Two sides of a coin: the phylum Kinorhyncha in Panama. II) Pacific Panama

Fernando Pardos^{1,*}, María Herranz² and Nuria Sánchez¹

ABSTRACT

Meiofaunal sampling was carried out in 2011 in the Pacific coast of Panama, West of Panama City and Las Perlas Archipelago. No kinorhynch species have previously been reported from the area. Seven species were found, four of them new to science: *Echinoderes belenae* sp. nov., *Echinoderes muricatus* sp. nov., *Echinoderes strii* sp. nov., and *Cristaphyes harrisoni* sp. nov. In addition, *Echinoderes intermedius* and *Pycnophyes alexandroi*, recently described from the Caribbean coast, are also reported, as well as an unidentified species of *Antygomonas*. With the present results, the kinorhynch fauna of Panama reaches 23 species; furthermore, the distribution of species at both sides of Panama is discussed biogeographically.

Keywords: Kinorhynchs, meiofauna, biogeography, taxonomy, morphology, Panama Canal

1. Introduction

The Isthmus of Panama connects the continents of North- and South America and at the same time separates the Atlantic (Caribbean) and Pacific oceans in the area. It is one of the most classical objects of study for biogeography, both terrestrial, as a bridge between continents, and marine, as a barrier between Atlantic and Pacific oceans. The presence of the Panama Canal, a waterway connecting both oceans, adds further biogeographical interest to any survey of marine fauna in the area. The phylum Kinorhyncha is known from Panamanian waters since the first descriptions by Sørensen (2006), reporting nine species from Bocas del Toro (Caribbean side), of which five were new to science (see Table 1). Later, Neuhaus et al. (2014) reported the presence of *Centroderes barbanigra* Neuhaus et al., 2014 at the same locality. Additionally, Pardos et al. (this issue) reported four additional species new to science, plus several new citations from the same Caribbean area (Table 1), giving a total of 19 species. However, all these records and descriptions refer only to the Caribbean (Atlantic) side of the isthmus, while the kinorhynch fauna of the Pacific side is completely unknown. The nearest

records include *Fissuroderes thermoi* Neuhaus and Blasche, 2006 from the continental shelf off the coast of Costa Rica, *Campyloderes* cf. *vanhoeffeni* Zelinka, 1913 from Cocos Ridge (Neuhaus 2004) and several undescribed species of the genera *Echinoderes* and *Antygomonas* reported from Cocos Ridge, Coiba Ridge and Malpelo Ridge (see Neuhaus 2013, Fig. 5.6.5 and references therein). Going north, the nearest record of kinorhynchs is the recent report of the phylum from the Gulf of California (Álvarez et al., 2015), with up to 12 species identified just to the genus level: seven species of Pycnophyidae and two species of *Echinoderes* plus one species of *Fissuroderes*. The Pacific coast of South America remains largely unexplored except for the records of *Cateria styx* Gerlach, 1956, *Cristaphyes chilensis* (Lang, 1953) and *Cristaphyes anomalus* (Lang, 1953).

In the present contribution, we describe four species of kinorhynchs new to science from the Gulf of Panama on the Pacific coast, including the first Pacific reports of *Echinoderes intermedius* Sørensen, 2006 and *Pycnophyes alexandroi* Pardos et al., 2016. In addition, we discuss the distribution of kinorhynch species at both sides of the Isthmus.

2. Materials and methods

Sediment samples were taken from the Pacific coast of Panama, in the area around Playa Venao (Veracruz), Isla Taboga and Isla Pedro González (Las Perlas Archipelago) (Fig. 1) in December 2011, during a workshop on meiofauna organized by the Smithsonian Tropical Research Institute (STRI, Smithsonian Institution). Kinorhynch specimens appeared at seven sampling stations, whose data are summarized in Table 2. Sediment samples were taken by hand intertidally and by scuba diving or snorkelling subtidally. The sediment was processed for extraction of meiofauna following the “bubbling and blot” technique developed by Higgins (1964) and revised and updated by Sørensen and Pardos (2008). Kinorhynch specimens were picked up with an Irwin loop under a stereomicroscope and fixed in either 7% formalin or 100% ethyl alcohol.

Individual specimens were mounted in Fluoromount G® for observation and measurement under light microscopy using an Olympus BX51 microscope equipped with interference contrast optics (DIC) and a DP70 Olympus camera. Dimensions appearing in tables were obtained with Cella software from LM observations; measurements taken from SEM images are indicated directly in the text. Several specimens were prepared for SEM by dehydration through a graded series of ethanol, critical point dried and coated with gold or Platinum-Palladium. SEM observation and photography were performed with JEOL 6335F and Hitachi

S4700 Scanning Electron Microscopes. Type material is deposited at the Natural History Museum of Denmark (NHMD). Additional non-type material is deposited at the Kinorhynch Collection of the Meiofauna Lab, Universidad Complutense de Madrid (Spain).

3. Results

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

Order Echinorhagata Sørensen et al., 2015

Family Echinoderidae Zelinka, 1894

Genus *Echinoderes* Claparède, 1863

3.1. *Echinoderes belenae* sp. nov.

(Figs. 2-4)

3.1.1. Material examined

A total of 28 specimens were studied from all sampling stations yielding kinorhynchs (Fig. 1, Table 2). Holotype, adult male from station NAOS18a, recorded at Isla Taboga, December 9, 2011; mounted in Fluoromount G[®] deposited at the NHMD under accession number ZMUC KIN-988. Paratypes, three males and four females in total, from the stations NAOS3 (one male), NAOS18a (one male, one female), NAOS19 (two females), and NAOS21 (one male, one female) mounted on slides in Fluoromount G[®] and deposited at the NHMD under accession numbers ZMUC KIN-989 to KIN-995. Three male specimens were mounted for SEM. Remaining 16 specimens were mounted on slides (labelled PANI/ 47, 49, 62, 64, 81, 84, 85, 89, 90, 92, 94-99) and deposited at the Kinorhynch Collection of the Meiofauna Lab, Universidad Complutense de Madrid (Spain).

3.1.2. Diagnosis

Echinoderes with middorsal spines on segments 4, 6, 8 and lateroventral spines on segments 6-9; subdorsal tubes on segment 2; laterodorsal tubes on segments 4, 8-10; midlateral tubes on segments 2, 3, 5-7; lateral accessory tubes on segment 8, lateroventral tubes on segment 5 and ventrolateral tubes on segment 2. Lateral terminal spines short and stubby. Sublateral glandular cell outlets type 2 on segment 2.

3.1.3. Etymology

The new species is dedicated to Ms. Belén Pardos, daughter of the first author.

3.1.4. Description

All relevant dimensions and measurements are summarized in Table 3, and distribution of cuticular characters in Table 4. Although some studied specimens, mounted both for LM and for SEM appeared with the introvert partially extended, the information on scalid numbers and arrangement is scarce or unavailable, so no detailed description is possible. Neck with 16 placids trapezoid in shape, wider posteriorly. Midventral placid remarkably wider (11 μm , from SEM images) than others (7 μm , from SEM images). Placids adjacent to the midventral one bearing trichoscalid plates (Fig. 3A); paradorsal and laterodorsal placids also bearing trichoscalid plates, smaller than ventral ones (Fig. 3B).

Segment 1 as a closed ring. Cuticular hairs non-bracteate, relatively scarce and leaving the posterior third of the segment naked. Sensory spots in subdorsal, laterodorsal and ventromedial positions (Fig. 2A, B). Primary pectinate fringe poorly developed, with short, thin and regularly spaced tips. Depending on the contraction state of the specimen, the fringe may appear folded inwards, allowing the observation of the secondary fringe of the next segment (Figs 4D, G).

Segment 2 as a closed ring. Tubes in subdorsal, midlateral and ventrolateral positions (Figs 2A, B; 3A-B, 4B, C, D, G). Single middorsal sensory spot flanked by cuticular hairs (Fig. 4D); subdorsal and laterodorsal pairs of flanked sensory spots. Ventromedial glandular cell outlets type 1 near the anterior edge of the segment (Fig. 2A). Glandular cell outlet type 2 in sublateral position, adjacent to the midlateral tube (Figs 2A, 3A, 4G). Cuticular hairs bracteate, arranged into three or four wavy lines and increasing in length posteriorly. Conspicuous secondary pectinate fringe at the anterior edge of the segment, only visible with SEM consisting of short and flexible fringe tips (Fig. 4G).

Segment 3 and following segments with one tergal plate and two sternal plates. One pair of tubes in midlateral position (Fig. 2A, B). One pair of subdorsal flanked sensory spots. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 4 with a middorsal spine and one pair of laterodorsal tubes (Figs 2B; 3B; 4C, E).

Cuticular hairs as on the preceding segment; pectinate fringe conspicuous, with regularly spaced tips, longer than in preceding segments. Secondary pectinate fringe very regular, with fine tips (Fig. 4E).

Segment 5 with midlateral and lateroventral tubes (Figs 2A; 3A; 4E). Hairs and pectinate fringes as on the preceding segment.

