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Zoantharia (Cnidaria: Hexacorallia) of the Dutch Caribbean and One New Species of *Parazoanthus*

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Abstract: Species of the anthozoan order Zoantharia (=Zoanthidea) are common components of subtropical and tropical shallow water coral reefs. Despite a long history of research on their species diversity in the Caribbean, many regions within this sea remain underexamined. One such region is the Dutch Caribbean, including the islands of St. Eustatius, St. Maarten, Saba, Aruba, Bonaire, and Curaçao, as well as the Saba Bank, for which no definitive species list exists. Here, combining examinations of specimens housed in the Naturalis Biodiversity Center collection with new specimens and records from field expeditions, we provide a list of zoantharian species found within the Dutch Caribbean. Our results demonstrate the presence at least 16 described species, including the newly described *Parazoanthus atlanticus*, and the additional potential presence of up to four undescribed species. These records of new and undescribed species demonstrate that although the zoantharian research history of the Caribbean is long, further discoveries remain to be found. In light of biodiversity loss and increasing anthropogenic pressure on declining coral reefs, documenting the diversity of zoantharians and other coral reef species to provide baseline data takes on a new urgency.

Keywords: Anthozoa; coral reefs; records; Macrocnemina; Brachycnemina

1. Introduction

Zoantharians (Anthozoa, Hexacorallia, Zoantharia) are commonly observed rock and reef-dwelling benthic organisms in the Caribbean and other subtropical to tropical regions of the Atlantic. Detailed information about the diversity of the zoantharian fauna at species level has been reported from various parts of the Atlantic Ocean and adjacent seas, although some records may not be complete or taxonomically not up to date anymore. For example, 13 species have been recorded from the coastline of Brazil [1], 11 from of the Gulf of Mexico [2], 10 from the Bahamas and Florida [3], 8 from the Cape Verde islands in the eastern Atlantic [4] and Saint Helena Island [5], 7 from Bermuda [6], 7 from the Mediterranean [7], 5 in Canary Islands [8], and 4 from Ascension Island in the central Atlantic [9]. In addition, five deep-water species from the Azores (eastern Atlantic) were described

[10,11]. While some recent progress has been made in assessing oceanic basin-wide diversity patterns [5], questions remain on the true numbers of species present in each region due to a general lack of field data and ambiguous or brief original species descriptions. Thus, detailed data with accurate species identifications, the basis of large-scale biodiversity analyses, are still needed from most regions of the Atlantic.

Information about the zoantharian fauna of the Dutch Caribbean is generally poor despite a long history of biodiversity research [12]. The Dutch Caribbean consists of the islands Aruba, Bonaire, and Curaçao off Venezuela in the southern Caribbean region, and the islands Saba, St. Eustatius, and St. Maarten, together with the submerged platform Saba Bank, in the eastern Caribbean region. Most zoantharian records from these regions concern shallow water specimens and are usually not identified to more specific than the genus level. For instance, Van der Horst [13] refers to "Zoanthacea" as social sea anemones covering rocks that partly reach above the seawater level in Caracas Bay in Curaçao Island. Wagenaar Hummelinck [14,15] reported *Zoanthus* in shallow waters of Aruba and Curaçao. Van den Hoek et al. [16] mentioned that the genera *Palythoa* and *Zoanthus* were common in Curaçao in waters less than ca. 1.2 m deep. Wanders [17] and Nagelkerken and Nagelkerken [18] only reported on the presence of zoantharians in benthic communities of the shallow reef zones here.

However, there is some detailed, species-level information on the zoantharian fauna in the Dutch Caribbean. For example, Bak [19] mentioned *Palythoa mammillosa* as living in very shallow water of the shore zone in front of cliffs of Bonaire and Curaçao. Van Duyl [20] refers to zoantharians in general and to *Palythoa caribaeorum* when discussing the shallow water ecosystems of these same two islands. More recently, Reimer [21] distinguished 14 species in a preliminary report from a marine biodiversity expedition in St. Eustatius, and Garcia-Hernandez et al. [22] reported associations between *Palythoa caribaeorum* (Duchassaing de Fonbressin & Michelotti, 1860) [23] and *Umimayanthus parasiticus* (Duchassaing de Fonbressin & Michelotti, 1860) [23] and a crab species at St. Eustatius. Finally, Reimer et al. [24] have provided a detailed list of the zoantharian species of the west coast of Curaçao on coral reefs to 30 m depth.

The present report aims to give an update on the zoantharian fauna throughout the Dutch Caribbean as a result of recent fieldwork (2014–2019) by the authors in Bonaire, Curaçao, and St Eustatius, during which Zoantharia specimens were photographed in situ and collected. In addition, previously collected specimens deposited in the zoological collections of Naturalis Biodiversity Center were newly studied and identified to genus or species-level. In this manner, we have been able to cover a wide range of species across the Dutch Caribbean. Since most previous publications dealing with the zoantharians in the Dutch Caribbean were not performed by zoantharian specialists, it is hoped that the present work will serve as a basis for others performing research on zoantharians in the Atlantic and particularly in the Caribbean.

2. Materials and Methods

2.1. Specimens Analyzed

Our examinations included specimens from the Coelenterata and Porifera collections (RMNH and ZMA) at Naturalis Biodiversity Center in Leiden, Netherlands, and from the Molecular Invertebrate Systematics and Ecology Laboratory (MISE) collection at the University of the Ryukyus in Okinawa, Japan. Specimens and surveys included the island states of Aruba, Curaçao, Sint Maarten (both Netherlands and French territories), and the Caribbean Netherlands including the islands of Bonaire, Sint Eustatius, and Saba, as well as the submerged Saba Bank. In total, 479 zoantharian specimens were analyzed in this study (Table S1), including 181 specimens belonging to the Naturalis collections (60 from the Porifera collection, 121 from the Coelenterata collection including 6 specimens were collected in Curaçao by the second author from the shallow and deep sea in 2014), and 298 to the MISE collection. Among the specimens from the MISE collection, 173 were collected in the Sint Eustatius survey of 2015 [21], 86 were collected in the Curaçao survey of 2017 [24], and 39 were collected in the Bonaire survey of 2019.

2.2. Specimen Identification

Most specimens in this study were identified by the first or last author between 2012 and 2019. For identification, we focused on external morphological characteristics that are utilizable in the field (e.g., general colony morphology, polyp sizes, tentacle numbers [25,26]). All measurement units were converted to the standard international metric system. The large majority of newly collected specimens in this study were identified via simple morphological and ecological analyses. We additionally conducted molecular phylogenetic analyses for one species that we formally describe in this work; these methods are given below.

Previously collected and identified specimens from earlier field work were also re-identified as much as possible by the first or last author (n = 173), although some of these earlier specimens (particularly type specimens) retain their original identification with no further amendment (n = 2). Such 'earlier' identifications, however, may be synonymous with other species [5,27,28], and have not been counted in species totals following the methodology in Santos et al. [5], and are instead listed within species groups (as "b", "c", etc, see Table 1).

Table 1. Depth distributions of Zoantharia species in the Dutch Caribbean. The Southern Caribbean region includes the islands of Aruba, Bonaire, and Curacao, while the Eastern Caribbean covers Saba, Saba Bank, Saint Eustatius, and Saint Maarten. We divided records into historic (earlier than 2000) and recent surveys (2001 and later). References for each species' depths are included in each species' section of the Results.

Index	Species	Range (m)	Southern Caribbean (m)		Eastern Caribbean (m)	
			Historic	Recent	Historic	Recent
1	Parazoanthidae sp. 1	140–248	x	140–248	x	x
2	*Antipathozoanthus* aff. *macaronesicus*	10	10	x	x	x
3	*Bergia catenularis*	6–50	6–36	10–38	20–50	12–26
4	*Bergia* cf. *cutressi* *	0–8	0–8	x	x	x
5	*Bergia puertoricense* *	10–55	10–55	10–38	x	13–37
6	*Parazoanthus swiftii*	10–40	10	19–40	unknown	14–29
7	Parazoanthidae? sp.	unknown	unknown	x	x	x
8	*Parazoanthus atlanticus*	10–34	x	10–34	x	x
9	*Umimayanthus parasiticus* *	1–44	1–40	15–38	16–44	3–34
10	*Umimayanthus* sp.	37	x	37	x	x
11	*Epizoanthus* sp.	980	x	x	980	x
12	*Hydrozoanthus antumbrosus* *	11–30	x	30	x	11–19
13	*Hydrozoanthus tunicans* *	2–30	2–4	30	x	14–19
14a	*Palythoa caribaeorum*	0–35	0–2	0–14	0–35	2–29
14b	*Palythoa caracasiana* *†	unknown	unknown	x	x	x
14c	*Palythoa horstii* *†	unknown	unknown	x	x	x
14d	*Palythoa mammilosa* *†	2	unknown	x	2	x
15	*Palythoa grandiflora*	1–6	intertidal	x	1–6	x
16	*Palythoa grandis*	11–64	18–64	11–12	x	13–18
17	*Palythoa variabilis*	0–37	0–24	37	intertidal	3
18	*Palythoa* sp.	intertidal	intertidal	x	x	x
19	*Zoanthus pulchellus*	0–24	0–24	1–11	0–20	15–16
20	*Zoanthus* aff. *pulchellus*	1	x	1	x	x
21	*Zoanthus sociatus*	0–24	0–3	intertidal	0–6	3–24
22	*Zoanthus solanderi*	0–21	intertidal	12–16	0–15	3–21
23	*Zoanthus* sp.	intertidal	intertidal	x	intertidal	x
24	*Isaurus tuberculatus*	0–15	intertidal	x	2	15
	Diversity recorded	24	18	16	14	15
			22		17	

* Species endemic to the Caribbean Sea. x = not reported. † Species most likely synonym of *P. caribaeorum*, and therefore not included in the species counts.

Zoantharian specimens belonging to the Naturalis collection were identified or re-identified using the gross external morphology of preserved specimens, and biological interactions/associations when applicable (e.g., [24,29]). All MISE specimens from Sint Eustatius, Bonaire, and Curaçao were identified using in situ or in vivo images.

For each species listed in the Results, we have also included a description following as close as possible the original description, with some small amendments to reflect additional information acquired after the first formal description. These descriptions should not be interpreted as formal descriptions, to the exception of the one new species we describe here, but as information provided

to workers to aid in field identification and to make the original descriptions accessible. A list of specimens, their collection information, and Naturalis or MISE registration numbers are given within each species section.

2.3. Cnidae Analyses

Analyses were conducted using undischarged nematocysts from tentacles, column, actinopharynx, and mesenteries filaments of holotype polyps (n = 2; specimen NSMT-Co 1706) under a Nikon Eclipse80i stereomicroscope (Nikon, Tokyo, Japan). Cnidae sizes were measured using ImageJ ver. 1.45s [30]. Cnidae classification generally followed England [31] and Ryland and Lancaster [32], while basitrichs and microbasic b-mastigophores were considered as the same type of nematocyst based on studies by Schmidt [33], Hidaka et al. [34], and Hidaka [35] and therefore these two types were pooled together.

2.4. DNA Extraction, Polymerase Chain Reaction (PCR) Amplification, and Sequencing

Total DNA was extracted using the Qiagen DNeasy Blood & Tissue Kit following the manufacturer's instructions for specimens NSMT-Co 1706, NSMT-Co 1707, MISE JDR170613-10-60, MISE JDR170613-10-61, MISE JDR170616-13-76, RMNH.COEL.42433, MISE JDR170609-2-6, MISE JDR170610-4-32, and MISE JDR170619-20-94. PCR amplification was performed for partial sequences of cytochrome oxidase subunit I (COI-mtDNA) following Folmer et al. [36], mitochondrial 16S ribosomal DNA (16S-rDNA) following Sinniger et al. [37], and the nuclear internal transcribed spacer region of ribosomal DNA (ITS-rDNA) following Reimer et al. [38] using standard Taq polymerase in ReadyMix solution (Qiagen, Tokyo, Japan). Successful amplifications were confirmed by 2% agarose gel electrophoresis, cleaned by shrimp alkaline phosphatase (SAP), and sent for external sequencing in both directions to Fasmac, Kanagawa, Japan.

2.5. Phylogenetic Analyses and Species Delimitations

The nucleotide sequences were initially aligned using Geneious v10.2.3 [39] and the plugin MAFFT [40] with the algorithm L-INS-i, thereafter the sequences were manually curated and trimmed. Trimmed alignments were subsequently realigned using the plugin MUSCLE [41] in Geneious v10.2.3 with default settings and aligned with previously reported sequences from family Parazoanthidae found in GenBank (Table 2). The resulting alignments were 446 sites of 30 sequences for COI-mtDNA, 576 sites for 51 sequences for 16S-rDNA, and 814 sites for 44 sequences for ITS-rDNA. These three alignments were then used to construct a concatenated alignment; missing data and gabs were replaced with "Ns". The final concatenated alignment consisted of 1836 sites and 57 sequences (Table 2). All alignments are available from the first and senior authors, and at treebase.org (ID: 26174).

Table 2. List of all Zoantharia sequences used in phylogenetic analyses, and their respective sequences GenBank ID number. NA = not available.

Species/specimens	COI-mtDNA	16S r-DNA	ITS r-DNA
Antipathozoanthus macaronesicus	NA	HM130467	EU591552
Bergia catenularis	NA	EU828757	EU418289
Bergia catenularis (TOB37)	NA	NA	EU418292
Bergia cutressi (1)	NA	EU828759	EU418264
Bergia cutressi (2)	NA	NA	EU418267
Bergia puertoricense (1)	AB247351	AY995933	EU591584
Bergia puertoricense (2)	NA	EU828758	EU418312
Bergia sp. Senegal	EF672656	EF687820	EU591582
Bergia sp. 5 Sulawesi	EU591627	AY995934	NA
Bullagummizoanthus emilyacadiaarum	NA	KC218434	NA

Corallizoanthus tsukaharai	NA	EU035625	EU035621
Epizoanthus arenaceus	AB247348	AY995926	EU591538
Hurlizoanthus parrishi	NA	KC218433	NA
Isozoanthus giganteus	NA	GQ464867	GQ464896
Kauluzoanthus kerbyi (SH12)	NA	KC218435	NA
Kulamanamana haumeaae (SH2)	NA	KC218431	NA
Mesozoanthus fossii	NA	EF687822	EU591545
Parazoanthid sp. 02_27	NA	EU333760	EU333810
Parazoanthid sp. 3 Madagascar	EF672664	EF687825	EU591576
Parazoanthid sp. Tasmania	EU591620	EU591610	NA
Parazoanthid sp. 3 Sulawesi	AB247354	AY995937	EU591575
Parazoanthus aff. *juanfernandezii* (CA128)	NA	GQ464849	GQ464878
Parazoanthus aff. *swiftii* (PER241)	NA	GQ464853	GQ464882
Parazoanthus aff. *swiftii* (PER249)	NA	GQ464854	GQ464883
Parazoanthus anguicomus (1)	EF672660	EF687827	EU591574
Parazoanthus anguicomus (2)	NA	GQ464851	GQ464880
Parazoanthus axinellae (1)	AB247355	AF398921	NA
Parazoanthus axinellae (2)	EF672659	NA	EU591571
Parazoanthus capensis (SA262)	NA	GQ464852	GQ464881
Parazoanthus darwini (1)	NA	EU333748	EU333802
Parazoanthus darwini (2)	NA	EU333751	NA
Parazoanthus elongatus (Chile)	EF672661	EF687829	EU591565
Parazoanthus elongatus (NZ)	EF672662	EF687828	EU591564
Parazoanthus sp. 1401	NA	HM130478	NA
Parazoanthus sp. 269	NA	HM130468	NA
Parazoanthus sp. 'hertwigi'	KC218397	NA	NA
Parazoanthus swiftii (1)	AB247350	AY995936	GQ848258
Parazoanthus swiftii (2)	KJ794176	EU828755	EU418332
Savalia savaglia	NA	HQ110948	EU346888
Umimayanthus chanpuru (16J)	KR092609	KR092469	KR092678
Umimayanthus chanpuru (33J)	KR092594	KR092504	KR092680
Umimayanthus miyabi (179TF)	KR092570	KR092453	KR092645
Umimayanthus miyabi (70JR)	KR092573	KR092454	KR092646
Umimayanthus nakama (363JR)	KR092577	KR092458	KR092644
Umimayanthus nakama (3J)	KR092579	KR092457	KR092643
Umimayanthus parasiticus (1)	EF672663	AY995938	GQ848263
Umimayanthus parasiticus (2)	NA	EU828756	EU418306
Zibrowius ammophilus (SH15)	NA	KC218439	NA
Parazoanthus atlanticus sp. n. (RMNH.COEL.42433)	NA	NA	MT103525
Parazoanthus swiftii (MISE JDR170609-2-6)	MT102228	MT103533	MT103530
Parazoanthus swiftii (MISE JDR170610-4-32)	MT102229	MT103534	MT103531
Parazoanthus atlanticus sp. n. (MISE JDR170613-10-60)	MT102223	MT103538	MT103528
Parazoanthus atlanticus sp. n. (MISE JDR170613-10-61)	MT102222	MT103539	MT103527
Parazoanthus atlanticus sp. n. (NSMT-Co 1706)	MT102224	MT103537	MT103526
Parazoanthus atlanticus sp. n. (NSMT-Co 1707)	MT102225	MT103536	MT103524
Parazoanthus atlanticus sp. n. (MISE JDR170616-13-76)	MT102226	MT103535	MT103529
Umimayanthus sp. (MISE JDR170619-20-94)	MT102227	NA	NA

Phylogenetic analyses were performed on the concatenated aligned dataset using maximum-likelihood (ML) and Bayesian posterior probability (BPP). TOPALi v2.5 [42] was used to select the best fitting model for each COI-mtDNA, 16S-rDNA, and ITS-rDNA regions, independently for ML and BPP analyses. For ML analyses, the best-fitting models were K80+G (010010), TrNef+G (010020), and HKY+G (010010); and for BPP K80+G (010010), K80+G (010010), and HKY+G (010010), respectively, for COI-mtDNA, 16S-rDNA, and ITS-rDNA regions. Independent phylogenetic analyses were performed for each region and for the concatenation in RAxML v8.2.11 [43] for ML, and Mr. Bayes v3.2.6 [44] for BPP. RAxML was configured to use the substitution model GTR+G with the "-f a –x 1" algorithm, 1000 bootstrap replicates, 1 parsimony random seed, and *Epizoanthus arenaceous* was specified as out-group. MrBayes was configured following the models and parameters as indicated by TOPALi, 4 MCMC heated chains were run for 10,000,000 generations with the temperature for the heated chain set to 0.2. Chains were sampled every 200 generations. Burn-in was set to 3,500,000 generations (35%), at which point the average standard deviation of split frequency (ASDOSF) values were <0.01.

For specimens with molecular sequences available, species identifications were determined using a combination of molecular and morphological data. Species were delimited according to monophyletic clades of our generated concatenated phylogenetic tree (genealogical species concept; [45,46]), and their validity was evaluated using available morphological characters.

3. Results

3.1. Diversity in the Dutch Caribbean

Overall, 126 unique locations were examined across the study area (Figure 1a,b; Table S2), although the specific collection site information for 20 specimens were not available. Four localities were investigated in Aruba, 30 in Bonaire, 44 in Curaçao, 6 in Saba, 11 in Saba Bank, 26 in Sint Eustatius, and 5 in Sint Maarten, 3 of which were located in French territory.

Most Zoantharia specimens were easily identifiable to species level, to the exception of 3 specimens that were identified as "confers with" (cf.), 4 as "affinity" (aff.), 14 to genera, and 5 only to supra-generic levels. In total, all specimens studied represented 9 genera and 17 described species. Four potentially undescribed species were found in this survey; one undescribed species belonging to genus *Umimayanthus* (sample ID: MISE JDR170619-20-94, MISE JDR191026-1-1) and one to *Epizoanthus* (RMNH.COEL.40667), while specimens RMNH.COEL.42429, RMNH.COEL.42430; RMNH.POR. 9219, 9234, and 9251 possibly belong to one or two species in a potentially undescribed Parazoanthidae genus from the deep sea around Curaçao Island. Additionally, in this study, we formally describe one species belonging to genus *Parazoanthus* from six specimens (RMNH.COEL.42433; NSMT-Co 1706 and NSMT-Co 1707; JDR170613-10-60 to 61; JDR170616-13-76) that superficially resembled *P. swiftii* (Duchassaing de Fonbressin & Michelotti, 1860) [23] but was shown to have clear differences in habitat, polyp size, colony arrangement, and in molecular data from *P. swiftii* and other *Parazoanthus* species.

Specimens are listed by species with information in the following order: Specimen number, latitude and longitude, location, depth, date, collectors.

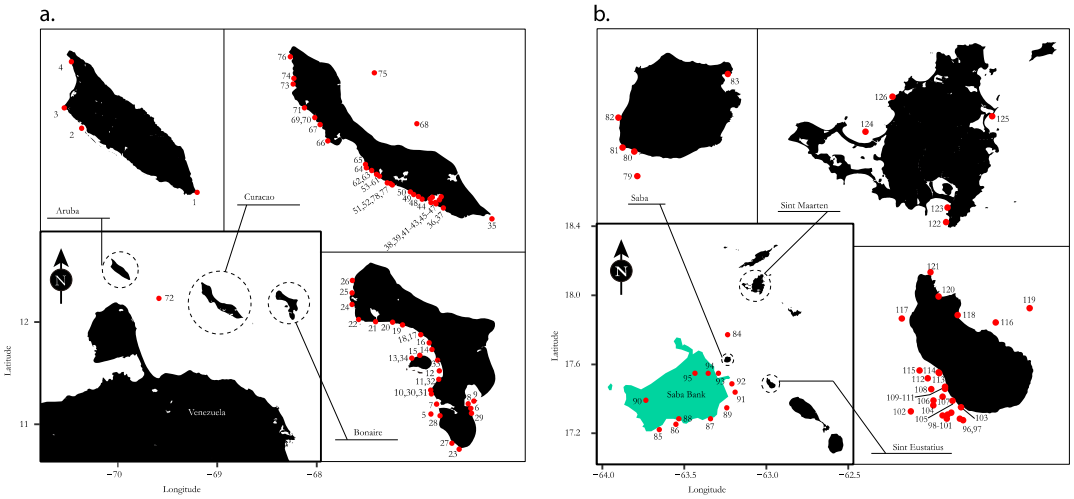

Figure 1. Map of the Dutch Caribbean islands. (**a**) Southern Caribbean region with Aruba, Bonaire, and Curaçao islands. (**b**) Eastern Caribbean region including Saba, Saba Bank, Sint Maarten, and Sint Eustatius. Red points indicate the approximate position of all localities included in this study. For detailed information on localities see Table S2 [47,48].

3.2. Specimens and Species

Order Zoantharia Rafinesque, 1815 [49]
Suborder Macrocnemina Haddon & Shackleton, 1891 [50]
Family Parazoanthidae Delage & Hérouard, 1901 [51]
Figures 2–26

3.2.1. Parazoanthidae sp. (Figure 2)

Specimens examined (*n* = 5). **Bonaire**. RMNH.POR.9234 (12°04′48″ N, 68°17′38″ W [point 5], Curasub, Cargill Pier, 223 m depth, 1.vi.2013, coll. L.E. Becking & E.H.W.G. Meesters); RMNH.POR.9251 (similar but from 248 m depth); RMNH.POR.9219 (12°08′49″ N, 68°16′56″ W [point 12], Kralendijk Pier, 140 m depth, 30.v.2013, coll. L.E. Becking & E.H.W.G. Meesters). **Curaçao** RMNH.COEL.42429 (12°14′01″ N, 68°53′32″ W [point 68], Curasub, Playa Porto, Curaçao, 61–243 m depth, 21.iii.2014, coll. BWH); RMNH.COEL.42430 (12°05′04″ N, 68°53′54″ W [point 49], Curasub, Substation Curaçao, ca. 200 m depth, 31.iii.2014, coll. BWH).

Photographic records (*n* = 5). In situ: Specimens RMNH.COEL.42429, RMNH.COEL.42430. Preserved: Specimens RMNH.POR.9219, 9234, 9251.

Remarks: All specimens were collected from the deep sea (depths 140–248 m), as symbiont of sponges. The examined specimens have cyclically transitional or cteniform marginal musculature, and these marginal musculature forms have been reported from the family Parazoanthidae [52,53]. Within this family, several *Isozoanthus* species are known to have association with stalked hexactinellid sponges within subclass Amphidiscophora Schulze, 1886 [54,55]. However, the examined specimens are associated with hexactinellid sponges within subclass Hexasterophora Schulze, 1886. Therefore, we consider that these specimens belong to an undescribed genus possibly containing more than one species. For now, we have listed specimens as one taxon in this work. Photographs of this species were published earlier as "zoanthids" living in association with the sponges *Cyrtaulon sigsbeei* (Schmidt, 1880) and *Verrucocoeloidea liberatorii* Reiswig & Dohrmann, 2014 (see [56] (Figure 4a,b); [57] (Figure 22f,g)), and were also recorded from Bonaire and Curaçao.

