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KINORHYNCH DIVERSITY IN THE SOUTHERN GULF OF MEXICO AND A DESCRIPTION OF *DRACODERES CHAAC* SP. NOV.

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ABSTRACT: Sediment collections from the southern Gulf of Mexico between the Texas–Mexico border and the Yucatán Peninsula have resulted in many new kinorhynch species distribution records and the finding and taxonomic description of a new species, *Dracoderes chaac* sp. nov. This study focused on the non–echinoderid members of the Phylum Kinorhyncha, many of which are rare or restricted to only a few locations. A total of 136 specimens were identified from 24 sediment stations, distributed among the following species: *Antygomonas gwenae*, *Campyloderes vanhoeffeni*, *Centroderes readae*, *Condyloderes flosimbriatus*, *Co. rohalorum*, *Cristaphyes panamensis*, *Dracoderes chaac* sp. nov., *Leiocanthus corrugatus*, *L. langi*, *L. quinquenudus*, *L. satanicus*, *Pycnophyes alexandroi*, *Semnoderes lusca*, and *Sphenoderes aspidochelone*. Additional undescribed species in the genera *Leiocanthus*, *Mixtophyes*, and *Paracentrophyes* were recovered. Statistical analysis of the stations revealed a grouping of locations where the majority of the pycnophyid species were recovered. Some species (e.g., *Ca. vanhoeffeni*, *S. aspidochelone*) had an extensive distribution, while others were recorded from one or few locations only (e.g., *A. gwenae*, *Co. rohalorum*). Most of the species were reported from earlier collections in the northern Gulf of Mexico on the U.S. continental shelf, between 700–1100 km away.

KEY WORDS: Ecology, Kinorhyncha, Meiofauna, Taxonomy

INTRODUCTION

Recent studies of Kinorhyncha in the northern Gulf of Mexico (nGOM) have resulted in numerous new species records and new species descriptions (Landers et al. 2019, 2020, Sánchez et al. 2019, Hoffman et al. 2021, Cepeda et al. 2022). Currently, 30 named species are known from the United States' nGOM waters. Community analysis studies from the nGOM (Hoffman et al. 2021, Landers et al. 2018, 2019, 2020) reported 88–90% of all kinorhynch individuals belonged to the Family Echinoderidae, which includes *Echinoderes*, known to be the most species–rich genus in the phylum and accounting for approximately one third of kinorhynch species diversity (Sørensen and Pardos 2020). The remainder of species from these 4 nGOM studies belonged to the families Antygomonidae, Campyloderidae, Centroderidae, Neocentrophoridae, Pycnophyidae, Semnoderidae, and Zelinkaderidae. Rarer taxa from these families are typically not encountered in high numbers in kinorhynch ecology studies, but are recovered from large sampling efforts.

The bathymetry of the nGOM is more uniform than the southern Gulf of Mexico (sGOM), having an expansive continental shelf that extends from southern Texas to southern Florida. The shelf extends to ~100–200 km off the Texas, Louisiana, Alabama, and Florida coasts, and narrows to as little as 10 km at the mouth of the Mississippi river. Thus, nGOM sampling efforts in previous studies were focused on more shallow stations (11–443 m) due to the distance to the continental slope from shore at most locations. In contrast, the coastline of the sGOM, which spans from the northern border of Mexico to the eastern margin of the Yucatán Peninsula, is characterized by the East Mexico and Yucatán Shelves. These shallow, relatively flat areas range from <10 km wide near Vera-

cruz to almost 150 km off the coast of the Yucatán Peninsula. The western portion of the sGOM, where the coastal shelf is narrowest, is characterized by steep continental slopes that grade into the Mexico Basin, with depths exceeding 3,800 m. A prominent benthic feature of the sGOM in the east is the Campeche Escarpment, the dividing line between the Yucatán Shelf and the Campeche Canyon, where depth can change from 200 m to over 2000 m in < 15 km (Davis 2017).

Given the more varied bathymetry of the sGOM, a study of kinorhynchs from various depths ranging from 16–3,214 m was undertaken. Currently there are few records of kinorhynchs from Mexico. Recently, *Echinoderes unispinosus* was reported from 2 deep (2,298 and 3,708 m) locations found in the middle of the study area of this report (Álvarez–Castillo et al. 2020), along with other Mexican records restricted to the Gulf of California in the Pacific (Álvarez–Castillo et al. 2015, 2018, Cepeda et al. 2019a), and anchialine caves in the Yucatan Peninsula (Sánchez and Martínez 2019). This current study reports new species records and distributions for the rarer non–echinoderid kinorhynch taxa, collected in the sGOM at multiple stations, and also provides a description of a new species, *Dracoderes chaac* sp. nov.

MATERIALS AND METHODS

Sample collection

Sediment samples were collected using an Oktopus MUC 12–100 multicorer on the Universidad Nacional Autónoma de México's R/V *Justo Sierra* (cruise JS–0815) between 30 July and 9 August 2015 in the sGOM (Figure 1). The samples were collected as part of the GOMRI C–IMAGE II consortium research program. Samples were fixed on the ship in 7% formalin, stored at the Harte Research Institute for Gulf of Mexico

FIGURE 1. Collection stations in the southern Gulf of Mexico.

Studies (Corpus Christi, TX) and eventually donated to Troy University for meiofauna analysis. CTD data were collected at each sediment core station (Table 1).

Sediment processing.

