A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Gulf of Mexico, with a redescription of *Echinoderes bookhouti* Higgins, 1964

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ABSTRACT

Sampling of meiofauna along the US continental shelf of the Gulf of Mexico has been carried out in an eight year period, from 2007 to 2014. Studies of the kinorhynch fauna from these collections have resulted in the description of two new species, *Echinoderes augustae* and *E. skipperae*. The present contribution includes new recordings of *E. augustae* and *E. skipperae*, as well as information on two additional kinorhynch species, *Echinoderes bookhouti* and *Echinoderes charlotteae* sp. nov. The latter species is new to science and a detailed morphological description is provided. *Echinoderes bookhouti* was originally described from shallow water localities off North Carolina, but comparison with the type material indicates that the same species occurs in the Gulf of Mexico. Based on the new material from the Gulf, *E. bookhouti* is redescribed using light- and scanning electron microscopy, and new taxonomically significant characters are provided. In addition, examination of other *Echinoderes* types from the collections of the Smithsonian Institution revealed that several species described before 1990 showed taxonomically significant structures, such as tubes and glandular cell outlets type 2, which were not included in their original descriptions. Hence, to ease future identification of *Echinoderes* species, we provide updated information about the nature and distribution of cuticular structures for a total of seven species, including *E. abbreviatus*, *E. andamanensis*, *E. imperforatus*, *E. kristenseni*, *E. pennaki*, *E. truncatus*, and *E. wallaceae*.

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4 **Keywords:** Echinoderidae, kinorhynchs, meiofauna, morphology, taxonomy
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10 **1. Introduction**
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12 Since 2007, comprehensive meiofauna sampling has been carried out in the Gulf of Mexico, along
13 the United States' continental shelf from the Texas/Mexico border to the Florida Keys. From 2007
14 to 2014, samples from over 240 sediment grabs have been collected, with approximately 50% of
15 those samples yielding kinorhynchs. This extensive sampling has revealed a rich kinorhynch fauna
16 of mostly undescribed or poorly known species. Descriptions of new kinorhynch species, notes on
17 the morphology and distribution of known species, and general information on distribution
18 patterns correlated with abiotic factors, are planned to be published in a series of papers. The first
19 contribution was made by Sørensen and Landers (2014) who described two echinoderid species,
20 *Echinoderes augustae* Sørensen & Landers, 2014 and *Echinoderes skipperae* Sørensen & Landers,
21 2014.
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24 The present contribution is the second in this series, and it includes the description of a third
25 new species of *Echinoderes* from the northern Gulf shelf. It furthermore includes a redescription of
26 *Echinoderes bookhouti* Higgins, 1964. This species was originally described from the Atlantic
27 Ocean, off the coast of South Carolina, USA (Higgins, 1964), but it also occurs in the Gulf of Mexico
28 where it turns out to be one of the most abundant kinorhynch species. For the first time,
29 morphological information revealed through scanning electron microscopy is provided for this
30 species, and new significant species diagnostic traits are provided. The new samples also provided
31 additional information about the distribution of *E. augustae* and *E. skipperae*. Finally, as part of
32 the exploration of the numerous new echinoderid species from the Gulf, the type material of
33 several similar or closely related species (deposited at the Smithsonian Institution) was re-
34 examined and novel information of taxonomic significance was revealed. This information is
35 summarized in the present contribution, which hopefully will be a help for future taxonomic and
36 morphological studies.
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2. Materials and methods

2.1. Sampling

Sediment samples were collected along the United States' Gulf of Mexico continental shelf during several cruises from 2007 to 2014. Details about collected specimens and stations for the present study are listed in Fig. 1 and Table 1. All samples taken from 2013-2014 were collected with a multicorer, whereas samples before that were taken with a box corer (WildCo©) or a Shipek® sediment grab on the NOAA (National Oceanic and Atmospheric Administration) ships *Gordon Gunter* and *Pisces*, in collaboration with the National Marine Fisheries Service Laboratory in Pascagoula, Mississippi.

The samples were fixed immediately in 5-10% formalin, and meiofauna was subsequently extracted by Ludox centrifugation (Burgess, 2001). After sorting under a dissecting microscope, the specimens were stored in isopropanol until prepared for light microscopy (LM) or scanning electron microscopy (SEM). Specimens for LM were dehydrated through a graded series of glycerin and mounted in Fluoromount G. They were examined and photographed with an Olympus BX51 microscope, equipped with an Olympus DP27 camera and a drawing tube. Line art illustrations were based on camera lucida drafts of mounted specimens that subsequently were scanned and drawn in Adobe Illustrator CS6. Measurements were made with CellSens software. All dimensions reported in the tables are based on LM measurements. Measures based on estimates are provided in the text only, and it is indicated clearly if the measures originate from SEM. Specimens for SEM were prepared and examined either at the Natural History Museum of Denmark (NHMD) or at the Auburn University Research Instrumentation Facility (AURIF). Specimens for SEM were transferred from 70% isopropanol to 100% ethanol through a graded series, critical point dried, mounted on aluminum stubs, and sputter coated with gold or platinum/palladium. Some specimens were postfixed in osmium tetroxide vapor. Specimens photographed at NHMD were examined with a JEOL JSM-6335F Field Emission SEM, and specimens photographed at AURIF were examined with a Zeiss EVO 50 SEM.

All type material is deposited at the Natural History Museum of Denmark.

3. Results

To date, kinorhynchs have been recorded from 121 stations in the Gulf of Mexico. Examination of samples and identification of specimens are still going on, but a current estimate suggests that the samples contain between 25 and 30 kinorhynch species, distributed among 9 to 10 genera.

Whereas species need to be identified/described from all samples (2007-2014), and some samples still need to be processed (some 2013-2014 samples), data from four species is now as updated as currently possible. These species includes *E. augustae*, *E. skipperae*, *E. bookhouti*, and *Echinoderes charlotteae* sp. nov. described herein. The distribution of these species is summarized in Table 1, and presented graphically in Fig. 1.

3.1 Taxonomic account

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

Order Echinorhagata Sørensen et al., 2015

Family Echinoderidae Bütschli, 1876

Genus *Echinoderes* Claparède, 1863

***Echinoderes charlotteae* sp. nov.**

Type material

Holotype, adult male, collected from mud on November 02, 2012, at station 050-2013 (Fig. 1), at 74 m depth near the rim of the continental shelf, south of the Louisiana coast line, and southwest of the submarine Mississippi Valley (28°14'21.29"N 090°52'01.81"W), mounted in Fluoromount G, deposited at the Natural History Museum of Denmark, under catalogue number ZMUC KIN-868.

Paratypes include two females (ZMUC KIN-869 and ZMUC KIN-918) and two males (ZMUC KIN-870 and ZMUC KIN-817) mounted in Fluoromount G, and one female (ZMUC KIN-871) mounted for SEM. Paratypic female (ZMUC KIN-869) was collected at same station as holotype; paratypic male (ZMUC KIN-870) at station 071-2008, paratypic female (ZMUC KIN-871) at station 075-2012, paratypic male (ZMUC KIN-917) at station 031-2014, and paratypic female (ZMUC KIN-918) at station 025-2014. All paratypes are deposited at the Natural History Museum of Denmark.

Additional non-type material includes one female from station 078-2013 and two males from station 135-2013. The non-type specimens are mounted for SEM and stored in the personal

reference collection of Stephen C. Landers. See Fig. 1 for localities and Table 1 for detailed station data.

Diagnosis

Echinoderes with middorsal spine on segment 4 only, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral positions on segments 2 and 5, and in lateral accessory positions on segment 8; males furthermore with well-developed tubes in laterodorsal positions on the posterior margin of segment 10, whereas females show much smaller laterodorsal tubes on segment 10, emerging through openings on the posterior segment half, but not at the margin. Glandular cell outlets type 2 in subdorsal and sublateral positions on segment 2. A conspicuous middorsal protuberance extends from the intersegmental border between segments 10 and 11. Tergal extensions of segment 11 are terminally pointed, with an additional point on each inferior margin. Males with three penile spines; females with lateral terminal accessory spines.

Etymology

This species is dedicated to Charlotte Windberg – the wife of the first author.

Description

Adults with head, neck and eleven trunk segments (Figs 2A-B, 3A, 4A-B). Trunk length in males appears to be slightly larger than in females (male trunk length of 194-204 μm vs. female trunk length of 152-169 μm), but more specimens would be needed to confirm this. For complete overview of measures and dimensions, see Table 2. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, is summarized in Table 3.

The head consists of a retractable mouth cone and an introvert (Fig. 4A-C). The pharynx has a terminal pharyngeal crown, and rings of inner oral styles, but their exact number and arrangement could not be determined. The external mouth cone armature consists of nine outer oral styles, apparently of the same or nearly the same size (Fig. 4C). Outer oral styles are arranged as one style

1 anterior to each introvert sector, except the middorsal sector 6. A fringe with three long spikes,
2 bordered laterally by one additional pair of spikes, is located at the base of each outer oral style.
3 The introverts were only partly everted in the three specimens available for SEM examinations,
4 hence, it is not possible to provide a complete description of the appearance and arrangement of
5 scalids. Anterior scalids rings include ten primary spinoscalids in Ring 01, followed in each sector
6 by four spinoscalids arranged in a diamond (Rings 02-04). The primary spinoscalids consist of a
7 basal sheath and an elongated, smooth end-piece. The basal sheath carries most proximally four
8 short spikes flanked by two longer spikes. Medially, it has three additional small spikes flanked by
9 two longer spikes, and then again at its distal margin, two small spikes. Spinoscalids of Rings 02
10 and 03 are each composed of a basal sheath with finely fringed distal margin, and an elongated,
11 pointed end-piece. Spinoscalids of Ring 04 have the same composition, but are smaller.

12 The neck has 16 placids, measuring 9 μm in length. The midventral placid is broadest,
13 measuring 9 μm in width at its base, whereas all other are narrower, measuring 6 μm in width at
14 their bases (Figs 2A-B, 3B-C). The trichoscalid plates are well-developed, with the ventral pair
15 being broader (6.5 μm in width) than the two dorsal pairs (4.5 μm in width).

