Two sides of a coin: the phylum Kinorhyncha in Panama. I) Caribbean Panama

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

¹Department of Zoology and Physical Anthropology. Universidad Complutense de Madrid. José Antonio Novais, 2, 28040 Madrid, Spain

²Departments of Zoology and Botany. University of British Columbia. Vancouver, Canada

*Corresponding author. Email address: fpardos@bio.ucm.es

ABSTRACT

Sampling for meiofauna was carried out in 2010 in Bocas del Toro, Northwest Caribbean Panama, as the first part of a study along Caribbean and Pacific coasts of Panama. Nine kinorhynch species were known previously from the area, some of them being confirmed in the present contribution plus several new citations. In addition, four species new to science are described, *Echinoderes rociae* sp. nov., *Echinoderes orestauri* sp. nov., *Cristaphyes panamensis* sp. nov. and *Pycnophyes alexandroi* sp. nov. Furthermore, and based on the present material, we redescribe *Echinoderes intermedius* providing new and more detailed morphological information. The presence of *Echinoderes truncatus* in the area, reported previously, is also discussed. Hence, an updated list of the kinorhynch fauna for the Caribbean Sea is provided, reaching 33 species.

Keywords: Kinorhynchs, meiofauna, biogeography, taxonomy, morphology

1. Introduction

In June, 2010, and December, 2011, the Smithsonian Institution organized two workshops at the marine stations of the Smithsonian Tropical Research Institute in Bocas del Toro (Caribbean Panama) and Naos (Pacific Panama), respectively. With the collaboration and support of Encyclopedia of Life (EOL), the workshops intended to survey and characterize the meiofauna at both sides of the Panama Canal with the aim of initiating a molecular library of lesser known taxa. This paper is one of the contributions on the kinorhynch fauna obtained

during such workshops, together with the corresponding study at the Pacific side of Panama (Pardos et al., this issue).

The kinorhynch fauna of Panama was completely unexplored until the study of Sørensen (2006), carried out at the Smithsonian Research Station of Bocas del Toro. Sørensen (2006) reported nine kinorhynch species, of which five were new to science (see Table 1). These latter included *Echinoderes intermedius* Sørensen, 2006 and *Echinoderes collinae* Sørensen, 2006, an undetermined species of *Centroderes* that later was described as *Centroderes barbanigra* Neuhaus et al., 2014 and two undetermined species of, respectively, *Echinoderes* and *Cephalorhyncha*. First reports for Panama were *Echinoderes spinifurca* Sørensen et al., 2005, *Echinoderes truncatus* Higgins, 1983 (but see Discussion section below), *Semnoderes pacificus* Higgins, 1967, and *Pycnophyes beaufortensis* Higgins, 1964.

Interestingly, and from the same locality in Bocas del Toro, the present contribution reports the presence of four additional species new to science, plus *Antygomonas* cf. *paulae* Sørensen, 2007, *Leiocanthus emarginatus* (Higgins, 1983), *Fujuriphyes distentus* (Higgins, 1983) and *Paracentrophyes praedictus* Higgins, 1983, together with two undetermined species of the genera *Campyloderes* and *Pycnophyes*, respectively. Additionally, a redescription of *Echinoderes intermedius* Sørensen, 2006 is provided herein in the light of new morphological information. The current picture of the kinorhynch fauna both in Panama and the Caribbean region is also summarized.

2. Materials and methods

Sediment samples were taken from the area around Bocas del Toro (Panama) (Fig 1) in June 6-19, 2010, during a training workshop organized by the Smithsonian Tropical Research Institute (STRI, Smithsonian Institution) and the Encyclopedia of Life. Seven sampling stations yielded kinorhynch specimens, both close to the Smithsonian Station or around the Bastimento Island. Sampling data are summarized in Table 2. Samples were taken by hand intertidally and by scuba diving or snorkelling subtidally. 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 selected from extracted samples and fixed in 7% formalin for standard morphological studies and storage or in 100% ethanol for future molecular studies.

Individual specimens were mounted in Fluoromount G[®] for observation and measurement with light microscopy with an Olympus BX51 microscope equipped with interference contrast optics

(DIC) and a DP70 Olympus camera. 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 a JEOL 6335F and Hitachi S4700 Scanning Electron Microscopes. Type material is deposited at the Natural History Museum of Denmark (NHMD).

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 intermedius* Sørensen, 2006

(Figs 2-4; Tables 4-5)

3.1.1. *Material examined*

One male specimen from Bocas del Toro, recorded at Solarte Island, station BRS 102 (Table 2). The specimen was mounted for LM, slide labelled PAN I/23. Two males and two females from the same locality were mounted for SEM. Three males and four females collected at Las Perlas Archipelago (Pacific Panama) 8° 23' 16.17'' N, 79° 7' 31.86'' W from coarse sand with shells, at 20 m depth, mounted for LM, slides labelled PAN I/55-61. All specimens were deposited in the kinorhynch collection of the UCM Meiofauna lab, Universidad Complutense de Madrid (Spain).

3.1.2. *Emended diagnosis*

Echinoderes with middorsal spines on segments 4, 6, 8, increasing in length posteriorly; subdorsal and ventrolateral tubes plus sublateral glandular cell outlet type 2 on segment 2; lateroventral tubes on segment 5; lateroventral acicular spines on segments 6-9 and lateral accessory tubes on segments 6-8; laterodorsal tubes on segment 8; laterodorsal, sexually dimorphic tubes on segment 10.

3.1.3. *Description*

All relevant dimensions and measurements are summarized in Table 3, and distribution of cuticular characters in Table 4. In the present redescription we will only record important features or structures that differ from the original description; otherwise see Sørensen (2006) for further details.

The introvert appeared partly or completely retracted into the trunk in all specimens, so no description of scolid arrangement was possible. Neck with 16 placids surrounding the trunk opening; all trapezoid in shape, wider posteriorly. Midventral placid larger (Figs 2, 3B, 4D). Intercalary areas of softer cuticle (interplacids) at both sides of each placid. Clover-like trichoscalid plates on midventral placids (Figs 2A, 4D); smaller and more rounded-triangular trichoscalid plates on subdorsal and laterodorsal placids.

Segment 1 as a closed ring. Sensory spots in subdorsal, laterodorsal and ventromedial positions. Subdorsal ones typically flanked by two long hairs. Cuticular hairs long, scarce and non-bracteate emerging from round perforation sites, with no defined pattern but distributed into one or two irregular lines around the anterior half of the segment. Posterior edge of the segment smooth ventrally; only very weak indentation dorsally, not forming a real pectinate fringe.

Segment 2 as a closed ring. Tubes in subdorsal and ventrolateral positions (Figs 2A-B, 4A, D, F). Sensory spots in middorsal, subdorsal, laterodorsal, and ventromedial positions. Subdorsal and laterodorsal ones flanked by long hairs (Fig. 4C). Big glandular cell outlet type 2 in sublateral positions (Figs 2A, 4F), appearing in SEM as perfectly round openings 2 μm in diameter with a marked rim. Cuticular hairs and posterior edge as in the precedent segment.

Segment 3 and following segments composed of one tergal and two sternal plates. Sensory spots in subdorsal and sublateral positions, both flanked by hairs (Figs 2A-B, 4A). Cuticular hairs bracteate, mostly distributed into two rows, the anterior one with much shorter hairs. Posterior half of the segment naked and smooth. Primary pectinate fringe short and well developed.

Segment 4 with a spine in middorsal position (Figs 2B, 3A, 4A), reaching the edge of the next segment. No sensory spots present. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 5 with long and thin tubes in lateroventral position (Figs 2A, 3B). Sensory spots in subdorsal, laterodorsal and ventromedial positions. Cuticular hairs and well developed pectinate fringe as in the precedent segment.

Segment 6 with spines in middorsal and lateroventral positions (Figs 2A-B, 3A, B). Tubes in lateral accessory positions and paradorsal, laterodorsal and ventromedial sensory spots. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 7 with spines in lateroventral positions and lateral accessory tubes (Figs 2A, 3B). Sensory spots in subdorsal, laterodorsal and ventromedial positions. Pectinate fringe well developed, with long and very regular points.

Segment 8 with spines in middorsal and lateroventral positions, plus tubes in lateral accessory and laterodorsal positions (Figs 2A-B, 3B). One pair of paradorsal sensory spots. Segment otherwise similar to precedent.

Segment 9 with lateroventral spines only (Figs. 2A, 3B). Sensory spots in paradorsal, subdorsal laterodorsal and ventrolateral positions. A pair of sieve plates appears in sublateral position, as a depressed circular area with 20-25 perforations (Fig. 4G). Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 10 with laterodorsal tubes, much longer in males than in females (Figs. 2B, D, 4B, E). Sensory spots present in subdorsal and ventrolateral positions. Posterior edge of sternal plates conspicuously extended paraventrally, forming a midventral V-shape.

Segment 11 short, with long lateral terminal spines (Figs. 2, 3D). Females with lateral terminal accessory spines. Males with three pairs of penile spines arising below the pectinate fringe of the precedent segment in midlateral positions (Figs 2C-D, 4B). Penile spines ps1 and ps3 are filiform, whereas ps2 is broad and ends in a tuft of hairs (Figs 2C-D, 4B). One pair of sensory spots in paradorsal position and two pairs in ventromedial positions. Tergal plate projected posteriorly into well developed, pointed tergal extensions surpassing the sternal extensions (Figs. 3B, C, D). A cuticular elevation or protuberance covered by hairy cuticular projections appears middorsally.

3.1.4. Associated kinorhynch fauna

Echinoderes intermedius co-occurred at Station BRS 102 (Table2) with *Echinoderes orestauri* sp. nov., *Pycnophyes alexandroi* sp. nov., *Cristaphyes panamensis* sp. nov., *Centroderes barbanigra*, *Leiocanthus emarginatus*, *Paracentrophyes praedictus*, *Fujuriphyes distentus* and *Pycnophyes* sp.

3.2. *Echinoderes rociae* sp. nov.

(Figs. 5-7; Tables 6-7)

3.2.1. Material examined

All specimens were collected from medium sand at Bastimento Island, Bocas del Toro, Station BRS 107 (Table 2). Holotype, female mounted in Fluoromount G®, deposited at the NHMD under catalogue number ZMUC KIN-974. Paratypes, two males and one female mounted in Fluoromount G®, deposited at the NHMD under catalogue numbers ZMUC KIN-975 to KIN-977. Two additional specimens, one male and two females from the same locality mounted for SEM.

3.2.2. Diagnosis

Echinoderes with middorsal spines on segments 4, 6, 8, increasing in length posteriorly; subdorsal and ventrolateral tubes plus sublateral glandular cell outlets type 2 on segment 2; lateroventral tubes on segment 5; lateroventral acicular spines on segments 6-9; lateral accessory tubes on segments 7 and 8; laterodorsal tubes on segment 8; laterodorsal, sexually dimorphic tubes on segment 10. Lateral terminal spines very short, stout and pointed, with several hairy projections along the distal end. Middorsal protuberance on segment 11.