Segment 6 with a middorsal spine and one pair of lateroventral spines (Fig. 3B, 4C). Tubes in midlateral position and sensory spots in paradorsal, subdorsal and ventromedial positions. Paradorsal sensory spots near the posterior edge of the segment. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 7 with lateroventral spines and midlateral tubes (Figs 2A, 3A). Sensory spots in subdorsal and ventromedial positions. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 8 with a middorsal spine and one pair of lateroventral spines. Tubes in lateral accessory and laterodorsal positions. One pair of paradorsal sensory spots near the posterior edge of the segment. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 9 one pair of lateroventral spines and one pair of laterodorsal tubes. Sensory spots in paradorsal, subdorsal and ventrolateral positions. Small oval sieve plate in sublateral position. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 10 with one pair of laterodorsal tubes. Sensory spots in subdorsal and ventrolateral positions. Subdorsal sensory spots flanked by a single long hair. Ventral posterior edge prolonged midventrally in a V shape (Figs 2A, 4F).

Segment 11 with lateral terminal spines short and coarse, ending in a sharp tip. The lateral terminal spines appear hollow, with a wide cavity, and bear short hairs on the lateral sides of their distal halves. Lateral terminal accessory spines in females, nearly as long as the lateral terminal spines, but much thinner. Males with three pairs of penile spines in midlateral position, the second pair shorter and coarser than the longer and filiform first (Figs 2B, 4F) and third pairs. Tergal plate extended dorsally into two well developed and pointed tergal extensions, showing an indentation on their medial edge.

3.1.5. Associated kinorhynch fauna

Echinoderes belenae sp. nov. seems to be widely distributed in the area, appearing in all sampling localities with kinorhynchs. Therefore, the new species co-occurs with all other species reported here for Pacific Panama: *Echinoderes muricatus*, sp. nov., *Echinoderes strii* sp. nov., *E. intermedius*, *P. alexandroi*, *Cristaphyes harrisoni* sp. nov., and *Antygomonas* sp.

3.2. *Echinoderes muricatus* sp. nov.

(Figs. 5-7)

3.2.1. *Material examined*

Only five specimens of *E. muricatus* sp. nov. were recorded intertidally from station NAOS7, at Playa Venao (Veracruz, Panama), December 2, 2011. Holotype, adult female, mounted on a glass slide with Fluoromount G[®] deposited at the NHMD under accession number ZMUC KIN-996. Paratypes, two adult females, mounted on glass slides deposited at the NHMD under accession numbers ZMUC KIN-997 to KIN-998. Two specimens, one male and one female, mounted for SEM.

3.2.2. *Diagnosis*

Echinoderes with middorsal spines on segments 4-8; spines very long and flexible; long tubes in ventrolateral position on segment 2 and in lateral accessory position on segment 8; smaller tubes in laterodorsal position on segment 10. Acicular spines in lateroventral position on segments 6-9. Lateral terminal spines extremely long.

3.2.3. *Etymology*

The species name, *muricatus*, is Latin and means “spiny like a *murex*”; it refers to the long spines of the new species that resembles the mollusk shells of the genus *Murex*.

3.2.4. *Description*

All relevant dimensions and measurements are summarized in Table 5, and distribution of cuticular characters in Table 6. Only very limited information on mouth cone and introvert scalds is available from the studied specimens, so no introvert description is addressed. Neck with 16 trapezoid placids articulated with the first trunk segment. Midventral placid clearly wider (11 μ m) and middorsal placid slightly slenderer (7 μ m) than others (7.4 μ m). Trunk with elongate proportions, cigar shaped and slightly slenderer towards posterior end (Figs. 5A, B, 7A, Table 5). Cuticular surface of trunk segments appears smooth except for the presence of

cuticular hairs. Cuticular hairs arranged into well-defined and characteristic patterns, always covering the anterior half of the respective segment, leaving the posterior half naked (Fig. 7C).

Segment 1 as a closed ring. Sensory spots in subdorsal, laterodorsal and ventromedial positions. The cuticle appears completely naked and smooth (Fig. 6A, D); no cuticular hairs present. Pectinate fringe well developed, with regular points.

Segment 2 as a closed ring. One pair of ventrolateral tubes very long, reaching the middle of the next segment (Figs. 5A, 6A). Tubes have the standard structure consisting of a basal part, broader and arising from a wide notch, and a distal shaft, thinner and showing lateral flaps or wing-like projections. The distal shaft ends with a terminal pore. Sensory spots in middorsal, laterodorsal and ventromedial positions. Paradorsal glandular cell outlets type 1 near the anterior margin of the segment, often overlapped by the pectinate fringe of the preceding segment. Cuticular bracteate hairs, arranged in a distinct pattern. They form 3 – 5 wavy rows regularly distributed around the anterior half of the segment, leaving the posterior half naked. The number of rows increases progressively on the following segments, to reach a maximum of 15-17 on the last segment (Fig. 7E). Hairs are remarkably short, except for the ones at the posteriormost row on each segment, conspicuously longer. Hair fields are interrupted by gaps of smooth cuticle in middorsal and laterodorsal areas (Fig. 7B, C, E). On this and the following segments, pectinate fringe well-developed, with regular points that become thinner and denser at the ventral region (Fig. 7F, G). Also, secondary pectinate fringe very conspicuous anterior to the hair areas and formed by very regular but short and thin points (Fig. 7B, C, F).

Segment 3 and following segments formed by one tergal and two sternal plates (Fig. 5A). One pair of subdorsal and midlateral sensory spots and one pair of anterior paradorsal glandular cell outlets type 1. Pectinate fringes, both primary and secondary, as on the preceding segment. Cuticular hairs as described for the preceding segment. Additionally, little patches of paraventral hairs are present in this and the following segments, without perforation sites and appearing as the free tips of longitudinal cuticular grooves (Fig. 7G).

Segment 4 with a middorsal acicular spine, long and flexible (Figs. 5B, 6A). One pair of paradorsal sensory spots slightly posterior to the MD spine. One pair of paradorsal glandular cell outlets type 1 located near the anterior edge of the segment and frequently overlapped by the free flap of the previous segment (Fig. 6D). Pectinate fringes and cuticular hairs as on the preceding segment, including paraventral patches.

Segment 5 with middorsal acicular spine, flexible and longer than the preceding one (Figs 5B, 7B). One pair of lateroventral tubes (Fig. 7B), similar in size and morphology to the ones

described for segment 2. One pair of midlateral sensory spots and one pair of paradorsal, anterior glandular cell outlets type 1. Pectinate fringes and cuticular hairs as on the preceding segment.

Segment 6 with middorsal acicular spine, flexible and longer than the preceding one (Figs. 5B, 6E, 7B). One pair of stiff acicular spines in lateroventral position. Sensory spots in paradorsal, midlateral and ventromedial positions (Figs. 5A-B, 7B). One pair of paradorsal glandular cell outlets type 1 near the anterior margin. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 7 with middorsal acicular spine, very long and flexible, plus one pair of lateroventral stiff acicular spines (Figs 5A-B, 6B, E). Sensory spots in paradorsal, laterodorsal, midlateral and ventromedial positions (Figs 5A-B, 7B). Paradorsal glandular cell outlet type 1 near the anterior margin. Cuticular hairs and pectinate fringes as on the preceding segment.

Segment 8 bearing the last and longest middorsal acicular spine (Figs 5B, 6B, E, 7B). Stiff acicular spine in lateroventral position plus a lateral accessory tube (Figs 5A, 6C, 7C). One pair of paradorsal sensory spots slightly posterior to the MD spine and one pair of glandular cell outlets type 1 near the anterior margin. Cuticular hairs arranged in a similar pattern as on previous segments, but with 9-10 hair rows. Segment otherwise similar to the preceding one.

Segment 9 with one pair of lateroventral stiff acicular spines (Figs 5A, 6C, 7C, F). Sensory spots in paradorsal, subdorsal, midlateral and ventrolateral positions (Figs. 7B, F). A pair of minute sieve plates present in sublateral positions, showing up to 9 perforations and with no distinct margins (Figs 5A, 7D). Cuticular hairs and pectinate fringes as on the preceding segments.

Segment 10 with one pair of laterodorsal tubes at least in females (Figs 5B, 7E). Sensory spots in subdorsal and ventrolateral positions. Posterior edge of the segment projected midventrally as a V shape (Figs 5A, 7F). Primary pectinate fringe with tips shorter than in preceding segments. Patches of cuticular hairs well extended, with up to 15 – 17 hair rows (Fig. 7E).

Segment 11 with extremely long lateral terminal spines (Fig. 5 A-B). Females with lateral terminal accessory spines and males with three pairs of penile spines in midlateral position, the second pair remarkable coarser and shorter than the others. Sensory spots in paradorsal and laterodorsal positions, close to the segment posterior edge (Fig. 5A-B). Middorsal elevation spindle-shaped, flanked by hair-like, filiform cuticular projections (Fig. 7E). Bracteate hairs absent. Glandular cell outlet type 1 middorsally, visible with SEM as a group of tiny perforations. Secondary pectinate fringe well developed. Tergal extensions pointed, covered by numerous filiform cuticular projections on the medial surface (Figs 5A-B, 6F, 7E).

3.2.5. Associated kinorhynch fauna

The new species appeared just on one single sampling station in Playa Venao (See Table 2) together with *Echinoderes belenae* sp. nov.

3.3. *Echinoderes strii* sp. nov.

(Figs. 8-10)

3.3.1. Material examined

All specimens studied appeared in station NAOS15, sampled December 6, 2011. Holotype, adult male, mounted on slide with Fluoromount G and deposited at the NHMD under accession number ZMUC KIN-999. Paratypes, 2 adult females and one male mounted on slides, deposited at the NHMD under accession numbers ZMUC KIN-1000 to KIN-1002. Four specimens, 2 males and two females, mounted for SEM. All 7 remaining specimens (labelled PAN I/65-68, 70, 72, 75) deposited at the Kinorhynch Collection of the Meiofauna Lab, Universidad Complutense de Madrid (Spain).