The 0–1 cm depth slices from 3 cores at each station were processed by Ludox® centrifugation (Burgess 2001). Kinorhynchs were isolated using a counting wheel and a stereomicroscope, and stored in microfuge tubes with 70% isopropanol until microscopically examined. Samples for light microscopy (LM) were mounted between 2 coverslips with Fluoromount G® (Sørensen and Pardos 2020) and affixed to a plastic coverslip holder (Electron Microscopy Sciences #72268), allowing the animals to be critically examined ventrally and dorsally by inverting the slide. Animals for scanning electron microscopy (SEM) were enclosed in a modified BEEM capsule with 35 µm nitex mesh on each end, which held the animals during critical point drying. Gold-coated samples were examined in a Zeiss EVO 50 SEM at the Auburn University Research Instrumentation Facility (Auburn, Alabama). Animals were identified to genus and species following Sørensen and Pardos (2020) and descriptions from the primary literature. Adult body types (type 1

versus type 2) were determined for the genera *Campyloderes*, *Centrodere*, *Condyloderes*, and *Sphenoderes* (Neuhaus and Sørensen 2013, Neuhaus et al. 2014, Sørensen et al. 2019, Sørensen and Herranz 2022, Sørensen and Landers pers. obs.). Type material is stored in the collection of the Natural History Museum of Denmark (NHMD). The holotype of *Dracoderes toyoshioae* was loaned from Hokkaido University Museum, Hokkaido University, Japan.

Statistical analysis

The samples varied in the amount of sediment (the top 1 cm of sediment was present in most samples, but some appeared to have less), and were thus analyzed for non-quantitative studies. To examine the relationship between physical-chemical variables among stations, we ordinated 6 physical-

chemical variables (bottom temperature (°C), bottom salinity, bottom dissolved oxygen (DO; mg/L), depth (m), and latitude and longitude) using principal component analysis (PCA) of the correlation matrix in Primer® software. We interpreted variables that loaded on a component at an absolute value ≥ 0.435 to make a significant contribution to interpreting that component (Hair et al. 1984). The species community

TABLE 1. Collection stations with positional and abiotic data. See Figure 1 for locations of each station.

Station	Cruise ID	Latitude	Longitude	Depth (m)	Bottom DO (mg/L)	Bottom Temp (°C)	Bottom Salinity
1	25–500	24.2174	–96.8213	946	2.533	5.53	34.92
2	26–500	22.3803	–97.2230	953	4.515	5.52	34.9
3	26–750	22.4123	–97.0886	1533	4.570	5.49	34.92
4	26a–250	21.2103	–96.8556	518	2.901	8.56	35.05
5	27–500	20.0827	–96.2339	990	4.682	5.33	34.93
6	27–750	20.1212	–96.1302	1522	5.887	4.27	34.97
7	28–500	19.2236	–95.6998	1155	5.258	5.04	34.94
8	30–100	18.6970	–94.4307	200	3.253	15.56	36.04
9	30–250	18.8575	–94.4249	518	3.075	9.16	35.12
10	30a–100	18.9335	–93.3615	190	3.082	16.22	36.15
11	30a–250	19.0923	–93.4017	496	2.974	9.72	35.18
12	LT1	18.8484	–92.0705	16	5.230	27.85	36.66
13	LT2	19.0564	–92.1245	21	5.460	28.47	36.65
14	Abkatun	19.3143	–92.2080	50	5.069	22.6	36.52
15	LT3	19.3568	–92.2759	51	3.364	20.11	36.45
16	31–100	19.5255	–92.5857	190	3.005	16.9	36.24
17	IXNW–350	19.6457	–92.7421	709	3.378	7.33	34.96
18	IXNW–600	20.1046	–93.5685	2043	5.530	4.33	34.97
19	IXNW–1600	20.8066	–94.8136	3214	5.236	4.38	35
20	IXN–100	19.8175	–92.3484	421	3.041	10.69	35.31
21	IXN–250	19.9143	–92.3432	725	4.000	6.5	34.9
22	IXN–750	20.1701	–92.4200	1647	6.203	4.32	34.97
23	IXN–1000	20.3525	–92.4946	2173	5.907	4.31	34.97
24	33–250	22.3319	–91.7015	391	3.306	10.84	35.32

at each station was analyzed using cluster analysis (presence/absence transformation) and SIMPROF (Similarity Profile) with Primer ® 6.0 software. The station map (Figure 1) was created using ArcGIS Pro 2.7.1.

RESULTS

Distribution of non—echinoderid Kinorhynchs

The 24 station locations varied greatly in depth and latitude, as the collections extended over a distance of >770 km. Depths varied from 16–3,214 m (Table 1). Principal components analysis separated the stations with principal component 1 (PC1) having the highest contributions to variation coming from depth, bottom temperature and bottom salinity, and PC2 having the highest contributions from bottom dissolved oxygen (Figure 2). Depth loaded onto both PC 1 and 2 similarly, but was at a lower and less important correlation than dissolved oxygen on PC 2 (see Figure 2 vectors). We interpret this as a similar number of deep stations had either lower or higher dissolved oxygen levels. Both longitude and latitude loaded on both axes but at much lower levels (see Figure 2 vectors). Overall, PC1 and PC2 accounted for 78.1% of the variation. We observed that the stations could be separated by PC1 into 3 groups based on depth: deep stations with depths ≥ 953 m (stations 1–3, 5–7, 18, 19, 22, 23), those between 391–725 m (stations 4, 11, 17, 20, 21, 24), and more shallow stations ≤ 200 m (stations 8, 10, 12–16).

A total of 136 non—echinoderid specimens, belonging to 19 species, were recovered from the families Antygomonidae, Campyloderidae, Centroderidae, Dracoderidae, Neocentro-

TABLE 2. A list of kinorhynch species collected at 24 southern Gulf of Mexico stations in 2015. See Figure 1 for locations of each station number. Stages were identified following Neuhaus and Sørensen (2013), Neuhaus et al. (2014), Sørensen et al. (2019), Sørensen and Herranz (2022), and Sørensen and Landers (pers. obs.).

