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DIVERSITY AND DISTRIBUTION OF BRYOZOANS IN THE PELICAN CAYS, BELIZE, CENTRAL AMERICA

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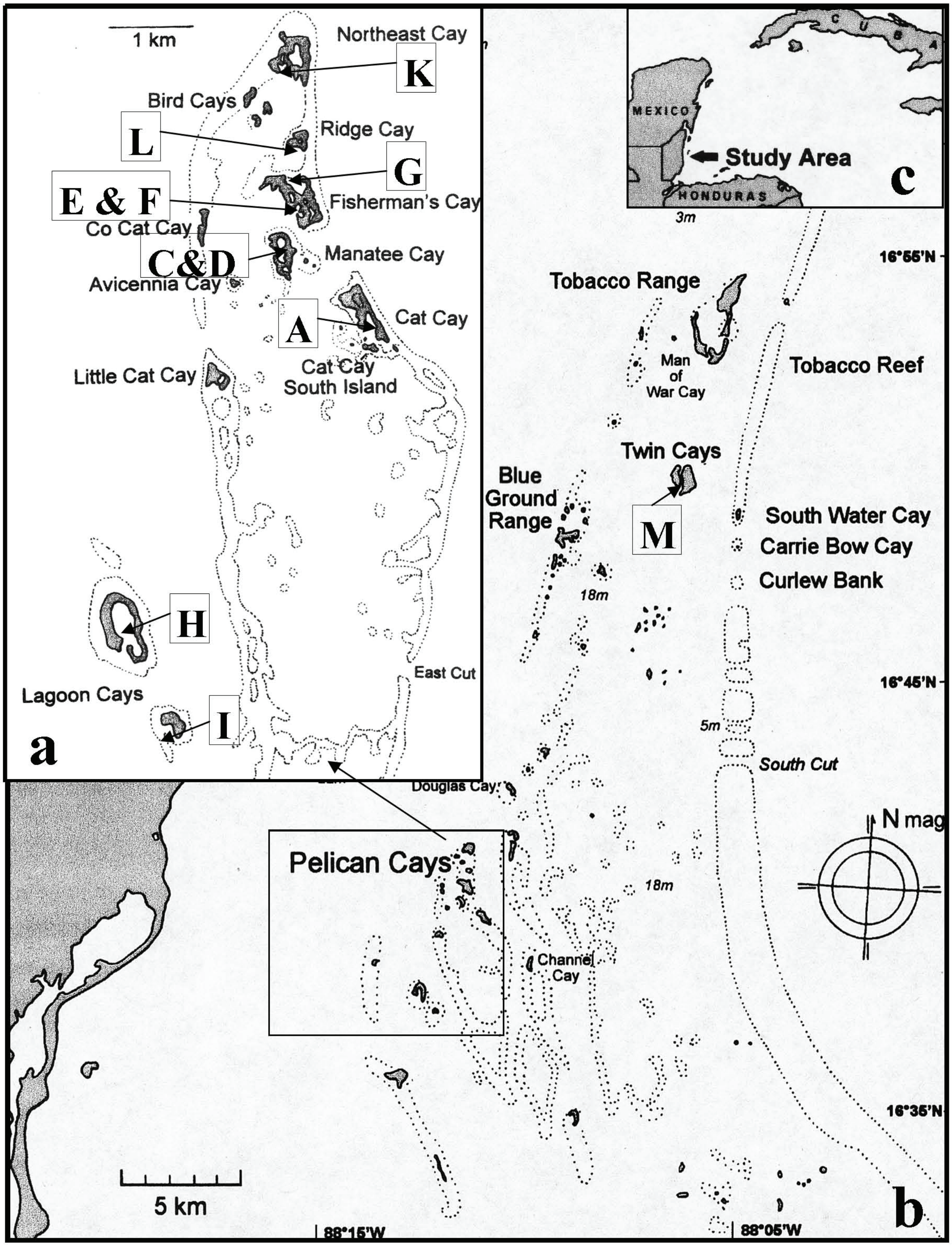

Figure 1. Maps of study sites. 1a. Enlargement of portion of the Pelican Cays to show study sites. 1b. Location of Pelican Cays and Twin Cays (site M), Central Province, Belize, Barrier Reef. 1c. Location of Belize and area of study on the barrier reef. Adapted from maps in Littler and Littler, 1997.

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ABSTRACT

Thirty-one species of bryozoans were found in mangrove communities in the Pelican Cays. Only in the large lagoon pond at Fisherman's Cay was the dominant bryozoan a common Caribbean fouling species, *Schizoporella pungens*. At Northeast Cay, Ridge Cay, Manatee Cay, and Cat Cay, as well as the small lagoon ponds at Fisherman's Cay, bryozoan species normally associated with shallow reef habitats formed extensive colonies on the submerged hanging roots of red mangroves along banks or undercuts bordering the lagoon ponds. *Stylopoma* sp., *Steginoporella magnilabris*, *Trematooecia aviculifera*, *Hippopodina feegeensis*, and *Rhynchozoon verruculatum* were the most abundant species overall. However, presence and relative abundance of these reef species varied from cay-to-cay. The overlapping thalli of *Lobophora variegata* covered much of the surface on vertical peat banks and on mangrove roots in well-shaded areas. The undersides of the thalli hosted a cryptic bryozoan fauna, consisting of delicate branching and encrusting colonies, which shared some species with both mangrove root and seagrass bryozoan assemblages. Eighteen species, including five undescribed species, were found in the *Lobophora* habitat.

INTRODUCTION

Mangroves are defined as a group of plants that share a life restricted to tidal swamps, a physiological mechanism for coping with salt-water life, production of aerial roots, reproduction via viviparity, and taxonomic isolation from terrestrial relatives (Rützler and Feller, 1987). Some ecologists have divided mangrove forests into two categories, mainland-fringing and oceanic (Rützler and Feller, 1996). Although an extensive literature exists on the ecology of mangal communities, most studies have focused on mangrove swamp habitats along mainland coasts. In many mainland mangrove habitats in the Western Atlantic, red mangrove trees occur in depths in which the prop roots are exposed to air during much of the tidal cycle. Their mostly intertidal biota consists of motile organisms like mangrove tree crabs, those like isopods, which bore into the roots, and sessile organisms like mangrove oysters, barnacles or certain

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algae that can survive periods of desiccation. Only in areas where deeper water exists can a subtidal community develop on the mangrove roots.

The Pelican Cays, 16°39.8'N; 88º11.5'W (Fig. 1), are of the rarer oceanic-island type. They form part of the northwestern area of the Rhomboid Shoals in the southern lagoon of the Belize Barrier Reef. The Pelican group consists of a network of mangrove islands overgrowing coral ridges. They are characterized by the presence of circular-to-irregularly-shaped pond-like lagoons whose entrances are restricted subtidally by coral ridges. The cays are scattered between areas of patch reef, shoals, and seagrass beds. Geologically, they developed over the last thousand years as coral reefs on a Pleistocene karst subsurface. Their mangrove overgrowth dates back to the last few hundred years (Macintyre et. al., 2000).

The attached and free-hanging prop roots of the mangroves around the lagoon ponds at many of the cays are submerged in deeper water (1-2 m) with peat banks, often undercut, creating additional shaded cryptic habitat in a number of places. Recent studies of the natural history of these cays (Macintyre and Rützler, 2000) have shown that they host an unusually high biological diversity of sessile organisms, sponges (Rützler et al., 2000), ascidians (Goodbody, 2000), corals (Macintyre et al., 2000), and algae (Littler et al. 2000) attached to the subtidal roots or to the peat, coral, and seagrass substrata. Although bryozoans are mentioned in several places in this work, they were not surveyed for the 2000 publication. This paper describes the results of a preliminary survey of the bryozoan fauna of the Pelican Cays.

Bryozoans are components of coral-reef and mangrove communities world-wide, but the ecology and taxonomic composition of such bryozoan faunas is well known in only a few areas (Hayward and Ryland, 1995; Ristedt and Hillmer, 1985; Ryland and Hayward, 1992; Tilbrook et al., 2001; Winston and Jackson, 1984; Winston, 1986b). Fortunately, in this part of the Belize barrier reef system knowledge of the bryozoan fauna is reasonably good, having been the focus of six publications on bryozoan taxonomy and ecology (Best and Winston, 1984; Winston, 1984a, 1984b, 1986a, 1991, 2004). As a result of these studies 38 species of bryozoans, including five new species and one new genus, have been collected and described from reef habitat around Carrie Bow Cay and mangrove habitat at Twin Cays. This information provided a taxonomic framework for the study of distribution and taxonomy of bryozoans from the Pelican Cays described below.

METHODS

The survey took place during two weeks in September, 2005. Very calm weather prevailed over the coast of Belize during much of this period, thanks to a hurricane in the Gulf of Mexico. The survey team (Winston and Reed) was able to examine mangrove roots, algae, and *Thalassia* substrata at eight of the Pelican Cays, the two adjacent Lagoon Cays (Fig. 1a), and at Twin Cays (inland of Carrie Bow Cay, to the north of the Pelican group (Fig. 1b)). The letters marking the sites sampled on Figure 1 are those used in the original survey of Pelican (Cays) with additions (K, L, and M) for sites that were not sampled in that project.

We did not sample quantitatively for two reasons: 1) the goal of this project was to sample as many sites as possible to get the broadest picture of the overall bryozoan diversity and taxonomic composition; and 2) we wanted to disrupt this fragile habitat as little as possible, taking only a few roots or sections of roots for voucher specimens when the colonies could not be detached from their substratum.