3.3.2. Diagnosis

Echinoderes without acicular spines except for lateral terminal spines. Lateral terminal accessory spines lacking in both sexes. Tubes in midlateral position on segment 3, in lateroventral and laterodorsal positions in segments 5 and 8, and in subdorsal positions on segment 10 of males. Large oval sieve plate midlaterally in segment 9. Tergal extensions of segment 11 conspicuously rounded in males and truncate with a filiform lateral projection in females. Trunk cuticle with tiny perforations interspersed among cuticular hairs. Segments 10 and 11 retractable into segment 9.

3.3.3. Etymology

The species name is dedicated to the Smithsonian Tropical Research Institute (STRI) with the deep gratitude of the authors.

3.3.4. Description

All relevant dimensions and measurements are summarized in Table 7, and distribution of cuticular characters in Table 8. Although some of the specimens studied showed the introvert fully extended (Figs 9A; 10B, I), the information on the number and arrangement of introvert appendages is too partial and incomplete so no introvert map is provided. Nevertheless,

primary spinoscalids appear quite characteristic showing four flaps along their proximal half (Fig. 10B). The most proximal has three stiff spikes, reduced to two in the second one. The third and fourth ones are overlapping tufts or fringes. The inner armature of the retractable mouth cone could not be examined in detail. The outer armature is composed by nine oral styles (Fig. 10B), formed by two jointed units. The basal units alternate between longer and shorter, making the joints appear at two different levels. The neck is formed by 16 trapezoid placids, being the midventral one clearly wider than others (Figs 8A-B, 9B, 10A).

The trunk is formed by 11 segments and is relatively short and wide, with a thickset outline. A remarkable feature is the telescopic retraction of the two terminal segments, 10 and 11, into segment 9 showed by some of the specimens (Figs 9E, I, J; 10 A, F, G, I) while other specimens displayed a normal, extended appearance (Figs 9A, F, H; 10H). This fact is hardly explained as a fixation artifact, because it does not happen to all specimens of the same sample and always the same segments are retracted. Moreover, the contraction state does not affect to the whole specimen, because some of the individuals appeared with the introvert fully extended and the posterior end completely retracted (Compare Figs 10A and 10I).

The whole trunk cuticle appears covered by non-bracteate cuticular hairs, long and regularly spaced, giving the animal a hairy aspect. Additionally, the cuticle show tiny perforations widespread over the tergal surface of segments 2-11, visible with both SEM at high magnification (Fig. 10D) and DIC (Fig. 9C). These perforations are easily distinguished from hair perforation sites by size (Figs 9C, 10D). Sensory spots are oval areas with filiform micropapillae and unusually big, measuring about 5 μm (estimated from SEM).

Segment 1 as a closed ring. Large and oval sensory spots in subdorsal, laterodorsal and ventrolateral positions (Fig. 8A, B). Dorsal sensory spots very close to the anterior edge of the segment (Figs 8B, 10A-B). Cuticular hairs widespread around the segment without a definite pattern and not as densely packed as on following segments. Cuticular surface smooth except for hair perforation sites. Primary pectinate fringe well-developed, with a quite regular pattern of alternating long and short tips (Fig. 8E).

Segment 2 as a closed ring. Sensory spots in subdorsal and laterodorsal positions (Fig. 8A, B). Cuticular hairs covering the segment surface densely with no definite pattern but regularly spaced. Tiny perforations interspersed but not very abundant around the segment. Primary pectinate fringe as on the preceding segment. Secondary fringe at the anterior edge, with regular and minute tips.

Segment 3 and following segments with one tergal and two sternal plates. One pair of midlateral tubes (Figs 8B; 10A, E) of standard structure. Sensory spots in subdorsal, laterodorsal and ventromedial positions. Cuticular hairs regularly distributed all around the segment. Tiny perforations only present on the tergal plate. Pectinate fringes as on the preceding segment.

Segment 4 with sensory spots in laterodorsal and ventromedial positions. Cuticular hairs, perforations and pectinate fringes as on the preceding segment.

Segment 5 with pairs of tubes in laterodorsal and lateroventral positions (Figs 8A, B; 9B, D; 10C, E, I). Subdorsal and ventrolateral sensory spots, the latter anterior to the tube level. Cuticular hairs and perforations as on the preceding segment. All tips of the primary pectinate fringe elongated and sharp, with no alternating pattern. Secondary pectinate fringe as on the preceding segment.

Segment 6 with sensory spots in laterodorsal, midlateral (Fig. 10C, E) and ventromedial positions. Cuticular hairs, perforations and pectinate fringes as on the precedent segment.

Segment 7 with sensory spots in laterodorsal, midlateral and ventrolateral positions. Cuticular hairs, perforations and pectinate fringes as on the precedent segment.

Segment 8 with pairs of tubes in laterodorsal and lateroventral positions (Figs 8A, B; 9D; 10A, F, G, I). Laterodorsal and ventrolateral sensory spots present, the former anterior to the tube level. Cuticular hairs, perforations and pectinate fringes as on the precedent segment.

Segment 9 with sensory spots in laterodorsal (2 pairs) (Figs 9A, B; 10G, H), midlateral and ventrolateral positions. The two laterodorsal sensory spots appear aligned, with the posterior one being twice as big as the anterior (Figs 8B, 10G). Conspicuously large sieve plate in midlateral position (Figs 8A, B; 9D, H; 10D, F-H). It is an elongated oval area 8 – 14.5 μm long and 3 - 5 μm wide (measured from SEM images) profusely perforated by hundreds of minute round holes and associated with a big pore in the centre of a circular area, 3 μm posterior (Fig. 10D). Cuticular hairs, perforations and pectinate fringes as on the precedent segment.

Segment 10 with one pair of subdorsal tubes in males only (Figs 8B; 9F; 10G, H). Sensory spots in laterodorsal and ventrolateral positions. Posterior edge of the segment slightly convex on dorsal side in both sexes and ventrally in females only (Fig. 8A-D)

Segment 11 with lateral terminal spines covered by cuticular filiform projections that give the spine a hairy appearance (Fig. 10G, H). Lateral terminal spines slightly longer in females (Table 7). Lateral terminal accessory spines absent in females (Figs 8C, D; 9A, E, H-J; 10H). Males with

3 pairs of penile spines (ps) in midlateral position (Figs 8A, B, 9G, 10G). First (ps1) and third (ps3) pairs filiform, ps1 slightly longer (Fig. 10G); second (ps2) pair coarser and shorter. Tergal extensions short and rounded in males (Figs 8A, B; 9E, G); females with tergal plate ending abruptly (Fig. 8C, D); only a filiform projection marks the position of tergal extensions (Figs 9H-J, 10H).

3.3.5. Associated kinorhynch fauna

Echinoderes strii sp. nov. appeared in a single station at a mangrove field in Pedro González Island (See Table 2), together with *Echinoderes belenae* sp. nov.

Class Allomalorhagida Sørensen et al., 2015

Family Pycnophyidae Zelinka, 1896

Genus *Cristaphyes* Sánchez et al., 2016

3.4. *Cristaphyes harrisoni* sp. nov.

(Figs. 11-13)

3.4.1. Material examined

Holotype, adult female, collected at Isla Taboga, station NAOS21, December 9, mounted in Fluoromount G®, deposited at the NHMD under accession number ZMUC KIN-1003. Paratypes, one adult male and two adult females, same collecting data as holotype. The male mounted on slide with Fluoromount G®, deposited at NHMD under accession number ZMUC KIN-1004; one female specimen mounted for SEM and stored at the Kinorhynch Collection of the Meiofauna Lab, Universidad Complutense de Madrid. One adult female, mounted on slide with Fluoromount G® stored as additional material (slide PAN II/60) at the Kinorhynch Collection of the Meiofauna Lab, Universidad Complutense de Madrid.

3.4.2. Diagnosis

Cristaphyes with middorsal processes on segments 1-9; unpaired paradorsal setae on segments 2, 4, 6 and 8, pairs of paralateral setae on segment 1, laterodorsal setae on segments 2-9, lateroventral setae on segments 2, 4, 6, 8 and 10, ventrolateral setae on segments 1, 5 and 10, and ventromedial setae on segments 3-8. Without lateral terminal spines.

3.4.3. Etymology

The species name is dedicated to Dr Frederick Harrison, eminent zoologist, scientific editor and closest friend of the first author.

3.4.4. Description

All relevant dimensions and measurements are summarized in Table 9, and distribution of cuticular characters in Table 10. Only very limited information on mouth cone and introvert scalds is available from the studied specimens, so no introvert description is provided. The neck is formed by four dorsal and four ventral placids. Dorsal placids are rectangular and of similar size (Fig. 12B). Ventral placids are similar but smaller than the dorsal ones. All placids appear robust and hard, strongly sclerotized.

The trunk is formed by 11 segments, the first one consisting of one tergal and three sternal plates, two episternal and one trapezoidal midsternal plate. Segments 2 to 11 with one tergal and two ventral sternal plates (Figs 11, 12A, B, 13A, B). Segments 1-9 with middorsal processes. Segments 2 to 10 with small, oval, subdorsal, ventrolateral and ventromedial glandular cell outlets (Fig. 12C). Similar glandular cell outlets on segment 1, but the dorsal side are displaced medially whereas the ventral ones are laterally displaced. Oval muscular scars in laterodorsal and ventromedial position along the trunk segments. Inconspicuous cuticular ridges. Pachycycli and peg and socket joints on segments 2-10. Apodemes absent. Two to three secondary pectinate fringes by segment (Fig. 11). Pectinate fringes only visible with SEM.