16 Segment 1 consists of a complete cuticular ring (Figs 2A-B, 3A-C, 4A-B, D). Sensory spots are
17 located anteriorly on the segment in subdorsal and laterodorsal positions (Figs 2A, 3B), and more
18 posteriorly in ventromedial positions (Figs 2B, 4D). The sensory spots are small and slightly
19 elongate, and the ventromedial ones are flanked by a pair of cuticular hairs. Glandular cell outlets
20 type 1 are present in ventrolateral positions. Cuticular hairs emerge through rounded perforation
21 sites, but are scarce, especially on the ventral side. The posterior segment margin is straight along
22 the dorsal and lateral side, but extends more posteriorly in the ventromedial and midventral
23 areas. The dorsal, lateral, ventromedial and midventral parts of the margin form a pectinate fringe
24 with well-developed fringe tips, whereas hardly any fringe tips are present from the midlateral to
25 the ventrolateral positions (Figs 2B, 4D).

26 Segment 2 consists of a complete cuticular ring, with tubes (ca. 8 μm from SEM) located in
27 lateroventral positions (Figs 2B, 3C, 4D). Pachycyclis of the anterior segment margin
28 uninterrupted and of regular thickness. Sensory spots are located in laterodorsal (two pairs but
29 not twin pairs) and ventromedial positions (Fig. 4D). Laterodorsal sensory spots are flanked by a
30 pair of cuticular hairs, whereas the ventromedial ones each have a single marginal cuticular hair.

Glandular cell outlets type 2 are located in subdorsal and sublateral positions (Figs 2A-B, 3B-C, 4D-E). Secondary pectinate fringe not detected. On this and all following segments, the cuticular hairs are bracteate. They are distributed around the segment, more densely than on the preceding segment, but still rather scarce. The posterior segment margin forms a pointed midventral extension, and consists of a pectinate fringe, with well-developed fringe tips.

Segment 3, and remaining segments, consisting of one tergal and two sternal plates (Figs 2A-B, 3A, 4B). Pachycyclis of the anterior segment margin of regular thickness. It is interrupted at the tergo-sternal junctions, but is in addition also interrupted middorsally. Sensory spots are located in subdorsal and midlateral positions. They are extremely small, consisting of two pores, and very few (7-8) cuticular micropapillae (Fig. 4E and inset). A single glandular cell outlet type 1 is located in middorsal position (Fig. 3B). Secondary pectinate fringe present on anterior part of segment, consisting of thin, flexible fringe tips. Cuticular hairs evenly distributed over tergal plate, between secondary fringe and intersegmental joint line, whereas the sternal plates only have a few hairs near their anterior corners. Posterior segment margin straight, with pectinate fringe formed by well-developed fringe tips.

Segment 4 with short acicular spine in middorsal position (Figs 2A, 3D, 4E), flanked by a pair of paradorsal glandular cell outlets type 1. In LM, the glandular cell outlets appear as elliptical, obliquely arranged areas with light refracting granules inside. Sensory spots not present. Pachycyclis, secondary fringe, pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segment 5 with tubes (ca. 7 μm from SEM) in lateroventral positions (Figs 2B, 3E). Sensory spots present in subdorsal and ventromedial (Fig. 3E) positions. Pachycyclis, secondary fringe, pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segments 6 and 7 are almost identical, with acicular spines in lateroventral positions (Figs 2B, 3E), and sensory spots in subdorsal and midlateral positions (Fig. 4F) (and in ventromedial positions on segment 6). Pachycyclis, secondary fringe, pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segment 8 with acicular spines in lateroventral positions, and tubes (ca. 8 μm from SEM) in lateral accessory positions (Figs 2B, 3H, 4F). Sensory spots present in subdorsal positions only (Fig.

3D). Pachycycli, secondary fringe, pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segment 9 with acicular spines in lateroventral positions (Figs 2B, 4G). Sensory spots present in subdorsal, laterodorsal and ventrolateral positions; subdorsal and ventrolateral sensory spots are flanked by a pair of cuticular hairs. Elliptical, transversely arranged glandular cell outlets type 1 present in paradorsal positions. A pair of minute sieve plates is located in sublateral positions (Figs 2B, 4G). Pachycycli, secondary fringe, pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segment 10 with laterodorsal tubes at or near posterior segment margin: tubes in males are relatively well-developed (ca. 9 μm from LM), resembling regular tubes with a thicker basal part and a thin distal part with wings, and located in small indentations in the posterior segment margin (Fig. 2C); tubes in females much shorter (ca. 1,5 μm from SEM), formed like simple tubes with bifurcating tips, but otherwise no further differentiation, and emerging through the cuticle at the posterior part of the segment, near but not at the posterior segment margin (Figs 2A, 4G and inset). Sensory spots, all flanked by a pair of cuticular hairs, are present in subdorsal and ventrolateral positions (Fig. 4I). Glandular cell outlets type 1 present as two middorsal ones on the anterior part of the segment, and much more posteriorly in subdorsal positions (Fig. 2A).

Middorsal outlets are elliptical and transversely arranged, whereas subdorsal ones are elliptical and longitudinally arranged. A prominent protuberance emerges in a middorsal position from the intersegmental joint between segments 10 and 11 (Figs 2A, 4H). The structure is cone-shaped with a distal tuft of hair-like cuticular extensions. The segment has a few cuticular hairs near its anterior margin, but is otherwise smooth. Pachycycli of tergal plate continues uninterrupted through the middorsal point. The posterior segment margin of the tergal plate is straight and with a weakly developed pectinate fringe (Fig. 4H), whereas the margins of the sternal ones are concave, extending posteriorly near the midventral junction, and with well-developed fringe tips (Fig. 4I-J).

Segment 11 with lateral terminal spines (Figs 2A-D, 3F-G, 4A-B, H-J). Females with lateral terminal accessory spines (Figs 2A-B, 3F, 4H-I), and males with three pairs of thin and flexible penile spines (Figs 2C-D, 3G, 4J). Sensory spots not present. Glandular cell outlets type 1 present in subdorsal positions; outlets are elliptical and longitudinally arranged. The segment is completely devoid of cuticular hairs. Tergal extensions are pointed, and appear in LM as if they have an

1 additional point on each inferior margin (Fig. 3G); SEM imaging reveals that this additional point is
2 actually elongated tips from the marginal fringes (Fig. 4H). Sternal extensions are triangular and
3 pointed, not extending beyond the tergal extensions (Fig. 4I-J).
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9 ***Echinoderes bookhouti* Higgins, 1964**

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12 *Material examined*

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14 Holotype (USNM 30981), allotype and ten paratypes (USNM 30982) were loaned from the
15 Smithsonian Institution, United States National Museum, and examined with light microscope. All
16 type specimens originate from Beaufort, North Carolina, USA (see Higgins, 1964). Additional
17 material includes 146 specimens collected from 25 stations in the Gulf of Mexico (see Fig. 1A and
18 Table 1). The specimens are mounted for either LM or SEM. 32 specimens mounted for LM are
19 deposited at the Natural History Museum of Denmark under catalogue numbers ZMUC KIN-886 to
20 KIN-916 and KIN-919. Remaining specimens, mounted for either LM or SEM are stored in the
21 personal reference collections of the authors.
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32 *Emended diagnosis*

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34 *Echinoderes* with middorsal spines on segments 4 to 8, and in lateroventral positions on segments
35 6, 7 and 9; spine on segment 8 displaced to a lateral accessory position. Tubes present in
36 lateroventral positions on segment 5; males furthermore with long, well-developed tubes in
37 laterodorsal positions on the posterior margin of segment 10, whereas females show only minute
38 laterodorsal tubes on segment 10. Two pairs of regular sized glandular cell outlets type 2 present
39 in subdorsal and lateroventral positions on segment 2, and one pair of considerably larger ones
40 present in midlateral positions on segment 8. Middorsal protuberance extends from the
41 intersegmental border between segments 10 and 11. Pectinate fringes at posterior segment
42 margins of segments 1 and 2 conspicuously strong on ventral side. Segment 10 in females with
43 three patches of cuticular hairs on tergal plate, and one patch on each sternal plate; segment 10 in
44 males completely devoid of hairs. Tergal extensions of segment 11 are terminally pointed, with an
45 additional point on each inferior margin. Males with three penile spines; females with lateral
46 terminal accessory spines.
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Description

Adults with head, neck and eleven trunk segments (Figs 5A-B, 6, 7A-B, 8A-B, 9A). For complete overview of measures and dimensions, see Table 4. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, is summarized in Table 5.

The head is formed by a retractable mouth cone and an introvert (Figs 6, 9A-B). The pharynx has a terminal pharyngeal crown, and rings of inner oral styles. The external mouth cone armature consists of nine outer oral styles that each are made up by two joined units (Fig. 9B). The styles have almost the same size, but appear to alternate between slightly smaller and slightly larger ones (Fig. 9B). They are arranged as one style anterior to each introvert sector, except for the middorsal sector 6 (Fig. 6). A fringe with three long spikes, bordered laterally by one additional pair of spikes, is located at the base of each outer oral style (Fig. 9B).

The introvert sectors are defined by ten primary spinoscalids in Ring 01 (Fig. 6). Each primary spinoscalid consists of a basal sheath and a distal end piece with a blunt tip. The basal sheaths have long extensions that form transverse fringes, whereas the end pieces are wrinkled on their proximal halves and smooth more distally. Spinoscalids of Rings 02 to 06 appear rather similar, consisting of a basal sheath with a fringed margin, and a pointed end piece. Spinoscalids in Rings 07 and 08 are considerably smaller and consist apparently of a single, pointed unit only. Rings 02 and 04 each have 10 spinoscalids, and Rings 03 and 5 have 20, meaning that the spinoscalids of these rings form a quincunx in each sector (Fig. 6). Sectors 2, 4, 8 and 10 have no spinoscalids posterior to Ring 05. Sectors 1, 3 and 9 have a single medial spinoscalid in Rings 06 and 08, and a pair in Ring 07, resulting in a total sector-wise arrangement with ten spinoscalids forming a triple diamond (Fig. 6). Sectors 5 and 7 have almost identical distributions of spinoscalids, except that one of the paired spinoscalids of Ring 07 is missing in each sector because a trichoscalid plate is taking up the space. The spinoscalids arrangement of sector 6 is also similar to the one of sectors 1, 3 and 9, except for the spinoscalid of Ring 08 that is missing in this sector (Fig. 6).