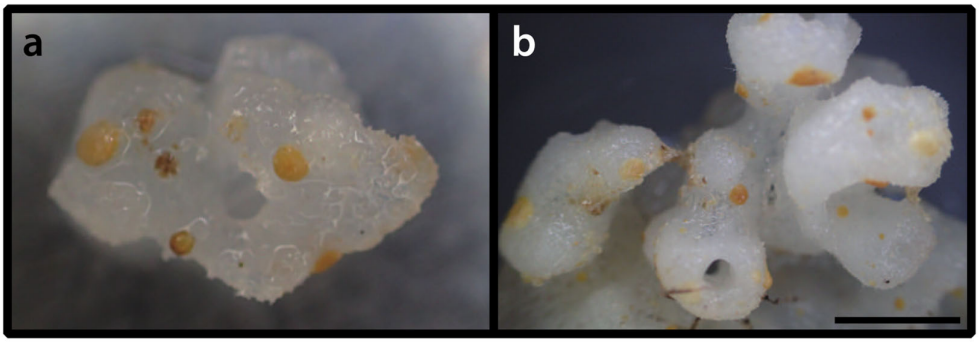

Figure 2. Preserved specimens of Parazoanthidae sp. from Naturalis collected from Bonaire; (**a**) specimen RMNH.POR.9219 from Kralendijk Pier [point 12], depth = 140 m, and (**b**) RMNH.POR.9234 from Cargill Pier [point 5], depth = 223 m. Scale bar in b) = approximately 1 cm.

Genus *Antipathozoanthus* Sinniger, Reimer & Pawlowski, 2010 [58]

3.2.2. *Antipathozoanthus* aff. *macaronesicus* Ocaña & Brito, 2003 [59] (Figure 3)

Specimens examined (*n* = 3). **Curaçao.** RMNH.COEL.40331, 40332, 40763 (12°04′30″ N, 68°51′51″ W [point 45], Caracas Baai, Buoy 9, >10 m depth, 9.ii.1955, coll. J.S. Zaneveld & P. Wagenaar Hummelinck).

Photographic records (*n* = 3). Preserved: Specimens RMNH.COEL.40331, 40332, 40763.

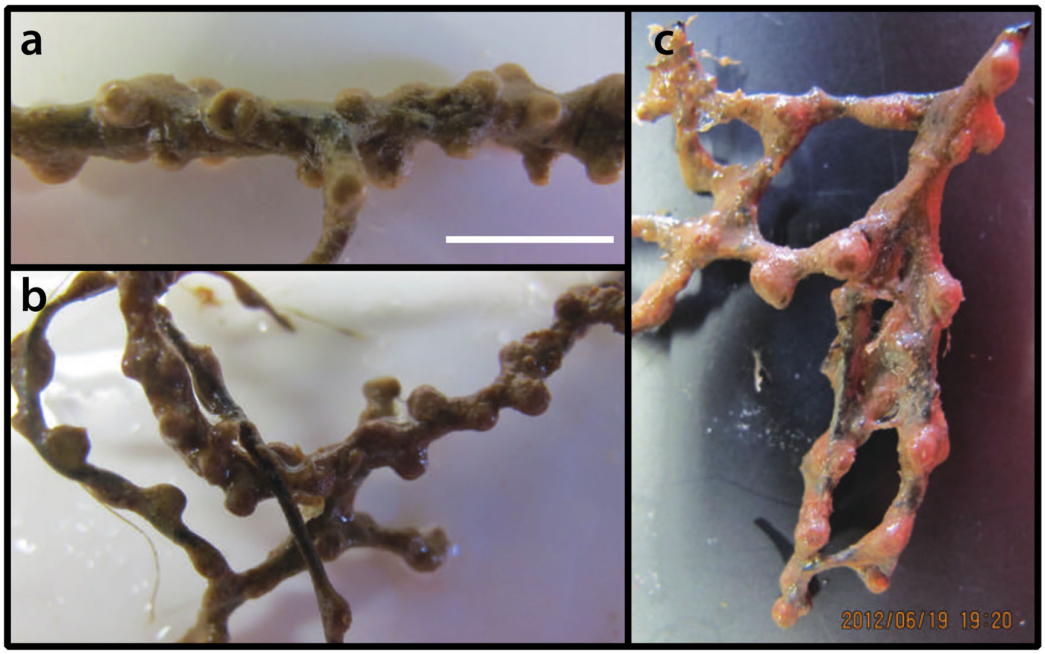

Figure 3. Preserved specimens of *Anthipathozoanthus* aff. *macaronesicus* from Naturalis collected from Buoy 9, Caracas Baai [point 45], Curaçao, all depth >10 m; (**a**) specimen RMNH.COEL.40331, (**b**) RMNH.COEL.40332, and c) RMNH.COEL.40763. Scale bar in (**a**) = approximately 1 cm.

Description of *A. macaronesicus* adapted from Ocaña & Brito [59]. Colonies present several forms of growth and a variable external appearance. When growing freely, the colony develops its own skeleton and generates branches in a single or multiple direction; although it may also present a poorly developed ribbon-like skeleton. The colony can also grow over anthipatharians and reach up

to one meter in height. In preserved material, polyp dimensions are variable from 0.2 to 1 cm in height and 0.2 to 0.5 in diameter; alive, the polyp sizes increase considerably to 2 to 3 cm. Tentacles are pointed, 42 in number, and, more or less, arranged in two entacmeic cycles. Polyps are overhanging from coenenchyme, but embedded polyps are also present. The colony can present several colors ranging from yellow to orange, in tentacles and column; colonies growing in antipatharians typically present brown color.

Remarks: All specimens were collected from colonies growing on antipatharians. Specimen RMNH.COEL.40332 was growing on an unidentified antipatharian. RMNH.COEL.40763 was growing on *Antipathes gracilis* Gray, 1860. No *Antipathozoanthus* were found during our recent surveys of Curaçao, and all known specimens were collected in 1955. Currently, only one species, *A. macaronesicus* (Ocaña & Brito, 2003) [59], is known for the genus *Antipathozoanthus* from the Atlantic. However, four species of the genus have been described from the Indian and Pacific Oceans [60,61]. Thus, given the distance from confirmed records of *A. macaronesicus* in the East Atlantic, we here identify all specimens as *Antipathozoanthus* aff. *macaronesicus*.

Genus *Bergia* Duchassaing de Fonbressin & Michelotti, 1860 [23]

3.2.3. *Bergia catenularis* Duchassaing de Fonbressin & Michelotti, 1860 [23] (Figure 4)

Specimens examined (*n* = 26). **Bonaire**. MISE JGH191024-2-1 (12°7′53.28″ N, 68°16′59.76″ W [point 32], Corporal Meiss, 27 m depth, 24.x.2019, coll. JGH); MISE JDR191025-1-1 (12°12′1.74″ N, 68°18′30.72″ W [point 18], Oil Slick, 17 m depth, 25.x.2019, coll. JDR); MISE JDR191025-2-2 (12°2′8.22″ N, 68°15′43.32″ W [point 27], Sweet Dreams, 30 m depth, 25.x.2019, coll. JDR); MISE JDR191103-2-6 (12°1′36.3″ N, 68°15′4.74″ W [point 23], Red Slave, 20 m depth, 3.xi.2019, coll. JDR); MISE JDR191103-2-7 (12°1′36.3″ N, 68°15′4.74″ W [point 23], Red Slave, 20 m depth, 3.xi.2019, coll. JDR). **Curaçao.** MISE JDR170610-3-26 (12°08′21″ N, 68°59′53″ W [point 64], Snake Bay, 31 m depth, 10.vi.2017, coll. JDR); MISE JDR170610-4-31 (12°08′53″ N, 69°00′00″ W [point 65], Sint Michiel's Bay, 20 m depth, 10.vi.2017, coll. JDR); MISE JDR170610-4-33 (12°08′53″ N, 69°00′00″ W [point 65], Sint Michiel's Bay, 10 m depth, 10.vi.2017, coll. JDR); MISE JDR170621-night-102 (12°07′20″ N, 68°58′08″ W [point 54], Carmabi, House Reef, Curaçao, unknown depth, 21.vi.2017, coll. J.E. Garcia-Hernandez); MISE NA (12°19′45″ N, 69°09′05″ W [point 74], Playa Jeremi, 12–38 m depth, 20.vi.2017, coll. JDR); ZMA.POR.14242 (12°08′21″ N, 68°59′53″ W [point 64], Snake Bay, 36 m depth, 18.iv.1989, coll. M.J. de Kluijver); ZMA.POR.14344 (12°07′32″ N, 68°58′27″ W [point 59], north of Piscadera Bay, Buoy 1, 35 m depth, 15.v.1998, coll. R. Gomez); ZMA.POR.15665 (12°08′01″ N, 68°59′07″ W [point 62], Blue Bay, 35 m depth, 25.ii.1989, coll. R.W.M. van Soest); ZMA.POR.19055 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, unknown depth, 2005, coll. N. van der Hal); ZMA.POR.4626 (12°07′30″ N, 68°58′23″ W [point 58], north of Piscadera Bay, Buoy 0, 6–12 m depth, 19.xii.1980, coll. R.W.M. van Soest). **Saba Bank.** ZMA.POR.5143 (17°14′00″ N, 63°34′00″ W [point 86], Sta. LUY-101, south-slope, 20–50 m depth, 24.x.1972, coll. Luymes Exp.). **Sint Eustatius.** MISE JDR150610-6, JDR150610-7 (17°27′44.2″ N, 62°58′46.7″ W [point 97], Sta. EUX007, 21 m depth, 10.vi.2015, coll. JDR; MISE JDR150610-12 (17°27′53.9″ N, 62°59′00.7″ W [point 101], Sta. EUX008, 17 m depth, 10.vi.2015, coll. JDR); MISE JDR150611-33, JDR150611-34 (17°28′19.2″ N, 62°59′15.6″ W [point 107], Sta. EUX010, 12 m depth, 11.vi.2015, coll. JDR); MISE JDR150612-81 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 16 m depth, 12.vi.2015, coll. JDR); MISE JDR150614-127 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 16 m depth, 14.vi.2015, coll. JDR); MISE JDR150616-147 (17°28′13.6″ N, 62°59′30.2″ W [point 106], Sta. EUX019, 18 m depth, 16.vi.2015, coll. JDR); MISE JDR150618-157 (17°27′56.6″ N, 63°00′07.2″ W [point 102], Sta. EUX022, 26 m depth, 18.vi.2015, coll. JDR); MISE JDR150619-166 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta EUX024, 25 m depth, 19.vi.2015, coll. JDR).

Photographic records (*n* = 24). In situ: Specimens MISE JDR150610-6, JDR150610-7, JDR150610-12, JDR170610-3-26, JDR170610-4-31, JDR170610-4-33, JDR150611-33, JDR150611-34, JDR150612-81, JDR150614-127, JDR150616-147, JDR150618-157, JDR150619-166, JGH191024-2-1, JDR191025-1-1, JDR191025-2-2, JDR191103-2-6, JDR191103-2-7. Preserved: Specimens ZMA.POR.4626, 5143, 14242, 14344, 15665, 19055.

Description as in Duchassaing de Fonbressin & Michelotti [23], West [26], Swain [62]. The colonies present very short polyps forming a chain-like incrustation on the surface of the sponges, with polyps arising from one another by stolons (propagules), not from a common membrane. This species is characterized by having a commensalistic and cateniform habit of colonization (p. 54 translated by Duerden [63] from Duchassaing de Fonbressin & Michelotti [23], also [29]). Polyps and coenenchyme present a golden–brown color, 10 capitular ridges, 20 tentacles with a maximum length of 1 mm, and the same number of mesenteries, the length and diameter of extended polyps is rarely more than 1 mm, and the symbiont sponges belonging to the order Halosclerida [26,62].

Recent and other previous records: Antilles [23], Bahamas [64], Barbados [65,66], Brazil [66], Colombia [67], Curaçao [24], Dominica [66], Jamaica [68], Panama [66], Puerto Rico [26], Tobago [66], USA (Gulf of Mexico, Navassa Island) [66,69], and Venezuela [70].

Remarks: This species, originally placed with the genus *Bergia*, was placed into *Parazoanthus* Haddon & Shackleton, 1891 [50] by Duerden [63], and thus appears in most literature as *P. catenularis*, until the resurrection of *Bergia* based on molecular data by Montenegro et al. [71]. *B. catenularis* was observed associated with *Petrosia* (*Petrosia*) aff. *weinbergi* Van Soest, 1980 in Curaçao [24] and Saba Bank; and with *Xestospongia muta* (Schmidt, 1870) in Sint Eustatius.

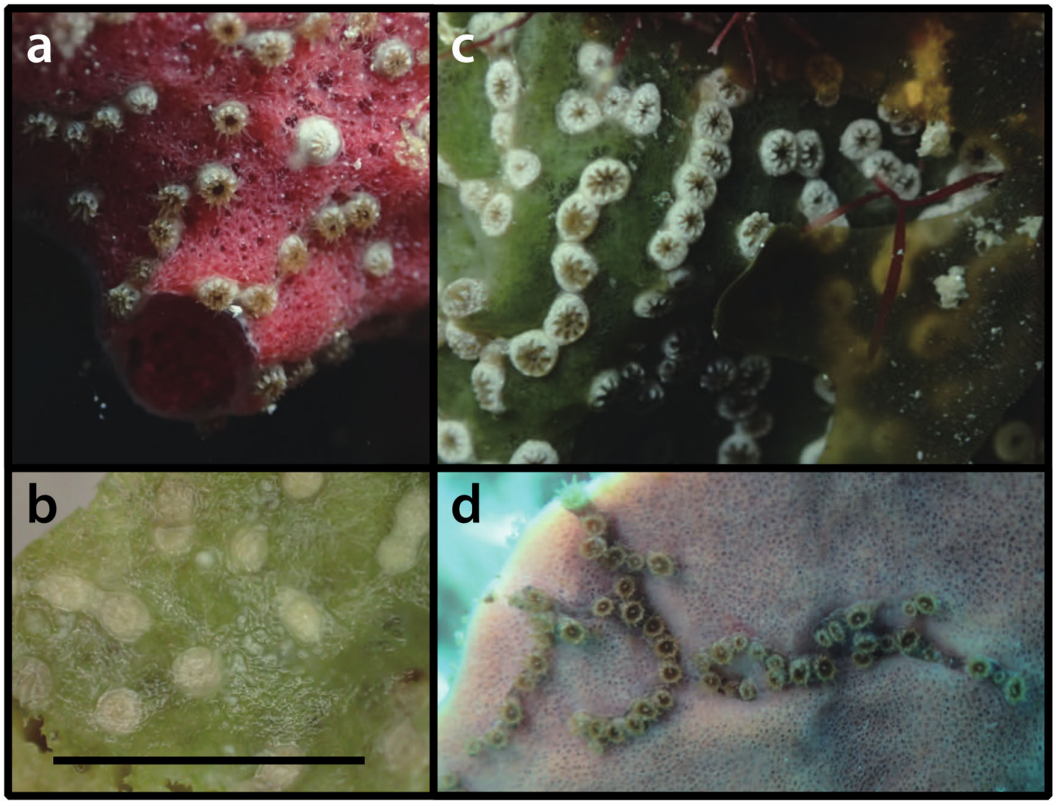

Figure 4. Specimens of *Bergia catenularis*. (**a**) specimen MISE JDR170610-4-31 in situ from Sint Michiel's Bay [point 65], Curaçao, depth = 20 m, (**b**) preserved ZMA.POR.19055 collected from Santa Marta, Water Factory, Curaçao, depth = unknown, (**c**) MISE JDR170610-4-33 in situ from Sint Michiel's Bay [point 65], Curaçao, depth = 10 m, and (**d**) MISE JDR150611-34 from Sta. EUX010 [point 107], Sint Eustatius, depth = 12 m. Scale bar in (**b**) = approximately 1 cm.

3.2.4. *Bergia* cf. *cutressi* (West, 1979) [26] (Figure 5)

Specimens examined (*n* = 3). **Bonaire**. MISE JDR191029-1-2 (12°13'24.42" N, 68°24'13.38" W [point 22], Taylor Made, 29 m depth, 29.x.2019, coll. JDR); MISE JDR191107-1-1, (12°6'37.74" N, 68°17'35.16" W [point 30], The Lake, 13 m depth, 7.xi.2019, coll. JDR). **Sint Maarten.**

RMNH.COEL.40278 (18°00′31″ N, 63°02′46″ W [point 122], Great Bay near Pointe Blanche, Sta. LUY-120, 0–8 m depth, 27.ix.1972, coll. JCH).

Photographic records (n = 3). In situ: MISE JDR191029-1-2, JDR191107-1-1. Preserved: Specimen RMNH.COEL.40278.

Description as in West [26]: Colonies embedded in *Xestospongia* sp. sponge, with only scapus of polyps projecting from the surface. The polyp dimensions are 1 mm in high and 0.3 mm in diameter. The polyps are connected beneath the sponge surface by a coenenchyme; scapulus thin-walled and clean, capitular ridges are 12 in number; tentacles and mesenteries are 12 in number. Coenenchyme, column, and tentacles are the color yellow.

Recent and other previous records: Barbados [65,66], Colombia [67], Dominica [66], Puerto Rico [26], Tobago, and USA (Navassa) [66].

Remarks: Similar to *B. catenularis*, this species was originally described as part of *Epizoanthus* Gray, 1867 [72] by West [26], later placed into *Parazoanthus* by Swain et al. [53], until the resurrection of *Bergia* by Montenegro et al. [71], where molecular evidence placed this species within genus *Bergia*. Thus, this species still appears in most literature as *E. cutressi*. The associated host sponge of specimen RMNH.COEL.40278 was not identified.

Figure 5. (**a**) Preserved *Bergia* cf. *cutressi* specimen RMNH.COEL.40278 from Great Bay near Pointe Blanche, Sta. LUY-120 [point 122], Sint Maarten, depth = 0–8 m, (**b**) and close-up of same specimen. Scale bar in (b) = approximately 1 cm.

3.2.5. *Bergia puertoricense* (West, 1979) [26] (Figure 6)

Specimens examined (n = 29). **Bonaire**. MISE JGH191106-2-1 (12°11′17.1″ N, 68°17′47.7″ W [point 16], Andrea I, 17 m depth, 6.xi.2019, coll. JGH). **Curaçao**. RMNH.COEL.42431 (12°08′06″ N, 68°59′16″ W [point 63], Blue Wall, 10 m depth, 2.iv.2014, coll. BWH); MISE JDR170609-1-4 (12°07′17″ N, 68°58′09″ W [point 53], Carmabi, Hilton Hotel, 20 m depth, 9.vi.2017, coll. JDR); MISE JDR170610-4-30 (12°08′53″ N, 69°00′00″ W [point 65], Sint Michiel's Bay, 20 m depth, 10.vi.2017, coll. JDR); MISE JDR170612-7-45 (12°05′24″ N, 68°54′19″ W [point 50], Marie Pampoen, 31 m depth, 12.vi.2017, coll. JDR); MISE JDR170612-7-46 (12°05′24″ N, 68°54′19″ W [point 50], Marie Pampoen, 31 m depth, 12.vi.2017, coll. JDR); MISE JDR170614-11-67 (12°22′29″ N, 69°09′30″ W [point 76], Playa Kalki, 30 m depth, 14.vi.2017, coll. JDR); MISE NA (12°19′45″ N, 69°09′05″ W [point 74], Playa Jeremi, 12-38 m depth, 20.vi.2017, coll. JDR); ZMA.POR.14209 (12°07′23″ N, 68°58′14″ W [point 56], west of Piscadera Bay, 30 m depth, 11.v.1998, coll. M.J. de Kluijver); ZMA.POR.14245 (12°08′21″ N, 68°59′53″ W [point 64], Snake Bay, 20 m depth, 18.v.1998, coll. M.J. de Kluijver); ZMA.POR.16222 (coordinates and depth unknown, 12.i.1999, coll. H. Ranner); ZMA.POR.16312 (coordinates and depth unknown, vii.1992, coll. P. Willemsen); ZMA.POR.18396 (coordinates unknown, 27 m depth, 13.i.2003, coll. F.J. Parra-Velandia); ZMA.POR.22404 (12°07′32″ N, 68°58′27″ W [point 59], Buoy 1, north of Piscadera Bay, 15 m depth, 9.ii.1992, coll. R.W.M. Van Soest); ZMA.POR.3593 (12°04′29″ N, 68°52′50″ W [point 44], Jan Thiel Bay, 23–32 m depth, 16.xi.1975, coll. unknown); ZMA.POR.3623 (coordinates unknown, 10 m depth, xi.1975, coll. E. Westinga); ZMA.POR.3670 (12°07′45″ N, 68°58′51″ W [point 61], 500 m west

of Piscadera Reef, 50 m depth, 7.xi.1975, coll. S. Weinberg); ZMA.POR.5703 (12°08′01″ N, 68°59′07″ W [point 62], Blue Bay, 55 m depth, 20.x.1984, coll. W.F. Hoppe & M.J.M. Reichert). **Sint Eustatius**. MISE JDR150610-2, JDR150610-3 (17°27′44.2″ N, 62°58′46.7″ W [point 97], Sta. EUX007, depth: 20 m depth, 10.vi.2015, coll. JDR); MISE JDR150610-17 (17°27′53.9″ N, 62°59′00.7″ W [point 101], Sta. EUX008, 16 m depth, 10.vi.2015, coll. JDR); MISE JDR150611-27 (17°27′42.1″ N, 62°58′41.2″ W [point 96], Sta. EUX009, 37 m depth, 11.vi.2015, coll. JDR); MISE JDR150611-64 (17°28′19.2″ N, 62°59′15.6″ W [point 107], Sta. EUX010, 13 m depth, 11.vi.2015, coll. JDR); MISE JDR150612-80 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 18 m depth, 12.vi.2015, coll. JDR); MISE JDR150612-97 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 13 m depth, 12.vi.2015, coll. JDR); MISE JDR150614-124 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 15 m depth, 14.vi.2015, coll. JDR); MISE JDR150615-135 (17°28′05.6″ N, 62°59′30.3″ W [point 104], Sta. EUX016, 21 m depth, 15.vi.2015, coll. JDR); MISE JDR150615-137 (17°28′05.6″ N, 62°59′30.3″ W [point 104], Sta. EUX016, 20 m depth, 15.vi.2015, coll. JDR); MISE JDR150616-145 (17°28′13.6″ N, 62°59′30.2″ W [point 106], Sta. EUX019, 19 m depth, 16.vi.2015, coll. JDR).

Photographic records (*n* = 28). In situ: Specimens RMNH.COEL.42431, MISE JDR150610-2, JDR150610-3, JDR150610-17, JDR150611-27, JDR150611-64, JDR150612-80, JDR150612-97, JDR150614-124, JDR150615-135, JDR150615-137, JDR150616-145, JDR170609-1-4, JDR170610-4-30, MISE JDR170612-7-45, JDR170612-7-46, JDR170614-11-67, JGH191106-2-1; Preserved: Specimens ZMA.POR.3593, 3623, 3670, 5703, 14209, 14245, 16222, 16312, 18396, 22404.

Description as in West [26]: Colonies with polyps regularly distributed over the sponge surface, but clusters formed by two or more polyps are also present; the distribution of polyps is variable depending on the host sponge. The polyp dimensions in living specimens are 1 mm in high and 1.5 mm in diameter; completely retracted polyps are mammiform, rising little above the surface of the coenenchyme, the coenenchyme surrounding the polyps is rarely more than 2 mm. Capitular ridges are 12 in number, mesenteries are 24 in number; tentacles arranged in two cycles and 24 in number with up to 1 mm in length in living and expanded specimens. The polyps present abundant pigmentation and a dense concentration of sponge spicules and calcareous sand grains, with an overall dark maroon color.

Recent and other previous records: Barbados [66], Colombia [67], Curaçao [24], Dominica [66], Puerto Rico [26], Tobago, USA (Navassa) [66], and Venezuela [70].

