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Expanding the *Echinoderes coulli* group (Kinorhyncha: Cyclorhagida) with a new species from the Chuuk Islands, Micronesia

María Herranz \(^a^{,}b^{*,} \), Alexis D. Moreleon \(^a\), Hyun Soo Rho \(^c\), Martin V. Sørensen \(^a\)

\(^a\) Natural History Museum of Denmark, University of Copenhagen, 2100, Copenhagen, Denmark
\(^b\) Department of Biology, University of Copenhagen, 2100, Copenhagen, Denmark
\(^c\) East Sea Environment Research Center, Korea Institute of Ocean Science and Technology, Uljin, 36315, Republic of Korea

A new species of *Echinoderes* is described from the Chuuk Islands, Micronesia. *Echinoderes inaequalis* sp. nov. clearly belongs to the *Echinoderes coulli* species group due to the presence of enlarged sieve plates, reduced trunk spines (excluding the terminal series) and a hairy habitus. *E. inaequalis* sp. nov. is characterised by the presence of a minute middorsal spine on segment 4; unpaired subdorsal tubes in alternating positions on segments 5–7; lateroventral tubes on segments 5, 7–9; midlateral tubes on segment 8; sexually dimorphic laterodorsal tubes on segment 10; numerous glandular cell outlets type 2 located on segments 2, 4–8; and very short and stout terminal spines (ca. 12% of the trunk length). The subdorsal unpaired tubes of segments 5–7 show intraspecific variation. *E. inaequalis* sp. nov. increases the count of the *E. coulli* group to 23 species.

1. Introduction

Kinorhynch exploration has greatly increased over the last decade resulting in the description of ca. 160 species, half of which belong to the diverse genus *Echinoderes* (Yamasaki, 2022). Thanks to such progress and the thorough redescription of multiple old species (e.g., Herranz and Leander, 2016; Yamasaki and Dal Zotto, 2019; Sørensen et al., 2020) certain morphological patterns started to be recognized within the genus, and putative monophyletic species groups were progressively defined. So far there are five species groups established, including the *Echinoderes cernunnos* group (Grzelak and Sørensen, 2022), *Echinoderes coulli* group (Sørensen, 2014), *Echinoderes dujardini* group (Sørensen et al., 2020), *Echinoderes horni* group (Anguas-Escalante et al., 2022), and *Echinoderes spinifurca* group (Landers and Sørensen, 2018; Sørensen et al., 2018). Of those, the *E. coulli* group was the first one defined, and also the one with the steepest increase in number of species, with around 18 new species over the last ten years, seven of which have been described in 2022 (Cepeda et al., 2022a; 2022b; Grzelak and Sørensen, 2022; Kennedy et al., 2022; Sørensen, 2022). The *E. coulli* group was originally characterised by the presence of an enlarged sieve plate, reduction or absence in number and size of trunk spines, occasionally present in a middorsal position on segment 4 and in the lateral series of segments 6–7, reduction or absence of lateral terminal accessory spines in females, and presence of tubes on segments 5 and 8 (Sørensen, 2014; Yamasaki and Fujimoto, 2014). However, over time the diagnostic characters of the group have slightly changed to accommodate the new species (e.g., Sørensen, 2014; Sørensen et al., 2016; Sørensen, 2022). Some of these changes refer to the habitat preference, which was thought to be shallow and highly fluctuating, with the majority of the species inhabiting intertidal marine or brackish waters (Sørensen, 2014; Yamasaki and Fujimoto, 2014). However, the recent description of a deep-sea *E. coulli* species, *Echinoderes blazeji* Grzelak and Sørensen, 2022, shakes the previous idea of their restricted bathymetric range (Grzelak and Sørensen, 2022) demonstrating that this group’s habitat ranges are more diverse than previously thought.

Here we describe yet another new species from the *E. coulli* species group collected from shallow localities in the atoll area of the Chuuk Islands, in the Central West Pacific. The samples belong to the same sampling campaign in which *Triodontoderes anulap* Sørensen and Rho, 2009 was described, and now, 13 years later, it is finally addressed.

