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ORIGINAL PAPER

Intertidal and shallow subtidal marine tardigrades from the British Virgin Islands with a description of a new *Batillipes* (Heterotardigrada: Batillipedidae)

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Abstract

This is the first survey of marine tardigrades from the British Virgin Islands, though two species were previously reported from St. Croix, U.S. Virgin Islands. In June 2016, we collected subtidal and intertidal sand samples from various locations throughout the British Virgin Islands. We found 602 tardigrades in 18 of 21 samples, and these included 12 taxa, one of which, *Batillipes wyedeleinorum* sp. nov., is new to science and described here. We compared abundance and species diversity in intertidal and subtidal samples and found significantly greater abundance in intertidal habitats but no significant difference in the number of observed species between the two habitats. We calculated Chao 1 species richness, which indicated higher estimated richness in intertidal habitats and 15 ± 3.7 species ($\bar{x} \pm$ SD) in both habitats combined. Non-metric Multidimensional Scaling revealed differences in species composition between the two habitats with some species showing clear preferences for one or the other.

Keywords *Batillipes wyedeleinorum* sp. nov. · Caribbean Sea · Community ecology · Meiofauna · Tardigrada · Water bears

Introduction

Meiofauna is the vast assemblage of hidden but ubiquitous microscopic animals occurring in virtually all marine benthic communities. They are an important component of marine trophic webs with more than 75% of their production being consumed by higher trophic levels (Danovaro et al. 2007), and they provide numerous ecosystem services including sediment structuring (Schratzberger and Ingels 2018). Relative abundance and diversity of meiofauna can be bioindicators of anthropogenic change (Zeppilli et al. 2015). Meiofauna communities are still poorly understood, however, and some taxonomic groups such as tardigrades are especially understudied.

Members of the phylum Tardigrada, commonly known as water bears, have five body segments, four pairs of lobopodous legs, paired eversible stylets as part of the feeding mechanism, and a cuticle requiring moulting for growth. Like most meiofauna, they have no planktonic dispersal stage. They are part of the Panarthropoda Nielsen, 1995 within Superphylum Ecdysozoa Aguinaldo et al., 1997. Tardigrades are well known for their extreme survival ability via cryptobiosis; however, only a small handful of marine tardigrades

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are known to possess this capability (see “Discussion” for further information). Hygum et al. (2016) suggest that cryptobiosis may have evolved in marine intertidal habitats, and the marine genus *Coronarctus* is thought to conserve the most plesiomorphic characters and occupy a basal position at least among heterotardigrades (Kihm et al. 2023). Thus, marine tardigrades warrant further investigation for both ecological and evolutionary considerations.

Approximately 1400 species of tardigrades are currently known, but only 260 species and subspecies are marine (Bartels et al. 2015a; Guidetti and Bertolani 2005; Degma and Guidetti 2019-2023) though many more remain to be discovered and many areas of the world have not been surveyed (Kaczmarek et al. 2015; Bartels et al. 2015a). Bartels et al. (2016) estimated the number of marine tardigrades remaining to be discovered, and their model indicated that the number of marine tardigrades may eventually rival the number of terrestrial tardigrades. There have been no previous collections in the British Virgin Islands (BVI), although Pollock (1982, 1983) reported *Orzeliscus belopus* du Bois-Reymond Marcus, 1952, and a newly described species, *Styraconyx craticulus* Pollock, 1983, from St. Croix, U.S. Virgin Islands.

Here we report findings from a survey of intertidal and shallow subtidal sand in the British Virgin Islands, and we compare tardigrade abundance, diversity, estimated species richness, and species composition between the two habitats. We also describe a new *Batillipes* species.

Material and methods

Collections were made by the lead author from 31 May to 12 June 2016. Specific sites and site characteristics are shown in Table 1, and a map of localities is provided in Fig. 1.

Samples were collected by scooping sand into 250 ml wide-mouth Nalgene jars using a small trowel on the beach or by hand while snorkelling for the subtidal samples. For most collecting sites, a sample was collected at mid-tide level on the beach and another nearby well below low tide level (1–2 m bsl). To extract the tardigrades, sand was treated with the freshwater shock method (Kristensen and Higgins 1984a). The sand was placed in a 1-L Erlenmeyer flask with freshwater for 1 min, agitated, and quickly decanted onto a 45 µm sieve. This was repeated twice more. Samples were preserved in a 4% buffered formaldehyde solution and transported to the lab at Warren Wilson College. We were unable to preserve specimens with any technique other than formalin, so DNA analysis was not possible. In the lab, tardigrades were sorted with a dissecting microscope. Specimens were transferred to microslides, mounted in polyvinyl alcohol or glycerine, and cover slips were sealed with nail polish.

Tardigrades were examined, measured (all measurements in micrometres — µm) and microphotographed under 1000× oil immersion, with a Zeiss Phase Contrast (PhC) microscope and a Zeiss Axioimager 2 Differential Interference Contrast Microscope (DIC), both equipped with digital cameras and Zen Imaging Software (Zeiss), an Olympus BX41 PhC microscope, or an Olympus BX60 PhC/DIC/FL microscope with Jenoptiks digital camera and Gryphax software. When symmetrical structures were measured, the larger value was recorded if different values were obtained. Identifications were based on Fontoura et al. (2017), Hansen and Kristensen (2020) and original species descriptions in the literature as cited in taxonomic accounts below. Generic abbreviations follow the recommendations in Perry et al. (2019).

In total, we sampled 11 localities, and at 10 of those we collected an intertidal sample and a nearby shallow subtidal sample, allowing a paired comparison of abundance, diversity, and community composition. Species counts are complicated by the florarctids, the most abundant group in our collection, a large number of which could not be identified beyond subfamily. Since these were such a dominant member of the community, we did not want to exclude them. For the purpose of these analyses, we chose to handle this by repeating the analyses twice. First, we treated the unidentified florarctids as a separate species, and in the second analysis, we lumped them together with *Florarctus yucatanensis* since these are likely to be the predominant species. We counted abundance and observed species (Sobs) for each sample, then compared them with a Wilcoxon matched-pairs signed rank test. Using both approaches for the florarctids, we also compared Chao1 species richness estimates (following the recommendation by Foggo et al. 2003) and used Nonmetric Multi-Dimensional Scaling (NMDS) and PERMANOVA to analyze the differences in species composition. For the paired Wilcoxon test, sample 3 was omitted since there was no matched intertidal sample. The software application PRISM 9.0.0 was used for the paired Wilcoxon test; PRIMER 6.1.18 was used to calculate the species richness estimates, NMDS, and PERMANOVA.

Results

Tardigrades were found in 18 of the 21 samples, and a total of 602 tardigrades was identified representing 12 species from 10 genera. Taxa recorded were *Anisonyches diakidius* Pollock, 1975, *Archechiniscus bahamensis* Bartels, Fontoura & Nelson, 2018, *Batillipes wyedeleinorum* sp. nov., *Batillipes pennaki* Marcus, 1946, *Dipodarctus subterraneus* (Renaud-Debyser, 1959), *Dipodarctus borrori* Pollock, 1995, *Florarctus yucatanensis* Anguas-Escalante, de Jesus Navarrete, DeMilio, Pérez-Pech & Hansen, 2020, *Halechiniscus remanei remanei* Schulz, 1955, *Orzeliscus belopus,*

Table 1 Collecting site characteristics. Latitude and longitude in degrees and decimal minutes. Note that sample 18 was excluded from this study because it was taken from floating algae, not sediment, and it yielded no tardigrades