At each site (e.g., Pl. 1a) we snorkeled completely around the perimeter of the lagoon ponds (if present) and the landward (west) sides of the cays, adjacent to the ponds, carefully examining the roots and associated substrata (mangrove oysters, barnacles, algae) for bryozoans and collecting voucher specimens. In the same manner we snorkeled around the north, south, and east (reefward and seaward) sides of the cays where the water was deep enough to make this possible, although on the seaward sides of most cays the red mangrove roots were in very shallow water, and a subtidal sessile fauna did not occur. To look for potential sources for bryozoan recruitment to the mangrove root community, we also snorkeled at some reefward patch reefs adjacent to cays, and made two SCUBA dives on the ridges that block the entrances to the “ponds” subtidally, to look for bryozoans on the coral rubble on both the inside and outside of the sills. While sampling at our second site (Cat Cay) we realized that the undersides of the thick flexible thalli of the brown alga *Lobophora variegata* hosted a number of bryozoans, mostly species which did not occur on the mangroves, so we began collecting *Lobophora* from the mangrove banks and roots. At each site we collected at least 50 pieces of *Lobophora* taken from several areas scattered around the site and at depths from near the water surface to whatever depth the roots or banks extended. We also collected *Thalassia* from the lagoon ponds for comparison. These substrata were taken back to the lab for sorting and determination under a dissecting microscope as most of the attached bryozoan colonies were too small to identify in the field.

Digital photographs of living colonies of the dominant species were taken at the Carrie Bow lab and are presented in the plates accompanying this paper as a guide to their identification. Samples of all species found on the roots were preserved for further taxonomic study with the scanning electron microscope.

RESULTS

Thirty-one species of bryozoans were obtained from mangrove communities in the vicinity of the Pelican Cays. Tables 1 and 2 show their distribution and abundance at each of the Cays surveyed.

Bryozoans Occurring on Mangrove Roots

At Northeast Cay, Ridge Cay, Manatee Cay, Cat Cay, and the small lagoon pond at Fisherman’s Cay, bryozoan species normally associated with shallow reef habitats formed extensive colonies on the submerged hanging roots of red mangroves along banks or undercuts bordering the lagoon ponds. *Stylopoma* sp., *Steginoporella magnilabris*, *Trematooecia aviculifera*, *Hippopodina feegeensis*, and *Rhynchozoon verruculatum* were the most abundant overall. Additional reef species occurred in small numbers on the roots or on shells or algae attached to the roots, suggesting that most common reef species could eventually be found in the mangrove root habitats of the Pelican Cays. Only at Twin Cays and the large lagoon pond at Fisherman's Cay was the dominant bryozoan a fouling species, *Schizoporella pungens.*

At each Cay where bryozoans occurred, the fauna varied in terms of which of the reef species dominated.

Cat Cay – Pond A. Steginoporella magnilabris (Pl. 1b-c), *Trematooecia aviculifera* (Pl. 2a-c), *Hippopodina feegeensis* (Pl. 3), *Rhynchozoon* sp. (Pl. 4), *Parellisina latirostris* (Pl. 5a-b). *Celleporaria albirostris* (Pl. 5c-d), *Smittina smittiella* (Pl. 6a-b), *Antropora leucocypha*, *Synnotum circinatum* and *Zoobotryon verticillatum* were found at this site. Bryozoans often encrusted old decaying hanging roots, especially those on which bark had come partially detached from the root. On such roots, bryozoan colonies were found both on the exposed wood and on the inside of the loose bark covering. *Trematooecia* and *Steginoporella* were more abundant at the outer edges of the pond, and *Rynchozoon* and *Stylopoma* most abundant on roots along the shadiest banks, in association with dense sponge coverage. Large *Stylopoma* colonies even encrusted the hanging pvc pipes that were part of an ongoing experiment. *Steginoporella* and *Hippopodina* formed large (several cm in length) colonies that wrapped completely around the roots, resulting in production of an additional layer by self-overgrowth. *Trematooecia*, *Stylopoma* and *Rhynchozoon* all produced large multilaminar colonies. All three, as well as *Smittiella* and *Hippopodina*, were mature and sexually reproductive, brooding embryos in ovicells.

At Cat Cay we also made SCUBA dives on both sides of the coral ridge blocking Pond A. Previous to the 1998 bleaching event (Macintyre, 2000) this ridge had stands of *Agaricia tenuifolia.* Little live coral remained at the time of our visit. Coral rubble, with a few live areas remaining on some pieces, was stuck together and anchored on the sediment-covered slope by massive and ropey sponges. The upper surfaces of most of the rubble was covered by sediment and undersurfaces were bare of sessile cryptic fauna. Only four species, small colonies of *Trematooecia aviculifera*, *Steginoporella connexa* (Pl. 6a-b), *Nolella stipata* and *Synnotum circinatum*, were found.

Manatee Cay – Ponds C & D. These ponds were the richest in sponge diversity (Rützler et al., 2000) and one of the two richest for ascidians (Goodbody, 2000) in the earlier studies. Roots in these ponds remained heavily covered by sponges. One branching bryozoan, *Bugula neritina*, a common warm-water fouling species, was found attached to roots, but the only reef bryozoan that occurred was *Stylopoma* sp., a species capable of forming extensive multilayered colonies (e.g., Pl. 2d).

Fisherman's Cay – Large embayment G. This site was a large, shallow lagoon, with a deep pond in its center. The outer left-hand side of the lagoon was very shallow with seagrass beds right up to the roots; just inside the lagoon was a deep bank with hanging roots. *Schizoporella pungens* (Pl. 7a-c), a common Caribbean and tropical western Atlantic fouling species, was the dominant bryozoan throughout, although a few scattered colonies of *Hippopodina feegeensis* and *Zoobotryon verticillatum* (Pl. 7d) were also observed. The central rim of the lagoon had many mangroves cut down, and dead branches in the water. That area was colonized chiefly by algae. The right-hand rim had a root-encrusting biota composed of sponges and ascidians, especially *Ascidia nigra*, and a white didemnid species. *Schizoporella* formed massive colonies, primarily coating the shaded side of roots, but sometimes completely enveloping their circumference and even overgrowing adjacent sponges.

Fisherman's Cay – Ponds E & F. The bryozoan faunas of these two adjoining lagoon ponds more closely resembled those of the Cat and Northeast Cays than that of the large lagoon above. *Stylopoma* sp. was the most abundant bryozoan, followed by *Trematooecia aviculifera*, *Steginoporella magnilabris* and *Hippopodina feegeensis*. Bryozoan diversity was highest at the outer left-hand rim of Pond E where all four species were present, and hanging roots extended from an undercut bank into water about 1.5 m deep. One large coral head encrusting a root was observed, but the environment was not as reef-like as Ridge Cay. Pond F had more algal encrusted roots but roots there also hosted *Stylopoma* and sponge colonies. On the right-hand rim of Pond E, leading back out to open water, most bryozoan colonies found were *Stylopoma* sp.

Northeast Cay – Pond K. The lagoon here had fewer large sponge and ascidian colonies, but the greatest bryozoan abundance. Bryozoan colonies encrusted large portions of many of the roots, with colonies of different species meeting and overgrowing each other. *Trematooecia aviculifera* was the dominant species, followed by *Hippopodina feegeensis*, *Stylopoma* sp. and *Steginoporella magnilabris*. Other species, *Exechonella antillaea* (Pl. 6e-f), *Savignyella lafontii*, *Smittina smittiella*, *Synnotum circinatum*, and *Bowerbankia maxima*, also occurred on the roots. As at other sites, the more shaded outer rim of the pond was most reef-like in having live hermatypic and ahermatypic corals, gorgonians and sponges and sponge-associated brittlestars, as well as the reef-associated bryozoan species.

Ridge Cay – West and South (channel) sides of Cay – L. Ridge Cay did not have a pond lagoon and was not part of the previous surveys. We surveyed its south side which consisted of mangrove forest, bordered by a narrow stretch of seagrass and patch reef edging a steep-sided deep water (20 m) channel which extends seaward toward the barrier reef (although according to the chart it does not penetrate all the way to open sea, but is eventually blocked by shoals). Instead of roots jammed together into a solid bank, the roots of the trees were open to water flow. Although the roots and trunks were too closely spaced to snorkel between, we could peer between them to see fish swimming and reef organisms, including bryozoans, attached to roots at least several meters into the forest. Bryozoans and other sessile organisms were abundant at this site, which exemplifies what Sterrer (2000) called "mangreef", truly a reef in a forest. *Trematooecia aviculifera* was the dominant species. *Steginoporella magnilabris*, *Steginoporella connexa*, *Hippopodina feegeensis*, *Rhynchozoon* and *Parellisina latirostris* were also found but, surprisingly, there were no colonies of *Stylopoma* sp. Reef fauna included platy- and mound-shaped colonies of *Porites astreoides*, fan and whip-shaped or plumy gorgonians, *Erythropodium, Millepora*, *Palythoa grandis*, and many anemones and hydroids.

Lagoon Cays, Larger Cay – H. At the larger of the two Lagoon Cays ascidians, including *Ascidia nigra*, *Distaplia corolla* and *Botrylloides* sp. dominated the hanging roots. Some sponges were present also but there were no encrusting bryozoans.