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\(^*\) Corresponding author. Natural History Museum of Denmark, University of Copenhagen, 2100, Copenhagen, Denmark.

E-mail addresses: maria.herranz@bio.ku.dk, mariaherranzm@gmail.com (M. Herranz).

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2. Materials and methods

2.1. Sampling

Sediment samples containing *Echinoderes inaequalis* sp. nov. were collected from the Chuuk Islands, Micronesia by SCUBA diving on March 9th and 21st, 2007 at localities MAP-01 (000°27’27”N 151°53’52”E) and MAP-19 (000°27’11”N 151°54’15”E) at 30 and 1–2 m depth respectively (Fig. 1).

Meiofaunal organisms were roughly extracted from the sediment using the freshwater shock technique (Giere, 2009), subsequently filtered through a 63 μm mesh and fixed in 4% buffered formalin in seawater. Kinorhynchs were isolated under a Leica MZ8 stereomicroscope.

2.2. Microscopy

Specimens for light microscopy (LM) were transferred to distilled water, dehydrated through a graded series of glycerine and mounted in Fluoromount G on glass slides. Mounted specimens were examined and photographed using an Olympus BX60 microscope equipped with Nomarski differential interference contrast and photographed with an Olympus DP27 camera. Measurements were carried out with CellSens software.

Specimens for scanning electron microscopy (SEM) were dehydrated through a graded series of ethanol, transferred to acetone and critical point dried. Once dried the specimens were mounted on aluminium stubs, sputter coated with platinum-palladium and examined with a JEOL JSM-6335F field emission scanning electron microscope.

Line art illustrations were made in Adobe Illustrator v.26.3.01 combining information from LM and SEM. Images were adjusted in Adobe Photoshop v.23.3.2 and assembled into plates in Adobe Illustrator.

3. Results

3.1. Taxonomic account

Class Cyclorhagida (Zelinka, 1896) sensu Herranz et al., 2022.

Order Echinorhagata Sørensen et al., 2015

Family Echinoheridae Carus, 1885.

Genus *Echinoderes* Claparède, 1863.

Species *E. inaequalis* sp. nov.


(Figs. 2–4, Tables 1–2).

3.1.1. Etymology

The species name comes from the Latin in- (un or not) and -aequalis (equal or even), meaning, the uneven one, referring to the distinctive asymmetric distribution of subdorsal tubes on segments 5 to 7.

3.1.2. Diagnosis

*Echinoderes* with a single, minute middorsal spine on segment 4. Lateroventral tubes on segments 5, 7–9, midlateral tubes on segment 8, and sexually dimorphic laterodorsal tubes on segment 10. Single subdorsal tubes usually in alternating positions on segments 5–7 with intraspecific variation. Small glandular cell outlets type 2 in subdorsal, laterodorsal and ventrolateral positions on segment 2, subdorsal position on segment 4, and midlateral positions on segments 5–7; large, conspicuous, laterodorsal glandular cell outlets type 2 are present on segment 8. Large nephridial areas composed of elongated sieve plates and a posterior pore in sublateral position on segment 9. Short and stout lateral terminal spines with fringed edges. Males with three pairs of slender penile spines, and well-developed laterodorsal tubes on segment 10. Females with short and thin lateral terminal accessory spines, and reduced laterodorsal tubes on segment 10.

3.1.3. Material examined

Holotypic female collected by HSR on March 21st, 2007 from coral sand at 1–2 m depth at Chuuk Islands, Micronesia (locality MAP-19: 000°27’11”N, 151°54’15”E) (Fig. 1); mounted in Fluoromount G on a glass slide and deposited at the Natural History Museum of Denmark, under catalogue number NHMD-1176540.