3.2.3. Etymology

The new species is dedicated to Ms. Rocío Pardo, daughter of the first author.

3.2.4. Description

All relevant dimensions and measurements are summarized in Table 5, and distribution of cuticular characters in Table 6. All studied specimens, mounted both for LM and for SEM appeared with the head completely retracted into the trunk, so no information is available on scald numbers and arrangement. Neck with 16 placids trapezoid in shape, wider posteriorly. Midventral placid remarkably wider than others (Fig. 7B). Cuticular surface of placids completely smooth except for a slight transverse line near the anterior margin (Figs 5A-B, 7B). Intercalary areas of soft cuticle connect placids to each other. Two big clover-like trichoscalid plates articulate on placids adjacent to the midventral one. Smaller trichoscalid plates on subdorsal and laterodorsal placids.

Segment 1 as a closed ring. Cuticle smooth. Cuticular hairs non bracteate and scarce, scattered through the anterior half of the segment with no definite pattern. One pair of subdorsal, laterodorsal and ventromedial sensory spots (Fig. 5). Posterior edge of the segment appears smooth in SEM (Figs 7A-B).

Segment 2 as a closed ring. Tubules in subdorsal and ventrolateral positions (Figs. 5A, B, 6B). One middorsal plus two pairs of laterodorsal and one pair of ventromedial sensory spots. Conspicuous glandular cell outlet type 2 in sublateral position, appearing as a circular opening 2 μ m in diameter (Fig. 7B). Cuticular hairs arranged into two irregular lines at the anterior half of the segment. Posterior edge of the segment showing a very weak indentation.

Segment 3 and following segments composed of one tergal and two sternal cuticular plates. One pair of sensory spots in subdorsal position, flanked by long cuticular hairs (Fig. 5B). Other hairs non bracteate, arranged into three rows at the anterior half of the tergal plate and forming two paraventral patches on the sternal plates. Segment edge with short pectinate fringe.

Segment 4 with a middorsal spine barely reaching the posterior edge of the segment (Figs 5B, 6B). Sensory spots in ventromedial positions. Hair pattern and segment edge as in the precedent segment.

Segment 5 with one pair of lateroventral tubes. Sensory spots flanked by two hairs in subdorsal and midlateral positions. Ventromedial sensory spots on the sternal plates. Cuticular hairs as in the precedent segment. Pectinate fringe well developed, with regular tips.

Segment 6 with a middorsal spine and one pair of stiff and robust lateroventral spines, (Figs 5A-B, 6B, C, F, 7E). Paired paradorsal and ventromedial sensory spots plus one pair of midlateral sensory spot flanked by two hairs. Dorsal cuticular hairs as in previous segment, paraventral patches of cuticular hairs not well defined. Pectinate fringe as in the precedent segment.

Segment 7 with lateroventral robust spines and lateral accessory tubes (Figs. 5A-B, 6C, F, 7E). Sensory spots flanked by cuticular hairs in subdorsal and midlateral positions. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 8 with a middorsal spine and robust lateroventral spines plus lateral accessory tubes (Figs 5A-B, 6C-D, F, 7C-D) and one additional pair of laterodorsal tubes (Figs. 5B, 7C). Only one pair of paradorsal sensory spots. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 9 with one pair of lateroventral spines (Figs. 5A-B, 6C, F, 7D). Sensory spots in paradorsal, subdorsal and ventrolateral positions. Rounded sieve plate in sublateral position (Fig. 5A). Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 10 with laterodorsal tubes, much longer in males than in females (Figs. 5B, D, 7F). In females the tubes lack the basal part, showing just a flexible and short tube-like structure (Figs 5B, 7F). Sensory spots in ventrolateral positions. Cuticular hairs on sternal plates leaving a naked ventromedial area. Posterior edge of segment deeply curved extending in the ventromedial area.

Segment 11 with lateral terminal spines short, robust and pointed, showing a hollow central cavity in LM (Fig. 5A-D, 6A, D-E, 7F). SEM images show several hairy extensions, towards the distal end of the spines. Lateral terminal accessory spines in females about two thirds of LTS (figs. 5A-B, 6E, 7F). Males with three pairs of penile spines arising laterally under the pectinate fringe of the precedent segment. Ventral and dorsal penile spines (ps1 and 3) filiform, midlateral penile spine (ps2) shorter and coarser (Figs 5C-D). Tergal plate with a middorsal, hairy protuberance, and two relatively long, pointed tergal extensions. One pair of paradorsal and ventromedial sensory spots.

3.3. *Echinoderes orestauri* sp. nov.

(Figs. 8-10)

3.3.1. *Material examined*

All specimens collected at Bastimento Island, Bocas del Toro, Station BRS 106 (Table 2). Holotype, male mounted in Fluoromount G®, deposited at the NHMD under catalogue number ZMUCKIN-978. Paratypes, one male and three females mounted in Fluoromount G®, deposited at the NHMD under accession numbers ZMUC KIN-979 to KIN-982. One additional female from Station BRS 106 mounted for SEM.

3.3.2. *Diagnosis*

Echinoderes with middorsal spines in segments 4-8, short but increasing in length posteriorly. Lateroventral acicular spines on segments 6-9. Laterodorsal tubes on segment 10. Up to 30 pairs of fringed tubes distributed mainly on tergal plates. Big glandular cell outlets type 2 laterodorsally on segments 8 and 9. Tergal extensions of segment 11 truncate.

3.3.3. *Etymology*

The species name, *orestauri*, refers to the Spanish name Bocas (L. *ores*, plural for *os*, mouth) del Toro (L. *tauri*, bull), the locality in northwest Caribbean Panama where the specimens were found.

3.3.4. Description

All relevant dimensions and measurements are summarized in Table 7, and distribution of cuticular characters in Table 8. None of the studied specimens allowed a detailed description of the head. Neck with 16 trapezoid to triangular placids, articulating with the first trunk segment (Figs 10A, B). Placid surface completely smooth. Midventral placid nearly twice as wide as the remaining ones (Figs 8A, 10B). All trunk segments densely covered by long, bracteate cuticular hairs.

Segment 1 as a closed ring. One pair of glandular cell outlets type 1 near the anterior margin in lateroventral positions. Pairs of sensory spots in paradorsal, subdorsal, midlateral and ventrolateral positions (Figs. 8A, B). All sensory spots on this and the following segments consist of round to oval areas of cuticular micropapillae, elongated posteriorly, surrounding one or two central pores. Cuticular hairs abundant, showing no definite pattern except for a broad ventral patch. Pectinate fringe well developed, with tips shorter dorsally. All tips consist of a broad proximal part followed by a long, filiform distal end (Fig. 10K).

Segment 2 as a closed ring. Seven pairs of short fringed tubes distributed as follows: two pairs in subdorsal position, two in laterodorsal, one midlateral, one sublateral and one ventrolateral (Figs 8A-B, 9A-B, 10C). All tubes on this and the following segments are fringed tubes (Sørensen 2006): short tubular structures arising from cuticular perforations and consisting of a very short proximal section and a longer distal one, ending as a fringe of several cuticular tips (Fig. 10I). Sensory spots in middorsal, subdorsal, laterodorsal and ventromedial positions, at the same level than fringed tubes. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 3 and following segments composed of one tergal plate and two ventral, sternal plates. Fringed tubes in paradorsal and subdorsal positions (Figs 8B, 10C). Sensory spots in paradorsal, subdorsal and midlateral positions. Cuticular hairs and pectinate fringe as on the precedent segment.

Segment 4 with a short middorsal spine (Fig. 9A). Two pairs of fringed tubes in subdorsal and one pair in laterodorsal positions (Fig. 8B). Sensory spots in paradorsal, subdorsal, midlateral and ventromedial positions. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 5 with a middorsal spine. Three pairs of fringed tubes in subdorsal position plus one pair in laterodorsal and lateroventral positions (Figs 8A-B, 10D). Sensory spots in

laterodorsal and ventromedial positions. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 6 with middorsal and lateroventral acicular spines (Figs 8A-B, 9B, 10 D-E, G). Three pairs of fringed tubes in subdorsal position plus one in laterodorsal and midlateral positions. Paradorsal, laterodorsal and ventromedial sensory spots. Laterodorsal fringed tube and sensory spot alternate in position with the precedent segment. Cuticular hairs and pectinate fringe as in the previous segment.

Segment 7 with middorsal and lateroventral acicular spines. Two pairs of fringed tubes in subdorsal and one pair in lateral accessory positions (Figs 8A-B, 9B, 10E-G). Paradorsal, laterodorsal and ventromedial sensory spots. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 8 with middorsal and lateroventral acicular spines. Two pairs of fringed tubes in subdorsal position plus one in laterodorsal and lateral accessory positions (Figs 8A-B, 9A-B, 10F-G). Paradorsal, laterodorsal and ventromedial sensory spots. Large glandular cell outlets type 2 laterodorsally, anterior to the fringed tube and sensory spot in the same position (Figs 9A, 10F). Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 9 with lateroventral acicular spines (figs. 8A, 9B). One pair of laterodorsal fringed tubes (fig. 8B). Sensory spots in paradorsal, laterodorsal and ventromedial positions. Large glandular cell outlets type 2 laterodorsally, anterior to the fringed tube and sensory spot in the same position (Fig. 8B, 9A, 10F). Round, small sieve plate in sublateral position. Cuticular hairs and pectinate fringe as in the precedent segment.

Segment 10 with a single pair of laterodorsal tubes, not fringed (Fig. 8B, D, 10H, J). These are the only non-fringed tubes. Two pairs of subdorsal sensory spots, one in the centre of the segment and the other close to the posterior edge. Bracteate cuticular hairs form a broad middorsal patch separated from lateral hairy areas by narrow longitudinal naked bands. Pectinate fringe as in the precedent segment.

Segment 11 short, with lateral terminal spines having a broad, hollow base that tapers considerably to become filiform from the middle of the spine to the tip (Figs 8A-D, 9B, 10A). Females with conspicuous lateral terminal accessory spines (Fig. 10H); males with three pairs of penile spines arising under the pectinate fringe of the precedent segment. Ventral penile spines (ps1) are long and filiform (Figs 8A, 9B) as well as the much shorter dorsal ones (ps3), whereas the lateral penile spines (ps2) are short and stout. One pair of subdorsal sensory

spots. Tergal plate undivided and without any middorsal specialization. Tergal plate with reduced tergal extensions; sternal plates nearly truncate, without any posterior extensions. Both tergal and external plates with a well-developed pectinate fringe (Figs 8A-D, 10J).