Segment 1 with posterior margin of tergal plate bearing a middorsal process not associated to intracuticular atria (Fig. 12C). Anterolateral margins of the plate projecting anteriorly into horn-shaped extensions. Anterior edge of tergal plate smooth, finely denticulate in the middle region. Two pairs of subdorsal and laterodorsal sensory spots (Fig. 12B) and one pair of paralateral setae present (Fig. 12D, E). Sternal plates with a smooth anterior area and paired ventrolateral setae (Fig. 12D, E). Pairs of ventromedial sensory spots present at the anterior third of the plate. Midsternal plate anteriorly narrow (Fig. 12D).

Segment 2 with posterior margin of tergal plate bearing a middorsal process similar to that of segment 1 (Fig. 12C). Unpaired paradorsal seta plus paired setae in laterodorsal and lateroventral positions (Fig. 12B, E). One pair of subdorsal and two pairs of laterodorsal sensory spots, with the laterodorsal setae being located between the sensory spots. Sternal plates of females with one pair of ventromedial sensory spots and one additional pair of glandular cell outlets. Males with one pair of large ventromedial tubes, setae and sensory

spots (Fig. 13E). The tubes are located between the more medial setae and the sensory spots (Fig. 12E). Ventrolateral glandular cell outlets present in both sexes.

Segment 3 with tergal plate similar to that on segment 2, but without paradorsal and lateroventral setae. Sternal plates with paired ventromedial setae and sensory spots, the latter slightly displaced laterally (Figs 11A, 12F).

Segment 4 with tergal plate similar to that on segment 2. Sternal plates similar to those on segment 3 (Fig. 12F).

Segment 5 with tergal and sternal plates similar to those on segment 3 (Fig. 13C), but with one pair of ventrolateral setae (Fig. 11A, B).

Segment 6 with tergal plate similar to that on segment 4 (Figs 11B, 13C). Sternal plates similar to segment 3 (Fig. 11A).

Segment 7 with tergal and sternal plates similar to those on segment 3 (Figs 11A, B, 13C, D).

Segment 8 with tergal plate similar to that on segment 4 (Fig. 13D), but with an additional pair of subdorsal sensory spots (Figs 11B, 12B). Sternal plates similar to segment 3 (Figs 11A, 13F).

Segment 9 with tergal plate similar to that on segment 3 (Fig. 11B). Paralateral protonephridial openings present, not sieve-like. Sternal plate similar to those on segment 3, although the ventromedial setae seem to be absent (Figs 11A, 13F).

Segment 10 without middorsal structure specializations or intracuticular atria. One pair of lateroventral setae and laterodorsal sensory spots present (Fig. 11B). Sternal plates with paired ventrolateral setae and ventromedial sensory spots (Fig. 13F). Posterior sternal segment margin straight in females and rounded in males (Fig. 11A, C). Remaining characters on both tergal and sternal plates uncheckable.

Segment 11 developed lateral terminal spines (Figs 12A, B, 13A, B, F), but with a pair of bulbous protuberances instead (Fig. 11). Males with two pairs of penile spines and genital pores surrounded by a tuft of long hairs. Remaining characters on both dorsal and ventral plates uncheckable.

3.4.5. Associated kinorhynch fauna

The new species appeared together with *Echinoderes belenae* sp. nov. in Isla Taboga (See Table 2).

4. Discussion

4.1. Remarks on diagnostic and taxonomic features of the new species

4.1.1. Remarks on *Echinoderes belenae* sp. nov.

Echinoderes belenae sp. nov. has a pattern of middorsal spines of segments 4, 6, and 8 that is very common for species of the genus. Also, the pattern of lateroventral spines/tubes is quite usual, with one pair of tubes in segment 5 and spines on segments 6 to 9, plus lateral accessory tubes on segment 8. However, the pattern of midlateral tubes on segments 2, 3, 5, 6 and 7 is unique and justifies by itself the erection of a new species. It should be noted, however, that midlateral tubes are difficult to be recognized in LM mountings, because of their location at the edges of the specimen; only SEM observations allow the accurate identification of this feature. Also, the presence of laterodorsal tubes in segments 4, 8-10 is a pattern not shared by any other kinorhynch species.

The presence and distribution of glandular cell outlets type 2 as a significant taxonomic character has been stressed very recently (see contribution of Sørensen et al., this special issue, and discussion therein). The presence of this type of glandular cell opening seems to be quite widespread among the species of *Echinoderes*. However, only *E. abbreviatus* Higgins, 1983, *E. intermedius*, *E. reicherti* Neves et al., 2016, and *E. rociae* Pardos et al., 2016 share with *E. belenae* sp. nov. a single pair of glandular cell outlets type 2 in sublateral position of segment 2. Interestingly, *E. abbreviatus*, *E. intermedius* and *E. rociae* have been described from the Caribbean. The exception is *E. reicherti*, recently described from Faro (Portugal). Both *E. intermedius* and *E. reicherti* have long lateral terminal spines and cannot be confused with the new species. However, *E. belenae* sp. nov. shares several characters with both *E. abbreviatus* and *E. rociae*, such as size, outline, middorsal spines on segments 4, 6, 8, lateroventral tubes on segment 5, lateroventral spines on segments 6-9 and the short and stubby lateral terminal spines. But *E. abbreviatus* has tubes only ventrolaterally on segment 2 and in lateral accessory position on segment 8, while *E. rociae* and *E. belenae* sp. nov. have a much more complex set of tubes.

Undoubtedly, the species that resembles *E. belenae* sp. nov. the most is *E. rociae*, described from the Caribbean side of Panama (see contribution of Pardos et al., in this special issue).

Although easily distinguishable by the series of midlateral tubes plus LD tubes of segments 4 and 9 in *E. belenae* sp. nov., they share the spine formula, LA tubes on segment 8, SD tubes on segment 2 and LD tubes on segment 8, plus the short and stubby LTS.

This last easy-to-detect feature, the presence of short and stubby lateral terminal spines is shared by 9 other species in the genus (see contribution of Pardos et al., 2016 in this special

issue, and discussion therein). Nothing is known about the taxonomic or adaptive value of short and stout LTS. However, there is no doubt about the applied utility of the character, which gives a characteristic general appearance to the specimens, allowing a very easy identification even with a stereomicroscope.

4.1.2. Remarks on *Echinoderes muricatus* sp. nov.

The generic identity of this species has been somehow problematic. The few specimens available mounted for LM are all in lateral orientation, probably because the long trunk and spines tend to rest in that position. Hence, articulation lines between ventral cuticular plates are not easy to discriminate, especially in the two first trunk segments, a main diagnostic character for cyclorhagid genera. SEM images clearly show the two first trunk segments as closed rings, pointing clearly to the genus *Echinoderes*. However, other cyclorhagid genera such as *Cephalorhyncha*, *Fissuroderes* and *Meristoderes* show a different configuration of those segments, in some cases with just subcuticular fissures delimiting sternal plates, only detectable with LM. In fact, species such as *Cephalorhyncha nibakkeni* (Higgins, 1986), *Fissuroderes sorenseni* Herranz and Pardos, 2013 and several species of *Meristoderes* (Herranz et al, 2012; Sørensen et al., 2012; Herranz and Pardos, 2014) are quite suggestive in terms of general outline and very long and flexible spines. Nevertheless, and in the absence of more conclusive material, we decided to ascribe the new species to the genus *Echinoderes*.

E. muricatus sp. nov. has a very common pattern of five middorsal spines in segments 4-8, shared with 46 other species in the genus. From these, only five share the ventral series pattern of ventrolateral tubes in segment 2, lateroventral in 5, and lateral accessory in 8, plus lateroventral spines in segments 6-9. These are *Echinoderes augustae* Sørensen and Landers, 2014, *Echinoderes adrianovi* Herranz et al., 2014, *Echinoderes dujardinii* Claparède, 1863, *Echinoderes gerardi* Higgins, 1978, and *Echinoderes kanni* Thormar and Sørensen, 2010. *E. muricatus* sp. nov. differs from *E. augustae* by the presence in the latter of midlateral tubes in segment 4 and by the presence in the former of laterodorsal tubes in segment 10. But mostly by the elongated outline and the very long lateral terminal spines of *E. muricatus* sp. nov. vs. the conspicuously short and stout lateral terminal spines of *E. augustae* (LTS/TL 66% in *E. muricatus* sp. nov. but only 11,4% in *E. augustae*). Both *E. adrianovi* and *E. kanni* have subdorsal tubes on segment 2 that are lacking in the new species. *E. dujardinii* and *E. gerardi* are fully coincident in the spine formula, but again *E. muricatus* sp. nov. has a longer trunk length and the middorsal spines of the new species are considerably longer than the

conspicuously short middorsal spines of the two species referred to above. Unfortunately, all specimens of *E. muricatus* sp. nov. studied with LM were females, and only one male was available for SEM and from ventral view. Consequently only very limited information is available on sexually dimorphic characters. Laterodorsal tubes in segment 10 are usually a sexually dimorphic feature appearing only in males of several species of the genus *Echinoderes*. However, females of the new species do show LD tubes in segment 10, so we would expect that males also have them, differing from females by the presence of penile spines and the lack of lateral terminal accessory spines.

