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Research Article

Effects of ocean exposure, substrate type, and depth on bryozoan species richness in the north Pacific of Costa Rica

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ABSTRACT. Bryozoa is a phylum of sessile, colonial filter-feeding organisms that are often understudied in tropical regions. Research on this group in Costa Rica is scarce, both in ecology and in diversity. Moreover, in the study area on the north Pacific coast, no studies on bryozoans have been published in more than 90 years. Considering this, the objective of this study was to investigate bryozoan diversity in the Área de Conservación Guanacaste (ACG) and to assess whether habitat factors, such as exposure to the open ocean, depth, and substrate type, influence bryozoan species distribution. Samples of bryozoans inhabiting shallow waters (0-16 m) from various localities in the ACG were obtained. Multivariate analyses were performed, and diversity indices were calculated to characterize the sampling sites. The results of the study demonstrated that the inner and medium exposed zones of the study area and hard substrates (such as under rocks and shell litter) had the highest species richness and the highest number of rare species. However, no preference for depth was noticed.

Keywords: bryozoans; nMDS; LDA; cluster; Jaccard; upwelling; Santa Elena Gulf; Northern Pacific coast; Costa Rica

INTRODUCTION

Bryozoa is a phylum of aquatic colonial and mostly sessile animals that tend to grow on hard substrates, as epibionts on algae (Rogick & Croasdale 1949, Ryland 2005, Flórez-Romero et al. 2007, Cortés et al. 2009, Cook et al. 2018a) or even on artificial substrates (Azevedo et al. 2006, Ruiz-Velasco et al. 2025). These animals are suspension feeders and compete for space on the substrate with other organisms that share with similar life strategies, such as ascidians, cirripedians, sponges, and algae (Winston & Jackson 1984, Labarbera 1985, Ciavatta et al. 2020). Bryozoans are preyed upon by a wide variety of other species, including nudibranchs, pycnogonids, mollusks, fish, starfish, and other incidental consumers (Ryland 1976). Therefore, habitat selection during larval settlement is a factor affecting bryozoan survival and may be dictating their regional distribution (Brancato & Woollacott 1982, McKinney & McKinney 1993). Some bryozoan species tend to prefer specific substrates. Examples of this include epibionts on algal fronds, encrusting colonies living on rocks and boulders, or growing on shell litter; even fouling species may have certain affinities for or an ease of colonization of new substrates (Ryland 1976, Humphries 1977, Duncan et al. 2022). The contrary can also be said, as non-fouling bryozoans can be found colonizing different types of substrates.

Although bryozoans are a diverse group with several representatives of fouling and exotic species, they are understudied ecologically (Yan & Huang 1990,

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Miranda et al. 2018, Ciavatta et al. 2020). The phylum has appeared in multiple articles about intertidal and rocky shore ecology of the tropical eastern Pacific, not as protagonists but as brief mentions of them as part of the encrusting colonial fauna (Reimer 1976, Menge et al. 1986, Witman & Smith 2003, Miloslavich et al. 2016) or potential threats as invasive species (Veitch et al. 2017). In Costa Rica, there are few studies have on extant species richness, as noted by Cortés et al. (2009). No exclusive bryozoan ecology publication has been published, aside from benthic community studies such as Sibaja-Cordero & García-Méndez (2014), which included several unidentified bryozoans and membraniporids in an intertidal community study influenced by open-ocean exposure. Or in the study conducted by Sibaja-Cordero et al. (2016), who found three species of Bryozoa as part of the macrofaunal assemblage on coarse sand bottom dredged from Isla del Coco, an oceanic island.

Efforts to inventory bryozoans have been made in other tropical and temperate countries due to the increase in reports of exotic and cryptic species over the last 20 years (Bock 1982, Miranda et al. 2018, Granthom-Costa et al. 2025). Bryozoan growth strategies make them potential fouling organisms, which may be a major cause of the introduction of exotic species (Ryland 1976, 2005, Yan & Huang 1990). Costa Rica is a tropical country with habitats that the introduction of exotic species could endanger. Therefore, determining the preexisting diversity and habitat selection of bryozoans is important to manage potential threats to native diversity.

The objective of this study was to describe and analyze patterns of bryozoan diversity and distribution in the Santa Elena Gulf, on the northern Pacific coast of Costa Rica. The study was designed to test the hypothesis that bryozoan diversity and distribution would vary with habitat characteristics (ocean exposure, type of colonized substrate, and depth at which organisms were collected). Higher diversity was expected in less-exposed areas of the study site, as they are less likely to be affected by environmental conditions associated with seasonal upwelling. For substrates, greater diversity was expected on stable, hard surfaces, such as large boulders and rocks. Regarding depth, higher diversity was expected at shallower depths.

MATERIALS AND METHODS

Study site

The Área de Conservación Guanacaste (ACG; 10.6 to 11.0°N, 86.5 to 85.3°W, Fig. 1a) is a conservation area in the north Pacific of Costa Rica. ACG encompasses 163,000 ha in northern Guanacaste, and its protected area represents 2% of Costa Rica's total territory. ACG includes the Santa Elena Peninsula, the Murciélago Archipelago, and Isla Bolaños. The peninsula has a diversity of marine habitats, including sandy beaches, soft bottoms, mudflats, rhodolith beds, coral reefs, rocky intertidal zones, mangroves, deep areas (more than 50 m), islets, and islands (Cortés 2017, ACG 2019). Most of the islands in ACG are outside the Santa Elena Peninsula, meaning they are directly exposed to Pacific Ocean influences.

Nevertheless, zones that are sheltered from the waves during the rainy season but exposed during the upwelling season, and occasionally affected by southern swells during the non-upwelling season, were sampled. The Santa Elena Peninsula is composed mainly of sedimentary rock outcrops, the oldest in Costa Rica. The peninsula's geological origin led to the formation of numerous cliffs and walls, creating environments conducive to marine life (Cortés & Quesada-Román 2024). The exposed rocks on the peninsula are mainly serpentinized peridotites, basaltic radiolarites, gabbros, basaltic intrusions, and plagiogranites, dating from around the end of the Cretaceous period (Denyer et al. 2005, Denyer & Gazel 2009, Whattam et al. 2016).

The waters in this region stay warm during the rainy season. Between May and November (non-upwelling season), water temperature is usually in the range of 26 to 30°C (Alfaro & Cortés 2012); pH tends to be close to 8.00, dissolved CO_2 is usually around 475 to 645 µatm, and dissolved oxygen is in the range of 228 to 144 µmol l-1 Rixen et al. 2012. Moreover, mean rainfall in the area ranges from 1.2 to 2.4 mm per day, while in the dry season (November to March) rainfall is typically below 1.0 mm per day Sánchez-Noguera et al. 2025. ACG experiences a strong seasonality due to powerful winds from November to April. During this period, the average wind velocity increases sharply, reaching 4 m s^{-1}. The winds and their direction cause an intense annual upwelling (Cortés & Joyce 2020, Fernández-García et al. 2021), leading to a decrease in surface seawater temperature from 30 to 24°C (Sibaja-Cordero et al. 2025). Previous studies in Bahía Salinas showed that water temperature at the bottom (depths of 3 to 6 and 6.5 to 9 m) could go down to 9°C cooler than in non-upwelling months (Sibaja-Cordero et al. 2025). Also, it can become 1 pH unit more acidic because dissolved carbon dioxide can increase by up to 150 units, while dissolved oxygen and sea level tend to decrease too (McCreary et al. 1989, Rixen et al. 2012).

Sampling

ACG was visited on four occasions: August 03 in 2022; June 29-30, July 07, and August 24-25 in 2023. All sampling periods were encompassed during the non-upwelling season. Samples from 14 Scuba dives and 2 freedives were collected during visits to the intertidal zones at low tide in ACG (Table 1, Fig. 1b). The dives had an average duration of 45 min. For the visits to the intertidal habitats, sampling took about 45 min, with the research team divided into teams to search the mid-intertidal zone and freedive in the low intertidal zone. In each sampling event, three to four researchers collected the material, and at least three of the four were the same researchers each time. In the research team, all members have at least 5 years of experience sampling marine benthic organisms in the area and have expertise in ascidians, sponges, algae, crustaceans, marine worms, hydroids, and bryozoans. The material extracted came from rocky habitats in shallow water (0 to 16 m), such as boulders, cobbles, or coral rubble; rocky shores, reefs, platforms, and walls; or sandy patches. During the dives, the upper and undersides of large rocks and coral rubble were inspected for colonies visible to the naked eye, and fragments were removed with a hammer and chisel. For smaller rocks and algae with colonies, the substrates were collected by hand. For this study, boring specimens were not considered. Sample collection follows the procedure detailed in Antillón-Obando et al. (2025).

At each sampling site, the maximum depth (m) and substrate type were annotated. The types of substrate included rock, pebbles, algae, invertebrates, shells, and dead coral. The 16 sampling sites differ in their open-ocean exposure, based on their location in the marine sector of ACG, their proximity to the Santa Elena Gulf, and whether they are within bays or part of the archipelago. Four main geographical zones with a gradient of exposure to the open ocean (EOO; Fig. 1b) were established: external, medium, internal, and intertidal. These categories ranged from the highest EOO (external) to the lowest (intertidal) in ACG. Each EOO category contained all substrate types.

Classification and identification of colonies

The colonies were maintained alive in seawater with air pumps throughout their manipulation, then preserved in 90% ethanol. Digital photographs of the live colonies were taken in a field laboratory using an AmScope SM-4TZ-144A microscope or an Omax 18MP camera, and the program Touplite (2010-2022, ToupTek Photonics) was used to capture close-up images of the zooids. For larger colony frames, a Canon EOS Rebel SL3 camera was used. After that, a fragment from a morphologically representative individual in each morphospecies group was prepared for Scanning Electron Microscope (SEM) imaging using a Hitachi S-3700n or a Zeiss Sigma300VP, both at the Centro de Investigación en Estructuras Microscópicas (CIEMic). Fragments with fresh tissue and mounts for SEM images were preserved and stored in the Bryozoa collection at the Museo de Zoología de la Universidad de Costa Rica (MZUCR). A more detailed description of these methods can be found in Antillón-Obando et al. (2025). For the morphological identification of the colonies the taxonomic keys provided by Banta & Carson (1977), Soule et al. (2007), Cook et al. (2018b), journal articles containing SEM images with thorough descriptions in Banta (1969), Badve & Sonar (1995), Dick et al. (2006), and web pages with public records of bryozoans in the region (Herrera-Cubilla 2017) were employed. As criteria for morphological classification, characteristics such as avicularia, spines, ovicells, shape of the opesia, denticles, and gymnocyst were prioritized. Photos of live colonies and SEM images for each species are available in the Supplementary Material (Figs. S1-S9 of Bryozoan species of the north Pacific coast of Costa Rica (https://kerwa.ucr.ac.cr/)).

Statistical analysis

Firstly, for the description of diversity, rare species were defined as colonies found in only one category of a variable (e.g. only one substrate type). Rare species depend on the specific variable highlighted at the moment; therefore, some species are specific to one category in one variable, but not the other variables (e.g. a colony found only in one EOO, across several substrates and depths). On the other hand, a colony could be found in a specific arrangement of single categories for each variable and still be a rare species (e.g. a colony found only in one EOO, one substrate, and one depth range). Secondly, for EOO and depth, a non-metric multidimensional scaling (nMDS) analysis was conducted using the presence-absence Jaccard index to visualize similarities among groups. In the case of EOO, the four main categories (external, medium, internal, and intertidal) were subdivided into six smaller zones (EOOsub) to have a better comparison in the nMDS analysis (Hammer et al. 2001). These areas were based on Table 1 separation categories including Isla Bolaños and Isla Loros. Moreover, for EOO and depth, a constrained seriation analysis was performed to compare the arrangement of species presence along each gradient and determine whether species presence-absence was randomly distributed. The test compares

Table 1. Sites visited for collecting marine bryozoans in Área de Conservación Guanacaste (ACG). Zone named based on geography. Depth corresponds to the maximum depth reached in each site during dives. Exposure to the open ocean (EOO) gradient with 4 categories (external, medium, internal, intertidal). The names used locally by the community in Cuajiniquil town were kept.