3.3.5. Associated kinorhynch fauna

Echinoderes orestauri co-occurs with *Echinoderes intermedius*, *Centroderes barbanigra*, *Leiocanthus emarginatus*, *Paracentrophyes praedictus*, *Fujuriphyes distentus*, *Pycnophyes alexandroi* sp. nov. and *Pycnophyes* sp.

Class Allomalorhagida Sørensen et al., 2015

Family Pycnophyidae Zelinka, 1896

Genus *Cristaphyes* Sánchez et al., 2016

3.4. *Cristaphyes panamensis* sp. nov.

(Figs. 11-13)

3.4.1. Material examined

Holotype, adult male, collected at Bastimento Island in Bocas del Toro, sample BRS 106 (Table 2), and mounted in Fluoromount G®, deposited at the NHMD under accession number ZMUC KIN-983. Paratypes, two adult males, two adult females and one specimen of undetermined sex; same collecting data as holotype. From these, one adult male mounted in Fluoromount G®, deposited at NHMD under accession number ZMUC KIN-984; paratypic adult females (slides labelled PAN II/33-34), one adult male (slide labelled PAN II/32) and the undeterminable specimen mounted for SEM are deposited in the Kinorhynch collection of the UCM Meiofauna lab, Universidad Complutense de Madrid (Spain).

3.4.2. Diagnosis

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

3.4.3. Etymology

The species name refers to Panama, the country in Central America where this and the remaining species of this study have been found.

3.4.4. Description

All relevant dimensions and measurements are summarized in Table 9, and distribution of cuticular characters in Table 10. Most studied specimens, mounted both for LM and for SEM appeared with the introvert completely retracted into the trunk, so the available information on scolid numbers and arrangement is insufficient to fulfil adequate descriptions. Neck with four dorsal and two ventral placids. Dorsal placids are rectangular and of similar size. Ventral ones are much more elongate, getting narrower towards the lateral sides. All placids appear robust and hard, strongly sclerotized.

Segments 2 to 10 with subdorsal oval glandular cell outlets (cuticular scars) and crescentic ones in ventromedial position. Similar cuticular scars on segment 1, but these are elongate, with the dorsal ones medially displaced, and the ventral ones laterally displaced. Oval muscular scars in laterodorsal and ventromedial position along the trunk segments. Inconspicuous cuticular ridges present. Well-developed peg and socket joints on segments 2-5. Pachycycli with a characteristic shape, tergal ones with notches at the middorsal line, ventral ones with a triangular profile at the lateral regions (Fig. 12E). Without apodemes. Pectinate fringe fringes not visible with LM. Three pairs of secondary pectinate fringes throughout the tergal and sternal plates present on segments 2-10

Segment 1 with the posterior margin of dorsal plate with a middorsal process, without intracuticular atria (Fig. 12C). Anterolateral margins of the plate projecting into horn-shaped extensions. Anterior edge of tergal plate slightly denticulated, followed by a narrow reticulated area. Paired paralateral setae. Three pairs of sensory spots, one in subdorsal and two in laterodorsal positions (Fig. 12C). Smooth ventral anterior area. Paired ventrolateral setae. Two pairs of ventromedial sensory spots present at the anterior and posterior third of the plate (Fig. 11A).

Segment 2 with the posterior margin of dorsal plate with a middorsal process. Paired paradorsal sensory spots associated with butterfly-like intracuticular atria. Pairs of paradorsal, subdorsal, laterodorsal (Fig. 12C) and lateroventral setae present. One pair of subdorsal sensory spots located mesial to the subdorsal setae. Two pairs of laterodorsal sensory spots present, one pair located mesial to the laterodorsal setae and the other one lateral to the setae. Ventral pachycycli with a characteristic shape, as tilted towards the midventral line. Sternal plates in males with one pair of large ventromedial tubes (Fig. 13C) and ventromedial

sensory spots located lateral to the tubes. Males with the sensory spots surrounded by a dense covering of cuticular hairs. Females with a pair of ventromedial setae instead of tubes (Fig. 11C). The setae are located mesial to the sensory spots.

Segment 3 with the tergal plate similar to that on segment 2, but only with a single, unpaired paradorsal seta. Sternal plates with paired ventrolateral setae and one pair of ventromedial sensory spots located lateral to the glandular cell outlets (Figs. 12E, 13C).

Segment 4 with the tergal plate similar to that on segment 2 (Figs. 12D, 13A, E). Sternal plates with one pair of ventromedial setae and sensory spots, with the setae located between the sensory spots and the glandular cell outlets (Figs. 12E, 13C).

Segment 5 with the tergal plate similar to that on segment 3 (Figs. 12D, 13A, E). Sternal plates similar to those on segment 4, but with one pair of ventrolateral setae and the ventromedial setae slightly displaced (Fig. 12E).

Segment 6 with the tergal plate similar to that on segment 2 (Figs. 12D, 13A, E). Sternal plates similar to those on segment 4 (Figs. 12A, 13B).

Segment 7 with the tergal plate similar to that on segment 3 (Figs. 11B, 12B, 13A, E). Sternal plates similar to those on segment 4 (Figs. 12A, 13B).

Segment 8 with the tergal plate similar to that on segment 2, but with an additional pair of subdorsal sensory spots (Fig. 11B). Paradorsal sensory spots seem to be absent. Sternal plates similar to those on segment 4 (Figs. 11A, 13D).

Segment 9 with the tergal plate similar to that on segment 8, but with unpaired paradorsal seta (Fig. 11B). Paralateral protonephridial openings present, not sieve-like. Sternal plate similar to those on segment 4 (Figs. 12F, 13D), with the ventromedial sensory spots laterally displaced and with conspicuous thickenings of ventral pachycycli at ventromedial position (Figs. 11A, D).

Segment 10 without middorsal structure specializations or intracuticular structures (Fig. 11B). Males with unpaired paradorsal setae, uncheckable in females. One pair of subdorsal sensory spots located near the posterior margin of the segment. Laterodorsal position uncheckable. One pair of ventromedial sensory spots present. Posterior sternal segment margin rounded at the paraventral area.

Segment 11 without lateral terminal spines (Fig. 13D), instead with a pair of bulbous protuberances (Figs. 11A, B, D). Uncheckable tergal and sternal plates. Hairy posterior margin. Males with two pairs of penile spines and genital pores surrounded by a tuft of long hairs.

3.4.5. Associated kinorhynch fauna

Cristaphyes panamensis sp. nov. co-occurs with *Pycnophyes* sp., *Leiocanthus emarginatus*, *Paracentrophyes praedictus*, *Fujuriphyes distentus*, *Pycnophyes alexandroi* sp. nov., *Echinoderes orestauri* sp. nov., *Echinoderes intermedius* and *Centroderes barbanigra*.

3.5. *Pycnophyes alexandroi* sp. nov.

(Figs. 14-16)

3.5.1. Type material

Holotype, adult male, collected on December 9, 2011 in Taboga Island (Table 2; sample NAOS21, Pacific Panama; see also Pardos et al., this issue); mounted in Fluoromount G®, deposited at deposited at the NHMD under accession number ZMUC KIN-985. Paratypes, one adult male and one adult female; collecting data as holotype; mounted in Fluoromount G®, deposited at NHMD under accession number ZMUC KIN-986 to ZMUC KIN-987. Two adult females mounted in Fluoromount G® (slides labelled PAN II/58 and PAN II/47) and an additional adult specimen of undetermined sex mounted for SEM, stored as additional material deposited in the Kinorhynch collection of the UCM Meiofauna lab, Universidad Complutense de Madrid (Spain); same collecting data as holotype for one female (PAN II/58), and the other one (PAN II/47) collected at Isla Colon in Bocas del Toro, sample BRS 008 (Table 2).

3.5.2. Diagnosis.

Pycnophyes with middorsal elevations on segments 1-9 (males on segment 10); paradorsal setae on some segments, subdorsal setae on segment 1, pairs of laterodorsal setae on segments 2-9, paralateral setae on segments 1, 3, 5 and 7, lateroventral setae on segments 2, 4, 6, 8 and 10 (two pairs), ventrolateral setae on segments 1 and 5, and ventromedial setae on segments 2-9. Without lateral terminal spines. Midsternal plate with a characteristic contoured profile.

3.5.3. Etymology

The species name is dedicated to Dr Alejandro Martínez, for his constant and enthusiastic help during sampling and processing.

3.5.4. Description

All relevant dimensions and measurements are summarized in Table 11, and distribution of cuticular characters in Table 12. All studied specimens, mounted both for LM and for SEM appeared with the introvert completely retracted into the trunk, so no information is available on scald numbers and arrangement. Neck with four dorsal and two ventral placids. All placids are rectangular and of similar size, robust and hard, strongly sclerotized.

Segments 2 to 10 with subdorsal elongate, groove-like glandular cell outlets (cuticular scars) and crescentic ones in ventromedial position. Similar glandular cell outlets appear on segment 1, but these are more conspicuous, with the dorsal ones displaced medially and the ventral ones being more laterally displaced. Oval muscular scars in laterodorsal and ventromedial position along the trunk segments. Segments 2 to 9 with one pair of laterodorsal and ventromedial cuticular ridges. Pachycycli and peg and socket joints on segments 2-10. Apodemes present on segments 9-10. Pectinate fringe fringes not visible with LM. Two parallel secondary pectinate fringes on segments 2-10.

Segment 1 with the anterolateral margins of the episternal plates projecting into horn-shaped extensions. Anterior edge of tergal plate smooth. Posterior margin of dorsal plate with a middorsal elevation and one pair of paradorsal sensory spots associated with butterfly-like intracuticular atria (Figs. 15B, C, 16B). Paired subdorsal and paralateral setae (Figs. 15B, 16B). Two additional pairs of sensory spots, one subdorsal and one laterodorsal. Ventral anterior margin is bulged and ornamented, followed by a contiguous depressed area. Midsternal plate with a characteristic contoured profile and slightly longer than the episternal plates, extending beyond the anterior edge of the segment (Fig. 15F, G). Paired ventrolateral setae (Fig. 15F, G). Paired ventromedial sensory spots present at the anterior third of the plate.

Segment 2 with the posterior margin of dorsal plate with a middorsal elevation. One pair of paradorsal sensory spots associated with butterfly-like intracuticular atria (Fig. 15C). Three additional pairs of sensory spots, one subdorsal and two laterodorsal. Pairs of laterodorsal and lateroventral setae present (Fig. 15C). The laterodorsal pair appears more mesially than the laterodorsal cuticular ridges and between the two laterodorsal sensory spots. Sternal plates on both sexes with one pair of ventromedial setae and sensory spots; sensory spots located lateral to the setae (Figs. 14A, C, 15F). Males with a pair of large ventromedial tubes. One female with one pair of ventrolateral setae.