The neck has 16 placids, measuring 12 μm in length. The midventral placid is broadest, measuring 14 μm in width at its base, whereas all other are narrower, measuring 8 μm in width at their bases. The trichoscalid plates are well-developed, and located in introvert sectors 2, 4, 5, 7, 8,

1 and 10 (Fig. 6). The ventral pair (sectors 2 and 10) are broader (14 μm in width) than the two
2 dorsal ones (10 μm in width). A trichoscalid attaches to each trichoscalid plate.
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5 Segment 1 consists of a complete cuticular ring (Figs 5A-B, 7A-B, 8A-B, 9C-D). Sensory spots
6 are located anteriorly on the segment in subdorsal and laterodorsal positions (Fig. 5A), and more
7 posteriorly in ventromedial positions (Figs 5B, 9D). The sensory spots are small and rounded, made
8 up by a circle of micropapillae around a central pore with a cilium. Glandular cell outlets type 1 are
9 present in middorsal and lateroventral positions. Cuticular hairs emerge through rounded
10 perforation sites, being most abundant on the dorsal side. The posterior segment margin
11 terminates into a pectinate fringe; fringe tips on the ventral side of the segment are conspicuously
12 well-developed (compare fringes on Fig. 9C and Fig. 9D).
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20 Segment 2 consists of a complete cuticular ring (Figs 5A-B, 7A-B, 8A-B, 9C-D). Pachycyclus of
21 the anterior segment margin is interrupted middorsally and in lateroventral positions. Sensory
22 spots are located in middorsal, laterodorsal (Fig. 9C), midlateral and ventromedial (Fig. 9D)
23 positions. Sensory spots on this and all following segments are slightly elongate, with about ten
24 micropapillae surrounding one or two pores; a cilium may eventually emerge from one of the
25 pores (see inset in Fig. 9E with representative sensory spot). Glandular cell outlets type 2 of
26 regular sizes are located in subdorsal and lateroventral positions (Figs 5A-B, 7C-D, 8C-D, 9C-D).
27 Glandular cell outlets type 1 are present in middorsal (Figs 7C, 8C) and ventromedial (Fig. 8D)
28 positions. Secondary pectinate fringe not detected. On this and all following segments, the
29 cuticular hairs are bracteate. Hairs are densely distributed around the segment. Pectinate fringe of
30 posterior margin with conspicuously well-developed fringe tips on ventral side, as observed on
31 preceding segment also.
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44 Segment 3, and remaining segments, consisting of one tergal and two sternal plates (Figs 5A-
45 B, 7A-B, 8A-B). Pachycyclus of anterior segment margin of regular thickness, interrupted at the
46 tergosternal junctions, but also middorsally until segment 9. Sensory spots are located in
47 subdorsal positions only. Glandular cell outlets type 1 are present in middorsal and ventromedial
48 positions. Secondary pectinate fringe present on anterior part of segment. Cuticular hairs evenly
49 distributed over tergal plate, between secondary fringe and intersegmental joint line, whereas the
50 sternal plates have hairs on their lateral halves. Pectinate fringe on posterior segment margin with
51 regular, minute fringe tips, like those on the dorsal side of the two preceding segments.
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1 Segment 4 with acicular spine in middorsal position (Fig. 5A), flanked by a pair of paradorsal
2 glandular cell outlets type 1. In LM, the glandular cell outlets on the tergal plates of this and all
3 following segments appear as elliptical, almost vertically arranged areas with light refracting
4 granules inside. Glandular cell outlets type 1 are furthermore present in ventromedial positions.
5 Sensory spots not present. Pachycycli, secondary fringe, pectinate fringe of posterior margin and
6 cuticular hairs as on preceding segment.

7 Segment 5 with acicular spine in middorsal position, and tubes in lateroventral positions (Fig.
8 5A-B). Sensory spots present in subdorsal, midlateral and ventromedial positions (although the
9 ventromedial sensory spots are laterally displaced, and hence getting close to the ventrolateral
10 positions, see Fig. 5B). Glandular cell outlets type 1, pachycycli, secondary fringe, pectinate fringe
11 of posterior margin and cuticular hairs as on preceding segment.

12 Segments 6 and 7 are almost identical, with acicular spines in middorsal and lateroventral
13 positions (Fig. 5A-B), and sensory spots in paradorsal, midlateral and ventromedial positions
14 (ventromedial sensory spots on segment 6 are perfectly centred on each sternal plate, whereas
15 those on segment 7 are laterally displaced as observed on segment 5 also, see Fig. 5B). Glandular
16 cell outlets type 1, pachycycli, secondary fringe, pectinate fringe of posterior margin and cuticular
17 hairs as on preceding segment.

18 Segment 8 with acicular spine in middorsal position (Figs 5A, 7E). Acicular spines are also
19 present in the lateral series, but on this segment they have been displaced to lateral accessory
20 position (Figs 5B, 7F, 8F, 9E). Sensory spots present in paradorsal, laterodorsal and ventromedial
21 (slightly laterally displaced) positions. A pair of large glandular cell outlets type 2 is present in
22 midlateral positions (Figs 5A, 7E, 8E, 9E). Cuticular hairs on tergal plate as on preceding segment;
23 hairs on sternal plates extend further towards the antero-inferior margins of the plates. Glandular
24 cell outlets type 1, pachycycli, secondary fringe and pectinate fringe of posterior margin as on
25 preceding segment.

26 Segment 9 without middorsal spine, but with acicular spines in lateroventral positions (Figs
27 5B, 8F, 9E). Sensory spots present in paradorsal and ventrolateral positions. Minute sieve plates
28 are located in sublateral positions. Glandular cell outlets type 1, pachycycli, secondary fringe,
29 pectinate fringe of posterior margin and cuticular hairs as on preceding segment.

Segment 10 with laterodorsal tubes at the posterior segment margin: tubes in males are elongate and well-developed (ca. 22 μm from SEM), resembling regular tubes (Figs 5A, 7G, 8G, 9G); tubes in females much shorter (ca. 1,5 μm from SEM), formed like simple tubes with bifurcating tips (Figs 5C, 9F). Sensory spots present in subdorsal (Fig. 9F-G) and ventrolateral (Fig. 9H) positions. Glandular cell outlets type 1 present as two middorsal ones on the anterior part of the segment (Fig. 7G), and in ventromedial positions. A prominent protuberance emerges in a middorsal position from the intersegmental joint between segments 10 and 11 (Figs 5A, 7G, I, 8G, 9G). The structure is cone-shaped with marginal hairs and a central glandular cell outlet type 1. Females with three patches of cuticular hairs on the tergal plate, and a lateral patch of hairs on each sternal plate (Figs 5C-D, 7I, 9F); males completely devoid of cuticular hairs on this segment (Figs 5A-B, 7G-H, 9G-H). Pachycyclus of tergal plate uninterrupted. Secondary fringe and pectinate fringe of posterior margin as on preceding segment.

Segment 11 with lateral terminal spines (Figs 5A-D, 7G-I, 8G-I, 9G-H). Females with rather thin lateral terminal accessory spines (Figs 5C-D, 8I), and males with three pairs of penile spines (Figs 5A-B, 7H, 8H, 9G-H): Dorsal- and ventralmost penile spines are thin and flexible; medial spines are thicker and with fringe-like ornamentation on their distal halves. Sensory spots present in subdorsal positions. Glandular cell outlets type 1 not present. The segment is completely devoid of cuticular hairs in both sexes. Tergal extensions are pointed, with an additional point on each inferior margin (Figs 5A-D, 8H), formed by elongated tips from the marginal fringes. Sternal extensions are short and broadly rounded.

3.2 Additional diagnostic characters on other species of *Echinoderes*

The collecting campaign in the Gulf of Mexico revealed several species of which some obviously are new to science, whereas others potentially could be conspecific with previously described species, with either rather simplistic or inaccurate descriptions. This uncertainty prompted a re-examination of type material of selected *Echinoderes* species deposited at the Smithsonian Institution (United States National Museum of Natural History). A bit surprisingly, new taxonomically significant structures were observed in several examined species, hence, to ease future identification of these species, we wish to make this information available. A total of twelve species were examined, of which eight showed structures that were either completely omitted or

at least not described in detail in their original descriptions. The eight species include: *Echinoderes abbreviatus* Higgins, 1983, *Echinoderes andamanensis* Higgins & Rao, 1979, *Echinoderes bookhouti*, *Echinoderes imperforatus* Higgins, 1983, *Echinoderes kristenseni* Higgins, 1985, *Echinoderes pennaki* Higgins, 1960, *Echinoderes truncatus* Higgins, 1983, and *Echinoderes wallaceae* Higgins, 1983. Information on distribution of cuticular structures (glandular cell outlets, spines and tubes) for eight of the species is provided in Table 6 (for *E. bookhouti* see above). *Echinoderes sublicarum* Higgins, 1977; *Echinoderes horni* Higgins, 1983, *Echinoderes newcaledoniensis* Higgins, 1967 and *Echinoderes worthingi* Southern, 1914 were also examined without finding any new structures.

4. Discussion

4.1 Notes on diagnostic and taxonomic features in *E. charlotteae* sp. nov.

Echinoderes charlotteae sp. nov. can be distinguished from all other congeners by its unique distribution pattern of tubes and acicular spines. Actually, the combination of having a single middorsal spine (on segment 4), and only a single pair of tubes on segment 2 (in lateroventral position) is not present in any other species of *Echinoderes*. The presence of a single spine in the middorsal series, and always on segment 4 specifically, is shared with only eight other species: *Echinoderes ajax* Sørensen, 2014; *Echinoderes cantabricus* Pardos et al., 1998; *Echinoderes capitatus* Zelinka, 1928; *Echinoderes isabelae* G^aOrdóñez et al., 2008; *Echinoderes maxwelli* Omer-Cooper, 1957; *Echinoderes ohtsukai* Yamasaki & Kajihara, 2012; *Echinoderes rex* Lundbye et al., 2011; and *Echinoderes teretis* Brown, 1985 in Adrianov & Malakhov, 1999 (see original descriptions and also Nebelsick (1992) for *E. capitatus*, and Lundbye et al. (2011) for *E. maxwelli*). However, the four latter (*E. maxwelli*, *E. ohtsukai*, *E. rex* and *E. teretis*) belong to the *E. coulli*-species group, in which all species easily are distinguished from other *Echinoderes* through characteristic traits such as enlarged sieve plates and general lack of acicular spines (see Sørensen (2014) for further notes on the *E. coulli*-species group). Neither the remaining four species (*E. ajax*, *E. cantabricus*, *E. capitatus*, and *E. isabelae*) can really be confused with *E. charlotteae* sp. nov., since they all possess four pairs of tubes on segment 2 (in subdorsal, laterodorsal, sublateral and ventrolateral position), opposed to *E. charlotteae* sp. nov. that has only a single pair of tubes on segment 2.