Paratypes series include five specimens, three females and two males all of them mounted in Fluoromount G on glass slides and deposited at the Natural History Museum of Denmark, under catalogue numbers NHMD-1176541 to 45. Of those, male paratypes NHMD-1176542, NHMD-1176545 and female paratype NHMD-1176541 were collected at the same locality as the holotype; whereas the two remaining female paratypes, NHMD-1176543 and NHMD-1176544, were collected on March 9th, 2007 from subtidal sediment at 30 m depth (locality MAP-01: 000°27’27”N, 151°53’52”E).

Additional material includes 17 specimens mounted for SEM and stored in MVS personal reference collection.

3.1.4. Description

Adults with head, neck and eleven trunk segments (Figs. 2, 3A and 4A). Measurements and dimensions are given in Table 1. A summary of sensory spots, spines, tubes and glandular cell outlet positions is provided in Table 2. Mouth cone and introvert could not be studied in detail due to the poor condition of the SEM specimens prepared 14 years ago.

The neck consists of 16 placids numbered clockwise from the midventral 1 (Fig. 3B and C). Placids 2–16 are trapezoidal measuring 9 μm at the base while the midventral placid is more rectangular and wider measuring 15 μm (Fig. 2B, 3B–C). All placids articulate with the first trunk segment. Trichoscalid plates bearing trichoscalids appear dorsally on placids 6, 8, 10, 12 and ventrally on placids 2 and 16. Ventral trichoscalid plates are triangular with rounded edges, while dorsal trichoscalid plates are rounded and smaller (Figs. 2, 3B–C).

Trunk segments 1 and 2 consist of one closed cuticular ring (Figs. 2, 3A-C, 4A-B) while segments 3–11 are composed of one tegral and two sternal plates (Figs. 2, 3A and 4A). Glandular cell outlets type 1 consist of numerous minute pores arranged in a circle, situated in the anterior part of the segments, usually hidden under the posterior part of the previous segment and quite inconspicuous. Dorsal glandular cell outlets type 1 are located middorsally on segments 1–3, 10–11 and paradosally on segments 4–9 (Fig. 2). Ventral glandular cell outlets type 1 are lateroventral on segment 1 and ventromedial on segments 2–10 (Fig. 2).

Primary penicinate fringe well developed in all segments, composed of very short fringe tips on segments 1 and 2 (Figs. 2 and 4B) and long and
flexible tips in remaining segments (Figs. 2 and 4B). Secondary pectinate fringe absent on segment 1, and on segments 2–11 consisting of a single line of minute and regular teeth usually hidden under the primary pectinate fringe of previous segment (Fig. 4B).

Segment 1 with rounded sensory spots formed by a collar of short papillae surrounding at least one pore (Fig. 4B); sensory spots are located near the anterior segment margin in subdorsal and laterodorsal positions, and centrally in ventromedial position (Figs. 2, 3B–C, 4B). Cuticular hairs are abundant and distributed forming a wide belt covering most of the dorsal and ventral surface of the segment, except for the anterior margin of the segment, ventral area with a less dense hair covering (Figs. 2, 3B–C, 4B). All cuticular hairs emerging from round perforation sites in this and the following segments. The posterior segment margin is straight along the dorsal and lateral side but extends slightly posteriorly in the ventromedial and midventral areas.

Segment 2 with glandular cell outlets type 2, located in subdorsal, laterodorsal and ventrolateral positions (Fig. 2A and B, 3B–C, 4B). These are small with delicate fringed margins. Sensory spots present in middorsal, laterodorsal, midlateral and ventromedial positions; sensory spots on this and the following segments are oval. Hairs densely distributed in a belt covering the segment showing hairless areas in the anterior margin of the segment in ventromedial position (Fig. 4B–C, E). Hairs increasing in length posteriorly.

Segment 3 with sensory spots in subdorsal and sublateral positions (Fig. 2A and B). Dorsal hair pattern dense, cuticular hairs on the ventral side are covering the sternal plates except for hairless areas on the anterior margin of the sternal plates and narrow patches in ventromedial positions in this and the following segments.

