THE SUBTIDAL BRYOZOAN FAUNA OFF CAPE ARAGO, OREGON

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A THESIS

Presented to the Department of Biology
And the Robert D. Clark Honors College of the University of Oregon
In partial fulfillment of the requirements
For the degree of
Bachelor of Science

May 2013

An Abstract of the Thesis of

Dylan Michael Cottrell for the degree of Bachelor of Science
In the Department of Biology to be taken June 17th, 2013.

Title: SUBTIDAL BRYOZOAN FAUNA OFF CAPE ARAGO, OREGON

Approved: ____
Dr. Craig M. Young

The subtidal marine biodiversity off the Oregon coast is poorly studied and not well understood. The few subtidal studies in Oregon have focused on vertebrates with little regard to invertebrate assemblages. Oregon’s subtidal Bryozoa play key roles in these assemblages by providing habitat, food, and, potentially, pollution sequestration. Using dredge samples collected over two years, we assembled a comprehensive list of Bryozoa found between 30-60 m depth off Cape Arago, Oregon. A total of 41 species were collected, including one new species in the genus *Fenestruloides*. Although 25 families were represented in our samples, 17 (68%) families were only represented by one species and only two families (8%) were represented by more than three species. This data provides the first comprehensive survey of Oregon’s subtidal bryozoan biodiversity and is an important first step in understanding the region’s biodiversity.

ACKNOWLEDGEMENTS

I would like to thank Dr. Craig Young for his support and guidance that made this research possible as well as his work editing this thesis. I would also like to extend a special thanks to Dr. Dave Bilderback for his invaluable insight, expertise, and passion, and his efforts in editing my thesis and guiding me through bryozoan taxonomy. I would like to thank Dr. Matthew Dick and Dr. Dennis Gordon for their guidance and opinion regarding the discovery of a new species. I would like to thank Nicholas Hayman for his work preserving bryozans from the first seven dredges as well as for sharing his data with me. Finally, I would like to thank all the members of OIMB's 2011 and 2012 subtidal and deep sea ecology classes and the 2012 marine ecology class for their work in collecting and preserving the samples used in this research.

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Introduction

Despite a long history of subtidal marine research on the Pacific Coast of North America, the subtidal invertebrate communities off the Oregon coast remain poorly studied. The most extensive work has been conducted in southern California, in Monterey Bay or in the Puget Sound region of Washington (e.g. Shaffer, 2000; Watanabe, 1984; Langstroth, Lovell, and Langstroth, 2000) where conditions are amenable for SCUBA diving. The majority of subtidal community studies in Oregon have been done with either submersibles or dredges, and most of these focused on fisheries while mostly disregarding the rich invertebrate assemblages that make up the majority of the faunal diversity. This is particularly true of Oregon’s bryozoans, which have never been studied in any depth. This study sought to collect and identify the bryozoan fauna off Cape Arago, Oregon in an attempt to catalogue one aspect of Oregon’s invertebrate assemblages.

The Underrepresentation of Invertebrates

The limited number of published works on subtidal invertebrates of Oregon is surprising given the relative ease with which many species may be collected using standard methods such as dredges, trawls, and cores. The lack of studies can be attributed largely to the emphasis in Oregon on commercially harvested species. In recent years with the development of new technologies such as ROV’s (Remotely Operated Vehicles) and multibeam mapping, we have the tools for characterizing these environments using more than simple collecting methods. Indeed, just within the past few years, millions of dollars have been invested in mapping the ocean floor in the Oregon Territorial Seas. Some ground-truthing has been done to correlate substratum types with the sonar returns. Nevertheless, the Oregon Marine Atlas, which brings together virtually all that is known about the nearshore environments and resources still recognizes only a few commercially important invertebrates. All of the other invertebrates remain unmapped and taxonomically unknown. The importance of characterizing invertebrate diversity has become apparent in recent years with the establishment and proposed expansion of a network of marine reserves and with a variety of exploitative proposals for offshore wind energy and wave energy projects.

Even with methodological advances, vertebrate studies still take precedence over invertebrate studies in Oregon. By 2004, the Oregon Department of Fish and Wildlife had conducted many studies of rockfish populations south of Cape Arago, and although these studies recorded the more conspicuous invertebrates collected, dedicated invertebrate studies have yet to become mainstream (Fox et al, 2004; Weeks and Merems, 2004; Fox et al., 1998; Merems, 2003). McCauley (1972) compiled the first published checklist of invertebrates found off the Oregon coast, though many invertebrates were not represented. Other publications used for identifying marine animals were prepared in California or Washington and therefore have limited use in Oregon. In one notable SCUBA study, Posey et al. (1984) conducted a study of a sabellariid (a polychaete worm) reef at Gregory Point, near Cape Arago. This shallow-water study is one of the very few studies to survey comprehensively an invertebrate community off the Oregon coast. Hayman (2012) conducted the first research of invertebrate communities off Cape Arago and compiled a list of 143 subtidal invertebrate species in the area.