Sample number	Coll. date	Island	Location	Lat/Lon	Zone	Depth (m bsl)	Sediment description
1	30-May-16	Little Jost Van Dyke	Sandy Spit, Green Cay	18°26.987N 64°42.515W	Intertidal	0	Coarse coralligenous sand
2	31-May-16	Little Jost Van Dyke	Sandy Spit, Green Cay	18°26.987N 64°42.515W	Subtidal	2	Coarse coralligenous sand with fine white silt
3	2-Jun-16	Virgin Gorda	Eustatia Reef	18°30.599N 64°20.968W	Subtidal	2	Coarse sand and shell fragments
4	2-Jun-16	Virgin Gorda	Vixen Point, Prickly Pear Island	18°30.147N 64°22.082W	Intertidal	0	Medium coralligenous sand
5	2-Jun-16	Virgin Gorda	Vixen Point, Prickly Pear Island	18°30.147N 64°22.082W	Subtidal	1	Medium coralligenous sand and silt
6	3-Jun-16	Cooper Island	Manchioneel Bay	18°22.813N 64° 30.980W	Subtidal	2	Coarse sand and shell fragments with silt
7	3-Jun-16	Cooper Island	Manchioneel Bay	18°22.813N 64° 30.980W	Intertidal	0	Coarse sand and shell fragments with silt
8	5-Jun-16	Peter Island	Little Harbour	18°21.259N 64°35.937W	Subtidal	1	Medium coralligenous sand with organic fragments
9	5-Jun-16	Peter Island	Little Harbour	18°21.259N 64°35.937W	Intertidal	0	Medium coralligenous sand with gravel
10	6-Jun-16	Norman Island	Privateer Bay	18°18.698N 64°37.425W	Intertidal	0	Coarse coralligenous sand and gravel
11	6-Jun-16	Norman Island	Privateer Bay	18°18.698N 64°37.425W	Subtidal	1	Coarse coralligenous sand and gravel
12	7-Jun-16	Peter Island	Little Harbour	18°21.169N 64°36.166W	Intertidal	0	Coarse coralligenous sand
13	7-Jun-16	Peter Island	Little Harbour	18°21.169N 64°36.166W	Subtidal	1	Coarse coralligenous sand with organic fragments
14	9-Jun-16	Salt Island		18°22.368'N 64°31.913'W	Intertidal	0	Coarse coralligenous sand with shell fragments
15	9-Jun-16	Salt Island		18°22.368'N 64°31.913'W	Subtidal	1	Coarse coralligenous sand with shell fragments
16	10-Jun-16	Great Camanoe Island	Marina Cay	18°27.652N 64°31.562W	Intertidal	0	Medium coralligenous sand with shell fragments
17	10-Jun-16	Great Camanoe Island	Marina Cay	18°27.652N 64°31.562W	Subtidal	2	Medium coralligenous sand with shell fragments and small coral pieces
19	11-Jun-16	Guana Cay	Monkey Point	18°27.925N 64°34.20W	Intertidal	0	Medium coralligenous sand
20	11-Jun-16	Guana Cay	Monkey Point	18°27.925N 64°34.20W	Subtidal	1	Medium coralligenous sand with anoxic layer of black silt
21	12-Jun-16	Jost Van Dyke		18°26.296N 64°43.283W	Intertidal	0	Medium coralligenous sand
22	12-Jun-16	Jost Van Dyke		18°26.296N 64°43.283W	Subtidal	2	Medium coralligenous sand

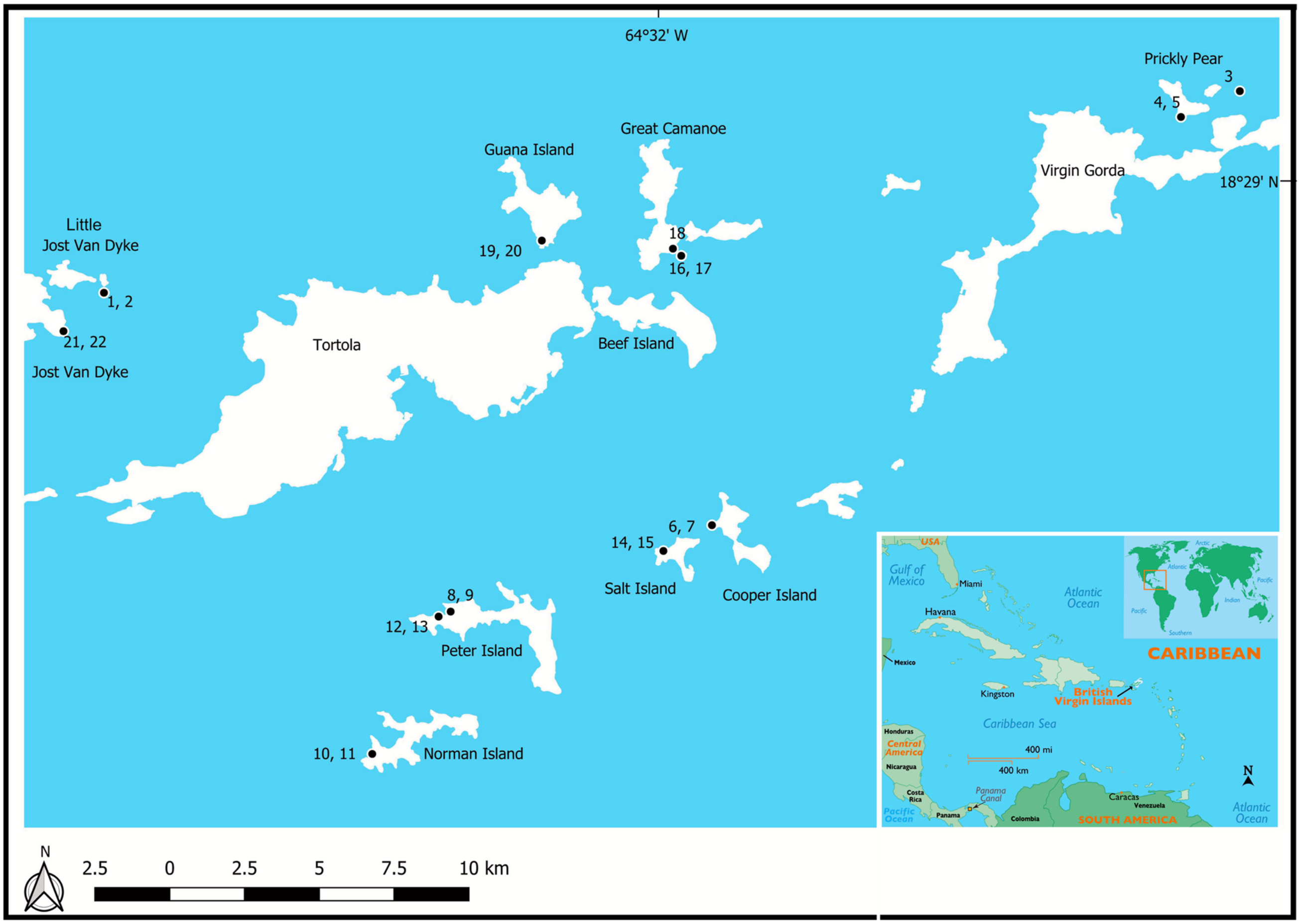

Fig. 1 Map of the British Virgin Islands collecting sites. Numbers correspond to sample numbers in Table 1. White and green = land masses, blue = ocean. Inset indicating larger geographic context adapted from worldatlas.com

Parastygarctus sterreri Renaud-Mornant, 1970, *Styraconyx craticulus,* and *Wingstrandarctus* cf. *intermedius*. Since these are the first reports of marine tardigrades from BVI, all of the species are new records for this country. Summaries of geographic distribution and habitats given in each account are from Kaczmarek et al. 2015 and Bartels et al. 2015a. Raw data for the species counts per sample are available in Online Resource 1.

Taxonomic accounts

Phylum: Tardigrada Doyère, 1840

Class: Heterotardigrada Marcus, 1927

Family: Anisonychidae Møbjerg, Jørgensen & Kristensen, 2019

Genus: *Anisonyches* Pollock, 1975 (amended by Bartels et al. 2018)

***Anisonyches diakidius* Pollock, 1975 (amended by Bartels et al. 2018)**

Voucher images Morphobank P4966:M897158-M897232 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Four specimens, all from intertidal sample 9 (two females and two damaged and gender indeterminant).

Taxonomic remarks: These specimens key to *Ani. diakidius* using the dichotomous key in Bartels et al. 2018, and they exactly match the amended description in Bartels et al. 2018. Identifying traits include the presence of primary clavae, sensory appendages on leg IV only, and details of claw structure including the basal spurs directed horizontally rather than downward.