4.1.3. Remarks on *Echinoderes strii* sp. nov.

E. strii sp. nov. can be distinguished from most other species in the genus by its complete lack of spines (except lateral terminal ones) and its tube formula, dorsal and ventral ones on segments 5 and 8 (LV5, 8; LD5, 8) plus midlateral tubes on segment 3 (ML3) and subdorsal tubes on segment 10 of males (LD10). The new species also show conspicuously rounded tergal extensions of segment 11 in males; the filiform projections of tergal extensions in females appear very similar to equivalent structures of female *Echinoderes applicitus* Ostmann et al, 2012. The most striking feature of the new species is the cuticle perforated by numerous tiny pores, which, together with the bigger perforation sites of cuticular hairs, give the whole surface of the cuticle a very characteristic appearance. This feature has not been described in any other species of kinorhynch. No subcuticular structure seems to be associated to these tiny perforations, whose function is completely unknown. Other remarkable feature is the presence of four sets of spines/flaps on the primary spinoscalids; the two proximal groups of spines are identical to those present in *E. applicitus*, but this latter species lacks the two distal fringes.

To our knowledge, no kinorhynch species has been described formally as retracting telescopically the posteriormost segments into the ninth one. However, the original description of *Echinoderes maxwelli* (Omer-Cooper, 1957) includes some illustrations that could suggest this phenomenon but without description or mention in the text (see Figs. 1, 1b, 1c in Omer-Cooper 1957). Recent revision of SEM material of *E. maxwelli* (Sørensen, pers. com.) confirms the retraction of the last two segments in some individuals. In addition, *E. applicitus* is clearly able to retract just the terminal segment (Ostmann et al. 2012). In our specimens, the retraction of the last two segments is nearly total and goes far beyond the expected flexibility of intersegmentary junctions. Although this behaviour should be

considered with caution, the situation has been found quite consistently in different specimens, and can hardly be attributed to a general shrinking by fixation. Whether this is a particular or exclusive ability of *E. strii* sp. nov. with unknown biological significance or just a very strong contraction state induced by natural or artificial causes, remains as an open question.

E. strii sp. nov. shows features that clearly point to a relationship with the so-called *E. coulli*-group (see Table 11): the nearly complete lack of spines other than the lateral terminal (LTS) and the presence of enlarged, oval sieve plates on segment 9. In addition, this group of species shares the estuarine/brackish water habitat, with a reduced salinity (see discussion in Ostmann et al., 2012), in good agreement with the mangrove habitat of the new species (salinity value: 27‰). To date, ten *Echinoderes* species have been cited as belonging to the *E. coulli*-group: *Echinoderes coulli* Higgins, 1977, *E. maxwelli*, *E. ohtsukai*, *E. applicitus*, *Echinoderes rex* Lundbye, Rho and Sørensen, 2011, *E. komatsui* Yamasaki and Fujimoto, 2014, *E. hwiizaa* Yamasaki and Fujimoto, 2014, *E. marthae* Sørensen, 2014, *Echinoderes annae* Sørensen, Gasiorowski, Randsø, Sánchez and Neves, 2016, and *Echinoderes teretis* Brown, 1999 in Adrianov and Malakhov 1999. The latter species is known from an unpublished PhD Thesis (Brown 1985) and has never been described formally. However, it should be considered as a valid species very often cited in the literature (see Neuhaus 2013 for explanation of its nomenclatorial status). Also *Echinoderes aspinosus* Sørensen, Rho, Ming, Kim and Chang, 2012 is considered as very close to the *E. coulli*-group, although not strictly included in it.

E. strii sp. nov. shares with *E. coulli* the lateroventral tubes in segments 5 and 8, but both species differ by the presence of midlateral tubes in segment 3 and laterodorsal tubes in segments 5, 8 and 10, lacking in the latter. Comparison with *E. maxwelli* is difficult because of the uncertain and incomplete description of the species (Omer-Cooper 1957), even after revision of type material (Higgins 1977; Lundbye et al. 2011; Ostmann et al. 2012). Nevertheless, tubes are present in lateroventral position of segments 5 and 8, as they are in the new species; but contrarily, *E. maxwelli* shows minute lateral accessory spines on segment 6 and sublateral on 7, lacking in *E. strii* sp. nov., and lacks the midlateral and laterodorsal tubes present in the new species. *E. applicitus* is, together with *E. komatsui*, *E. marthae* and *E. coulli*, the species most resembling *E. strii* sp. nov. They share the absence of spines and the presence of lateroventral tubes on segments 5 and 8, plus the laterodorsal/subdorsal tubes on 10. Differences regard the midlateral tubes on segment 3 and the laterodorsal tubes on segments 5 and 8 of the new species. Only *E. marthae* has laterodorsal tubes on segment 8, but not on 5. The three species are furthermore distinguished by the characteristic middorsal extension of

segment 11 in *E. applicitus* (Ostmann et al. 2012) and *E. komatsui* (see Fig. 6C in Yamasaki and Fujimoto 2014) vs. the conspicuously rounded, paired tergal extensions in males of *E. strii* sp. nov. and truncate posterior end in females. *E. ohtsukai* differs from the new species by the presence of a middorsal spine on segment 4, presence of LTAS in females, presence of fringed tubes and by the absence of laterodorsal tubes on segments 5 and 8 present in *E. strii* sp. nov. Both *E. teretis* and *E. rex* differ from *E. strii* sp. nov. by the presence of a middorsal spine on segment 4 and the presence of lateroventral spines on segments 6 and 7. *E. annae* shares with *E. strii* sp. nov. the lateroventral tubes on segments 5 and 8, but both species differ in the presence of laterodorsal tubes on segments 5 and 8, absent in *E. annae*, and in the location of midlateral tubes, on segment 3 in *E. strii* sp. nov. and on segment 9 in *E. annae*. Moreover, *E. annae* also shows a middorsal spine on segment 4, lacking in *E. strii* sp. nov.

4.1.4. Remarks on *Cristaphyes harrisoni* sp. nov.

Cristaphyes harrisoni sp. nov. shares with seven congeners the lack of well-developed lateral terminal spines, having a pair of bulbous protuberances instead: *C. anomalus*, *Cristaphyes belizensis* (Higgins, 1983), *Cristaphyes panamensis* Pardos et al., 2016, *Cristaphyes phyllotropis* (Brown and Higgins, 1983), *Cristaphyes rabaulensis* (Adrianov, 1999 in Adrianov and Malakhov, 1999), *Cristaphyes spinosus* (Lang, 1949), and *Cristaphyes yushini* (Adrianov, 1989). However, none of these species have paradorsal setae only on segments 2, 4, 6 and 8, as does *C. harrisoni* sp. nov. *Cristaphyes yushini* and *C. belizensis* have paradorsal setae also on segment 9 (Higgins, 1983; Adrianov, 1989), *C. anomalus* has paradorsal setae on segments 3-6, 8-9, and *C. phyllotropis* on segments 2, 5-6, 8 (no data for segments 4 and 9) (Lang, 1953) (see also Sánchez et al, 2016; Appendix S1 and Table S1). According to the original descriptions *C. rabaulensis* and *C. spinosus* do not have paradorsal setae at all (Lang, 1949; Adrianov and Malakhov, 1999).

Moreover, *Cristaphyes harrisoni* sp. nov. lacks a keel-like middorsal process on segment 10, a feature useful to separate it from a group of species in the genus: *Cristaphyes abyssorum* (Adrianov and Maiorova, 2015), *Cristaphyes arctous* (Adrianov, 1999) in Adrianov and Malakhov, 1999, *Cristaphyes chukchiensis* (Higgins, 1991), *Cristaphyes cristatus* (Sánchez et al., 2013), *Cristaphyes cryopygus* (Higgins and Kristensen, 1988), *Cristaphyes furugelmi* (Adrianov, 1999) in Adrianov and Malakhov, 1999, *Cristaphyes nubilis* (Sánchez et al., 2014), and *Cristaphyes odhneri* (Lang, 1949), in which the process appears conspicuously extended beyond the segment 11.

4.2. Kinorhynch fauna of Panama: biogeographical considerations

The present study allows for the first time the comparison of the kinorhynch fauna of two areas relatively close in terms of distance, but belonging to two different oceans, the Atlantic and the Pacific. From the biogeographical point of view, the Isthmus of Panama is a bridge connecting North and South America, allowing the terrestrial fauna of both continents to cross in both directions. However, the rising of the Isthmus operates as a barrier for marine life. The Isthmus is the narrowest land mass from the Arctic to the Antarctic seas, and its rising was a pivotal event in the history of the whole planet, with great consequences in oceanography, climate and distribution of living organisms. The classical hypothesis to date the raising of the Isthmus places the event 3.5 MY ago (Haug and Tiedemann 1998; Coates et al. 2003). However, recent studies bring the event even further back in time to 13-15 MY (Bacon et al. 2015; Montes et al. 2015), increasing considerably the time lapse for evolutionary events to occur in a classical process of allopatric speciation. Hence, we could expect that the kinorhynch fauna at both sides of Panama is formed by different species, with Atlantic and Pacific populations being isolated since long time ago.

The present results agree with such hypothesis in general terms, showing a group of species with Caribbean affinities in the Atlantic side (see Pardos et al., this special issue) and a different group of species in the Pacific. However, *E. intermedius* and *P. alexandroi* deviate from this disjunct distribution pattern appearing both in Bocas del Toro (Caribbean) and Pacific Panama. Three possible scenarios would explain their presence at both sides.