Lagoon Cays, Smaller Cay – I. The smaller of the two cays has an active pelican rookery. The lagoon water near the rookery was shallow and turbid with some patches of seagrass. On the shallowly submerged red mangrove roots, there were a few of the same ascidians as at the previous site, but no encrusting bryozoans. Only one colony of an arborescent ctenostome bryozoan, *Zoobotryon verticillatum*, was found in the seagrass bed. It was heavily fouled by filamentous algae and many of the zooids had sloughed off the stolons.

Twin Cays – M. Previous studies (Winston 1984b, 2004) had documented five bryozoans from Twin Cays mangrove roots. During this survey we snorkeled much of the interior channel from Boston Bay to Cuda Cut at the other end of the channel, as well as the Lair and Hidden Creek. Mangrove root sessile faunas had dwindled since previous visits. In the Lair and Hidden Creek we found *Zoobotryon verticillatum* (senescent colonies, some lacking any zooids on stolons), *Bowerbankia maxima* (large senescent colonies covered with filamentous algae and sediment) and *Schizoporella pungens*. *Schizoporella* colonies were alive, with dark coloration, but lacked the orange margin that denotes active growth. We did not find any colonies of *Synnotum circinatum*, a species which was originally described from Twin Cays (Winston, 2004). For comparison with Pelican sites we also looked at bryozoans from Twin Cays *Thalassia* blades. Bryozoans were infrequent colonizers on the blades, but four species were collected: *Celleporaria* sp. 2, *Bugula minima*, *Mimosella firmata*, and *Schizoporella floridana*.

Bryozoans Occurring on *Lobophpora variegata*

The bracket-fungus shaped alga *Lobophora variegata,* common on shaded banks and roots in many areas, also hosted a diverse assemblage of species that overlapped both the mangrove root and the adjacent *Thalassia* communities taxonomically. This previously unstudied habitat yielded 18 bryozoan species, including seven undescribed species, one of them also requiring designation of a new genus.

Cat Cay – Pond A. Overlapping flexible thalli of *Lobophora variegata* blanketed many of the roots in more shaded areas of the lagoon. The undersides of the fleshy thalli attracted a different assemblage of bryozoans: ephemeral species with small or runner-like growth forms, characteristic of algal habitats, or young colonies of species also found on mangrove roots and cryptic reef habitats. Examples of species from this habitat are shown in Plate 8. Ten species were collected at this cay (Table 2) including *Aetea* sp., *Microporella* new sp., *Mimosella firmata*, *Scrupocellaria* new sp. and *Celleporaria* new sp.

Manatee Cay – Ponds C & D. Manatee Cay was the first of the Pelican Cays sampled, and we had not yet realized the importance of *Lobophora* as a bryozoan habitat, so no samples were taken.

Fisherman's Cay – Large embayment G. Six species were collected from *Lobophora* at this site: *Aetea* sp., *Mimosella firmata, Scrupocellaria* new sp., *Catenicella contei, Nolella stipata*, and *Bugula minima*. In contrast to the mangrove root encrusting bryozoans, the taxonomic composition of the species found on the *Lobophora* at this site resembled that of other Pelican Cays samples, but there were more spirorbid tubeworms encrusting the algae than at other sites

Fisherman's Cay – Ponds E & F. Eleven species were found on *Lobophora* in these smaller lagoon ponds (Table 2), including *Beania mirabilis*, and *Beania klugei*. One small *Hippopodina* colony was collected although it is doubtful if larger colonies of this fragile and inflexible calcified species can persist for long on the flexible thalli.

Northeast Cay – Pond K. Eleven *Lobophora* encrusting bryozoan species were found at Northeast Cay. They included a new aetiid cheilostome, which was not found at any of the other cays, and a juvenile colony of *Trematooecia aviculifera*, one of the most abundant reef-mangrove root species.

Ridge Cay – West and South (channel) sides of Cay – L. At this cay, where the roots extended into shallower water, and *Lobophora* was not as abundant, we collected six species. We found only two colonies of *Aetea* sp. which was very common at Cat and Northeast Cays. The *Lobophora* was also encrusted by sponges and filamentous algae.

Lagoon Cays, Larger Cay – H. At this site there was no *Lobophora.* However, we collected bryozoans from other brown algae, *Padina* and *Dictyota* spp, for comparison (Table 2). Six bryozoan species were found, all of them also occurring on *Lobophora* at other Pelican Cays sites.

Twin Cays – M. At Twin Cays, we found four species on *Thalassia*: *Schizoporella floridana*, *Celleporaria* pink sp., *Bugula minima* and *Mimosella firmata*. All but *S. floridana* also occurred on *Lobophora* at other sites.

DISCUSSION

Although not as diverse taxonomically as the sponges and ascidians found there, bryozoans are clearly an important component of the suspension-feeding community of submerged mangrove roots and *Lobophora* thalli in the Pelican Cays.

Despite the large literature on mangrove ecology, few studies of epibionts on submerged mangrove roots mention bryozoans. Kolehmainen (1973) and Yoshioka (1974) studied the ecology of sessile and free-living organisms on mangrove roots in

Jobos Bay, Puerto Rico as part of environmental studies for the Aguirre power plant. Three bryozoans were named in the first study: *Crisia* sp., *Savignyella lafontii*, and *Schizoporella errata* (probably *Schizoporella pungens*, a member of the *Schizoporella errata* species complex). All algal and 11 macroinvertebrate phyla were found on the roots although composition and biomass of the epibionts varied throughout the bay. Yoshioka (1974) reported that *Schizoporella* "when found usually occurred on the lower part of branches" and that it occasionally overgrew and smothered living *Balanus eburneus*. Yoshioka's general conclusion was that two types of mangrove communities occurred in Jobos Bay. One, along the shipping channel, was made up of epibionts characteristic of coastal waters and one, in channels in the vicinity of the Mar Negro Lagoon, was made of species characteristic of embayments. Water depths at all of their stations were less than one meter.

Sutherland (1980) listed three bryozoans associated with red mangroves at Bahía de Buche, Venezuela, but did not identify them to species, although his "purple, encrusting (*Schizoporella*?)" is almost certainly *Schizoporella pungens*. Bryozoa are noted as present, but not further identified, in Farnsworth and Ellison's (1996) study of dynamics of the mangrove root communities of several Belizean cays, including Twin Cays.

The most thorough survey of mangrove-root bryozoans in the Caribbean is that of Creary (2003a, 2003b) who studied the spatial distribution of bryozoans found on *Rhizopora mangle* roots in Kingston Harbour, Jamaica. Eighteen species of bryozoans were collected from 848 roots. Only six species were in common with the Pelican Cays mangrove bryozoan fauna: *Schizoporella pungens*, *Savignyella lafontii, Bugula neritina*, *Zoobotryon verticillatum*, *Bowerbankia maxima*, and *Nolella stipata.* Two of that group also occurred in the Jobos Bay studies. All of them, and most of the other species in Creary's survey, are warm-water species typically found in shallow coastal, estuarine and harbor environments on both artificial (fouling) and natural substrata. The Pelican Cays appear unique in having a bryozoan fauna dominated by cryptic coral-reef species at most sites surveyed.

The dominant reef bryozoans of the mangrove roots are perennial species with large zooids, rapid growth and excellent competitive ability relative to other cryptic reef species (Winston and Jackson, 1984). *Steginoporella* spp overgrow most other cryptic bryozoans. Although they cannot produce massive colonies by frontal budding they can form colonies several layers deep by self-overgrowth. *Stylopoma sp.* is usually overgrown by *Steginoporella* but out-competes most other cryptic-reef species. Its growth rate is enhanced by the fact that the settled larva metamorphoses into a compound 9-zooid rosette-shaped ancestrula, rather than producing a single ancestrular zooid, enabling the young colony to grow outward in all directions immediately. *Trematooecia aviculifera* can produce large mound-like colonies several cm in diameter and is one of the few reef bryozoans able to grow on open vertical surfaces in direct competition for space with corals, sponges, and crustose algae. *Hippopodina feegeensis* can occur on very shallow coral rubble (2 m or less). *Rhynchozoon verruculatum* forms small patches on coral substrata, but they become raised and multilayered with age (Winston, 1984).

Being dominated by shallow reef species, the bryozoans are very much like the Pelican Cays sponge fauna (Rützler et al., 2000; Wulff, 2005). Wulff (2005) even suggests for the sponges that the mangroves might be the better habitat for the "reef" species, and the reef their refuge habitat.

The reasons for the differences in spatial distribution and dominance of different bryozoans at the different cays are not known, but are probably the result of a blend of biotic and abiotic factors. Studies of mangrove-root community ecology have considered all of the following to play a role: temperature, salinity, tides, water flow rates, sediment, light, nutrient levels, food supply, recruitment, competition, succession, seasonality, predation, epibiont or substratum toxicity, and root history.

The survey of the Pelicans reported in 2000 included preliminary data on hydrography and physical conditions at some of the lagoon ponds and mangrove margins (Ulrish, 2000; Villareal et al., 2000; Shyka and Sebens, 2000). Tides are microtidal, mixed semidiurnal with a range of only 15 cm, and flow rates were low, although wind and tide combined provided fairly rapid flushing of pond margins. Water temperatures averaged 31.4° C (in May of 1994), and salinity 35.3 ppt (Ulrish, 2000). Dissolved oxygen and nitrogen, and sometimes phosphorus, were elevated (but within natural limits). Goodbody (2000) pointed out that these conditions, when added to the shade provided by the heavy canopy of undisturbed trees, layers of hanging roots, steep or undercut banks were ideal for ascidians. The same conditions are very favorable for bryozoans as they usually prefer shaded or cryptic habitats. In our survey it was very noticeable that where mangroves had been cut, or had fallen naturally, the much brighter conditions led to a change in the subtidal biota of the roots (e.g., at Fisherman's Cay) which in such areas consisted mainly of algae. Phytoplankton in the Pelican Cays consisted mostly of dinoflagellates, which could reach bloom conditions (Morton, 2000; Faust, 2000). Dinoflagellates and small unarmored flagellates are known to be good food for many bryozoans (McKinney, 1990).