Biogeographical and ecological comments: There are 14 published records of this species from around the world, including the Bahamas (Bartels et al. 2018) and Guadeloupe Island (Renaud-Mornant and Gourbault 1981, 1984). Ten of the 14 records are from intertidal sediment, and four are from subtidal sediment to a maximum depth of 110 m bsl.

Family: Archechiniscidae Binda, 1978

Genus: *Archechiniscus* Schulz, 1953

***Archechiniscus bahamensis* Bartels, Fontoura & Nelson, 2018**

Voucher images Morphobank P4966:M897237-M897361 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Nine specimens all from subtidal samples 3, 11 and 17 (three females, one male, one two-clawed larva, and four damaged of unknown gender).

Taxonomic remarks: These specimens key to *Arc. bahamensis* using the dichotomous key in Bartels et al. 2018, and they exactly match the description there. Identifying traits include transverse dorso-cuticular folds, T-shaped stylet furcae, bifurcated internal and external cirri tips, and gonopore and seminal receptacle openings located in a depression protected by cuticular platelets.

Biogeographical and ecological comments: There are 10 published records of this species from the Bahamas, Mexico, and the Caribbean coast of Costa Rica (Bartels et al. 2018, Pérez-Pech et al. 2020, Bartels et al. 2021), and all but one of these records are from subtidal samples to a maximum depth of 40 m bsl. This species may be endemic to the Caribbean Basin.

Family: Batillipedidae Ramazzotti, 1962 (amended by Gallo D'Addabbo et al. 2005)
Genus: *Batillipes* Richters, 1909
***Batillipes pennaki* Marcus, 1946**
Voucher images Morphobank P4966:M897410-M897455
https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Three specimens all from intertidal sample 21 (one female, one unknown gender, one four-toed larva).

Taxonomic remarks: A key to the species of *Batillipes* can be found in Santos et al. (2018). Two additional species were described by Bartels et al. (2021) and another one by Vishnudattan et al. (2023). The BVI specimens match all characters for *Bat. pennaki*. Middle toes (3 and 4) on feet of legs IV are equal in length (toe pattern A), primary clavae are divided in two with an obvious constriction, body projections between legs III and IV are lobate, and femur of legs IV are very broad and short.

Biogeographical and ecological comments: This species has been reported broadly from around the world, including Guadeloupe Island (Renaud-Mornant and Gourbault 1981, 1984) in the Caribbean Sea. Of the 145 published records, 120 are from intertidal sediments, the others are subtidal to a maximum depth of 200 m bsl.

***Batillipes wyedeleinorum* sp. nov.**
Figures 2, 3 and 4, Table 2
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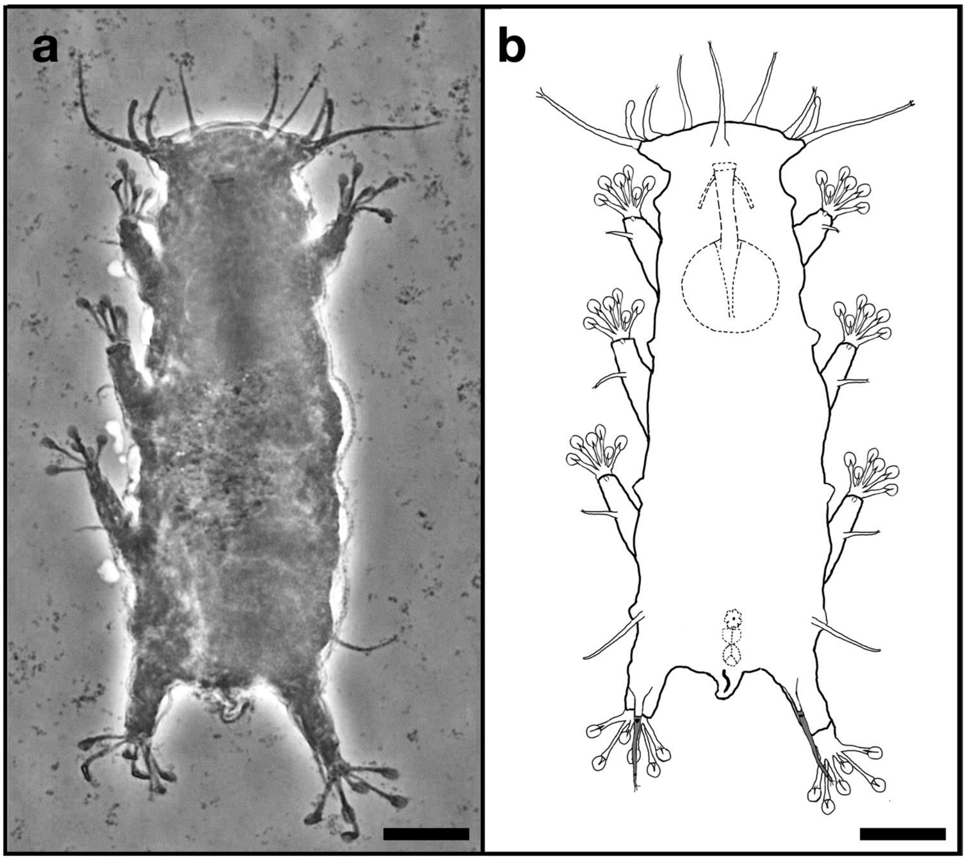

Fig. 2 *Batillipes wyedeleinorum* sp. nov. habitus, holotype. **a** Photo (focus merged and stitched from multiple photographs, PhC); **b** drawing based on holotype with additional input from paratype 16-29 dorsal view with internal buccal apparatus and ventral anus and gonopore indicated with dashed lines. Scale bars = 20 µm

Table 2 Morphometric data for *Batillipes wyedeleinorum* sp. nov. Body projection 1 is anterior to leg I, 2 is between leg I and II, 3 is between leg II and III, and 4 is between leg III and IV. Note: one additional specimen was damaged and not measurable. All measurements in microns. ? = unmeasurable traits

Structures	Holotype 16-19	Paratype 16-29	Paratype 16-30	Paratype 16-22	Paratype 16-31	Paratype 16-32	Specimen 3-1
Gender	F	M	M	?	?	?	F
Body length	108.4	90.1	91.7	63.8	97.0	87.3	97.0
Body width	20.9	18.0	19.6	?	22.5	18.8	20.9
Head width	32.2	31.2	34.4	?	31.7	29.0	32.1
Pharyngeal bulb	18.7 × 21.9	13.8 × 15.5	14.8 × 15.0	?	19.0 × 17.8	16.3 × 14.8	20.0 × 20.7
Median cirrus	20.9	21.7	21.9	16.0	16.2	?	23.8
Internal cirrus	15.6	?	16.2	11.1	12.2	10.9	17.5
External cirrus	11.8	11.4	12.1	9-7	10.9	9.9	14.8
Lateral cirrus A	26.1	23.6	24.8	?	23.2	22.1	28.1
Primary clava	11.5	10.0	10.4	8.8	8.8	8.7	11.8
Cirrus E	14.5	18.8	15.5	?	17.2	11.3	17.6
Leg spine I	5.9	6.1	5.0	?	5.8	5.6	7.3
Leg spine II	6.1	8.2	?	?	6.0	6.3	10.0
Leg spine III	7.4	7.4	8.4	?	7.3	6.4	9.1
Leg IV sensory organ	17.0	16.1	16.7	14.5	14.7	13.7	23.8
Leg IV sensory organ base	6.8	6.7	6.4	6.1	5.1	5.6	9.3
Leg IV sensory organ spine	10.2	9.4	10.3	8.4	9.6	8.1	14.5
Body projection 1	2.4	1.7	2.3	?	2.4	2.1	2.9
Body projection 2	2.2	2.1	2.4	?	2.3	?	3.3
Body projection 3	2.7	3.1	2.9	?	?	2.0	?
Body projection 4	2.4	2.8	2.4	?	2.7	2.0	3.2
Caudal apparatus	5.9	3.1	5.2	2.1	2.4	3.1	5.2
Legs I–III Toe 1	6.7	6.0	?	?	6.2	5.7	6.0
Toe 2	4.2	4.0	?	?	3.5	3.7	3.6
Toe 3	9.2	8.1	?	?	8.1	6.0	9.1
Toe 4	6.5	6.0	?	?	6.1	5.9	7.5
Toe 5	11.2	9.5	?	?	9.0	8.1	12.9
Toe 6	7.8	7.3	?	?	6.4	7.5	7.8
Legs IV Toe 1	10.0	8.3	8.7	?	8.7	8.2	9.7
Toe 2	13.7	12.4	12.7	?	12.4	11.4	15.3
Toe 3	6.7	6.6	6.3	?	4.8	4.6	6.4
Toe 4	9.4	8.9	7.3	?	7.8	6.5	9.5
Toe 5	15.4	12.7	15.4	?	13.4	12.9	17.9
Toe 6	10.5	9.7	10.7	?	9.8	7.9	11.4
Gonopore-anus	6.7	?	?	?	?	?	?