1) Both species are very widely distributed, at least along a broad area around the Americas or even worldwide, so their distribution patterns are independent from the presence of the Isthmus. This reflects the idea that “everything is everywhere”, the well-known EiE hypothesis especially applied to meiofaunal organisms (Finlay, 2002; Fenchel and Finlay, 2004). However, new methodologies of study, singularly DNA sequencing and confocal laser scanning microscopy point to a high degree of cryptic speciation in meiofauna communities (Curini-Galletti et al., 2012; Leasi and Todaro, 2009). The knowledge on these two species is still very limited to make any guess about their distribution patterns, but it seems quite unlikely that they are so widespread to appear at both sides of the Isthmus and at the same time have passed unnoticed all around the world or at least along the well-known Atlantic coast of North America.

2) Both species were already present at the area (the so-called Central American Seaway) before the rising of the Panama Isthmus. However, and as stated above, this would mean that after isolation, both species remained unchanged at both sides for about 12 MY. Even with the lowest evolutionary rate this is again unlikely.

3) Both species have been able to migrate across the Isthmus through the Panama Canal. This reasoning brings into scene the long debated issue of the Canal as a passageway for the exchange of fauna between the two oceans (Menziez 1968; McCosker and Dawson 1975; Miloslavich et al. 2011). Today, it is well accepted that better than a passageway, the Canal acts as a highly selective filter for migration of fauna between the two oceans. In the particular case of kinorhynchs, that can be extended to meiofauna in general, animals find three kinds of constraints to migrate through the Canal. First one is physical: the Canal is not Sea-level, but proceeds through a series of locks to save the 29 m slope up and down to Gatun and Miraflores lakes, in the middle of the Isthmus. Locks make the direct migration of meiofaunal organisms by themselves totally unlikely. Second one is chemical: all water inside the Canal is freshwater, a completely unsuitable habitat for marine meiofaunal organisms. Third one is biological: kinorhynchs have no planktonic larvae for dispersion through the water mass. Only transportation by the ships traversing the Canal would allow the passage of kinorhynchs. The well-known way of ballast water (Rubinoff 1970; Cohen 2006; Briski et al. 2012) or through hull biofouling (Davidson et al. 2009; Schlöder et al. 2013) would be possible. However, transport in ballast water seems quite improbable, for ships take ballast water well off the coast, making very unlikely to bring bottom-living kinorhynchs. Interestingly, a very recent study (Herranz and Leander 2016, this issue) reports the first case of human vectored migration for a kinorhynch, *E. ohtsukai*, between Japan and British Columbia (Canada). The application of molecular techniques gives a very strong support to the study, which points to aquacultural activities as the most probable source of introduced fauna. These authors also find the ways of ship ballast water and bio-fouling unlikely. We have no data on aquacultural activity and traffic across the Panama Canal, but here the influence of regular commercial traffic is overwhelming. On the other hand, kinorhynchs have been found on several algae, though this is not their most common habitat. Hence, the transport by fouling algae on ship hulls seems the only possibility for a recent passage from one side of the Canal to the other, although kinorhynchs have never been reported as part of the bio-fouling communities. The search for meiofauna in hull bio-fouling could be a very interesting subject for future research.

Of course, deeper investigations beyond the descriptive scope of this paper will be needed to determine the real status of *E. intermedius* and *P. alexandroi* populations at both sides of the

Isthmus. Although molecular sequencing was one of the main goals of the two workshops hosted by the Smithsonian Institution in Panama, the posterior processing of specimens failed unexpectedly. Undoubtedly, new and more exhaustive sampling in the area together with the use of molecular techniques will shed light on this issue, revealing ongoing speciation processes or the presence of cryptic species.

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Figure Captions

Fig. 1. Map of the Gulf of Panama area at the Pacific coast of Panama. Dots indicate sampling stations yielding kinorhynch specimens. See also Table 2.

Figure 2. Line drawings of *Echinoderes belenae* sp. nov. (A) Adult male, ventral view. (B) Same, dorsal view. (C) Adult female, ventral view of segment 11. (D) Same, dorsal view.

Abbreviations: go2, glandular cell outlet type 2; lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; mlt, midlateral tube; pdss, paradorsal sensory spot; pf, pectinate fringe; ps1-3, penile spines 1-3; sdss, subdorsal sensory spot; sdt, subdorsal tube; ss, sensory spot; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Figure 3. Light micrographs of *Echinoderes belenae* sp. nov. (A) Adult male, ventral view. (B) Same, dorsal view of segments 1-7. (C) Adult female, ventral view of segments 8-11. (D) Adult

male, ventral view of segments 6-9. Dotted circles mark ventromedial sensory spots. (E) Adult male, dorsal view of segments 7-10. Abbreviations: go2, glandular cell outlet type 2; lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; md, middorsal spine; mlt, midlateral tube; mvpl, midventral placid; pf, pectinate fringe; ps1,2, penile spines 1,2; sdt, subdorsal tube; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Figure 4. SEM micrographs of *Echinoderes belenae* sp. nov. (A) Overview, adult male, ventral. (B) Same, segments 1-5. (C) Same, segments 3-7. (D) Same, Dorsal view of introvert and segments 1-3. (E) Detail of segments 4 and 5, lateral view. (F) Ventral view of segments 10 and 11. (G) Detail of segment 2 showing the midlateral tube (mlt) and associated glandular cell outlet type 2 (go2). Abbreviations: go2, glandular cell outlet type 2; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; mlt, midlateral tube; pf, pectinate fringe; ps1, penile spine 1; sdt, subdorsal tube; spf, secondary pectinate fringe; ss, sensory spot; te, tergal extension; vlt, ventrolateral tube.

Figure 5. Line drawings of *Echinoderes muricatus* sp. nov. (A) Adult female, ventral view. (B) Same, dorsal view. (C) Adult male, ventral view of segments 10, 11. (D) Same, dorsal view of segments 10, 11. Abbreviations: go1, 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; mdpl, middorsal placid; mds, middorsal spine; mdss, middorsal sensory spot; mlss, midlateral sensory spot; pdss, paradorsal sensory spot; sdss, subdorsal sensory spot; sp, sieve plate; ss, sensory spot; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube. Question mark in D points to the assumed laterodorsal tube on segment 10 of males.

Figure 6. Light micrographs of *Echinoderes muricatus* sp. nov., adult female, A-C, focus on tergal plates; D-F, focus on sternal plates. (A) Lateral view of segments 1-6. (B) Segments 6-9. (C) Segments 8-11. (D) Segments 1-6. (E) Segments 6-9. (F) Segments 8-11. Abbreviations: go1, glandular cell outlet type 1; ij, intersegmentary junction line; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Figure 7. SEM micrographs of *Echinoderes muricatus* sp. nov., adult female. (A), Laterodorsal overview. (B) Adult female, laterodorsal view of segments 5-9. (C) Lateral view of segments 8-11. (D) Detail of sieve plate in segment 9. Dotted circle marks the midlateral sensory spot. (E) Dorsolateral view of segments 10 and 11. Dotted circles mark sensory spots. (F) Ventral view of segments 9-11. Dotted circles mark sensory spots. (G) Ventral view of segments 5 and 6. Dotted circles mark sensory spots. Abbreviations: bh, bracteate hair; 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; sp, sieve plate; spf, secondary pectinate fringe; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Figure 8. Line drawings of *Echinoderes strii* sp. nov. (A) Adult male, ventral view. (B) Same, dorsal view. (C) Adult female, ventral view of segment 11. (D) Same, dorsal view. (E) Detail of pectinate fringe pattern of segments 1-4. Abbreviations: g, gonopore; ldt, laterodorsal tube; lts, lateral terminal spine; lvt, lateroventral tube; mdpl, middorsal placid; mlt, midlateral tube; mvpl, midventral placid; p, pachycyclus; ps1-3, penile spines 1-3; sp, sieve plate; ss, sensory spot; te, tergal extension.

Figure 9. Light micrographs of *Echinoderes strii* sp. nov. Numbers denote trunk segments. (A) Adult female, lateral view of fully extended specimen. (B) Adult female, ventral view of segments 1-5. (C) Detail of tergal plates of segments 5 and 6. Arrowheads mark big perforation sites corresponding to cuticular hairs; arrows mark tiny cuticular perforations of unknown function. (D) Adult female, lateral view of segments 4-9. (E) Adult female, ventral view of segments 8-11. Note the retraction of segments 10 and 11, nearly covered by segment 9. Compare with Fig. 10A, F, G, I. (F) Adult male, dorsal view of segments 9-11, fully extended. (G) Adult male posterior end, ventral view, fully extended. Arrows mark the rounded tergal extensions of segment 11. (H) Adult female posterior end, lateral view, fully extended. Note the filiform projection of tergal extensions (te). (I) Adult female dorsal view of segments 9-11, contracted. Note the lack of laterodorsal tubes in segment 10 (compare with Fig. 9F). (J) Same, ventral view. Note the filiform projection of tergal extensions (te, compare with Figs 9H, 10H) instead the rounded tergal extensions of males. Abbreviations: go, gonopore; ldt, laterodorsal tube; lts, lateral terminal spine; lvt, lateroventral tube; mvp, midventral placid; pf, pectinate fringe; ps1, 2, penile spine 1, 2; sp, sieve plate; te, tergal extension.