The roles of seasonality and succession on mangrove roots have varied with the location of the study. Bingham and Young (1994) found Florida Keys mangrove root communities to be extremely dynamic, with great variability and changing species composition on individual roots over a short (1-2 month) time period. In contrast, Sutherland (1980) found long-term stability and lack of seasonality in a Venezuelan mangrove root community. Dynamics of mangrove root communities at the Pelican Cays is probably somewhere between the two extremes. Growth of corals and perennial bryozoans indicates some degree of long-term stability. However, some of the bryozoan species that also occur in Florida show marked seasonality, with greatest growth, reproduction and recruitment in both Florida and Belize taking place in the cooler months. Such species include *Amathia vidovici*, *Bowerbankia maxima*, *Bugula neritina* and *Zoobotryon verticillatum*. During this survey, which took place at the end of the summer, *Bowerbankia maxima, Bugula neritina*, and *Zoobotryon* were rare or present as large, but senescent colonies. *Synnotum circinatum,* while present, consisted of old algae-fouled colonies with limited or no motility of branches (which curl up completely when a young colony is disturbed).

History of both cays and roots may affect distributions. The bryozoan assemblage present at a particular cay might also reflect the cay's proximity to cryptic reef habitat from which larvae could be carried. Dives made on both sides of the ridge blocking the lagoon entrance at Cat Cay yielded very few bryozoans, indicating that the recruitment source there was not the lagoon itself. However, during the calm weather days we experienced while working there, the upper layer of water in the lagoon pond at Cat Cay, with its very narrow eastern rim, was brimming with tiny bright-colored particles of plastic debris. This mangrove filter could just as well collect invertebrate larvae, many of which are similar in size and buoyancy to the plastic particles we observed.

In the cryptic reef community, recruitment rates of bryozoans are low and relatively constant year-round (Winston and Jackson,1984). Sutherland (1980) also documented low recruitment rates in Venezuelan mangroves. This may also apply to the reef species dominating mangrove roots in this study. Recruitment rates of sponges at the Pelican Cays are also low (Rützler et al., 2000).

The study of Belizean mangrove communities by Farnsworth and Ellison (1996) also indicated the importance of larval supply in shaping community composition. Their analysis found statistical correlation between assemblages found on roots within two-to-three meters of each other, perhaps indicating the distance non-feeding larvae can travel in this low-flow environment. Once a root is successfully colonized by one of the dominant bryozoans, the colony's offspring, large yolky non-feeding larvae, may settle on nearby roots.

Predation is important for some groups encrusting mangrove roots, but not for others. Wulff (2000, 2005) documented the importance of fish predation in structuring sponge assemblages in the Pelican Cays, but Goodbody (2000) did not find evidence of fish predation on ascidians there.

One of the most striking findings of this study was that the dominant bryozoans formed colonies as large or larger or than they do in cryptic reef habitats. How can these species grow so large out in the open on roots when there are so many apparent potential predators present? We saw numerous reef- and mangrove-associated fish swimming among the roots (e.g., French Angelfish, Barracuda, silversides, needlefish, snappers, small parrotfish, seahorses, sting rays, puffers, Scrawled Cowfish) but did not observe any fish feeding on bryozoans. Perhaps this is not significant, as only a few fish, like filefish, actually feed on bryozoans, although on the reef itself encrusting colonies can be grazed out of existence by coral-feeding parrotfish. Maybe it is the invertebrate grazers (limpets, chitons, urchins, and gastropods) responsible for much of the partial predation observed in the reef cryptic community, which do not occur on the roots or occur in much lower densities.

Is the lack of spatial competition a factor? Do spatial competitors like calcareous algae not penetrate as far down the roots, leaving open space for bryozoan growth? Is the bare space on the roots structured by sloughing of heavy masses of sessile organisms over time? The dominant species are all known to be good competitors with long-lived colonies (Winston and Jackson, 1984). In this survey they were sometimes observed to overgrow sponges (e.g., Pl. 3b and 6c) and ascidians as well other bryozoans and solitary organisms such as serpulid worms and vermetid gastropods (e.g., Pl. 4e).

Finally, is there a chemical exudate from the mangrove roots, the overlapping masses of *Lobophora* which blanket roots and banks in places, or from the sessile organisms themselves that discourages predation on colonies, but not settlement by recruits? Experimental work will be needed to answer these questions.

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Table 1. Bryozoans found on *Rhizopora* roots at the Pelican Cays.

Bryozoan species	**Sites Present**								
	Pelican Cays						**Lagoon Cays**		**Twin Cays**
	Northeast Cay	**Ridge Cay**	**Fishermans G**	**Cay E+F**	**Manatee Cay**	**Cat Cay**	**Larger Cay**	**Smaller Cay**	**Boston Bay**
On *Rhizopora* roots									
*Antropora leucocypha**						**X**			
Bowerbankia maxima	**X**								**X**
Bugula neritina					**X**				
Celleporina albirostris						**X**			
Exechonella antillea	**X**								
Hippopodina feegeensis**	**X**	**X**	**X**	**X**		**X**			
Parellisina latirostris		**X**				**X**			
Rhynchozoon verruculatum		**X**				**X**			
Savignyella lafontii	**X**								
Schizoporella pungens			**X**			**X**			**X**
Smittina smittiella	**X**					**X**			
Steginoporella connexa		**X**							
Steginoporella magnilabris	**X**	**X**		**X**		**X**			
***Stylopoma* sp.**	**X**			**X**	**X**	**X**			
Synnotum circinatum	**X**								
Trematooecia aviculifera	**X**	**X**		**X**		**X**			
Zoobotryon verticillatum			**X**			**X**		**X**	**X**

*on oyster clump on root
** names in bold = dominant spp

Table 2. Bryozoans found on *Lobophora*, other algae and, seagrass.

Bryozoan species	**Sites Present**							
	Pelican Cays					**Lagoon Cays**		**Twin Cays**
	Northeast Cay	**Ridge Cay**	**Fishermans G**	**Cay E+F**	**Cat Cay**	**Larger Cay**	**Smaller Cay**	**Boston Bay**
	All on	***Lobophora***				**On other algae***		***Thalassia***
Aetiid sp.**	**X**							
Aetea sp.* **	**X**	**X**	**X**	**X**		**X**	**X**	
Beania klugei	**X**			**X**	**X**			
Beania mirabilis				**X**				
Bowerbankia maxima	**X**			**X**	**X**			
Bugula minima			**X**					**X**
Catenicella contei			**X**	**X**	**X**	**X**		
Celleporaria sp. 1**	**X**			**X**	**X**			
Celleporaria sp. 2**				**X**				**X**
Hippopodina feegeensis				**X**	**X**			
Hippothoa sp.	**X**	**X**						
Microporella sp.**	**X**			**X**	**X**			
Mimosella firmata	**X**		**X**	**X**	**X**			**X**
Nolella stipata		**X**	**X**			**X**		
Savignyella lafontii		**X**		**X**	**X**	**X**		
Schizoporella floridana								**X**
Scrupocellaria* sp.*	**X**	**X**	**X**		**X**	**X**		
Synnotum circinatum	**X**	**X**				**X**		
Trematoecia aviculifera	**X**							

**Padina, Dictyota* and a brown filamentous alga
** =new species
*** names in bold=dominant spp

REFERENCES

Best, B.A. and J.E. Winston
1984. Skeletal strength of encrusting cheilostomes. *Biological Bulletin* 167**:**390-409.

Bingham, B.L. and C.M. Young
1995. Stochastic events and dynamics of a mangrove root epifaunal community. *P. S. Z. N. I. Marine Ecology* 16(2):145-163.

Canu, F. and R.S. Bassler
1928. Fossil and Recent Bryozoa of the Gulf of Mexico region. *Proceedings of the United States National Museum* 72:1-199.

Creary, M.M.
2003a. Spatial distribution of epibenthic bryozoans found on the roots of *Rhizophora mangle*, Kingston Harbour, Jamaica, W. I. *Bulletin of Marine Science* 73(2):477- 490.

Creary, M.M.
2003b. A simplified field guide to the bryozoan species found on the roots of the red mangrove (*Rhizophora mangle*) in and around Kingston Harbour, Jamaica, W. I. *Bulletin of Marine Science* 73(2):521-526.

Farnsworth, E.J. and A.M. Ellison
1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. *Ecological Monographs* 66(1):45-96.

Goodbody, I.
2000. Diversity and distribution of ascidians (Tunicata) in the Pelican Cays, Belize**.** *Atoll Research Bulletin* 480:303-326.

Hayward, P.J. and J.S. Ryland
1995. Bryozoa from Heron Island, Great Barrier Reef, 2. *Memoirs of the Queensland Museum* 38:533-573.

Kolehmainen, S.
1973. Ecology of sessile and free living organisms on mangrove roots in Jobos Bay. *Aguirre Environmental Studies, Jobos Bay, Puerto Rico: 1972 Annual Report.* Mayaguez, Puerto Rico Nuclear Center, University of Puerto Rico.141-173.