Type material: Seven specimens from intertidal sample 16. Holotype, female (slides 16-19) and six paratypes, two males (slides 16-29, 16-30) and four specimens of unknown gender (slides 16-22, 16-28, 16-31, 16-32). An additional female specimen, not included in the type series, was found in subtidal sample 3 (slide 3-1). We also re-examined Bahamian specimens recorded as *Batillipes* sp. in Bartels et al. 2018, which also belong to the new species.

Type locality: Great Camanoe Island, B.V.I., Caribbean Sea. 18°27.652N, 64°31.562W.

Type depository: Holotype (female, slide 16-19) and one paratype (male, slide 16-29) are deposited at the Department of Animal Taxonomy and Ecology, Faculty of Biology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61-680 Poznań, Poland. The remainder of the paratypes are deposited at the Natural History Museum

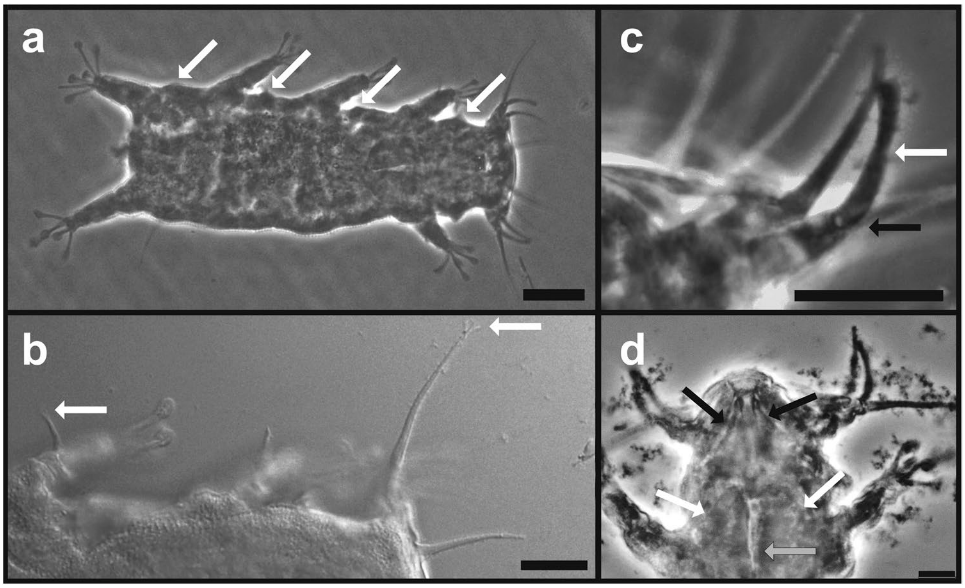

Fig. 3 Taxonomically important traits of *Batillipes wyedeleinorum* sp. nov. **a** Habitus, focused on lateral body projections (white arrows), holotype, PhC; **b** Left anterior dorsum, white arrows = tufts visible on tips of cirrus A and leg II sensory appendage, holotype, DIC; **c** primary clava, ventral view, white arrow = medial constriction, black arrow = van der Land's organ, holotype, PhC; **d** Buccal apparatus, white arrows indicate margins of pharynx, black arrows = stylets, gray arrow = placoid, paratype 16-29, PhC. Scale bars = 20 µm for A, 10 µm for all others

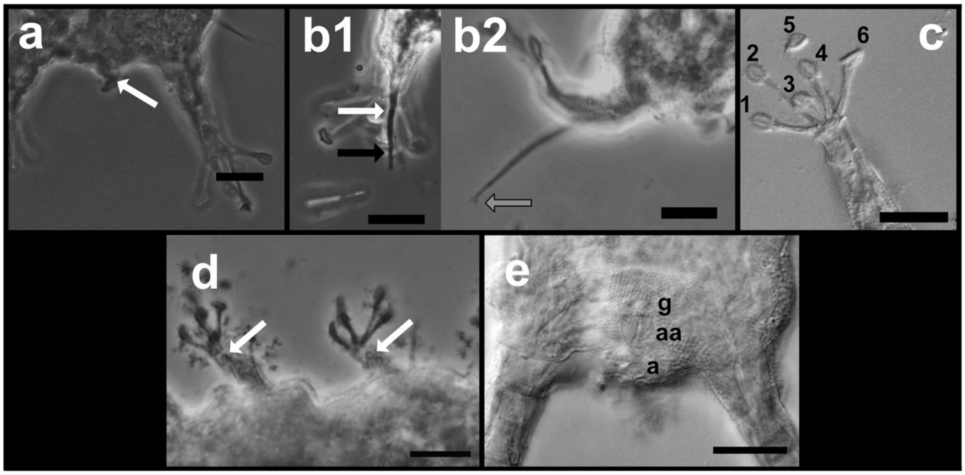

Fig. 4 Additional taxonomically important traits of *Batillipes wyedeleinorum* sp. nov. (**a**) caudal appendage, white arrow = S-shaped thickening, holotype, PhC; (**b1**) sensory appendage leg IV, white arrow = van der Land's organ, black arrow = optically dense point, holotype, PhC; (**b2**) sensory appendage leg IV, gray arrow = frayed tip, paratype 16-29, PhC; (**c**) right claw IV showing toe pattern with toes numbered from exterior to interior, holotype, focus merged, DIC; (**d**) legs I and II, dorsal view, white arrows = papillae, paratype 16-29, PhC; (**e**) posterior ventrum with gonopore (g), anus (a), and apunctate area (aa) between them, holotype, PhC. Scale bars = 10 µm

of Denmark, accession numbers (NHMD-171106, 171107, 171108, 171109, 171110).

Etymology: The specific epithet recognizes the lead author's intrepid field assistants and grandchildren, Wyeth Droege and Madeleine Droege. The combined form of their first names (*wyedeleinorum* = *wye* + *delein* + the Latin masculine plural ending -*orum*) was their creation.

Diagnosis: Batillipes with drumstick-like tubular, undivided, but medially slightly constricted, primary clavae, ending with a swollen tip. Long cephalic cirri with swollen distal tips. A tuft of additional sensory filaments is present on the tip of all cephalic cirri. Sensory spines on all legs. Tuft of additional sensory filaments also present at tip of all leg sensory organs. Cirrus *E* lacking tuft of sensory filaments. A distinct head separated from the body by a neck constriction followed by a short triangular lateral process. Small ventro-lateral body projections between all leg pairs present; triangular shaped with blunt vertices between the first three pairs of legs, roundish between legs III and IV. The caudal apparatus consists of a short triangular cuticular projection with a short longitudinal medial thickening. Dorsal cuticle uniformly granulated constituted by small pillars (*ca.* 1.0 µm high). Ventral cuticle also finely granulated. Toes with oval discs and conspicuous braces. Toe pattern of the fourth foot shows toe 3 shorter than toe 4 (toe 3 being the more cephalically situated), and smaller than the other toes. Rosette-like female gonopore separated from the three-lobed anus by a subtriangular smooth area with a medial groove.