Segment 3 with the posterior margin of dorsal plate with a middorsal elevation (Fig. 15C). One pair of paradorsal sensory spots associated with butterfly-like intracuticular atria. Three additional pairs of sensory spots, two subdorsal and one laterodorsal (Fig. 15B, C). Pairs of laterodorsal and paralateral setae present (Fig. 15B, C). Females with unpaired paradorsal setae. Sternal plates with paired ventromedial setae (Fig. 15E) and sensory spots; setae located

mesial to the sensory spots (Fig. 15A, H). Females with their ventromedial setae located closer to the paraventral position (Fig. 15H). Two females with a ventrolateral seta on one of the sternal plates. One male with the ventromedial setae located lateral to the sensory spots.

Segment 4 with the posterior margin of dorsal plate with a middorsal elevation (Fig. 16D). One pair of paradorsal sensory spots associated with butterfly-like intracuticular atria. Three additional pairs of sensory spots, two subdorsal and one laterodorsal (Fig. 15B). Pairs of laterodorsal and lateroventral setae present (Figs. 15B, 16D). Males with unpaired paradorsal seta (Fig. 16D). Sternal plates with pairs of ventromedial setae and sensory spots (Fig. 15E), with the sensory spots located lateral to the setae (Fig. 15A).

Segment 5 with the tergal plate similar to that on segment 3 (Figs. 15B, 16D), but without paradorsal setae in any of the sexes. Sternal plates similar to those on segment 4 (Fig. 15A), but with one pair of ventrolateral setae.

Segment 6 with the tergal and sternal plates similar to those on segment 4 (Figs. 15A, B, 16C, D). Unpaired paradorsal seta seems to be present in the specimens of undetermined sex checked by SEM (Fig. 16C, D).

Segment 7 with the tergal plate similar to that on segment 3 (Figs. 15B, 16A, C), but without paradorsal setae on both sexes. Sternal plates similar to those on segment 4 (Fig. 15A).

Segment 8 with the tergal plate similar to that on segment 4, but with an additional pair of laterodorsal sensory spots (Figs. 14B, 15B, D, 16E). Females with unpaired paradorsal seta. Paradorsal seta also present in the specimens of undetermined sex checked by SEM (probably a male) (Fig. 16E). Sternal plates similar to those on segment 4 (Figs. 14A, 15A).

Segment 9 with the tergal plate with a middorsal elevation and paradorsal sensory spots (Figs. 15B, D, 16E). Three additional pairs of sensory spots, two subdorsal and one laterodorsal (Figs. 15B, D, 16E). One pair of laterodorsal setae (Figs. 15B, D, 16E). Unpaired paradorsal setae observed in one female and two males (Figs. 15B, D, 16E). Paralateral protonephridial openings present, not sieve-like. Sternal plate similar to those on segment 4 (Fig. 15A). Females with the ventromedial seta mesially displaced.

Segment 10 without middorsal structure specializations or intracuticular atria. Two pairs of lateroventral setae (Fig. 14A, B). Males with unpaired paradorsal seta (Fig. 16E), uncheckable in females. One pair of ventromedial sensory spots present, located more mesially than those of the previous segments. Posterior sternal segment margin projected and rounded at the paraventral area in males, straight in females (Figs. 14A, D).

Segment 11 without lateral terminal spines (Figs. 15A, B, 16A), instead with a pair of bulbous protuberances. Males with two pairs of penile spines and genital pores surrounded by a tuft of long hairs. Other characters uncheckable.

3.5.5. Associated kinorhynch fauna

Pycnophyes alexandroi sp. nov. only appeared in Bocas del Toro at the sampling locality near the Station dock (BRS 008; see Table 2). For Pacific Panama, see Pardos et al. 2016, this issue.

4. Discussion

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

4.1.1 *Echinoderes intermedius*

The original description of *Echinoderes intermedius* reports the presence of subdorsal, sublateral and ventrolateral tubes (but referred to as both “tubules” and “spines”) on segment 4 (now segment 2). The examination of the material presented herein, confirmed by reexamination of the original material (Sørensen, pers. com.) allows us to conclude that segment 2 has just subdorsal and ventrolateral tubes plus a big, conspicuous glandular cell outlet type 2 in sublateral position, originally mistaken for a sublateral tube. Also the ventrolateral tube in this segment is reported but illustrated as lateroventral. The presence and distribution of all other spines and tubes agree with the original description by Sørensen (2006), including the sexual dimorphism of the laterodorsal tubes of segment 10 (originally described as subdorsal).

The number and distribution of sensory spots has also been revised, resulting in the location of ten new sensory spots (compare Table 4 herein with Table 12 in Sørensen (2006)).

Noteworthy, some of the sensory spots appear always flanked by a pair of long cuticular hairs. Such hairs are not different from others on the segment, except for their consistent association with sensory spots. In *Echinoderes intermedius* such flanked sensory spots appear in the anteriormost segments, subdorsal on segment 1, subdorsal and laterodorsal on segment 2 and sublateral on segment 3. The feature corresponds to the subtype (a) sensory spot described by Herranz et al. (2012), but only recently noticed in this genus (see *Echinoderes rociae* sp. nov. Pardos et al., this paper and *Echinoderes belenae* sp. nov. Pardos et al., this issue) and the closely related *Meristoderes* and *Cephalorhyncha* (Herranz et al., 2012; Sørensen et al., 2013).

The middorsal protuberance described on segment 11 was unnoticed in the original description (Sørensen 2006), but recently has been reported from various *Echinoderes* (see Sørensen et al. 2016, this Special Issue). Probably this feature is quite widespread among the genus and at least present in *E. bookhouti* Higgins, 1964, *E. charlotteae* Sørensen et al. 2016, *E. augustae* Sørensen and Landers, 2014, *E. eximus* Higgins and Kristensen, 1988, and *E. tchefouensis* Lou, 1934.

Besides the new information and redescription included herein, the *Echinoderes* species that show the closest resemblance with *E. intermedius* are still *Echinoderes peterseni* Higgins and Kristensen, 1988, *Echinoderes hispanicus* Pardos et al., 1998, and *Echinoderes newcaledoniensis* Higgins, 1967 as discussed in Sørensen (2006). It should be remarked, however, that such similarity refers just to the spine/tube formula and do not reflect any kind of well supported phylogenetic analysis of the Echinoderidae.

4.1.2. *Echinoderes rociae* sp. nov.

Echinoderes rociae sp. nov. shares the presence of middorsal spines on segments 4, 6, 8 with other 13 species in the genus, including *E. intermedius* redescribed above. From these, only *Echinoderes abbreviatus* Higgins, 1983, *E. peterseni*, *E. newcaledoniensis*, *E. hispanicus* and *E. intermedius* have one pair of subdorsal/laterodorsal tubes on segment 2 as present in the new species (Higgins, 1967; Higgins and Kristensen, 1988; Sørensen, 2006). And only *E. intermedius* has laterodorsal tubes on segment 8 plus lateral accessory tubes on segments 7 and 8. However, *Echinoderes rociae* sp. nov. lacks the lateral accessory tube on segment 6 present in *E. intermedius*. Moreover, both species can be easily distinguished by their lateral terminal spines, long in *E. intermedius* and conspicuously short in *Echinoderes rociae* sp. nov.

The short and stubby lateral terminal spines, is an easy-to-detect feature that is shared by 8 species in the genus: *Echinoderes abbreviatus*, *Echinoderes augustae*, *Echinoderes brevicaudatus* Higgins, 1966, *Echinoderes cavernus* Sørensen et al., 2000, *Echinoderes hwiizaa* Yamaski and Fujimoto, 2014, *Echinoderes obtuspinosus* Sørensen et al., 2012, *Echinoderes ulsanensis* Adrianov, 1999 in Adrianov and Malakhov (1999), and *Echinoderes belenae* Pardos et al., this issue. But only *E. abbreviatus* and *E. belenae* have middorsal spines on segments 4, 6 and 8 (Higgins, 1983; Pardos et al., this issue). However these two species can be easily differentiated from *Echinoderes rociae* sp. nov. by the complete absence of tubes on the tergal plates of *E. abbreviatus* and by a series of midlateral tubes in *E. belenae*.

4.1.3. *Echinoderes orestauri* sp. nov.

The species most resembling *Echinoderes orestauri* sp. nov. is *Echinoderes truncatus* (Higgins, 1983). After its original description, this species was not reported again until 2006, when M.V. Sørensen found new cuticular structures termed fringed tubes in specimens collected in Bocas del Toro, Panama. In spite of the initial considerations, new observations and reevaluation of the material have now lead to consider the Panamanian specimens as a new, yet undescribed species (Sørensen et al., this issue). The species described herein, *Echinoderes orestauri* sp. nov., seems to differ from both *E. truncatus* and the Panamanian specimens of Sørensen (see Table 13).

Unfortunately, the study of type material of *Echinoderes truncatus* revealed difficult for the condition of the specimens was really bad, as already noted by Sørensen (2006) (but see below and Sørensen et al., this issue). This is particularly important because the structures to be studied, the fringed tubes, are not well discriminated with LM and only SEM images allow a complete identification. Differences of *Echinoderes orestauri* sp. nov. and *E. truncatus* are: the presence of big gland cell openings type 2 on segment 2 of the latter that do not occur in *E. orestauri* sp. nov., the presence of a standard tube in lateroventral position of segment 5 instead of a fringed tube in the same position as showed by the new species; the presence of a fringed tube in lateral accessory position of segments 7 and 8 of the new species, absent in *E. truncatus*; and the lateroventral spine in the segment 10 of *E. truncatus*, lacking in *E. orestauri* sp. nov (Higgins, 1983). Instead, the new species shows a laterodorsal standard tube on this last segment. Moreover, the lateroventral spines of *E. truncatus* show sexual dimorphism, a feature not displayed in *Echinoderes orestauri* sp. nov. Of course, the presence of numerous pairs of fringed tubes not reported in the original description of *E. truncatus* should be taken into consideration. Such tubes were overlooked by Higgins (1983), but observed and reported by Sørensen et al. (2016, this issue) after revising the type material from Belize deposited at the Smithsonian Institution. We consider that the differences reported herein between *E. truncatus* and *E. orestauri* sp. nov. justify the description of a new species.

Regarding the differences between *Echinoderes orestauri* sp. nov. and the Panamanian specimens reported by Sørensen (2006) but not described as new species, the presence of ventrolateral standard tubes on segment 2 (see Fig 2E in Sørensen 2006), which are lacking in the *E. orestauri* sp. nov, is remarkable. Both species also differ greatly in the number and

distribution of fringed tubes, very numerous in *E. orestauri* sp. nov. (up to 30 pairs) while reaching only 20 pairs in the Panamanian specimens of Sørensen (2006) (see Table 13).

The final picture shows three different species: *Echinoderes truncatus*, *Echinoderes orestauri* sp. nov. and the undescribed species from Sørensen (2006). Undoubtedly, the three species are very similar from morphological and biogeographical points of view. Moreover, their unusual features, mostly related to the presence of numerous fringed tubes and the truncate appearance of the last segment, might suggest a closer phylogenetic relationship of these species within *Echinoderes*.