Littler, D.S. and M.M. Littler
1997. An illustrated marine flora of the Pelican Cays, Belize. Bulletin of the Biological Society of Washington 9:1-149.

Littler, D.S., M.M. Littler, and B.L. Brooks
2000. Checklist of marine algae and seagrasses from the ponds of the Pelican Cays, Belize. *Atoll Research Bulletin* 474:151-206.

Macintyre, I.G.
2000. Appendix: status of scleractinian corals in some Pelican Cays ponds following the 1998 bleaching event. *Atoll Research Bulletin* 467:35-37.

Macintyre, I.G., W F. Precht, and R.B. Aronson
2000. Origin of the Pelican Cays, Belize. *Atoll Research Bulletin* 466:1-11.

Macintyre, I.G., I. Goodbody, K. Rützler, D.S. Littler and M.M. Littler
2000. A general biological and geological survey of the rims of ponds in the major mangrove islands of the Pelican Cays, Belize. *Atoll Research Bulletin* 467:13-34.

McKinney, F.K.
1990. Feeding and associated colonial morphology in marine bryozoans. *Critical Reviews in Aquatic Sciences* 2(2):255-280.
Morton, S.L.
2000. Phytoplankton ecology and distribution at Manatee Cay, Pelican Cays, Belize. *Atoll Research Bulletin* 472:123-132.
Ristedt, H. and G. Hillmer
1985. The cheilostomate bryozoan fauna from shallow waters of the Hiluntangan Channel, Cebu Philippines: Part 1. *Philippine Scientist* 22:133-143.
Rützler, K. and I.C. Feller
1987. Mangrove swamp communities. *Oceanus* 30:16-25.
Rützler, K. and I.C. Feller
1996. Caribbean mangrove swamps. *Scientific American* 274:92-99.
Rützler, K., M.C. Diaz, R.W.M. Van Soest, S. Zea, K.P. Smith, B. Alvarez, and J. Wuff
2000. Diversity of sponge fauna in mangrove ponds. Pelican Cays, Belize. *Atoll Research Bulletin* 476:231-250.
Ryland, J.S. and Hayward, P.J.
1992. Bryozoa from Heron Island, Great Barrier Reef. *Memoirs of the Queensland Museum* 32:223-301.
Shyka, T.A. and K.P. Sebens
2000. Community structure, water column nutrients, and water flow in two Pelican Cays Ponds, Belize. *Atoll Research Bulletin* 471:105-121.
Sterrer, W.
2000. Gnathostomulida in the Pelican Cays, Belize. *Atoll Research Bulletin* 478:265-271.
Sutherland, J.P.
1980. Dynamics of the epibenthic community on roots of the mangrove *Rhizopora mangle*, at Bahía Buche, Venezuela. *Marine Biology* 58:75-84.
Tilbrook, K.J., P.J. Hayward, and D.P. Gordon
2001. Cheilostomatous Bryozoa from Vanuatu. *Zoological Journal of the Linnean Society* 131:35-109.
Urish, D.W.
2000. Preliminary hydrographic surveys of some ponds in the Pelican Cays, Belize. *Atoll Research Bulletin* 469:59-85.
Villareal, T.A., S.L. Morton, and G.B. Gardner
2000 . Hydrography of a semi-enclosed mangrove lagoon, Manatee Cay, Belize. *Atoll Research Bulletin* 470:87-103.
Winston, J.E.
1984a. Why bryozoans have avicularia -- a review of the evidence. *American Museum Novitates* 2789:1-26.
Winston, J.E.
1984b. Shallow-water bryozoans of Carrie Bow Cay, Belize. *American Museum Novitates* 2799:1-38.

Winston, J.E. and J.B.C. Jackson
1984. Ecology of cryptic coral reef communities. IV. Life histories of cryptic reef cheilostomes. *Journal of Experimental Marine Biology and Ecology* 76:1-21.
Winston, J.E.
1986a. Victims of avicularia. *P.S.Z.N.I: Marine Ecology* 7**:**193-199.
Winston, J.E.
1986b. A checklist of coral-associated bryozoans. *American Museum Novitates* 2859:1-39.
Winston, J.E.
1991. Avicularian behaviour -- a progress report. *Société des Sciences Naturelles de l'Ouest de la France. Mémoire. hors series* 1:531-540.
Winston, J.E.
2004. Bryozoans from Belize (II). *Atoll Research Bulletin* 523:1-14.
Wulff, J.L.
2000. Sponge predators may determine differences in sponge fauna between two sets of mangrove Cays, Belize Barrier Reef. *Atoll Research Bulletin* 477:249-263.
Wulff, J.L.
2005. Trade-off in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. *Journal of Animal Ecology* 74:313-321.
Yoshioka, P.M.
1974. Mangrove communities. *Jobos Bay. Aguirre Environmental Studies, Jobos Bay, Puerto Rico: Final Report.* Mayaguez, Puerto Rico Nuclear Center, University of Puerto Rico vol.1, 50-65.

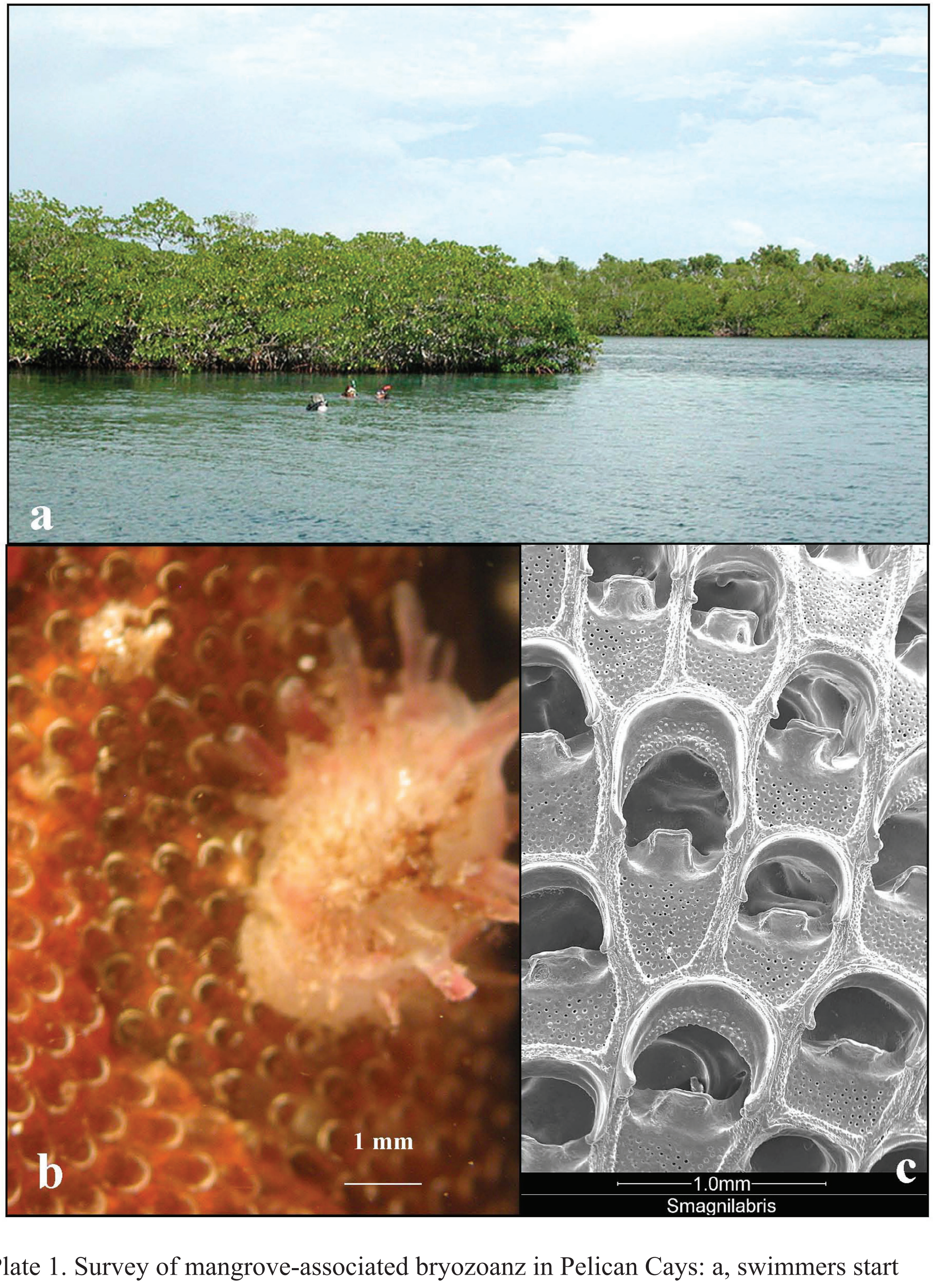

Plate 1. Survey of mangrove-associated bryozoanz in Pelican Cays: a, swimmers start to survey a lagoon pond; b, Living colony of *Steginoporella magnilabris*, one of the dominant bryozoans of red mangrove roots; c, *S. magnilabris* zooid structure (SEM).