Zone	Site	Coordinates	Depth (m)	EOO
Murciélago Archipelago	San Pedrito	10°51'21"N, 85°57'4"W	5	External
	Bajo Pochote	10°51'30"N, 85°''55"23W	7	
	Jardín San José Island	10°51'45"N, 85°54'43"W	6.8	
Santa Elena Gulf	David Island a	10°57'28"N, 85°43'25"W	9	Internal
	David Island b	10°57'27"N, 85°43'23"W	4	
	Bajo Viejón	10°57'18"N, 85°43'42"W	15	
	Casa Verde/Bajo Chaca	10°58'56N, 85°42'15"W	6-4	
	Muñecos Island	10°58'45"N, 85°42'54"W	4-5	
Intertidal (Bahía Junquillal)	Intertidal zone	10°58'43"N, 8541'26"°W	0	Intertidal
	Intertidal rocky zone	10°58'44"N, 85°41'32"W	0	
Santa Elena Bay	Pitahaya	10°56'15"N, 85°48'6"W	3.5-5.5	Medium
	Punta Matapalito	10°56'18"N, 85°47'24"W	5-10	
	Playa Pochote	10°56'45"N, 85°49'06"W	8	
	Las Gemelas	10°56'22"N, 85°47'08"W	10	
Bahía Salinas	Loros Island - lado Refugio	11°00'09"N, 85°44'50"W	5-9	Internal
	Bolaños Island	11°03'01"N, 85°42'46"W	5-13	

the constrained matrix with 30 random matrices generated via a Monte Carlo simulation to determine whether the constrained matrix is more informative than a random one (Brower & Kile 1988). Thirdly, for substrate, a cluster analysis was carried out using an unweighted pair-group method with arithmetic averages (UPGMA) based on the Jaccard index of the general species list for the different types of surfaces colonized by bryozoans. After this, a principal coordinates analysis (PCoA) was applied to the presence-absence matrix for each sample, using all axes to capture the total variance, and a linear discriminant analysis (LDA) was then performed to assess differences between substrates.

Additionally, a one-way permutational multivariate analysis of variance (PERMANOVA), a non-parametric multivariate analysis of variance (Anderson 2001), was applied on each of the three environmental variables based on the Jaccard index, to determine if there were differences in the composition of bryozoan species between the groups (EOO, substrate, and depth). Lastly, two individual rarefaction curves of species richness were generated for the environmental variables that showed statistical differences, and a species accumulation curve (SAC) was genrated using dive immersions as units of effort. All analyses were performed using PAST 4.15 (Hammer et al. 2001) and the SAC in Google Colab in Python.

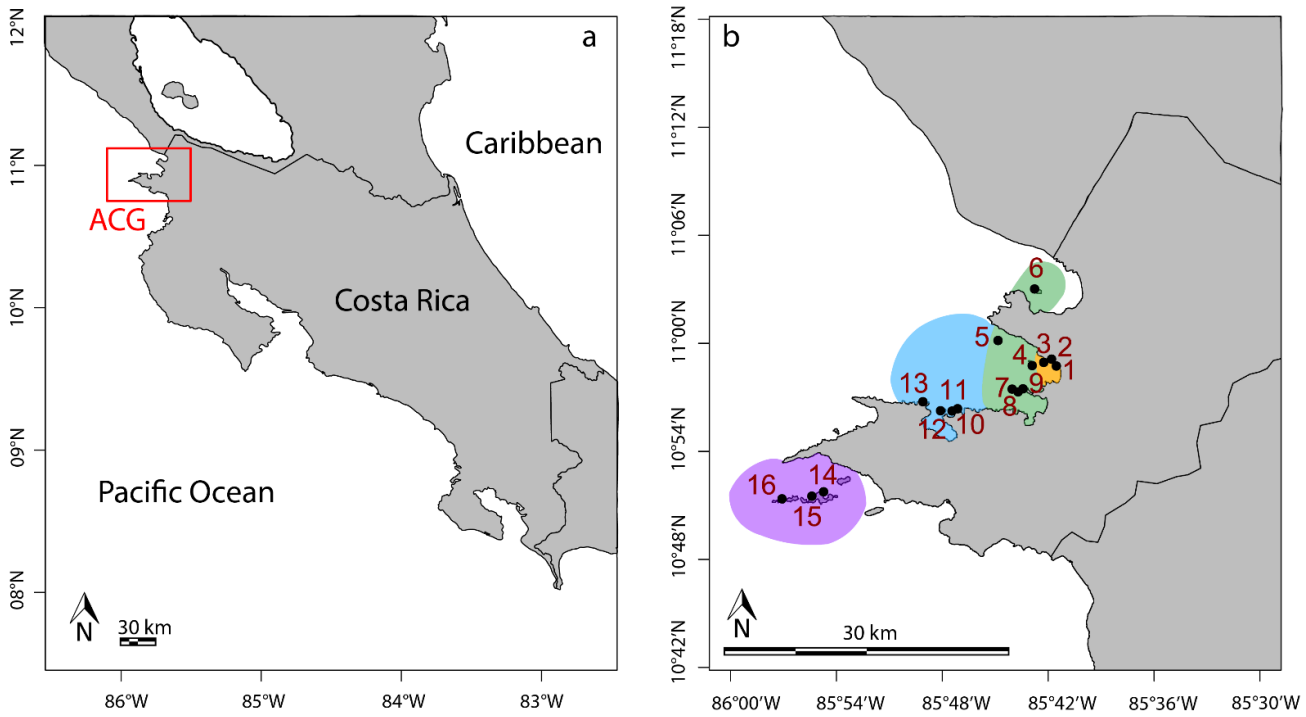

Figure 1. a) Map of Costa Rica with Área de Conservación Guanacaste (ACG) in a red square. b) Map of the coastline of ACG with the sampling sites. Numbers 1 to 16 correspond to the names of the locations visited: 1. Junquillal intertidal; 2. Junquillal rocky shore; 3. Casa Verde/Bajo Chaca; 4. Muñecos Island; 5. Loros Island; 6. Bolaños Island; 7. David Island; 8. Bajo Rojo; 9. Bajo Viejón; 10. Las Gemelas; 11. Punta Matapalito; 12. Pitahaya Island; 13. Playa Pochote; 14. Jardín San José Island; 15. Bajo Pochote; 16. San Pedrito. Colors indicate exposure to the open ocean distribution: yellow-intertidal, green-internal, blue-medium, purple-external.

RESULTS

A total of 174 bryozoan colonies corresponding to 32 taxa in 16 sampling sites were recorded, with an average richness of 9 ± 3 (standard deviation) taxa per site. The highest species richness (24 species) was recorded in the medium EOO, and the lowest value was at intertidal EOO (Table 2). Fifty-nine percent of the species were found in more than one EOO, while 65% of the species were found growing on more than one type of substrate (Table 2). The species accumulation curve (SAC) by dive sampling number showed that the number of species found was close to the estimate by extrapolation of around 35 expected species for this specific habitat and depth range (Fig. 2) (Fig. S1). The substrate type with the highest richness was "under rocks" (25 species), followed by "shells" (22 species; Table 3). Algae and invertebrates had the least bryozoan abundance and richness (Table 3). The highest Jaccard index similarities were observed between internal-medium, external-medium, and internal-intertidal (0.33, 0.26, and 0.26, respectively; Table 4). EOO medium had the highest number of rare species (7), while external and intertidal had the least number of rare species (one each, Table 4). Ten species in the study were rare species with a specific single arrangement of categories in each variable; they occurred only once in the EOO, substrate, and depth categories (Table 2: *Alderina smitti*, *Biflustra* sp., *Bugula neritina*, Calloporidae indet., *Floridina* sp., *Hippaliosina* sp., Lichenoporidae indet., *Puellina* sp., *Tubulipora* sp., *Watersipora arcuata*).

The nMDS for the EOOsub (stress = 0.13, Fig. 3a) showed similarities between areas of the same exposure to the ocean and had the closest distances between areas with the same EOO (Table 1). The islands in EOOsub (Loros, Bolaños, and Murciélago Archipelago) were closer to each other than to other EOOsub, with Loros and Bolaños being the closest of the three. The next similar EOOsub was Santa Elena Gulf, associated with intertidal, as well as Santa Elena Bay. Following coordinate 1, intertidal and Murciélago Archipelago were the furthest apart. While following coordinate 2, Santa Elena Bay was the furthest from Bolaños and

Table 2. Species of Bryozoa recorded in the present study and characteristics of the habitats exposure to the open ocean (EOO) zones: Ext: external, Med: medium, Int: internal, Intl: intertidal. Substrate: Al: Algae, DC: dead coral, Inv: invertebrate, Pe: pebble, Sh: shell, UR: under rock. In bold: rare species only occurring once in one category of each variable.

Species	EOO	Substrate	Depth (m)
Alderina smitti	**Int**	**Sh**	**4-5**
Antropora granulifera	Med; Int	Pe; Sh UR	8; 10; 16; 5-10
Antropora minor	Ext; Med; Int; Intl	DC; Inv; Pe; Sh; UR	0; 4; 7; 9; 10; 15; 4-5; 5-13; 6.8
Antropora sp.	Ext; Med; Int; Intl	DC; Pe; Sh; UR	0; 5; 8; 9; 15; 16; 4-5; 5-10; 5-9; 6-4
Beania cf. *hirtissima*	**Int**	Sh; UR	9, 6-4
Biflustra sp.	**Med**	**UR**	**3.5-5.5**
Biflustra tenuis	Ext; Med; Int; Intl	Al; Sh; UR	0; 4; 8; 10; 16; 4-5; 5-13; 5-9; 6-4; 6.8
Bugula neritina	**Med**	**Al**	**6-4**
Calloporidae indet.	**Med**	**Sh**	**3.5-5.5**
Cigclisula sp.	Med; Int; Intl	DC; Pe; Sh; UR	0; 4; 8; 10; 15; 16; 4-5; 5-10; 5-13; 5-9; 6-4
Conopeum sp.	Int; Intl	Pe; Sh; UR	0; 9
Copidozoum sp.	Med Int	DC; UR	16; 5-13; 5-9
Cradoscrupocellaria sp.	Med; Int	Al; DC; Sh; UR	9; 15; 16; 4-5; 6-4
Disporella sp.	Med; Int	Sh; UR	8; 9; 10; 3.5-5.5; 5-10
Floridina sp.	**Int**	**UR**	**9**
Hippaliosina sp.	**Int**	**UR**	**15**
Hippoporidridae indet.	**Med**	Pe; Sh	5-10; 5-13
Lichenoporidae indet.	**Med**	**Sh**	**3.5-5.5**
Membraniporidae indet.	**Ext**	**UR**	**0**
Microporella sp.	Med; Int	Sh; UR	4; 5-13
Parasmittina crosslandi	Ext; Med Int; Intl	DC; Inv; Pe; UR	0; 7; 10; 3.5-5.5; 5-13; 5-9; 6-4
Phidoloporidae indet.	Ext; Med	Sh; UR	5-10; 6.8
Plesiocleidochasma porcellaniforme	Ext; Med; Int	Pe; Sh; UR	4; 7; 10; 3.5-5.5; 5-10; 5-13; 5-9; 6-4
Pleuromucrum sp.	Int; Intl	Sh; UR	0; 15; 6-4
Puellina sp.	**Med**	**UR**	**5-10**
Reptadeonella bipartita	Ext; Med; Int	Pe; Sh; UR	7; 10; 15; 16; 4-5; 5-10; 5-13; 5-9; 6.8
Rhynchozoon sp.	Ext; Med; Int	DC; Inv; Sh; UR	5; 10; 15; 3.5-5.5; 4-5; 5-13; 5-9; 6-4; 6.8
Smittinidae indet.	Med; Int; Intl	Sh; UR	0; 8; 9; 5-9
Smittipora acutirostris	Ext; Med; Int	Pe; Sh; UR	8; 15; 3.5-5.5; 4-5; 5-10; 5-13; 5-9; 6-4; 6.8
Smittipora levinseni	Med; Int	Sh; UR	4; 9; 10; 15; 16; 4-5; 5-10; 5-13; 5-9
Tubulipora sp.	**Med**	**Al**	**5-13**
Watersipora arcuata	**Intl**	**Pe**	**0**

Loros Island. The seriation analysis confirmed a pattern of bryozoan distribution according to the EOO (*P*-value > 0.001, Fig. 3b). Therefore, it could be said that there was a non-random distribution of the bryozoan diversity, following a gradient of EOO in ACG.