Furthermore, none of the four species have glandular cell outlets type 2 on segment 2, whereas *E. charlotteae* sp. nov. has a pair on subdorsal and sublateral positions. Finally, three of the species display spines or tubes in unusual positions, such as subdorsal or laterodorsal spines on segments 6 to 8 in *E. capitatus*, in laterodorsal position of segment 7 and subdorsal position of segment 8 in *E. isabelae*, and midlaterally on segment 1 in *E. cantabricus*. Such spines or tubes are not present in *E. charlotteae* sp. nov. Hence, the new species cannot really be confused with any existing ones. The presence of subdorsal and sublateral glandular cell outlets type 2 on segment 2 in *E. charlotteae* sp. nov. makes it even easier to distinguish the species from others. Co-occurrence of glandular cell outlets type 2 in these positions is only known from three other species of *Echinoderes*, i.e., *E. abbreviatus* Higgins, 1983 (see Table 6 in present contribution), *Echinoderes cernunnos* Sørensen et al., 2012 and *Echinoderes obtuspinosus* Sørensen et al., 2012, but these three species have five middorsal spines, and cannot be confused with *E. charlotteae* sp. nov.

4.2 Notes on distribution and diagnostic features in *E. bookhouti*

Echinoderes bookhouti was described by Higgins (1964), and hence belongs to his earliest described kinorhynch species. Of the 224 kinorhynch species that we today recognize as valid species based on descriptions of adult specimens, only 48 species were known back then. Naturally, our understanding of taxonomically significant characters has also been improved considerably since then, and based solely on the information provided in the original description of *E. bookhouti*, and without comparison with the type material of the species, it would today be difficult to identify this species among similar congeners. The reason for this is that *E. bookhouti* displays the most stereotypical spine configuration found among species of *Echinoderes*. The presence of middorsal spines on segments 4 to 8, and lateral tubes/spines on segments 5 to 9 is shared by no less than 35 species of *Echinoderes*, and out of these, 21 also possess laterodorsal tubes. Since the original description of *E. bookhouti* did not really provide any additional useful diagnostic features, a redescription of the species is highly needed. When the species turned out to be extremely abundant in the material collected from the Gulf of Mexico, this seemed to be the perfect opportunity to do so. The redescription was based on a combination of data from the type material from North Carolina, as well as newly collected material from the Gulf of Mexico,

1 mounted for light microscopy but also supplemented with information from specimens mounted
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3 for scanning electron microscopy.
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5 Examination of the type specimens and newly collected material revealed several
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7 taxonomically important characters that are either only briefly mentioned or not mentioned at all
8
9 in the original description. These new characters in combination enable fast and easy
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11 identification of *E. bookhouti*. The species is most easily distinguished by its lateral spines on
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13 segment 8 that have been displaced to a lateral accessory position, and by its large glandular cell
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15 outlets type 2, also on segment 8. Both character traits are very rare among species of
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17 *Echinoderes*. The displacement of the spines, from lateroventral to lateral accessory positions may
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19 seem like a highly subtle diagnostic character, but it is actually extremely easy to visualize with
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21 both LM and SEM (see Figs 7F, 8E, 9E). Among species of *Echinoderes* such a displacement is
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23 known only from *E. eximus* Higgins and Kristensen, 1988 and *E. tchefouensis* Lou, 1934 (see
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25 Sørensen et al., 2012). The two species are easily distinguished from *E. bookhouti* though, since
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27 they lack spines in the lateral series of segments 6 and 7 (Higgins and Kristensen, 1988; Sørensen
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29 et al., 2012).
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31 The presence of large glandular cell outlets type 2 in midlateral positions of segment 8 is
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33 only shared with *E. truncatus* Higgins, 1983 (see below in present contribution). However, *E.*
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35 *truncatus* stands out in several other ways, partly due to its conspicuous rectangular trunk shape
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37 and truncate tergal extensions, and partly to the presence of numerous tubes in paradorsal,
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39 subdorsal or laterodorsal positions, revealed during the present study (see Table 6). Hence, *E.*
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41 *bookhouti* and *E. truncatus* cannot be confused with each other. Other species have glandular cell
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43 outlets of type 2 in nearby (i.e., laterodorsal and sublateral) positions on this segment though.
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45 Type 2 outlets in sublateral positions are found in *E. obtuspinosus* only, but with its short and stout
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47 lateral terminal accessory spines (Sørensen et al., 2012), this species cannot be confused with *E.*
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49 *bookhouti*. The presence of type 2 outlets in laterodorsal positions on segment 8 is more common
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51 though, and is found in six species of *Echinoderes*. These include (information on position of
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53 glandular cell outlets from original description unless other source is mentioned): *Echinoderes*
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55 *eximus* (information from unpublished observations by M.V. Sørensen), *Echinoderes gerardi*
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57 Higgins, 1978 (information from unpublished observations by N. Özlem Köroğlu and M.V.
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59 Sørensen), *Echinoderes hwiizaa* Yamasaki and Fujimoto, 2014, *Echinoderes komatsui* Yamasaki and
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Fujimoto, 2014, *Echinoderes microaperturus* Sørensen et al., 2012 and *Echinoderes tchefouensis* (see Sørensen et al., 2012). As mentioned above, *E. eximus* and *E. tchefouensis* cannot be confused with *E. bookhouti*. This is also the case for *E. hwiizaa* and *E. komatsui* since they both belong to the *E. coulli*-species group, which accommodates an assemblage of highly characteristic species, e.g., recognized by enlarged sieve plates and the complete lack of spines in the lateral series (see Sørensen, 2014; Yamasaki and Fujimoto, 2014). *E. gerardi* and *E. microaperturus* may superficially resemble *E. bookhouti*, but in these species the type 2 glandular cell outlets are very minute, and definitely much smaller than those found in *E. bookhouti*. Furthermore, both species possess lateroventral/ventrolateral tubes on segment 2, and in addition they have one additional pair of laterodorsal glandular cell outlets type 2, located on segment 7 in *E. microaperturus* and on segment 9 in *E. gerardi*.

Other conspicuous or significant morphological traits in *E. bookhouti* that should be mentioned include the glandular cell outlets type 2 on segment 2, the well-developed pectinate fringes ventrally on segments 1 and 2, the middorsal protuberance between segments 10 and 11, and the sexual dimorphism expressed in the hair covering of segment 10. The strong pectinate fringes on the ventral sides of segments 1 and 2 were already mentioned in the original description (Higgins, 1964), but we would like to highlight this character trait here also, since it is actually very easily observed (compare Figs 7C and 8C with Figs 7D and 8D) and to our knowledge not present in other species of *Echinoderes*. Higgins (1964) also mentions the presence of a middorsal protuberance, emerging between segments 10 and 11. A structure like this has also been described from *E. augustae* Sørensen and Landers, 2014, and it might also be present in *E. eximus*. However, its presence in the latter species needs to be confirmed by more careful examinations with SEM (see Sørensen and Landers, 2014).

The occurrence of glandular cell outlets type 2 in subdorsal and lateroventral positions on segment 2 was also indicated by Higgins (1964) who illustrated them as pairs of weak markings on the line art illustrations (see Figures 17-18 in Higgins, 1964). The understanding of the morphology and nature of glandular cell outlets type 2 and their use as diagnostic characters are a much more recent acquisition in kinorhynch systematics (see, e.g., Neuhaus and Blasche, 2006; Sørensen et al. 2012), and were not known by the time of the description of *E. bookhouti*. Today we know though, that such outlets are fairly common in species of *Echinoderes*, and especially on segment 2 they

1 appear to occur quite frequently. Only three species, *Echinoderes astridae* Sørensen, 2014, *E.*
2 *kristenseni* Higgins, 1985 (see Table 5 in present contribution), and *E. wallaceae* Higgins, 1985 (see
3 Table 5 in present contribution) show the same distribution of type 2 outlets on segment 2 as we
4 see in *E. bookhouti*.
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9 Lastly, the sexual dimorphism regarding hair distribution on segment 10 is noteworthy.
10 Usually, sexual dimorphism among species of *Echinoderes* is expressed in the presence of either
11 lateral terminal accessory spines or penile spines, the development of laterodorsal tubes on
12 segment 10, and in a few cases distribution of certain sensory spots. To our knowledge, a sexual
13 dimorphism expressed as complete lack of hairs on segment 10 in males, and a more regular hair
14 covering in females, is rather unusual and might not have been reported before.
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19 Based on the comparison of specimens of *E. bookhouti* collected in the Gulf of Mexico for
20 the present study and the type specimen, we can conclude that the species has a distribution that
21 stretches from the Northwest Atlantic, off North Carolina to the Gulf of Mexico. Higgins (1964)
22 already reported that the species had been recorded as far south as Marineland, Florida, but with
23 the observations from the present study we can extent this distributional range considerably.
24 Knowing that species of *Echinoderes* tend to have rather limited distributions this obviously makes
25 us speculate whether the Atlantic populations and the Gulf populations actually represent two
26 genetically different species. Nothing in the morphology indicates this, but the habitats of the two
27 populations could maybe point us in that direction, since the Atlantic specimens were collected in
28 a shallow water river estuary (Higgins, 1964), i.e., a habitat that must be affected by fluctuating
29 salinities. Oppositely, all specimens from the present study are strictly marine and subtidal,
30 collected between 37 and 125 m depth. This could indicate the occurrence of two cryptic species
31 that are morphologically similar, but have different habitat choices. To test this, specimens from
32 the two areas should obviously be sequenced and compared at the molecular level, but it would
33 be equally interesting to examine if *E. bookhouti* in the Gulf also occurs at more coastal localities,
34 i.e., the swamps and estuaries of the U.S. Gulf Coast.
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53 4.3 Notes on other species of *Echinoderes* from the collections of the Smithsonian Institution

