinoderes* (Kinorhyncha: Cyclorhagida), with the proposition of a new

- species group – the *Echinoderes dujardinii* group. *European Journal of Taxonomy* **730**, 1–101. <https://doi.org/10.5852/ejt.2020.730.1197>
- Sørensen MV and Pardos F** (2008) Kinorhynch systematics and biology – an introduction to the study of kinorhynchs, inclusive identification keys to the genera. *Meiofauna Marina* **16**, 21–73.
- Sørensen MV and Pardos F** (2020) Kinorhyncha. In Smith-Rhaesa A (ed), *Guide to the Identification of Marine Meiofauna*. Munich: Verlag Dr Friedrich Pfeil, pp. 391–414.
- Sørensen MV, Rho HS, Min WG, Kim D and Chang CY** (2013) Occurrence of the newly described kinorhynch genus *Meristoderes* (Cyclorhagida: Echinoderidae) in Korea, with the description of four new species. *Helgoland Marine Research* **67**, 291–319. <https://doi.org/10.1007/s10152-012-0323-2>
- Sørensen MV, Rohal M and Thistle D** (2018) Deep-sea Echinoderidae (Kinorhyncha: Cyclorhagida) from the Northwest Pacific. *European Journal of Taxonomy* **456**. <https://doi.org/10.5852/ejt.2018.456>
- Yamasaki H and Dal Zotto M** (2019) Investigation of echinoderid kinorhynchs described 90 years ago: redescription of *Echinoderes capitatus* (Zelinka, 1928) and *Echinoderes ferrugineus* Zelinka, 1928. *Zoologischer Anzeiger* **282**, 189–205. <https://doi.org/10.1016/j.jcz.2019.05.013>
- Yamasaki H, Neuhaus B and George KH** (2018) New species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from Mediterranean seamounts and from the deep-sea floor in the Northeast Atlantic Ocean, including notes on two undescribed species. *Zootaxa* **4387**, 541–566. <https://doi.org/10.11646/zootaxa.4387.3.8>
- Yamasaki H, Neuhaus B and George KH** (2019) Echinoderid mud dragons (Cyclorhagida: Kinorhyncha) from Senghor Seamount (NE Atlantic Ocean) including general discussion of faunistic characters and distribution patterns of seamount kinorhynchs. *Zoologischer Anzeiger* **282**, 64–87. <https://doi.org/10.1016/j.jcz.2019.05.018>
- Yıldız NÖ, Sørensen MV and Karaytuğ S** (2016) A new species of *Cephalorhyncha* Adrianov, 1999 (Kinorhyncha: Cyclorhagida) from the Aegean Coast of Turkey. *Helgoland Marine Research* **70**, 24. <https://doi.org/10.1186/s10152-016-0476-5>
- Zelinka K** (1928) *Monographie der Echinodera*. Leipzig: Verlag Wilhelm Engelmann.