Holotype description: Eyes not observed. Trapezoid head well separated from the body by a neck constriction followed by a triangular lateral process (body projection 1) (Figs. 2 and 3a). Internal cephalic cirri, with small cirrophores, are inserted dorsally on the frontal edge of the head. External cephalic cirri, also with cirrophores, inserted more ventrally, very near the pedestal bearing lateral cirri *A* and primary clavae. Long median cirrus with cirrophore present. Lateral cirrus *A* is located dorsally in relation to the primary clava (Figs. 2 and 3b). These two appendages share a thin common pedestal. A van der Land's organ is present at the base of primary clavae, which is undivided, drumstick-like, medially slightly constricted and exhibiting a swollen tip with a terminal pore (Fig. 3c). A tuft of additional sensory filaments is present on the tip of all cephalic cirri (Fig. 3b); more developed in lateral cirri *A* (sensory filaments ca. 2.0 µm long) and shorter and very hard to see in the other cephalic cirri (about 1.0 µm long). A very small indentation is present in the frontal edge of the head between the external cephalic cirrus and the pedestal with the primary clava and lateral cirrus. Papillary secondary clavae present but barely visible. Ventral mouth opening in a protruded circular structure. Very large, ovoid pharyngeal bulb with placoids (Figs. 2b and 3d). Length of buccal tube (2.8 µm wide) and stylets not discernible after slide mounting (in a paratype 90.1 µm long, the buccal tube is 14.1 µm long and 2.1 µm wide, the placoids about 9.7 µm long and the stylets, with stylet supports, about 17.4 µm).

Small triangular ventro-lateral granulated processes, with blunt apices, between the first three pairs of legs. Between legs III and IV, a small blunt roundish process is present (Figs. 2 and 3a). The caudal apparatus consists of a short triangular dorsal cuticular projection with a short longitudinal medial S-shaped thickening (Figs. 2 and 4a).

Sensory spines with blunt tips present on all legs, increasing in length from leg I to IV (Figs. 2 and 3a, b). A tuft of additional sensory filaments is present on the tip of all sensory organs, very hard to see in sensory organs on legs I–III (Figs. 3b and 4b2). The sensory organ on leg IV divided into a basal portion (6.8 µm long) separated from a distal portion (10.2 µm long) by a van der Land's organ. The tip of the distal portion with tuft of sensory filaments (2.0 µm long) with an optically dense dot (dark when observed under PhC) at the base (Figs. 2b and 4b1). Robust cirrus *E* with a blunt tip lacking tuft of sensory filaments (Figs. 2, 3a and 4a).

Telescopic legs with average-sized toes with the distal stalk not particularly enlarged distally, ovoid suction discs (2.7 × 2.0 µm) and conspicuous braces (Figs. 2 and 4c). On feet of the first three pairs of legs, toe 2 (considering toe 1 the most cephalically situated) is the shortest, almost sessile; toes 3 and 5, both more dorsally implanted, are the longest, especially toe 5, and toes 1, 4, and 6 are medium-sized. On feet of the fourth pair of legs, medial toes 3 and 4 are the shortest and of different lengths, with toe 4 longer than toe 3. Toes 1 and 6 are medium sized; toe 2 and especially toe 5 are the longest (i.e., group B, subgroup B1 in Santos et al. 2018). A very small papilla, difficult to see, is present on the extremity of legs I–III (Figs. 2b and 4d).

Dorsal cuticle uniformly and finely granulated (Fig. 3b), ca. 14 pillars/10 µm (each pillar about 1.0 µm long), without visible metameric folds. Ventrally the cuticle granulation is more delicate.

Rosette-shaped gonopore is separated from the three-lobed anus by a subtriangular smooth area with a medial groove (Figs. 2b and 4e).

Additional remarks: The precise shape of the caudal apparatus is difficult to describe because it exhibits some variability and is covered by detritus; the S-shaped medial thickening observable in the holotype and a paratype is straighter in two other specimens. In one specimen the caudal thickening is not perceptible and it seems doubled in another paratype. Tufts of additional sensory filaments on cephalic cirri and leg sensory spines were barely visible and most easily seen in PhC. Except for lateral cirri *A* and sensory organs on legs IV, the additional filaments are very small and can be easily overlooked. The faint secondary clava is visible in only two specimens. The observation of the very small papillae on the extremity of legs I-III depends on the orientation of the leg itself and is another structure that can be easily overlooked.

Differential diagnosis: In having the medial toes 3 and 4 on feet of the fourth pair of legs of different lengths, with toe 4 longer than toe 3, toes 2 and 5 the longest ones and toes 1 and 6 not shorter than middle toes 3 and 4, the new species exhibits a *Batillipes* toe pattern of the group B, subgroup B1 (Santos et al. 2018). This subgroup comprises nine species. However, only one other *Batillipes* species of this subgroup, *Batillipes similis* Schulz, 1955, shares with *Bat. wyedeleinorum* sp. nov. the presence of undivided, single pointed lateral body projections between all leg pairs. These two very similar species can be distinguished by the presence of tufts of additional filaments on all the cephalic cirri and leg sensory organs in the new species (lacking in *Bat. similis*). Moreover, the two species exhibit different shaped and sized body projections between legs III and IV and caudal apparatuses. The new species has small, sometimes difficult to see, blunt fourth body projections, contrary to the large conical and backward-turned projections typical in *Bat. similis*. Although variable in both species, the caudal apparatus is much smaller in *Bat. wyedeleinorum* sp. nov. than in *Bat. similis* and exhibits a medial thickening often S-shaped (lacking in *Bat. similis*). In addition, contrary to *Bat. similis*, in the new species papillae are present at the distal extreme of legs I-III and cuticular pillars are shorter (ca. 1.0 µm high in the new species, ca. 2.0 µm in *Bat. similis*). Moreover, the basal cuticular ring is present at the tip of the primary clava of *Bat. similis* is not visible in *Bat. wyedeleinorum* sp. nov. On the contrary, primary clavae of the new species have a slight medial constriction. Finally, the two species can also be distinguished by having different gonopore apparatuses: in the new species a smooth (apunctate) subtriangular area with a medial grove separates the rosette-like female gonopore from the anus, while *Bat. similis* lacks this structure.

Among all the 40 known *Batillipes* species (including the new species), the tuft of additional sensory filaments on cephalic cirri is only shared by *Batillipes bullacaudatus* McGinty & Higgins, 1968 and *Batillipes solitarius* Jørgensen, Boesgaard, Møbjerg & Kristensen, 2014. Both species clearly differ from *Bat. wyedeleinorum* sp. nov. in having a different toe pattern on the fourth foot, with the medial toes 3 and 4 equal in length (group A, according to Santos et al. 2018). Contrary to the new species, *Bat. bullacaudatus* lacks lateral body projections between the first three pairs of legs and exhibits a peculiar caudal apparatus consisting of an elongate spine terminating in a hollow bulbous structure. In addition, *Bat. bullacaudatus* and the new species differ in toe morphology (toes with very small circular toe disks, short braces and considerably enlarged distal stalks in *Bat. bullacaudatus*). Frayed tips on external cephalic cirri and sensory organs of legs I–III were not described in *Bat. bullacaudatus*; however, these characters are very difficult to observe and their presence cannot be excluded. As in the new species, *Batillipes* specimens from Florida (Gulf of Mexico) attributed to *Bat. bullacaudatus* by McKirdy (1975) had discrete lateral body projections between all leg pairs and a fourth foot toe pattern of the group B, subgroup B1, and despite having the elongated caudal spike terminating in a bulbous structure, they probably belong to a new unnamed species. Those Florida specimens also differ from *Bat. bullacaudatus senso stricto* and from *Bat. wyedeleinorum* sp. nov. by having the dorsomedial cuticle with smaller granulations than the remaining dorsal and lateral areas and by having nonuniform granulation.

In addition to the different toe patterns above mentioned, *Bat. solitarius* can be distinguished from the new species in having large lens-shaped secondary clavae (indistinct or poorly visible in the new species), an indistinct caudal appendage (versus a triangular projection with a medial thickening often S-shaped in *Bat. wyedeleinorum* sp. nov.) and in lacking tufts on external cephalic cirri and leg sensory organs.