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55 Recent years' progress in kinorhynch systematics, combined with the introduction of more
56 advanced microscopy (especially SEM) in kinorhynch taxonomy, have improved our understanding
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of *Echinoderes* morphology and pointed out new taxonomically significant characters that are needed to distinguish the continuously increasing amount of known echinoderid species. The combined use of LM and SEM in taxonomic and systematic studies has helped us understanding the nature of cuticular structures. For instance, we know now that structures previously reported as ‘cuticular scars’ and ‘muscle scars’ often turn out to be sensory spots or glandular cell outlets, and especially the glandular cell outlets type 2 are today considered important taxonomic characters. Without this distinction between the different morphological structures, it would be impossible to distinguish certain species. The occurrence and positions of glandular cell outlets type 2 were only relatively recently introduced as taxonomic characters among echinoderids. Neuhaus and Blasche (2006) used the character to distinguish between species of *Fissuroderes*, and subsequently the occurrence of the outlets have proved useful to discriminate species of *Meristoderes* and *Echinoderes* also (see e.g., Herranz et al., 2012; Sørensen et al. 2012; 2013; Yamasaki and Kajihara 2012; Herranz and Pardos 2013; Sørensen 2014; Sørensen and Landers 2014; Yamasaki and Fujimoto 2014). Information on the distribution of glandular cell outlets type 2 might be missing in older descriptions, but as part of the present project, a considerable part of the *Echinoderes* types stored at the Smithsonian Institution were examined, and this study confirmed that 1) glandular cell outlets type 2 appear in many species even though it is not reported in the literature, and 2) the outlets of this type do not appear to show intraspecific variation in their occurrence, which supports the taxonomic value of the character.

In general, examinations revealed the presence of several structures, in particular tubes and/or glandular cell outlets type 2, that have been left either unnoticed or received very little emphasis in their original descriptions (see summary of cuticular structures in Table 6). Especially examination of *E. truncatus* revealed much new information, as the species turned out to present numerous pairs of minute tubules arranged in paradorsal, subdorsal and laterodorsal series along segments 2 to 9. In addition, the species has a pair of glandular cell outlets type 2 in ventrolateral positions of segment 2, and in midlateral positions of segments 8 and 9. The species was originally described from Belize (Higgins, 1983), and has since then been reported from Bocas del Toro on the Atlantic side of Panama (Sørensen, 2006). The identity of the Panamanian specimens is questionable though. Sørensen (2006) already noted that the Panamanian specimens had lateroventral tubes on segment 2. Such tubes are not present in the type species of *E. truncatus*.

Furthermore, Sørensen (2006) noted the presence of minute “fringed tubules” in dorsal series of the Panamanian specimens. Interestingly we can now show that similar tubes are present in the holotype of *E. truncatus* also, but comparison with the material collected in Panama reveals that the distribution of the tubes differs considerably between specimens of the Belizean and Panamanian populations. Hence, based on our current observations we can conclude that the Panamanian specimens reported as *E. truncatus* by Sørensen (2006) are not conspecific with *E. truncatus*, but represents a closely related, but yet undescribed species. The Panamanian material is available through the Natural History Museum of Denmark.

Also *E. imperforatus* revealed some interesting cuticular structures. In the original description, Higgins (1983) already noted the presence of “brace-shaped muscle scars” in ventrolateral positions of segment 6. He furthermore shows the presence of a small structure in ventrolateral positions of segment 7 (see Figure 33 in Higgins (1983)). We were able to identify the same “brace-shaped” marking in segment 6. This could be a glandular cell outlet type 2, but we are not certain about this, and confirmation from SEM would be required. As for the tiny structures shown on segment 7, we interpret these as minute papillae. In addition, we found similar papillae in ventromedial positions on segment 8, but the papillae on both segment 7 and 8 are present in females exclusively. Female specific papillae on the sternal plates were also recently observed in *E. gerardi* (unpublished observations by N. Özlem Köroğlu and M.V. Sørensen), and together with the two species’ conspicuously short middorsal spines this may suggest a closer relationship.

For five of the remaining species new findings mostly regard the presence of glandular cell outlets type 2, and eventually, tubes. In *E. abbreviatus* ventrolateral tubes have been reported from segment 2 (Higgins, 1983), but our examinations revealed one additional set of tubes in subdorsal positions, and a pair of sublateral glandular cell outlets type 2. *E. abbreviatus* belongs to an easily recognizable assemblage of species that all have conspicuously short and stout lateral terminal spines. Among these, *E. abbreviatus* is the only species with middorsal spines on segments 4, 6 and 8 only, hence the observation of these additional structures on segment 2 does not bring the validity of the species into question. However, we expect that the addition of these characters might help to prevent future confusion with new species.

Glandular cell outlets type 2 on segment 2 were also observed in *E. kristenseni* and *E. wallaceae* (the structures are reported as ‘muscle scars’ in the original descriptions (see Higgins, 1983, 1985)). The two species are already very similar and consider by Higgins (1985) as close relatives, hence it was not surprising to confirm the presence of type 2 outlets in both of them. According to Higgins (1985) the two species are most easily identified by spine lengths relative to trunk length, with *E. kristenseni* generally presenting longer spines than *E. wallaceae*. Besides this difference we noted that the lateral accessory tubes on segment 8 in *E. wallaceae* appear to slightly more laterally displaced, towards the sublateral positions, whereas the corresponding tubes in *E. kristenseni* are perfectly located in the lateral accessory positions.

In *E. pennaki* glandular cell outlets type 2 were found in subdorsal positions on segments 2 and 4, and in ventrolateral positions on segment 2. The finding of type 2 outlets in this species was in particular welcome, since it otherwise belong to this highly stereotypic group of *Echinoderes* species with five middorsal spines, lateroventral tubes/spines on segments 5 to 9, and basically no other conspicuous characters. Especially the presence of subdorsal type 2 outlets makes it very easy to recognize *E. pennaki* amongst other *Echinoderes*, since only three other species have subdorsal type 2 outlets on this segment. These are *E. hwiizaa* and *E. komatsui* that both belong to the *E. coulli*-species group (see Yamasaki and Fujimoto, 2014) and hence cannot be confused with *E. pennaki*, and *E. obtuspinosus* that differs from *E. pennaki* in several different ways, but in particular by its short and stout lateral terminal spines (Sørensen et al., 2012).

In *E. andamanensis* glandular cell outlets type 2 appear in subdorsal positions on segments 6 and 8. The species was already easy to recognize by the presence of lateroventral tubes/spines on segments 8 and 9 only – a trait that does not appear in any other species – but the occurrence of type 2 outlets on segments 6 and 8 makes it even easier to identify the species. Having subdorsal type 2 outlets on these two particular segments is also unique among congeners.

4.4 Distribution of *E. augustae* and *E. skipperae*

E. augustae and *E. skipperae* were first two species to be described from the ongoing project that focuses on the meiofauna of the United States’ Gulf of Mexico continental shelf (Sørensen and Landers, 2014). Since their original description, *E. augustae* has been recorded from eleven additional stations and *E. skipperae* from nine (see boldfaced records in Table 1). Compared to

1 their recorded distributions in Sørensen and Landers (2014) several data points have been added
2 in the area south and southeast of the Mississippi River Delta (Fig. 1B), whereas the two species
3 still do not appear in the De Soto Valley and are rare along the Floridian coast. This distribution
4 could indicate that both *E. augustae* and *E. skipperae* have a preference for the silty Louisiana
5 sediments that are formed by the efflux of the Mississippi River, and this explains why the species
6 do not appear east of Station 012-2014 (see Fig. 1B) where the sediment is coarser and less
7 affected by the river. We still see a single record of each species on the West Florida Escarpment,
8 but in this context it is noteworthy that they occur on fairly deep stations (110 m and 178 m),
9 where the sediment turns siltier again due to the depth.

10 11 12 13 14 15 16 17 18 19 20 **Acknowledgements**

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27 series of *E. bookhouti* on loan for further examination. In addition, our thanks go to the
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30 This publication and the species *Echinoderes charlotteae* sp. nov. were registered in Zoobank
31 (www.zoobank.org) under LSID number: urn:lsid:zoobank.org:pub:E4DE2A89-8C53-4483-8584-
32 805B208157FD. Raw data is available at <https://data.gulfresearchinitiative.org>

33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 **References**

- 49 Adrianov, A.V., Malakhov, V.V., 1999. Cephalorhyncha of the world ocean. KMK Scientific Press,
50 Moscow.
51 Brown, R., 1985. Developmental and taxonomic studies of Sydney Harbour Kinorhyncha. Ph.D.-
52 thesis. Macquarie University, Australia.
53
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60
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- Burgess, R., 2001. An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Mar. Ecol. Prog. Ser.* 214, 161–165.
- Bütschli, O., 1876. Untersuchungen über freilebende Nematoden und Gattung *Chaetonotus*. *Z. wiss. Zool.* 23, 363–413.
- Claparède. A.R.E., 1863. Zur Kenntnis der Gattung *Echinoderes* Duj. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt. Verlag von Wilhelm Engelmann, Leipzig, pls. XVI-XVII, pp. 90-92, 119.
- G^aOrdóñez, D., Pardos, F., Benito J., 2008. Three new *Echinoderes* (Kinorhyncha, Cyclorhagida) from North Spain, with new evolutionary aspects in the genus. *Zool. Anz.* 247, 95–111.
- Herranz, M., Pardos, F., 2013. *Fissuroderes sorenseni* sp. nov. and *Meristoderes boylei* sp. nov.: First Atlantic recording of two rare kinorhynch genera, with new identification keys. *Zool. Anz.* 253, 93–111.
- Herranz, M., Thormar, J., Benito, J., Sánchez, 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, 191–179.
- Higgins, R.P., 1960. A new species of *Echinoderes* (Kinorhyncha) from Puget Sound. *Trans. Am. Microsc. Soc.* 79, 85–91.
- Higgins, R.P., 1964. Three new kinorhynchs from the North Carolina Coast. *Bull. Mar. Sci. Gulf and Caribbean* 14, 479–493.
- Higgins, R.P., 1967. The Kinorhyncha of New-Caledonia. In: *Expédition Française sur les Récifs Coralliens de la Nouvelle-Calédonie* 2, 75–90.
- Higgins, R.P., 1977. Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. *Trans. Am. Microsc. Soc.* 96, 340–354.
- Higgins, R.P., 1978. *Echinoderes gerardi* n. sp. and *E. riedli* (Kinorhyncha) from the Gulf of Tunis. *Trans. Am. Microsc. Soc.* 97, 171–180.
- 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., 1985. The genus *Echinoderes* (Kinorhyncha, Cyclorhagida) from the English Channel. *J. Mar. Biol. Assoc. UK.* 65, 785–800.
- Higgins, R.P., Kristensen, R.M., 1988. Kinorhyncha from Disko Island, West Greenland. *Smithson. Contrib. Zool.* 458, 1–56.