Remarks: As with other *Bergia* congeners listed above, this species appears in most literature as *P. puertoricense* as the genus *Bergia* was only recently resurrected [71]. *B. puertoricense* was found associated to *Petrosia* (*Petrosia*) *weinbergi* van Soest, 1980, *Petrosia* (*Petrosia*) aff. *weinbergi*, *Agelas clathrodes* (Schmidt, 1870), *Agelas conifera* (Schmidt, 1870), *Agelas* cf. *conifera* (Schmidt, 1870), *Svenzea zeai* (Alvarez, van Soest & Rützler, 1998), *Topsentia* sp., and *Xestospongia* sp. in Curaçao; and with *Svenzea zeai* in Sint Eustatius.

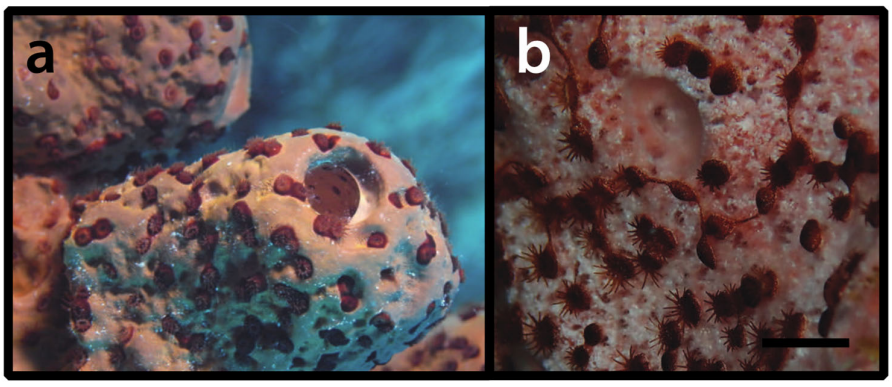

Figure 6. *Bergia puertoricense* in situ; (**a**) specimen MISE JDR170609-1-4 from Carmabi, Hilton Hotel [point 53], Curaçao, depth = 20 m, and (**b**) image (not collected) from Red Slave, Bonaire, depth = 30 m. Scale bar in (**b**) = approximately 1 cm.

Genus *Parazoanthus* Haddon & Shackleton, 1891 [50]

3.2.6. *Parazoanthus swiftii* (Duchassaing de Fonbressin & Michelotti, 1860) [23] (Figure 7)

Specimens examined (*n* = 22). **Bonaire**. MISE JDR191024-2-1 (12°7′53.28″ N, 68°16′59.76″ W [point 32], Corporal Meiss, 20 m depth, 24.x.2019, coll. JDR); MISE JDR191029-1-1 (12°13′24.42″ N, 68°24′13.38″ W [point 22], Taylor Made, 37 m depth, 29.x.2019, coll. JDR); MISE JDR191101-2-3 (12°15′49.8″ N, 68°24′49.2″ W [point 25], Boka Slaagbaai, 8 m depth, 1.xi.2019, coll. JDR). **Curaçao.** RMNH.COEL.42432 (12°06′33″ N 68°57′15″ W [point 52], Santa Marta, Water Factory, 20 m depth, 27.iii.2014, coll. BWH); MISE JDR170609-2-6 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 21 m depth, 9.vi. 2017, coll. JDR); MISE JDR170610-4-32 (12°08′53″ N, 69°00′00″ W [point 65], Sint Michiel's Bay, 19 m depth, 10.vi.2017, coll. JDR); MISE JDR170614-11-66 (12°22′29″ N, 69°09′30″ W [point 76], Playa Kalki south, 40 m depth, 14.vi.2017, coll. JDR); ZMA.POR.5839 (12°07′38″ N, 68°58′39″ W [point 60], Buoy 2, north of Piscadera Bay, 10 m depth, 2.i.1981, coll. R.W.M. Van Soest); ZMA.POR.10110 (coordinates and depth unknown, 1992, coll. P. Willemsen). **Saba.** ZMA.POR.15667 (17°36′29.7″ N, 63°15′07.6″ W [point 79], 800 m off Fort Bay, depth unknown, 12.iii.1986, coll. J. Vermeulen); RMNH.COEL.17763 (17°37′05″ N, 63°15′26″ W [point 81], Sta. LUY-021, between Fort Bay and Ladder Point, depth unknown, 10.iii.1986, coll. JCH). **Sint Eustatius.** MISE JDR150612-85, JDR150612-86 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 14–15 m depth, 12.vi.2015, coll. JDR); MISE JDR150612-94, JDR150612-98, JDR150612-101 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 14–15 m depth, 12.vi.2015, coll. JDR); MISE JDR150614-116, JDR150614-118 (17°29′00.6″ N 62°59′52.9″ W [point 96], Sta. EUX014, 21–22 m depth, 14.vi.2015, coll. JDR); MISE JDR150614-120 (17°29′00.6″ N, 62°59′52.9″ W [point 115], Sta. EUX014, 16 m depth, 14.vi.2015, coll. JDR); MISE JDR150617-150 (17°28′48.3″ N, 62°59′39.4″ W [point 112], Sta. EUX020, 17 m depth, 17.vi.2015, coll. JDR); MISE JDR150618-159 (17°27′56.6″ N, 63°00′07.2″ W [point 102], Sta. EUX022, 27 m depth, 18.vi.2015, coll. JDR); MISE JDR150619-165 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta. EUX024, 29 m depth, 19.vi.2015, coll. JDR).

Photographic records (*n* = 20). In situ: Specimens RMNH.COEL.42432, MISE JDR150612-85, JDR150612-86, JDR150612-94, JDR150612-98, JDR150614-116, JDR150614-118, JDR150614-120, JDR150617-150, JDR150618-159, JDR150619-165, JDR170609-2-6, JDR170610-4-32, JDR170614-11-66, JDR191024-2-1, JDR191029-1-1, JDR191101-2-3. Preserved: Specimens ZMA.POR.5839, 15667, 10110.

Description as in Duchassaing de Fonbressin & Michelotti [23]: Small species with brownish/orange coloration, growing on the surface of the sponge in a linear pattern. The lines are formed by polyps connected to each other by short propagules. The lines are generally composed of 2 to 7 polyps, however solitary polyps and clusters of three to four polyps with no particular linear distribution are also present. Polyps are 1 mm in height and diameter and are not immersed in the sponge tissues.

Recent and other previous records: Ascension Islands [9,73], Barbados [65,66], Brazil [1,66], Colombia [67], Cuba [74], Curaçao [24,66], Dominica [66,75], Jamaica [68,76,77], Panama [66,78], Puerto Rico [26], Saint Thomas [23], Tobago, US Virgin Islands, USA (Georgia, Florida) [66], and Venezuela [70].

Remarks: This species has been shown to be closely related to *P. darwini* from the Galapagos in the Eastern Pacific via molecular studies [61]. *P. swiftii* was found associated with *Topsentia ophiraphidites* (Laubenfels, 1934) and *Topsentia* sp. in Curaçao [24]; with *Dragmacidon reticulatum* (Ridley & Dendy, 1886) in Saba; and with *Iotrochota birotulata* (Higgin, 1877) in Sint Eustatius.

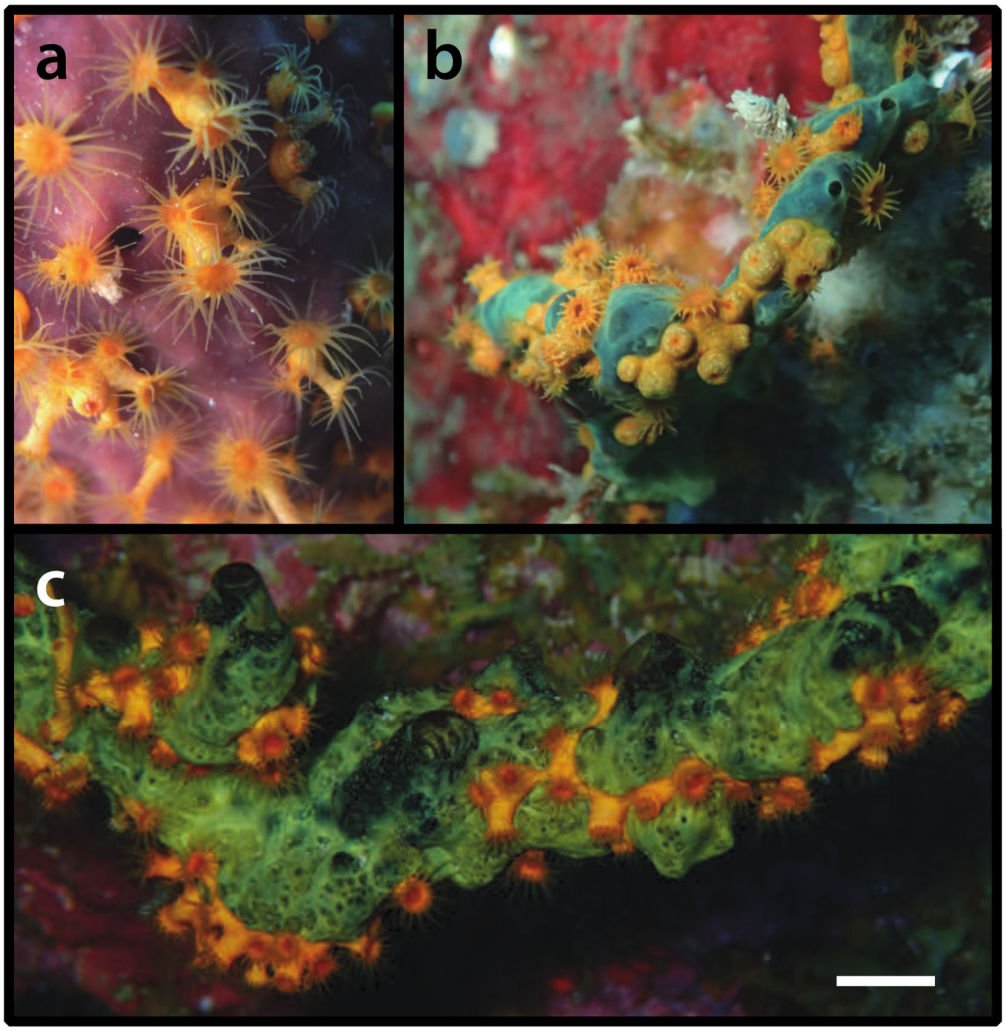

Figure 7. In situ images of *Parazoanthus swiftii* (**a**) RMNH.COEL.42432 from Santa Marta, Water Factory, Curaçao [point 52], depth = 20 m, (**b**) MISE JDR170610-4-32 from Sint Michiel's Bay [point 65], Curaçao, depth = 19 m, and (**c**) image (not collected) from Bari Reef, Bonaire, depth = 18 m. Scale bar in (**c**) = approximately 1 cm.

3.2.7. Parazoanthidae? sp. (Figure 8)

Specimens examined (*n* = 1). **Curaçao.** RMNH.COEL.40264 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Bay, depth unknown, 11.ix.1972, coll. JCH).

Photographic records (*n* = 1). Preserved: specimen RMNH.COEL.40264.

Remarks: The specimen RMNH.COEL.40264 was poorly preserved and was not possible to confidently identify to species level. While the polyp arrangement and size resembled preserved specimens of *P. swiftii*, there is also the possibility it is an *U. parasiticus* specimen. Future examination of the host sponge species should help more confidently identify this specimen as these zoantharian species do not have overlapping host species.

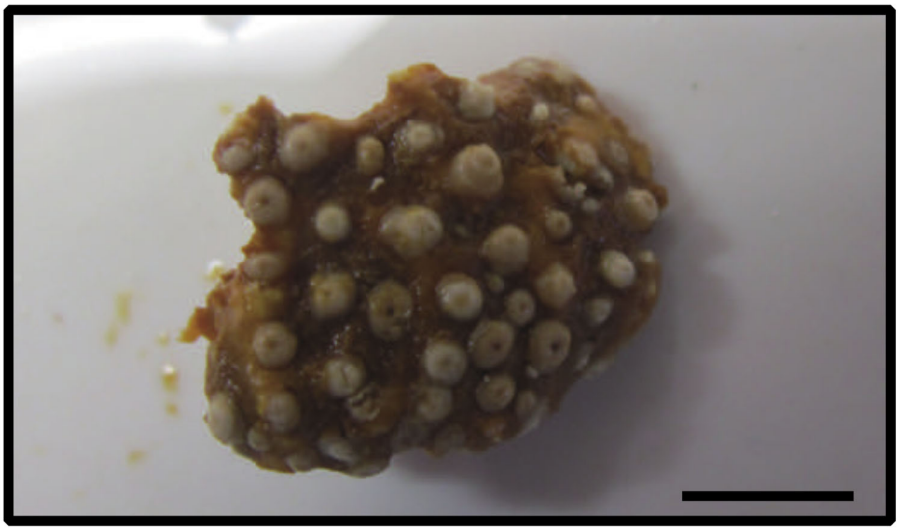

Figure 8. Preserved specimen RMNH.COEL.40264 Parazoanthidae? sp. from north of Piscadera Bay [point 61], Curaçao, depth = unknown. Scale bar = approximately 1 cm.

3.2.8. *Parazoanthus atlanticus* sp. n. (Figure 9)

http://zoobank.org/urn:lsid:zoobank.org:act:151E1AAA-7CAD-46AF-83B6-BFC0D0E0C931

Synonymy: *Parazoanthus* sp. 269 *sensu* Reimer et al. 2010 [4] (p. 162, Figure 2e)

Etymology: "atlanticus" in reference to the wide Atlantic distribution of this species, known from the Cape Verde Islands (East Atlantic) and Curaçao and Bonaire in the Caribbean.

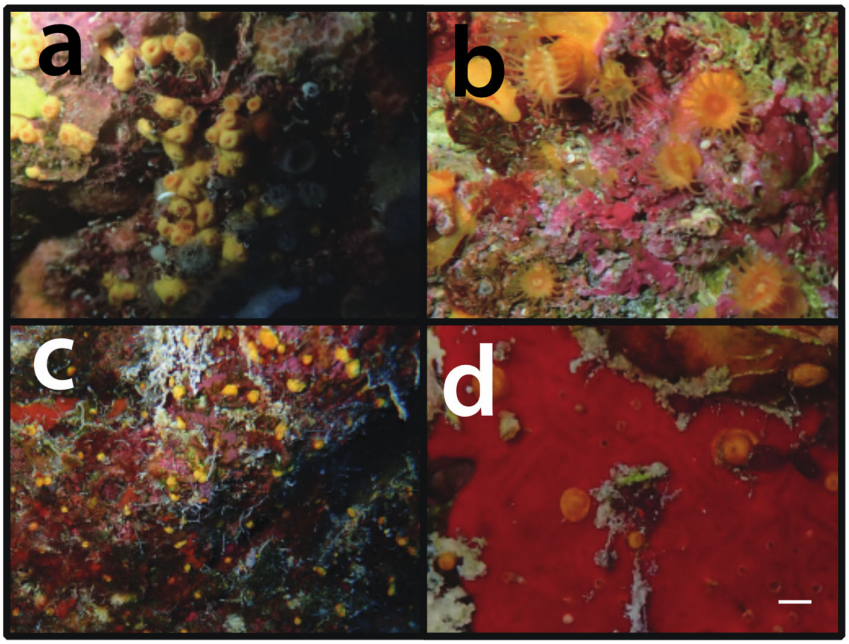

Figure 9. In situ images of *Parazoanthus atlanticus* sp. n. (**a**) specimen MISE JDR170613-10-61 from Caracas Bay, Tugboat [point 42], Curaçao, depth = 18 m, (**b**) specimen MISE JDR170616-13-76 from north of Blue Bay [point 62], Curaçao, depth = 34 m, (**c**) specimen MISE JDR191103-1-1 from Small Wall [point 14], Bonaire, depth = 16 m, and (**d**) specimen MISE JDR191103-1-1 from Small Wall, Bonaire, depth = 16 m, with presence of much smaller *Umimayanthus* sp. Note the small sizes of the colonies formed by *P. atlanticus* sp. n. and the high frequency of solitary polyps. Scale bar in d) = approximately 3 mm.

Material examined: Type locality Curaçao, Director's Bay [point 40], 12°03′59″ N, 68°51′38″ W (Table S1). **Holotype**: NSMT-Co 1706 (12°03′59″ N, 68°51′38″ W [point 40], Director's Bay, Curaçao, 27 m depth, 13.vi.2017, coll. JDR). **Paratype 1**: RMNH.COEL.42433 (12°08′06″ N, 68°59′16″ W [point 63], Blue Wall, Curaçao, on the ceiling of a cave at 10 m depth, 2.iv.2014, coll. BWH). **Paratype 2**: NSMT-Co 1707 (12°03′59″ N, 68°51′38″ W [point 40], Director's Bay, 20 m depth, 13.vi.2017, coll. JDR). **Other material** (n = 5). Other specimens are deposited in the Molecular Invertebrate Systematics and Ecology (MISE) Laboratory collection at the University of the Ryukyus, Nishihara, Okinawa, Japan. **Bonaire**. MISE JDR191029-1-3 (12°13′24.42″ N, 68°24′13.38″ W [point 22], Taylor Made, 25 m depth, 29.x.2019, coll. JDR); MISE JDR191103-1-1 (12°10′41.1″ N, 68°17′32.34″ W [point 14], Small Wall, 16 m depth, 3.xi.2019, coll. JDR). **Curaçao.** MISE JDR170613-10-60 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, 29 m depth, 13.vi.2017, coll. JDR); MISE JDR170613-10-61 (similar but at 18 m depth); MISE JDR170616-13-76 (12°08′01″ N, 68°59′07″ W [point 62], north of Blue Bay, 34 m depth, 16.vi.2017, coll. JDR).

Photographic records (n = 8). **Bonaire.** In situ: Specimens MISE JDR191029-1-3, JDR191103-1-1. **Curaçao.** In situ: Specimens RMNH.COEL.42433, NSMT-Co 1706, NSMT-Co 1707, MISE JDR170613-10-60, JDR170613-10-61, JDR170616-13-76.

Sequences: All sequences were deposited in GenBank with accession numbers MT102222-MT102229 for the mitochondrial cytochrome oxidase subunit I region (COI-mtDNA), MT103533-MT103540 for mitochondrial ribosomal subunit 16S ribosomal DNA, and MT103524-MT103531 for the nuclear ribosomal internal transcribed spacer sequences (ITS-rDNA).

Description. Size: Preserved polyps are on average 3.117 mm ± 0.640 mm (σ^2 = 0.427, n = 24 polyps) in diameter and 1.446 mm ± 0.569 mm (σ^2 = 0.337, n = 24 polyps) in height. All measurements were performed on closed polyps of specimens preserved in 99% ethanol.

Morphology: *Parazoanthus atlanticus* sp. n. presents a bright yellow color, almost orange, in all collected material and in situ. The polyps have approximately 24 to 30 tentacles. Colonies generally consist of clusters of three polyps scattered over the sponge surface, but single polyps and groups of up to 14 polyps were also observed. Polyps were solitary or connected to each other by the stolon over the sponge surface. Distance between polyps was variable and no noticeable pattern was found.

Cnidae: All cnidocyte categories previously reported in Zoantharia [32] were found, however holotrichs and p-mastigophores were particularly low in frequency in all examined tissues (tentacles, column, pharynx and mesenterial filaments); p-mastigophores were only found in mesenterial filaments, and holotrichs medium were found only in the pharynx. Spirocysts were absent in column and mesenterial filaments. For details on sizes, lengths, and widths of each cnidocyte categories, refer to Table 3 and Figure 10.

Table 3. Results of the cnidocyte analyses of all categories found per examined tissue. Notice the differential distribution and frequency of each cnidocyte category across tissues.

	Sample ID: NSMT-Co 1706	Length (Min-Max, Average) µm	Width (Min-Max, Average) µm	*n*
Tentacles	Spirocysts	13–29, 20	2–6, 3.5	222
	Holotrichs (L)	32	15	1
	Bastrichs and microbasic b-mastigophores	14–23, 19.8	2–5, 4.3	24
	Microbasic p-mastigophores	-	-	-
Column	Spirocysts	-	-	-
	Holotrichs (L)	20–47, 29.2	11–15, 13.1	16
	Bastrichs and microbasic b-mastigophores	-	-	-
	Microbasic p-mastigophores	-	-	-
Pharynx	Spirocysts	23	3	1
	Holotrichs (M)	17	8	1
	Bastrichs and microbasic b-mastigophores	14–18, 16.1	2–4, 3.3	17
	Microbasic p-mastigophores	-	-	-
Filaments	Spirocysts	-	-	-
	Holotrichs (L)	25–31, 28.4	9–16, 13.5	32
	Bastrichs and microbasic b-mastigophores	-	-	-
	Microbasic p-mastigophores	12–20, 16	3–6, 4.8	10

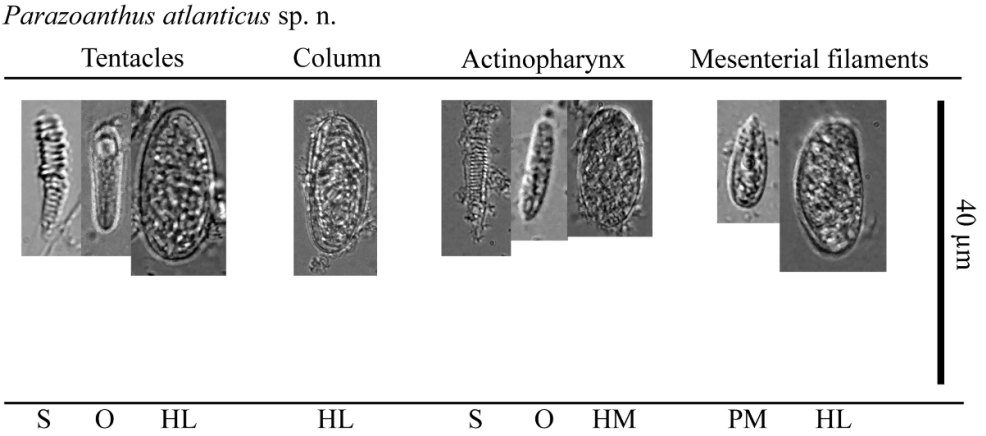

Figure 10. Images of all cnidae categories and average size of found across different tissues in polyps of *P. atlanticus* sp. n.; S = Spirocysts, O = basitrich & microbasic b-mastigophores, HL = Holotrichs (L), HM = Holotrichs (M), and PM = microbasic p-mastigophores.

Differential diagnosis: *Parazoanthus atlanticus* sp. n. can be distinguished from *P. anguicomus* (Norman, 1869) [79], *P. haddoni* Carlgren, 1913 [54], *P. antarcticus* Carlgren, 1927 [80], *P. aruensis* Pax, 1911 [81], *P. elongatus* McMurrich, 1904 [82], and *P. juan-fernandezii* Carlgren, 1922 [83] by polyp diameter and numbers of tentacles, which are larger in all the above species (see also [71]). As well, *P. darwini* Reimer & Fujii, 2010 [61] and *P. lividum* Cutress, 1971 [84] differ in distribution ranges, being only found in the South and East Pacific; additionally, multiple morphological characteristics set *P. lividum* apart, including polyp size and colonies formed by polyps organized in a band-like arrangement [84]. Although the descriptions of *P. axinellae* (Schmidt, 1862) [85] and *P. capensis* Duerden, 1907 [86] overlap with *P. atlanticus* sp. n. regarding the number of tentacles and polyp diameters, both *P. axinellae* and *P. capensis* associate with a different sponge species. *P. axinellae* was reported associated with *Axinella verrucosa*, *A. damicornis*, *Petrosia ficiformis,* and *Hippospongia*

communis; while for *P. capensis,* the associated sponge species remains unknown, but the sponges are arboresent/branching in shape [86]. On the other hand, the sponges associated to *P. atlanticus* sp. n., although not identified, are all encrusting in morphology. *P. capensis* from South Africa was described with pale yellow polyps with colorless tentacles [86], different from the brighter yellowish coloration in *P. atlanticus* sp. n. Within genus *Parazoanthus,* the species that most resembles *P. atlanticus* sp. n. in colony shape and polyp color is *P. swiftii* (Duchassaing de Fonbressin & Michelotti, 1860) [23], however it may be slightly differentiated by polyp size; 2.5 mm in diameter for *P. swiftii* and 3.1 mm for *P. atlanticus* sp. n. Additionally, in colonies of *P. swiftii*, solitary polyps are only exceptionally found while in *P. atlanticus* sp. n., solitary polyps are relatively frequently observed. As well, while *P. swiftii* is often found in environments with abundant light exposure and is associated to a wide range of sponges, *P. atlanticus* sp. n. has only been found in cave-like environments and exclusively associates with encrusting sponges.

Encrusting sponges in caves and cracks of Bonaire have been reported to have high levels of diversity and contain many cryptic species [87]. Accurate identification of the host encrusting sponges of *P. atlanticus* sp. n. in the future would further help characterize differences with closely related species. As well, microanatomical analyses (e.g., [53]) should also help further differentiate *P. atlanticus* sp. n. from closely related species.