Importance of Biodiversity

Just as marine research is beginning to focus more on Oregon's invertebrate communities, so too are policymakers beginning to consider these communities when making policy decisions. A new management regime, known as ecosystem-based management (EBM) has been proposed by various advisory panels (Pikitch et al., 2004). The EBM scheme seeks to account for all the characteristics of an ecosystem when making a policy decision. This includes human impacts such as fishing as well as the role and sources of nutrients, sediments, and complex marine food webs. Under current management schemes, the connections among organisms, the environment, and their physical surroundings are seldom accounted for, often meaning that existing management methods are ineffective as evidenced by the number of collapsed fisheries worldwide (Ruckelshaus et al., 2008). Some habitats required by fish are destroyed by commercial fishing methods such as bottom trawling (Thrush et al. 1998). Not only is fish habitat being destroyed in current management practices, but also invertebrate assemblages are being heavily disturbed while we remain ignorant of the scale and effects of such disturbance. Unless benthic communities are studied to establish baseline data, future studies will be unable to quantify the success of management practices.

The conservation and protection of biodiversity is not simply important for resource management. Changes in biodiversity are often magnified through the nonlinear nature of ecosystems (Levin and Lubchenco, 2008). In worst case scenarios, low diversity may result in regime changes, population collapses, or even collapses of whole ecosystems. The Millennium Ecosystem Assessment (2006) determined that marine ecosystems that have higher biodiversity are more robust and less susceptible to parasites, population collapse, or regime change. The threats posed by climate change and associated ocean acidification and the associated loss of ecosystem diversity makes biodiversity conservation all the more important.

In addition to facing pressure from commercial fisheries, marine ecosystems also experience the pressures of climate change, pollution, and resource extraction. Interest in wave-generated power continues to increase, and test-sites are being planned in areas that have not been fully explored. Oregon is a global leader in renewable wave energy and there are several pilot projects underway off the Oregon coast. These programs have the potential to address Oregon’s energy needs. However, these projects are currently being developed without fully understanding what species are present, or how such projects will affect biodiversity. Although Oregon’s Territorial Sea Plan Advisory Committee has proposed legislation to “review standards and criteria for determining the possible adverse impacts of [wave power] development on protected marine resources and uses,” there is still little mention of studying the impacts of development on unprotected marine species. As mentioned earlier, most of Oregon’s marine laws focus of maintaining and protecting commercial fisheries while ignoring invertebrates, which are ecologically important. This is a serious problem, particularly if wave-generated power is to be fully implemented.

If biodiversity levels are to be maintained and protected, knowing the initial state of marine habitats is key. As Vecchione et al. (2000) pointed out, basic knowledge of a site’s biodiversity is needed before the effectiveness of conservation efforts can be judged. Such preliminary biodiversity exploration provides researchers with a baseline by which to measure species composition and distribution changes. In turn, these baseline data could be used to determine how effective marine reserves and management practices are, as well as the impacts of climate change and wave power development projects.

Correct identification of organisms in an area of study is the first step toward acquiring a basic knowledge of biodiversity (Vecchione and Collette, 1996b). When exploring biodiversity, studying taxonomic groups for which there is little reliable information offers rewarding results and a large return for the investment of limited time and money. In the Pacific Northwest, bryozoans are prime candidates for such studies as few studies have been conducted on bryozoan taxonomy in the region, and there are likely to be many undiscovered species. In one recent study conducted in California, 23 new species of bryozoans were reported (Soule, Soule, and Chaney, 1995). Similarly, Grischenko, Dick, and Mawatari (2007) reported 39 species from only 10 study sites in Alaska, of which 21 (54%) were new to science. Such results demonstrate the vast number of bryozoans that have yet to be described. To date, no comprehensive survey of bryozoan fauna has been conducted in Oregon. One expert has predicted that more than 20% of the Oregon's bryozoan fauna have yet to be described (Matthew Dick, Hokkaido University, personal communication).

Natural History and Ecology of Bryozoans

Bryozoans are small aquatic animals found in both marine and freshwater habitats. Marine bryozoans are common on sea floors and coastlines worldwide. The Phylum Bryozoa has a long fossil record, extending back to a rich diversity in the Paleozoic Era (Soule, Soule, and Chaney, 1995). Although the Phylum Echinodermata has roughly the same number of species, bryozoans are typically overlooked by the casual beachcomber and extremely underrepresented in scientific literature, possibly due to their small size and difficulty in identifying and studying them.

This underrepresentation, as well as the fascinating biology and uniqueness of bryozoans, makes their study both exciting and rewarding. Nearly all bryozoans are colonial, and colony sizes range from just a few to thousands of individuals. The growth pattern of a colony is highly variable because colonies respond to water currents as well as predation or overgrowth (Soule, Soule, and Chaney, 1995; Harvell 1990; Harvell and Padilla 1990). Colonies are clearly visible with the naked eye, though observation of a species' defining characteristics (other than color) requires magnification. Researchers often use coloration and colony form for preliminary identification in the field, though a sample must generally be brought back to the laboratory for positive identification.