Segment 4 with a very short acicular middorsal spine (ca. 11 μm measured from SEM) (Fig. 2A and B, 3E, 4C). Glandular cell outlets type 2 present in subdorsal position (Figs. 2A, 3E and 4C). Sensory spots present in laterodorsal position. Other characters similar to previous segment.

Segment 5 with lateroventral tubes and a single additional tube in subdorsal position (Fig. 2A and B, 3D–E, 4D, G). Each tube consists of a short and smooth basal part, and a longer distal part in this and the
Fig. 3. Light micrographs (DIC) showing traits in *Echinoderes inaequalis* sp. nov. Male paratype NHMD-1176545 (A, B, D, E, H), female holotype NHMD-1176540 (C, K, I) female paratype NHMD-1176543 (F, G), and male paratype NHMD-1176542 (J). (A) Male overview, ventral view. (B) Segments 1–2, ventral view. (C) Segments 1–2, dorsal view. (D) Segments 5–7, ventral view. (E) Segments 4–5, dorsal view. (F) Segments 7–8, lateroventral view. (G) Segments 6–7, dorsolateral view. (H) Male, segments 10–11 ventral view. (I) Female, segment 11, ventral view. (J) Segments 9–10, ventral view. (J’) Detail of sieve plate. (K) Segment 8, focused on laterodorsal area. Abbreviations: ldgco2, laterodorsal glandular cell outlet type 2; ldss, laterodorsal sensory spot; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvgco1, lateroventral glandular cell outlet type 1; lvlt, lateroventral tube; mdgco1, middorsal glandular cell outlet type 1; mlgco2, midlateral glandular cell outlet type 2; mlit, midlateral tube; mvp, midventral placid; pdgco1, paradorsal glandular cell outlet type 1; pe, penile spine; sdgco2, subdorsal glandular cell outlet type 2; sdss, subdorsal sensory spot; sdt, subdorsal tube; si, sieve plate; te, tergal extension; tp, trichoscalid plate; vlgco2, ventrolateral glandular cell outlet type 2; vmgco1, ventromedial glandular cell outlet type 1; vmss, ventromedial sensory spot. Circles indicate the position of glandular cell outlets type 1. Dashed circles indicate the position of sensory spots. Digits after abbreviations refer to segment number.
Fig. 4. Scanning electron micrographs (SEM) showing overviews and details of *Echinoberes inaequalis* sp. nov. (A) Male, lateroventral overview. (B) Segments 1–2 ventral view. (C) Segments 2–4, dorsal view. (D) Segments 5–6, lateroventral view. (E) Segment 2, laterodorsal view. (F) Detail of segment 8, lateral view. (G) Detail of segment 5, lateroventral view. (H) Segments 6–7, middorsal view. (I) Detail of sieve plate. (J) Female, segments 10–11, dorsal view. (K) Segments 9–11, ventral view. (L) Male, detail of penile spines, lateral view. (M) Male, detail of penile spines and laterodorsal tube, laterodorsal view. Abbreviations: ldgo2, laterodorsal glandular cell outlet type 2; lds, laterodorsal sensory spot; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvgco1, lateroventral glandular cell outlet type 1; lvts, lateroventral tube; mds, middorsal spine; mdss, middorsal sensory spot; mlgco2, midlateral glandular cell outlet type 2; mlss, midlateral sensory spot; mlss, midlateral tube; pe, penile spine; sdgo2, subdorsal glandular cell outlet type 2; sds, subdorsal sensory spot; sdt, subdorsal tube; si, sieve plate; spf, secondary pectinate fringe; te, tergal extension; vgco2, ventrolateral glandular cell outlet type 2; vlss, ventrolateral sensory spot; vmgo1, ventromedial glandular cell outlet type 1; vmss, ventromedial sensory spot. Circles indicate the position of glandular cell outlets type 1. Dashed circles indicate the position of sensory spots. Digits after abbreviations refer to segment number.
located in subdorsal position, the latter usually alternating in position (Figs. 2A, 3G and 4H). Glandular cell outlets type 2 present in midlateral position (Figs. 2A and 4G). Sensory spots present in subdorsal, laterodorsal and ventromedial positions (Fig. 2A and B, 4H). Remaining characters as on previous segments.