Phylogenetic analyses using the sequences of the ITS-rDNA region also support *P. atlanticus* sp. n. as a monophyly with complete support in both ML and BPP analyses. Similar tree topologies for the COI-mtDNA and 16S-rDNA analyses were seen but with weaker support (Figure S1). When the sequences of COI-mtDNA, 16S-rDNA, and ITS-rDNA were concatenated, the monophyly of *P. atlanticus* sp. n. was moderately supported (ML = 71%, BPP = 0.86; Figure 11). Although the phylogenetic position of *P. atlanticus* sp. n. within genus *Parazoanthus* remains uncertain, both the ITS-rDNA and concatenated phylogenies weakly support *P. atlanticus* sp. n. as a basal or sister clade to a clade formed by *P. axinellae*, *P. anguicomus*, and *P. capensis*. Remarkably, in the COI-mtDNA region, a single nucleotide substitution from "C" to "T" at position 178 of our alignment was found to be unique to *P. atlanticus* sp. n. across all species of sponge-associated zoantharian in genera *Bergia*, *Parazoanthus* and *Umimayanthus*; several substitutions and indels were also found to be unique to *P. atlanticus* sp. n. in ITS-rDNA and 16S-rDNA regions.

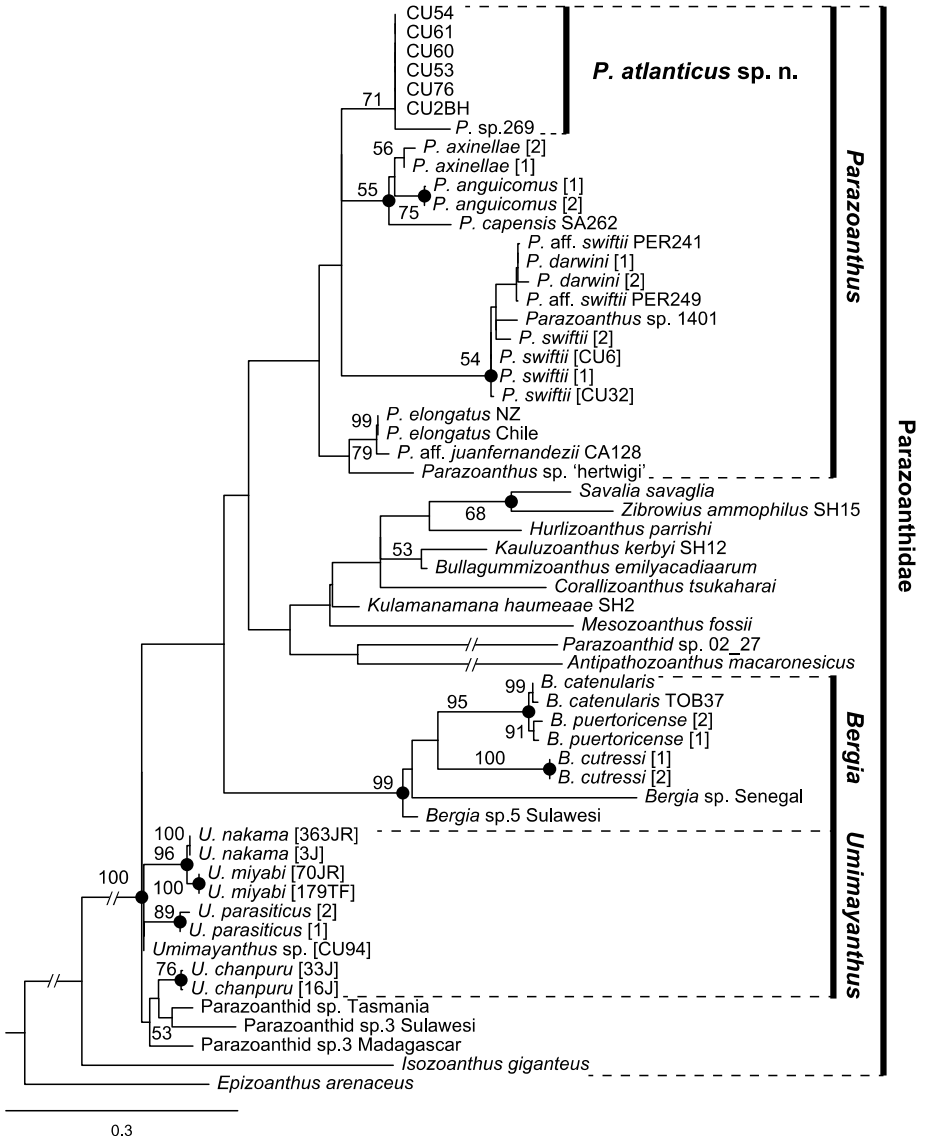

Figure 11. Maximum likelihood (ML) phylogenetic reconstruction using the concatenated alignment of one nuclear DNA region ITS-rDNA, and two mitochondrial regions 16S-rDNA and COI mt-DNA. Values on branches represent bootstrap support >50 from maximum likelihood analyses and black circles indicate Bayesian posterior probabilities >95%. Note the clear monophyly form by *P. atlanticus* sp. n. in reference to other species in genus *Parazoanthus*. CU53 = NSMT-Co 1706; CU54 = NSMT-Co 1707; CU60 = MISE JDR170613-10-60; CU61 = MISE JDR170613-10-61; CU76 = MISE JDR170616-13-76; CU2BH = RMNH.COEL.42433; CU6 = MISE JDR170609-2-6; CU32 = MISE JDR170610-4-32; CU94 = MISE JDR170619-20-94.

Distribution. Localities and islands recorded in this study: **Bonaire**. Taylor Made [point 22] and Small Wall [point 14]. **Curaçao**. Director's Bay [point 40], Caracas Bay [point 42], Piscadera Bay [point 61], Blue Bay [point 62], and Blue Wall [point 63].

Recent and other previous records: *P. atlanticus* sp. n. was previously reported in Reimer et al. [4] as *Parazoanthus* sp. 269; the specimen was collected at Danger, Tarrafal Bay, Santiago I. in Cape Verde from a submerged cave at 20 m depth.

Genus *Umimayanthus* Montenegro, Sinniger & Reimer, 2015 [88]

3.2.9. *Umimayanthus parasiticus* (Duchassaing de Fonbressin & Michelotti, 1860) [23] (Figure 12)

Specimens examined (*n* = 78). **Bonaire**. RMNH.COEL.40255 (12°05′40″ N, 68°17′06″ W [point 7], Inlet Salt Lake West Coast, 1–2 m depth, 10.iv.1978, coll. JCH). **Curaçao**. RMNH.COEL.42434 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 20 m depth, 27.iii.2014, coll. BWH); MISE JDR170609-1-1, JDR170609-1-2, JDR170609-1-5 (12°07′17″ N, 68°58′09″ W [point 53], Carmabi, Hilton Hotel, 15–32 m depth, June 9, 2017, coll. JDR); MISE JDR170613-9-55 (12°03′59″ N, 68°51′38″ W [point 40], Director's Bay, 20 m depth, 13.vi.2017, coll. JDR); MISE JDR170619-21-97 (12°13′55″ N, 69°05′44″ W [point 67], Playa Cas Abao, 20 m depth, 19.vi.2017, coll. JDR); MISE NA (12°19′45″ N, 69°09′05″ W [point 74], Playa Jeremi, 24–38 m depth, 20.vi.2017, coll. JDR); RMNH.COEL.40239 (12°07′45″ N, 68°58′51″ W [point 61], Buoy 2, north of Piscadera Bay, 5 m depth, 9.ix.1972, coll. JCH); RMNH.COEL.40258 (12°04′47″ N, 68°50′25″ W [point 47], Spaanse Water east side, depth unknown, 9.vi.1971, coll. JCH); RMNH.COEL.40269 (12°04′25″ N, 68°50′37″ W [point 43], Spaanse Water near Fosfaatberg, shallow, 12.xi.1972, coll. JCH); ZMA.POR.10756 (12°03′48″ N, 68°51′04″ W [point 38], Spaanse Water, depth unknown, 1989, coll. M. Kuenen); ZMA.POR.14194 (12°04′49″ N, 68°53′18″ W [point 48], Jan Thiel, Curaçao, 38 m depth, 10.v.1998, coll. M.J. de Kluijver); ZMA.POR.14198 (12°04′29″ N, 68°52′50″ W [point 44], Jan Thiel Bay, 24 m depth, 10.v.1998, coll. M.J. de Kluijver); ZMA.POR.14271 (12°07′23″ N, 68°58′14″ W [point 56], west of Piscadera Bay, 34 m depth, 22.v.1998, coll. M.J. de Kluijver); ZMA.POR.14353 (12°07′17″ N, 68°58′09″ W [point 53], Carmabi, Hilton Hotel, 18 m, 21.v.1998, coll. R. Gomez); ZMA.POR.20902 (12°6′16.6″ N, 68°56′36.6″ W [point 77], Superior Producer wreck, 33 m depth, 23.v.1998, coll. R. Gomez); ZMA.POR.20913 (12°6′26.6″ N, 68°56′51.7″ W [point 78], Holiday Beach, 19 m depth, 30.i.2000, coll. M.J. de Kluijver); ZMA.POR.20914 (12°6′26.6″ N, 68°56′51.7″ W [point 78], Holiday Beach, depth unknown, 18.ii.2000, coll. R. Gomez); ZMA.POR.22251 (12°07′20″ N, 68°58′08″ W [point 54], Carmabi, house reef, 22 m depth, 1.v.1991, coll. P. Willemsen); ZMA.POR 3304, 3634 (12°04′03″ N, 68°51′10″ W [point 41], Santa Barbara Beach, Spanish Lagoon, 3 m depth, 17.i.1974, 18.i.1974, coll. J.H. Stock); ZMA.POR.3305, 3306 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Reef, 32–40 m depth, 19.xii.1973, 22.iii.1974, coll. J.H. Stock); ZMA.POR.3315 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Reef, 10-18 m depth, 21.xi.1973, coll. J.H. Stock); ZMA.POR.3486 (12°08′01″ N, 68°59′07″ W [point 62], Blue Bay, 3 m depth, 17.x.1958, coll. J.H. Stock); ZMA.POR.3581 (12°07′20″ N 68°58′08″ W [point 54], Carmabi, House Reef, 10–25 m depth, 10.xii.1975, coll. E. Westinga); ZMA.POR.3600, 3647 (12°08′01″ N, 68°59′07″ W [point 62], Blue Bay, 20–30 m depth, xi.1975, coll. S. Weinberg & E. Westinga); ZMA.POR.3601 (12°07′23″ N, 68°58′14″ W [point 56], west of Piscadera Bay, 15 m depth, 13.xi.1975, coll. unknown); ZMA.POR.3609, 3648, 3653, 3644 (12°07′20″ N, 68°58′08″ W [point 54], Carmabi, House Reef, 11–20 m depth, 14.xi.1978, 16.xi.1978, coll. unknown); ZMA.POR.3614 (12°08′01″ N, 68°59′07″ W [point 62], Blue Bay, 15–20 m depth, xi.1975, coll. S. Weinberg & E. Westinga); ZMA.POR.3646 (12°07′32″ N, 68°58′27″ W [point 59], Buoy 1, north of Piscadera Bay, 40 m depth, 22.iii.1974, coll. J.H. Stock); ZMA.POR.3877 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Reef, 35 m depth, 13.xi.1975, coll. unknown). **Saba**. ZMA.POR 15745 (17°36′29.7″ N, 63°15′07.6″ W [point 79], 800 m off Fort Bay, Saba, depth unknown, 12.iii.1986, coll. J. Vermeulen). **Saba Bank**. RMNH.POR.5102, 5152, 5153 (17°33′00″ N, 63°22′00″ W [point 94], Sta. LUY-124, northeast side, 24 m depth, 12.xi.1972, coll. Luymes Exp.); RMNH.POR.5103 (17°12′00″ N, 63°40′00″ W [point 85], Sta. LUY-111, southwest side, 28 m depth, 24.v.1972, coll. Luymes Exp.); RMNH.POR.5104 (17°14′00″ N, 63°34′00″ W [point 86], Sta. LUY-055, northeast side, 39 m depth, 15.x.1972, coll. Luymes Exp.); RMNH.POR.5105 (17°29′00″ N, 63°13′00″ W [point 92], Sta. LUY-144, east side, 16 m depth, 14.xi.1972, coll. Luymes Exp.); RMNH.POR.5148 (17°23′00″ N, 63°45′00″ W [point 90], Sta. LUY-069, 44 m depth, 17.x.1972, coll. Luymes Exp.); RMNH.POR.5149 (17°33′00″ N, 63°27′00″ W [point 95], Sta. LUY-126, 36 m depth, 12.xii.1972, coll. Luymes Exp.); RMNH.POR Sta-146 (17°26′00″ N, 63°12′00″ W [point 91], Sta. LUY-146, east-slope, 30 m depth, 14.vi.1972, coll. Luymes Exp.). **Sint Eustatius**. MISE JDR150610-1, JDR150610-5, JDR150610-8 (17°27′44.2″ N, 62°58′46.7″ W [point 97], Sta. EUX007, 19–21 m depth, 10.vi.2015, coll. JDR); MISE JDR150610-10, JDR150610-11, JDR150610-13, JDR150610-14, JDR150610-22 (17°27′53.9″ N, 62°59′00.7″ W [point 101], Sta. EUX008, Sint Eustatius, 16–17 m depth, 10.vi.2015, coll. JDR); MISE JDR150610-25, JDR150610-26 (17°27′53.9″ N, 62°59′00.7″ W [point 101], Sta. EUX008,

depth unknown, 10.vi.2015, coll. JDR); MISE JDR150611-28 (17°27′42.1″ N, 62°58′41.2″ W [point 96], Sta. EUX009, 34 m depth, 11.vi.2015, coll. JDR); MISE JDR150611-32, JDR150611-41, JDR150611-63, JDR150611-76 (17°28′19.2″ N, 62°59′15.6″ W [point 107], Sta. EUX010, 11–13 m depth, 11.vi.2015, coll. JDR); MISE JDR150612-78, JDR150612-82, JDR150612-83 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 10–17 m depth, 12.vi.2015, coll. JDR); MISE JDR150612-91, JDR150612-99 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 12–15 m depth, 12.vi.2015, coll. JDR); MISE JDR150613-109 (17°28′56.3″ N, 62°59′20.3″ W [point 113], Sta. EUX013, 3 m depth, 13.vi.2015, coll. JDR); MISE JDR150614-117 (17°29′00.6″ N, 62°59′52.9″ W [point 115], Sta. EUX014, 22 m depth, 14.vi.2015, coll. JDR); MISE JDR150614-126, JDR150614-133 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 15–17 m depth, 14.vi.2015, coll. JDR); MISE JDR150615-134 (17°28′05.6″ N, 62°59′30.3″ W [point 104], Sta. EUX016, 21 m depth, 15.vi.2015, coll. JDR); MISE JDR150615-141 (17°28′31.5″ N, 62°59′33.6″ W [point 108], Sta. EUX017, 19 m depth, 15.vi.2015, coll. JDR); MISE JDR150616-143, JDR150616-144 (17°28′13.6″ N, 62°59′30.2″ W [point 106], Sta. EUX019, 19 m depth, 16.vi.2015, coll. JDR); MISE JDR150619-162 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta. EUX024, 28 m depth, 19.vi.2015, coll. JDR); RMNH.POR.5099 (17°28′02.7″ N, 62°58′44.7″ W [point 103], Sta. LUY-121, <15 m depth, 9–10.xi.1972, coll. Luymes Exp.). **Sint Maarten**. RMNH.POR.5150 (18°04′00″ N, 63°06′00″ W [point 124], Sta. LUY-122, Baie Marigot, <15 m depth, 11.xi.1972, coll. Luymes Exp.).

Photographic records (*n* = 73). In situ: Specimens RMNH.COEL.42434, MISE JDR150610-1, JDR150610-5, JDR150610-8, JDR150610-10, JDR150610-11, JDR150610-13, JDR150610-14, JDR150610-22, JDR150611-28, JDR150611-32, JDR150611-41, JDR150611-76, JDR150612-78, JDR150612-82, JDR150612-83, JDR150612-91, JDR150612-99, JDR150613-109, JDR150614-117, JDR150614-126, JDR150615-134, JDR150615-141, JDR150616-143, JDR150616-144, JDR150619-162, JDR170609-1-1, JDR170609-1-2, JDR170609-1-5, JDR170613-9-55, JDR170619-21-97; Preserved: Specimens RMNH.COEL.40239, 40255, 40258, 40269, RMNH.POR.5099, 5102, 5103, 5104, 5105, 5148, 5149, 5150, 5152, 5153, Sta-146, ZMA.POR.3304, 3305, 3306, 3315, 3486, 3581, 3600, 3601, 3609, 3614, 3634, 3644, 3646, 3647, 3648, 3653, 3877, 10756, 14194, 14198, 14271, 14353, 15745, 20902, 20913, 20914, 22251.

Description as in Duchassaing de Fonbressin & Michelotti [23] and West [26]: A very small species living in sponges, and given its parasitic habits is similar to genus *Bergia* (note this species is now not thought to be generally parasitic [89]). It is a zoantharian without tissues reinforced with sand deposits. The propagules are basilar. The oral disk, including tentacles, is about ¾ of the total polyp diameter. The length and diameter off expanded polyps are between 1 and 1.5 mm, the retracted polyps are mammiform in shape and rising little from above the sponge surface; the diameter of the coenenchyme surrounding the polyps is about 2 mm. Polyps are usually solitary or occasionally in groups of 2-3; the polyps present 14 ridges and 28 tentacles. The tentacles are yellow–brown in color, due to the symbiotic zooxanthellae.

Recent and other previous records: Bahamas [64], Barbados [65,66], Bermudas [90–93], Colombia [67], Cuba [74], Curaçao [24,66], Dominica [66,75], Mexico [94], Panama [66,78], Puerto Rico [26], Sint Eustatius [22], Saint Thomas [23], Tobago, US Virgin Islands [66], USA (Florida; Navassa) [64,66,95,96], Venezuela [70].

Remarks: Endemic to the Caribbean Sea, this species was the second most commonly observed zoantharian in the Dutch Caribbean, recorded to all islands with exception of Aruba. This species was placed in *Parazoanthus* until recent phylogenetic analyses followed by description of the genus *Umimayanthus* changed its placement [88]. *U. parasiticus* was found associated with *Callyspongia* (*Cladochalina*) *vaginalis* (Lamarck, 1814), *Niphates erecta* Duchassaing de Fonbressin & Michelotti, 1864, *N. amorpha* Van Soest, 1980, and *Svenzea zeai* in Curaçao [24, this study); with *Callyspongia* (*Cladochalina*) *armigera* (Duchassaing de Fonbressin & Michelotti, 1864) in Saba; with *Niphates digitalis* (Lamarck, 1814), *Niphates erecta*, *Callyspongia* (*Cladochalina*) *vaginalis* in Saba Bank; with *Niphates digitalis* in Sint Eustatius; and with *Niphates amorpha* in Sint Maarten.

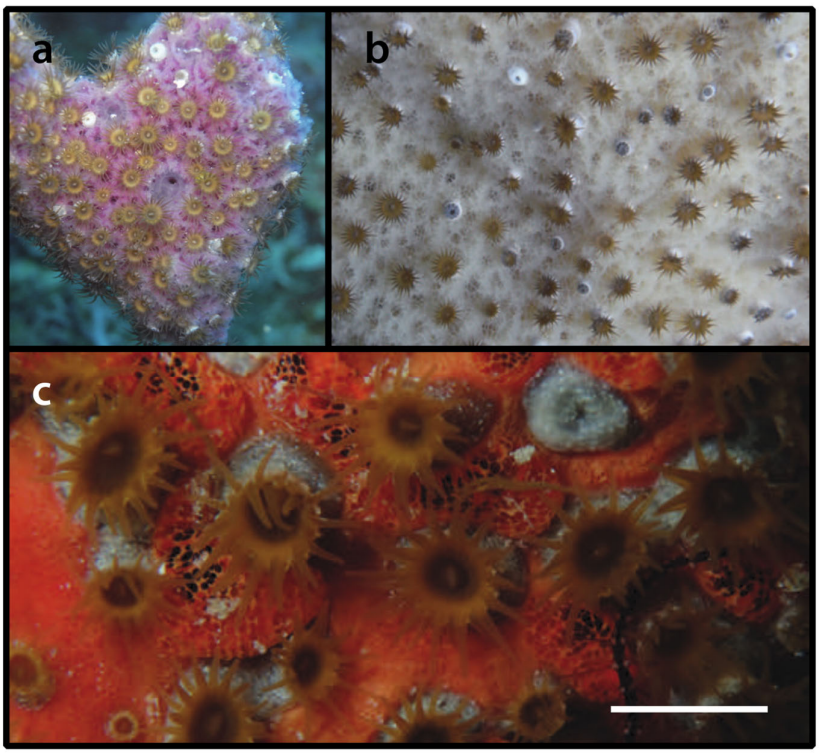

Figure 12. In situ images of *Umimayanthus parasiticus* (**a**) Specimen RMNH.COEL.42434 from Santa Marta, Water Factory [point 52], Curaçao, depth = 20 m, (**b**) image M0057481 (not collected) from Sta. EUX31 (Mushroom), Sint Eustatius, depth = 13 m, and (**c**) image PB045491 (not collected) from Front Porch, Bonaire, depth = 9 m. Scale bar in (**c**) = approximately 5 mm.

3.2.10. *Umimayanthus* sp. (Figure 13)

Specimens examined (*n* = 2). **Bonaire**. MISE JDR191026-1-1 (12°13′10.26″ N, 68°21′7.38″ W [point 20], Karpata, 37 m depth, 26.x.2019, coll. JDR). **Curaçao.** MISE JDR170619-20-94 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, 37 m depth, 19.vi.2017, coll. JDR).

Photographic records (*n* = 2). In situ: Specimens MISE JDR170619-20-94, MISE JDR191026-1-1.

Remarks: The specimens generally resemble *U. chanpuru* Montenegro, Sinniger & Reimer, 2015 [88] widely distributed across the Indo-Pacific region, but no similar species has been previously reported in the Atlantic Ocean or Caribbean Sea. Preliminary molecular analyses of the ITS-rDNA nuclear region indicate that specimen MISE JDR170619-20-94 is an undescribed species of genus *Umimayanthus* (GenBank Accession Number MT102227). Additional specimens and observations are needed to formally describe this species.

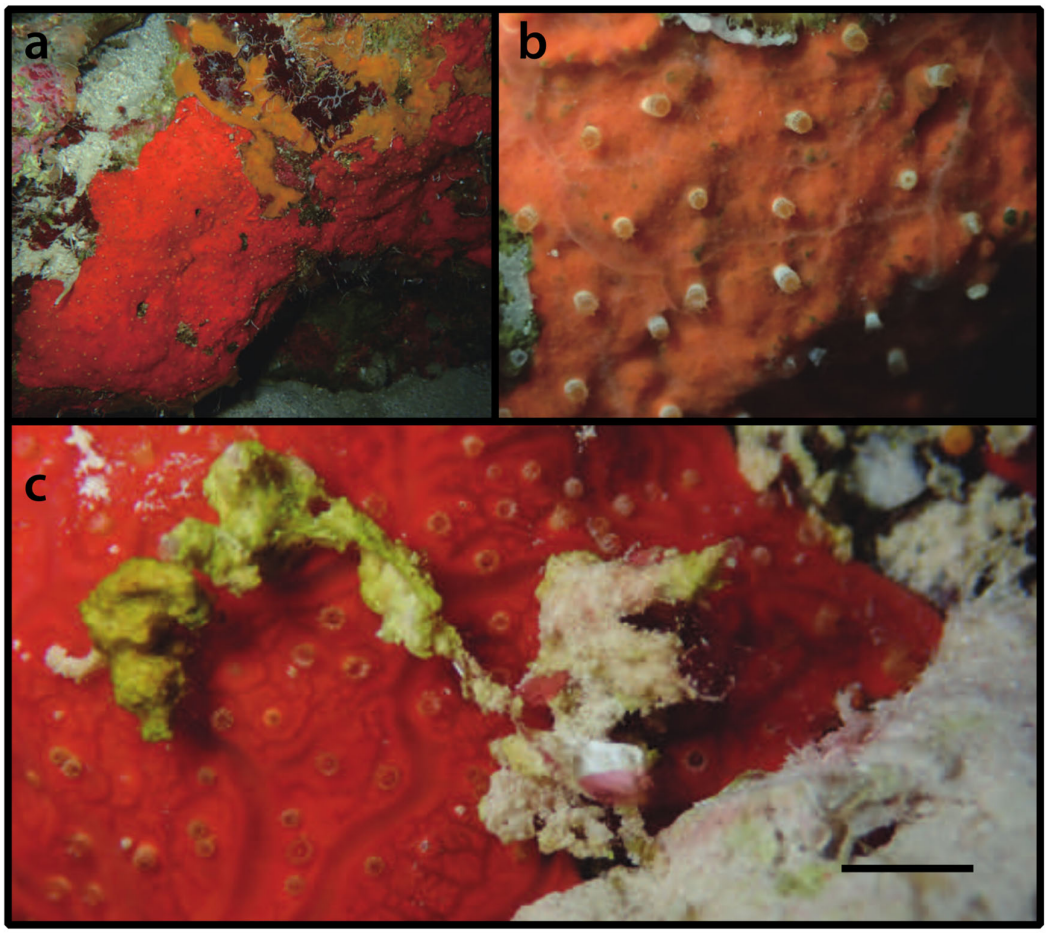

Figure 13. In situ images of *Umimayanthus* sp. (**a**) specimen MISE JDR170619-20-94 from Caracas Bay, Tugboat [point 42], Curaçao. Depth = 37 m, (**b**) close-up of same specimen, and (**c**) specimen MISE JDR191026-1-1 from Karpata, Bonaire, depth = 37 m. Scale bar in (**c**) = approximately 5 mm.