Each individual in a colony is less than a millimeter long and is known as a zooid (Woollacott and Zimmer, 1977). Zooids are often differentiated into various polymorphs even though they are genetically identical. These polymorphs include avicularia, gynozooids, androzooids, kenozooids, ancestrula, and autozooids. An avicularium (Greek for bird beak) is a zooid whose role is to defend the colony from predation or from being overgrown. Gynozooids and androzooids are reproductive zooids (females and males, respectively). A kenozooid is simply a supporting zooid, and fills various roles. An ancestrula is the colony's founding member, and thus each colony has only one. Finally, an autozooid (the most common type of zooid) is a feeding individual with no specialized task. A colony arises via asexual budding of the ancestrula, meaning all zooids in a colony are genetically identical even though its ancestrula was sexually produced. Typically, a colony broods its eggs and larvae until mature. Brooding takes place either in gonozooids or in specialized brood chambers known as ovicells (if the species is a cheilostome).

Broadly, individuals may be placed into two groups. Heterozooids are individuals that have a specialized task (and, often, specialized morphology) such as defense or reproduction. The remaining individuals are simply autozooids. Once an individual is created via budding, its role is permanent. Thus if a colony does not produce enough avicularia, it is more likely to be eaten or overgrown. Clearly, a delicate balance must be found in the number of individuals produced for each role.

This balance becomes even more important when one considers how a colony obtains its food. Each autozooid has a lophophore (an inverted cone-shaped ring of tentacles) surrounding the mouth. The lophophore can be retracted into the autozooid's body cavity if it is disturbed. Heterozoids lack both a lophophore and a digestive tract and are thus incapable of capturing their own food or digesting it. Nutrients are transported to the heterozoids through funicular tissue**,** which connects all individual zooids the colony (Woollacott and Zimmer, 1977). This funicular tissue also allows for the coordination of behavioral responses among individuals through neural connections. Interestingly, the interior portion of a zooid, or polypide, can be broken down and regenerated during the zooid's life. Additionally, if a portion of the colony is lost due to overgrowth, predation, or injury, the rest of the colony can survive unharmed. If a colony is divided, both parts can survive and grow.

Nearly all bryozoans are sessile animals found on hard substrates such as rocks, seagrasses, algae, or shells. Colonies are either encrusting (sheets or runners) or erect (bushes, lattices, or fronds) though this morphology can be rather plastic, meaning that morphology is often not unique enough to facilitate identification. Indeed, several species have been observed to change their growth pattern based on water current direction and strength (Soule, Soule, and Chaney, 1995).

The study of colony morphology and ecology have seen growth in the past few decades (Taylor, 1990). Bryozoans play important roles in the stabilization of coral and algal reefs (Soule, Soule, and Chaney, 1995). They also play important roles for fish by providing a suitable substratum for algal growth (eaten by fish) as well as providing shelter and hiding places for larval and juvenile fish (Woollacott and Zimmer, 1977). As noted, the bottom trawling and dredging conducted by many fisheries often breaks up these habitat-forming colonies.

Not only do bryozoans act as habitat engineers, but they are typically filter feeders and thus act are important in water filtration (Taylor, 1990). Autozooids will also feed on bacteria (which coat detritus), nonplankton (algal spores, protists, etc.) as well as the occasional small worm or crustacean further helping maintain water quality (Soule, Soule, and Chaney, 1995).

Although state agencies are beginning to include invertebrates in marine planning, invertebrates still remain undersampled. Studies like Hayman (2012) are proving valuable in helping policy makers incorporate invertebrates into their considerations. Although Hayman’s study provided a strong case for the importance of considering overall species diversity, much work remains to be done on the taxonomy of various important components of the subtidal fauna. The present study undertook the identification of bryozoans from the same collection area where Hayman’s research was conducted. The goal of this study was to provide a more complete picture of subtidal invertebrate, specifically bryozoan, communities off Cape Arago. Further, as this is the first in-depth study of bryozoans in Oregon, it is hoped this study will be used in future studies regarding policy effectiveness and environmental change.

Materials and Methods

The central question of my thesis is easily articulated as what bryozoan species are found off Cape Arago, Oregon but difficult to answer because of a paucity of bryozoan studies in the area. I collected samples from the sea floor during 12 dredges all conducted at different locations (Figure 1). All offshore dredges were conducted between April-May 2011 and between May-July 2012. Dr. Craig Young and students enrolled in his subtidal and deep sea ecology course obtained the samples collected during the 2011 session. Dr. Young's class preserved their samples for later research, allowing me to use their collection in my study. Dr. Young and his students repeated this same procedure in the May 2012, though this time I participated in collection and preservation of the samples. Dr. Cynthia Trowbridge and her students again repeated this procedure in July 2012, though only bryozoans were preserved for study.

Qualitative dredges were conducted in an area of rocky outcrops with patches of mixed gravel and sand. Each dredge haul was conducted for ten minutes with a 0.5 m wide dredge and 2 cm net. Dredge tracks varied in length from 500-1000 m, depending on currents, wind strength, and boat speed. The net boat speed was approximately one knot for each dredge and dredge depths varied between 30 and 60 meters.

Collected specimens were roughly sorted immediately after retrieval of each dredge. Macrofaunal specimens, if known, were recorded and returned to the ocean if they were not needed for further study. All other specimens were placed in plastic tubs to be brought back to the laboratory for identification. If numerous specimens of the same unknown species were collected during a dredge, only one was kept and brought to the laboratory. The remaining sample, consisting of clams, scallops, annelids, ophiuroids, brachiopods, bryozoans, rocks, and mud, was also placed in plastic tubs and brought to the laboratory.