4.1.4. *Cristaphyes panamensis* sp. nov.

Cristaphyes panamensis sp. nov. is characterized by the presence of middorsal processes on all segments 1-9. The lack of the structure on segment 10 enables us to distinguish the new species from eight of its congeners, which have a keel-shaped middorsal, appearing conspicuously extended beyond the segment 11. These species are as follows: *Cristaphyes abyssorum* (Adrianov and Maiorova, 2015); *Cristaphyes arctous* (Adrianov, 1999); *Cristaphyes chukchiensis* (Higgins, 1991); *Cristaphyes cristatus* (Sánchez et al., 2013); *Cristaphyes cryopygus* (Higgins and Kristensen, 1988); *Cristaphyes furugelmi* (Adrianov, 1999); *Cristaphyes nubilis* (Sánchez et al., 2014); and *Cristaphyes odhneri* (Lang, 1949). On the remaining *Cristaphyes* species, only six share with *Cristaphyes panamensis* sp. nov. the absence of lateral terminal spines, having a pair of bulbous protuberances instead. These include: *Cristaphyes anomalus* (Lang, 1953); *Cristaphyes belizensis* (Higgins, 1983); *Cristaphyes phyllotropis* (Brown and Higgins, 1983); *Cristaphyes rabaulensis* (Adrianov, 1999); *Cristaphyes spinosus* (Lang, 1949); and *Cristaphyes yushini* (Adrianov, 1989). However, none of the referred species present paradorsal setae on all segments 1-10, present in *Cristaphyes panamensis* sp. nov. The remaining three species in the genus, *C. carinatus* (Zelinka, 1928), *C. chilensis* (Lang, 1953) and *C. longicornis* (Higgins, 1983) differ greatly from the new species in many characters, so are not discussed any longer here.

4.1.5. *Pycnophyes alexandroi* sp. nov.

Pycnophyes alexandroi sp. nov. can be easily discriminated from the other pycnophyid species by the presence of middorsal elevations and its distribution of paradorsal setae. The presence of both characters is quite common among the species of the family, but the presence of middorsal elevations on segments 1-9 usually runs with paradorsal setae only on even-

numbered segments or on all segments 1-9. The new species has the particular feature of having paradorsal setae on even-numbered as well as uneven-numbered segments, but not on all of them. Three species share with *Pycnophyes alexandroi* sp. nov. the presence of paradorsal setae on segment 9 and on some even-numbered segments: *Cristaphyes abyssorum* (2-4, 8-9), *Cristaphyes belizensis* (2, 4, 6, 9), and *Cristaphyes yushini* (on segments 2, 4, 6, 8-9) (Adrianov, 1989; Adrianov and Maiorova, 2015; Higgins, 1983). Of these species, only *C. yushini* and *C. belizensis* share with the new species the presence of bulbous protuberances instead of well-developed lateral terminal spines (Adrianov, 1989; Higgins, 1983). However, the outline of the midsternal plate in *Pycnophyes alexandroi* sp. nov. is clearly different from the two referred species. The characteristic features of *Pycnophyes alexandroi* sp. nov. do not fit with the diagnostic characters of none of the newly pycnopyid genera erected by Sánchez et al. (2016).

4.2. The kinorhynch fauna of the Caribbean region

The Caribbean Sea is limited by the coastline of Central America, from Belize to Venezuela, and by the Greater Antilles, with Cuba, La Española and Puerto Rico, followed by the Lesser Antilles until Trinidad. In spite of the high zoological diversity of the area, the phylum Kinorhyncha was not reported from the Caribbean until Kirsteuer (1964) described *Echinoderes caribiensis* Kirsteuer, 1964 from the Mochima Bay in Venezuela. Much later, Higgins (1983) sampled extensively at Carrie Bow Cay, a coral sand island off Belize, which made its kinorhynch fauna the best known in the Caribbean, with 18 new species described. Sørensen (2006) found nine species in Bocas del Toro (Panama), two of them, *E. collinae* and *E. intermedius*, new to science. However, his report of *E. truncatus* finally resulted in a new, yet undescribed species (see above and Sørensen et al. 2016, this issue). Recently, Neuhaus et al. (2014) described from the same locality a new species of *Centroderes*, *C. barbanigra* in a survey of the genus along the Eastern coast of America. This latter species was reported before by Sørensen (2006) but not described.

The present study, carried out also at Bocas del Toro, adds four new species plus four new records to the previous list. All these makes a total of 33 species in the Caribbean region (Table 1), of which 18 are from Belize, 14 from Bocas del Toro (Panama) and one from Venezuela. The list includes three undescribed species of the genera *Campyloderes*, *Echinoderes* and *Cephalorhyncha*. However, it probably only reveals a small fraction of the actual diversity because just two localities, Carrie Bow Cay (Belize) and Bocas del Toro (Panama), both in the continental coast of Central America yielded such results. The coasts of Honduras, Guatemala,

Costa Rica, Colombia and most Venezuela, and most important, the long line of islands of the Greater and Lesser Antilles still remain unexplored. New sampling will complete the picture of the Caribbean kinorhynchs and most probably will uncover an even higher diversity in the area.

Moreover, and from a biogeographical point of view, these findings would complement the ongoing comprehensive studies along the Gulf of Mexico (Sørensen et al., this issue) and the well sampled kinorhynch fauna from Florida and Bermuda (Higgins, 1983, Herranz et al., 2014), making Caribbean Central America one of the best known and most extensive areas for kinorhynchs around the world, paralleling the coasts of the Iberian (Sánchez et al., 2012) and Korean Peninsulas (Sánchez et al., 2013; Sørensen et al., 2012, 2013).

5. Acknowledgements

The authors deeply acknowledge the support of the Smithsonian Institution through its Smithsonian Tropical Research Institute, and the Encyclopedia of Life (EOL). Special thanks are given to Dr Jon Norenburg, organizer of the Panamanian workshops, and to the staff of the Smithsonian Marine Station at Bocas del Toro. We want to express our gratitude to the participating scientists at the workshops, who contributed with sampling effort and a really friendly atmosphere. K. Worsaae and D. Gouge collected several kinorhynch-rich samples by scuba diving. We are also grateful to the staff of the Bioimaging Facility at University of British Columbia for their help with SEM. This research has been partially funded by grants CGL2009-08928 and CGL2013-42908-P to FP from the Ministerio de Ciencia y Tecnología, Government of Spain.

References

- Adrianov, A.V., 1989. The first report on Kinorhyncha of the Sea of Japan. Zool. Zhur. 68, 17–27.
- Adrianov, A.V., Maiorova, A.S., 2015. *Pycnophyes abyssorum* sp. n. (Kinorhyncha: Homalorhagida), the deepest kinorhynch species described so far. Deep-Sea Res. II: Topical Studies in Oceanography. 111, 49–59.
- Adrianov, A.V., Malakhov, V.V., 1999. Cephalorhyncha of the world ocean. KMK Scientific Press, Moscow.

- Brown, R., Higgins, R.P., 1983. A new species of *Kinorhynchus* (Homalorhagida, Pycnophyidae) from Australia with a redescription and range extension of other Kinorhyncha from the South Pacific. Zool. Scr. 12, 161–169.
- Claparède, A.R.E., 1863. Zur Kenntnis der Gattung Echinoderes Duj. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt, 119. Verlag von Wilhelm Engelmann, Leipzig, pp.90–92 (pls. XVI–XVII).
- Herranz, M., Sánchez, N., Pardos, F., Higgins, R. P., 2014. New Kinorhyncha from Florida coastal waters. Helgol. Mar. Res. 68, 59–87.
- Herranz, M., Thormar, J., Benito, J., Sanchez, N., Pardos, F., 2012. *Meristoderes* gen. nov., a new kinorhynch genus, with the description of two new species and their implications for echinoderid phylogeny (Kinorhyncha: Cyclorhagida, Echinoderidae). Zool. Anz. 251, 161–179.
- Higgins, R. P., 1964. Three new kinorhynchs from the North Carolina coast. Bull. Mar. Sci. Gulf Caribb. 14, 479–493.
- Higgins, R. P., 1966. Faunistic studies in the Red Sea (In winter, 1961–62). Kinorhynchs from the Area of Al-Ghardaqa. Zool. Jb. Syst. Bd. 93, 118–126.
- Higgins, R.P., 1967. The Kinorhyncha of New-Caledonia. In: Expedition Française sur les Récifs Coralliens de la Nouvelle-Calédonie 2, 75–90.
- Higgins, R.P., 1983. The Atlantic Barrier reef ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. Smithson. Contrib. Mar. Sci. 18, 1–131.
- Higgins, R.P., 1991. *Pycnophyes chukchiensis*, a new homalorhagid kinorhynch from the Arctic Sea. Proc. Biol. Soc. Wash. 104, 184–88.
- Higgins, R.P., Kristensen, R.M., 1988. Kinorhyncha from Disko Island, West Greenland. Smithson. Contrib. Zool. 458, 1–56.
- Kirsteuer, E., 1964. Zur Kenntnis der Kinorhynchen Venezuelas. Zool. Anz. 173, 388–393.
- Lang, K., 1949. Echinoderida. In N. H. Odhner (Ed.), Further zoological results of the Swedish Antarctic Expedition 1901–1903, Vol. IV, No. 2 (pp. 1–22). Stockholm: Norstedt and Söner.
- Lang, K., 1953. Reports of the Lund University Chile Expedition 1948–49. 9. Echinoderida. Kunngl. Fysiografiska. Sällskapet i Lund Handlingar, N.F. 64, 1–8.