Family Epizoanthidae Delage & Hérouard, 1901 [51]
Genus *Epizoanthus* Gray, 1867 [72]

3.2.11. *Epizoanthus* sp. (Figure 14)

Specimens examined (*n* = 1). **Saba.** RMNH.COEL.40667 (17°49′00″ N, 63°16′00″ W [point 84], Sta. LUY-155, 980 m depth, 16.vi.1972, coll. Luymes Exp.).

Photographic records (*n* = 1). Preserved: Specimen RMNH.COEL.40667.

Remarks: Specimen RMNH.COEL.40667 does not resemble any known species in genus *Epizoanthus*, thus we consider it an undescribed species from the deep sea. Additional specimens and observations are needed to formally describe this species. Future collections of such material would do well to additionally collect detailed in situ images and information on host species (if present).

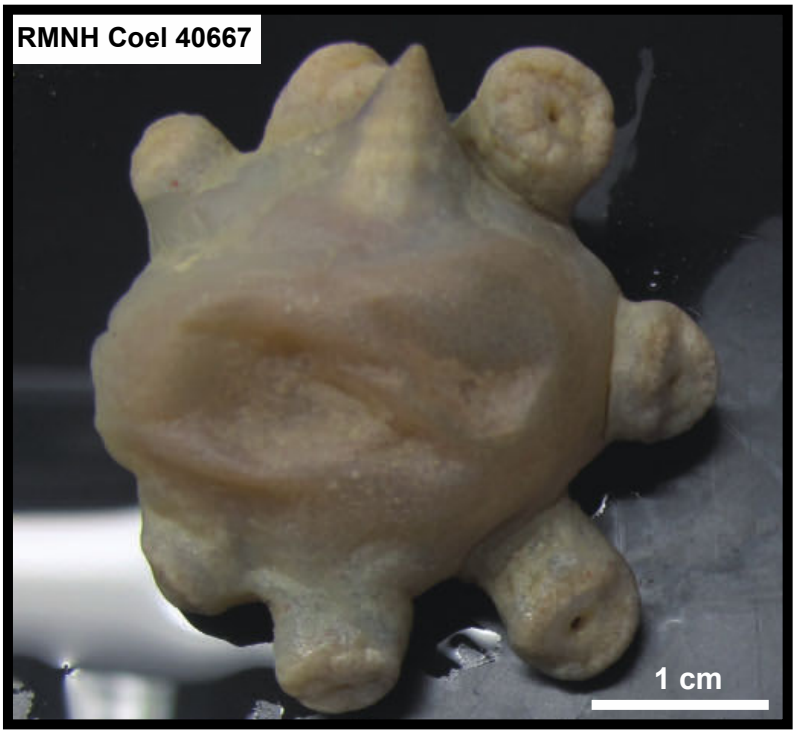

Figure 14. *Epizoanthus* sp. specimen RMNH.COEL.40667 from Sta. LUY-155 [point 84], Curaçao, depth = 980 m.

Family Hydrozoanthidae Sinniger, Reimer & Pawlowski, 2010 [58]
Genus *Hydrozoanthus* Sinniger, Reimer & Pawlowski, 2010 [58]

3.2.12. *Hydrozoanthus antumbrosus* (Swain, 2009) [62] (Figure 15)

Specimens examined (*n* = 14). **Bonaire**. MISE JDR191030-2-2 (12°4′52.92″ N, 68°13′55.56″ W [point 29], Baby Beach (Pretty Rough), 25 m depth, 30.x.2019, coll. JDR); MISE ML191108-1-1 (12°9′53.16″ N, 68°19′22.74″ W [point 34], Carl's Hill, Klein Bonaire, 20 m depth, 8.xi.2019, coll. Marianne Ligthart). **Curaçao.** MISE JDR170609-2-8 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 30 m depth, 9.vi.2017, coll. JDR). **Sint Eustatius.** MISE JDR150611-53, MISE JDR150611-61, MISE JDR150611-62 (17°28′19.2″ N, 62°59′15.6″ W [point 107], Sta. EUX010, 11 m depth, 11.vi.2015, coll. JDR); MISE JDR150612-92, JDR150612-96 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 15 m depth, 12.vi.2015, coll. JDR); MISE JDR150614-128 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 15 m depth, 14.vi.2015, coll. JDR); MISE JDR150615-142 (17°28′31.5″ N, 62°59′33.6″ W [point 108], Sta. EUX017, 19 m depth, 15.vi.2015, coll. JDR); MISE JDR150617-151 (17°27′50.4″ N, 62°59′15.0″ W [point 99], Sta. EUX021, 15 m depth, 17.vi.2015, coll. JDR); MISE JDR150617-152, JDR150617-154, JDR150617-155 (17°27′50.4″ N, 62°59′15.0″ W [point 99], Sta. EUX021, 15–17 m depth, 17.vi.2015, coll. JDR).

Photographic records (*n* = 13). In situ: Specimens MISE JDR170609-2-8, JDR150611-53, JDR150611-62, JDR150612-92, JDR150612-96, JDR150614-128, JDR150615-142, JDR150617-151, JDR150617-152, JDR150617-154, JDR150617-155, JDR191030-2-2, ML191108-1-1.

Description as in Swain [62]: The expanded polyps are dichromatic; coenenchyme, column, and oral disk are seal-brown and tentacles are golden. The polyps' column dimensions are 4.1 to 8.9 mm in length and 2.2 to 4.3 mm in diameter, and the oral disk is 2.7 to 4.8 mm in diameter. The contracted polyps are monochromatic, mammiform, 2.2 to 4.2 mm in diameter, and extending 3.3 to 9.9 mm above the surrounding coenenchyme. The capitulum has 15-19 distinct ridges. The tentacles are 30 to 38 in number, 1.9 to 5.0 mm long, and 0.4 to 0.7 mm diameter at the insertion point in the oral disk.

The colony present a thin and encrusting coenenchyme densely infiltrated with calcareous sediment and siliceous spicules. Polyps are separated by intervals of approximately 1.5 to 2.5 times a polyp diameter, often organized in an orthogonal or distichous arrangement with oral disk nearly parallel to the plane of the pinnate hydroid branches. The colony completely envelopes the central and secondary axial branches of the hydroid host, *Dentitheca dendritica* (Nutting, 1900), but usually not covering the pinnate branches where the hydroid zooids are located.

Recent and other previous records: Colombia, Dominica [62], Curaçao [24,62], Honduras [37,62], Panama, and Surinam [62].

Remarks: This species was locally common at sites around Bonaire, Curaçao, and Sint Eustatius where there was consistently strong current, which may be a prerequisite for the hydroid host species *Dentitheca* Stechow, 1920.

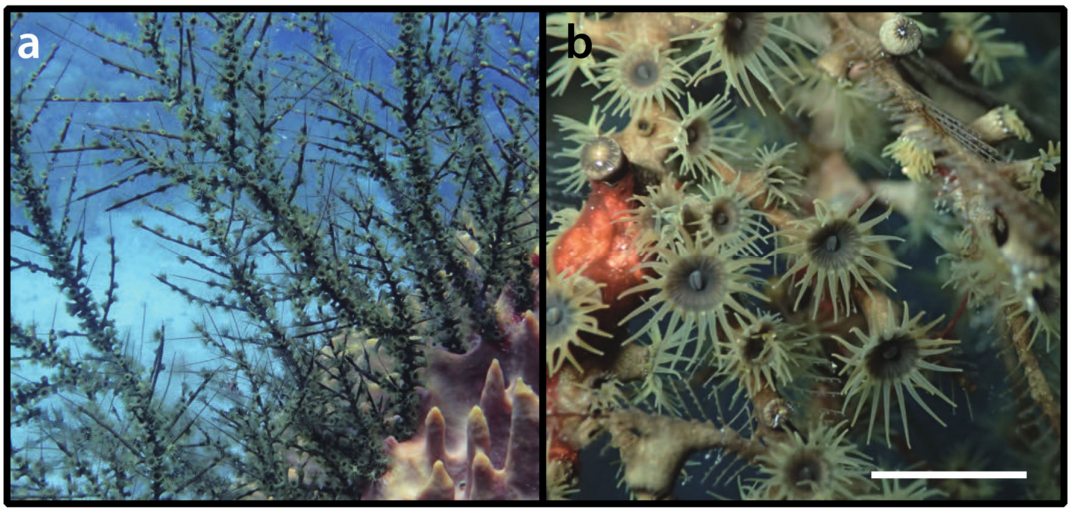

Figure 15. In situ images of *Hydrozoanthus antumbrosus*; (**a**) specimen MISE JDR150611-62 from Sta. EUX010 [point 107], Sint Eustatius, depth = 11 m, and (**b**) specimen MISE JDR170609-2-8 from Santa Marta, Water Factory [point 52], Curaçao, depth = 30 m. Scale bar in (**b**) = approximately 1 cm.

3.2.13. *Hydrozoanthus tunicans* (Duerden, 1900) [68] (Figure 16)

Specimens examined (*n* = 11). **Bonaire**. MISE JDR191030-2-1 (12°4′52.92″ N, 68°13′55.56″ W [point 29], Baby Beach (Pretty Rough), 25 m depth, 30.x.2019, coll. JDR). **Curaçao.** MISE JDR170609-2-7 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 30 m depth, 9.vi.2017, coll. JDR); RMNH.COEL.13201 (coordinates unknown, south Coast, 2–4 m depth, 9.iv.1972, coll. JCH). **Sint Eustatius.** MISE JDR150610-9 (17°27′53.9″ N, 62°59′00.7″ W [point 101], Sta. EUX008, 18 m depth, 10.vi.2015, coll. JDR); MISE JDR150612-93 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 14 m depth, 12.vi.2015, coll. JDR); MISE JDR150614-123 (17°27′50.9″ N ,62°59′06.8″ W [point 100], Sta. EUX015, 15 m depth, 14.vi.2015, coll. JDR); MISE JDR150615-138, JDR150615-139, JDR150615-140 (17°28′31.5″ N, 62°59′33.6″ W [point 108], Sta. EUX017, 19 m depth, 15.vi.2015, coll. JDR); MISE JDR150616-146 (17°28′13.6″ N, 62°59′30.2″ W [point 106], Sta. EUX019, 16 m depth, 16.vi.2015, coll. JDR); MISE JDR150617-153 (17°27′50.4″ N, 62°59′15.0″ W [point 99], Sta. EUX021, 17 m depth, 17.vi.2015, coll. JDR).

Photographic records (*n* = 10). In situ: Specimens MISE JDR150610-9, JDR150612-93, JDR150614-123, JDR150615-138, JDR150615-139, JDR150615-140, JDR150616-146, JDR150617-153, JDR170609-2-7, JDR191030-2-1.

Description as in Duerden [68]: Each colony consists of a thin coenenchyme with multiple polyps arising close to each other, covering the main stems and smaller branches of hydroids. On the smaller branches, the polyps are arranged in a distichous manner, in a plane at right angles to the pinnulae of the hydroid, and polyps at the two sides are either opposite or alternate. On the thicker

stems, their distribution becomes more irregular, and the polyps extend all around; they often arise obliquely to the surface of the coenenchyme. The coenenchyme and column wall present white granulations, foreign inclusions, which determine the color of the colony; tentacles and oral disk are usually brown in color. Tentacles are short, rounded at their apex, and dicyclic, with 14 to 16 occurring in each cycle. The mouth is rounded or slit-like and the lips are prominent. The capitular ridges are wedge-shaped and acute and vary in number from 14 to 16. The polyps are capable of complete retraction and present mammiform shape; or they may be slightly longer, and flattened or rounded above, a small aperture remains in the middle. The polyps' diameter and height over the coenenchyme is 2 mm.

Recent and other previous records: Curaçao [24,66], Dominica [66], Jamaica [68], Puerto Rico [26], and Tobago [66].

Remarks: Similar to *H. antumbrosus*, *H. tunicans* was locally common at sites around Curaçao and Sint Eustatius where there was consistent strong current, which may be a prerequisite for the host *Dentitheca* hydroid species. Consequently, both Atlantic *Hydrozoanthus* species often co-occur in the same location, at least around Bonaire, Curaçao [24], and Sint Eustatius [21].

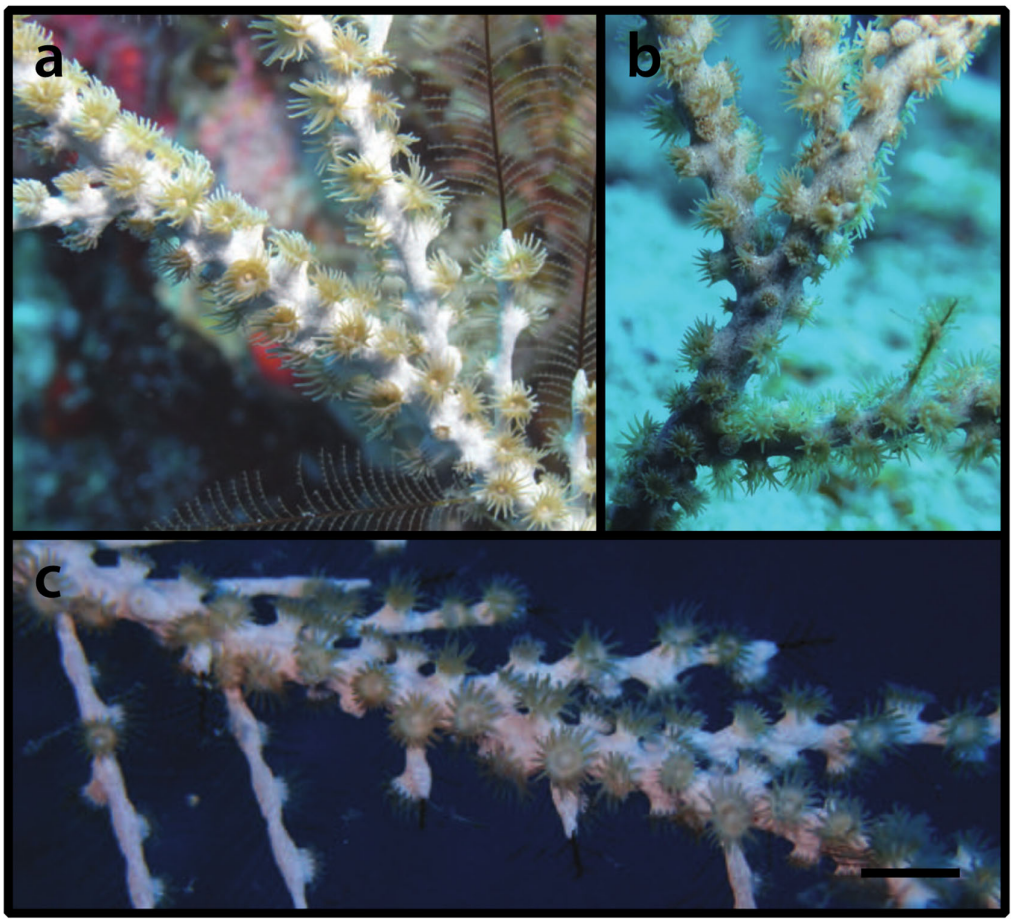

Figure 16. In situ images of *Hydrozoanthus tunicans*; (**a**) image M0054611 (not collected) from Sta. EUX04 (Hangover), Sint Eustatius, depth = 16 m, (**b**) specimen MISE JDR150612-93 from Sta. EUX012 [point 117], Sint Eustatius, depth = 14 m, and (**c**) specimen MISE JDR191030-2-1 from Baby Beach (Pretty Rough) [point 29], Bonaire, depth = 25 m. Scale bar in (**c**) = approximately 1 cm.

Suborder Brachycnemina Haddon & Shackleton, 1891 [50]
Family Sphenopidae Hertwig, 1882 [97]

Genus *Palythoa* Lamouroux, 1816 [98]

3.2.14. (a) *Palythoa caribaeorum* (Duchassaing de Fonbressin & Michelotti, 1860) [23] (Figure 17a,c)

Specimens examined (*n* = 156). **Aruba.** RMNH.COEL.40308 (12°25′04″ N, 69°51′57″ W [point 1], Seru Colorado (Ceru Cora), East Point, intertidal, 2.v.1955, coll. PWH); RMNH.COEL.40307 (12°36′29″ N, 70°03′13″ W [point 4], Malmok, Arashi Beach, depth unknown, 14.viii.1955, coll. PWH). **Bonaire.** RMNH.COEL.40235 (12°05′19″ N, 68°14′00″ W [point 6], 1 km south of Sorobon, shallow water, 13.iv.1973, coll. JCH); RMNH.COEL.40265 (12°12′01″ N, 68°18′38″ W [point 17], ca. 3 km north of Kralendijk, depth unknown, 9.iv.1973, coll. JCH); RMNH.COEL.40299, 40326 (12°08′02″ N, 68°16′55″ W [point 11], De Hoop, south of Kralendijk, intertidal, 10.ix.1948, coll. PWH); RMNH.COEL.40300 (12°09′53″ N, 68°19′24″ W [point 13], West Point, Klein Bonaire, depth unknown, 28.iii.1955, coll. PWH); RMNH.COEL.40309, 40322 (12°07′00″ N, 68°17′43″ W [point 10], north of Point Vierkant, intertidal, 9.ix.1948, coll. PWH); RMNH.COEL.40320 (12°05′59″ N, 68°13′43″ W [point 9], Lac Boca, 1–2 m depth, 1.xi.1948, coll. PWH); MISE JDR191103-2-10 (20 m depth), JDR191103-2-11, JDR191103-2-12, JDR191103-2-13, JDR191103-2-14, JDR191103-2-15, JDR191103-2-16, JDR191103-2-17, JDR191103-2-18 (12°1′36.3″ N, 68°15′4.74″ W [point 23], Red Slave, 5-10 m depth, 3.xi.2019, coll. JDR. **Curaçao.** MISE JDR170609-2-15, JDR170609-2-16, JDR170609-2-17, JDR170609-2-18, JDR170609-2-19, JDR170609-2-20, JDR170609-2-21, JDR170609-2-22, JDR170609-2-23, JDR170609-2-24 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 5–7 m depth, 9.vi.2017, coll. JDR); MISE JDR170609-2-9, JDR170609-2-10, JDR170609-2-11, JDR170609-2-12, JDR170609-2-13, JDR170609-2-14 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, 10 m depth, 9.vi.2017, coll. JDR); MISE JDR170611-5-34, JDR170611-5-35, JDR170611-5-36, JDR170611-5-37, JDR170611-5-38 (12°06′27″ N, 68°56′56″ W [point 51], Double Reef, 10–14 m depth, 11.vi.2017, coll. JDR); MISE JDR170611-5-39, JDR170611-5-40, JDR170611-5-41, JDR170611-5-42, JDR170611-5-43 (12°06′27″ N, 68°56′56″ W [point 51], Double Reef, 7–8 m depth, 11.vi.2017, coll. JDR); MISE JDR170612-7-47, JDR170612-7-48, JDR170612-7-49, JDR170612-7-50, JDR170612-7-51, JDR170612-7-52 (12°05′24″ N, 68°54′19″ W [point 50], Marie Pampoen, 3–5 m depth, 12.vi.2017, coll. JDR); MISE JDR170613-10-63 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, 11 m depth, 13.vi.2017, coll. JDR); MISE JDR170613-10-64 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, <1 m depth, 13.vi.2017, coll. JDR); MISE JDR170613-9-57, JDR170613-9-58, JDR170613-9-59 (12°03′59″ N, 68°51′38″ W [point 40], Director's Bay, <1 m depth, 13.vi.2017, coll. JDR); MISE JDR170618-18-84, JDR170618-18-85, JDR170618-18-86, JDR170618-18-87, JDR170618-18-88 (12°16′02″ N, 69°07′43″ W [point 71], south of Santa Martha Bay, 1–2 m depth, 18.vi.2017, coll. JDR); RMNH.COEL.2991 (coordinates and depth unknown, 1920, coll. C.J. van der Horst). Saba. RMNH.COEL.40333 (17°36′29.7″ N, 63°15′07.6″ W [point 79], Sta. LUY-153, <1 m depth, 15.vi.1972, coll. Luymes Exp.); RMNH.COEL.40236 (12°03′59″ N, 68°51′04″ W [point 39], Spaanse Water, tidal pools east of Boca, intertidal, 5.ix.1972, coll. JCH); RMNH.COEL.40243 (12°02′00″ N, 68°44′00″ W [point 35], Oostpunt from open sea, intertidal, August 30, 1972, coll. JCH); RMNH.COEL.40252 (17°37′05″ N, 63°15′26″ W [point 81], Sta. LUY-021 between Fort Bay and Ladder Point, depth unknown, 10.iii.1986, coll. JCH); RMNH.COEL.40267 (17°38′35″ N, 63°13′15″ W [point 83], Cove Bay, 1–2 m depth, x.1972 coll. JCH); RMNH.COEL.40284, 40738 (12°14′49″ N, 69°06′25″ W [point 70], Playa Hulu, intertidal, 19.iii.1949, coll. PWH); RMNH.COEL.40295, 40750 (17°37′00″ N, 63°15′11″ W [point 80], west of Fort Bay, intertidal, 6.x.1963, coll. PWH); RMNH.COEL.40302 (12°16′41″ N, 69°38′39″ W [point 72], Boca Pos Spaño, Spaanse Put, depth unknown, 27.ii.1955, coll. PWH); RMNH.COEL.40335 (17°37′41.8″ N, 63°15′30.9″ W [point 82], Sta. LUY-114, 35 m depth, 26.v.1972, coll. Luymes Exp.). **Saba Bank.** RMNH.COEL.40334 (17°20′00″ N, 63°15′00″ W [point 89], Sta. LUY-067, 20 m depth, 16.v.1972, coll. Luymes Exp.); RMNH.COEL.40337 (17°33′00″ N, 63°18′00″ W [point 93], Sta. LUY-084, 17 m depth, 19.v.1972, coll. Luymes Exp.); RMNH.COEL.40345 (17°16′00″ N, 63°21′00″ W [point 87], Sta. LUY-102, 16 m depth, 24.v.1972, coll. Luymes Exp.); RMNH.COEL.40346 (17°29′00″ N, 63°13′00″ W [point 92], Sta. LUY-144, 16 m depth, 14.vi.1972, coll. Luymes Exp.); RMNH.COEL.40748 (17°16′00″ N, 63°33′00″ W [point 88], Sta. LUY-074, 23 m depth, 18.v.1972, coll. Luymes Exp.). **Sint Eustatius**. MISE JDR150610-15, JDR150610-16, JDR150610-20, JDR150610-23, JDR150610-24 (17°27′53.9″ N, 62°59′00.7″

W [point 101], Sta. EUX008, 15–17 m depth, 10.vi.2015, coll. JDR); MISE JDR150611-30, JDR150611-35, JDR150611-36, JDR150611-37, JDR150611-38, JDR150611-39, JDR150611-40, JDR150611-42, JDR150611-43, JDR150611-44, JDR150611-45, JDR150611-46, JDR150611-47, JDR150611-48, JDR150611-49, JDR150611-50, JDR150611-51, JDR150611-52, JDR150611-54, JDR150611-55, JDR150611-56, JDR150611-57, JDR150611-58, JDR150611-59, JDR150611-60, JDR150611-65, JDR150611-66, JDR150611-67, JDR150611-68, JDR150611-69, JDR150611-70, JDR150611-71, JDR150611-72, JDR150611-73, JDR150611-74, JDR150611-75 (17°28′19.2″ N, 62°59′15.6″ W [point 107], Sta. EUX010, 11–13 m depth, 11.vi.2015, coll. JDR); MISE JDR150612-77 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 18 m depth, 12.vi.2015, coll. JDR); MISE JDR150612-88, JDR150612-89, JDR150612-90 (17°30′57.4″ N, 62°59′21.6″ W [point 120], Sta. EUX011, 10 m depth, 12.vi.2015, coll. JDR); MISE JDR150612-95 (17°30′22.6″ N, 63°00′22.0″ W [point 117], Sta. EUX012, 17 m depth, 12.vi.2015, coll. JDR); MISE JDR150613-102, JDR150613-103, JDR150613-104, JDR150613-105, JDR150613-106, JDR150613-107, JDR150613-111, JDR150613-112, JDR150613-113, JDR150613-114, JDR150613-115 (17°28′56.3″ N, 62°59′20.3″ W [point 113], Sta. EUX013, 2–3 m depth, 13.vi.2015, coll. JDR); MISE JDR150614-121, JDR150614-130, JDR150614-131 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 15 m depth, 14.vi.2015, coll. JDR); MISE JDR150615-136 (17°28′05.6″ N, 62°59′30.3″ W [point 104], Sta. EUX016, 18 m depth, 15.vi.2015, coll. JDR); MISE JDR150617-149 (17°28′48.3″ N, 62°59′39.4″ W [point 112], Sta. EUX020, 17 m depth, 17.vi.2015, coll. JDR); MISE JDR150617-156 (17°27′50.4″ N, 62°59′15.0″ W [point 99], Sta. EUX021, 15 m depth, 17.vi.2015, coll. JDR); MISE JDR150619-163, JDR150619-164, JDR150619-167 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta. EUX024, Sint Eustatius, 24–29 m depth, June 19, 2015, coll. JDR); MISE JDR150619-172, JDR150619-173, JDR150619-174, JDR150619-175 (17°30′16.4″ N, 62°57′47.8″ W [point 116], Sta. EUX025, 15 m depth, 19.vi.2015, coll. JDR); RMNH.COEL.40230 (17°28′35″ N, 62°59′11″ W [point 111], Sta. Gallows Bay, 1–3 m depth, 30.ix.1972, coll. JCH); RMNH.COEL.40240 (17°28′58″ N, 62°59′23″ W [point 114], Oranjestad Bay, 2–3 m depth, 30.ix.1972, coll. JCH); RMNH.COEL.40311 (17°28′33″ N, 62°59′11″ W [point 110], south of Gallows Bay, 2 m depth, 15.vii.1949, coll. PWH); RMNH.COEL.40336, 40338 (17°28′02.7″ N, 62°58′44.7″ W [point 103], Sta. LUY-121, 10–15 m depth, 9–10.vi.1972, coll. Luymes Exp.). **Sint Maarten.** RMNH.COEL.40247, 40263 (18°00′31″ N, 63°02′46″ W [point 122], Great Bay near Pointe Blanche, <5 m depth, 17.ix.1972, coll. JCH); RMNH.COEL.40321 (18°01′05″ N, 63°02′44″ W [point 123], Great Bay, east side, intertidal, 11.vi.1949, coll. PWH).