Species	Number of Individuals	Station #
<i>Antygomonas gwenae</i>	5 specimens (2 identifiable as ♀)	20
<i>Campyloderes vanhoeffeni</i>	3 specimens (2 ♂)	2
	1 ♂	5
	1 ♀	6
	2 ♀	8
	4 ♂	10
	9 specimens (3 ♀ stage 1, 5 ♂)	20
	1 ♂	24
<i>Centroderes readae</i>	1 ♀, 1 ♂ stage 1	2
& <i>Centroderes</i> cf. <i>C. readae</i>	1 ♂ stage 1	7
	2 specimens (1 ♂ stage 2)	10
	1 ♀	16
	1 ♂ stage 2	18
	4 ♀	20
<i>Condyloderes flosfimbriatus</i>	2 ♂	2
& <i>Condyloderes</i> cf. <i>C. flosfimbriatus</i>	1 specimen	4
	2 specimens (1 ♂)	8
	2 specimens	9
	1 ♀ stage 2	10
	6 specimens (1 ♀ stage 2, 1 ♀ stage 1, 3 ♂)	20
<i>Condyloderes rohalorum</i>	2 ♀ stage 2, 4 ♂	20
<i>Cristaphyes</i> cf. <i>C. panamensis</i>	2 ♂	14
	1 ♀	15
<i>Dracoderes chaac</i> sp. nov.	1 ♀	3
	1 ♀	8
	1 ♂	9
<i>Leiocanthus corrugatus</i> & <i>Leiocanthus</i> cf. <i>L. corrugatus</i>	1 ♀, 3 ♂	14
	2 ♀, 1 ♂	15
<i>Leiocanthus langi</i>	1 ♂	13
	6 ♀, 3 ♂	14
	3 ♀, 2 ♂	15
<i>Leiocanthus quinquenudus</i>	2 ♀, 1 ♂	14
<i>Leiocanthus satanicus</i>	1 ♀	14
	2 ♂	15
<i>Leiocanthus</i> sp. 3	1 ♀, 1 ♂	24
<i>Leiocanthus</i> sp. 4	1 ♂	22
<i>Leiocanthus</i> sp. 5	1 ♂	20
<i>Mixtophyes</i> sp. 1	1 ♂	23
<i>Paracentrophyes</i> sp. 1	1 ♀	2
<i>Pycnophyes alexandroi</i> & <i>Pycnophyes</i> cf. <i>P. alexandroi</i>	1 ♂	12
	1 ♀, 1 ♂	14
	1 ♀	15
<i>Semnoderes lusca</i>	1 specimen	7
	1 specimen	10
	3 specimens	20
	1 specimen	21
	1 specimen	22
	1 specimen	23
	1 specimen	24
<i>Sphenoderes aspidochelone</i>	2 specimens (1 ♂, 1 unk stage 1)	1
	2 specimens (1 ♀ stage 1)	2
	2 ♀ stage 1	5
	1 ♂ stage 1	7
	2 specimens (1 ♀ stage 1, 1 unk stage 1)	8
	3 specimens (1 ♀ stage 2, 2 ♂ stage 1)	10
	4 ♀ stage 1	11
	1 specimen	16
	1 ♀ stage 1	17
	1 specimen stage 1	19
	1 ♀ stage 1, 1 ♂ stage 2	20
	1 ♂ stage 1	21
	1 ♀ stage 1	22
	2 ♀ stage 1, 1 ♂ stage 1	24

FIGURE 2. Principal components analysis (PCA) of collection stations (see Figure 1) based on abiotic data. Three depth strata have been indicated.

FIGURE 3. Cluster analysis of collection stations based on kinorhynch communities. Solid lines indicate significant ($p < 0.05$) grouping using SIMPROF. The 4 shallow stations, with most of the family Pycnophyidae data, are indicated by the rectangle.

phyidae, Pycnophyidae, and Semnoderidae. These specimens were identified to either existing species or unique, but unidentified, species within existing genera (Table 2). All represent new species records for Mexico. Four of these species were represented by a single specimen. The most abundant species was *Sphenoderes aspidochelone*, with 26 specimens recovered from 14 stations. The second most abundant species was *Campyloderes vanhoeffeni*, with 21 specimens recovered from 7 stations. A rare species, *Semnoderes lusca*, was found in 7 sampling localities, reaching a relatively high abundance with 9 specimens reported from the area. A cluster analysis of stations (Figure 3) revealed a significant grouping of the shallow stations 12–15, as these stations provided the majority (36/39) of the specimens belonging to the Family Pycnophyidae. The stations had a depth range of 16–51 m. Outliers to this observation were *Leiocanthus* sp. 3, 4 and 5. These shallow stations yielded no specimens outside of the Family Pycnophyidae, resulting in their grouping on the cluster analysis.

Description of a new species

Class: Allomalorhagida Sørensen et al. 2015

Order: Anomoirhaga Herranz et al. 2022

Family: Dracoderidae Higgins & Shirayama, 1990

Genus: *Dracoderes* Higgins & Shirayama, 1990

Species: *Dracoderes chaac* sp. nov. (urn:lsid:zoobank.org:act:EAEB7425–9069–4374–90E3–8E9545C9B126)

Diagnosis

Dracoderes with acicular spines in middorsal position on segment 1; spines of the dorsal series on the following segments are alternately laterally displaced to paradorsal position on segment 2, and subdorsal positions on segments 3 to 9; addi-

tional acicular spines present in ventrolateral positions on segment 1, lateroventral positions on segments 2 to 4, and 6 to 9, and in lateral accessory positions on segment 5 (Figure 4). Tubes present in lateral accessory positions on segment 2 and in lateroventral positions on segment 5. Glandular cell outlets type 2 present in lateroventral positions on segment 10.