- Neuhaus, B., Pardos, F., Sørensen, M.V., Higgins R. P., 2014. New species of *Centroderes* (Kinorhyncha: Cyclorhagida) from the Northwest Atlantic Ocean, life cycle and ground pattern of the genus. *Zootaxa*, 3901, 1–69.
- Pardos, F., Higgins, R.P., Benito, J., 1998. Two new *Echinoderes* (Kinorhyncha, Cyclorhagida) from Spain, including a reevaluation of kinorhynch taxonomic characters. *Zool. Anz.* 237, 195–208.
- Sanchez, N., Herranz, M., Benito, J., Pardos, F., 2012. Kinorhyncha from the Iberian Peninsula: new data from the first intensive sampling campaigns. *Zootaxa*. 3402, 24–44.
- Sánchez, N., Pardos, F., Sørensen, M.V., 2014. Deep-sea Kinorhyncha: two new species from the Guinea Basin, with evaluation of an unusual male feature. *Org. Divers. Evol.* 14, 349–361.
- Sánchez, N., Rho, S.H., Min, W.G., Kim, D., Sørensen, M.V. 2013. Four new species of *Pycnophyes* (Kinorhyncha: Homalorhagida) from Korea and the East China Sea. *Sci. Mar.* 77, 353–380.
- Sánchez, N., Yamasaki, H., Pardos, F., Sørensen, M.V., Martínez, A., 2016. Morphology disentangles the systematics of a ubiquitous but elusive meiofaunal group (Kinorhyncha: Pycnophyidae). *Cladistics*. <http://dx.doi.org/10.1111/cla.12143>
- Sørensen, M.V., 2006. New kinorhynchs from Panama, with a discussion of some phylogenetically significant cuticular structures. *Meiofauna Marina*, 15, 51–77.
- Sørensen, M.V., 2007. A new species of *Antygomonas* (Kinorhyncha: Cyclorhagida) from the Atlantic coast of Florida, USA. *Cah. Biol Mar.* 48, 155–168.
- Sørensen, M.V., Dal Zotto, M., Rho, H.S., Herranz, M., Sánchez, N., Pardos, F., Yamasaki, H., 2015. Phylogeny of Kinorhyncha based on morphology and two molecular loci. *PLoS ONE* 10(7), e0133440.
- Sørensen, M. V., Heiner, I., Ziemer, O., 2005. A new species of *Echinoderes* from Florida (Kinorhyncha: Cyclorhagida). *Proc. Biol. Soc. Wash.* 118 (3), 499–508.
- Sørensen, M.V., Herranz, M., and Landers, S. C., 2016. A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Gulf of Mexico, with a redescription of *Echinoderes bookhouti* Higgins, 1964. *Zool. Anz.* (this issue), <http://dx.doi.org/10.1016/j.jcz.2016.04.004>

- Sørensen, M.V., Jørgensen, A, Boesgaard, T.M., 2000. A new *Echinoderes* (Kinorhyncha: Cyclorhagida) from a submarine cave in New South Wales, Australia. *Cah. Biol Mar.* 41, 167–179.
- Sørensen, M.V., Landers, S.C., 2014. Two new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Gulf of Mexico. *Front. Mar. Sci.* 1:8.
- Sørensen, M.V., Pardos, F., 2008. Kinorhynch systematics and biology-an introduction to the study of kinorhynchs, inclusive identification keys to the genera. *Meiofauna Mar.* 16, 21–73.
- Sørensen, M.V., Rho, H.S. , Min, W.-G., Kim, D., Chang, C.Y., 2012. An exploration of *Echinoderes* (Kinorhyncha: Cyclorhagida) in Korean and neighboring waters, with the description of four new species and a redescription of *E. tchefouensis* Lou, 1934. *Zootaxa*.3368, 161–196.
- Sørensen, M.V., Rho, H.S, Min, W.G., Kim, D., Chang, C.Y., 2013. Occurrence of the newly described kinorhynch genus *Meristoderes* (Cyclorhagida: Echinoderidae) in Korea, with the description of four new species. *Helgol. Mar. Res.* 67(2), 291–319.
- Yamasaki, H., Fujimoto, S., 2014. Two new species in the *Echinoderes coulli* group (Echinoderidae, Cyclorhagida, Kinorhyncha) from the Ryukyu Islands, Japan. *Zookeys* 382 27-52.
- Zelinka, C., 1894: Über die Organisation von *Echinoderes*. *Verh. Deutsch Zool. Gesellsch.* 4: 46–49.
- Zelinka, C., 1896: Demonstration der Tafeln der *Echinoderes*- Monographie. *Verh. Deutsch Zool. Gesellsch.* 6: 197–199.
- Zelinka, C., 1928. Monographie der Echinodera. Verlag W. Engelmann, Leipzig.

Figure Captions

Fig. 1. Map of Bocas del Toro area in Panama. Dots indicate sampling stations yielding kinorhynch specimens. See also Table 2.

Fig. 2. Line drawings of *Echinoderes intermedius*. (A) Adult female, ventral view. (B) Same, dorsal view. (C) Adult male, 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; mdpl, middorsal placid; mds, middorsal spine; mvp, midventral placid; pdss, paradorsal sensory spot; ps1-3, penile spines 1-3; sdt, subdorsal tube; sp, sieve plate; ss, sensory spot; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Fig. 3. Light micrographs of *Echinoderes intermedius*. (A) Adult female, habitus, ventral view. (B) Adult female, ventral view of segments 1-4. Arrow points to a glandular cell outlet type 2 in segment 2. (C) Adult female, dorsal view of segments 1-5. (D) Adult female, ventral view of segments 3-7. (E) Adult female, dorsal view of segments 6-11. (F) Adult female, ventral view of segments 8-11. Lateral terminal accessory spines are out of focus. Dotted circles indicate selected sensory spots. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; mvp, midventral placid; sdt, subdorsal tube; te, tergal extension; tp, trichoscalid plate; vlt, ventrolateral tube.

Fig. 4. SEM micrographs of *Echinoderes intermedius*. (A) Dorsal view of segments 1-4. (B) Posterior end of a male specimen, laterodorsal view. (C) Bracteate hairs on tergal plate. Arrow points to a sensory spot flanked by hairs. (D) Ventral view of segments 1-4. Arrow points to left ventrolateral tube of segment 2. (E) Posterior end of a female specimen, lateral view. (F) Lateral view of segment 2. Arrow points to gland opening type 2. (G) Pectinate fringe of segment 8 overlapping anterior part of segment 9. Arrow points to excretory sieve plate. Lateroventral spine and lateral accessory tube of segment 8 can be seen at left margin. Abbreviations: ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mvp, midventral placid; ps2/3, penile spine 2/3; sdt, subdorsal tube; te, tergal extension; tp, trichoscalid plate. Dotted circles mark sensory spots.

Fig. 5. Line drawings of *Echinoderes rociae* sp. nov. (A) Adult female, ventral view. (B) Same, dorsal view. (C) Adult male, 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; lvt, lateroventral tube; mdpl, middorsal placid; mds, middorsal spine; ps1-3, penile spines 1-3; sdt, subdorsal tube; sp, sieve plate; ss, sensory spot; tp, trichoscalid plate.

Fig 6. Light micrographs of *Echinoderes rociae* sp. nov. (A) Holotypic female, habitus, ventral view. (B) Same, dorsal view of segments 1-6. (C) Same, dorsal view of segments 6-10. (D) Paratypic male segments 10-11. (E) Holotypic female, ventral view of segments 1-6. Numbers mark the segment numbers. (F) Holotypic female, ventral view of segments 6-11. Abbreviations: 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; ps1-3, penile spines 1-3; sdt, subdorsal tube; te, tergal extension.

Fig. 7. SEM micrographs of *Echinoderes rociae* sp. nov. (A) Panoramic lateral view of a female specimen. (B) Lateroventral view of segments 1-4. Arrow points to right sublateral glandular cell outlet type 2. (C) Left lateral view of segments 5-8. (D) Ventral view of segments 8-10. (E) Left lateral view of segments 6-7. (F) Laterodorsal view of segments 10-11. Abbreviations: lat, lateral accessory tube; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine;.mvp, midventral placid; te, tergal extension.

Fig. 8. Line drawings of *Echinoderes orestauri* sp. nov. (A) Adult female ventral view. (B) Same, dorsal view. (C) Adult male, ventral view of segment 11. (D) Same, dorsal view. Abbreviations: ft, fringed tube; go1/2, glandular cell outlet type 1/2; ld, laterodorsal; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mdpl, middorsal placid; mds, middorsal spine; ml, midlateral;.mvp, midventral placid; ps1-3, penile spines 1-3; sp, sieve plate; ss, sensory spot; tp, trichoscalid plate.

Fig 9. Light micrographs of *Echinoderes orestauri* sp. nov. (A) Holotypic male, dorsal view. Arrows point to some of the fringed tubes of the same segment. (B) Same, ventral view. Arrows point to some of the fringed tubes of segment 2. Abbreviations: go2, glandular cell outlet type 2; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; ps, penile spine.

Fig. 10. SEM micrographs of *Echinoderes orestauri* sp. nov. (A) Panoramic lateral view of an adult female. (B) Neck and first segment. The introvert is retracted. (C) Laterodorsal view of segments 2-3. Arrows point to fringed tubes. (D) Laterodorsal view of segments 5-6. Arrows point to fringed tubes. (E) Laterodorsal view of segments 6-7. Arrows point to fringed tubes. (F) Lateral view of segments 7-9. Black arrows point to type 2 gland cell opening in segments 8 and 9. White arrows point to fringed tubes in lateral accessory position. (G) Ventral view of segments 4-9. Arrows point to fringed tubes. (H) Lateral view of segments 10-11. (I) Detail of cuticular structures. Arrows point to fringed tubes. (J) Dorsal view of segments 10-11. (K) Detail of area between segments 1 and 2. Note the scarce hairs on segment 1 compared with segment 2. The secondary pectinate fringe is barely visible under the primary pectinate fringe (pf). Arrow points to a type 1 gland cell outlet. Abbreviations: ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; mvpl, midventral placid; pf, pectinate fringe; tp, trichoscalid plate. Dotted circles mark sensory spots.

Fig. 11. Line drawings of *Cristaphyes panamensis* sp. nov. (A) Male, ventral view. (B) Same, dorsal view. (C) Female, 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; pdss, paradorsal sensory spot; pls, paralateral seta; ps, penile spine; sds, subdorsal seta; sdss, subdorsal sensory spot; spf, secondary pectinate fringe; tp, thickening of ventral pachycycli; tu, male tubes; vls, ventrolateral seta; vms, ventromedial seta; vmss, ventromedial sensory spot.

Fig. 12. Light micrographs of *Cristaphyes panamensis* sp. nov., holotypic male. (A) Ventral view. (B) Dorsal view. (C) Dorsal view of right side of segments 1-2. (D) Dorsal view of right side of segments 4-6. (E) Ventral view of right side of segments 3-5. (F) Ventral view of right side of

segment 9. Abbreviations: go, glandular cell outlet; lds, laterodorsal seta; mdp, middorsal process; pds, paradorsal seta; sds, subdorsal seta; spf, secondary pectinate fringe; vls, ventrolateral seta; vms, ventromedial seta. Dotted circles indicate sensory spots. Solid circlets indicate setae.

Fig. 13. SEM micrographs of *Cristaphyes panamensis* sp. nov., paratypic specimens. A, B, D, E, paratypic female. C, paratypic male. (A) Dorsal view. (B) Ventral view of left side of segments 6-7. (C) Ventral view of segments 2-4. (D) Ventral view of left side of segments 8-11. (E) Lateral view. Scale bar a-b, e = 100 μ m; c-d = 10 μ m. Abbreviations: go, glandular cell outlet; lds, laterodorsal seta; lvs, lateroventral seta; mdp, middorsal process; pds, paradorsal seta; pls, paralateral seta; sds, subdorsal seta; tu, tube; vls, ventrolateral seta; vms, ventromedial seta. Dotted circles indicate sensory spots.