Figure 10. SEM micrographs of *Echinoderes strii* sp. nov. Numbers denote trunk segments. (A) Adult male, lateroventral view, fully contracted. (B) Adult female, lateral overview of introvert and mouth cone. Arrows mark the four sets of spines on primary spinoscalids. (C) Detail of laterodorsal tube (ldt) of segment 5 and midlateral sensory spot (dotted circle) of segment 6. (D) Detail of sieve plate in segment 9. Arrowheads mark tiny cuticular perforations; compare with Fig. 9C. (E) Lateral view of segments 1-6. Dotted circle marks midlateral sensory spot. (F) Adult female, lateral view of segments 5-11; same specimen than Fig. 10B, I; note segments 10 and 11 retracted into segment 9. Circle marks the sieve plate in segment 9. (G) Adult male, detail of posterior end. Note segments 10 and 11 retracted into segment 9. Circle marks sieve plate; dotted circles mark sensory spots. (H) Adult female, detail of posterior segments fully extended. Note the filiform projection of tergal extensions (te, compare with Fig. 9H, J) instead the rounded tergal extensions of males. Circle marks sieve plate; dotted circle mark sensory spot. (I) Lateroventral overview of same female specimen than in Fig. 10B, F. Note the fully extended anterior end and the fully retracted posterior end. Abbreviations: h, cuticular hair; ldt, laterodorsal tube; lts, lateral terminal spine; lvt, lateroventral tube; mc, mouth cone; mlt, midlateral tube; mvp, midventral placid; os, oral styles; po, pore associated to the sieve plate; ps1-3, penile spines 1-3; sp, sieve plate; spf, secondary pectinate fringe; te, tergal extension.

Figure 11. Line drawings of *Cristaphyes harrisoni* sp. nov. (A) Female, ventral view. (B) Same, dorsal view. (C) Male, ventral view, segments 1-2. (D) Same, ventral view, segments 9-11. Abbreviations: bp, bulbous protuberance; go, glandular cell outlet; lds, laterodorsal seta; ldss, laterodorsal sensory spot; lvs, lateroventral seta; mdp, middorsal process; ms, muscular scar; pds, paradorsal seta; pls, paralateral seta; sdss, subdorsal sensory spot; spf, secondary pectinate fringe; vls, ventrolateral seta; vms, ventromedial seta; vmss, ventromedial sensory spot.

Figure 12. Light micrographs of *Cristaphyes harrisoni* sp. nov. A-D, holotypic female. E-F, paratypic male. (A) Ventral view. (B) Dorsal view. (C) Dorsal view of segments 1-2. (D) Ventral view of segments 1-2. (E) Ventral view of segments 1-2. (F) Ventral view of segments 3, 4. Abbreviations: bsj, ball and socket joint; go, glandular cell outlet; lvs, lateroventral seta; mdp, middorsal process; pls, paralateral seta; tu, tube; vls, ventrolateral seta; vms, ventromedial seta. Dotted circles indicate sensory spots. Circles indicate setae.

Figure 13. SEM micrographs of *Cristaphyes harrisoni* sp. nov. A-E, paratypic male. F, paratypic female. (A) Ventral view. (B) Lateral view. (C) Lateral view, right side of tergal plates 5-7. (D) Lateral view, right side of tergal plates 7-8. (E) Ventral view, detail of the left sternal plate, showing the male tube and sensory spot. (F) Ventral view, segments 8-10. Abbreviations: lvs, lateroventral seta; mdp, middorsal process; tu, tube; vls, ventrolateral seta; vms, ventromedial seta. Dotted circles indicate sensory spots.

/Pardos et al.

Two sides of a coin: the phylum Kinorhyncha in Panama. II) Pacific Panama

Tables

Table 1. List of the species of kinorhynchs from Panama, including original descriptions and other reports. Type localities marked in boldface. Allomalorhagid species appear with the new generic names after Sánchez et al. (2016), although old names are also indicated between brackets.

Species	First reference in Panama	Locality; Caribbean (C)/ Pacific (P)	Other localities
<i>Antygomonas</i> cf. <i>paulae</i>	Pardos et al. 2016, this issue; this study	Bocas del Toro (C); Las Perlas (P)	Fort Pierce (Florida)
<i>Campyloderes</i> sp.	Pardos et al. 2016, this issue	Bocas del Toro (C)	
<i>Centroderes barbanigra</i>	Neuhaus et al. 2014	Bocas del Toro (C)	Gulf of Mexico (USA)
<i>Cephalorhyncha</i> sp.	Sørensen 2006	Bocas del Toro (C)	
<i>Cristaphyes panamensis</i>	Pardos et al. 2016, this issue	Bocas del Toro (C)	
<i>Cristaphyes harrisoni</i> sp. nov.	This study	Isla Taboga (P)	
<i>Echinoderes belenae</i> sp. nov.	This study	Isla Taboga (P)	Las Perlas (Pacific Panama)
<i>Echinoderes collinae</i>	Sørensen 2006	Bocas del Toro (C)	
<i>Echinoderes intermedius</i>	Sørensen 2006	Bocas del Toro (C); Las Perlas (P)	
<i>Echinoderes muricatus</i> sp. nov.	This study	Playa Venao (P)	
<i>Echinoderes orestauri</i>	Pardos et al. 2016, this issue	Bocas del Toro (C)	
<i>Echinoderes rociae</i>	Pardos et al. 2016, this issue	Bocas del Toro (C)	
<i>Echinoderes spinifurca</i>	Sørensen 2006	Bocas del Toro (C)	Fort Pierce (Florida)
<i>Echinoderes strii</i> sp. nov.	This study	Las Perlas (P)	
<i>Echinoderes truncatus</i>	Sørensen 2006	Bocas del Toro (C)	Carrie Bow Cay (Belize)

<i>Fujuriphyes distentus</i> [<i>Kinorhynchus distentus</i> prior to Sánchez et al., 2016]	Pardos et al. 2016, this issue	Bocas del Toro (C)	
<i>Leiocanthus emarginatus</i> [<i>Pycnophyes emarginatus</i> prior to Sánchez et al., 2016]	Pardos et al. 2016, this issue	Bocas del Toro (C)	Carrie Bow Cay (Belize)
<i>Paracentrophyes praedictus</i>	Pardos et al. 2016, this issue	Bocas del Toro (C)	Carrie Bow Cay (Belize)
<i>Pycnophyes alexandroi</i>	Pardos et al. 2016, this issue; this study	Bocas del Toro (C); Isla Taboga (P)	
<i>Pycnophyes beaufortensis</i>	Sørensen 2006	Bocas del Toro (C)	Beaufort (North Carolina, USA)
<i>Semnoderes cf. pacificus</i>	Sørensen 2006	Bocas del Toro (C)	New Caledonia; Redondo beach (California)

Table 2. Sampling data in Naos area (Pacific Panama)

Station number	Date	Local name	Latitude	Longitude	Depth	Sediment	Salinity	Tide	Kinorhynchs found
NAOS3	Dec. 2, 2011	Playa Venao, Veracruz	8°53'29"N	79°35'43"W	intertidal	Coarse sand and shells	n.a.	Low tide 1.0m	<i>E. belenae</i>
NAOS7	Dec. 2, 2011	Playa Venao, Veracruz	8°53'27"N	79°35'43"W	intertidal	Mud with more coarse sand and foraminiferans	n.a.	Low tide 1.0m	<i>E. belenae</i> ; <i>E. muricatus</i>
NAOS11	Dec. 6, 2011	Pedro González Las Perlas	8°23'16"N	79°07'32"W	20 m	Coarse sand with shells	30	medium level tide 2.5m	<i>E. belenae</i> ; <i>Antygomonas</i> sp.; <i>E. intermedius</i>
NAOS15	Dec. 6, 2011	Pedro González Las Perlas	8°23'15"N	79°05'2"W	intertidal	Mangrove mud	27	medium level tide 2.5m	<i>E. belenae</i> ; <i>E. strii</i>
NAOS18a	Dec. 9, 2011	Isla Taboga	8°48'13"N	79°33'15"W	11 m	Sandy mud	30	low tide 0.6m	<i>E. belenae</i>
NAOS19	Dec. 9, 2011	Isla Taboga	8°46'56"N	79°32'13"W	8 m	Coarse-medium sand	30	low tide 0.6m	<i>E. belenae</i>
NAOS21	Dec. 9, 2011	Isla Taboga	8°48'08"N	79°33'19"W	2 m	Sandy mud	30	low tide 0.6m	<i>E. belenae</i> ; <i>C. harrisoni</i> ; <i>P. alexandroi</i>

Table 3. Measurements (μm) and proportions of *E. belenae* sp. nov. Number of specimens measured indicated in parentheses. Numbers in the first column indicate the corresponding segment. Abbreviations: LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral spine/tube; MD, Middorsal spine; MSW, maximum sternal width, measured on segment 6; S, segment length; SD, standard deviation; SW, standard width, measured on segment 10.