Segment 8 with tubes in lateroventral and midlateral positions (Fig. 2A and B, 4F). Large glandular cell outlets type 2 with fringed edges present in laterodorsal position (Fig. 2A and B, 3K, 4F). Sensory spots present in subdorsal position. Other characters similar to previous segments.

Segment 9 with tubes in lateroventral position. Sensory spots present in subdorsal, laterodorsal, midlateral and ventrolateral positions (Fig. 2A and B, 3J). Elongated nephridial areas present in sublateral position, and consisting of an oval perforated sieve plate (ca. 12 μm) with a posterior round pore (Fig. 3J-J’, 4I). Other characters similar to previous segments.

Segment 10 with tubes in laterodorsal positions, at or near the posterior segment margin. In males the tubes are long and similar of those described on segments 5–9 (Figs. 2C and 4M), whereas in females the tubes lack the basal part, showing just a flexible and short tubular structure (Figs. 2A and 4J). Very elongated sensory spots composed of two or three rows of short parallel papilae present in subdorsal and ventrolateral positions (Figs. 2, 4J-K). The posterior segment margin of the tergal plate is straight and with a small, but well-developed, pectinate fringe, whereas the margins of the sternal plates are concave, extending posteriorly near the midventral junction, and with well-developed fringe tips (Fig. 2B, D, 4K).

Segment 11 with short and stout lateral terminal spines with lateral fringes, and a short fringe wrapping the spine medially (Figs. 2 and 3A, H–I, 4J). Males with three pairs of tubular, and flexible penile spines, two of them long, and one slightly shorter (Fig. 2B and C, 3H, 4L-M). Females with a pair of short, thin and hairy lateral terminal accessory spines (Fig. 2A and B, 3I, 4J-K). Sensory spots are present in subdorsal position (two pairs) and in ventromedial position. The ventromedial sensory spots are very small, and located at the posterior margin of the sternal plate (Fig. 4K). One of the subdorsal pairs of sensory spots is also small and located on the margin of the tegal extensions (Fig. 2). The tegal plate is covered in hair-like extensions without perforation sites; sternal plates with a ventromedial fringed area (Fig. 2B, D, 4K). The margins of the sternal plates are curved and covered by long hairs that get shorter towards the lateroventral area (Fig. 4K). Tegal extensions are pointed extending further than the sternal plates and with a small distal notch (Figs. 2, 3H–I, 4J–K).

4. Discussion

4.1. Notes on diagnostic features

E. inaequalis sp. nov. clearly belongs to the E. coulli species group (Sørensen, 2014; Yamasaki and Fujimoto, 2014) based on the presence of the following features (Fig. 4G). Glandular cell outlets type 2 present in midlateral position (Figs. 2A and 4G). Sensory spots present in subdorsal, laterodorsal and ventromedial positions (Fig. 2A and B). Other characters similar to previous segment.

Segment 6 with a single subdorsal tube usually, but not consistently, in alternating position in respect to the single tube on segment 5 (Figs. 2A, 3G and 4H). Glandular cell outlets type 2 present in midlateral position (Figs. 2A and 3G). Sensory spots present in subdorsal, sublateral and ventromedial positions (Fig. 2A and B). Remaining characters as on previous segments.

Segment 7 with lateroventral tubes, and an additional single tube located in subdorsal position, the latter usually alternating in position with the unpaired tube of the preceding segment (Fig. 2A and B, 3F–G, 4H). Glandular cell outlets type 2 present in midlateral position (Fig. 3G). Sensory spots present in subdorsal, laterodorsal and ventrolateral positions (Fig. 2A and B, 4H). Remaining characters as on previous segments.