- Higgins, R.P., Rao, G.C., 1979. Kinorhynchs from the Andaman Islands. Zool. J. Linn. Soc. 67, 75–85.
- Lou, T.-H., 1934. Sur la presence d'un nouveau kinorhynque a Tchefou: *Echinoderes tchefouensis* sp. nov. Contrib. Inst. Zool., Nat. Acad. Peiping 1, 1–9. [In Chinese with French translation]
- Lundbye, H., Rho, H.S., Sørensen, M.V., 2011. *Echinoderes rex* n. sp. (Kinorhyncha: Cyclorhagida) – the largest *Echinoderes* species found so far. Sci. Mar. 75, 41–51.
- Nebelsick, M., 1992. Ultrastructural investigations of three taxonomic characters in the trunk region of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida). Zool. Scr. 21, 335–345.
- Neuhaus, B., Blasche T., 2006. *Fissuroderes*, a new genus of Kinorhyncha (Cyclorhagida) from the deep sea and continental shelf of New Zealand and from the continental shelf of Costa Rica. Zool. Anz. 245, 19–52.
- Omer-Cooper, J., 1957. Deux nouvelles espèces de Kinorhyncha en provenance de L'Afrique du Sud. Bull. Mens. Soc. Linn. Lyon 26, 213–216.
- Pardos, F., Higgins, R.P., Benito, J., 1998. Two new *Echinoderes* (Kinorhyncha, Cyclorhagida) including a reevaluation of kinorhynch taxonomic characters. Zool. Anz. 237, 195–208.
- 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., 2014. First account of echinoderid kinorhynchs from Brazil, with the description of three new species. Marine Biodiv. 44, 251–274.
- Sørensen, M.V., Landers, S.C., 2014. Two new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from the Gulf of Mexico. Front. Mar. Sci. 1, article 8, 1–18.
- 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., 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. Helgoland Mar. Res. 67, 291–319.
- Southern, R., 1914. Nematelmia, Kinorhyncha and Chaetognatha. Clare Island Survey, part 54. Proc. R. Irish Acad. 31, 1–80.

- 1 Yamasaki, H., Fujimoto, S., 2014. Two new species in the *Echinoderes coulli* group (Echinoderidae,
2 Cyclorhagida, Kinorhyncha) from the Ryukyu Islands, Japan. ZooKeys 382, 27–52.
3
4 Yamasaki, H., Kajihara, H., 2012. A New Brackish-water Species of *Echinoderes* (Kinorhyncha:
5 Cyclorhagida) from the Seto Inland Sea, Japan. Species Div. 17, 109–118.
6
7 Zelinka, K., 1896. Demonstration von Tafeln der *Echinoderes*-Monographie. Verh. Deutsch. Zool.
8 Gesellsch. 6, 197-199.
9
10 Zelinka, C., 1928. Monographie der Echinodera. Verlag Wilhelm Engelmann, Leipzig.
11
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Figure legends

Fig. 1. Maps showing the sampling locations in the Gulf of Mexico. Station numbers are given for each collection site. **A.** Collection sites for *Echinoderes bookhouti* and *E. charlotteae* sp. nov. **B.** Collection sites for *E. augustae* and *E. skipperae* (updated after Sørensen and Landers, 2014).

Fig. 2. Line art illustrations of *Echinoderes charlotteae* sp. nov. **A.** Female, dorsal view. **B.** Female, ventral view. **C.** Male, segments 10 to 11, dorsal view. **D.** Male, segments 10 to 11, ventral view.

Abbreviations: gco1/2, glandular cell outlet type 1/2; ld, laterodorsal sensory spot; ldt, laterodorsal tube; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; ml, midlateral sensory spot; pe, penile spine; pr, protuberance; si, sieve plate.

Fig. 3. Light micrographs showing overviews and details in male holotype ZMUC KIN-868 (**A-E, G**), female paratype ZMUC KIN-869 (**F**) and male paratype ZMUC KIN-870 (**H**) of *Echinoderes charlotteae* sp. nov. **A.** Ventral overview of male holotype. **B.** Segments 1 to 4, dorsal view. **C.** Segments 1 to 4, ventral view. **D.** Segments 4 to 8, dorsal view. **E.** Segments 4 to 8, ventral view. **F.** Right lateral terminal spine and lateral terminal accessory spine of female. **G.** Segments 10 to 11 of male, ventral view. **H.** Left half of segments 8 to 9, ventral view. Abbreviations: gco1/2, glandular cell outlet type 1/2; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; mvp, midventral placid; pe, penile spine; sd, subdorsal sensory spot; te, tergal extension; vm, ventromedial sensory spot.

Fig. 4. Scanning electron micrographs showing overviews and details in head and trunk morphology of *Echinoderes charlotteae* sp. nov. **A.** Laterodorsal overview of female specimen. **B.** Ventrolateral overview of male specimen. **C.** Mouth cone with outer oral styles. **D.** Neck region and segments 1 to 2, ventrolateral view. **E.** Segments 2 to 6, subdorsal view. Inset shows subdorsal sensory spot on segment 3; scale bar = 1 μ m. **F.** Segments 6 to 8, lateral view. **G.** Segments 9 to 10 of female, lateral view. Inset shows the minute female laterodorsal tube on segment 10; scale bar = 500 nm. **H.** Segments 10 to 11 of female, dorsal view. **I.** Segments 10 to 11 of female, ventral

view. **J.** Segments 10 to 11 of male, ventral view. Abbreviations: gco1/2, glandular cell outlet type 1/2; ldt, laterodorsal tube; lat, lateral accessory tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; ml, midlateral sensory spot; oos, outer oral style; pe, penile spine; pr, protuberance; sd, subdorsal sensory spot; si, sieve plate; te, tergal extension; vl, ventrolateral sensory spot; vm, ventromedial sensory spot.

Fig. 5. Line art illustrations of *Echinoderes bookhouti*. **A.** Male, dorsal view. **B.** Male, ventral view. **C.** Female, segments 10 to 11, dorsal view. **D.** Female, segments 10 to 11, ventral view. Abbreviations: gco1/2, glandular cell outlet type 1/2; las, lateral accessory spine; ld, laterodorsal sensory spot; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; lvt, lateroventral tube; mds, middorsal spine; ml, midlateral sensory spot; pe, penile spine; pr, protuberance; si, sieve plate; vl, ventrolateral sensory spot.

Fig. 6. Diagram of mouth cone (grey area), introvert and placids in *Echinoderes bookhouti*, showing distribution of outer oral styles, spinoscalids and trichoscalids. The table below shows the scalid arrangement by sector (S1 to S10), and summarized scalid numbers by rings and sectors. Question marks indicate that the occurrences of eventual inner oral styles are uncertain.

Fig. 7. Light micrographs showing overviews and details in male allotype, USNM 30982 (**A, E-H**) and female holotype USNM 30981 (**B-D, I**) of *Echinoderes bookhouti*, collected in the Northwest Atlantic by Higgins (1964). **A.** Dorsal overview. **B.** Ventral overview. **C.** Segment 2, dorsal view. **D.** Segment 2, ventral view. **E.** Segment 8, dorsal view. **F.** Segment 8, ventral view. **G.** Segments 10 to 11 of male, dorsal view. **H.** Segments 10 to 11 of male, ventral view. **I.** Segments 10 to 11 of female, dorsal view. Abbreviations: gco1/2, glandular cell outlet type 1/2; las, lateral accessory spine; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral spine; mds, middorsal spine; pe, penile spine; pr, protuberance.

Fig. 8. Light micrographs showing overviews and details in male, ZMUC KIN-888 (**A-H**) and female ZMUC KIN-869 (**I**) specimens of *Echinoderes bookhouti*, collected in the Gulf of Mexico. **A.** Dorsal

overview. **B.** Ventral overview. **C.** Segment 2, dorsal view. **D.** Segment 2, ventral view. **E.** Segment 8, focused medially in trunk in order to visualize midlateral glandular cell outlets type 2. **F.** Segments 7 to 9, ventral view. **G.** Segment 11 of male, dorsal view. **H.** Segment 11 of male, ventral view. **I.** Segment 11 of female, dorsal view. Abbreviations: gco1/2, glandular cell outlet type 1/2; las, lateral accessory spine; ldt, laterodorsal tube; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lvs, lateroventral spine; pr, protuberance; pe, penile spine; te, tergal extension; vm, ventromedial sensory spot.

Fig. 9. Scanning electron micrographs showing overviews and details in head and trunk morphology of *Echinoderes bookhouti*, collected in the Gulf of Mexico. **A.** Lateral overview. **B.** Mouth cone, ventral overview. **C.** Segment 2, dorsal view; note the weak pectinate fringe, pf. **D.** Segments 1 to 3, ventral view; note the strong pectinate fringe, pf. **E.** Segments 8 and 9, lateroventral view. Inset shows midlateral sensory spot of segment 5, representing the appearance of most sensory spots from segments 3 to 10; scale bar = 1 μ m. **F.** Segments 10 and 11 of female, laterodorsal view; note the cuticular hairs on segment 10. **G.** Segments 10 and 11 of male, dorsal view; note the lack of cuticular hairs on segment 10. **H.** Segments 10 and 11 of male, ventral view. Abbreviations: gco2, glandular cell outlet type 2; las, lateral accessory spine; ld, laterodorsal sensory spot; ldt, laterodorsal tube; lts, lateral terminal spine; lvs, lateroventral spine; md, middorsal sensory spot; oos, outer oral style; pf, pectinate fringe of posterior segment margin; pr, protuberance; pe, penile spine; sd, subdorsal sensory spot; sfr, style fringe; te, tergal extension; vl, ventrolateral sensory spot; vm, ventromedial sensory spot.