Once back in the laboratory, the sample was spread out on trays and allowed to air dry for a week. Once dried, the sample was hand-sorted to isolate the bryozoans, which were in turn placed into operational taxonomic units (OTUs). Initially, several of the dredges were sorted into OTUs before being allowed to air dry, though this procedure was later changed to make sorting easier. When possible, color photographs were taken of specimens using a Nikon camera mounted on an Olympus dissecting microscope.

It should be noted that I was only able to sort the samples collected by the Marine Ecology course (July 2012). The first ten dredges were conducted either before I attended OIMB or before I had selected my thesis topic. As a result, only two dredges were thoroughly sorted by species of bryozoa; unless one is looking closely (often using a hand lens or microscope) at a colony, it is difficult to differentiate species. This may be reflected in the data I collected: only 18 species were found during all seven dredges in 2011 while I found 24 species during a single dredge in the summer of 2012. This discrepancy in consistency likely resulted in a slightly more incomplete species list than one would hope.

After sorting and drying, each OTU was again hand-sorted and the best (large, intact, relatively clean) specimens were selected for further study. The representative samples were then cleaned using methods modified from Toscano (2008) and Gordon (2009) in order to remove cuticular membranes, dirt, iron deposits, and any biotic substrata to which the specimen was attached.

If the specimen was highly calcified (often characterized by an upright branching or encrusting morphology) it was immersed in a hydrogen peroxide (H_2O_2) solution (30% m/v in water) for 60-90 minutes. Immediately upon being removed from the H_2O_2, the specimen was re-immersed in 5% sodium hypochlorite (household bleach) for an additional 60-90 minutes. If the specimen was encrusted on a rock, the bryozoans were removed post-cleaning by careful use of a razor blade. This process was repeated at least twice for each specimen, and sometimes more if the specimen was particularly dirty, contained iron minerals, or was thoroughly encrusted on other biotic material. Once cleaned, each specimen was rinsed with distilled water.

If a specimen was only lightly calcified (often characterized by a colony's flexibility or ability to "stand" upright when out of water), it was immersed in the H_2O_2 solution (30% m/v) for 30 minutes. Following H_2O_2 immersion, the specimen was briefly immersed in 5% sodium hypochlorite for no more than 10 minutes before being transferred to a graded alcohol bath series to near-absolute ethanol concentrations (45 minutes each in a 10%, 20%, 40%, 60%, and 90% ethanol). The ethanol bath helped prevent surface-tensional effects such as curling, bending, and cracking.

Following cleaning, samples of each OTU were cut and mounted on SEM stubs with double-sided tape. Samples were chosen so that each stub had several individuals showing their dorsal side and others showing their ventral side. Each stub was then placed in an Emscope SC 500 Sputter Coater and coated by gold-plated electrodes. Following gold plating, micrographs of each OTU were taken using a Hitachi S-510 Scanning Electron Microscope.

Several published works were used to identify the specimens. If possible, multiple works were used to verify a proper identification. Dr. David Bilderback (University of Montana, Professor Emeritus) also helped verify questionable identifications. Soule, Soule, and Chaney's report (1995) on bryozoans in the *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel* was used most heavily, followed by *Bryozoa of the Pacific Coast of America* (Osburn, 1950). As both of these works focused primarily on California's bryozoa, the key produced by Bergey and Denning in *Marine Invertebrates of the Pacific Northwest* (Kozloff, 1987) was also used. Soule, Soule, Morris, and Chaney's key in *The Light and Smith Manual* (Carlton, 2007, 4th ed.) was similarly drawn from but to a lesser extent.

Results

All the bryozoan species found in dredges from off the coast of Cape Arago are listed according to their taxonomic relationship in Table 1. This table is also a tentative list of Oregon's subtidal Bryozoa, compiled from the few published studies in Oregon, as well as unpublished data. This study identified a total of 41 species, including one new species in genus *Fenestruloides* (described below). Defining characteristics of the new species, *F. n. sp.*, and its comparison with *F. morrisae* and *F. umbonata* are listed in Table 2. Micrographs of each of the collected bryozoan species are presented in Appendix A.

New Species Description

(Plate 13)

Name. *Fenestruloides n. sp.*

Material Examined. Dredge site 12 (see Figure 1).

Diagnosis/Description. Colonies thin, fragile, encrusting rocks. Zooids covered with an ectocyst of medium thickness, hexagonal, 512-697 µm long , 432-615 µm wide, length-to-width ratio 1.13-1.18, inflated frontal wall. Marginal gymnocyst rim around zooids and ovicells; numerous, fairly regularly spaced frontal pores 17-24 µm in diameter. Aperture arched distally with 2-3 spines, straight promixally. Ovicellate zooids have only two visible spines (flanking the ovicell), although the third median spine may be seen if the roof of the ovicell is removed. Aperture 117-138 µm long, 147-167 µm wide (131-141µm long, 161-186 µm wide if ovulate), length-to-width ratio of 0.80-0.83. Ascopore narrow, opening 33-39 µm wide, with a wide, thin uvulate process 10-13 µm long, weakly denticulate, seldom rimmed. Ascopore length to frontal pore diameter ratio 1.49-1.60. Ovicell inflated, about 20 ridges, with chevron at proximal margin, 312-358 µm wide and 265-394 µm long (length to width ratio 1.12), rimmed by gymnocyst and bordered by one row of irregular marginal pores.