Table 1

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Table 2

Summary of the nature and location of sensory spots, glandular cell outlets, spines and tubes in E. inaequalis sp. nov. Abbreviations: LA: lateral accessory; LD: laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradozial; SD: subdorsal; SI: sieve plate; SS: sensory spot; TU: tube; TU*: unpaired tube; (δ), male condition of sexually dimorphic character; (♀), female condition of sexually dimorphic character.
of enlarged and conspicuous sieve plates with a posterior round pore, the absence of acicular trunk spines other than a minute middorsal spine on segment 4 and the terminal spine series, reduced lateral accessory terminal spine in females, and dense hair coverage on the trunk. Within the E. coulli group, E. inaequalis sp. nov. is very easily distinguished by the presence of single subdorsal tubes alternating in positions on segments 5–7. This character is unique not only across the E. coulli group but also among all Echinoderes.

Within the E. coulli group the species resembling E. inaequalis sp. nov. the most is Echinoderes hwitaaz Yamasaki and Fujimoto, 2014, from the Ryukyu Islands, Japan. E. hwitaaz and E. inaequalis sp. nov. show an identical pattern and appearance of glandular cell outlets type 2, short and stout lateral terminal spines, presence of lateral terminal accessory spines and similar pattern of tubes in the lateral series (Yamasaki and Fujimoto, 2014). The only differences between the two species are the presence of additional single subdorsal tubes on segments 5–7 in E. inaequalis sp. nov. and the absence of a middorsal spine on segment 4 in E. hwitaaz. However, the latter character could have been easily overlooked due to the dense hair pattern covering the trunk and the inconspicuous appearance of the spine, which is quite reduced and mostly resembles a hair. Based on the striking morphological similarities among E. inaequalis sp. nov. and E. hwitaaz and their Central Western Pacific distribution we hypothesize them to be closely related.

4.2. Intraspecific variation of cuticular characters

E. inaequalis sp. nov. shows intraspecific variation in the arrangement of the subdorsal single tubes of segments 5–7. The majority of the examined specimens show alternating tubes starting on the left side of segment 5, right side of segment 6, and left side of segment 7 (Fig. 2A). Other specimens showed two consecutive tubes aligned either in segments 5 and 6, or 6 and 7, and the remaining tube alternating in position with the previous. Given the low number of specimens studied it is hard to draw conclusions on the occurrence of the variation, however it is worth mentioning that out of ten specimens with visible tubes, at least three showed different combinations of the subdorsal tube pattern. Since the differences observed only involve changes in the position of the subdorsal tubes, left or right from the middorsal line, and one morpotype is the dominant whereas the rest are relatively rare, it is more likely that those changes respond to intraspecific variation. Nonetheless, molecular sequencing would be necessary to confirm this hypothesis.

Intraspecific variation of cuticular characters such as sensory spots, setae, glandular openings or tubes is not uncommon and has been reported widely across Kinorhyncha in species of e.g., Cristaphyes, Campyloderes, Condyloderes, Echinoderes (Neuhaus and Sørensen, 2013; Grzelak and Sørensen, 2018; Cepeda et al., 2019; Neuhaus et al., 2019). Within Echinoderes, variation in the presence of glandular cell outlets type 2 was so far only described in Echinoderes hamiltonorum Sørensen Rohal and Thistle, 2018 (Sørensen et al., 2018), whereas variation in the position of tubes is much more frequent. Grzelak and Sørensen (2018, 2019, 2022) and Sørensen (2018) described variation in the position and absence/presence of tubes in several Echinoderes species. Yamasaki and Dal Zotto (2019) also found tube and sensory spot pattern variations among and within populations of Echinoderes capitatus (Zelinka, 1928). The lack of molecular data in all the previous studies has led multiple open questions about the degree of intraspecific variation. Recently, Angua-Escalante et al. (2022) demonstrated that differences in the absence/presence of a single pair of tubes, among otherwise identical echinoderrid specimens from the same population, can be the result of sympatric speciation. This outcome stresses the importance of the inclusion of molecular sequencing in future taxonomical studies, and the urge to revisit and sequence already described species.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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