Similar to the new species, another unnamed species from the Gulf of Mexico wrongly identified by McKirdy (1975) as *Batillipes dicrocercus* Pollock, 1970 (see Santos et al. 2018) also has tufts of additional sensory filaments on cephalic cirri and leg IV sensory organs, fourth foot with medial toe 4 longer than toe 3, corresponding to toe arrangement pattern B, subgroup B1, and small dorsal papillae on the extremity of the legs. However, these two species differ in the following characters: (a) dorsal cuticle uniformly granulated in the new species and mid-dorsal cuticle with smaller granulations than cephalic and caudal dorsal areas in the unnamed species; (b) an evident indentation located on the anterior edge of the head, between external cirri and pedestals bearing primary clava and lateral cirrus *A,* is visible in the unnamed species while it is absent or barely visible in *Bat. wyedeleinorum* sp. nov.; c) the caudal apparatus is two-branched in specimens from the Gulf of Mexico and triangular-shaped in specimens of the new species; d) the toes have very small circular toe disks, short braces and considerably enlarged distal stalks in the unnamed species compared to ovoid discs with evident toe braces and relatively thin distal stalks in the new *Batillipes*.

Distribution and ecology: Specimens listed as *Batillipes* sp. in Bartels et al. (2018) match the description of *Bat. wyedeleinorum* sp. nov. in all observable characters. In the Bahamas, they were found in only one subtidal sample (3 m bsl). Thus, this species is now known from only the Bahamas and the British Virgin Islands. In BVI samples it was more abundant in intertidal samples, but it occurs in both habitats.

Family: Halechiniscidae Thulin, 1928 (amended by Fujimoto et al. 2017)

Subfamily: Dipodarctinae Pollock, 1995 (amended by Jørgensen et al. 2014)

Genus: *Dipodarctus* Pollock, 1995 (amended by Jørgensen et al. 2014)

***Dipodarctus borrori* Pollock, 1995**

Voucher images Morphobank P4966:M897515-M897556 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: One specimen from intertidal sample 1 (unknown gender).

Taxonomic remarks: A discussion of identification of the five species of *Dipodarctus* can be found in Bartels et al. 2018. This specimen exactly matches the description of *Dipodarctus borrori* (Pollock, 1995). Key characters are an elongated outermost toe on legs I–III, cuticular bars under shorter toes on legs I–III, and a unique protrusible mouth cone with a large subterminal opening. All characters including the opening for the retractable mouth cone were visible in our specimen.

Biogeographical and ecological comments: This species has only been reported previously six times, from Hawaii, Japan and Italy. Four of those records were intertidal, one was from 20 m bsl, and the other location was not reported. This is the first record of this species from the Caribbean Sea and the Western Atlantic Ocean, representing a significant range extension.

Dipodarctus subterraneus **(Renaud-Debyser, 1959)**
Voucher images Morphobank P4966:M897557-M897599
https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: One specimen from subtidal sample 13 (female).

Taxonomic remarks: The only two characters clearly identifying *Dpo. subterraneus* are a small lateral projection just anterior to leg IV and segmented cephalic cirri. Both of these characters are visible in the BVI specimen.

Biogeographical and ecological comments: This species has been reported broadly from around the world, including the Bahamas and Mexico in the Caribbean Basin (Bartels et al. 2018, Pérez-Pech et al. 2020). Out of 75 published records, 61 were from subtidal samples to a maximum depth of 260 m bsl.

Subfamily: Florarctinae Renaud-Mornant, 1982 (amended by Kristensen 1984 and Hansen and Kristensen 2021)
Genus: *Florarctus* Delamare-Deboutteville & Renaud-Mornant, 1965
Florarctus yucatanensis **Anguas-Escalante, de Jesus-Navarrete, DeMilio, Pérez-Pech & Hansen, 2020**
Voucher images Morphobank P4966:M897800-M897-813
https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Five specimens from intertidal samples 7 and 16 and one from subtidal sample 17 (three females, one male, two of unknown gender and the other unmeasurable). An additional 417 florarctids were found, but they did not do well in the polyvinyl alcohol mounting medium and we can only say that they are members of Subfamily Florarctinae. We also compared the BVI material with "*Florarctus* sp. 1" and "*Florarctus* sp. 2" specimens from the Bahamas (Bartels et al. 2018).

Taxonomic remarks: These specimens match the original description of *Flo. yucatanensis.* The shape of both lateral and caudal caesti are diagnostic.

Biogeographical and ecological comments: Florarctus yucatanensis was described recently from Mexico. The BVI specimens are just the second record of this species, but a re-examination of our samples from the Bahamas revealed that the species we listed as *Florarctus* sp. 1 also belongs to *Flo. yucatanensis.* Thus, this species appears to be endemic to the Caribbean Basin and occurs in both intertidal and subtidal habitats (in BVI it was more abundant in intertidal samples).

Genus: *Wingstrandarctus* Kristensen, 1984
Wingstrandarctus* cf. *intermedius
Voucher images Morphobank P4966:M898322-M898335
https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Three specimens from intertidal samples 9 and 10 and subtidal sample 17 (two males, one unknown gender).

Taxonomic remarks: These specimens have ornamented cuticles and divided alae which clearly contain no caesti, however, other characters are poorly preserved so we cannot make a species level identification. The cuticle is ornamented with large wide caudal alae, most similar to *Wingstrandarctus intermedius* (Renaud-Mornant, 1967) <Amended by Renaud-Mornant 1989>.

Biogeographical and ecological comments: Wingstrandarctus intermedius has been reported widely from around the world but only once from the Atlantic (da Rocha et al. 2009). *Wingstrandarctus corallinus* (Kristensen 1984) is the only species of the genus that has been recorded in the Caribbean Basin (Kristensen 1984, Bartels et al. 2018, Pérez-Pech et al. 2020). For *Win. intermedius,* previous records are fairly evenly divided between subtidal and intertidal habitats (11/18 records from subtidal).

Subfamily: Halechiniscinae Thulin, 1928 (amended by Grimaldi de Zio et al. 1990)
Genus: *Halechiniscus* Richters, 1908 (amended by Grimaldi de Zio et al. 1990)
Halechiniscus remanei remanei **Schulz, 1955**
Voucher images Morphobank P4966:M897829-M897907
https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: There were 133 individuals all from intertidal samples 9, 14, 16, 19, and 21. Of these, 10 individuals were measured (eight females, one male, one with gonopore not visible, all four-toed).

Taxonomic remarks: Body length was 50–98 µm for the measured specimens, considerably smaller than the range of 86–120 µm reported by Schulz (1955). Other than the smaller size, the specimens match the original description. Chang and Rho (2002) provide a key for all species in the genus except for the two most recent species described by Fujimoto (2015). The only species with a caudal protrusion is *Hal. remanei*, which is divided into two subspecies (Renaud-Mornant 1984). The sole character distinguishing the subspecies is the presence of a proximal spine on the cuticular expansion above the P4 sensory structure in *Hal. remanei antillensis* Renaud-Mornant 1984. Our specimens lack this structure.

Biogeographical and ecological comments: This species has been reported broadly from around the world, including Guadeloupe Island (Renaud-Mornant and Gourbault 1981, 1984) in the Caribbean Sea, and both coasts of Costa Rica (Bartels et al. 2021). Of the 75 previously published records, 61 are from intertidal habitats, but they have been found in subtidal sediments to a maximum depth of 150 m.

Subfamily: Orzeliscinae Schulz, 1963 (amended by Gross et al. 2014)

Genus: *Orzeliscus* du Bois-Raymond Marcus, 1952

***Orzeliscus belopus* du Bois-Reymond Marcus, 1952**

Voucher images Morphobank P4966:M897908-M897968 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Five specimens from subtidal sample 8 and three specimens from subtidal sample 22 (four with visible female gonopores). Note that no males have been reported for this species and at least some populations are known to be simultaneous hermaphrodites (Suzuki and Kristensen 2014).

Taxonomic remarks: See Bartels et al. 2018 for a discussion of this genus. Only two species are currently recognized according to Degma & Guidetti (2009–2023). Distinguishing characteristics of *Orz. belopus* according to Lee et al. (2017) include primary clavae that are much broader proximally, then abruptly narrowed at the distal half, cheek region of head not strongly swollen, and lateral projections between legs III and IV lacking or very weak. The BVI specimens match this description. Not all characters are visible on all specimens.