Biology. Encrusting rocks and presumably other hard substrates. Recovered from 49-58 meters deep.

Taxonomic Remarks. This species most resembles *Fenestruloides morrisae,* and *F. umbonata* (Table 2). The zooids of *F. n. sp.* are shorter and tend to be narrower, with a length-to-width ratio of 1.13-1.18 compared to *F. morrisae* (1.14-1.24) and *F. umbonata* (1.12-1.17). The ascopore of *F. n. sp.* is smaller than these other species, and its weakly denticulate morphology is unique. Ascopore width to frontal pore diameter ratio of 1.49-1.60, compared to *F. morrisae* (3.89) and *F. umbonata* (2.43-2.55). No avicularia were observed. Whereas ovicells in *F. morrisae* are flattened and smooth, the ovicells of *F. n. sp.* and *F. umbonata* are inflated. *F. n. sp.* ovicells can be distinguished from *F. umbonata* by the presence of approximately 20 ridges on lateral and distal walls of the ovicell and a chevron on the proximal margin.

Type Locality and Type Specimens. Dredge Station 12, off of Cape Arago, Oregon. Collected 18 July, 2012. OIMB Byrozoa OTU No. 11.3.

Distribution. No other locality known at present.

Discussion

The number of species collected in each dredge varied greatly, ranging from 6 to 24 species (Figure 1). There is also a noticeable increase in species richness between dredges 1-10 and dredges 11-12, with the later having at least double the number of species than the former (Figure 1). Although bryozoan habitat suitability is influenced greatly by sediment type, the proximity of the dredges makes it unlikely that sediment differences are responsible for such large differences in bryozoan species richness. The most likely explanation for this discrepancy is that only the final two dredges were sorted with special attention to bryozoans while the others were sorted with more attention on larger invertebrates (holothuroids, ophiuroids, mollusks, echinoderms, etc.). Bryozoan morphology is often quite similar, and unless special attention is paid to this phylum, operational taxonomic units (OTUs) tend to be coarse. If OTUs were coarse enough, it could account for the low number of species recorded. To the casual observer, only colony morphology (i.e. erect/branching or encrusting) and color are quickly discernible. With closer inspection, finer resolution OTUs can be easily established.

The prevalence of these coarse OTUs clearly demonstrates the importance of conducting phylum-specific surveys off the Oregon coast if Oregon's marine fauna are to be catalogued. Hayman (2012) found that sponges and bryozoans account for roughly 40% of the known species off Cape Arago. During Hayman's study, only 18 bryozoan species were identified. An additional 22 bryozoan species were recorded by this study, underscoring the importance of such focused taxonomic efforts. If these two studies are used as the basis for a hypothetical rarefaction curve, it is clear that the resulting graph would not be near asymptotic, indicating there are still many more Bryozoa yet to be identified off Cape Arago. If this is indeed the case, much work remains to be done on the Bryozoa of Cape Arago.

As previously mentioned, it has been estimated that 20% (or more) of species in Oregon's bryozoan assemblages have yet to be described (Dick, personal communication). This study identified only one previously unknown species, *Fenestruloides n. sp.*. The low number of new species is likely due to the coarse OTUs rather than an affect of prior exhaustive studies. It is likely that future studies will discover many more new species. In turn, these data can be used to begin to determine the overall bryozoan species richness off Cape Arago by adding data to the rarefaction curve.

Species from 25 families (excluding *Cyclostomatida incertae sedis*) were collected (Table 1). It is interesting to note that 17 families (68%) are only represented by one species and only two families (8%), *Bugulidae* and *Smittinidae*, are represented by four species each. Additionally, 32 (78.1%) of all species are in a single class, Gymnolaemata and all 32 species of Gymnolaemata belong to the order Cheilostomatida. Although specimens from only one order of Stenolaemata were collected (Cyclostomatida), there were seven suborders represented. This is particularly interesting, as there were only nine species (21.9%) identified as stenolaemates.

The preliminary checklist of Oregon's subtidal Bryozoa (Table 1) indicates that total of 90 species have been collected and identified, though there are likely additional species that have yet to be collected. This compiled list draws heavily on bryozoans found on kelp holdfasts and associated rocks collected on the driftline (Bilderback, unpublished data) and a preliminary checklist compiled by McCauley (1972). This study reported 24 species in Oregon for the first time (Table 1 and Appendix A), although many of them have been reported both north and south of the state in previous studies. Their presence in Oregon state waters indicates that populations in Puget Sound and southern California may not be disjunct populations, though this certainly needs further study if a strong conclusion is to be drawn. The presence of many of these species was expected due to the dispersal range of bryozoans. Although bryozoans can be transported via ballast water, this dispersal method is unlikely to lead to the establishment of several disjunct populations unless the species is particularly invasive.

Due to the collection method used in this study, the abundance of various species could not be quantified, nor could colony growth patterns with regards to other species and water flow be examined. This would be a rich area of future study, particularly if it resulted in the niche of a few chosen species being defined.