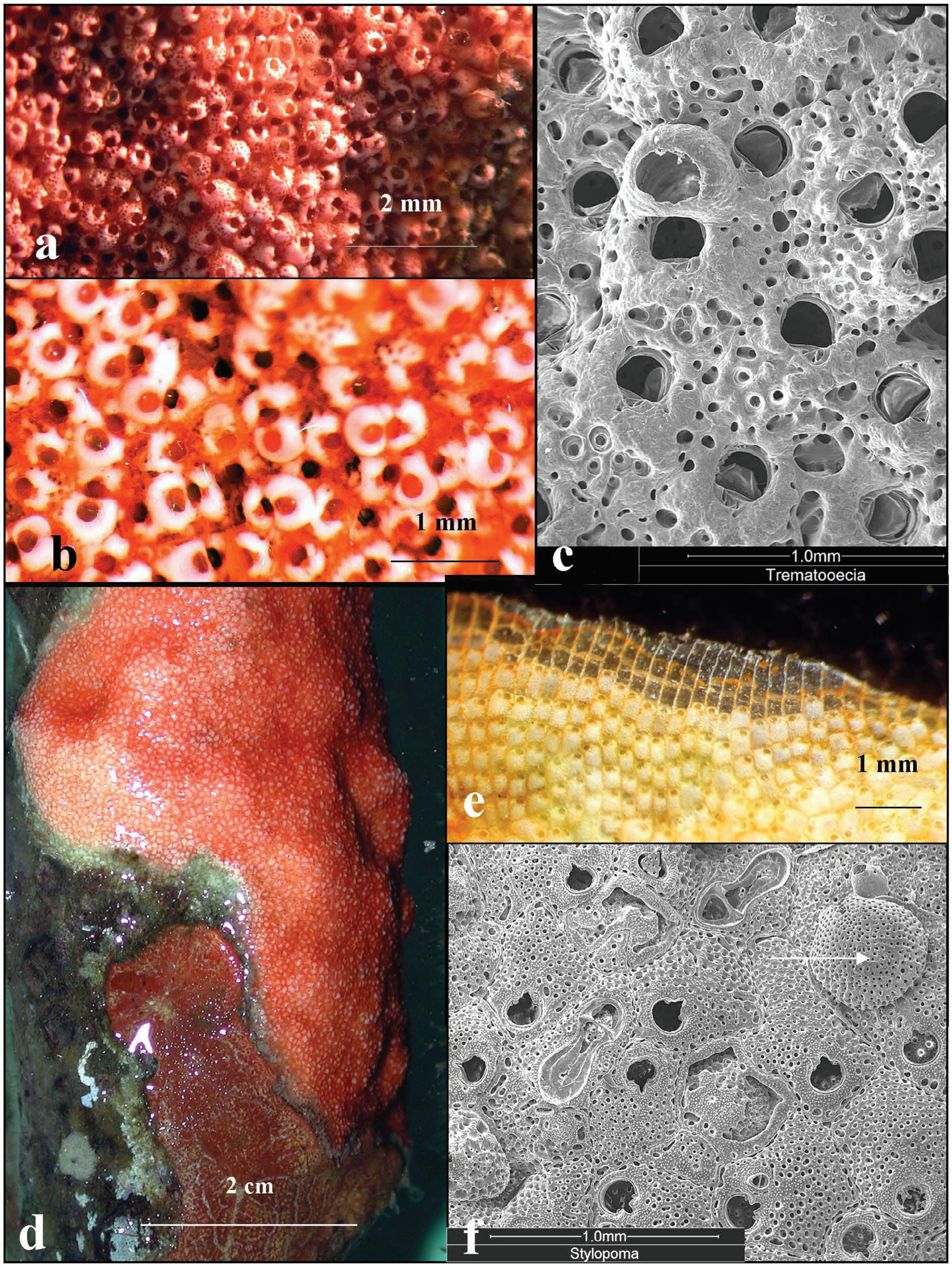

Plate 2. a-c: *Trematooecia aviculifera*, a, colony from mangrovr root; b, closer view of zooids and ovicells with rec embryos; c, SEM of zooids and ovicell (arrow) skeletons; d-f: *Stylopoma* sp., d, colony growing above red sponge on root; e, growing edge of colony, showing budding zone; f, SEM of zooids, spatulate avicularia, and ovicell (arrow).

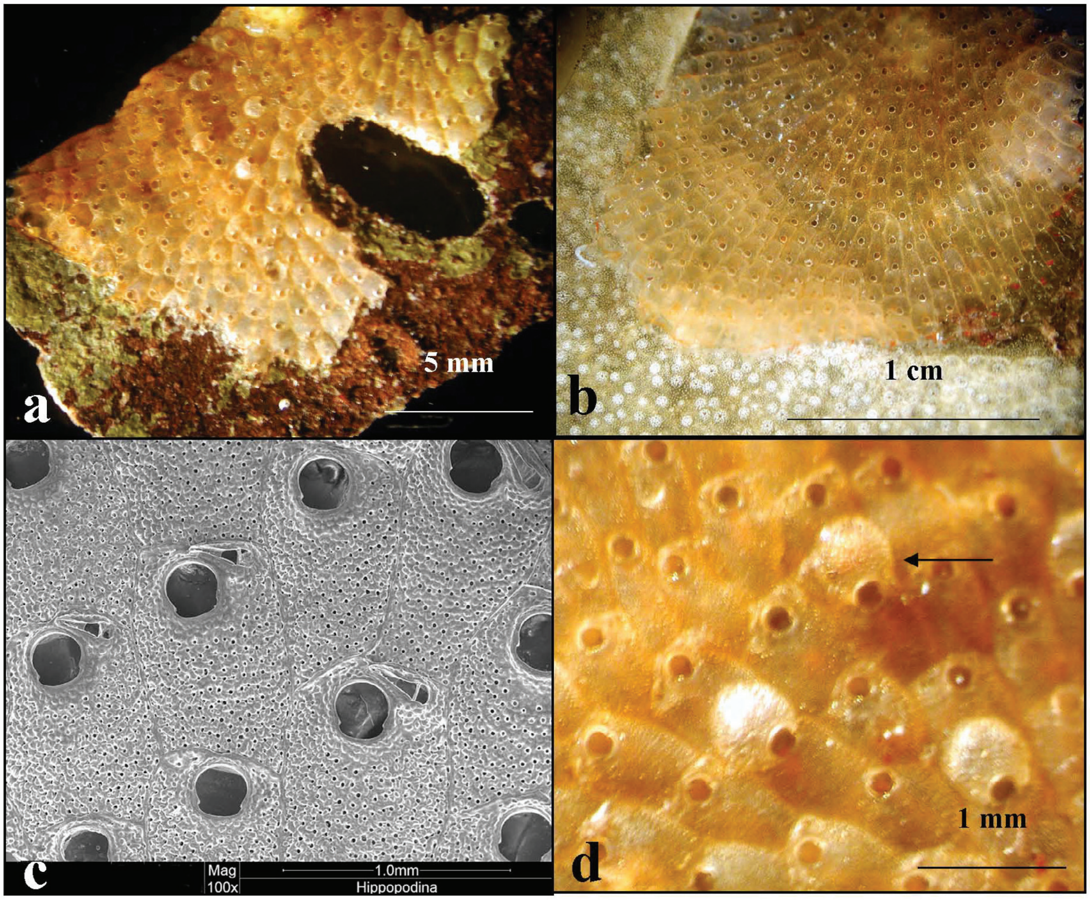

Plate 3. *Hippopodina feegeensis*: a, colony growing on mangrove root bark; b, colony overgrowing didemnid ascidian on mangrove root; c, SEM of zooids with triangular avicularia; d, living zooids, some with ovicells, one (arrow) containing an embryo.