Biogeographical and ecological comments: This species has been broadly reported from around the world including the U.S. Virgin Islands (Pollock 1992), Bermuda (Coull 1970, Renaud-Mornant 1970, Kristensen and Neuhaus 1999, Suzuki and Kristensen 2014), Guadeloupe Islands (Renaud-Mornant and Gourbault 1984), Florida, U.S.A. (Kristensen and Higgins 1989), and South Carolina, U.S.A. (Bartels et al. 2017). Thirty-one of the 57 previously published records are from intertidal sediments, and the maximum depth of subtidal records is 100 m bsl.

Family: Stygarctidae Schulz, 1951 (amended by Hansen et al. 2012)

Subfamily: Stygarctinae Schulz, 1951

Genus: *Parastygarctus* Renaud-Debyser, 1965 (amended by Hansen et al. 2012)

***Parastygarctus sterreri* Renaud-Mornant, 1970**

Voucher images Morphobank P4966:M897969-M898068 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Two specimens from intertidal sample 4 (one female, one male).

Taxonomic remarks: A key to four of the seven species of this genus can be found in Grimaldi de Zio et al. (1987). A fifth species was described by Gallo D'Addabbo et al. (2001), and Hansen et al. (2012) described two additional species. Our specimens match the description of *Pas. sterreri* with four claws per foot, body plates with only one lateral expansion, cephalic plate with straight lateral processes and club-shaped secondary clavae.

Biogeographical and ecological comments: This species has been broadly reported worldwide, including Florida, U.S.A. (Hansen et al. 2012), Guadeloupe Islands (Renaud-Mornant 1984b), Martinique Island (Renaud-Mornant et al. 1983, Renaud-Mornant 1984b) and the Caribbean coast of Costa Rica (Bartels et al. 2021). Forty-seven out of the 63 previously published records have been from subtidal sediments with a maximum depth of 200 m bsl.

Family: Styraconyxidae Kristensen & Renaud-Mornant, 1983 (elevated to family level and amended by Fujimoto et al. 2017)

Genus: *Styraconyx* Thulin, 1942 (amended by Kristensen and Higgins 1984b)

***Styraconyx craticulus* (Pollock, 1983)**

Voucher images Morphobank P4966:M898141-M898306 https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4966

Material examined: Six specimens from subtidal samples 6, 13, and 17 and one specimen from intertidal sample 14 (five females and two specimens of unknown gender).

Taxonomic remarks: A key to 11 of the 16 species in the genus can be found in D'Addabbo Gallo et al. (1989). The five newer species descriptions are provided in Chang and Rho (1998), Pérez-Pech et al. (2020), Fujimoto et al. (2020), and Bartels et al. (2015b, 2021). The BVI specimens match the original description of *Sty. craticulus*. A unique feature identifying *Sty. craticulus*, *Styraconyx craticuliformis* Chang & Rho, 1998 and *Styraconyx robertoi* Pérez-Pech, Jesús-Navarrate, Demilio, Anguas-Escalante & Hansen, 2020 is a grid-like pattern on the dorsal cuticle. The grid-like pattern is visible in some of the BVI specimens, but they clearly differ from *Sty. craticuliformis* and *Sty. robertoi* by having primary clavae and lateral cirri enveloped by a common membrane extending beyond the base.

Biogeographical and ecological comments: This species has been reported broadly from around the world including the U.S. Virgin Islands (Pollock 1983, Kristensen and

Higgins 1984b), Dominican Republic (Pollock 1983), Haiti (Pollock 1983), Guadeloupe Islands (Pollock 1983), Bahamas (Bartels et al. 2018), and the Caribbean coast of Costa Rica (Bartels et al. 2021). Sixteen of 26 previously published records are from intertidal sediments, and they have been found to a maximum of 200 m bsl.

Intertidal and subtidal comparisons

Paired subtidal and intertidal sampling allowed us to compare abundance, number of observed species, estimated species richness, and species composition in these two habitats. In all 10 matched samples, the subtidal samples were very shallow (< 2 m bsl) and very near the intertidal samples, thus effectively isolating the factor of tidal exposure as the primary ecological difference between the two habitats examined (periodic exposure to diurnal tides for intertidal samples, lack of exposure for subtidal samples).

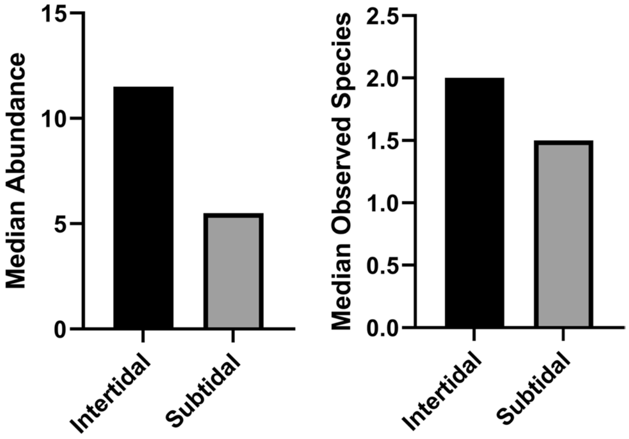

Fig. 5 Comparison of abundance and observed species (Sobs) between intertidal and subtidal samples ($n = 10$ for each). Due to lack of normality, median values are displayed. The results shown treat Florarctinae sp. as a separate taxon. Lumping or splitting Florarctinae sp. had no impact on the statistical results. Abundance was significantly higher in intertidal samples, Sobs was not significantly different in the two habitats

A total of nine species (plus Florarctinae sp.) was found in the intertidal samples and six species (plus Florarctinae sp.) in the subtidal samples. *Anisonyches diakidius*, *Bat. pennaki*, *Dpo. borrori*, *Flo. yucatanensis*, and *Pas. sterreri* were only collected in intertidal samples, while *Arc. bahamensis*, *Dpo. subterraneus*, and *Orz. belopus* were only collected in subtidal samples. *Halechiniscus r. remanei* was strongly dominant in intertidal sample 14, and Florarctinae sp. was the dominant taxon in intertidal samples 12 and 16.

Abundance and Sobs are compared in Fig. 5. These data were not normally distributed, so we present the median values and compare them with a Wilcoxon matched-pairs signed rank test. Abundance was significantly higher in the intertidal samples ($W = -43$, $P = 0.0078$), but there was no significant difference in Sobs ($W = -14$, $P = 0.3281$). Splitting or lumping Florarctinae sp. had no effect on these results. Results for the lumped treatment can be found in Online Resource 2.

Chao1 species richness estimates the asymptotic species richness with infinite sampling effort. Species richness and Sobs as a function of sampling effort are shown in Fig. 6 while treating Florarctinae sp. as a separate taxon. The only effect of lumping those unidentified specimens with *Flo. yucatanensis* was to reduce the total estimates by one species (see Online Resource 2B). Asymptotic species richness for subtidal samples is 8 ± 4.5 ($\bar{x}$ ± SD), reflecting the patchiness of these samples, while that of intertidal samples is 11 ± 1.9 ($\bar{x}$ ± SD). For all samples combined from both habitats, asymptotic species richness is 15 ± 3.7 ($\bar{x}$ ± SD).