Etymology

The species is named after the Mayan God Chaac – the deity for rain and thunder.

Examined Material

Holotype, adult female, collected from mud on 8 August 2015, Cruise ID 26–750 (Map station 3) at 1,533 m depth off Tampico, Mexico (22.41226833, –97.088555), mounted in Fluoromount G, and deposited at NHMD under catalogue number NHMD–915291. One paratype adult female, collected from mud on 7 August 2015, Cruise ID 30–100 (Map station 8) at 200 m depth off Coatzacoalcos (the southernmost sGOM station in this study), Mexico (18.69697667, –94.43065333), mounted in Fluoromount G, and deposited at NHMD under catalogue number NHMD–

915292. The paratype specimen was unfortunately squeezed so hard during mounting that spines and segments were broken apart; whereas it was no longer possible to make any measures on the specimen, it was still possible to observe cuticular structures such as sensory spots and glandular cell outlets. Additional material includes one non-type male, collected from mud on 7 August 2015, Cruise ID 30–250 (Map station 9) at 518 m depth (18.857535, –94.42491) slightly north of map station 8, mounted for SEM, and stored in the personal reference collection of the first author.

Description

Adults with head, neck and eleven trunk segments (Figures 4A–B, 5A, 6A). For complete overview of measurements and dimensions, see Table 3. Distribution of cuticular structures, i.e., spines, tubes, sensory spots and glandular cell outlets, is summarized in Table 4. Only the paratype female, mounted for LM, had its head everted, but it was not possible to observe any taxonomically relevant details in mouth cone, introvert, or neck region.

The anterior 6–7 segments are very broad, compared to their length, which gives a dorso–ventrally squeezed specimen mounted for LM a conspicuously chubby appearance (Figures 4A–B, 5A). Another noteworthy metric trait is the segment lengths that remain nearly constant from segment 2 to 11, whereas sternal widths drop from segment 7 and towards the posterior segments. Segment 1 consists of a closed cuticular ring, whereas segments 2 to 11 consist of one tergal and 2 sternal plates. All acicular spines appear very long and thin, and those on segments 1 to 9 have distinct, subcuticular anchor–like structures. Sensory spots were detected on several segments, but they appear rather indistinct in LM, and nearly

FIGURE 4. Line art illustrations of *Dracoderes chaac* sp. nov. A. Female, dorsal overview. B. Female, ventral view. C. Male, segments 10 to 11, ventral view, with lateral terminal spines drawn in full length; inset shows close-up of the minute penile spines. Abbreviations: las—lateral accessory spine; lat—lateral accessory tube; ldss—laterodorsal sensory spot; lts—lateral terminal spine; lvgo2—lateroventral glandular cell outlet type 2; lvs—lateroventral spine; lvt—lateroventral tube; lvss—lateroventral sensory spot; mlss—midlateral sensory spot; mds—middorsal spine; pds—paradorsal spine; pdgco1—paradorsal glandular cell outlet type 1; pe—penile spine; pvgo1—paraventral glandular cell outlet type 1; sdgco1—subdorsal glandular cell outlet type 1; sds—subdorsal spine; sdss—subdorsal sensory spot; vls—ventrolateral spine; vlss—ventrolateral sensory spot.

TABLE 3. Measurements (μm) from light microscopy for female holotype of *Dracoderes chaac* sp. nov. Abbreviations are followed by segment number. LA–lateral accessory; LTS–lateral terminal spine; LV–lateroventral; MD–middorsal; PD–paradorsal; S–segment lengths; SD–subdorsal; SW–sternal widths; TL–trunk length; VL–ventrolateral. Refer to Figure 4 for structure location.

Trunk and segments	Sternal widths	Dorsal spines	Lateral spines
TL	273		
S1	57	MD1 54	VL1 50
S2	37	SW2 75	PD2 55
S3	36	SW3 83	SD3 62
S4	36	SW4 90	SD4 67
S5	36	SW5 91	SD5 63
S6	36	SW6 91	SD6 64
S7	36	SW7 88	SD7 66
S8	38	SW8 83	SD8 64
S9	38	SW9 75	SD9 68
S10	39	SW10 68	
S11	39	SW11 63	LTS 364
			LTS/TL 133.3%

undetectable in SEM, which is why the sensory spot mapping most likely is incomplete.

Segment 1 with middorsal and ventrolateral acicular spines (Figures 4A–B, 5B–C, 6B, F). Acicular spines on this and following 9 segments are very slender, and show conspicuous subcuticular structures around their attachment sites. All spines (except for the lateral terminal ones) show a subcuticular con-

striction at their attachment point, which could suggest that the spines break off easily. Proximal to this attachment point they show a double, anchor-like structure; the exact structure of this anchor differs, depending on the position of the spines, but for those on segment 1 it is a crescentic structure, with the tips of the crescent pointing in an anterior direction (Figure 5B–C). Rounded glandular cell outlets type 1, only visible with LM, are present in paradorsal and ventromedial positions (Figures 4A–B, 5B). Sensory spots are present in subdorsal, laterodorsal, lateroventral and ventromedial positions; sensory spots appear in LM as small V-shaped intracuticular markings (Figure 5B–C), which are distinct in segment 1 but much more indistinct on the following segments. In SEM the sensory spots appear as very minute depressions with a few hairs but no well-defined papillae (Figure 6B), and except for the ventromedial sensory spots on segment 1 it was not possible to observe any other sensory spots with SEM. Long, slender cuticular hairs are scattered around the segment without showing any distinct pattern. The posterior segment margin is nearly straight, and terminates into a finely serrated pectinate fringe, with well-spaced slender fringe tips (Figure 6B).