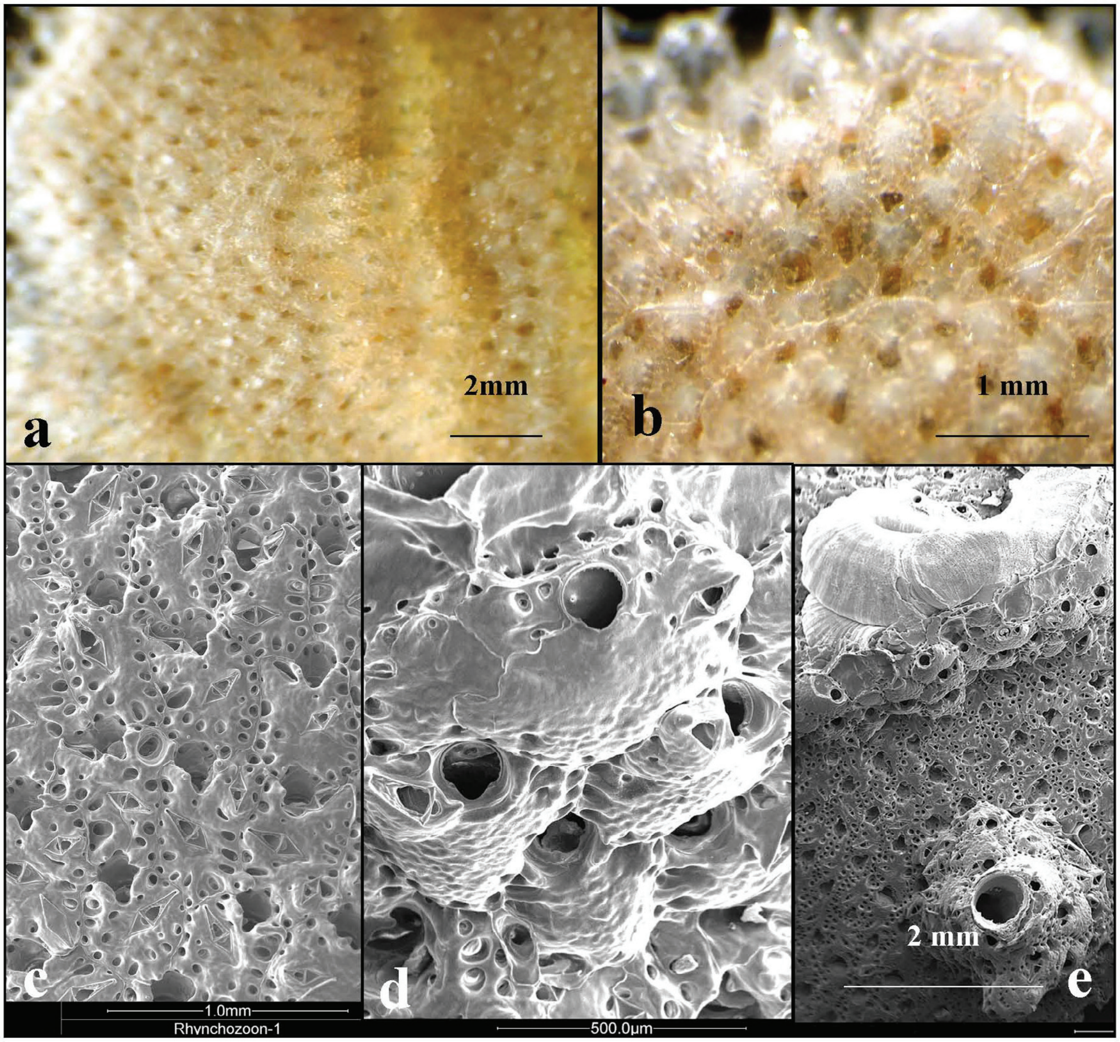

Plate 4. *Rhynchozoon verruculatum*: a, colony from mangrove root; b, closer view of zooids at growing edge of colony; c, SEM of zooid skeletons; d, SEM close-up showing zooids and avicularia; (arrows) e, as in reef cryptic communities, bryozoans usually overgrow solitary organisims such as the tubes of polychaetes or vermetids shown here.

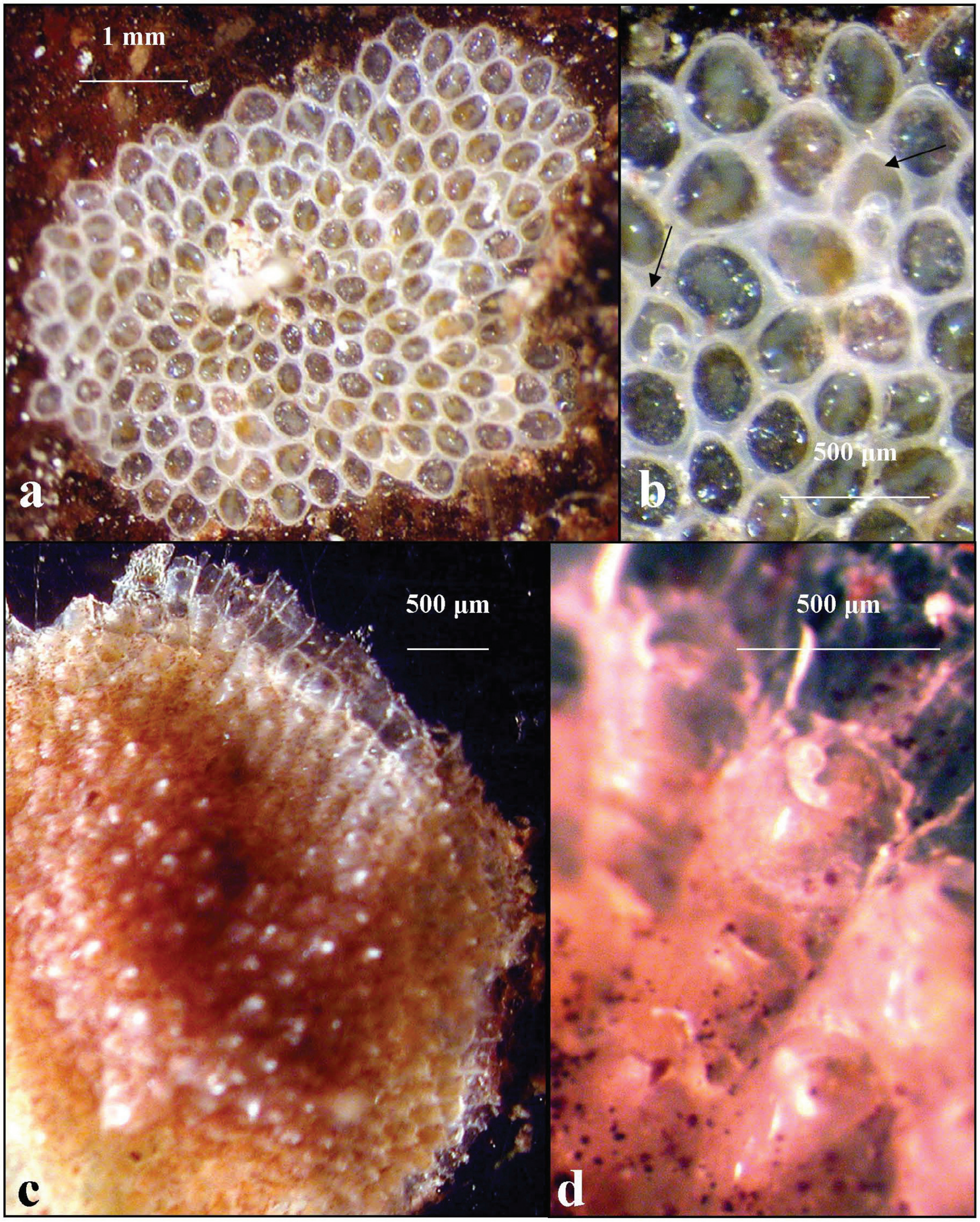

Plate 5. a-b, *Parellisina latirostris*: a, Colony encrusting mangrove root; b, colony enlarged to show two avicularia (arrows); c-d, *Celleporaria albirostris*, c, small colony from mangrove root, note purplish-red color and white spike-like projections of zooids; d, close-up of zooids showing dark pigment spots that cause coloration.

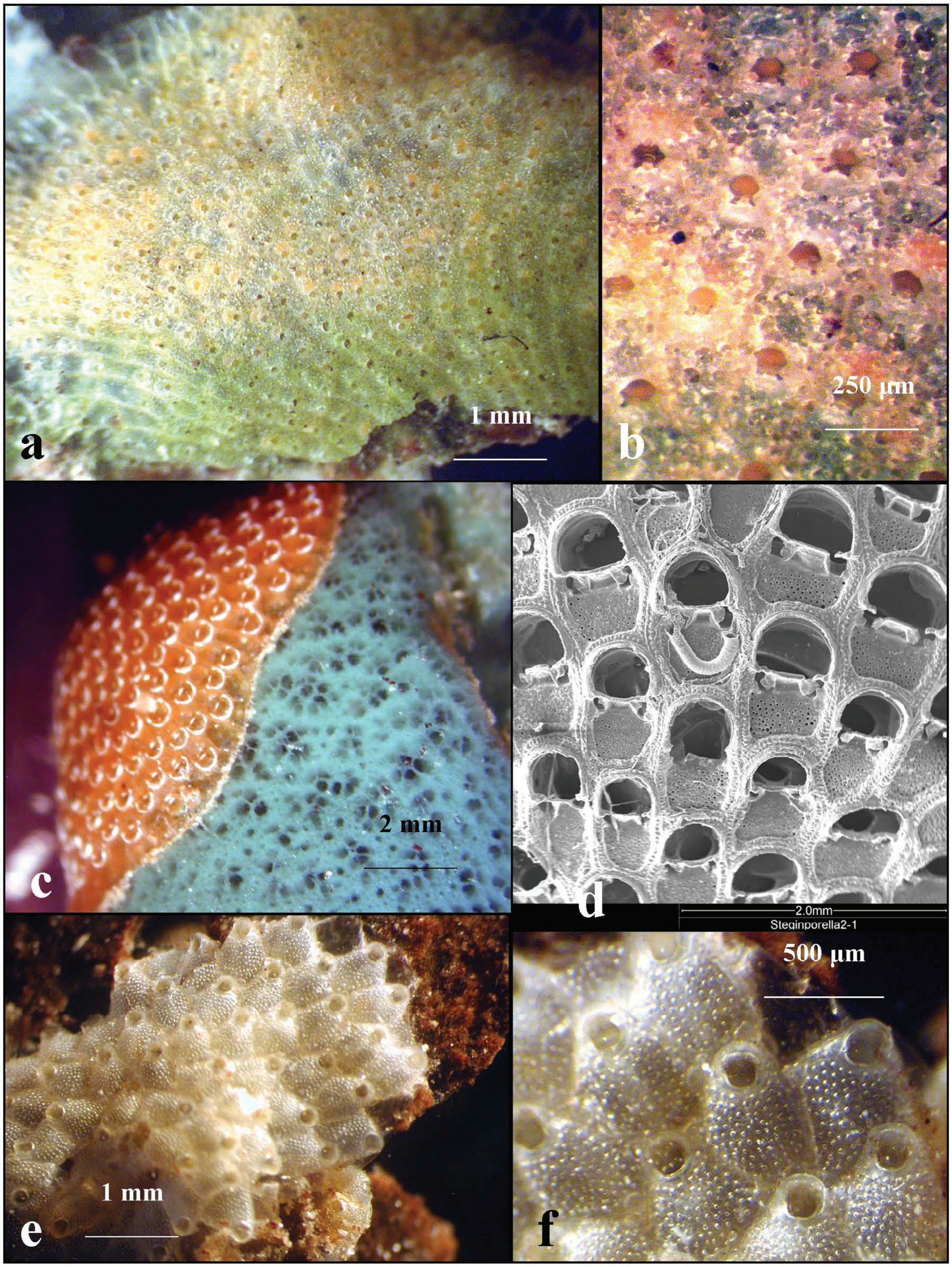

Plate 6. a-b, *Smittina smittiella*: a, colony attached to root; b, close-up of zooids; c-d, *Steginoporella connexa*; c, colony overgrowing sponge; d, SEM of skeletal structure for comparison with *Steginoporella magnilabris* (Pl. 1c); e-f, *Exechonella antillaea*, e, encrusting root; f, close-up of zooids.