	Holotype	Mean ♂ (4)	Mean ♀ (4)	Mean (8)	Range	SD
TL	283	255	252	254	236 - 298	25.04
MSW 6	30	29	28	29	27 - 30	0.83
MSW/TL	11%	11%	11%	11%	10% - 12%	0.89
SW10	24	23	24	23	22 - 25	0.88
S1	26	26	26	26	23 - 27	1.21
S2	26	26	28	27	25 - 29	1.33
S3	28	28	27	28	26 - 29	1.23
S4	29	29	30	29	28 - 31	1.18
S5	31	32	32	32	31 - 34	1.07
S6	34	34	34	34	32 - 37	1.54
S7	36	37	38	37	36 - 39	1.09
S8	39	35	40	37	20 - 41	6.88
S9	41	41	42	42	41 - 43	0.97
S10	52	47	39	43	38 - 52	5.24
S11	29	30	29	30	28 - 31	1.14
MD4	21	18	17	17	13 - 21	2.93
MD6	-	20	22	21	19 - 22	1.44
MD8	34	26	25	25	20 - 34	4.32
LV5	12	12	12	12	12 - 13	0.46
LV6	16	15	16	16	14 - 17	0.79
LV7	16	16	17	16	15 - 18	1.24
LV8	14	16	17	17	14 - 19	1.97
LV9	17	19	22	20	17 - 23	2.04
LTS	38	38	37	37	35 - 39	1.43
LTAS	-	-	29	29	26 - 31	1.91
LTS/TL	14%	15%	15%	15%	12% - 16%	1.40

Table 4. Summary of relevant cuticular characters and positions of *Echinoderes belenae* sp. nov. Abbreviations: LA, lateral accessory; LD, laterodorsal; LV, lateroventral; ML, midlateral; MD, middorsal; PD, paradorsal; SD, subdorsal; SL, sublateral; VL, ventrolateral; VM, ventromedial; ac, acicular spine; go2, gland cell outlet type 2; lta, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spines; ss, sensory spot; tu, tube; ♂, male condition of sexually dimorphic characters; ♀, female condition of sexually dimorphic characters.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1			ss	ss						ss
2	ss		tu, ss	ss	tu	go2			tu	
3			ss		tu					
4	ac			tu						
5					tu			tu		
6	ac	ss	ss		tu			ac		ss
7			ss		tu			ac		ss
8	ac	ss		tu			tu	ac		
9		ss	ss	tu				ac	ss	
10			ss	tu					ss	
11					ps(♂)		lta(♀)	lts		

Table 5. Measurements (μm) and proportions of *E. muricatus* sp. nov. The three individuals measured were females. Numbers in the first column indicate the corresponding segment. Abbreviations: LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral spine/tube; MD, middorsal spine; MSW, maximum sternal width, measured on segment 7; S, segment length; SW, standard width, measured on segment 10.

	Holotype	Paratype 1	Paratype 2	Mean
TL	345	350	319	338
MSW 7	26	27	25	26
MSW/TL	8%	8%	8%	8%
SW10	21	22	21	21
S1	35	37	35	36
S2	38	37	36	37
S3	42	47	41	43
S4	46	52	43	47
S5	49	54	46	50
S6	51	55	49	51
S7	53	56	50	53
S8	57	57	54	56
S9	56	57	52	55
S10	50	57	49	52
S11	32	35	32	33
MD4	55	36	54	48
MD5	70	52	69	64
MD6	85	75	82	80
MD7	94	109	-	102
MD8	-	127	145	136
VL2	32	-	31	32
LV5	33	22	28	28
LV6	25	24	24	24
LV7	27	30	27	28
LV8	33	35	32	34
LV9	36	38	38	37
LTS	227	238	205	224
LTAS	44	46	45	45
LTS/TL	66%	68%	64%	66%

Table 6. Summary of relevant cuticular characters and positions of *Echinoderes muricatus* sp. nov. Abbreviations: LA, lateral accessory; LD, laterodorsal; LV, lateroventral; ML, midlateral; MD, middorsal; PD, paradorsal; SD, subdorsal; SL, sublateral; VL, ventrolateral; VM, ventromedial; ac, acicular spine; go2, gland cell outlet type 2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spines; sp, sieve plate; ss, sensory spot; tu, tube; ♀, female condition of sexually dimorphic characters.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1			ss	ss						ss
2	ss	go1		ss					tu	ss
3		go1	ss		ss					
4	ac	ss; go1								
5	ac	go1			ss			tu		
6	ac	ss; go1			ss			ac		ss
7	ac	ss; go1		ss	ss			ac		ss
8	ac	ss; go1					tu	ac		
9		ss; go1	ss		ss	sp		ac	ss	
10			ss	tu					ss	
11		ss		ss			ltas(♀)	lts		

Table 7. Measurements (μm) and proportions of *E. strii* sp. nov. Number of specimens measured indicated in parentheses. Numbers in the first column indicate the corresponding segment. Abbreviations: LDT, laterodorsal tube; LTS, lateral terminal spine; LVT, lateroventral tube; MSW, maximum sternal width, measured on segment 8; S, segment length; SD, standard deviation; SW, standard width, measured on segment 10. High values of standard deviation are related to the different sizes of LTS in males and females and to the different contraction state of the specimens (TL).

	Holotype	Mean ♂ (4)	Mean ♀ (4)	Mean (8)	Range	SD
TL	235	250	258	254	235 - 277	14.3
MSW 8	34	35	35	35	31 - 41	2.9
MSW/TL	14%	14%	13%	14%	13% - 16%	1.2
SW10	28	26	30	28	21 - 32	3.8
S1	31	30	29	30	27 - 32	1.4
S2	30	31	31	31	28 - 33	1.7
S3	33	34	35	35	30 - 37	2.8
S4	34	37	40	38	32 - 43	4.4
S5	37	41	43	42	37 - 46	4.2
S6	41	44	49	47	37 - 53	6.3
S7	45	49	54	51	41 - 60	7.0
S8	51	54	59	57	48 - 63	5.7
S9	57	63	68	66	57 - 72	5.5
S10	37	37	37	37	35 - 40	1.6
S11	23	24	25	24	22 - 26	1.3
LVT5	-	24	26	25	24 - 28	1.7
LDT8	28	26	27	26	24 - 29	2.1
LVT8	27	27	30	29	27 - 32	2.0
LTS	59	59	77	68	58 - 78	9.3
LTS/TL	25%	24%	30%	27%	22% - 32%	3.6

Table 8. Summary of relevant cuticular characters and positions of *Echinoderes strii* sp. nov.
Abbreviations: LA, lateral accessory; LD, laterodorsal; LV, lateroventral; ML, midlateral; MD, middorsal; PD, paradorsal; SD, subdorsal; SL, sublateral; VL, ventrolateral; VM, ventromedial; ac, acicular spine; go2, gland opening type 2; lts, lateral terminal spine; ps, penile spines; sp, sieve plate; ss, sensory spot; tu, tube; ♂, male condition of sexually dimorphic characters.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1			ss	ss					ss	
2			ss	ss						
3			ss	ss	tu					ss
4				ss						ss
5				ss, tu				tu	ss	
6				ss	ss					ss
7				ss	ss				ss	
8				ss, tu				tu	ss	
9				ss, ss	ss, sp				ss	
10			tu(♂)	ss					ss	
11					ps(♂)			lts		

Table 9. Measurements (μm) and proportions of *C. harrisoni* sp. nov. Numbers in the first column indicate the corresponding segment. Abbreviations: MSW7, maximum sternal width measured at segment 7; S, segment length; SW10, standard width, measured on segment 10; TL, trunk length.

Character	Holotype ♀	Paratype 1♀	Paratype 2♂
TL	558	512	452
SW10	119	115	112
MSW7	150	152	141
MSW/TL	27%	30%	31%
S1	72	69	69
S2	48	41	41
S3	51	45	45
S4	60	45	45
S5	57	52	45
S6	67	59	50
S7	72	65	52
S8	71	65	58
S9	68	60	61
S10	45	40	54
S11	-	-	-

Table 10. Summary of relevant cuticular characters and positions of *C. harrisoni* sp. nov. Abbreviations: LD, laterodorsal; LV, lateroventral; PD, paradorsal; PL, paralateral; SD, subdorsal; VL, ventrolateral; VM, ventromedial; ps, penile spines; se, seta; ss, sensory spot; tu, tube; (*) indicates that the seta is unpaired; ♀, female condition of sexually dimorphic character; ♂, male condition of sexually dimorphic character.

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

Table 11. *Echinoderes* species of the so-called *coulli*-group showing some relevant characters. Abbreviations: LD, laterodorsal tube; LTAS, lateral terminal spine; LV, lateroventral spine/tube; MD, middorsal spine.

Character <i>Echinoderes</i> species	♀ LTAS	Large sieve plate	Spine formula reduced/absent	Tube formula	Estuarine/brackish/ mangrove/low salinity
<i>E. coulli</i>	-	*	-	LV5, 8	*
<i>E. maxwelli</i>	-	*	MD4?; LV6, 7	LV5, 8	*
<i>E. applicitus</i>	-	*	-	LV5, 8; LD10	*
<i>E. ohtsukai</i>	*	*	MD4	LV5, 8; LD10	*
<i>E. annae</i>	*	*	MD4	LV5, 8; ML9; LD10	*
<i>E. teretis</i>	-	*	MD4; LV6, 7	LV5, 8; LD 10	*
<i>E. rex</i>	-	*	MD4; LV6, 7	LV5, 8; LD 10	-
<i>E. komatsui</i>	*	*	-	LV5, 8; LD 10	*
<i>E. hwiizaa</i>	*	*	-	LV5, 7-9; ML8; LD10	*
<i>E. marthae</i>	-	*	-	LV5, 8; LD 8, 10	-
<i>E. strii</i> sp. nov.	-	*	-	ML3; LV5, 8; LD5, 8, 10	*

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

Figure 13