Segment 2 with an unpaired dorsal acicular spine laterally displaced to paradorsal position, paired lateroventral acicular spines, and paired lateral accessory tubes (Figures 4A–B, 5B–C, 6B, F). Subcuticular anchor-like structure of paradorsal spine crescentic as for spines on preceding segment; similar anchor-like structures present for spines in dorsal series on all following segments. Subcuticular anchor-like structures of lateroventral spines form 2, thin projections, with one pointing in an anterolateral direction and one in a posteroventral direction (see inset in Figure 5E for similar anchor-like structures on segments 8 and 9); similar anchor-like structures

TABLE 4. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Dracoderes chaac* sp. nov. LA–lateral accessory; LD–Laterodorsal; LV–lateroventral; MD–middorsal; ML–midlateral; PD–paradorsal; PV–paraventral; SD–subdorsal; VL–ventrolateral; VM–ventromedial; ac–acicular spine; gco1/2–glandular cell outlet type 1/2; lts–lateral terminal spine; pe–penile spines; ss–sensory spot; tu–tube; (σ)–male condition of sexually dimorphic character; * marks unpaired structures.

Position Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM	PV
1	ac*	gco1, ss*	ss	ss			ss	ac	ss, gco1	
2		gco1, ac	ss*			tu	ac			gco1
3		gco1*	ss*, ss*, gco1*, ac*		ss		ac			gco1
4		gco1*	ss*, ss*, gco1*, ac*		ss		ac			gco1
5		gco1*	gco1*, ac*		ss	ac	tu			gco1
6		gco1*	gco1*, ac*		ss		ac			gco1
7		gco1*	gco1*, ac*				ac			gco1
8		gco1*	ss*, gco1*, ac*	ss*			ac	ss		gco1
9		gco1*	ss, gco1*, ac*				ac	ss		gco1
10		gco1*	gco1*				gco2	ss		gco1
11			ss, ss			2xpe (σ)	lts			

present for spines in lateral series on the following 7 segments. The lateral accessory tube is simple, without any distinct differentiations (Figure 6F). Paired glandular cell outlets type 1 present in paradorsal and paraventral positions. Most sensory spots in the dorsal series of this and the following segments appear asymmetrical in their position, likely as an adjustment following the lateral displacement of the dorsal spine, i.e., an

unpaired paradorsal sensory spot occurs in the side opposite to the paradorsal spine, and another unpaired subdorsal sensory spot occurs near the base of this spine (Figure 4A). Thin cuticular hairs arranged in 2 rows that extend around the segment from middorsal to midventral; hairs in the posterior row are longer than those in the anterior. Posterior segment margin as on preceding segment.

Segment 3 with an unpaired dorsal acicular spine being even more laterally displaced to a subdorsal position (on the opposite side of the spine from the preceding segment), and paired lateroventral acicular spines (Figures 4A–B, 5B–C, 6B, F); subcuticular anchor-like structures as described for preceding segment. From this segment and onwards also the glandular cell outlets type 1 of the dorsal series start appearing asymmetrically in their positioning, i.e., an unpaired paradorsal outlet occurs in the side opposite to the subdorsal spine, and another unpaired

FIGURE 5. Light micrographs of female holotype of *Dracoderes chaac* sp. nov., NHMD-915291. A. Dorsal overview. B. Segments 1 to 4, dorsal view. C. Segments 1 to 4, ventral view. D. Segments 5 to 9, dorsal view. E. Segments 5 to 9, ventral view; inset shows subcuticular anchors for lateroventral spines on segments 8 and 9. F. Segments 9 to 11, dorsal view. G. Segments 9 to 11, ventral view; inset shows close-up of lateroventral glandular cell outlet type 2 on segment 10. Abbreviations: las—lateral accessory spine; lat—lateral accessory tube; ldss—laterodorsal sensory spot; lts—lateral terminal spine; lvco2—lateroventral glandular cell outlet type 2; lvs—lateroventral spine; lvt—lateroventral tube; lvss—lateroventral sensory spot; mds—middorsal spine; pds—paradorsal spine; pdgco—paradorsal glandular cell outlet type 1; pvgco—paraventral glandular cell outlet type 1; sdgco—subdorsal glandular cell outlet type 1; sds—subdorsal spine; sdss—subdorsal sensory spot; vls—ventrolateral spine; vlss—ventrolateral sensory spot; vmss—ventromedial sensory spot.

FIGURE 6. Scanning electron micrographs of male *Dracoderes chaac* sp. nov. A. Ventrolateral overview. B. Segments 1 to 3, lateroventral view; inset shows close-up of ventromedial sensory spot on segment 1, scale bar: 5 µm. C. Segments 4 to 6, ventrolateral view. D. Segments 6 to 8, ventrolateral view. E. Segments 8 to 9, ventrolateral view. F. Detail showing attachment of lateral accessory to ventromedial appendages on segments 1 to 3. G. Detail showing attachment of lateral accessory to lateroventral appendages on segments 5 to 7. H. Detail showing lateral structures on segments 10 and 11. Abbreviations: las—lateral accessory spine; lat—lateral accessory tube; lts—lateral terminal spine; lvgco2—lateroventral glandular cell outlet type 2; lvs—lateroventral spine; lvt—lateroventral tube; pe—penile spine; vls—ventrolateral spine; vmss—ventromedial sensory spot.

subdorsal outlet occurs near the base of this spine (Figure 4A); additional paired glandular cell outlets type 1 present in paraventral positions. Sensory spots are present in subdorsal positions on both halves of the tergal plate, but they still appear asymmetrical as the sensory spot in the same side as the spine is more lateral than the one in the other side (Figure 4A); additional paired and symmetrically arranged sensory spots present in midlateral positions. Cuticular hairs and posterior segment margin as on preceding segment.