Fig. 14. Line drawings of *Pycnophyes alexandroi* sp. nov. (A) Male, ventral view. (B) Same, dorsal view. (C) Female, ventral view, segments 1-2. (D) Same, ventral view, segments 9-11. Abbreviations: a, apodemes of ventral pachycycli; bp, bulbous protuberance; cr, cuticular ridge; go, glandular cell outlet; lds, laterodorsal seta; ldss, laterodorsal sensory spot; lvs, lateroventral seta; mde, middorsal elevation; ms, muscular scar; pds, paradorsal seta; pdss, paradorsal sensory spot; pls, paralateral seta; ps, penile spine; sds, subdorsal seta; sdss, subdorsal sensory spot; spf, secondary pectinate fringe; tu, male tubes; vls, ventrolateral seta; vms, ventromedial seta; vmss, ventromedial sensory spot

Fig. 15. Light micrographs of *Pycnophyes alexandroi* sp. nov., A-F, holotypic male. G-H, paratypic female. (A) Ventral view. (B) Dorsal view. (C) Dorsal view of segments 1-3. (D) Dorsal view of segments 8-9. (E) Ventral view of segments 3-4, male. (F) Ventral view of segments 1-2, male. (G) Ventral view of segments 1-2, female. (H) Ventral view of segments 2-3, female. Abbreviations: bsj, ball and socket joint; cr, cuticular ridge; go, glandular cell outlet; lds, laterodorsal seta; lvs, lateroventral seta; mde, middorsal elevation; pds, paradorsal seta; sca, subcuticular atria; tu, tube; vls, ventrolateral seta; vms, ventromedial seta. Dotted circles indicate sensory spots. Solid circlets indicate setae.

Fig. 16. SEM micrographs of *Pycnophyes alexandroi* sp. nov., adult specimen (probably a male). (A) Dorsal view of segments 4-11. (B) Dorsal view of segment 1. (C) Dorsal view of segments 6-7. (D) Dorsal view of segments 4-6. (E) Dorsal view of segments 8-11. Abbreviations: lds, laterodorsal seta; lvs, lateroventral seta; mde, middorsal elevation; pds, paradorsal seta; pls, paralateral seta; sds, subdorsal seta. Dotted circles indicate sensory spots. Solid circlets indicate setae.

Pardos et al.

Two sides of a coin: the phylum Kinorhyncha in Panama. I) Caribbean Panama

Tables

Table 1. List of the species of kinorhynchs from the Caribbean region, 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 the area	Caribbean locality	Other localities
<i>Antygomonas</i> cf. <i>paulae</i>	This study	Panama (Bocas del Toro)	Florida , Bermuda
<i>Campyloderes</i> sp.	This study	Panama (Bocas del Toro)	
<i>Centroderes barbanigra</i>	Neuhaus et al. 2014	Panama (Bocas del Toro)	
<i>Cephalorhyncha</i> sp.	Sørensen 2006	Panama (Bocas del Toro)	
<i>Cristaphyes belizensis</i> [<i>Kinorhynchus belizensis</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Cristaphyes longicornis</i> [<i>Pycnophyes longicornis</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Cristaphyes panamensis</i> sp. nov.	This study	Panama (Bocas del Toro)	
<i>Echinoderes abbreviatus</i>	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Echinoderes caribiensis</i>	Kirsteuer 1964	Venezuela (Mochima)	
<i>Echinoderes collinae</i>	Sørensen 2006	Panama (Bocas del Toro)	
<i>Echinoderes horni</i>	Higgins 1983	Belize (Carrie Bow Cay)	Florida, Hawaii
<i>Echinoderes imperforatus</i>	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Echinoderes intermedius</i>	Sørensen 2006	Panama (Bocas del Toro)	
<i>Echinoderes orestauri</i> sp. nov.	This study	Panama (Bocas del Toro)	
<i>Echinoderes rociae</i> sp. nov.	This study	Panama (Bocas del Toro)	
<i>Echinoderes</i> sp.1	Sørensen 2006	Panama (Bocas del Toro)	
<i>Echinoderes spinifurca</i>	Sørensen 2006	Panama (Bocas del Toro)	Florida
<i>Echinoderes truncatus</i>	Higgins 1983	Belize (Carrie Bow Cay)	Panama
<i>Echinoderes wallaceae</i>	Higgins 1983	Belize (Carrie Bow Cay)	Panama
<i>Fujuriphyes deirophorus</i> [<i>Kinorhynchus deirophorus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Fujuriphyes distentus</i> [<i>Kinorhynchus distentus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	Panama (Bocas del Toro)

<i>Higginsium erismatum</i> [<i>Kinorhynchus erismatus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Higginsium trisetosum</i> [<i>Kinorhynchus trisetosus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Leiocanthus corrugatus</i> [<i>Pycnophyes corrugatus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Leiocanthus ecphantor</i> [<i>Pycnophyes ecphantor</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Leiocanthus emarginatus</i> [<i>Pycnophyes emarginatus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	Panama (Bocas del Toro)
<i>Paracentrophyes praedictus</i>	Higgins 1983	Belize (Carrie Bow Cay)	Panama (Bocas del Toro)
<i>Pycnophyes alexandroi</i> sp. nov.	This study	Panama (Bocas del Toro)	
<i>Pycnophyes apotomus</i> [<i>Kinorhynchus apotomus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Pycnophyes beaufortensis</i>	Sørensen 2006	Panama (Bocas del Toro)	North Carolina (USA)
<i>Pycnophyes stenopygus</i> [<i>Kinorhynchus stenopygus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	
<i>Semnoderes</i> cf. <i>pacificus</i>	Sørensen 2006	Panama (Bocas del Toro)	New Caledonia; California
<i>Setaphyes iniorhaptus</i> [<i>Pycnophyes iniorhaptus</i> prior to Sánchez et al., 2016]	Higgins 1983	Belize (Carrie Bow Cay)	

Table 2. Sampling data in Bocas del Toro (and Naos21, Pacific Panama, for *P. alexandroi* sp. nov.)

Station number	Date	Locality	Coordinates	Depth	Sediment	Kinorhynch species
BRS 100	June 8, 2010	Bird Rock, north Isla Colon	9° 27' 30"N-82° 18.0'W	1-3 m	Clean, coarse sand, well sorted	<i>Antygomonas paulae</i>
BRS 102	June 8, 2010	Hospital Point, Solarte Island	9° 20.041'N-82° 13.137'W	12 m	Silty, fine grain / mud	<i>Echinoderes intermedius</i> ; <i>Centroderes barbanigra</i> ; <i>Leiocanthus emarginatus</i> ; <i>Leiocanthus corrugatus</i> ; <i>Paracentrophyes praedictus</i>
BRS 104	June 10, 2010	Wild Cane Rock, Bastimento Island	9° 21.016'N-82° 10.335'W	14 m	Medium coarse sand	<i>Antygomonas</i> cf. <i>paulae</i>
BRS 106	June 13, 2010	Punta Vieja, Bastimento Island	9° 17.175'N-82° 05.065'W	10 m	Medium sand	<i>Echinoderes orestauri</i> sp. nov.; <i>Cristaphyes panamensis</i> sp. nov. <i>Pycnophyes</i> sp., <i>Leiocanthus emarginatus</i> , <i>Paracentrophyes praedictus</i> , <i>Fujuriphyes distentus</i> , <i>Echinoderes intermedius</i> and <i>Centroderes barbanigra</i> .
BRS 107	June 13, 2010	Crawl Cay Channel, Bastimento Island	9° 15.126'N-82° 07.717'W	10 m	Medium sand	<i>Echinoderes rociae</i> sp. nov.
BRS 008	June 16, 2010	Station dock	9° 21' 0.0"N-82°15' 24.2"W	1 m	Mangrove mud	<i>Pycnophyes alexandroi</i> sp. nov.
off Bocas	June 15, 2010	Bocas dock	9° 20' 16.4"N-82° 14' 21.2"W	10 m	Muddy sand	<i>Centroderes barbanigra</i>
NAOS21	Dec. 9, 2011	Isla Taboga	8°48'08.0"N-79°33'19.0"W	2 m	Sandy mud	<i>Pycnophyes alexandroi</i> sp. nov.

Table 3. Measurements (μm) and proportions of *E. intermedius*. Number of measured specimens indicated in parentheses. Numbers in the first column indicate the corresponding segment. Abbreviations: LA, lateral accessory tube; LD, laterodorsal spine/tube; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral spine/tube; MD, Middorsal spine; MSW, maximum sternal width, measured on segment 5; S, segment length; SD, standard deviation; SW, standard width, measured on segment 10; TL, trunk length.

	Mean ♂ (3)	Mean ♀ (3)	Mean (6)	Range	SD
TL	222	236	229	214 - 267	19.6
MSW5	30	29	30	29 - 31	0.8
MSW/TL	14	13	13	12 - 14	0.9
SW10	21	21	21	20 - 22	0.6
S1	27	26	26	25 - 28	1.6
S2	28	29	29	28 - 30	0.8
S3	27	28	27	26 - 29	1.0
S4	28	29	28	27 - 30	0.9
S5	30	30	30	29 - 31	0.6
S6	32	33	33	31 - 34	1.1
S7	35	35	35	34 - 36	0.7
S8	38	39	38	37 - 41	1.7
S9	37	37	37	35 - 39	1.3
S10	38	45	41	34 - 51	6.7
S11	34	34	34	32 - 35	1.2
MD4	41	41	41	39 - 43	1.1
MD6	67	55	61	47 - 71	8.6
MD8	88	77	82	66 - 91	10.2
LV5	12	14	13	11 - 14	1.2
LV6	23	22	22	20 - 24	1.4
LA6	14	14	14	13 - 15	0.8
LV7	26	24	25	23 - 29	2.0
LA7	14	14	14	14 - 15	0.6
LV8	28	28	28	26 - 29	1.1
LA8	14	15	14	13 - 16	1.3
LD8	20	21	20	18 - 25	2.7
LV9	27	28	28	24 - 33	2.8
LTS	151	150	150	130 - 165	11.4
LTAS	-	27	27	26 - 29	1.8
LTS/TL	68	64	66	58 - 72	5.5

Table 4. Summary of relevant cuticular characters and positions of *Echinoderes intermedius*. 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, glandular cell outlet type 2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spine; ss, sensory spot; sp, sieve plate; tu, tube; ♀, female condition of sexually dimorphic characters; ♂, male 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		go2			tu	ss
3			ss			ss				
4	ac									
5			ss	ss				tu		ss
6	ac	ss		ss			tu	ac		ss
7			ss	ss			tu	ac		ss
8	ac	ss		tu			tu	ac		
9		ss	ss	ss		sp		ac	ss	
10			ss	tu					ss	
11		ss			ps(♂)		ltas(♀)	lts		ss, ss