Meanwhile, for the depth nMDS, a stress value of 0.19 (Fig. 4a) and a graphical arrangement that didn't clarify the similarities among diving sites were obtained. In this study, it was not possible to determine whether the distribution pattern in bryozoan diversity was related to depth. The distribution of colonies in 0 to 16 m seemed to be random, as confirmed by the seriation analysis (*P*-value = 0.72, Fig. 4b), in which no pattern in bryozoan distribution could be found.

In the cluster analysis for substrates, three main groups were found: the first group contained calcareous substrates (dead corals and invertebrates), the second group was conformed mainly by rocky substrates (pebbles, under rock) and shells (shell litter), and a third outer branch contained the algae (Fig. 5a). A similar pattern was observed with the set of samples in the LDA (Fig. 5b), that had an eigenvalue of 13.42 on the first axis and explained 58.92% of the variance, and an eigenvalue of 4.70 that explained 20.65% of the variance in the second axis. In the case of the LDA, there was an overlap between the groups of calcareous and rocky substrates, shell, invertebrates, pebble, and under rock, though under rock had the least overlap.

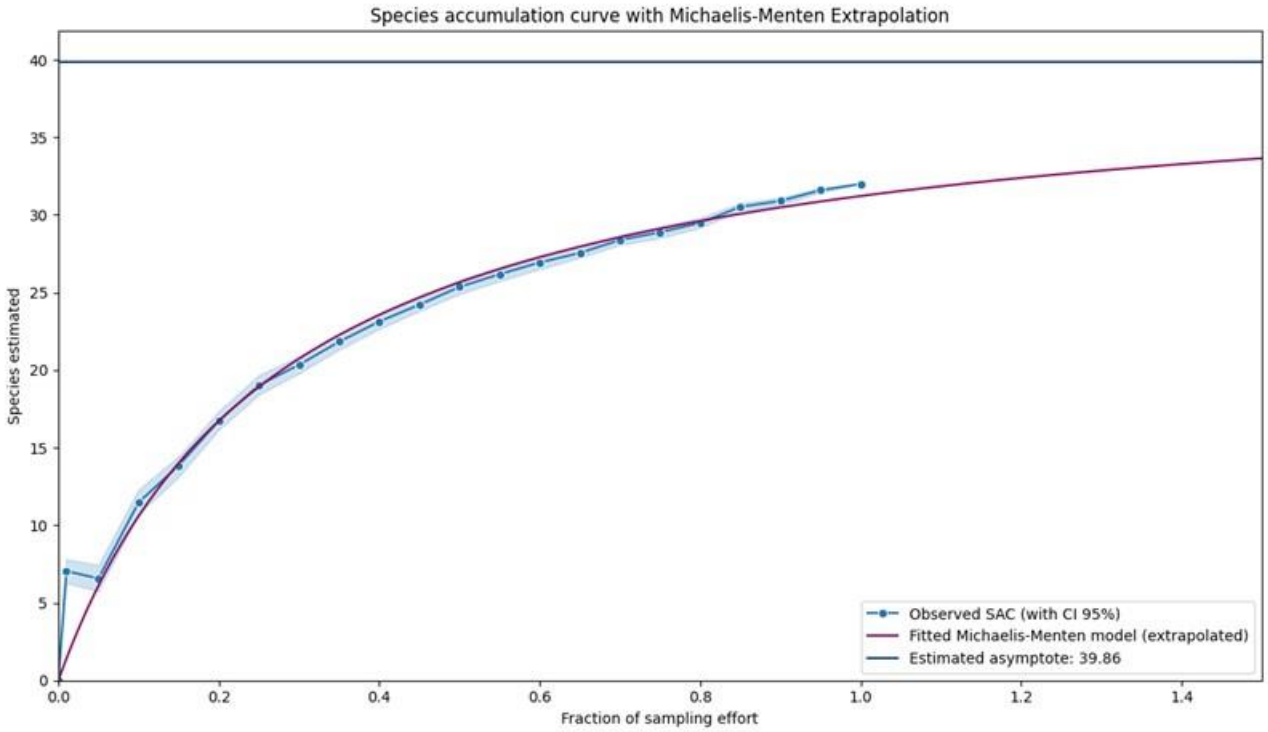

Figure 2. Species accumulation curve (SAC) of organisms found in the study with 95% confidence interval.

Table 3. Total bryozoan abundance, species richness, and rare species (only found in one type of substrate) for the six types of substrates.

	Invertebrate	Algae	Dead coral	Pebble	Shell	Under rock
Species	3	4	7	11	22	25
Individual	3	6	8	20	50	87
Rare species	0	2	0	1	3	5

Table 4. Exposure to the open ocean (EOO) zone similarities. Diagonals represent the unique species of the zone relative to the total species of the zone. In bold, shared species between zones. Decimals represent Jaccard similarity.

	External	Medium	Internal	Intertidal
External	1/10	**9**	**8**	**4**
Medium	0.26	7/24	**15**	**6**
Internal	0.25	0.33	4/22	**8**
Intertidal	0.21	0.18	0.26	1/9

The PERMANOVA for EOO indicated differences between groups (*P*-value < 0.001; Table 5). Therefore, environmental factors associated with each EOO may have influenced the distribution of bryozoan diversity in ACG. The PERMANOVA for substrates also indicated differences (*P*-value = 0.042; Table 5), suggesting that bryozoans' preferences for specific substrates vary by species. Nonetheless, the PERMANOVA for depth did not reveal significant differences between groups (*P*-value = 0.604; Table 5). As stated in the previous analyses (nMDS and seriation), there was no indication of a difference in depth.

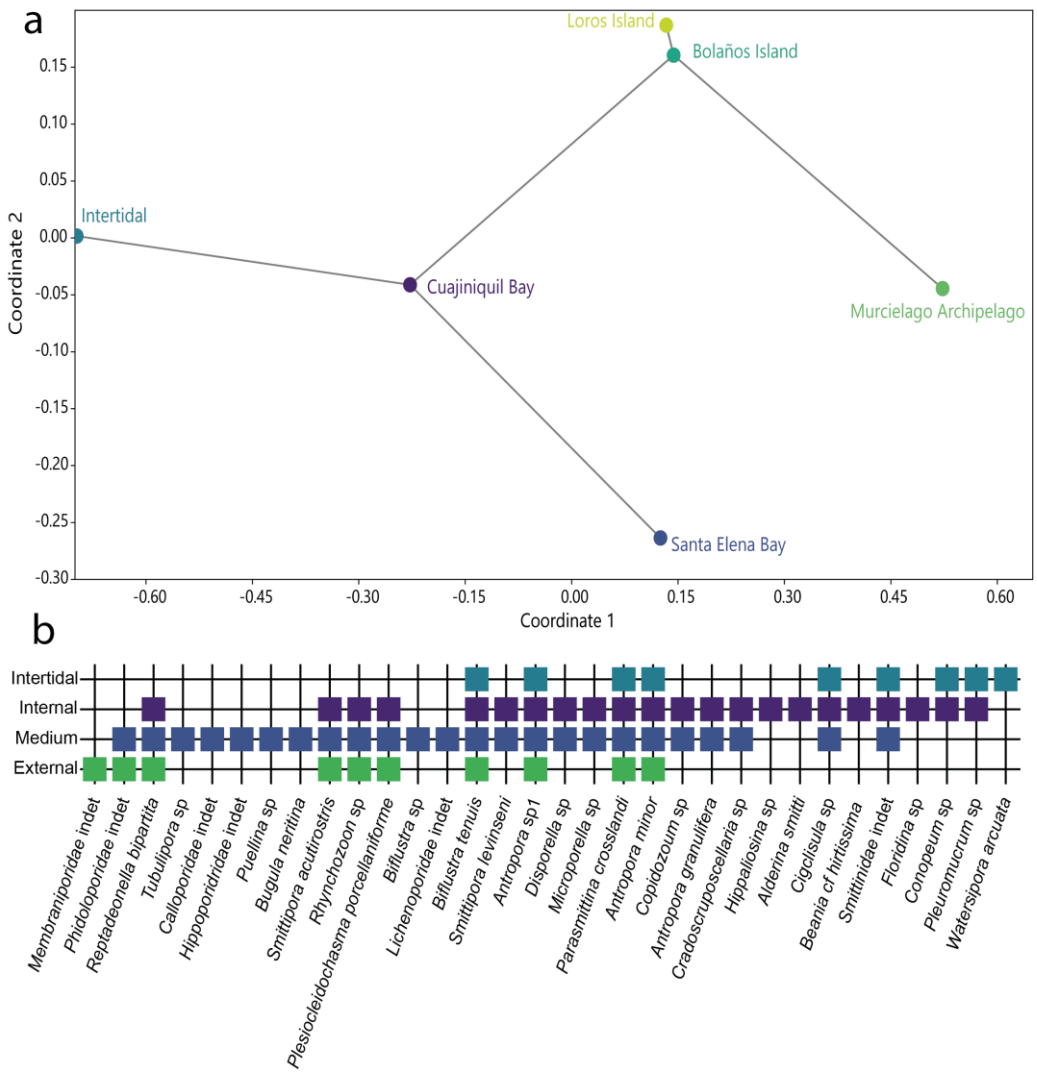

Figure 3. a) Non-metric multidimensional scaling (nMDS) plot for exposure to the open ocean (EOO) subzones (stress = 0.13) with similarity links by minimal spanning tree, using presence-absence Jaccard index as distance, b) constrained seriation analysis of the EOO zones (*P*-value > 0.001).

Lastly, for the individual rarefaction curves, a higher number of taxa was found in the medium and internal EOO (Fig. 6a). In comparison, a lower number was found in the external and intertidal (Fig. 6a). For substrates, the group with the most taxa was under rock, followed by shell, an intermediate number of taxa for pebble, and the lowest taxa achieved were in dead coral, algae and invertebrate (Fig. 6b).

DISCUSSION

The present study was conducted between 0 and 16 m depth, yielding a species count close to the expected 39, based on the extrapolated SAC (Fig. 2). A total of 32 species in the study region were recorded, with an average of nine species per site, and a Jaccard index similarity of 0.25 between EOO on average. For comparison, Hughes & Jackson (1992) report a maximum of 52 species per reef, but usually 30 or fewer bryozoan species per reef site in the Caribbean of Panama. Similarly, bryozoan assemblages on shells from dredge sampling in Schäfer et al. (2012) ranged from 9 to 39 species per site in shallow waters (<30 m). In another case, Cárdenas-Calle et al. (2020) found 13 species, ranging from 1 to 4 per site, using 50×50 cm quadrats in subtidal and intertidal habitats at the Equator. The finding of 32 species from only 16 sites in the northern Pacific of Costa Rica suggests the poten-