Segment 4 with an unpaired dorsal acicular spine in subdorsal position (on the opposite side of the spine from the preceding segment), and paired lateroventral acicular spines (Figures

4A–B, 5B–C, 6C); subcuticular anchor-like structures as described for preceding segment. Glandular cell outlets type 1 and sensory spots as on preceding segment, but with positions of asymmetrical structures switched to opposite sides, following the position of the subdorsal spine (Figure 4A). Cuticular hairs and posterior segment margin as on preceding segment.

Segment 5 with an unpaired dorsal acicular spine in subdorsal position (on the opposite side of the spine from the preceding segment), paired lateroventral tubes and paired lateral accessory acicular spines (Figures 4A–B, 5D–E, 6C, G); tubes simple, and subcuticular anchor-like structures of spines as described for preceding segment. Glandular cell outlets type

1 as on preceding segment, but with positions of asymmetrical structures switched to opposite sides, following the position of the subdorsal spine. Sensory spots only observed in midlateral positions, but more undetected ones might be present. Cuticular hairs and posterior segment margin as on preceding segment.

Segment 6 with an unpaired dorsal acicular spine in subdorsal position (on the opposite side of the spine from the preceding segment), and paired lateroventral acicular spines (Figures 4A–B, 5D–E, 6C–D, G); subcuticular anchor-like structures as described for preceding segment. Glandular cell outlets type 1 as on preceding segment, but with positions of asymmetrical structures switched to opposite sides, following the position of the subdorsal spine. Sensory spots, cuticular hairs and posterior segment margin otherwise as on preceding segment.

Segment 7 as preceding segment (although with dorsal structures switched to the opposite side) (Figures 4A–B, 5D–E, 6D, G), except for the midlateral sensory spots that are absent.

Segment 8 with an unpaired dorsal acicular spine in subdorsal position (on the opposite side of the spine from the preceding segment), and paired lateroventral acicular spines (Figures 4A–B, 5D–E, 6E); subcuticular anchor-like structures as described for preceding segment. Glandular cell outlets type 1 as on preceding segment, but with positions of asymmetrical structures switched to opposite sides, following the position of the subdorsal spine. Unpaired sensory spots present in subdorsal position (same side as spine) and laterodorsal position (opposite side of spine), and as a paired set in ventrolateral positions (Figures 4A–B, 5E). Cuticular hairs and posterior segment margin as on preceding segment.

Segment 9 with an unpaired dorsal acicular spine in subdorsal position (on the opposite side of the spine from the preceding segment), and paired lateroventral acicular spines (Figures 4A–B, 5D–G, 6E); subcuticular anchor-like structures as described for preceding segment. Glandular cell outlets type 1 as on preceding segment, but with positions of asymmetrical structures switched to opposite sides, following the position of the subdorsal spine (Figure 5D–G). Nearly symmetrical sensory spots present in subdorsal positions, and perfectly paired ones in ventrolateral positions (Figure 5E, G).

Segment 10 without spines, but with large, rounded glandular cell outlets type 2 in lateroventral positions (Figures 4B–C, 5G, 6H). Glandular cell outlets type 1 as on preceding segment, and without having the positions switched to opposite sides (Figure 5F–G). Sensory spots only observed in ventrolateral positions (Figure 5G).

Segment 11 with long lateral terminal spines, exceeding the length of the trunk (Figures 4, 5A, F–G, 6A, H). Males with 2 pairs of short, thin, fringed and flexible penile spines in lateral accessory positions (Figures 4C, 6H); females without any distinct secondary sexual characters. Glandular cell outlets not present. Sensory spots present as 2 subdorsal pairs: one pair medially on tergal plate and one pair at the tips of the tergal extensions (Figures 4A, 5F). Tergal extensions triangular with fringed, pointed tips (Figures 5F–G, 6H). Cuticular hairs absent.

DISCUSSION

Diversity of Kinorhynchs

This study focused on the diversity of non–echinoderid kinorhynchs from 24 collection stations in the sGOM. The species with the widest distribution was *S. aspidochelone*, recovered from 14 stations, and is known to have a distribution range of >700 km in the nGOM from Louisiana to Florida (Landers et al. 2018, Sørensen and Landers 2018). Another relatively common species, *Campyloderes vanhoeffeni*, was collected at 7 stations. This species is known to have a worldwide distribution, though it is not resolved whether *Campyloderes* is represented by one worldwide species or many subspecies with infraspecific variation (Neuhaus and Sørensen 2013). One rare species, *Semnoderes lusca*, with a known distribution range restricted to 2 nGOM locations (Sørensen and Landers 2018) was recovered from 7 additional stations in our study. Species of *Dracoderes*, here represented by the new species *D. chaac* sp. nov., have never previously been recovered from the GOM, but are now reported from 3 locations in Mexican waters at depths of 200, 518 and 1,533 m.

Notes on diagnostic features of *Dracoderes chaac* sp. nov.