The similarity among bryozoans in diet, habitat, and reproduction makes the sheer number of species collected globally nearly unfathomable. This is even more impressive when one considers that bryozoans are also competing with countless other species for space and food. All bryozoans are suspension feeders, so it is unlikely that dietary niches exist between species or even among families or orders. With 41 species and 25 families in such a small area, this possibility seems incredibly slim.

Although varying diets may not explain the great diversity of bryozoans off Cape Arago, the frequency of disturbances may. The ability to produce adequate avicularia to deter predators as well as the ability to maintain or increase colony size in the face of grazing by fish, limpets, and sea urchins among others is imperative. Colonies that grow larger would likely achieve a colonial size refuge, giving them an advantage over smaller colonies that could be completely overgrown or grazed. Colonies likely grow fast at the expense of colony defense (i.e. avicularia). This would make them more susceptible to predation, although it would limit the threat of overgrowth and increase the chances that a fragment will survive if the colony is heavily damaged. Smaller colonies likely put more resources into defense and are thus better suited to rebuff grazers or overgrowth. However, small colonies lack a size refuge with regards to disturbance, thus increasing the likelihood that the entire colony could be destroyed by a catastrophic event.

Although disturbance tolerance may account for the vast diversity in theory, the reality is not quite so simple. Colonial and zooid morphology is incredibly plastic and responds to predation/overgrowth and to water currents. If a colony is routinely grazed or threatened by overgrowth, the colony will have many more avicularia than a similar one that experiences a smaller threat. Thus, some colonies of the same species may have many interzooecial avicularia (zooids whose sole role is defense) and adventitious avicularia (avicularia that are only a part of a zooid) while another may have no interzooecial avicularia and only a few adventitious avicularia. Additionally, zooid shape and size vary dramatically from colony to colony. The type of substratum as well as water currents affect colony and zooid shapes and sizes. Such plastic morphology makes determining niches difficult.

Perhaps the biggest factor in a bryozoan species niche is its fundamental morphology (i.e. encrusting, erect, uniserial or multiserial). A colony’s fundamental morphology is not plastic and thus is likely an evolutionary response to an empty niche. A uniserial colony is one which zooids are budded distally, such that a single row of zooids develops over time. Multiserial colonies bud either distally or frontally, but colonies are shaped as fans or discs rather than as a single row.

The majority of species collected were multiserial encrusting followed by multiserial erect, massive multiserial encrusting, uniserial erect, and finally uniserial encrusting. McKinney and Jackson (1989) who proposed that colony growth forms could be interpreted as an evolutionary response to disturbances found this same trend at a similar depth in the Atlantic Ocean. Uniserial colonies are best suited to frequent disturbance because of their rapid growth rate and the large area colonies are able to cover. Multiserial encrusting colonies also may be favored over erect colonies because they are faster growing, reproduce faster, and are more difficult to break or be consumed by predators. At sites with low levels of disturbance, erect colonies would likely be favored because their morphology allows them to elevate into the water column where food may be more readily available thus ‘shading’ the encrusting colonies beneath them. This theory was not tested in this study due to collection methods and the limited range of dredge depths, though this is a rich area for future research.

Colony location also may have a huge role in establishing a species’ niche. Erect colonies have a slow growth rate, and are thus unlikely to grow on horizontal surfaces where sediments can build up and bury the colony. Instead, they are more likely to grow on vertical faces of boulders, where risk of burial is minimal. Indeed, this was observed in several videos filmed by Oceana in 2011 off the Oregon coast (Enticknap et al., 2013). It may be that some species specialize on growing on horizontal surfaces while others are found only on vertical faces. Yet, other species may be generalists and survive on either surface. Unfortunately, collecting samples via dredge did not allow for niche analysis although this is an interesting area to direct future research.

The taxonomic diversity of bryozoans underscores the importance of detailed surveys such as this one. Taxonomic diversity is a key component of biodiversity. Indeed, taxonomic diversity is often used as a measure of biodiversity. Though this study did not address biomass or percent cover for each species, it did demonstrate the vast amount of taxonomic diversity and varied levels of taxonomic representation.

The low number of species collected in each family indicates that local disturbances could have a large impact on local biodiversity. If only a few species become locally or functionally extinct, not only will genetic diversity be lost, but higher-order taxonomic diversity will be lost too. Such losses could be magnified through the ecosystem's nonlinear relationships as discussed by Levin and Lubchenco (2008).

Stability helps ecosystems withstand and recover from frequent disturbances such as bottom trawling. Biodiversity can enhance ecosystem production and help maintain the ecosystem's stability (Worm et al., 2006). Worm et al. (2006) concluded that globally, diverse ecosystems produce 78 to 80% more primary and secondary products than monoculture sites. One reason for this is that intact, diverse assemblages contain redundant species that share ecosystem functions. One classic example of this is herbivory on coral reefs. The macroalgal densities on these reefs are maintained by a wide array of herbivores including various types of fish and urchins. If one species of fish or urchin were to become locally extinct, the remaining species of grazers could still regulate macroalgal populations, and the ecosystem could survive. However, in lower diversity systems such as the kelp beds of California, such redundancy is absent. In an undisturbed ecosystem, sea otters keep urchin populations in check. When otter populations crashed in the early 1900s, urchin populations were relieved of predatory pressure and their population increased. Unchecked, urchins ate many of the kelp holdfasts, destroying kelp beds and creating urchin barrens where no macroalgae could grow. No other species could adequately maintain the ecological function of sea otters that led to an ecosystem collapse.