Table 5. Measurements (μm) and proportions of *E. rociae* sp. nov. Number of measured specimens indicated in parentheses. Numbers in the first column indicate the corresponding segment. Abbreviations: LA, lateral accessory; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral spine/tube; MD, Middorsal spine; MSW, maximum sternal width, measured on segment 5; S, segment length; SD, standard deviation; SW, standard width, measured on segment 10

	Holotype	Mean ♂ (3)	Mean ♀ (2)	Mean (5)	Range	SD
TL	225	217	220	218	206 - 233	10.5
MSW5	32	30	32	31	28 - 35	2.8
MSW/TL	14%	14%	14%	14%	13% - 16%	1.2
SW10	24	21	22	22	21 - 24	1.3
S1	24	23	23	23	22 - 24	0.7
S2	28	26	26	27	24 - 28	1.7
S3	25	25	24	25	23 - 27	1.5
S4	27	27	27	27	25 - 27	0.9
S5	31	29	29	30	26 - 31	1.9
S6	32	32	32	32	31 - 32	0.7
S7	36	34	34	34	33 - 36	1.1
S8	39	36	37	37	34 - 39	2.0
S9	38	37	37	37	34 - 39	1.8
S10	34	38	36	37	34 - 39	2.1
S11	25	30	29	29	25 - 31	2.2
MD4	16	12	13	13	11 - 16	2.1
MD6	18	16	16	16	15 - 18	1.3
MD8	22	20	20	20	19 - 22	1.3
LV5	10	10	10	10	9 - 11	0.7
LV6	15	15	15	15	12 - 20	3.0
LV7	19	18	18	18	16 - 21	2.1
LA7	12	11	11	11	10 - 13	1.0
LV8	19	19	19	19	16 - 22	2.1
LA8	12	11	11	11	10 - 12	0.8
LV9	20	19	19	19	17 - 20	1.3
LTS	31	33	31	32	30 - 36	2.3
LTAS	23	-	22	22	20 - 23	1.9
LTS/TL	14%	15%	14%	15%	14% - 17%	1.4

Table 6. Summary of relevant cuticular characters and positions of *Echinoderes rociae* 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; go, glandular cell outlet type 2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spine; sp, sieve plate; ss, sensory spot; tu, tube; ♀, female condition of sexually dimorphic characters; ♂, male 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		go2			tu	ss
3			ss							
4	ac									ss
5			ss		ss			tu		ss
6	ac	ss			ss			ac		ss
7			ss		ss		tu	ac		
8	ac	ss		tu			tu	ac		
9		ss	ss			sp		ac	ss	
10				tu					ss	
11		ss			ps(♂)		ltas(♀)	lts		ss

Table 7. Measurements (μm) and proportions of *E. orestauri* 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 9; S, segment length; SD, standard deviation; SW, standard width, measured on segment 10

	Holotype	Mean M (2)	Mean F (3)	Mean (5)	Range	SD
TL	360	343	373	357	327 - 408	30.9
MSW9	36	35	36	36	34 - 37	1.0
MSW/TL	10	10	10	10	9 - 11	3.1
SW10	34	33	33	33	31 - 35	1.5
S1	40	39	42	41	37 - 45	2.9
S2	39	36	39	36	30 - 41	4.4
S3	41	38	42	39	32 - 45	5.5
S4	42	38	46	41	32 - 51	7.5
S5	42	39	48	42	33 - 57	9.4
S6	46	41	53	47	36 - 64	10.8
S7	48	47	55	51	44 - 66	8.8
S8	51	53	59	56	49 - 72	9.4
S9	52	53	58	56	52 - 66	5.8
S10	50	50	51	49	43 - 53	3.4
S11	30	26	32	30	23 - 34	4.2
MD4	13	13	13	13	11 - 14	1.3
MD5	14	14	14	14	12 - 15	1.1
MD6	17	16	18	18	15 - 21	2.0
MD7	26	27	23	25	21 - 28	2.5
MD8	29	29	28	29	24 - 32	3.1
LV5	12	12	12	12	12 - 12	0.4
LV6	12	12	14	13	12 - 15	1.1
LV7	14	13	16	15	13 - 20	2.8
LV8	17	16	18	17	15 - 20	1.8
LV9	19	19	20	19	19 - 20	0.5
LTS	168	174	163	167	156 - 180	8.7
LTS/TL	47	51	44	47	44 - 48	28.3
LTAS	-	-	42	42	41 - 43	1.2

Table 8. Summary of relevant cuticular characters and positions of *Echinoderes orestauri* 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; ft, fringed tube; go1/2, glandular cell outlets type 1 /2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; ps, penile spine; ss, sensory spot; tu, tube; ♀, female condition of sexually dimorphic characters; ♂, male condition of sexually dimorphic characters

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1		ss	ss		ss			go1	ss	
2	ss		ft, ft, ss	ft, ft, ss	ft	ft			ft	ss
3		ft, ss	ft, ss		ss					
4	ac	ss	ft, ft, ss	ft	ss					ss
5	ac		ft, ft, ft	ft,ss				ft		ss
6	ac	ss	ft, ft, ft	ss, ft	ft			ac		ss
7	ac	ss	ft, ft	ss			ft	ac		ss
8	ac	ss	ft, ft	go2, ft, ss			ft	ac		ss
9		ss		go2, ft, ss		sp		ac		ss
10			ss, ss	tu						
11			ss		ps(♂)		ltas(♀)	lts		

Table 9. Measurements (μm) of male holotype of and male paratype of *Cristaphyes panamensis* sp. nov. Abbreviations: MSW-7, maximum sternal width of segment 7; S1–S11, segment lengths of trunk segments 1–11; SW10, sternal width of trunk segment 10; TL, trunk length; ♂, male

Character	Holotype ♂	Paratype ♂
TL	571	622
SW10	119	119
MSW-7	151	147
MSW/TL	26%	23%
S1	94	99
S2	41	55
S3	50	57
S4	54	61
S5	56	61
S6	54	61
S7	60	65
S8	61	65
S9	67	69
S10	60	64
S11	58	51

Table 10. Summary of location of setae and sensory spots in *Cristaphyes panamensis* sp. nov. Abbreviations: LD, laterodorsal; LV, lateroventral; PD, paradorsal; PL, paralateral; SD, subdorsal; VL, ventrolateral; VM, ventromedial; lts, lateral terminal spine; ps, penile spine; se, seta (*) indicates that the seta is unpaired; ss, sensory spot; ss3, sensory spot type 3; tu, tube; ♀, female condition of sexually dimorphic character; ♂, male condition of sexually dimorphic character; ?, uncheckable

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

Table 11. Measurements (μm) of male holotype and male paratype of *Pycnophyes alexandroi* sp. nov. Abbreviations: LTS, lateral terminal spine; MSW-6, maximum sternal width of segment 6; n, number of measured specimens; SD, standard deviation; S1–S11, segment lengths of trunk segments 1–11; SW10, sternal width of trunk segment 10; TL, trunk length; ♀, female; ♂, male.

Character	Holotype ♂	Paratype ♀	n ♂	n ♀	Range ♂	Range ♀	Mean ♂	Mean ♀	SD ♂	SD ♀
TL	497	473	2	3	472-497	473-594	485	519	65.29	17.68
SW10	93	90	2	3	93	90-98	93	93	4.16	0.00
MSW-6	116	123	2	3	116-121	123-144	119	131	11.59	3.54
MSW/TL	23.3%	26%	2	3	23.3-25.6%	24.2-26%	24.5%	25.2%	1%	2%
S1	68	65	2	3	64-68	65-79	66	70	8.08	2.83
S2	48	51	2	3	46-48	40-51	47	47	5.86	1.41
S3	52	49	2	3	50-52	49-55	51	52	3.00	1.41
S4	55	54	2	3	51-55	54-68	53	60	7.37	2.83
S5	59	56	2	3	55-59	56-72	57	63	8.33	2.83
S6	58	55	2	3	53-58	55-69	56	60	8.08	3.54
S7	56	54	2	3	52-56	54-71	54	61	8.89	2.83
S8	57	55	2	3	56-57	55-69	57	61	7.37	0.71
S9	55	60	2	3	54-55	60-70	55	66	5.13	0.71
S10	29	40	2	3	29-40	35-42	35	39	3.21	7.78
S11	-	-	1	0	28	-	-	-	-	-

Table 12. Summary of location of setae and sensory spots in *Pycnophyes alexandroi* sp. nov. Abbreviations: LD, laterodorsal; LV, lateroventral; PD, paradorsal; PL, paralateral; SD, subdorsal; VL, ventrolateral; VM, ventromedial; lts, lateral terminal spine; ps, penile spine; se, seta (*) indicates that the seta is unpaired; ss, sensory spot; ss3, sensory spot type 3; tu, tube; ♀, female condition of sexually dimorphic character; ♂, male condition of sexually dimorphic character; (¹), appeared on a single female specimen.

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

Table 13. Comparative summary of relevant cuticular structures in trunk segments of *Echinoderes orestauri* sp. nov. and closely related species and specimens. Abbreviations: FT, fringed tube; go, glandular cell outlet; LA, lateral accessory; LD, laterodorsal; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral; MD, middorsal; ML, midlateral; PS, penile spine; VL, ventrolateral; ♂, male conditions of sexually dimorphic characters; ♀, female conditions of sexually dimorphic characters. * Character not present in the original description

	<i>Echinoderes truncatus</i> Higgins, 1983	<i>Echinoderes</i> cf. <i>truncatus</i> sensu Sørensen 2006	<i>Echinoderes orestauri</i> sp. nov.
MD spines	4-8	4-8	4-8
Seg. 2	VL go*	VL standard tube + 4 dorsal FT	5 dorsal + 2 ventral FT
Seg. 3	-	2 dorsal FT	2 dorsal FT
Seg. 4	-	3 dorsal FT	3 dorsal FT
Seg. 5	LV spine/tube	LV standard? tube + 3 dorsal FT	LV FT + 4 dorsal FT
Seg. 6	LV spine	LV spine + 2 dorsal FT	LV spine + 5 dorsal FT
Seg. 7	LV spine	LV spine + 2 dorsal FT	LV spine + LA FT + 2 dorsal FT
Seg. 8	LV spine + ML go*	LV spine + ML go + 2 dorsal FT	LV spine+ ML go + LA FT + 3 dorsal FT
Seg. 9	LV spine + ML go*	LV spine + ML go + 2 dorsal FT	LV spine+ ML go + 1 dorsal FT
Seg. 10	LV spine ♀>♂	LV spine ♀>♂ ?	LD standard tube ♀=♂
Seg. 11	LTS + LTAS♀ + 3 PS♂	LTS + LTAS♀ + 3 PS♂	LTS + LTAS♀ + 3 PS♂

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure

Figure