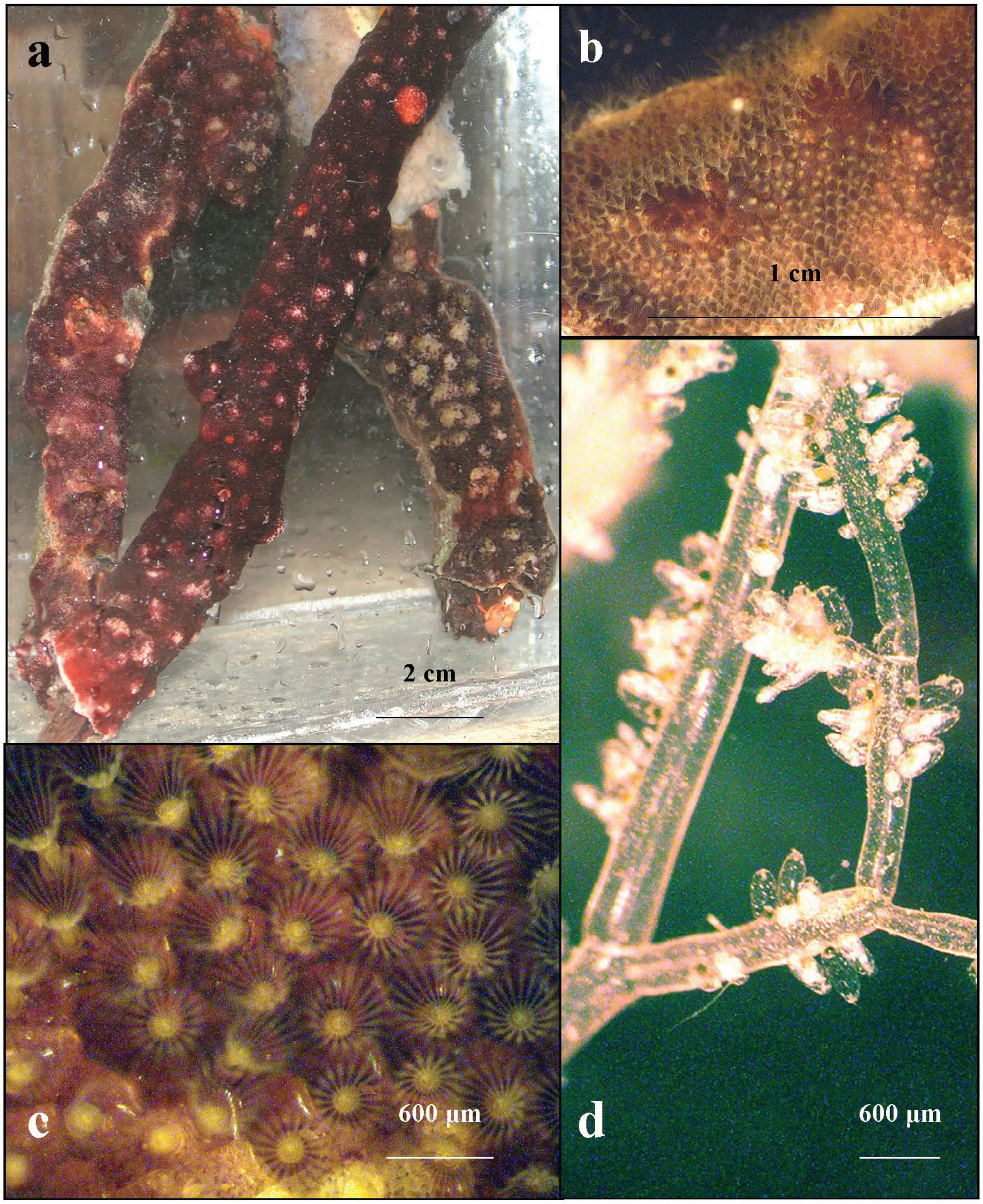

Plate 7. a-c, *Schizoporella pungens*; a, *Schizoporella*-encrusted roots in laboratory tank; b, portion of a colony with lophophores expanded; c, close-up of expanded lophophores; d, *Zoobotryon verticillatum*, showing small bottle-shaped zooids attached to thick, transparent stolons.

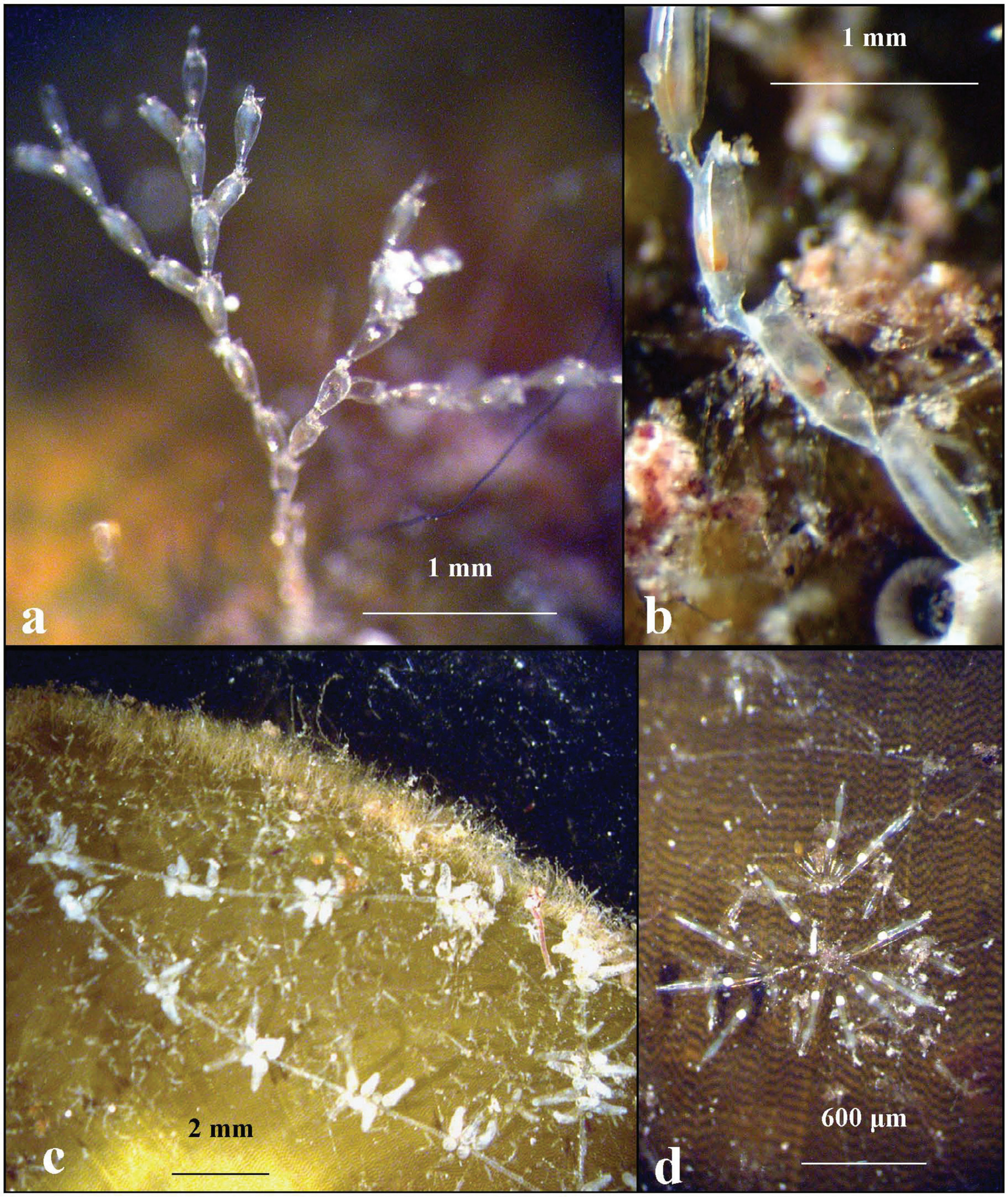

Plate 8. Examples of bryozoans found on the undersides of *Lobophora* thalli: erect growth habit; a, *Catenicella contei*; b, *Beania klugei*; c, vine-like growth habit, part of a thallus with *Bowerbankia maxima* (larger white stolons and zooids) and *Mimosella firmata* (almost transparent, spindle-shaped zooids); d, close-up of Mimosella cluster.