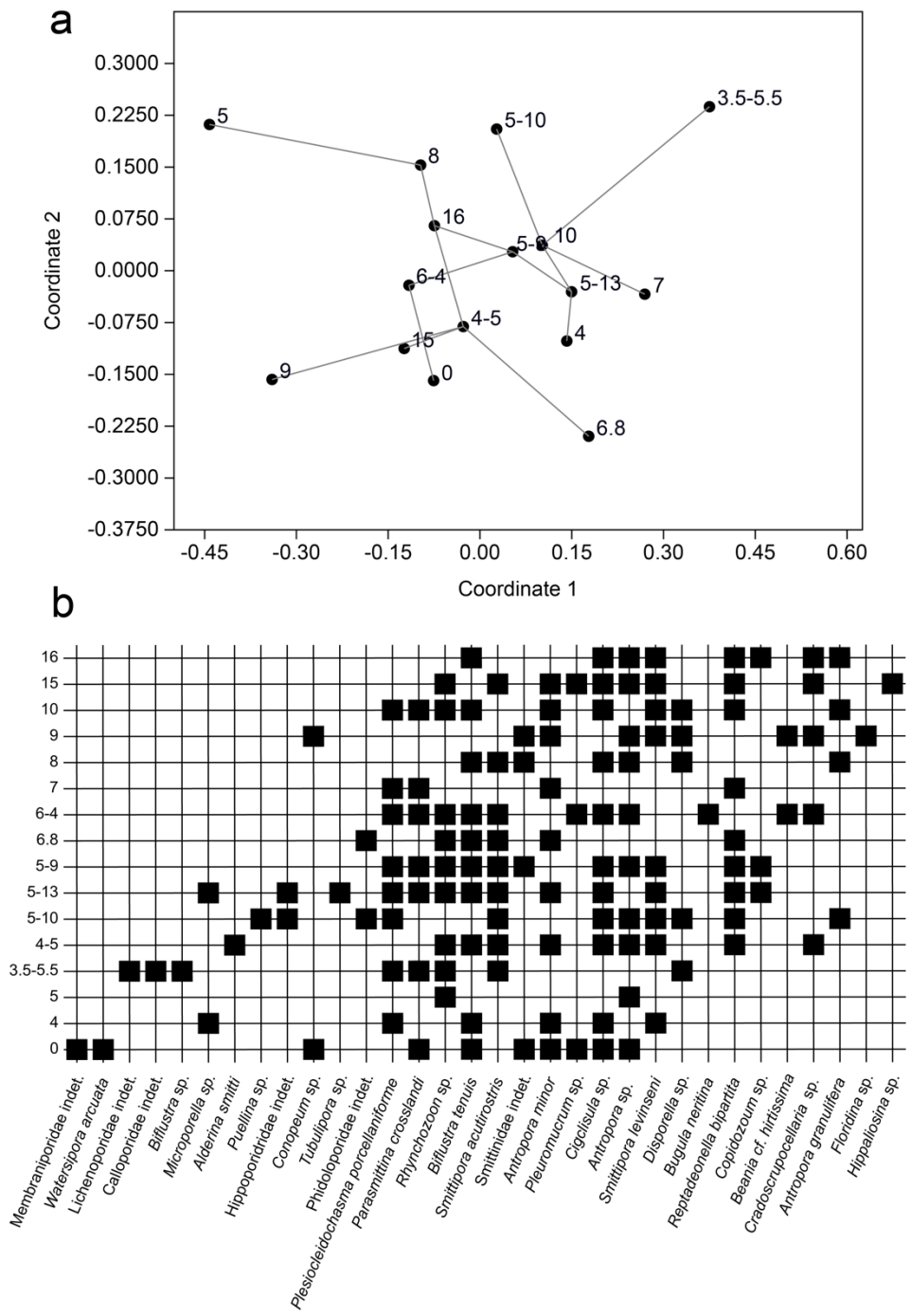

Figure 4. a) Non-metric multidimensional scaling (nMDS) plot for depth (stress = 0.19) with similarity links by minimal spanning tree, using presence-absence Jaccard index as distance, b) constrained seriation analysis of depth (*P*-value = 0.64).

tial for even greater bryozoan diversity in Costa Rican waters. Comparable examples include the Galápagos Islands, where Crossland (1927) reported 37 species at 11 sites, and Banta & Carson (1977) reported 30 species during snorkeling, resulting in seven new records. Deeper-water records have further expanded the Galápagos list to 184 species (Banta & Redden 1990). More recent studies in the Galápagos Islands reported 8-17 species in shallow subtidal and intertidal habitats, along with new records (Witman & Smith 2003, McCann et al. 2019).

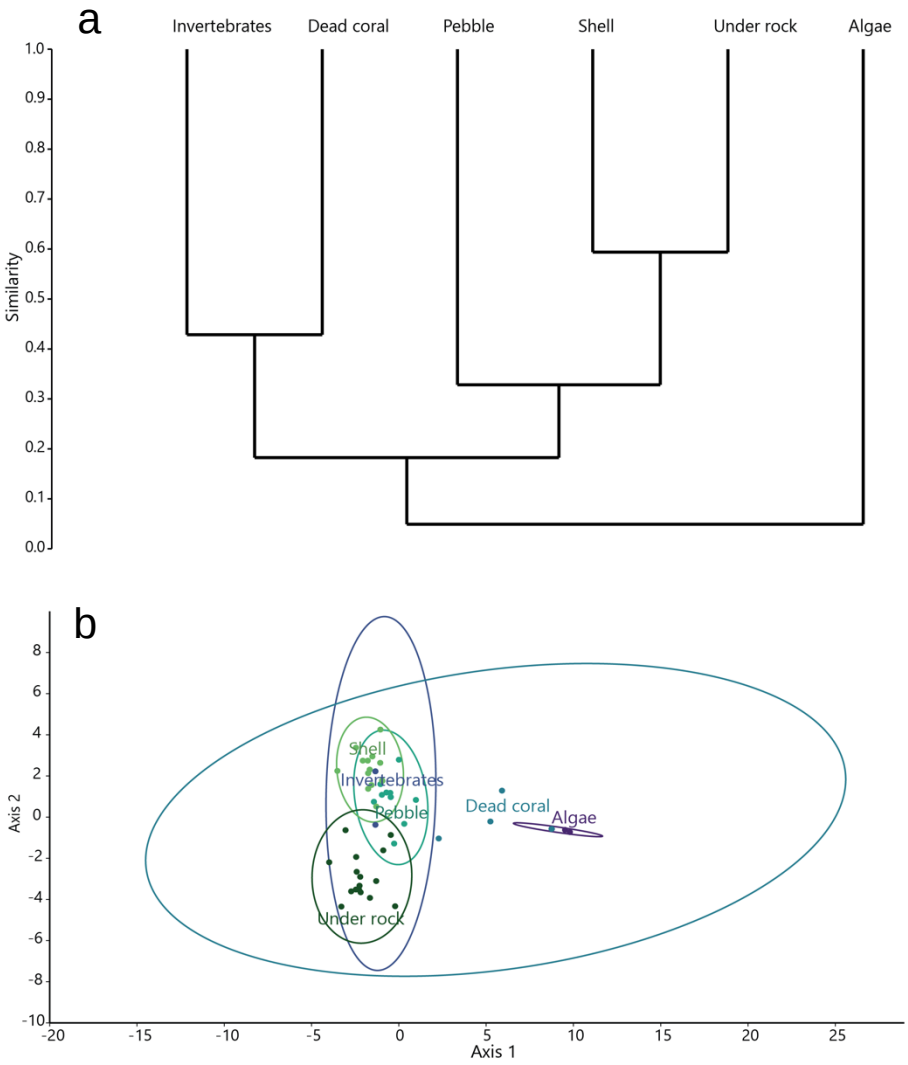

Figure 5. a) Cluster analysis (UPGMA algorithm) based on the Jaccard index for presence-absence of species of Bryozoa according to the substrate they were found growing on, b) linear discriminant analysis (LDA) plot of the different groups of substrates using the scores of a principal coordinates analysis (PcoA) previously performed with 95% confidence ellipses.

Table 5. Results of the PERMANOVAs with 9999 permutations for the three environmental variables in the study. EOO: exposure to the open ocean.

Variable	Sum of squares	Within groups sum of squares	F	*P*-value
EOO zones	24.03	20.81	1.52	<0.001
Substrates	4.51	2.70	1.34	0.042
Depth (m)	101.20	94.04	0.98	0.604

It was originally hypothesized that bryozoan diversity and distribution would vary with habitat characteristics, including ocean exposure, substrates, and the depth at which colonies could be found. The present study shows that, for both EOO and substrate, there are differences in diversity and species distribution. In the case of EOO, the highest diversity was found in medium and internal, while the lowest was

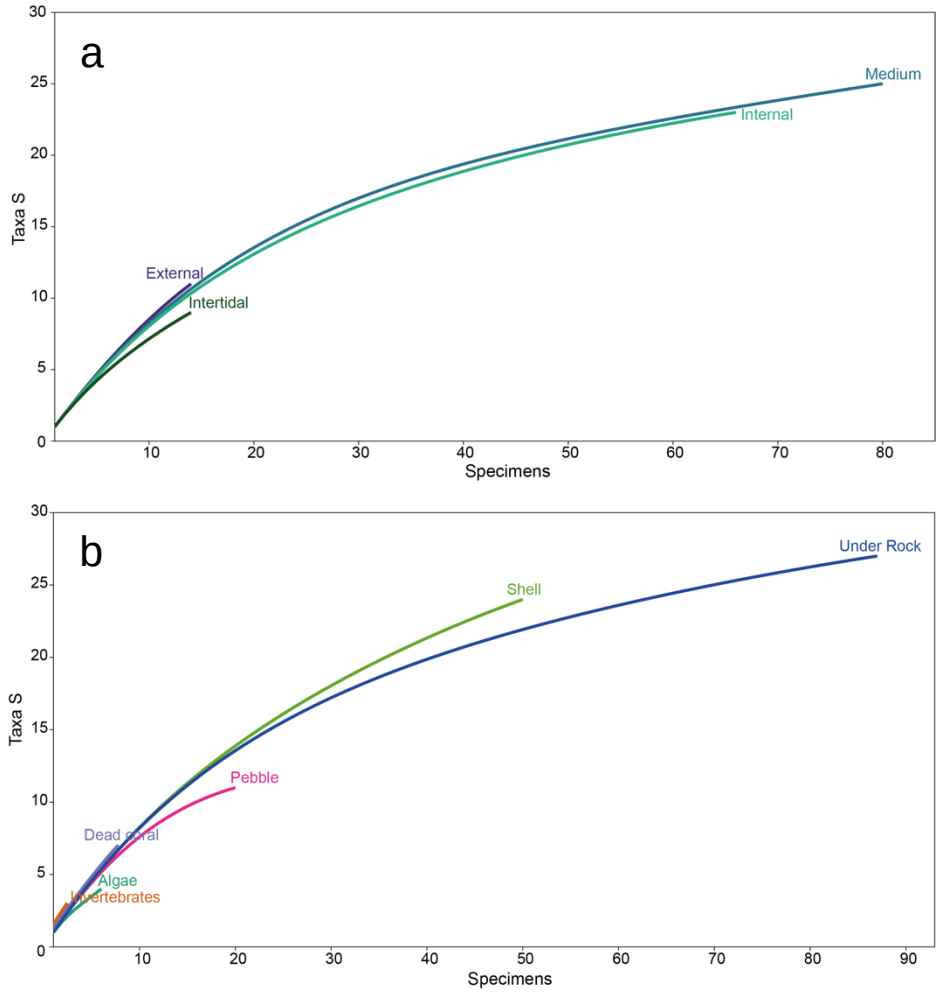

Figure 6. a) Individual rarefaction curve for exposure to the open ocean (EOO) zones, b) individual rarefaction curve for substrate.

in intertidal, followed by external. Originally, it was expected to find higher diversity for the inner, less exposed areas in the gulf due to these areas being more sheltered from the effects of the upwelling season (Sibaja-Cordero & Cortés 2008), which causes a drop in water temperature and pH, and an increase in carbon dioxide and chlorophyll concentration (Rixen et al. 2012, Sibaja-Cordero et al. 2025). Previous studies in the tropical eastern Pacific have shown that upwelling, as a natural disturbance, can alter the species composition of sessile organisms on rocky bottoms and in intertidal zones (Witman & Smith 2003, Sibaja-Cordero & Cortés 2008), in part because filter feeders benefit from microplankton blooms. Moreover, a few of the species found in previous studies about intertidal colonies in Panama and the north Pacific of Costa Rica matched the ones found in internal, intertidal, and medium EOOs from this study, such as *Antropora* sp, *Microporella* sp., *B. tenuis*, *S. acutirostris*, *S. levinseni*, and *Floridina* sp. (Labarbera 1985, Sibaja-Cordero & García-Méndez 2014).

Overall, 16 of the 32 species of bryozoans were shared between the medium and internal EOO, possibly due to less environmental variation or physical stress conditions than in the external and intertidal EOO. Some species in the medium and internal EOO zones are known as fouling taxa, such as *B. neritina* and *W. arcuata* (Yan & Huang 1990, Mackie et al. 2006, Miranda et al. 2018). Currently, there is insufficient enough information to confirm the presence of cryptogenic or exotic species in the area, so hull fouling could contribute to increase diversity in the gulf. In the internal EOO, there is a fishing dock, since artisanal fishing is the main economic activity in the Gulf of Santa Elena (Farías-Tafolla et al. 2022). Moreover, eight of the nine intertidal species were present in at

least two of the other EOO zones; only four were distributed across all four zones (*B. tenuis*, *Antropora* sp., *P. crosslandi* and *A. minor*). The medium EOO zone harbors the highest number of exclusive species, with 7 of its 24 recorded species occurring only there. This situation evidenced some restriction in the distribution of bryozoan species, with only four well dispersed in the region. Knowledge of water currents in this region is scarce. Still, Lizano & Alfaro (2014) pointed out that at the mouth of Bahía Santa Elena (sites 10-13 of the medium EOO zone), superficial water can flow in the opposite direction to the bottom water by influence of wind force and tide direction, outflow or inflow to the bay. During the dry season, the north-easterly jet winds drive Ekman transport that deflects surface waters westward and offshore, producing upwelling and increased wave height; during the rainy season, the winds are weak or shut down entirely, and the intense water transport ceases (Cambronero-Solano et al. 2021). During upwelling, some regions of the medium and internal sections of the gulf are sheltered by mountains, while others are exposed to wave action or water export. These processes influence larval movement within and outside the gulf, similar to the process of larval exportation described by Roughgarden et al. (1988), in that oceanographic forces limit or facilitate the return of species to coastal habitats in California and Oregon. Other factors that can influence the distribution of certain species are tolerance to freshwater input in the internal and medium regions, or the availability of settlement substrate, such as boulders, which are scarce in the intertidal cliffs of the external zone and only available in subtidal sections.