Photographic records (n = 112). In situ: Specimens MISE JDR150610-15, JDR150610-16, JDR150610-20, JDR150610-23, JDR150610-24, JDR150611-30, JDR150611-35, JDR150611-36, JDR150611-37, JDR150611-38, JDR150611-39, JDR150611-40, JDR150612-77, JDR150612-88, JDR150612-89, JDR150612-90, JDR150612-95, JDR150613-102, JDR150614-121, JDR150614-130, JDR150614-131, JDR150615-136, JDR150617-149, JDR150617-156, JDR150619-163, JDR150619-164, JDR150619-167, JDR150619-172, JDR150619-173, JDR150619-174, JDR150619-175, JDR170609-2-9, JDR170609-2-10, JDR170609-2-11, JDR170609-2-12, JDR170609-2-13, JDR170609-2-14, JDR170609-2-15, JDR170609-2-16, JDR170609-2-17, JDR170609-2-18, JDR170609-2-19, JDR170609-2-20, JDR170609-2-21, JDR170609-2-22, JDR170609-2-23, JDR170609-2-24, JDR170611-5-34, JDR170611-5-35, JDR170611-5-36, JDR170611-5-37, JDR170611-5-38, JDR170611-5-39, JDR170611-5-40, JDR170611-5-41, JDR170611-5-42, JDR170611-5-43, JDR170612-7-47, JDR170612-7-48, JDR170612-7-49, JDR170612-7-50, JDR170612-7-51, JDR170612-7-52, JDR170613-10-63, JDR170613-10-64, JDR170613-9-57, JDR170613-9-58, JDR170613-9-59, JDR191103-2-10, JDR191103-2-11, JDR191103-2-12, JDR191103-2-13, JDR191103-2-14, JDR191103-2-15, JDR191103-2-16, JDR191103-2-17, JDR191103-2-18; Preserved: Specimens RMNH.COEL.2991, 40230, 40235, 40236, 40240, 40243, 40247, 40252, 40263, 40265, 40267, 40284, 40295, 40299, 40300, 40302, 40307, 40308, 40309, 40311, 40320, 40321, 40322, 40326, 40333, 40334, 40335, 40336, 40337, 40338, 40345, 40346, 40738, 40748, 40750.

Description as in Duchassaing de Fonbressin & Michelotti [23]: The living polyps are color yellow citrus, with 30 to 32 tentacles pointed at the end and wider at the bases. When contracted, the polyps do not present a mammiform shape as in other *Palythoa* species; on the contrary, they form a depression.

Recent and other previous records: Ascension [9], Barbados, Belize [99], Brazil [1,100–141], Canary Islands [142], Cape Verde [4,25,143,144], Colombia [145], Costa Rica [146,147], Cuba [74,148,149], Curaçao [24,150], Jamaica [77,148,151–153], Mexico [94,154,155], Panama [78,135,156–158], Puerto Rico [148], Sint Eustatius [22], Saint Helena [5], Saint Thomas [23,148], U.S. Virgin Islands [158], USA (Florida) [159–161], and Venezuela [70,162,163].

Remarks: This is the most widespread zoantharian in shallow waters of the subtropical and tropical Atlantic Ocean [5], as well the most common zoantharian species across the Caribbean, as evidenced by the records listed above. Of interest is that many specimens from older surveys around Sint Eustatius and Curaçao in the 1920s to 1980s are from intertidal depths, while recent surveys in 2015 and 2017 from the same islands found very few colonies in such shallow waters.

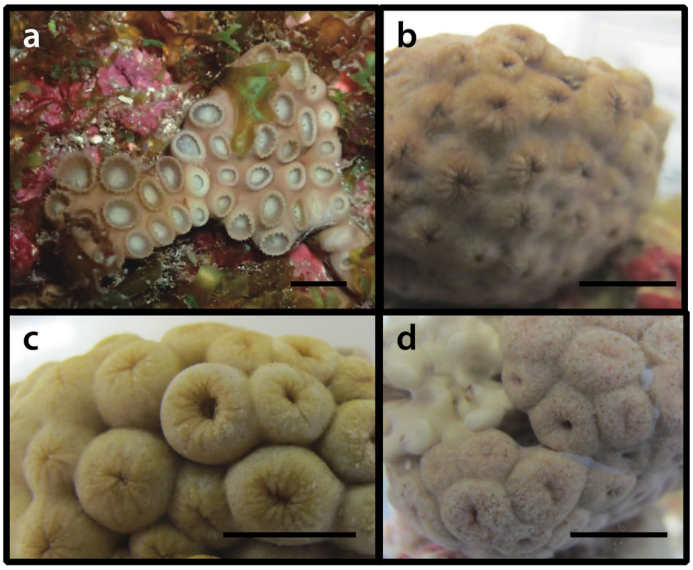

Figure 17. (**a**) *Palythoa caribaeorum* specimen MISE JDR150612-89 in situ at Sta. EUX011 [point 120], Sint Eustatius, depth = 10 m, (**b**) *P. caracasiana*, preserved type specimen RMNH.COEL.2990, coordinates and depth unknown, Curaçao, (**c**) preserved *P. caribaeorum* specimen RMNH.COEL.40265 from ca. 3 km north of Kralendijk [point 17], Sint Eustatius, depth = unknown, and (**d**) *P. mammillosa*, preserved type specimen RMNH.COEL.3810 from Aruba, coordinates, depth, date, and collector unknown. Scale bars = approximately 1 cm.

14(b) *Palythoa caracasiana* Pax, 1924 [150] (Figure 17b)

Specimen examined (*n* = 1). **Curaçao.** Holotype, RMNH.COEL.2990 (coordinates and depth unknown, 1920, coll. C.J. van der Horst).

Photographic records (*n* = 1). Preserved: Specimen RMNH.COEL.2990.

Description as in Pax [150]: The coenenchyme and the polyps are dark brown in preserved specimens. The colony tissues are heavily encrusted with pieces of lime and sand grains but remain flexible and present a significant tensile strength. The outline of the colonies is irregularly oval or polygonal. The polyps rise over the coenenchyme, close to each other, and are 3 to 5 mm in diameter. The characteristic feature of *P. caracasiana* are 14 capitular ridges very well demarcated, which are hardly seen in other species of *Palythoa*. The number of mesenteries varies from 28 to 32.

Recent and other previous records: Curaçao [150].

Remarks: This species is almost certainly *P. caribaeorum*, which like many *Palythoa* and *Zoanthus* species, is known to have considerable intraspecific morphological variation in external colony and polyp features (e.g., [164]). For now, as this is a type specimen, we have listed the species as separate from *P. caribaeorum* pending formal revision of these and similar species (see below). As discussed in Burnett et al. [27], it is likely that inadvertent repeated descriptions of the same species from different localities has overly inflated the species counts in both *Palythoa* and *Zoanthus*.

14(c) *Palythoa horstii* Pax, 1924 [150]

Specimens examined (*n* = 1). **Curaçao.** Holotype, RMNH.COEL.2993 (coordinates and depth unknown, 1920, coll. C.J. van der Horst).

Photographic records (*n* = 1). Preserved: Specimen RMNH.COEL.2993.

Description as in Pax [150]: The colony of preserved specimens present a circular outline, with contracted polyps that do not rise above the surface of the coenenchyme, although in some specimens, the polyps rise in the form of small humps. The polyps present 13 to 14 capitular grooves and in average a diameter of 5 mm. The coenenchyme and polyps are heavily encrusted with calcareous granules, and occasionally sponge spicules and foraminiferous skeletons. The number of tentacles is around 28 and mesenteries 30 in dissected specimens; all mesenteries present a distinct basal channel.

Recent and other previous records: None.

Remarks: As with *Palythoa caracasiana* above, this species is almost certainly *P. caribaeorum*.

14(d) *Palythoa mammillosa* (Ellis & Solander, 1786) [165] (Figure 17d)

Specimens examined (*n* = 2). **Aruba.** RMNH.COEL.3810 (coordinates, depth, date, and collector unknown). **Sint Maarten.** RMNH.COEL.2994 (coordinates and collector unknown, ca. 2 m depth, ii.1959).

Photographic records (*n* = 2). Preserved: Specimens RMNH.COEL.2994, 3810.

Description as in Ellis & Solander [165]: The colony is lather-like and spread over the rock surface. Polyps are tightly clustered together, projected over the coenenchyme in a convex mammiform shape, with a hollow in the middle and with a faint start-like appearance. Each polyp has 12 mesenteries and, when expanded, the same number of tentacles.

Recent and other previous records: Bermudas [93], Colombia [145], Guadeloupe [23], Jamaica [23,165–167], Saint Thomas [23], USA (Florida) [159], and Venezuela [162].

Remarks: Although the original description is lacking, if [92] is correct, based on Figure 17d in his work, there is a high probability that this species is the senior synonym of *P. caribaeorum*. Examination of the type species is needed to confirm or refute this idea. For now, the identity of the species remains uncertain, and we have informally placed it within the *caribaeorum-caracasiana-horstii* species grouping.

3.2.15. *Palythoa grandiflora* (Verrill, 1900) [92] (Figure 18)

Specimens examined (*n* = 7). **Aruba.** RMNH.COEL.40312 (12°32′27″ N, 70°03′51″ W [point 3], Bucuti, south point, intertidal, 17.i.1949, coll. PWH). **Bonaire**. MISE JDR191105-2-2 (12°14′46.86″ N, 68°24′49.5″ W [point 24], Playa Frans, 5 m depth, 5.xi.2019, coll. JDR); MISE JDR191106-3-3 (12°6′54.48″ N, 68°17′39.54″ W [point 31], Dolphin Reef, 13 m depth, 6.xi.2019, coll. JDR). **Curaçao.** RMNH.COEL.40241 (12°02′00″ N, 68°44′00″ W [point 35], Oostpunt from open sea, intertidal, 30.viii.1972, coll. JCH). **Sint Eustatius.** RMNH.COEL.40259 (17°30′28″ N, 62°58′51″ W [point 118], west side of Concordia Bay, intertidal, 1.x.1972, coll. JCH); RMNH.COEL.40276 (17°28′35″ N, 62°59′11″ W [point 111], Gallows Bay, 1–6 m depth, 9.iii.1986, coll. JCH). **Sint Maarten.** RMNH.COEL.40232 (18°04′36″ N, 63°00′55″ W [point 125], Baie de l'Embouchure, 1 m depth, x.1972, coll. JCH).

Photographic records (*n* = 7). In situ: MISE JDR191105-2-2, MISE JDR191106-3-3. Preserved: Specimens RMNH.COEL.40232, 40241, 40259, 40276, 40312.

Description as in Verrill [92]: Polyps are large, often spaced by half their length, and form clusters of 12 to 24 polyps of different sizes. When contracted, the polyps form large, rounded mammillae, often higher than wider, strongly sulcated longitudinally, the grooves (~ 26) converging to the central depression of the summit; surface covered with a firm coat of sand. In partial expansion, the summit becomes considerably swollen or turbinated; in full expansion, broad saucer shaped. Tentacles are 52 to 56 in number, short, subequal, with half as many marginal tentacles. The colony is the color buff or light ochre to dark ochre; disks are dull orange or brownish yellow, usually marked

with radial lines and specks of white; tentacles are dull orange, often tipped with white; marginal denticles; flake-white. The polyps are 15 to 20 mm in height, 10 to 13 mm in diameter, and the expanded oral disk 14 to 16 mm in diameter.

Recent and other previous records: Bermudas [92], Brazil [1,131], Canary [8], Cuba [149,168], and USA (Florida) [161].

Remarks: Sibling species of Indo-Pacific *P. mutuki* (Haddon & Shackleton, 1891) [169] as shown by molecular data [161]. Recent surveys in both Sint Eustatius in 2015 and Curaçao in 2017 did not find this species, although it was found in Bonaire. Colonies were seen in the Curaçao Sea Aquarium, however reportedly collected from the "Spaanse Water" site on Curaçao (M Jove, Curaçao Sea Aquarium, personal communication).

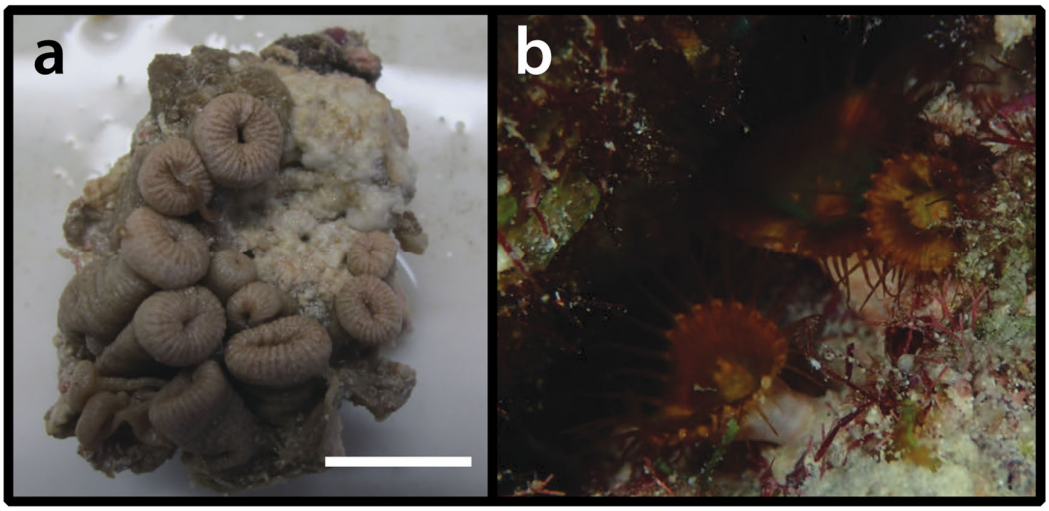

Figure 18. Specimens of *Palythoa grandiflora*; (**a**) preserved specimen RMNH.COEL.40232 from Baie de l'Embouchure [point 125], Sint Maarten, depth = 1 m, and (**b**) specimen MISE JDR191106-3-3 in situ from Dolphin Reef [point 31], Bonaire, depth = 13 m. Scale bar in (**a**) = approximately 1 cm.

3.2.16. *Palythoa grandis* (Verrill, 1900) [92] (Figure 19)

Specimens examined (*n* = 10). **Bonaire**. MISE JDR191101-2-1 (12°15′49.8″ N, 68°24′49.2″ W [point 25], Boka Slaagbaai, 21 m depth, 1.xi.2019, coll. JDR); MISE JGH191107-3-2 (12°10′9.18″ N, 68°18′38.88″ W [point 15], Sampler, Klein Bonaire, 12 m depth, 7.xi.2019, coll. JGH). **Curaçao.** MISE JDR170613-10-62, JDR170619-20-95 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, 11–12 m depth, 13.vi.2017 and 19.vi.2017, coll. JDR); MISE JDR170616-13-77 (12°08′01″ N, 68°59′07″ W [point 62], north of Blue Bay, 11 m depth, 16.vi.2017, coll. JDR) RMNH.COEL.40238 (12°04′29″ N, 68°52′50″ W [point 44], Jan Thiel Bay, 18 m depth, 1.v.1971, coll. J.C. Post); RMNH.COEL.40251 (12°07′20″ N, 68°58′08″ W [point 54], Carmabi House Reef, 64 m depth, 17.viii.1972, coll. J.C. Post). **Sint Eustatius.** MISE JDR150618-161 (17°27′44.5″ N, 62°59′08.1″ W [point 98], Sta. EUX023, 18 m depth, 18.vi.2015, coll. JDR); MISE JDR150619-170 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta. EUX024, depth unknown, 19.vi.2015, coll. JDR); MISE JDR150619-178 (17°30′16.4″ N, 62°57′47.8″ W [point 116], Sta. EUX025, 13 m depth, 19.vi.2015, coll. JDR).

Photographic records (*n* = 10). In situ: Specimens MISE JDR170613-10-62, JDR170616-13-77, JDR150618-161, JDR150619-170, JDR150619-178, JDR170619-20-95, JDR191101-2-1, JGH191107-3-2. Preserved: Specimens RMNH.COEL.40238, 40251.

Description as in Verrill [92]: A large species with polyps forming small divergent clusters joined by short stolons, furcate in the base, or sometimes isolated: Walls are thickly encrusted with fine sand. The expanded column is usually clavate, obconic, or long and trumpet-shaped, with the basal part tapered and rather narrow; often two to three times as high as wide. Oral disk broad, cup-

shaped, or when fully expanded convex or umbrella shaped, with recurved borders. Tentacles are numerous, about 60 to 66 arranged in two alternating rows, all similar, short, obtuse; outside the tentacles is a circle of marginal papillae, nearly as large as the tentacles and alternating with the outer rows. Sometimes one tentacle (directive) aligned with the longitudinal axis of the mouth is larger and lighter colored than the rest. The color of column is usually pale orange, salmon, or buff, under the coat of white sand; disk is usually orange or orange–brown, sometimes light orange, buff, or ochre–yellow, the color is variable in between the same cluster; the outer part, near the tentacles, is darker than the central, and usually with darker radial lines, sometimes tinged with green; lips are white or orange; the tentacles are similar in color to the disk but usually a shade paler, often darker at base, but the tentacles may be darker than the disk in pale specimens. The largest polyps are 30 to 36 mm in height, and the diameter of the expanded oral disk is 12 to 16 mm.

Recent and other previous records: Barbados [99], Belize [99,170], Bermudas [92,93,171], Canary Islands [142], Costa Rica [146,147], Cuba [149], Curaçao [24], Jamaica [171], Madeira [8], Mexico [94,154,155], Panama [78,157], USA (Florida) [161], and Venezuela [70,162,163].

Remarks: This species is known only from the greater Caribbean, and has no Pacific sibling species, unlike many shallow water zoantharian and *Palythoa* species. Additionally, unlike many *Palythoa* spp., this species seems to be found at deeper areas (e.g., >10 m), and may be a lower-light specialist. One specimen in this study (RMNH.COEL.40251) was found from 64 m, indicating a mesophotic distribution.

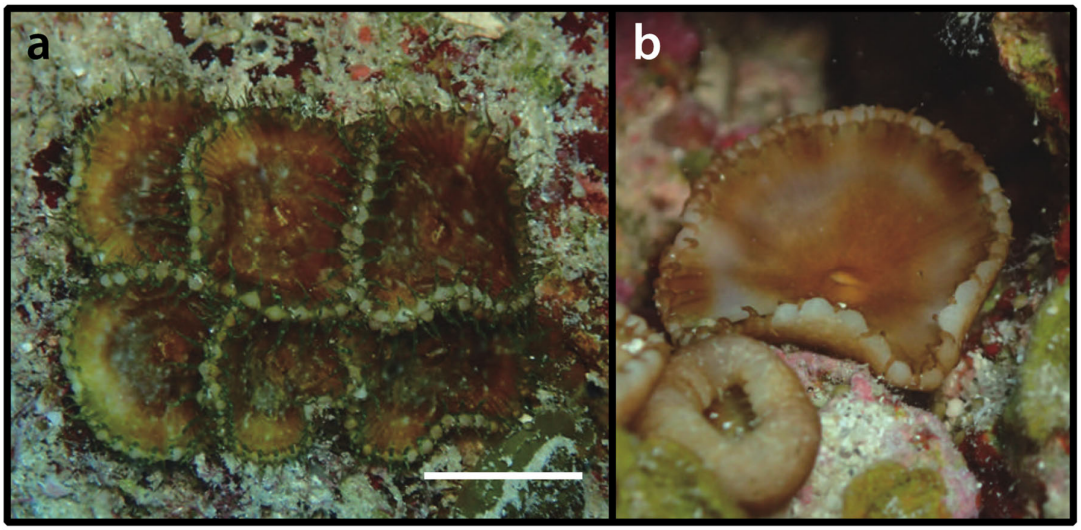

Figure 19. In situ images of *Palythoa grandis*; (**a**) specimen MISE JDR170613-10-62 from Caracas Bay, Tugboat [point 42], Curaçao, depth = 11–12 m, and (**b**) specimen MISE JDR150618-161 from Sta. EUX023 [point 98], Sint Eustatius, depth = 18 m. Scale bar in (**a**) = approximately 1 cm.

3.2.17. *Palythoa variabilis* (Duerden, 1898) [76] (Figure 20)

Specimens examined (*n* = 6). **Curaçao.** MISE JDR170617-16-83 (12°11′51″ N, 69°04′46″ W [point 66], Habitat, 37 m depth, 17.vii.2017, coll. JDR); RMNH.COEL.40248 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Bay, 24 m depth, 6.ix.1972, coll. JCH); RMNH.COEL.40736 (12°14′49″ N, 69°06′25″ W [point 70], Playa Hulu, intertidal, 19.iii.1949, coll. PWH). **Sint Eustatius.** RMNH.COEL.40271 (17°30′39″ N, 62°56′52″ W [point 119], boundary of Zeelandia Bay in the north, intertidal, 8.iii.1986, coll. JCH); MISE JDR150621-191 (17°28′12.8″ N, 62°58′58.7″ W [point 105], Sta. EUX029, 3 m depth, 21.vi.2015, coll. JDR); MISE JDR150616-148 (17°28′13.6″ N, 62°59′30.2″ W [point 106], Sta. EUX019, depth unknown, 16.vi.2015, coll. JDR).

Photographic records (*n* = 5). In situ: Specimens MISE JDR150616-148, JDR170617-16-83. Preserved: Specimens RMNH.COEL.40248, 40271, 40736.