Table 1

Summary of data on stations, species identities and catalogue numbers (KIN-) for species deposited at the Natural History Museum of Denmark. Boldfaced recordings are new; recordings with regular font are from Sørensen and Landers (2014).

Station	Date	Position	Depth	Species	Mounting	Type status and catalogue numbers
163-2008	Nov. 9, 2008	26° 37' 40.55" N 84° 22' 49.33" W (26.62793 ⁰ , -84.38037 ⁰)	178 m	<i>Echinoderes augustae</i>	SEM	Non-type in Landers collection
071-2008	Oct. 22, 2008	28° 07' 44.32" N 90° 38' 08.77" W (28.12898 ⁰ -90.63577 ⁰)	109 m	<i>Echinoderes charlotteae</i> sp. nov.	LM	1 ♂ paratype: KIN-870
007-2010	Oct. 15, 2010	27° 12' 24.12" N 96° 40' 26.76" W (27.2067 ⁰ , -96.6741 ⁰)	72 m	<i>Echinoderes skipperae</i>	LM	2 ♀ paratypes: KIN-731, KIN-732; 1 ♂ paratype (broken): KIN-733
013-2010	Oct. 17, 2010	27° 40' 07.32" N 96° 18' 48.24" W (27.6687 ⁰ , -96.3134 ⁰)	73 m	<i>Echinoderes skipperae</i>	LM	1 ♂ paratype: USNM- 1231478
031-2010	Oct. 20, 2010	27° 54' 12.60" N 94° 28' 50.88" W (27.9035 ⁰ , -94.4808 ⁰)	135 m	<i>Echinoderes skipperae</i>	LM	1 ♀ paratype: USNM- 1231479; 1 damaged paratype: KIN-734
062-2010	Oct. 26, 2010	28° 30' 11.15" N 90° 01' 49.44" W (28.5031 ⁰ , -90.0304 ⁰)	78 m	<i>Echinoderes bookhouti</i>	LM	1 Non-type in Sørensen collection
067-2010	Oct. 27, 2010	29° 20' 49.20" N 88° 34' 06.60" W (29.3470 ⁰ , -88.5685 ⁰)	61 m	<i>Echinoderes bookhouti</i>	LM	1 Non-type: KIN-906
100-2010	Nov. 10, 2010	26° 15' 44.28" N 83° 53' 56.04" W (26.2623 ⁰ , -83.8989 ⁰)	110 m	<i>Echinoderes skipperae</i>	LM	1 paratype: KIN-735
033-2011	Oct. 21, 2011	28° 09' 50.90" N 94° 14' 26.23" W (28.16414 ⁰ , -94.24062 ⁰)	56 m	<i>Echinoderes augustae</i>	SEM	1 ♂ paratype: KIN-713
042-2011	Oct. 22, 2011	28° 14' 14.17" N 92° 22' 34.72" W (28.23727 ⁰ , -92.37631 ⁰)	64 m	<i>Echinoderes augustae</i>	-	Specimen lost during preparation
049-2011	Oct. 23, 2011	28° 22' 20.96" N 91° 11' 03.98" W (28.37249 ⁰ , -91.18444 ⁰)	53 m	<i>Echinoderes bookhouti</i>	SEM	2 Non-types in Sørensen collection
068-2012	Oct 22, 2012	28° 05' 12.52" N 91° 38' 12.62" W (28.08681 ⁰ , -91.63684 ⁰)	102 m	<i>Echinoderes augustae</i> sp. nov.	LM	1 ♀ paratype: KIN-711
073-2012	Oct. 23, 2012	28° 18' 47.59" N 91° 10' 33.81" W (28.31322 ⁰ , -91.17606 ⁰)	65 m	<i>Echinoderes bookhouti</i>	SEM	2 Non-types in Sørensen collection
075-2012	Oct. 23, 2012	28° 07' 28.49" N 90° 53' 37.32" W (28.12458 ⁰ , -90.89370 ⁰)	113 m	<i>Echinoderes charlotteae</i> sp. nov. <i>Echinoderes augustae</i>	SEM SEM	1 ♀ paratype: KIN-871 2 ♀ paratypes: KIN-714, KIN-715; 1 ♂ paratype: KIN-716
				<i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM LM	1 Non-type: KIN-887 1 ♀ paratype: KIN-736
077-2012	Oct. 24, 2012	28° 22' 07.50" N 90° 30' 44.06" W (28.36875 ⁰ , -90.51224 ⁰)	49 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i>	SEM SEM	3 ♀ paratypes: KIN-717 to KIN-719; 1 ♂ paratype: KIN-720 2 Non-types in Sørensen collection
080-2012	Oct. 24, 2012	28° 49' 22.76" N 89° 42' 38.63" W (28.82299 ⁰ , -89.71073 ⁰)	70 m	<i>Echinoderes augustae</i>	LM	1 ♂ paratype (mounted laterally): KIN-712
082-2012	Oct. 25, 2012	28° 37' 59.34" N 89° 13' 16.32" W	242 m	<i>Echinoderes skipperae</i>	SEM	1 ♂ paratype: KIN-739

083-2012	Oct. 25, 2012	(28.63315 ⁰ , -89.22120 ⁰) 28° 46' 27.19" N 89° 04' 30.18" W (28.77422 ⁰ , -89.07505 ⁰)	361 m	<i>Echinoderes skipperae</i>	LM	1 ♂ paratype: KIN-737
084-2012	Oct. 25, 2012	28° 58' 51.02" N 88° 59' 56.47" W (28.98084 ⁰ , -88.99902 ⁰)	85 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i>	LM SEM LM SEM	♀ holotype: KIN-705; 1 ♀ paratype: KIN-706 3 ♀ paratypes: KIN-721 to KIN-723 2 Non-types: KIN-888 to KIN-889 1 Non-type in Sørensen collection
085-2012	Oct. 25, 2012	29° 07' 56.71" N 88° 42' 27.47" W (29.13242 ⁰ , -88.70763 ⁰)	86 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM SEM LM SEM LM SEM	1 ♀ paratype: USNM-1231476; 1 ♂ paratype: USNM-1231477 4 ♂ paratypes: KIN-724 to KIN-727 3 Non-types: KIN-890 to KIN-892 9 Non-types in Sørensen collection ♀ holotype: KIN-730; 1 ♀ paratype: KIN-738 2 ♀ paratypes: KIN-740, KIN-741; 1 ♂ paratype: KIN-742
086-2012	Oct. 25, 2012	29° 17' 21.16" N 88° 33' 21.24" W (29.28921 ⁰ , -88.55590 ⁰)	66 m	<i>Echinoderes augustae</i> sp. nov. <i>Echinoderes bookhouti</i>	LM SEM LM SEM	3 ♀ paratypes: KIN-707 to KIN-709; 1 ♂ paratype: KIN-710 1 ♀ paratype: KIN-729; 1 ♂ paratype: KIN-728 1 Non-type: KIN-893 1 Non-type in Sørensen collection
001-2013	Oct. 24, 2013	26° 14' 35.33" N 96° 36' 25.41" W (26.24315 ⁰ , -96.60706 ⁰)	51 m	<i>Echinoderes bookhouti</i>	LM SEM	2 Non-types: KIN-894 to KIN-895 7 Non-types in Sørensen collection
031-2013	Oct. 30, 2013	28° 01' 55.27" N 93° 13' 29.46" W (28.03202 ⁰ , -93.22485 ⁰)	99 m	<i>Echinoderes bookhouti</i>	LM	1 Non-type: KIN-896
050-2013	Nov. 02, 2013	28° 14' 21.29" N 90° 52' 01.81" W (28.23925 ⁰ , -90.86717 ⁰)	74 m	<i>Echinoderes charlotteae</i> sp. nov. <i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM LM LM SEM LM SEM	♂ holotype: KIN-868; 1 ♀ paratype: KIN-869 1 Non-type: KIN-872 1 Non-type: KIN-897 2 Non-types in Sørensen collection 3 Non-types: KIN-876 to KIN-878 1 Non-type in Sørensen collection
055-2013	Nov. 03, 2013	28° 20' 17.8" N 90° 00' 52.27" W (28.33828 ⁰ , -90.01452 ⁰)	107 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM LM SEM SEM	1 Non-type: KIN-873 1 Non-type: KIN-898 1 Non-type in Sørensen collection 1 Non-type in Sørensen collection
056-2013	Nov. 03, 2013	28° 20' 16.72" N 90° 17' 42.57" W (28.33798 ⁰ , -90.29516 ⁰)	63 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i>	LM LM	1 Non-type: KIN-874 8 Non-types: KIN-899 to KIN-905 and KIN-919
057-2013	Nov. 04, 2013	28° 38' 05.81" N 90° 04' 56.42" W (28.63495 ⁰ , -90.08234 ⁰)	146 m	<i>Echinoderes augustae</i> <i>Echinoderes skipperae</i>	LM LM LM	1 Non-type: KIN-875 2 Non-types in Landers collection 4 Non-types: KIN-879 to KIN-882
067-2013	Nov. 12, 2013	29° 10' 13.18" N 88° 48' 53.24" W (29.17033 ⁰ , -88.81479 ⁰)	74 m	<i>Echinoderes skipperae</i> <i>Echinoderes bookhouti</i>	LM LM LM	3 Non-types: KIN-883 to KIN-885 2 Non-types in Landers collection 10 Non-types: KIN-907 to KIN-916
078-2013	Nov. 15, 2013	29° 53' 7.72" N 86° 47' 31.2" W (29.88548 ⁰ , -86.792 ⁰)	142 m	<i>Echinoderes charlotteae</i> sp. nov.	SEM	1 ♀ Non-type in Landers collection
079-2013	Nov. 15, 2013	29° 48' 20.77" N 86° 36' 2.37" W (29.80577 ⁰ , -86.60066 ⁰)	125 m	<i>Echinoderes bookhouti</i>	SEM	2 Non-types in Landers collection
135-2013	Nov. 25, 2013	29° 50' 20.97" N 87° 07' 08.97" W (29.83916 ⁰ , -87.11916 ⁰)	154 m	<i>Echinoderes charlotteae</i> sp. nov.	SEM	2 ♂ Non-types in Landers collection
001-2014	Nov. 2, 2014	28° 25' 48.71" N 90° 14' 10.31" W (28.4302 ⁰ , -90.2362 ⁰)	57 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM LM LM	6 Non-types in Landers collection 22 Non-types in Landers collection 9 Non-types in Landers collection