The lowest richness was recorded in intertidal EOO, which had only one rare species among the nine species found at these sites (Table 4). Based on personal observations, the zones where samples were collected tended to have boulders on the smaller side, rocks relatively easy to move and displace, and were more prone to physical disturbance by the tide, aside from the usual stressor factors in this habitat, like desiccation and drastic temperature changes (Connell 1978). Intertidal bryozoans, like other sessile invertebrates, were restricted to low-intertidal rock pools and under rocks due to intense desiccation stress in the Tropical Pacific (Lubchenco et al. 1984, Firth et al. 2026). Additionally, encrusting bryozoans could survive at these sites on stable boulders due to cooling and continual splashing from the waves. Maximal bryozoan diversity is rarely reported from high-energy sites (Dick et al. 2006). Moreover, external EOO had the second-lowest richness in ACG (Table 4). San Pedrito (external EOO), one of the sites sampled in the Murciélago Archipelago, was a patch of dead coral with few bryozoans recorded. As stated in the methods, only colonies visible to divers were sampled; bryozoans encrusting debris, as reported by Winston & Vieira (2013), were not considered. Therefore, the richness here reported could be underestimated.

On the other hand, groups by type of substrate were formed, making a supergroup with the hard substrates and an outer group with algae (Fig. 5a). In this study, two of the four species were growing on algae, but also were reported to encrust two or more types of substrate (*B. tenuis* and *Cradoscrupocellaria* sp.). An important part of the shell litter consisted of the families Pinnidae and Pteridae (personal observation). In both the cluster and LDA results, these substrates were associated (Fig. 5). It has been reported that marine sessile organisms tend to compete strongly for surface area on hard substrates and employ diverse strategies to secure space for growth and feeding (Labarbera 1985). Brachiopods and ascidians are typically competitors with bryozoans for surface area; consequently, some species may avoid settling near them (Brancato & Woollacott 1982, Yan & Huang 1990). It is common for bryozoans to prefer substrates with large potential surface areas; as stated by Ryland (1976), small-surface-area substrates are not suitable for bryozoan settlement. Since these organisms do not delay metamorphosis, larval settlement is important. Still, the remainder of bryozoan distribution may be dictated by post-settlement mortality (Hurlbut 1991), which may explain why almost half of the individuals recorded (87 colonies from 26 species, Table 3) were encrusting under rock surfaces and another portion of them were also encrusting shell litter (50 colonies from 24 species, Table 3).

However, competition and substrate preference are not quite as straightforward in bryozoans (Ward & Thorpe 1989). The groups formed in this study might reflect specialized and generalist mechanisms previously reported in various Bryozoa species (Ryland 1976, McKinney & McKinney 1993, Liuzzi & López-Gappa 2011). Aside from organisms that tend to colonize algae and usually show a certain level of specificity toward their hosts (Liuzzi & López-Gappa 2011), generalist groups might explain why the hard-substrate groups (under rock, shell, pebble, dead coral, and invertebrate) were together. It is possible that, at least among bryozoans, competition for substrate space is not the rule (Sale 1978, Ward & Thorpe 1989). The reported substrate groups could reflect additional biological behaviors. Different species of bryozoans with cyphonaute larvae tend to exhibit diverse

mechanisms of selection, ranging from alternating positive and negative phototropism and geotropism to selection based on microbial films (Humphries 1977, McKinney & McKinney 1993). Larval settlement may even depend on specific species of colonial organisms previously settled in a substrate, as in *Bugula pacifica*, which delays settlement in the presence of the colonial ascidian *Diplosoma macdonaldi*, which tends to outgrow it (Brancato & Woollacott 1982). Moreover, most species occur on more than one substrate. Among the species found, the substrate with the highest number of rare species was under rock, and it also had the highest species richness (5 rare species out of 25 species found). The rest of the species were usually found on two or more substrates. As previously mentioned, the genus *Cradoscrupocellaria* was found growing on four of the six substrates studied.

Roughly 35% of the species observed showed preferences for substrate type, while the rest were seemingly generalists, encrusting more than one type of substrate. Both EOO and substrate distribution may be factors allowing bryozoans to cohabit this tropical region while reducing competition for resources such as food and encrusting space. Similar examples are the coexistence of 12 bryozoan genera in the intertidal of Andaman Island (11°35'S) by the diversity of substrates (Naufal et al. 2018), or in the Hawaii intertidal, the 32 bryozoans species present minimize their competition by occupying distinct microhabitats such as cavities, undersides, or exploit secondary substrates like worm tubes, coralline algae, or dead coral colonies (Dick et al. 2006).

On the other hand, no relation between depth and bryozoan distribution was noticed in this study. Most species have previously been reported in ranges of 0-200 m (Ryland 1976, Cook et al. 2018a,b). There is a tendency for a higher frequency of encrusting cheilostomes in shallower waters, while erect ramified species usually colonize deeper waters (Grünbaum 1997). This distribution might explain the high prevalence of encrusting cheilostomes observed in this study. Of the 32 taxa reported, only three species of erect or ramifying bryozoans were found living at depths from 4 to 16 m (*B.* cf. *hirtissima*, *Cradoscrupocellaria* sp., and *B. neritina*).

Thus, expanding sampling to greater depths or employing additional techniques, such as trawling or artificial settlement plates, could reveal more species for the Guanacaste coast. After almost 30 years since the last study on bryozoan diversity in Costa Rica, this study opens the way for further research on this group in the tropical eastern Pacific region.

Credit author contribution

B. Antillón-Obando: conceptualization, methodology, formal analysis, investigation, data curation, writing-original draft preparation, writing-review and editing, visualization. J. Cortés: validation, resources, project administration and funding acquisition; J.A. Sibaja-Cordero: conceptualization, methodology, validation, investigation, resources, writing-original draft preparation, writing-review and editing, supervision, project administration and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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SUPPLEMENTARY MATERIAL

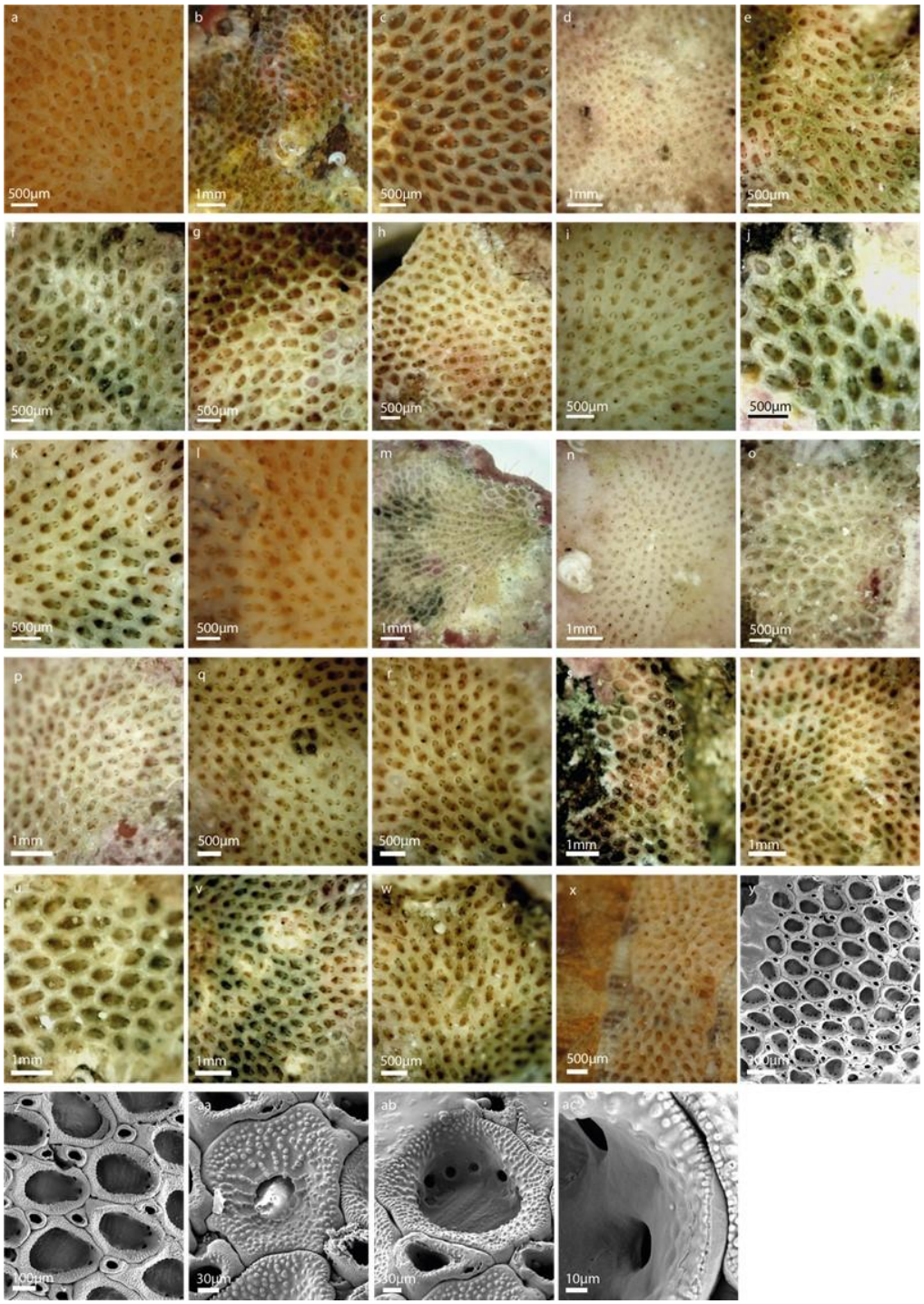

Figure S1. a-k) Live specimens of *Antropora minor*: a) MZUCR-0056, b) MZUCR-0065, c) MZUCR-0077, d) MZUCR-0120, e) MZUCR-0162, f) MZUCR-0164, g) MZUCR-0166, h) MZUCR-0201, i) MZUCR-0229, j) MZUCR-0244 and k) MZUCR-0250; l-x) live specimens of *Antropora* sp.: l) MZUCR-0075, m) MZUCR-0099, n) MZUCR-0105, o) MZUCR-0122, p) MZUCR-0137, q) MZUCR-0145, r) MZUCR-0157, s) MZUCR-0158, t) MZUCR-0191, u) MZUCR-0203, v) MZUCR-0212, w) MZUCR-0240, x) MZUCR-0063; y-ac) electron microscope images of MZUCR-0056 chosen as a representative specimen: y) colony, z) close up of a few zoids, aa) autozoid developing, ab) avicularium and pores, ac) close up of pores.