Description as in Duerden [76]: Polyps erect, firm, smooth, arising independently from a lamellar coenenchyme, or from the base of one another; or solitary; often cylindrical in retraction; slightly enlarged and flattened distally, or occasionally narrowing and terminating bluntly. The coenenchyme is not well developed and mostly preset only around the base of each polyp. The tissues are heavily incrusted with sand, sponge spicules, diatoms, and test of radiolarians. Capitulum with about 30 ridges and furrows; tentacles acuminate and arranged in two alternating rows of about 30 in each row. Peristome is considerably raised, and the mouth elongated and slit like. In full expansion, the capitulum and disk are much enlarged in proportion to the diameter of the column; the individuals in a colony are closely aggregated, the oral disk is at the same level in all individuals, capitulum margin in contact and by mutual pressure a polygonal outline is formed, leaving no interstices. Thus, a living colony when fully expanded present the appearance of a mosaic work of brown or green depressed disks, with margins of a dark-brown color. The lower part of the columns is a light buff color, and the upper is dark brown; tentacles are usually dark brown, but in some cases olive or green; the disk is either dark brown or bright green, with green radiating lines, and the peristome is the same color as the disk or different but always brown or bright green. In the largest specimen, the length of the column is 5 cm, the diameter 1.2 cm; the average height is 1.5 cm, and diameter 0.7 cm; the diameter of expanded disk is 2.3 cm; tentacles 0.3 cm in length. Given the rigidity of the column wall there is not much contraction in preserved specimens. The mesenteries are usually brachycnemic; in most polyps, 15 perfect mesenteries occur on each side and the same number of imperfect mesenteries.

Recent and other previous records: Brazil [1,100,104,106,109,110,113,114,117,124,130,133–135,138,172–179], Cape Verde Islands [180], Cuba [74,149,168], Jamaica [76,77,181], and Panama [78,135,157,182].

Remarks: Widely distributed across the tropical and subtropical Atlantic, and apparently common in some areas [175], this species was only found a handful of times during current surveys. It may be relatively rare in the central Caribbean.

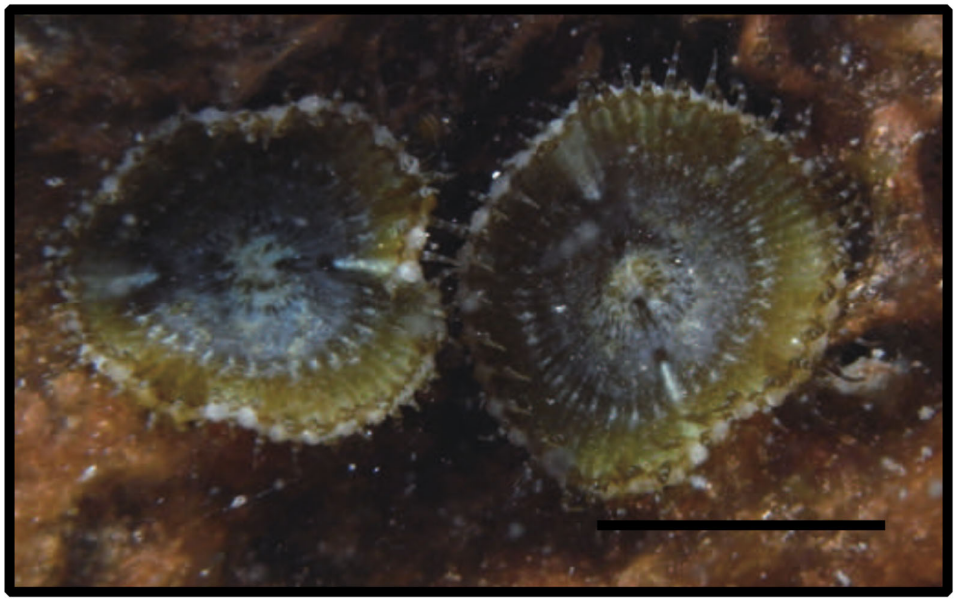

Figure 20. In situ image of *Palythoa variabilis* specimen MISE JDR150616-148 from Sta. EUX019 [point 106], Sint Eustatius, depth = unknown. Scale bar = approximately 5 mm.

3.2.18. *Palythoa* sp. (Figure 21)

Specimens examined (*n* = 1). **Aruba.** RMNH.COEL.40329 (12°32′27″ N, 70°03′51″ W [point 3], Bucuti, south point, intertidal, 17.i.1949, coll. PWH).

Photographic records (*n* = 1). Preserved: Specimen RMNH.COEL.40329.

Remarks: This specimen was in poor condition, making it difficult to identify to species level.

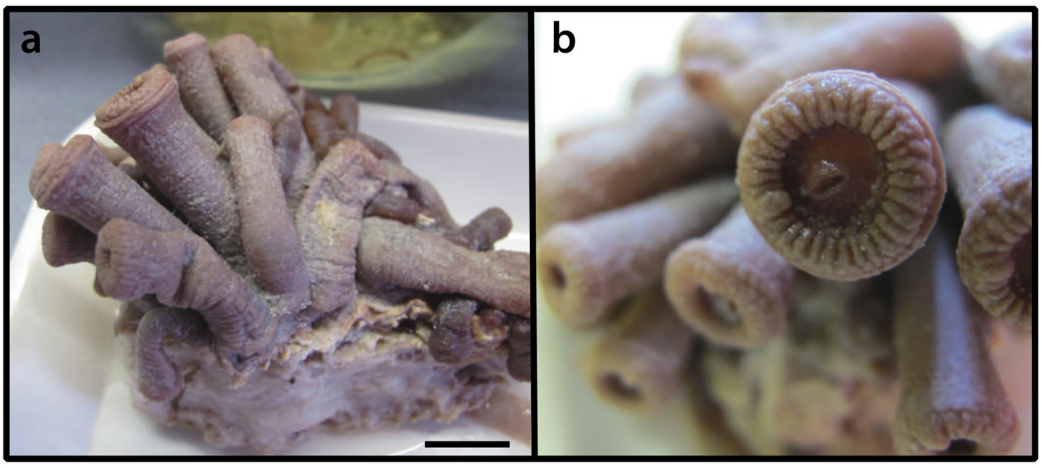

Figure 21. (**a**) and (**b**) images of preserved *Palythoa* sp. specimen RMNH.COEL.40329 from Bucuti, south point [point 3], Aruba, depth = intertidal. Scale bar in (**a**) = approximately 1 cm.

Family Zoanthidae Rafinesque, 1815 [49]
Genus *Zoanthus* Lamarck, 1801 [183]

3.2.19. *Zoanthus pulchellus* (Duchassaing de Fonbressin & Michelotti, 1860) [23] (Figure 22)

Specimens examined (*n* = 15). **Bonaire**. MISE JDR191103-1-4 (12°10′41.1″ N, 68°17′32.34″ W [point 14], Small Wall, 11 m depth, 3.xi.2019, coll. JDR). **Curaçao.** MISE JDR170613-9-56 (12°03′59″ N, 68°51′38″ W [point 40], Director's Bay, 10 m depth, 13.vi.2017, coll. JDR); MISE JDR170616-14-79 (12°08′01″ N, 68°59′07″ W [point 62], south of Blue Bay, 11 m depth, 16.vi.2017, coll. JDR); MISE JDR170621-x-101 (12°04′43″ N, 68°51′37″ W [point 46], Spaanse Water, 1 m depth, 21.vi.2017, coll. JDR); RMNH.COEL.3728 (coordinates and collector unknown, 6 m depth, 21.x.1958); RMNH.COEL.3729 (coordinates and depth unknown, 1920, coll. C.J. van der Horst); RMNH.COEL.40254 (12°07′45″ N, 68°58′51″ W [point 61], north of Piscadera Bay, 24 m depth, 6.ix.1972, coll. P. Creutzberg); RMNH.COEL.40262 (12°07′17″ N, 68°58′09″ W [point 53], Carmabi, Hilton Hotel, 24 m depth, 13.ix.1972, coll. P. Creutzberg & H. de Windt); RMNH.COEL.40327 (12°14′48″ N, 69°06′25″ W [point 69], south of Playa Hulu, intertidal, 2.iv.1949, coll. PWH). **Saba.** RMNH.COEL.40294 (17°37′00″ N, 63°15′11″ W [point 80], west of Fort Bay, intertidal, 6.x.1963, coll. PWH); RMNH.COEL.40340 (17°36′29.7″ N, 63°15′07.6″ W [point 79], Sta. LUY-153, 5–20 m depth, 15.vi.1972, Luymes Exp.). **Sint Eustatius.** MISE JDR150619-171, JDR150619-179, JDR150619-180 (17°30′16.4″ N, 62°57′47.8″ W [point 116], Sta. EUX025, 15–16 m depth, 19.vi.2015, coll. JDR); RMNH.COEL.40257 (17°28′35″ N, 62°59′11″ W [point 111], Sta. LUY-020, Gallows Bay, 1–3 m depth, 30.ix.1972, coll. JCH).

Photographic records (*n* = 14). In situ: Specimens MISE JDR150619-171, JDR150619-179, JDR150619-180, JDR170613-9-56, JDR170616-14-79, JDR191103-1-4. Preserved: Specimens RMNH.COEL.3728, 3729, 40254, 40257, 40262, 40294, 40327, 40340.

Description as in Duchassaing de Fonbressin & Michelotti [23]: Polyps are tightly packed together with oral disk in contact when fully expanded. Tentacles are 60–70 in number, the radio of the oral disk is 5.8 to 7.74 mm in size. The center of the disk is red with green borders and green tentacles.

Recent and other previous records: Bahamas [92], Barbados [99], Brazil [1,105,130,184], Cape Verde [8], Colombia [25], Costa Rica [146], Cuba [74,149,168], Curaçao [24,150], Jamaica [25,76,77,181], Lesser Antilles, Margarita [25], Mexico [94], Panama [78], Puerto Rico [148], Saint Helena [5], Saint Thomas [23,25,76], USA (Florida) [25,161], and Venezuela [70,163].

Remarks: *Zoanthus* spp. are notoriously difficult to identify without either detailed in situ images or histological examinations, and some of the specimens grouped here (and in other *Zoanthus* spp. in this paper) may be incorrectly placed, particularly for older specimens in which no in situ images exist. In particular, recent molecular examinations have indicated that *Zoanthus pulchellus* includes both the species sensu stricto as well as a cryptic species (*Z.* aff. *pulchellus*) that is not yet well delineated morphologically and is different by closely related phylogenetically [161].

This species appears to be, based on recent surveys, distributed in deeper (>10 m) waters in Bonaire, Curaçao, and Sint Eustatius, yet specimens collected from the same islands in the 1940s to 1970s include intertidal specimens. Similar to *P. caribaeorum*, it is not known if this is an artifact from sampling methods (reef-walking vs. SCUBA), due to shallow water bleaching events, or perhaps in this case, specimens of different species inadvertently being put together. More detailed molecular and morphological examinations of both recent and older specimens are needed to examine this, and results may provide important insights into recent climate change.

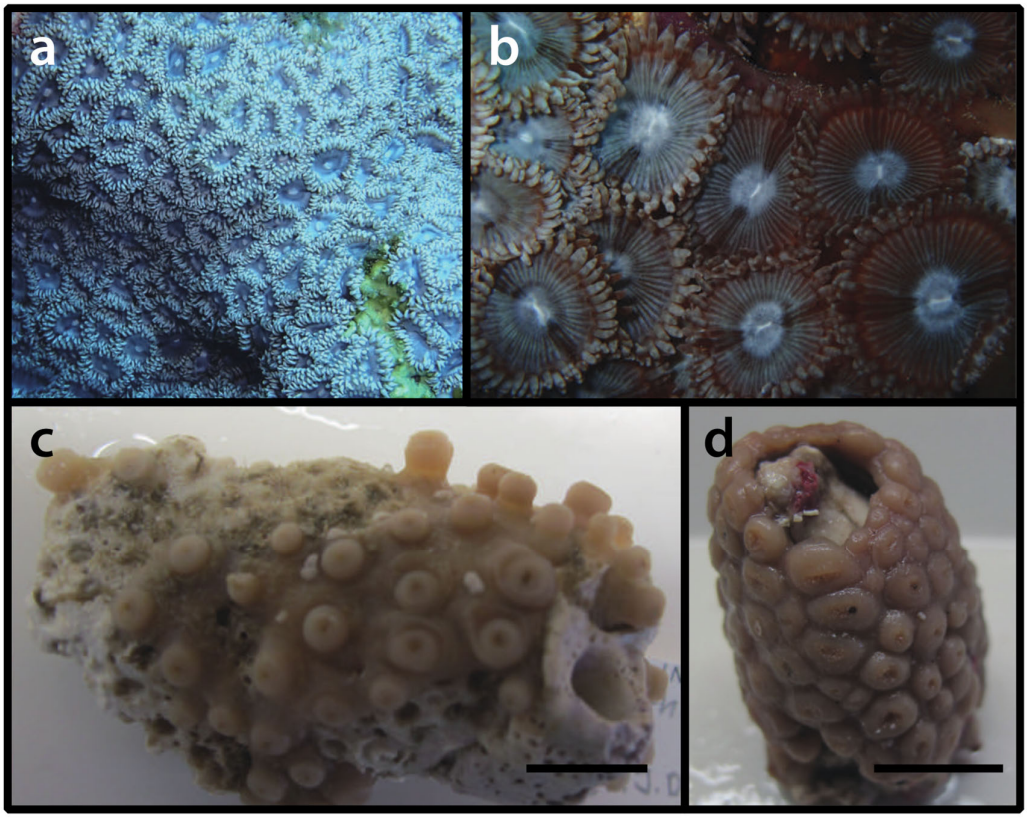

Figure 22. In situ images of *Zoanthus pulchellus*; (**a**) specimen MISE JDR170613-9-56 from Director's Bay [point 40], Curaçao, depth = 10 m, (**b**) specimen MISE JDR191103-1-4 from Small Wall, Bonaire, depth = 11 m, and preserved specimens c) RMNH.COEL.40262 from Carmabi, Hilton Hotel [point 53], Curaçao, depth = 24 m, and d) RMNH.COEL.40257 from Sta. LUY-020, Gallows Bay [point 111], Sint Eustatius, depth = 1–3 m. Scale bars in (**c**) and (**d**) = approximately 1 cm.

3.2.20. *Zoanthus* aff. *pulchellus* (Duchassaing de Fonbressin & Michelotti, 1860) [23]

Specimens examined (*n* = 1). **Curaçao.** MISE JDR170621-x-100 (12°04′43″ N 68°51′37″ W [point 46], Spaanse Water, 1 m depth, 21.vi.2017, coll. JDR).

Photographic Records (*n* = 0).

Description: See *Zoanthus pulchellus*.

Remarks: This single specimen was morphologically different from *Z. pulchellus* specimens above in being almost completely 'immersae' [25], with polyps barely protruding above a well-developed coenenchyme. However, phylogenetic analyses are needed to confirm the identity of this specimen, particularly given the intraspecific morphological plasticity of *Zoanthus* spp. [164].

3.2.21. *Zoanthus sociatus* (Ellis, 1768) [185] (Figure 23)

Specimens examined (*n* = 33). **Aruba.** RMNH.COEL.3731 (coordinates, depth, date, and collector unknown); RMNH.COEL.40325 (12°30′40″ N, 70°02′18″ W [point 2], Bucuti, north lagoon-side, intertidal, 8.ii.1937, coll. PWH). **Bonaire.** MISE JGH191025-1-3 (12°12′1.74″ N, 68°18′30.72″ W [point 18], Oil Slick, 18 m depth, 25.x.2019, coll. JGH. **Curaçao.** MISE JDR170610-3-27, MISE JDR170610-3-28, MISE JDR170610-3-29 (12°08′21″ N, 68°59′53″ W [point 64], Snake Bay, intertidal, 10.vi.2017, coll. JDR); MISE JDR170613-10-65 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, intertidal, 13.vi.2017, coll. JDR); RMNH.COEL.17819 (12°03′22″ N, 68°50′14″ W [point 37], Fuikbaai, depth unknown, 9.vi.1971, coll. JCH); RMNH.COEL.3730 (coordinates and depth unknown, 1920, coll. C.J. van der Horst); RMNH.COEL.3732 (coordinates and collector unknown, 1–3 m depth, 2.vii.1958). Saba. RMNH.COEL.40749, 40293 (17°37′00″ N, 63°15′11″ W [point 80], west of Fort Bay, intertidal, 6.x.1963, coll. PWH); RMNH.COEL.40261 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, intertidal, 1.vi.1971, coll. JCH); RMNH.COEL.40266 (17°38′35″ N, 63°13′15″ W [point 83], Cove Bay, 1–2 m depth, x.1972, coll. JCH); RMNH.COEL.40285, 12°14′49″ N, 69°06′25″ W [point 70], Playa Hulu, Curaçao, intertidal, March 19, 1949, coll. PWH; RMNH.COEL.40291 (12°03′21″ N, 68°50′05″ W [point 36], Fuikbaai, intertidal, 2.iii.1949, coll. PWH); RMNH.COEL.40297, 12°14′48″ N 69°06′25″ W [point 69], south of Playa Hulu, Curaçao, intertidal, April 2, 1949, coll. PWH; RMNH.COEL.40304 (12°16′41″ N, 69°38′39″ W [point 72], Boca Pos Spaño, Spaanse Put, depth unknown, 27.ii.1955, coll. PWH); RMNH.COEL.40314 (12°19′02″ N, 69°09′09″ W [point 73], Playa Lagun, intertidal, 13.vi.1948, coll. PWH); RMNH.COEL.40323 (coordinates and depth unknown, 1948, coll. PWH). Curaçao. RMNH.COEL.40272 (12°02′00″ N, 68°44′00″ W [point 35], Oostpunt from open sea, intertidal, 30.v.1972, coll. JCH). **Sint Eustatius**. MISE JDR150614-125 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 17 m depth, 14.vi.2015, coll. JDR); MISE JDR150618-160 (17°27′56.6″ N, 63°00′07.2″ W [point 102], Sta. EUX022, 24 m depth, 18.vi.2015, coll. JDR); MISE JDR150619-176 (17°30′16.4″ N, 62°57′47.8″ W [point 116], Sta. EUX025, 14 m depth, 19.vi.2015, coll. JDR); MISE JDR150621-183, MISE JDR150621-184, MISE JDR150621-185 (17°28′12.8″ N, 62°58′58.7″ W [point 105], Sta. EUX029, 3 m depth, 21.vi.2015, coll. JDR); MISE JDR150621-186, JDR150621-188, JDR150621-189, JDR150621-190 (17°28′12.8″ N, 62°58′58.7″ W [point 105], Sta. EUX029, 3–4 m depth, 21.vi.2015, coll. JDR); RMNH.COEL.40275 (17°28′35″ N, 62°59′11″ W [point 111], Gallows Bay, 1–6 m depth, 9.iii.1986, coll. JCH); **Sint Maarten.** RMNH.COEL.40231 (18°05′20″ N, 63°04′55″ W [point 126], Anse des Perres, 1–3 m depth, x.1972, coll. JCH).

Photographic records (*n* = 30). In situ: Specimens MISE JDR150614-125, JDR150618-160, JDR150619-176, JDR150621-183, JDR150621-184, JDR150621-186, JDR150621-188, JDR150621-189, JDR170610-3-27, JDR170610-3-28, JDR170610-3-29, JDR170613-10-65, JGH191025-1-3. Preserved: Specimens RMNH.COEL.3730, 3731, 3732, 40231, 40261, 40266, 40272, 40275, 40285, 40291, 40293, 40297, 40304, 40314, 40323, 40325, 40749.

Description as in Ellis [185]: This compound animal, formed by a tender fleshy substance, consists of many tubular bodies gently elongated towards the upper part and ending in a bulb, similar to a very small onion; on top of which is the mouth, surrounded by one or two rows of tentacles, which when contracted, look like a circle of beads. The lower parts of each tubular body are in communication with each other through a firm fleshy wrinkled tube, which sticks flat to the rocks. The tubular bodies present multiple sizes rising up irregularly in groups near to one another. The tubular bodies are strongly attached to the coral rock by a fleshy substance with incrusted pieces of shells.

Recent and other previous records: Bahamas [92,186,187], Bermudas [92,93], Brazil [100,105,106,115,117,121,123,130,131,133–135,138,141,188–191], Cape Verde [8], Colombia [145], Costa Rica [146], Cuba [74,149], Curaçao [150], Dominica [165], Guadeloupe [192], Haiti [25], Jamaica [25,151–153,171,181,193], Mexico [154,155], most of the West Indies [25], Panama [78,135,156,157], Puerto Rico [148], USA (Florida) [161], and Venezuela [70,162].

Remarks: The first species of zoantharian formally described, this species is widely distributed across the Atlantic [5], and is a sibling species to *Z. sansibaricus* Carlgren, 1900 [194] based on molecular data [161]). It is commonly found forming large colonies in shallow waters, although it was found to 24 m in this study, indicating it may be a depth generalist, similar to *Z. sansibaricus* as seen in Okinawa, Japan [195].

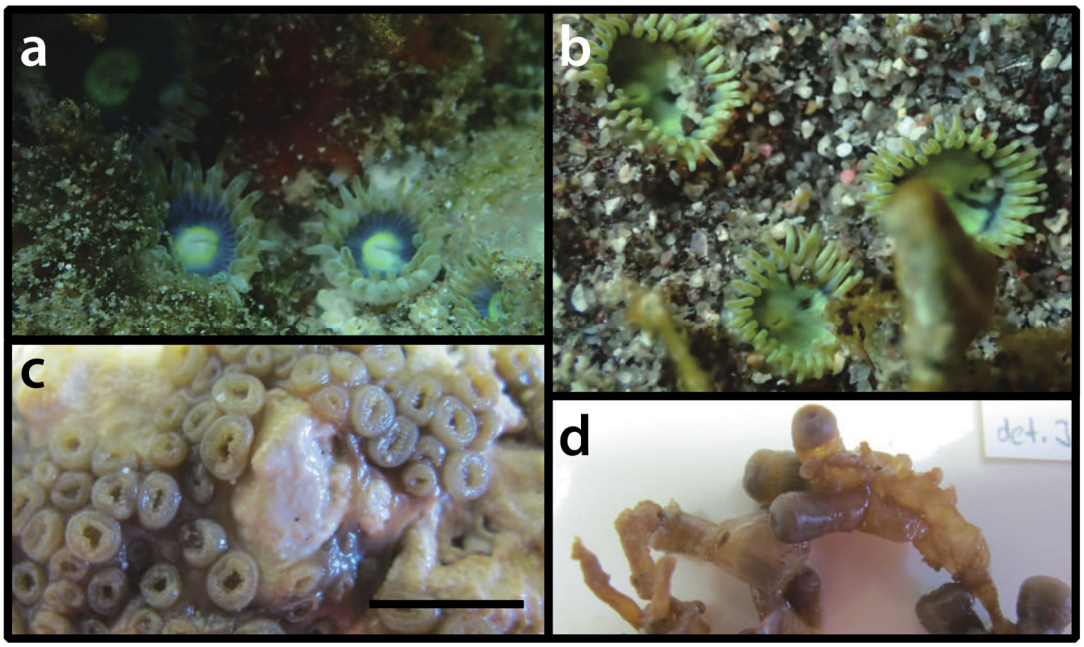

Figure 23. In situ images of *Zoanthus sociatus* (**a**) specimen MISE JDR150621-183 from Sta. EUX029 [point 105], Sint Eustatius, depth = 3 m, (**b**) specimen MISE JDR150621-186 from Sta. EUX029 [point 105], Sint Eustatius, depth = 3–4 m, and preserved specimens (**c**) RMNH.COEL.40314 from Playa Lagun [point 73], Curaçao, depth = intertidal, and (**d**) RMNH.COEL.40291 from Fuikbaai [point 36], Curaçao, depth = intertidal. Scale bar in (**d**) = approximately 1 cm.