Worm et al. (2006) concluded in survey of global marine habitats that diverse ecosystems are more robust and had lower rates of collapse. Importantly, loss of biodiversity was shown to impair the number of viable fisheries while water filtering and detoxification decreased by 68%. Such services would be greatly impacted by local loss of entire families or orders of bryozoans. Limited bryozoan larval dispersal (typically only a few meters) would preclude “rescue” by distant populations that may otherwise act as a source population.

In 2009, the Oregon Legislature passed House Bill 3013, which established the process for establishing a network of marine reserves along the Oregon coast. The data collected on these bryozoans assemblages not only contribute to knowledge of biodiversity off the Oregon coast, but they could assist in the establishment of a marine reserve off of Cape Arago. Past efforts to establish a reserve in this location have focused mostly on vertebrate diversity. This study in conjunction with Hayman’s study (2012) and others could encourage policy makers to consider invertebrate assemblages in the planning process. The great majority of studies off Oregon’s coast have focused on commercially important fisheries; so, biodiversity data are scarce and incomplete. Ideally, these data will be used not only for planning marine reserves but also for establishing new management techniques and determining the impact of offshore development projects like wave power.

Another policy body, the Ocean Policy Advisory Council (OPAC), advises Oregon’s governor on ocean policy. In 2002, OPAC stated in a report to the governor that its primary goal is to protect “important” marine habitat and to maintain the “functional integrity” of marine ecosystems. If these goals are to be accomplished, data on invertebrate communities must be collected. Invertebrates play extremely important roles in marine ecosystems, such as water filtration, pollution sequestration, and specialized habitat formation. Invertebrates also are integral to marine food webs. If the proposed marine reserve network in Oregon is to succeed and wave power projects are to have minimal impacts on marine habitats, invertebrates must be included in the planning process.

Characterizing the marine invertebrate community off Cape Arago is extremely important if the success of a marine reserve or the impacts of offshore development is to be determined. Without measures of the site’s baseline biodiversity, it will be impossible to determine if a reserve is affecting local biodiversity. Likewise, the impacts of wave power projects will remain largely unknown. This study is a small part of the effort to determine such a diversity baseline.

Collecting baseline information on bryozoan biodiversity also may be helpful in studying the impacts of ocean acidification. Smith (2009) demonstrated that bryozoans can be used to study the carbonate dynamics of continental shelves in temperate regions. The abundance of bryozoans on continental shelves and at various depths offers a perfect analogue to corals, which are often studied for this purpose in the tropics. Bryozoans have the potential to help us study the effects of ocean acidification, which affects marine calcification and thus many biomineralizing fauna. As global warming continues, the oceans are expected to become more acidic as they absorb carbon dioxide from the atmosphere. Smith (2009) identified several species of bryozoans that are particularly vulnerable to acidification and may act as early indicators of ocean acidification. Species identified as most vulnerable to acidification include *Cellaria immersa* and *Diaperoecia purpurascens*. Both these genera were collected in this study. Hopefully this study provides a baseline on bryozoan diversity which can be compared with future studies in an effort to determine the local effects of ocean acidification.

Measuring and understanding subtidal biodiversity is becoming increasingly important, both in Oregon and globally. If biodiversity conservation in Oregon is to be successful, the full range of organisms, not simply vertebrates, must be identified and studied. This study, the first such study in the state, provides biologists and policy makers with detailed data on bryozoan assemblages off of Cape Arago. These assemblages are important for maintaining ecosystem health, providing valuable habitat, and serving as a source of food. Subtidal ecosystems face the threats of commercial fisheries trawling, climate change, ocean acidification, and off-shore development of wave power. Yet, much more work remains in studying Oregon's Bryozoa as well as other invertebrates. Hopefully, this study provides a baseline by which to judge the success of any future marine reserves, as well as establishes some groundwork necessary for Cape Arago's bryozoans to be used as indicators of ocean acidification. This study may also be useful when determining the impacts of wave-power projects, which will almost certainly become increasingly important and common in the future. Although not all of these changes will have negative effects, understanding the composition of bryozoan assemblages that are of fundamental environmental importance is key if such effects are to be fully assessed and monitored.