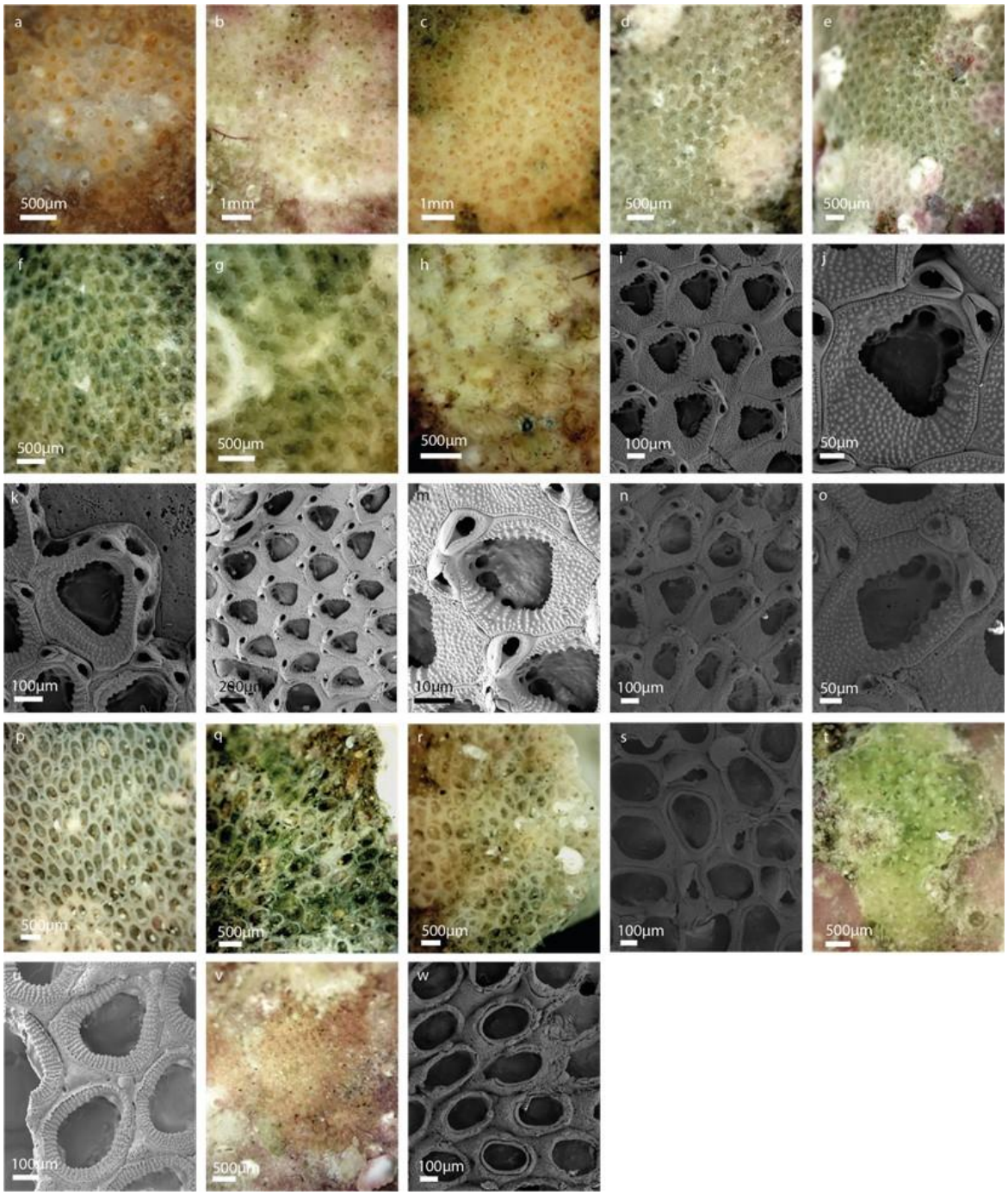

Figure S2. a-h) Live specimens of *Antropora granulifera*: a) MZUCR-0051, b) MZUCR-0136, c) MZUCR-0195, d) MZUCR-0114, e) MZUCR-0132, f) MZUCR-236, g) MZUCR-0237, h) MZUCR-0216; i-o) electron microscope images of *A. granulifera*, images from MZUCR-0136 i) colony, j) close up of a zoid, k) lateral growth of colonies, MZUCR-0132 l) colony and m) close up of a zoid, MZUCR-0216 in n) colony and o) close up of a zoid; p-w) colonies of Calloporidae indet., live colonies of *Copidozoum* sp. p) MZUCR-0139, q) MZUCR-0146, r) MZUCR-0163, s) electron microscope image of MZUCR-0163; t) MZUCR-0205 live colony of *Alderina smitti*, u) electron image of MZUCR-0205; v) live colony of Calloporidae indet. MZUCR-0089, w) electron image of MZUCR-0089.

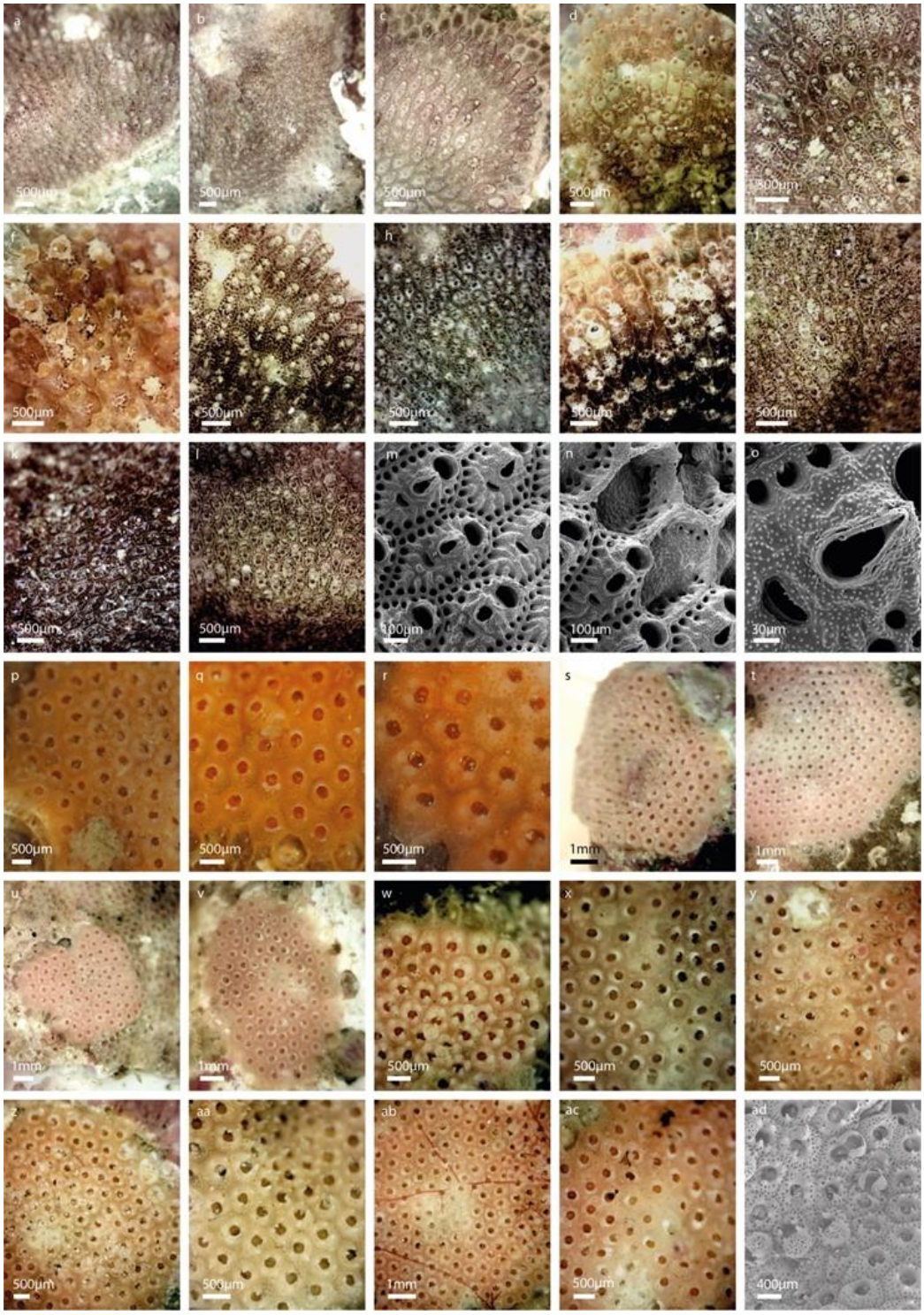

Figure S3. a-l) Live colonies of *Reptadeonella bipartita*: a) MZUCR-0108, b) MZUCR-0125, c) MZUCR-0138, d) MZUCR-0150, e) MZUCR-0156, f) MZUCR-0175, g) MZUCR-0209, h) MZUCR-0228, i) MZUCR-0235, j) MZUCR-0239, k) MZUCR-0243, l) MZUCR-0253; m-o) electron microscope images of *R. bipartita* MZUCR-0108 m) close up of zoids, n) developing zoids showing pores, o) adventitious avicularium; p-ac) live colonies of *Cigclisula* sp.: p) MZUCR-0054, q) MZUCR-0060, r) MZUCR-0085, s) MZUCR-0100, t) MZUCR-0113, u) MZUCR-0123, v) MZUCR-0131, w) MZUCR-0149, x) MZUCR-0155, y) MZUCR-0167, z) MZUCR-0192, aa) MZUCR-0204, ab) MZUCR-0215, ac) MZUCR-0223; ad) electron microscope image of *Cigclisula* sp. MZUCR-0060.

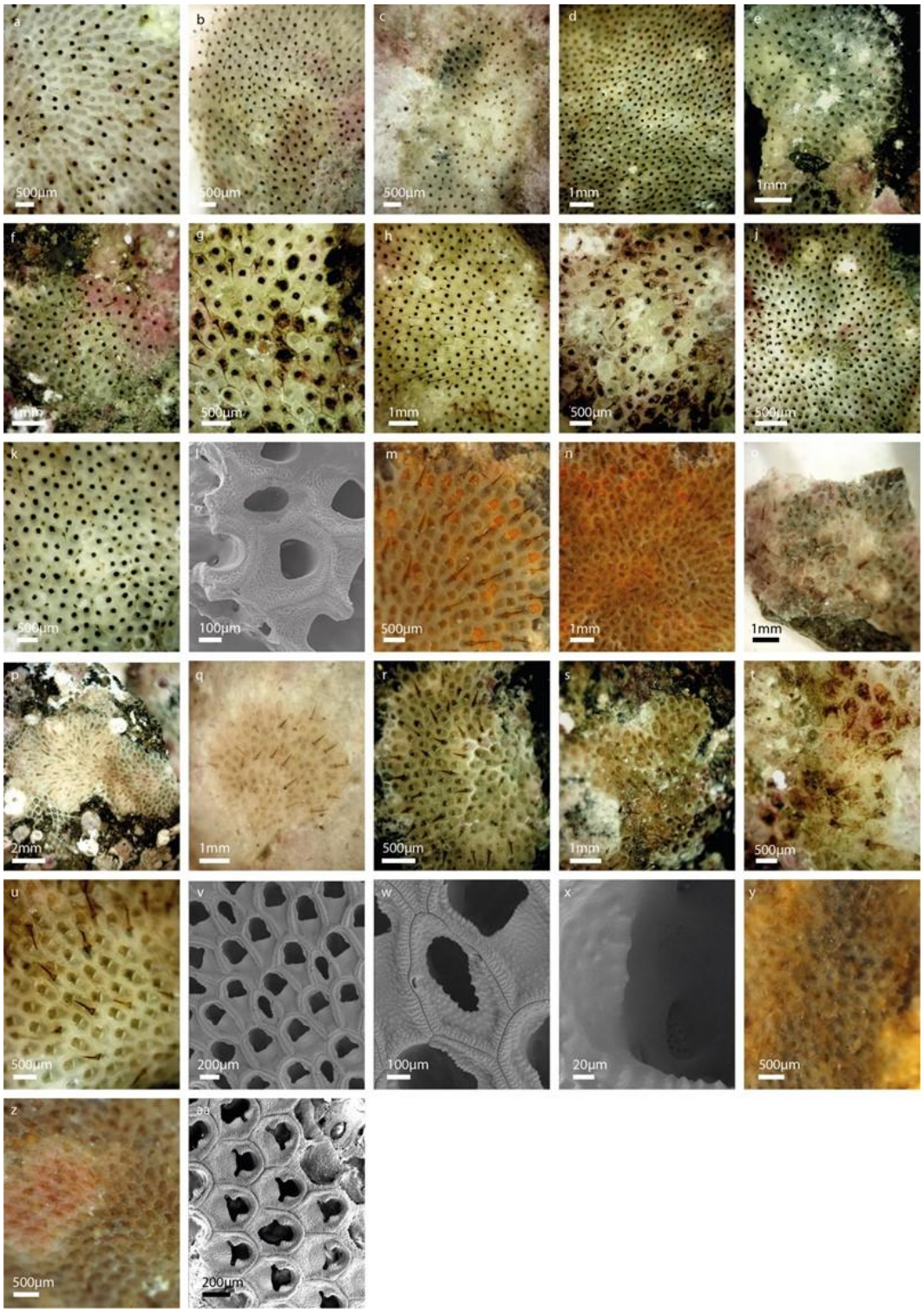

Figure S4. a-k) Live colonies of *Smittipora acutirostris*: a) MZUCR-0097, b) MZUCR-0110, c) MZUCR-0121, d) MZUCR-0141, e) MZUCR-0159, f) MZUCR-0174, g) MZUCR-0190, h) MZUCR-0199, i) MZUCR-0208, j) MZUCR-0213, k) MZUCR-0248; l) electron microscope image of MZUCR-0141 chosen as representative specimen; m-u) live colonies of *Smittipora levinseni*: m) MZUCR-0066, n) MZUCR-0080, o) MZUCR-0112, p) MZUCR-0118, q) MZUCR-0133, r) MZUCR-0148, s) MZUCR-0172, t) MZUCR-0207, u) MZUCR-0230; v-x) electron microscope images of *Smittipora levinseni* MZUCR-0080: v) colony, w) interzoidal avicularium, x) pore plates; y-z) live colonies of *Floridina* sp.: y) MZUCR-0067, z) MZUCR-0072; aa) electron microscope image of MZUCR-0067 *Floridina* sp.