Species composition in subtidal and intertidal habitats is compared using NMDS in Fig. 7. The correlation between the ordination and multidimensional space is good with a stress value of 0.08, and while there is overlap of some samples, a clear difference in species composition is evident. The NMDS presented is for

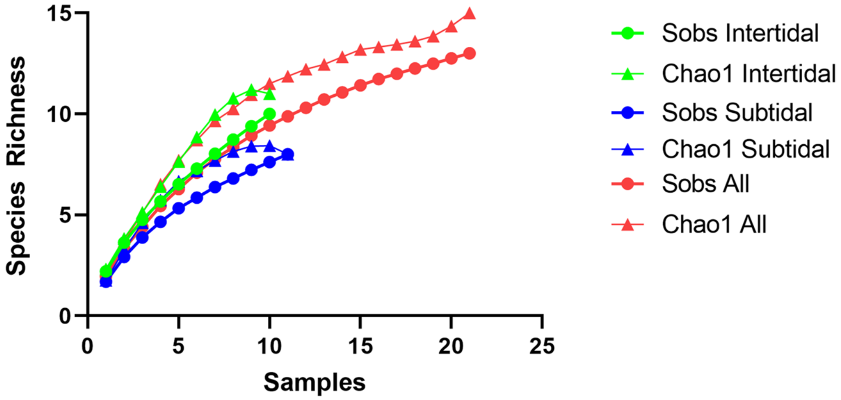

Fig. 6 Average observed species (Sobs) and Chao1 Species Richness Estimates as a function of sampling effort for subtidal samples, intertidal samples, and all samples combined. Florarctinae sp. treated as a separate species, permutations = 999

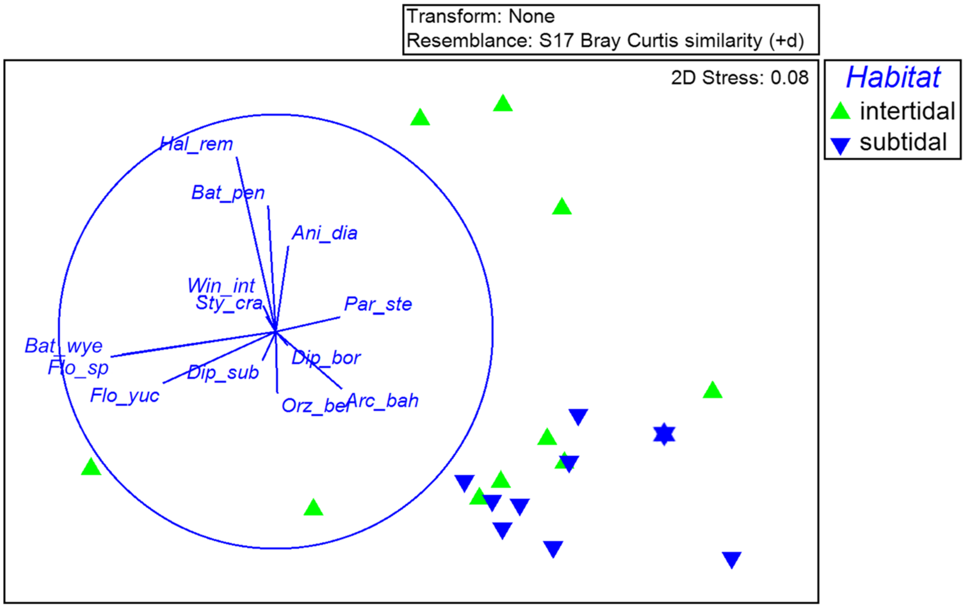

Fig. 7 Non-metric multi-dimensional scaling (Florarctinae sp. treated as separate species, no data transformation, dummy value on, 100 restarts) with species vector overlay using Pearson correlation. Each triangle is a sample, the blue star indicates 3 identical samples. *Ani_dia = Anisonyches diakidius, Arc_bah = Archechiniscus bahamensis, Bat_wye = Batillipes wyedeleinorum* sp. nov., *Bat_pen = Batillpes pennaki, Flo_yuc = Florarctus yucatanensis, Flo_sp* = Floractinae sp., *Hal_rem = Halechiniscus remanei, Orz_bel = Orzeliscus belopus, Par_ste = Parastygarctus sterreri, Sty_cra = Styraxonyx craticulus and Win_int = Wingstrandarctus* cf. *intermedius*

treating Florarctinae sp. as a separate taxon, but little difference in pattern was found when they were lumped with *Flo. yucatanensis* (Online Resource 2C). The species vector correlation indicates that *Hal. r. remanei*, *Bat. pennaki*, *Ani. diakidius*, *Bat. wyedeleinorum* sp. nov., *Flo. yucatanensis*, and Florarctinae sp. are associated with intertidal habitats while *Arc. bahamensis* is associated with subtidal habitats. Differences between species assemblages were significant (PERMANOVA pseudo-F = 1.9741, $P = 0.042$ when separating Florarctinae sp., pseudo-F = 1.9878, $P = 0.042$ when lumping Florarctinae sp.).

Discussion

In this first inventory of marine tardigrades from BVI, 12 taxa (13 including Florarctinae sp.) were identified, and *Bat. wyedeleinorum* sp. nov. was described. This is only the fourth location reported for *Arc. bahamensis,* and only the second for *Flo. yucatanensis*, and all of the records for these two species have been in the Caribbean Basin. Thus, these two species appear to be endemic to this region. The other species recorded have broader geographic ranges, and all but one have previously been found in the Caribbean Basin. This is the first record of *Dpo. borrori* in the Caribbean and an interesting range extension since previously it was known only from the central and western Pacific Ocean and the Mediterranean Sea. The BVI florarctids need further investigation. Our specimens were poorly preserved, especially the alae which are crucial for taxonomic analysis. These animals should be examined in water or glycerine, using fresh specimens when possible. It is entirely possible that additional species exist in BVI but were missed in this inventory.

Riera et al. (2012) compared intertidal and subtidal meiofaunal communities in Spain and found that species diversity was higher in the subtidal due to greater dominance of a few species in the intertidal, and they noted that this is consistent with the idea that high disturbance reduces diversity. However, tardigrades were not found in their samples. Bartels et al. (2018) suggested that subtidal and intertidal tardigrade communities may be quite distinct, deserving further study. For 10 sites in our BVI inventory, intertidal samples were paired with nearby, very shallow subtidal samples, allowing us to compare tardigrade communities in these two habitats. The obvious ecological distinction between these sites is periodic tidal exposure in the intertidal.

Contrary to results from Riera et al. (2012) for mixed meiofauna, we found greater tardigrade abundance and diversity (based on the Chao1 species richness estimates) in the intertidal samples. Tardigrade species assemblages differed in the two habitats, as well, with *Arc. bahamensis* more common in the subtidal while *Hal. r. remanei*, *Bat. pennaki*, *Ani. diakidius*, *Bat. wyedeleinorum*, *Flo. yucatanensis*, and Florarctinae sp. were more common in the intertidal. These habitat associations are largely consistent with previously published records as summarized in the species accounts, so some clear habitat “preferences” are evident.

Greater abundance and diversity in intertidal habitats compared to subtidal habitats may seem counterintuitive, but in this project, the subtidal area examined was a very narrow strip extremely close to the low tide mark. If a broader subtidal zone was examined with various depths and a greater range of ecological communities, then we would expect very different results. Furthermore, extensive mixing of sediment from the two habitats was likely, and the relative degree of disturbance in the two areas is not clear. Nonetheless, we observed clear differences in tardigrade distributions between these habitats, and it is interesting to consider possible causes. In general, marine (and freshwater) tardigrades are thought to have minimal or no cryptobiotic capabilities (Nelson et al. 2018). However, this has been checked in very few marine species. *Echiniscoides groenlandicus* Kristensen & Hallas, 1980 living on intertidal barnacles was found to be strongly cryptobiotic (Møbjerg et al. 2011), as is the barnacle-dwelling *Ecn. sigismundi* and probably other *Echiniscoides* as well (Møbjerg pers. comm.). *Styraconyx haploceros* Thulin, 1942 living on intertidal lichens was also found to be cryptobiotic, whereas *Bat. pennaki* from beach sediment did not survive desiccation (Jørgensen and Møbjerg 2014). Additionally, an unnamed *Archechiniscus* living on upper intertidal barnacles was reported to enter a tun state in response to high salinity and survive desiccation (Hansen and Fujimoto 2018). We wonder if cryptobiosis may be more frequent than previously thought among intertidal marine tardigrades, providing a competitive advantage in these habitats regularly exposed to drying and fluctuations of temperature and salinity. Fluctuating conditions might be especially likely for tardigrades living at the upper reaches of the high tide zone, for example. It would be very interesting to assay cryptobiosis and compare between *Arc. bahamensis* with its strong association with subtidal habitats and the species we found associated with intertidal habitats. See Jørgensen and Møbjerg (2014) and Vecchi et al. (2023) for possible experimental protocols for such an assay.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-024-01450-8.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability Data supporting the findings of this study are available within the paper and its Supplementary Information. Supplementary information includes a Supplementary Data document available through the journal's website and voucher photographs of all reported taxa in Morphobank.

Author contribution statement PB conceived and designed research, collected specimens, prepared slides, analyzed distribution data, and wrote the first draft of the manuscript. All authors contributed to species diagnoses, descriptions and text editing.

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