The segment composition and the laterally displaced dorsal spines easily identify the new species as a congener of *Dracoderes*. The genus currently accommodates 7 additional species, but only one of them, *Dracoderes toyoshioae* Yamasaki, 2015, can be confused with the new species. The 6 other species are all characterized by having segment 1 completely devoid of spines, and dorsal spines on the following segments only alternating between the paradorsal positions (Higgins and Shirayama 1990, Adrianov and Malakhov 1999, Sørensen et al. 2012, Thomsen et al. 2013, Yamasaki 2015, Cepeda et al. 2019b). Instead, *D. toyoshioae* and *D. chaac* sp. nov. both have middorsal and ventrolateral spines on segment 1, and the lateral displacement of dorsal spines on the following segments is more extreme. In his description of *D. toyoshioae*, Yamasaki (2015) refers to the dorsal spines of segments 2 to 9 as paradorsal, but at the same time the provided image documentation of the species shows that the lateral displacement gradually gets more extreme from segment 4 and on, and it would be fair to argue that its dorsal spines on the more posterior segments are subdorsal. This was also confirmed by the re-examination of the holotype of *D. toyoshioae*. The same extremely lateral displacement of dorsal spines can be observed in *D. chaac* sp. nov., and this trait, together with the spines on segment 1, easily discriminate *D. chaac* sp. nov. and *D. toyoshioae* from other congeners. In fact, the differences are so distinct that it might be worth to explore in future studies if the 2 species could be relocated from *Dracoderes* and united in a new genus under Dracoderidae. Another trait that potentially separates *D. chaac* sp. nov. and *D. toyoshioae* from other *Dracoderes* species regards the secondary sexual characters in males. Males of other *Dracoderes* species have 3 sets of prominent penile spines, and especially the penile spines of the dorsal pair are thick and long, extending well beyond the terminal segment (Adrianov and Malakhov 1999, Sørensen et al. 2012, Thomsen et al. 2013, Yamasaki 2015, Cepeda et al. 2019b). This is very different from the situation in *D. chaac*

sp. nov. that only has two pairs of minute, fringy penile spines (Figure 6H). Unfortunately, only female morphology is known for *D. toyoshioae*, but if their males turn out also to have similar, small penile spines, this would support the designation of *D. chaac* sp. nov. and *D. toyoshioae* to a new genus.

The two close congeners, *D. chaac* sp. nov. and *D. toyoshioae* can be distinguished by the tube patterns in their lateral series. Unfortunately, Yamasaki (2015) had only a single specimen available for the description of *D. toyoshioae*, and most of the spines and many tubes were broken off the specimen. Thus, the described spine/tube patterns of the species were based on assumptions, deducted from the occurrence of cuticular scars interpreted as spine or tube attachment sites. However, we agree with Yamasaki's (2015) suggested spine/tube patterns, and reinvestigation of the holotype confirmed this. In addition to the actual spine attachment sites, we also noted crescentic anchor-like structures for the dorsal and ventrolateral spines, as well as the posteroventral anchor-like projection for the lateroventral spines. Such anchor-like intracuticular structures are also associated with the spines of *D. chaac* sp. nov. Thus, trusting that we can use the presence of larger cuticular scars and posteroventral anchor-like projections in the lateral series as indication of acicular spines, and the smaller scars without anchor structures as tube indications, the spine pattern in *D. toyoshioae* will be the same as in *D. chaac* sp. nov., whereas the tube pattern would differ. *Dracoderes toyoshioae* appears to have lateral accessory tubes on segments 2 to 8 (except on segment 5, which has lateroventral tubes), different from *D. chaac* sp. nov. that only has tubes on segments 2 and 5. It remains unclear whether the 2 species differ in regards to the presence or absence of glandular cell outlets on segment 10. *Dracoderes toyoshioae* has lateroventral intracuticular markings that indicate the presence of structures in these positions, but their nature remains uncertain. Yamasaki (2015) reports it as potential spines or tubes, but the absence of anchor-like structures suggests no presence of spines. Based on the single available specimen of *D. toyoshioae* it is impossible to determine whether these markings are tubes or glandular cell outlets type 2. But despite this uncertainty, the 2 species are easily distinguished by the presence/absence of lateral accessory tubes on segments 3, 4 and 6 to 8.

Summary of known Kinorhynch species and their distributions

Notably, this survey recovered species known from distant locations, such as *Condyloderes flosfimbriatus* and *C. rohalorum*, known from the nGOM but also from deep locations off the California coast (Sørensen et al. 2019). All of the remaining known species recovered in this survey are known from the nGOM with the exception of *Cristaphyes panamensis*, described from the Caribbean coast of Panama (Pardos et al. 2016a), and *Dracoderes chaac* sp. nov.

Antygomonas gwenae Herranz, Sánchez, Pardos, & Higgins 2014

Five specimens were recovered from station 20 at a depth of 421 m. This species has been previously described from the Atlantic Ocean near Fort Pierce, FL at a depth of 140 m (Herranz et al. 2014). It has since been recovered from one location on

the nGOM continental shelf of Louisiana, at a depth of 37 m (Sørensen and Landers 2018, Landers et al. 2019). The current study extends the depth range of this species.

Campyloderes vanhoeffeni Zelinka, 1913

Twenty-one specimens were recovered from 7 stations, with depths ranging from 190–1,522 m. This cosmopolitan species is known from locations across the globe, in the Atlantic, Pacific, Indian, and Southern Oceans (Neuhaus 2004, Neuhaus and Sørensen 2013). Two locations in the nGOM are reported to have this species, at 344 m and 1,386 m depths (Neuhaus and Sørensen 2013).

Centroderes readae Neuhaus, Pardos, Sørensen & Higgins, 2014

Eleven specimens were recovered from 6 stations, with depths ranging from 190–2,043 m. This species was described from the Florida coast near Ft. Pierce (140 m depth). Other reported locations are near Fort Pierce at other depths (131–135 m), Buzzards Bay MA (3–9 m depths), North Atlantic, NJ (72–78 m depths), Bonn Bay, Newfoundland, Canada (16–30 m depths; Neuhaus et al. 2014). Additionally, the species is known from 3 locations in the nGOM (91–126 m depths, Landers et al. 2018). The specimens collected in the current study extends the known depth range of this species.

Condyloderes flosfimbriatus Sørensen, Thistle & Landers 2019

Fourteen specimens were recovered from 6 stations with a depth range of 190–953 m. This species was described from the nGOM off the Florida panhandle at a depth of 163 m (Sørensen et al. 2019). It was also reported from 4 additional nGOM stations from the Florida and Louisiana coasts that had a depth range of 88–125 m. Additionally, this species is known from 2 locations on the US West Coast off of northern California (2,719 m and 2,733 m depths; Sørensen et al. 2019).