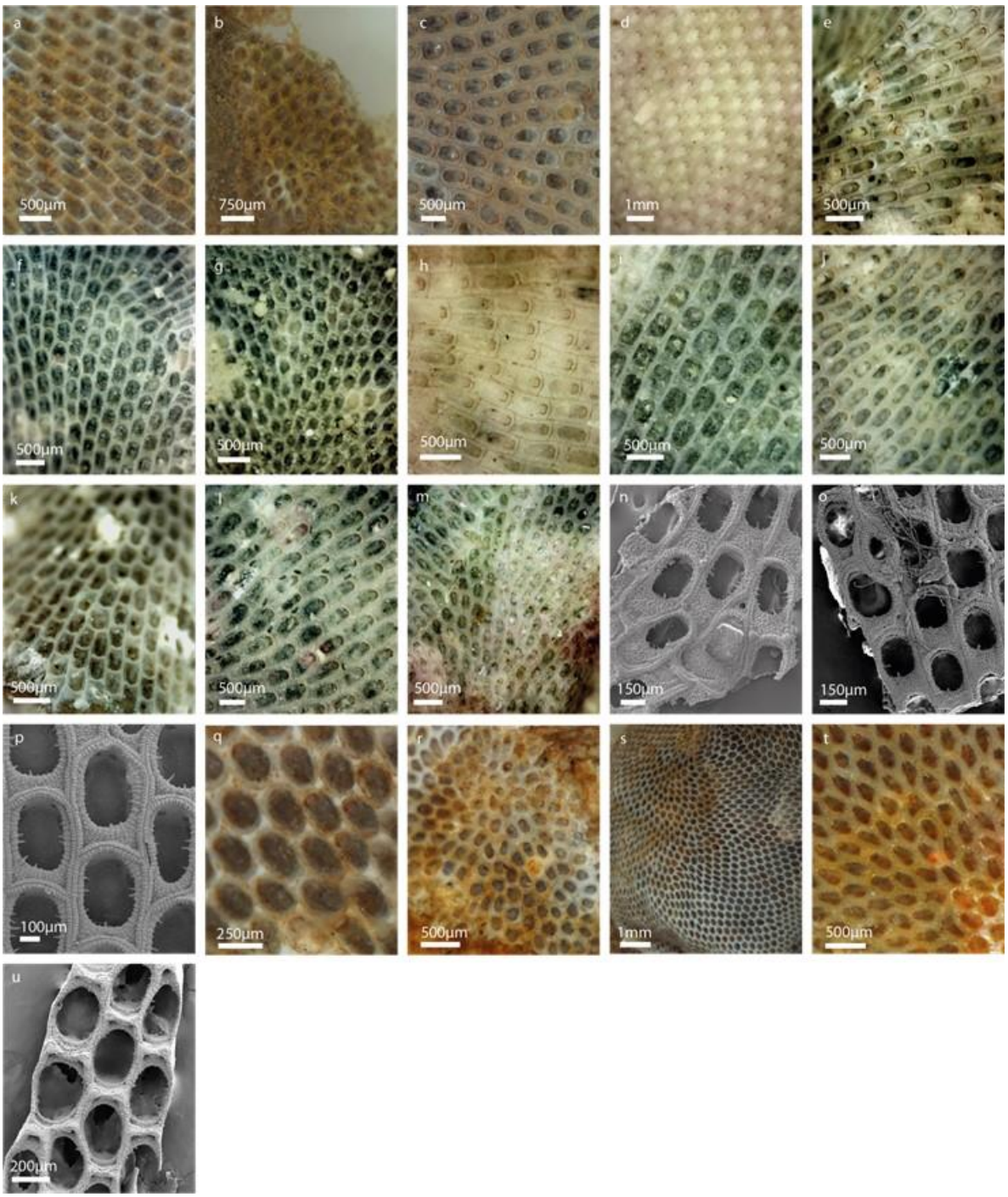

Figure S5. a-m) Live colonies of *Biflustra tenuis*: a) MZUCR-0048, b) MZUCR-0052, c) MZUCR-0076, d) MZUCR-0130, e) MZUCR-0161, f) MZUCR-0165, g) MZUCR-0184, h) MZUCR-0197, i) MZUCR-0198, j) MZUCR-0200, k) MZUCR-0218, l) MZUCR-0221, m) MZUCR-0254; n-p) electron microscope images of *B. tenuis*: n) MZUCR-0198, o) MZUCR-0090, p) MZUCR-0076; q-t) live colonies of *Conopeum* sp.: q) MZUCR-0047, r) MZUCR-0055, s) MZUCR-0057, t) MZUCR-0070; u) electron microscope image of *Conopeum* sp. MZUCR-0047.

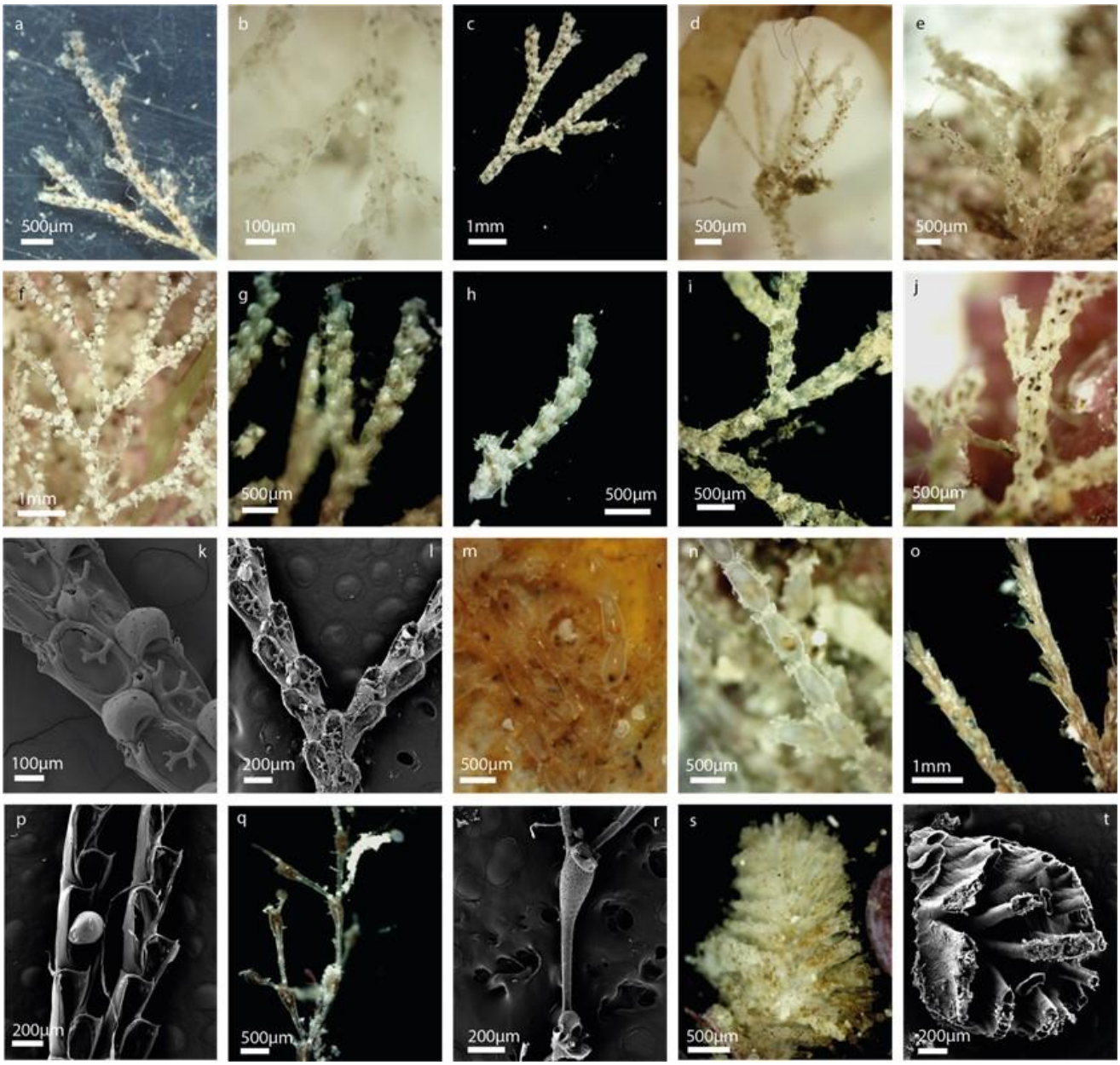

Figure S6. a-j) Live colonies of *Cradoscrupocellaria* sp.: a) MZUCR-0069, b) MZUCR-0086, c) MZUCR-0117, d) MZUCR-0128, e) MZUCR-0129, f) MZUCR-0135, g) MZUCR-0180, h) MZUCR-0189, i) MZUCR-0206, j) MZUCR-0211; k-l) electron microscope images of *Cradoscrupocellaria* sp.: k) MZUCR-0086, l) MZUCR-0189; m-n) live colonies of *Beania* cf. *hirtissima*: m) MZUCR-0073, n) MZUCR-0194; o-p) MZUCR-0179 *Bugula neritina*: o) live colony, p) electron microscope image; q-r) MZUCR-0188 *Savignyella lafontii*: q) live colony, r) electron microscope image; s-t) MZUCR-0169 *Tubulipora* sp.: s) live colony, t) electron microscope image.