002-2014	Nov. 2, 2014	28° 20' 30.83" N 90° 28' 20.63" W (28.3419°, -90.4724°)	53 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM LM LM	2 Non-types in Landers collection 8 Non-types in Landers collection 3 Non-types in Landers collection
004-2014	Nov. 2, 2014	28° 8' 30.83" N 90° 57' 5.39" W (28.1419°, -90.9515°)	97 m	<i>Echinoderes bookhouti</i>	SEM	3 Non-types in Landers collection
012-2014	Nov. 13, 2014	29° 15' 10.08" N 88° 18' 23.76" W (29.2528°, -88.3066°)	90 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i>	LM SEM SEM	15 Non-types in Landers collection 2 Non-types in Landers collection 3 Non-types in Landers collection
015-2014	Nov. 13, 2014	29° 3' 1.43" N 88° 52' 5.15" W (29.0504°, -88.8681°)	112 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM SEM LM SEM LM SEM	26 Non-types in Landers collection 9 Non-types in Landers collection 5 Non-types in Landers collection 15 Non-types in Landers collection 40 Non-types in Landers collection 2 Non-types in Landers collection
016-2014	Nov. 14, 2014	28° 53' 37.31" N 89° 14' 53.88" W (28.8937°, -89.2483°)	67 m	<i>Echinoderes augustae</i> <i>Echinoderes skipperae</i>	LM LM	16 Non-types in Landers collection 1 Non-type in Landers collection
019-2014	Nov. 14, 2014	28° 43' 52.68" N 89° 34' 16.32" W (28.7313°, -89.5712°)	94 m	<i>Echinoderes augustae</i> <i>Echinoderes bookhouti</i> <i>Echinoderes skipperae</i>	LM SEM SEM LM	3 Non-types in Landers collection 1 Non-type in Landers collection 4 Non-types in Landers collection 8 Non-types in Landers collection
025-2014	Nov. 16, 2014	28° 07' 06.60" N 91° 49' 34.32" W (28.1185°, -91.8262°)	88 m	<i>Echinoderes bookhouti</i> <i>Echinoderes charlotteae</i> sp. nov.	LM LM	1 Non-type in Landers collection 1 ♀ paratype: KIN-918
026-2014	Nov. 16, 2014	28° 27' 25.92" N 91° 31' 53.04" W (28.4572°, -91.5314°)	52 m	<i>Echinoderes bookhouti</i> <i>Echinoderes augustae</i>	LM SEM SEM	14 Non-types in Landers collection 9 Non-types in Landers collection 1 Non-type in Landers collection
031-2014	Nov. 20, 2014	29° 39' 35.28" N 86° 34' 58.08" W (29.6598°, -86.5828°)	163 m	<i>Echinoderes charlotteae</i> sp. nov.	LM	1 ♂ paratype: KIN-917
033-2014	Nov. 20, 2014	29° 32' 32.28" N 86° 11' 33.35" W (29.5423°, -86.1926°)	98 m	<i>Echinoderes charlotteae</i> sp. nov.	SEM	1 ♂ Non-type in Landers collection
039-2014	Nov. 22, 2014	29° 46' 22.79" N 88° 06' 04.32" W (29.7730°, -88.1012°)	37 m	<i>Echinoderes bookhouti</i>	SEM	1 Non-type in Landers collection

Table 2. Measurements from light microscopy of the five type specimens of *Echinoderes charlotteae* sp. nov. (in μm). Abbreviations: MD: middorsal spine; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral spine; MSW-5: maximum sternal width, measured on segment 5 in this species; S: segment lengths; SW-10, standard width, always measured on segment 10; TL: trunk length; –, missing data.

Character	Holotype KIN-868 Male	Paratype KIN-869 Female	Paratype KIN-870 Male	Paratype KIN-917 Male	Paratype KIN-918 Female
TL	204	169	194	199	152
MSW-5	43	35	40	44	40
MSW-5/TL	21.1%	20.7%	20.6%	22.1%	26.3%
SW-10	33	37	34	38	39
SW-10/TL	16.2	21.9%	17.5%	19.1%	25.7%
S1	18	18	20	21	18
S2	18	19	20	20	17
S3	18	20	21	19	18
S4	18	21	22	19	19
S5	20	22	25	23	21
S6	22	23	26	24	22
S7	24	25	28	27	25
S8	25	28	28	28	26
S9	27	26	27	30	28
S10	30	24	29	32	26
S11	29	31	35	29	35
MD4	12	–	17	20	13
LV6	11	13	15	14	17
LV7	15	14	17	18	17
LV8	16	16	20	21	20
LV9	17	20	22	23	20
LTS	85	116	150	147	149
LTS/TL	41.7%	68.6%	77.3%	73.9%	98.0%
LTAS	N/A	35	N/A	N/A	55

Table 3. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes charlotteae* sp. nov. Abbreviations: LA: lateral accessory; LD: Laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac, acicular spine; gco 1/2, glandular cell outlet type 1/2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; pe, penile spines; si, sieve plate; ss, sensory spot; tu, tube; (♀), female and (♂), male conditions of sexually dimorphic characters.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1			ss	ss					gco1	ss
2			gco2	ss,ss		gco2		tu		ss
3	gco1		ss		ss					
4	ac	gco1								
5			ss					tu		ss
6			ss		ss			ac		ss
7			ss		ss			ac		
8			ss				tu	ac		
9		gco1	ss	ss		si		ac	ss	
10	2xgco1		ss,gco1	tu					ss	
11			gco1		pe(♂)		ltas(♀)	lts		

Table 4. Measurements from light microscopy of *Echinoderes bookhouti* (in μm) from the Gulf of Mexico, including number of measured specimens (n) and standard deviation (SD). Abbreviations: (ac): acicular spine; LA: lateral accessory; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD, middorsal; MSW-7: maximum sternal width, measured on segment 7 in this species; S: segment lengths; SW-10, standard width, always measured on segment 10; TL: trunk length; (tu): tube.

Character	n	Range	Mean	SD
TL	10	295 – 372	343	22.28
MSW-7	10	59 – 70	66	3.12
MSW-7/TL	10	17.7 – 20.4%	19.2%	0.92%
SW-10	10	49 – 59	54	3.31
SW-10/TL	10	14.0 – 16.7%	15.7%	1.00%
S1	10	34 – 39	37	1.84
S2	10	34 – 39	36	1.99
S3	10	34 – 39	37	1.81
S4	10	32 – 40	37	2.41
S5	10	33 – 44	40	3.07
S6	10	39 – 47	43	2.50
S7	10	42 – 49	46	2.21
S8	10	42 – 51	48	2.58
S9	10	39 – 51	47	3.31
S10	10	35 – 52	45	6.04
S11	10	30 – 38	33	1.91
MD4 (ac)	8	33 – 48	42	4.81
MD5 (ac)	9	40 – 62	54	7.45
MD6 (ac)	9	51 – 70	63	6.95
MD7 (ac)	9	61 – 83	71	6.47
MD8 (ac)	10	70 – 83	77	4.52
LV5 (tu)	5	20 – 31	23	4.39
LV6 (ac)	10	27 – 36	33	2.45
LV7 (ac)	10	28 – 40	36	3.39
LA8 (ac)	10	34 – 41	39	2.37
LV9 (ac)	10	32 – 47	37	5.80
LTS	10	142 – 192	171	15.48
LTS/TL	10	40.5 – 55.3%	50.0%	4.41 %
LTAS	5	39 – 78	65	17.10

Table 5. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes bookhouti*. Abbreviations: LA: lateral accessory; LD: Laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; ac, acicular spine; gco 1/2, glandular cell outlet type 1/2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; pe, penile spines; si, sieve plate; ss, sensory spot; tu, tube; (♀), female and (♂), male conditions of sexually dimorphic characters.

Position Segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss				gco1		ss
2	gco1, ss		gco2	ss	ss			gco2		ss,gco1
3	gco1		ss							gco1
4	ac	gco1								gco1
5	ac	gco1	ss		ss			tu		ss,gco1
6	ac	gco1,ss			ss			ac		ss,gco1
7	ac	gco1,ss			ss			ac		ss,gco1
8	ac	gco1,ss		ss	gco2		ac			ss,gco1
9		gco1,ss				si		ac	ss	gco1
10	2xgco1, gco1		ss	tu					ss	gco1
11			ss		pe(♂)		ltas(♀)	lts		

Table 6. Summary of nature and location of cuticular spines, tubes, papillae and glandular cell outlets type 2 arranged by segments in the re-examined echinoderid species from the Smithsonian Institution, United States National Museum collection. Abbreviations: LA: lateral accessory; LD: Laterodorsal; LV: lateroventral; MD: middorsal; ML: midlateral; PD: paradorsal; SD: subdorsal; SL: sublateral; VL: ventrolateral; VM: ventromedial; gco2, glandular cell outlet type 2; ltas, lateral terminal accessory spine; lts, lateral terminal spine; pe, penile spines. “t”, “s” and “p” refer to tube, spine and papillae when accompanying uppercase abbreviations.

[illegible]

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Scalid and style arrangement

Ring/Sector	1	2	3	4	5	6	7	8	9	10	Total
00 outer oral styles +	1	1	1	1	1	0	1	1	1	1	9
01 primary spinoscalids ▼	1	1	1	1	1	1	1	1	1	1	10
02 spinoscalids ○	1	1	1	1	1	1	1	1	1	1	10
03 spinoscalids ○	2	2	2	2	2	2	2	2	2	2	20
04 spinoscalids ○	1	1	1	1	1	1	1	1	1	1	10
05 spinoscalids ○	2	2	2	2	2	2	2	2	2	2	20
06 spinoscalids ○	1	0	1	0	1	1	1	0	1	0	6
07 spinoscalids ○	2	0	2	0	1	2	1	0	2	0	10
08 spinoscalids ○	1	0	1	0	1	0	1	0	1	0	5
trichoscalids ●	0	1	0	1	1	0	1	1	0	1	6
Total spinoscalids	10	6	10	6	9	9	9	6	10	6	81

Figure 7

Figure 8

Figure 9