Condyloderes rohalorum Sørensen, Thistle & Landers 2019

Six specimens were recovered from one station (20) with a depth of 421 m. This species was described from the US West Coast off northern California (2,733 depth m; Sørensen et al. 2019). Other locations where this species has been found included a separate California site (2,719 m depth) and 3 locations in the nGOM on the Florida and Louisiana shelf with a depth range of 97–163 m (Sørensen et al. 2019).

Cristaphyes panamensis Pardos, Sánchez & Herranz 2016

Three specimens were recovered from 2 stations, with depths of 50 and 51 m. This species was described from the Caribbean coast of Panama at depth of 10 m (Pardos et al. 2016a). The current study extends the depth range of this species.

Dracoderes chaac sp. nov.

Three specimens, described in the current article, were recovered from 3 locations in the sGOM with depths of 1,533 m, 518 m, and 200 m. The distribution of the animals spanned 497 km and they were located in all 3 depth zones sampled. This is the first report of this genus in the GOM.

Leiocanthus corrugatus (Higgins 1983) Sánchez, Yamasaki, Pardos, Sørensen and Martinez, 2016

Seven specimens were recovered from 2 stations, with depths of 50 and 51 m. This species was described from Carrie Bow Cay, Belize, at a depth of 1–2 m (Higgins 1983) and later

assigned to the genus *Leiocanthus* (Sánchez et al. 2016). It was reported from the Caribbean coast of Panama at one location at a depth of 12 m (Pardos et al. 2016a) and has been recovered from one location on the Louisiana continental shelf in the nGOM at a depth of 32 m (Landers et al. 2019). The current study extends the depth range of this species.

Leiocanthus langi (Higgins, 1964) Sánchez, Yamasaki, Pardos, Sørensen and Martínez, 2016

Fifteen specimens were recovered from 3 stations, with a depth range of 21–51 m. This species was originally described as *Trachydemus langi*, and collected from the Newport River estuary in NC at a depth of about 1 m (Higgins 1964). It was later assigned to the genus *Leiocanthus* (Sánchez et al. 2016). The species *L. fimbriatus* (described as *Kinorhynchus fimbriatus* (Higgins, 1982) by Higgins (1982)) was later synonymized with *L. langi* (Sánchez et al. 2019), thus adding Castle Harbor, Bermuda, to the *L. langi* distribution. In the nGOM, *L. langi* has been reported from 24 locations on the shelf and Louisiana/Alabama coast, with a depth range of 0.5–83 m (Hoffman et al. 2021, Landers et al. 2019, 2020, Sánchez et al. 2019).

Leiocanthus quinquenudus Cepeda et al. 2022

Three specimens were recovered from station 14 at a depth of 50 m. This species was reported as *Leiocanthus* sp. 2 from 3 locations on the nGOM Alabama coast at depths of 16 and 18 m, and is known from a third location on the nGOM Louisiana coast at a depth of 52 m (Hoffman et al. 2021; Landers et al. 2020). The 3 specimens collected from this study were reported in the new species description of *L. quinquenudus* (Cepeda et al. 2022).

Leiocanthus satanicus Cepeda et al. 2022

Three specimens were recovered from 2 stations, with depths of 50 and 51 m. This species was reported from 7 locations on the nGOM Louisiana continental shelf with a depth range of 32–85 m (Landers et al. 2018 reported as *Pycnophyes* A, Landers et al. 2019 reported as *Leiocanthus* W). The 3 specimens collected from this study were reported in the recent species description of *L. satanicus* (Cepeda et al. 2022).

Undescribed *Leiocanthus* sp.

Three undescribed species of the genus were collected dur-

ing this study. Two specimens of *Leiocanthus* “species 3” were recovered from station 24 (391 m), and one specimen each of “species 4 and species 5” was recovered from stations 22 (1,647 m), and 20 (421 m), respectively. The genus was created in 2016 (Sánchez et al. 2016).

Mixtophyes “species 1”

One specimen of the undescribed species was recovered from station 23 at a depth of 2,173 m. The genus was described from the Guinea Basin deep-sea at a depth exceeding 5000 m (Sánchez et al. 2014).

Paracentrophyes “species 1”

One specimen from this genus was recovered from station 2 at a depth of 953 m. The genus was established by Higgins (1983) from specimens collected in Belize at shallow depths (3 m).

Pycnophyes alexandroi Pardos, Sánchez & Herranz 2016

Four specimens were recovered from 3 stations, with a depth range of 16–51 m. This species was described from the Caribbean and Pacific coast of Panama at 2 locations, at depths of 1–2 m (Pardos et al. 2016a, 2016b). This species was also reported from 2 locations on the nGOM Alabama and Louisiana shelf at depths of 20 and 32 m, respectively (Landers et al. 2019; Hoffman et al. 2021).

Semnoderes lusca Sørensen and Landers 2018

Nine specimens were recovered from 7 stations, with a depth range of 190–2,173 m, much deeper waters than previous reports. This species was described from the nGOM on the Louisiana shelf at a depth of 77 m. Two other locations in that description on the Alabama and Florida shelf had depths of 50 and 98 m, respectively (Sørensen and Landers 2018).

Sphenoderes aspidochelone Sørensen and Landers 2018

Twenty-six specimens were collected from 14 stations, with depths ranging from 190–3,214 m. This species was described from the nGOM Florida continental shelf at a depth of 125 m. Additional records from the same report include 11 stations on the Louisiana–Alabama–Florida shelf at depths ranging from 88–377 m (Sørensen and Landers 2018) and at a single location with a depth of 6 m in Mobile Bay (Hoffman et al. 2021). The current study extends the depth range of this species.

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