3.2.22. *Zoanthus solanderi* Le Sueur, 1817 [192] (Figure 24)

Specimens examined (*n* = 22). **Bonaire.** RMNH.COEL.40301 (12°09′53″ N, 68°19′24″ W [point 13], West Point, Klein Bonaire, depth unknown, 28.iii.1955, coll. PWH); MISE JGH191025-1-2 (12°12′1.74″ N, 68°18′30.72″ W [point 18], Oil Slick, 20 m depth, 25.x.2019, coll. JGH); MISE JDR191031-1-1 (12°9′41.76″ N, 68°17′0.96″ W [point 33], Something Special, 13 m depth, 31.x.2019, coll. JDR); MISE JDR191101-1-1 (12°16′57.42″ N, 68°24′49.32″ W [point 26], Playa Funchi, 20 m depth, 1.xi.2019, coll. JDR); MISE JDR191101-1-2 (12°16′57.42″ N, 68°24′49.32″ W [point 26], Playa Funchi, 20 m depth, 1.xi.2019, coll. JDR); MISE JDR191103-2-5 (12°1′36.3″ N, 68°15′4.74″ W [point 23], Red Slave, 30 m depth, 3.xi.2019, coll. JDR); MISE JDR191104-2-2 (12°4′38.76″ N, 68°16′48″ W [point 28], Invisibles, 10 m depth, 4.xi.2019, coll. JDR); MISE JDR191105-1-3 (12°12′55.38″ N, 68°20′13.08″ W [point 19], Tolo, 6 m depth, 5.xi.2019, coll. JDR). **Curaçao.** MISE JDR170609-2-25 (12°06′33″ N, 68°57′15″ W [point 52], Santa Marta, Water Factory, depth unknown, 9.vi.2017, coll. JDR); MISE JDR170619-20-96 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, 12 m depth, 19.vi.2017, coll. JDR); MISE JDR170620-23-98, JDR170620-23-99 (12°19′45″ N, 69°09′05″ W [point 74], Playa Jeremi, 12–16 m depth, 20.vi.2017, coll. JDR); RMNH.COEL.40303 (12°16′41″ N, 69°38′39″ W [point

72], Boca Pos Spaño, Spaanse Put, depth unknown, 27.ii.1955, coll. PWH); RMNH.COEL.40310, 40737, 40743 (12°14′49″ N, 69°06′25″ W [point 70], Playa Hulu, intertidal, 28.x.1948 and 19.iii.1949, coll. PWH); RMNH.COEL.40330 (coordinates and depth unknown, south side, 13.i.1972, coll. JCH). **Saba.** RMNH.COEL.40292 (17°37′00″ N, 63°15′11″ W [point 80], west of Fort Bay, intertidal, 6.x.1963, coll. PWH). **Sint Eustatius.** MISE JDR150619-169 (17°31′35.7″ N, 62°59′35.3″ W [point 121], Sta. EUX024, 21 m depth, 19.vi.2015, coll. JDR); MISE JDR150619-177 (17°30′16.4″ N,62°57′47.8″ W [point 116], Sta. EUX025, 13 m depth, 19.vi.2015, coll. JDR); MISE JDR150621-187 (17°28′12.8″ N, 62°58′58.7″ W [point 105], Sta. EUX029, 3 m depth, 21.vi.2015, coll. JDR). **Sint Maarten.** RMNH.COEL.40342 (18°04′00″ N, 63°06′00″ W [point 124], Sta. LUY-122, Baie Marigot, <15 m depth, 11.vi.1972, coll. Luymes Exp.).

Photographic records (*n* = 21). In situ: Specimens MISE JDR150619-169, JDR150619-177, JDR150621-187, JDR170609-2-25, JDR170619-20-96, JDR170620-23-98, JGH191025-1-2, JDR191031-1-1, JDR191101-1-1, JDR191101-1-2, JDR191103-2-5, JDR191104-2-2, JDR191105-1-3. Preserved: Specimens RMNH.COEL.40292, 40301, 40303, 40310, 40330, 40342, 40737, 40743.

Description as in Le Sueur [192]: The oral disk of the polyps is of a deep reddish brown color and the peduncle reddish yellow. The tentacles are short and 60 in number. When contracted, the polyp's summit is marked with a deep blue angular spot, and white lines. The polyps are united in groups by the base of their peduncles, in middle of the sand, at the surface of which they raise their discs. The polyps are about 5 cm in length.

Recent and other previous records: Bahamas [92], Brazil [100,112,113,130], Cape Verde [8], Colombia [145], Curaçao [24], Guadeloupe [76], Jamaica [153,181,193,196], Panama [78,135,156,157], Saint Thomas [23,76,192], USA (Florida) [161], and Venezuela [70,162].

Remarks: Although widely distributed, this species is not common, and forms small colonies of <20 cm in diameter. Similar to *P. caribaeorum* and *Z. pulchellus* above, this species was not found in the intertidal zone during recent surveys on Bonaire, Curaçao, and Sint Eustatius despite several specimens from in the intertidal zone in older collections.

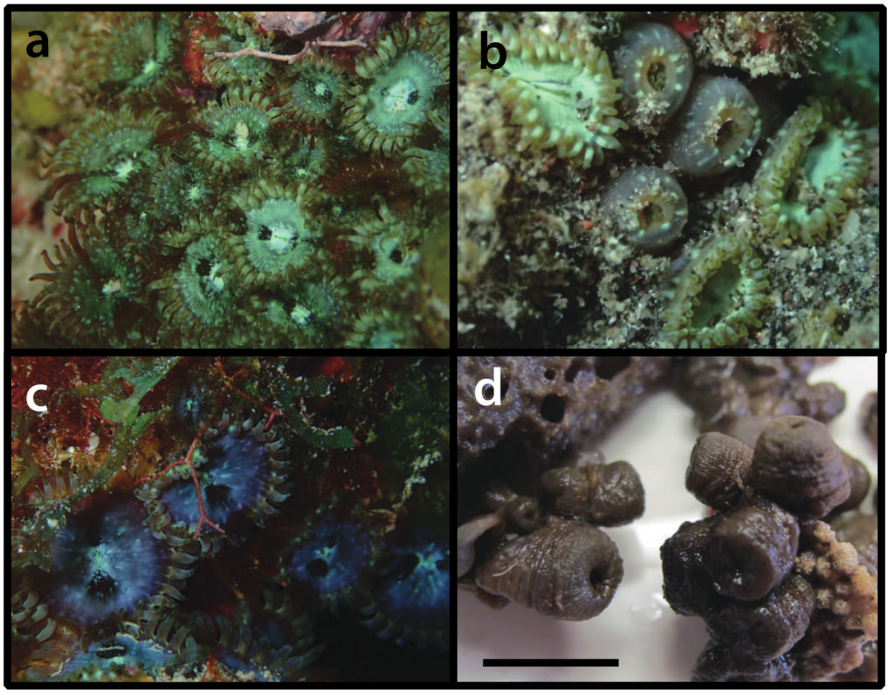

Figure 24. In situ images of *Zoanthus solanderi* (**a**) specimen MISE JDR170619-20-96 from Caracas Bay, Tugboat [point 42], Curaçao, depth = 12 m, (**b**) specimen MISE JDR150621-187 from Sta. EUX029 [point 105], Sint Eustatius, depth = 3 m, and (**c**) specimen MISE JDR191101-1-1 from Playa Funchi [point 26], Bonaire, depth = 20 m, and d) preserved specimen RMNH.COEL.40292 from west of Fort Bay [point 80], Saba, depth = intertidal. Scale bar in (**d**) = approximately 1 cm.

3.2.23. *Zoanthus* sp. (Figure 25)

Specimens examined (*n* = 10). **Aruba.** RMNH.COEL.40290, 40313, 40328 (12°32′27″ N, 70°03′51″ W [point 3], Bucuti, south point, intertidal, 17.i.1949, coll. PWH). **Bonaire.** RMNH.COEL.40234 (12°13′12″ N, 68°22′41″ W [point 21], southwest coast opposite Lake Goto, shallow water, 11.iv.1978, coll. JCH); RMNH.COEL 40246 (12°05′44″ N, 68°14′14″ W [point 8], Lac Cai, Punta Calbas, depth unknown, 8.iv.1973, coll. JCH). **Curaçao.** RMNH.COEL.40245 (12°03′22″ N, 68°50′14″ W [point 37], Fuikbaai, depth unknown, 9.vi.1971, coll. JCH); RMNH.COEL.40282 (12°03′21″ N, 68°50′05″ W [point 36], Fuikbaai, intertidal, 2.iii.1949, coll. PWH); RMNH.COEL.40296 (12°16′41″ N, 69°38′39″ W [point 72], Boca Pos Spaño, Spaanse Put, depth unknown, 27.ii.1955, coll. PWH); RMNH.COEL.40324 (12°16′02″ N, 69°07′43″ W [point 71], Santa Martha Beach, depth unknown, 29.vii.1955, coll. PWH). **Sint Eustatius.** RMNH.COEL.40242 (17°28′35″ N, 62°59′11″ W [point 111] Gallows Bay, depth unknown, x.1972, coll. JCH).

Photographic records (*n* = 10). Preserved: Specimens RMNH.COEL.40234, 40242, 40245, 40246, 40282, 40290, 40296, 40313, 40324, 40328.

Remarks: These specimens, although some were in good condition, could not be identified to species level, and thus we identify them here to generic level as *Zoanthus* sp. Note, while they are included as one species, material could possibly contain multiple species.

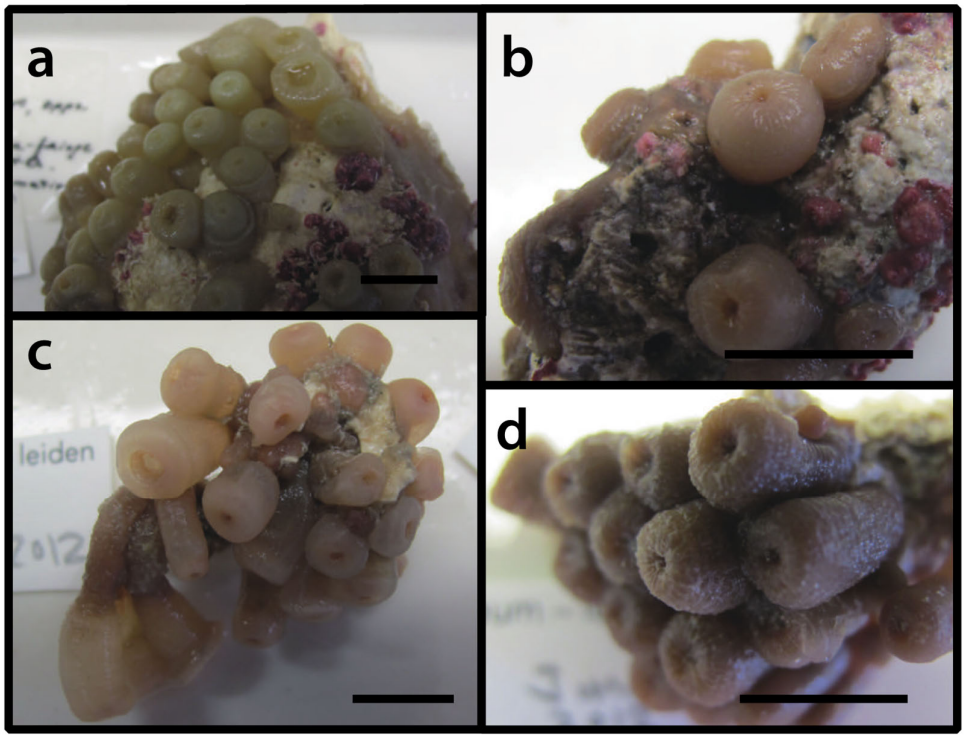

Figure 25. Preserved *Zoanthus* sp. (**a**) specimen RMNH.COEL.40234 from southwest coast opposite Lake Goto [point 21], Bonaire, depth = shallow water, (**b**) specimen RMNH.COEL.40282 from Fuikbaai [point 36], Curaçao, depth = intertidal, (**c**) specimen RMNH.COEL.40245 from Fuikbaai [point 36], Curaçao, depth unknown, and (**d**) specimen RMNH.COEL.40328 from Bucuti, south point [point 3], Aruba, depth = intertidal. Scale bars = approximately 1 cm.

Genus *Isaurus* Gray, 1828 [197]

3.2.24. *Isaurus tuberculatus* Gray, 1828 [197] (Figure 26)

Specimens examined (*n* = 11). **Curaçao.** RMNH.COEL.40244, 40256 (12°04′05″ N, 68°51′44″ W [point 42], Caracas Bay, Tugboat, intertidal, 1.vi.1971, coll. JCH); RMNH.COEL.40260 (12°07′21″ N,

68°58′20″ W [point 55], south of Piscadera Bay, depth unknown, 30.xii.1972 and 13.ix.1972, coll. JCH); RMNH.COEL.40237, 40273 (12°20′27″ N, 68°58′51″ W [point 75], Playa Chikitu (Kleine Knip), 1 m depth, 8.v.1971 and 29.iv.1971, coll. JCH); RMNH.COEL.40283 (12°07′26″ N 68°58′08″ W [point 57], east of Piscadera Bay, depth unknown, 13.ix.1972, coll. JCH), RMNH.COEL.2707, 2708 (coordinates and depth unknown, 1920, coll. C.J. van der Horst). **Sint Eustatius.** MISE JDR150614-129, JDR150614-132 (17°27′50.9″ N, 62°59′06.8″ W [point 100], Sta. EUX015, 15 m depth, 14.vi.2015, coll. JDR); RMNH.COEL.40287 (17°28′32″ N, 62°59′11″ W [point 109], south of Gallows Bay, 2 m depth, 15.vii.1949, coll. PWH).

Photographic records (*n* = 11). In situ: Specimens MISE JDR150614-129, JDR150614-132. Preserved: Specimens RMNH.COEL.2707, 2708, 40237, 40244, 40256, 40260, 40273, 40283, 40287.

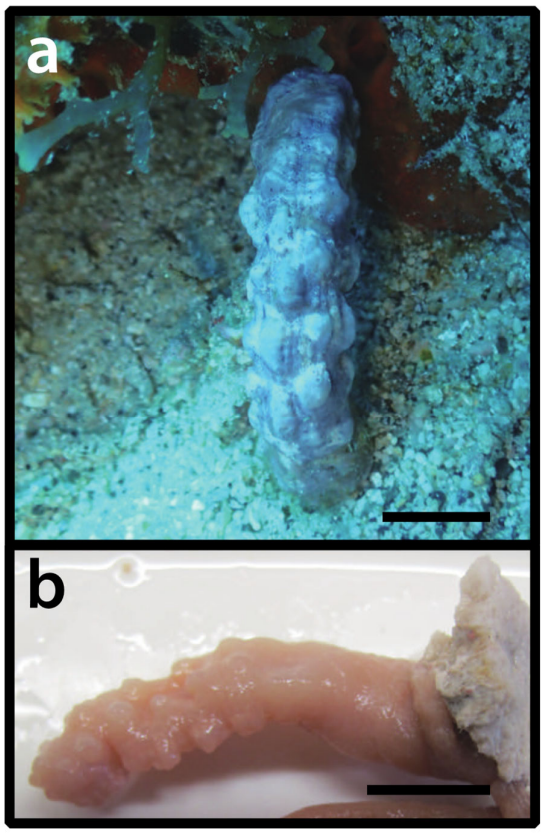

Figure 26. *Isaurus tuberculatus* images; (**a**) in situ specimen MISE JDR150614-129 from Sta. EUX015 [point 100], Sint Eustatius, depth = 15 m, and (**b**) preserved specimen RMNH.COEL.40244 from Caracas Bay, Tugboat [point 42], Curaçao, depth = intertidal. Scale bars = approximately 1 cm.

Description as in Gray [197]: Polyps are gregarious, sub-cylindrical, curved, and with longitudinal and transversal grooves and tubercles; tentacles are acute. Polyps are 5.08 cm in length and 1.27 cm in diameter.

Description of *I. gelatinosus* as in Pax [150]: The coenenchyme is poorly developed, and reduced to a lamellar enlargement in the base of the polyps. The shape of the polyps is approximately cylindrical; some specimens show a clear division between scapus and capitulum, while in others, the differentiation is blurred. The curvatures and tubercles typical of genus *Isaurus* are almost completely absent; even less developed than in var. *microtuberculata*. When tubercles are detectable, they occupied less than the 10% of the total body length and can only be recognized by a careful examination of the material. The diameter of the base of the polyps range from 5 to 18 mm and 11 mm in average; the apical diameter ranges from 4 to 10 mm and 7 mm in average; the polyps length

ranges from 20 to 56 mm and 35 mm in average. The tentacles are short and pronounced marginally; the mesenteries were 42 in number and consistent across polyps of different ages.

Recent and other previous records: Ascension [198], Belize [199], Bermudas [93], Brazil [130,138,188,189,200,201], Canary Islands [202], Cape Verde [4], Caribbean [197], Cuba [74,149], Curaçao [150], Guadeloupe [23], Panama [78,157], Saint Helena [5], USA (Florida) [161]. Also reported to the Indo-Pacific [203,204].

Remarks: Specimen RMNH.COEL.2707 was initially described as *Isaurus duchassaingi microtuberculata* Pax, 1924 [150], a subspecies of *Isaurus tuberculatus*. Additionally, RMNH.COEL.2708 is the type specimen for *Isaurus gelatinosus* Pax, 1924 [150]. Both of these species and others were merged into *I. tuberculatus* by Muirhead and Ryland [203].

This species is rare but widely distributed, and in the examined islands, forms small colonies of single or only a few polyps. Currently, based on the revision by Muirhead and Ryland [203], all Atlantic and most Pacific *Isaurus* belong to *I. tuberculatus*, although this is most likely not correct and these are different species, given the isolation of tropical and subtropical zooxanthellate benthic species from each other (discussed in 161].

3.2.25. Zoantharian Species Distribution across the Dutch Caribbean

There are 24 zoantharian species (described and putative) across the Dutch Caribbean in at least nine genera of five families (above and Table 1). Curaçao showed the highest richness of zoantharians (21 species), followed by Bonaire (16), St. Eustatius (15), Saba (7), St. Marten (6), Aruba (5), and Saba Bank (3). In the Southern Caribbean (SC; Aruba, Bonaire and Curaçao), a total of 22 species were observed, while in the Eastern Caribbean (EC; Saba, Saba Bank, St. Eustatius, and St Marten) there were 17 zoantharians. Both SC and EC host species of the genera *Bergia*, *Hydrozoanthus*, *Isaurus*, *Palythoa*, *Parazoanthus*, *Umimayanthus,* and *Zoanthus*. However, *Antipathozoanthus* was only reported from SC, and *Epizoanthus* from EC. There are nine species reported exclusively from the SC and another one from the EC.

Most species occurred in shallow waters (< 200 m depth), with the exception of two species (*Epizoanthus* sp. and Parazoanthidae sp.) found in a deeper zone. Moreover, many species had a wide depth range distribution (Table 1). Six genera (*Bergia*, *Hydrozoanthus*, *Palythoa*, *Parazoanthus*, *Umimayanthus*, *Zoanthus*) occur from the intertidal to the upper mesophotic zone (30–70 m depth), with *Isaurus* extending from the intertidal to 15 m depth. Three colonies of the *Antipathozoanthus* aff. *macaronesicus* were collected at around 10 m depth and *Epizoanthus* sp. was found only in deep waters (980 m).

4. Discussion

Biodiversity loss is one of the gravest threats facing the planet [205] and the Caribbean is under high anthropogenic stress [206–211]. Despite the zoantharian fauna of the Caribbean having been studied for over 250 years, recent works have shown that still much remains to be learned about Caribbean zoantharian diversity, with formal species descriptions ([62]; this study) and indications of other undescribed or unrecognized species ([1,4,161], also as in this study). The Dutch Caribbean is no exception, as our current study describes one new species, *Parazoanthus atlanticus* sp. n., and specimens indicate the presence of other potentially undescribed species (*Antipathozoanthus* aff. *macaronesicus*, *Epizoanthus* sp., *Umimayanthus* sp., *Zoanthus* sp., and Parazoanthidae sp.). Therefore, it is clear that diversity surveys in this region still have much to uncover and are urgently needed.

Furthermore, specimen collection and curating can help provide important baseline data for future analyses. In the current study, we noticed that many zooxanthellate *Palythoa* and *Zoanthus* spp. were collected from intertidal or very shallow waters in surveys until the 1980s, while our more recent surveys between 2015 and 2019 found very few specimens in such shallow waters. While these data alone do not indicate climate change or loss from bleaching, combined with temperature data and information from other taxa, they could be an important part of the picture of how coral reefs have changed over recent history. As our recent expeditions (Curaçao 2017, Bonaire 2019) also surveyed extensively the depth zone between 0 and 3 m, we do not attribute this shift to a change in sampling

effort. Additionally, the more recent scuba surveys (2014, 2017, 2019) by trained experts did reveal new depth records for many zoantharian species (Table 1), along with undescribed species, demonstrating the value of having trained taxonomists in the field searching for their specific target taxa.

It is relevant to remark here that many of the present species records are based on historical collection material (RMNH, ZMA), including specimens sampled by C.J. van der Horst from Curaçao (1920), PWH from Aruba (1937, 1955), Bonaire (1948, 1955), Curaçao (1949, 1953, 1955, 1977), Saba (1963), Sint Maarten (1949), and Sint Eustatius (1949), by JCH from Curaçao and Bonaire (1971–1973, 1978, 1986), and the Luymes Expedition to Saba, Saba Bank, Sint Eustatius, and Sint Maarten (1972). Information on some of the sampling localities during which material was collected is well documented in expedition reports [14,15,23]. Examples of Dutch Caribbean zoantharians only known from collections are *Anthipathozoanthus* aff. *macaronesicus* and *Epizoanthus* sp. It is possible that some of these taxa have become, locally, very rare or extinct since they were not observed during intensive fieldwork at Sint Eustatius (2015), Curaçao (2017), and Bonaire (2019). These findings underline the importance of specimen collecting and the continued curation of historical collections [212,213].

Out of the nine families of the order Zoantharia, at least five are recorded to the Dutch Caribbean, covering nine genera and 24 species. Among these, at least five species are endemic to the Caribbean Sea (*Bergia cutressi*, *B. puertoricense*; *Umimayanthus parasiticus*, *Hydrozoanthus antumbrosus*, and *H. tunicans*; [5,26,214]). The Caribbean is the diversity center of reef taxa in the Atlantic Ocean [209,215,216], including Zoantharia [5], and our results provided important insights on the distribution of zoantharians in a regional scale. For example, the SC region had a higher richness than EC (22 and 17 species, respectively; Table 1) and includes the newly described *Parazoanthus atlanticus* sp. n.; a similar pattern was reported by Miloslavich and colleagues [207] for other marine invertebrates across Caribbean regions. Additionally, 17 zoantharian species were distributed across both SC and EC, and some zooxanthellate species were found from intertidal to mesophotic depths, noted by historic and recent surveys. Such results confirm the wide distribution of Zoantharia across localities and depth range [5]. Moreover, two species were reported from deeper than 200 m and are probably unknown to science, highlighting the need of surveys in mesophotic and deep-sea ecosystems [11,217,218].

5. Conclusions

In conclusion, curated specimen collections are an invaluable resource. The Naturalis collections, combined with field surveys, have contributed much to our knowledge of zoantharians in both the Central Indo-Pacific [219] and in this study in the Dutch Caribbean. In addition, photographic records have also been useful during the present research, as previously was demonstrated the South China Sea [220]. For many marine taxa, there is a dearth of information despite their commonality, and basic science as conducted here is a foundation to further studies on different fields and management of species.

Supplementary Materials: The following are available online at www.mdpi.com/1424-2818/12/5/190/s1, Figure S1: Phylogenetic reconstructions using the sequences of one nuclear marker (a) ITS-rDNA, and two mitochondrial markers (b) 16S-rDNA, and (c) COI-mtDNA (cytochrome c oxidase I). Table S1: List of specimens examined in this study. Table S2: List of localities recorded in this study.

Author Contributions: Conceptualization, J.D.R. and B.W.H.; field work, J.D.R. and B.W.H.; methodology, all authors; molecular experiments and analyses, J.M., M.E.A.S., H.K., and J.D.R.; resources, J.D.R. and B.W.H.; data curation, all authors; writing—original draft preparation, J.M.; writing—review and editing, all authors; project administration, funding acquisition, J.M., H.K., J.D.R., and B.W.H. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

NA = information not available.
RMNH = Rijksmuseum van Natuurlijke Historie (at Naturalis Biodiversity Center), Leiden, Netherlands
ZMA = Zoological Museum Amsterdam (at Naturalis Biodiversity Center), Leiden, Netherlands
NSMT = National Science Museum, Tsukuba, Ibaraki, Japan
MISE = Molecular Invertebrate Systematics and Ecology Laboratory, University of the Ryukyus, Nishihara, Okinawa, Japan
Por = Porifera collection
Coel = Coelenterata collection
Sta. LUY = Station number Luymes Expedition [47]
Sta. EUX = Station number Marine Biodiversity Expedition to Sint Eustatius, 2015 [48]
coll. BWH = collector: Bert W. Hoeksema
coll. JCH = collector: J.C. (Koos) den Hartog
coll. JDR = collector: James D. Reimer
coll. JGH = collectoer: Jaaziel E. Garcia-Hernandez
coll. PWH = collector: P. Wagenaar Hummelinck

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