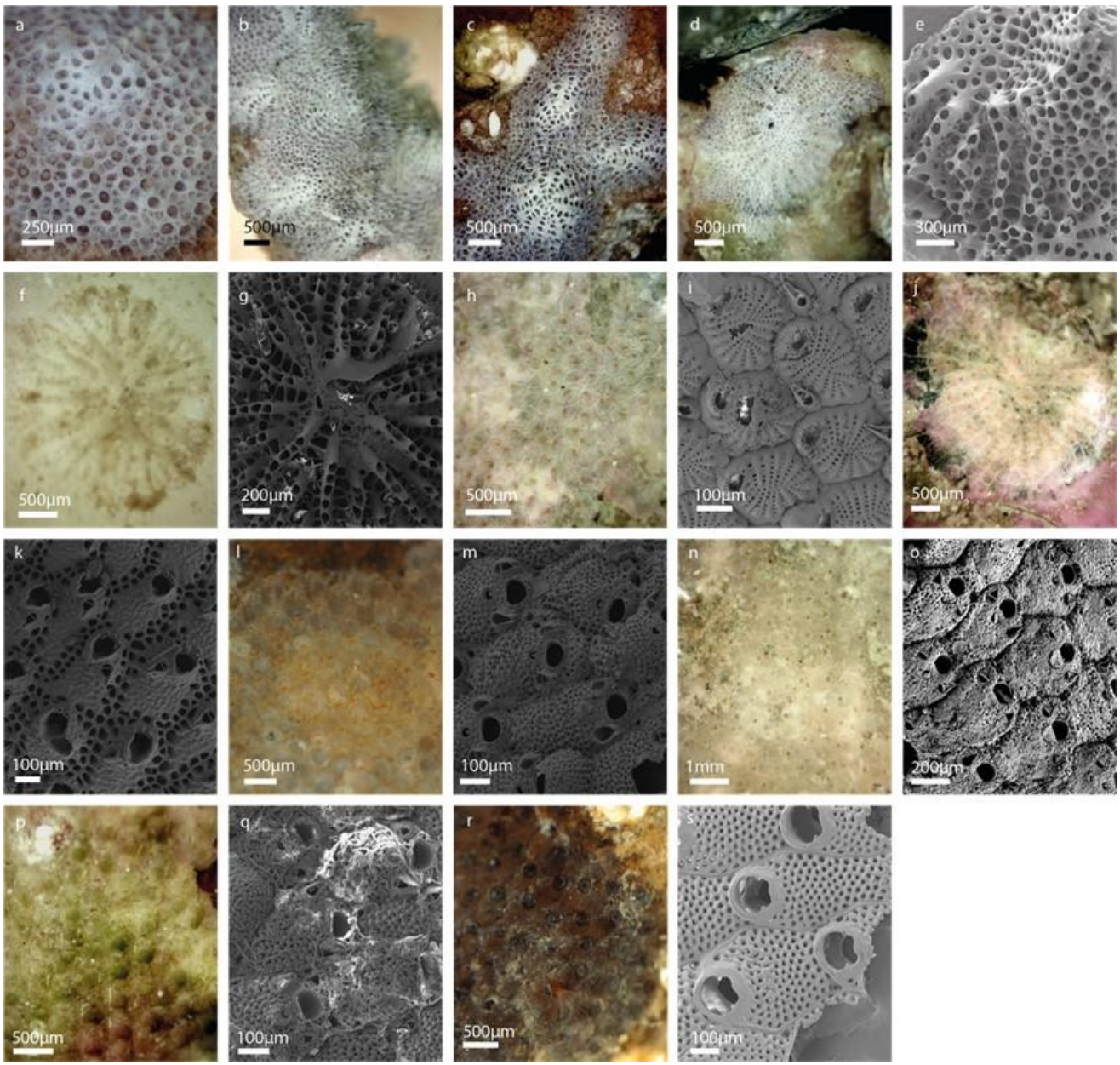

Figure S7. a-d) Live colonies of *Disporella* sp.: a) MZUCR-0068, b) MZUCR-0103, c) MZUCR-0217, d) MZUCR-0226; e) electron microscope image of *Disporella* sp. MZUCR-0103; f-g) Lichenoporidae indet. MZUCR-0088: f) live colony, g) electron microscope image; h-i) *Puellina* sp. MZUCR-0115: h) live colony, i) electron microscope image; j-k) *Hippaliosina* sp. MZUCR-0119: j) live colony, k) electron microscope image; l-q) *Microporella* sp. MZUCR-0082: l) live colony, m) electron microscope image; n-o) MZUCR-0126: n) live colony, o) electron microscope image; p-q) MZUCR-0173: p) live colony, q) electron microscope; r-s) *Watersipora arcuata* MZUCR-0059: r) live colony, s) electron microscope image.

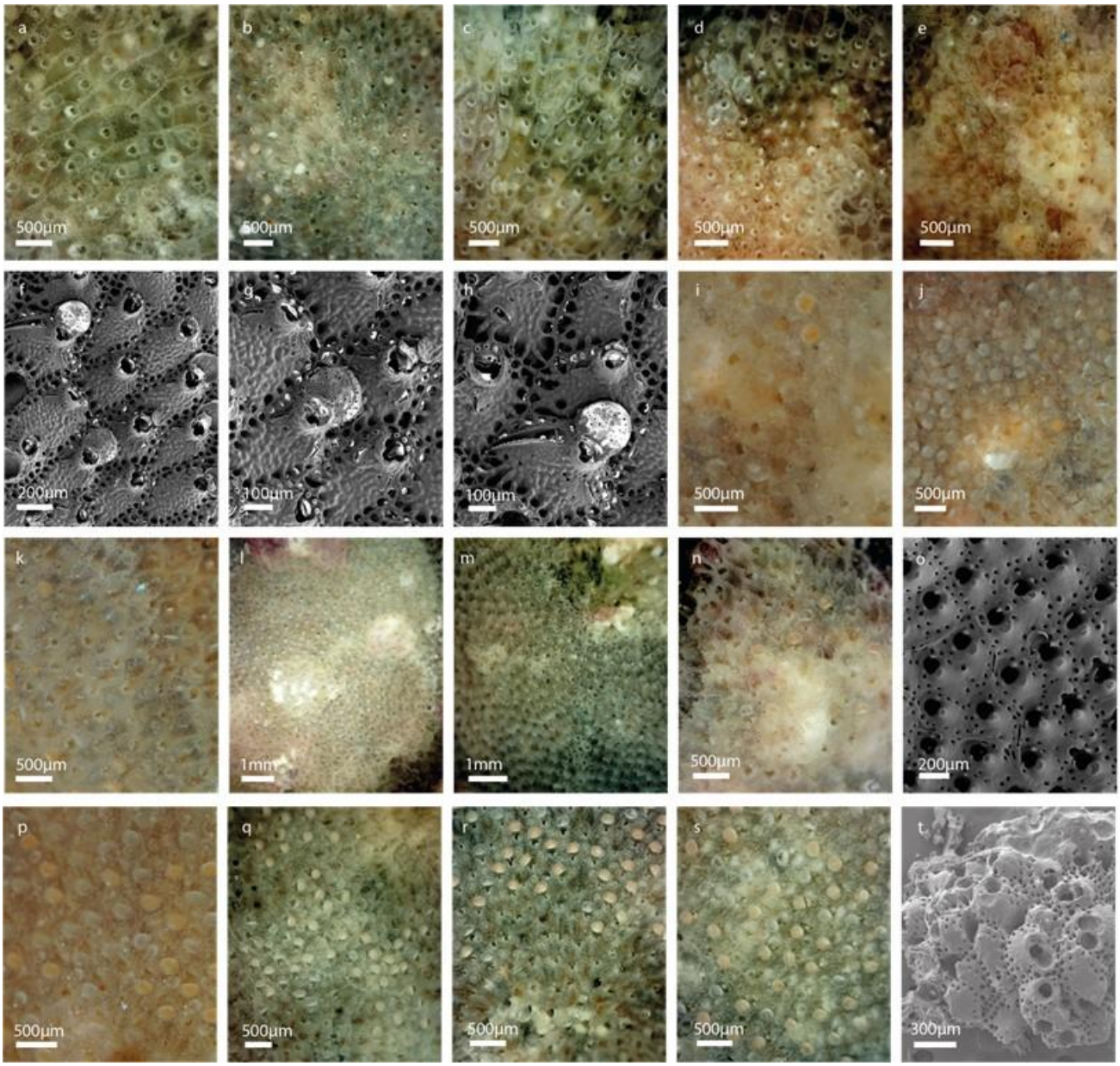

Figure S8. a-e) Live colonies of *Parasmittina crosslandi*: a) MZUCR-00177, b) MZUCR-00183, c) MZUCR-00217, d) MZUCR-00233, e) MZUCR-000234; f-h) electron microscope images of a representative specimen of *P.crosslandi* MZUCR-00177: f) colony, g) close up of colony showing an ovicell, h) zoid showing ovicell and a large adventitious avicularium; i-n) live colonies of *Parasmittina* sp.1: i) MZUCR-00061, j) MZUCR-00071, k) MZUCR-00062, l) MZUCR-00096, m) MZUCR-00153, n) MZUCR-00242; o) electron microscope image of a representative specimen of *Parasmittina* sp.1. MZUCR-00096; p-s) live colonies of Smittinidae indet.: p) MZUCR-00074, q) MZUCR-00142, r) MZUCR-00151, s) MZUCR-00174; t) electron microscope image of a representative specimen of Smittinidae indet. MZUCR-00061.

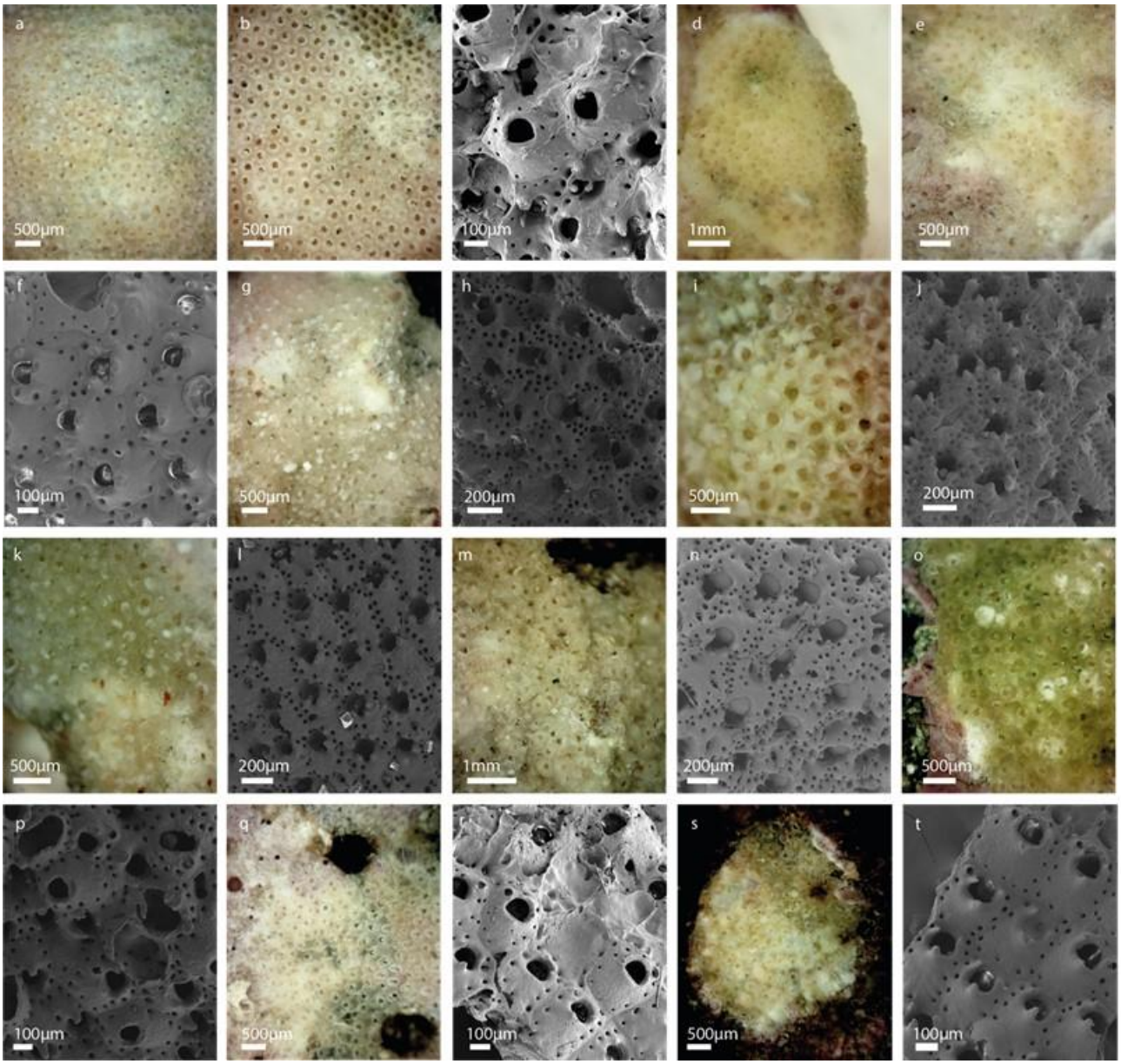

Figure S9. a-b) Live colonies of Hippoporidridae indet.: a) MZUCR-00098, b) MZUCR-00102; c) electron microscope image of Hippoporidridae indet. MZUCR-00102; d-e) live colonies of Hippoporidridae indet.: d) MZUCR-00106, e) MZUCR-00111; f) electron microscope image of Hippoporidridae indet. MZUCR-00106; g) live colony of Phidoloporidae indet. MZUCR-00116; h) electron microscope image of Phidoloporidae indet. MZUCR-00116; i) live colony of Phidoloporidae indet. MZUCR-00251; j) electron microsope image of Phidoloporidae indet. MZUCR-00251; k) live colony of Phidoloporidae indet. MZUCR-00252; l) electron microscope image of Phidoloporidae indet. MZUCR-00252; m) live colony of *Rhynchozoon* sp. MZUCR-00186; n) electron microscope image of *Rhynchozoon* sp. MZUCR-00186; o) live colony of *Pleuromucrum* sp1. MZUCR-00182; p) electron microscope image of *Pleuromucrum* sp. MZUCR-00182; q) live colony of *Pleuromucrum* sp. MZUCR-00127; r) electron microscope image of *Pleuromucrum* sp. MZUCR-00127; s) live colony of Hippoporidridae indet. MZUCR-00170; t) electron microscope image of Hippoporidridae indet. MZUCR-00170.