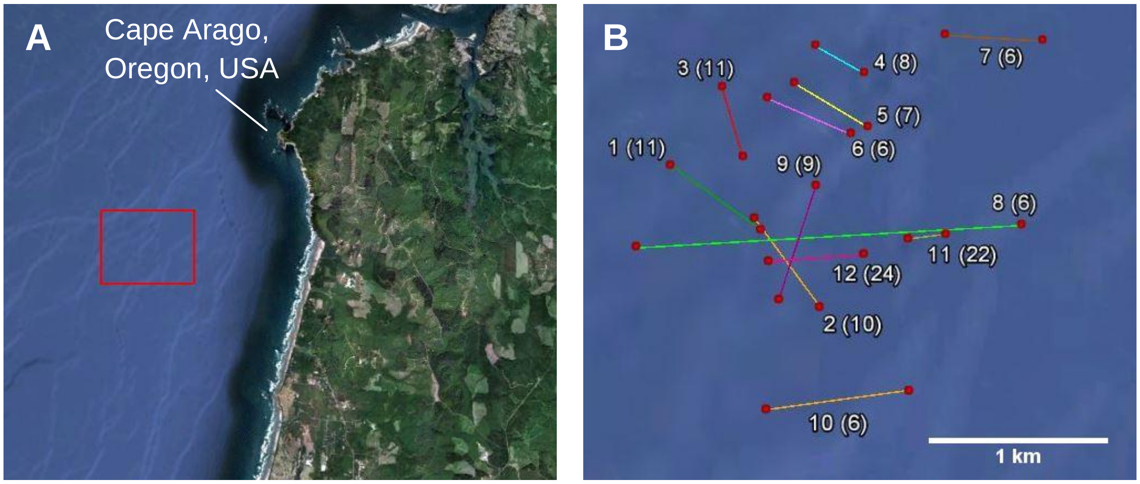

Figure 1: A. Map of the dredging locations conducted about 6.5 km SW of Cape Arago, Oregon, USA. A. Large-scale map; the red box indicates the subset map in 1B. B. Map of dredge locations and lengths. Numbers indicate dredge number while numbers in parentheses indicate the number of species collected in each dredge.

Table 1: A list of subtidal bryozoa in Oregon state waters. Species are listed by taxonomic order and the studies in which they were collected.

Class Gymnolaemata	Collected by:		
Order Cheilostomatida	This Study	Bilderback (unpublished data)	McCauley (1972)
Suborder Malacostegina			
Family Electridae			
Conopeum reticulum (Linnaeus, 1767)		+	
Conopeum tenuissimum (Canu, 1908)		+	
Electra venturaensis (Banta & Crosby, 1994)		+	
Family Membraniporidae			
Membranipora spp.	+		
Membranipora villosa (Hincks, 1880)		+	
Suborder Neocheilostomatina			
Infraorder Flustrina			
Family Bugulidae			
Bugula californica (Robertson, 1905)		+	
Bugula flabellata (J.V. Thompson, 1847)			+
Bugula pacifica (Robertson, 1905)		+	
Dendrobeania curvirostrata (Robertson, 1905)	+		
Dendrobeania laxa (Robertson, 1905)	+	+	
Dendrobeania lichenoides (Robertson, 1910)		+	
Dendrobeania longispinosa (Robertson, 1905)	+		
Dendrobeania murrayana (Bean, 1847)	+		
Family Calloporidae			
Alderina brevispina (O'Donoghue & O'Donoghue, 1926)	+		
Callopora corniculifera (Hincks, 1882)		+	+
Cauloramphus spp.	+		

	Collected by:		
Family Calloporidae (cont.)	This Study	Bilderback (unpublished data)	McCauley (1972)
Cauloramphus californiensis (Soule, Soule, & Chaney,1995)		+	
Cauloramphus echinus (Hincks, 1882)		+	
Copidozoum adamantum (Soule, Soule, & Chaney, 1995)		+	
Tegella circumclathrata (Hincks, 1881)		+	
Tagella horrida (Hincks, 1880)		+	
Family Candidae			
Caberea ellisi (Flemming, 1828)			+
Scrupocellaria diegensis (Robertson, 1905)		+	
Scrupocellaria varians (Hincks, 1882)	+	+	
Tricellaria circumternata (Soule, Soule, & Chaney, 1995)		+	
Tricellaria occidentalis (Trask, 1857)		+	
Family Chaperiidae			
Chaperiopsis patula (Hincks, 1881)		+	
Family Cellariidae			
Cellaria diffusa (Robertson, 1905)	+	+	+
Family Flustridae			
Hincksina alba (O'Donoghue & O'Donoghue, 1923)	+		
Hincksina pallida (Hincks, 1884)	+	+	
Hincksina velata (Hincks, 1881)		+	
Infraorder Ascophora			
Ascophora I	+		
Ascophora II	+		

	Collected by:		
Family Bitectiporidae	This Study	Bilderback (unpublished data)	McCauley (1972)
Neodakaria islandica (Soule, Soule, & Chaney, 1995)	+	+	
Neodakaria umbonata (Soule, Soule, & Chaney, 1995)		+	
Family Bryocryptellidae			
Porella columbiana (O'Donoghue & O'Donoghue, 1923)	+	+	
Porella major (Hincks, 1884)		+	
Porella porifera (Hincks, 1884)		+	
Family Celleporidae			
Celleporina robertsoniae (Canu & Bassler, 1923)	+	+	
Family Cribrilinidae			
Puellina californiensis (Soule, Soule, & Chaney, 1995)		+	
Puellina perplexa (Soule, Soule, & Chaney, 1995)		+	
Reginella hippocrepis (Soule, Soule, & Chaney, 1995)		+	
Family Eurystomellidae			
Integripelta bilabiata (Hincks, 1884)		+	
Family Hippothoidae			
Celleporella cornuta (Busk, 1854)		+	
Celleporella hyalina (Linnaeus, 1767)	+	+	
Family Hippoporinidae			
Hippoporina insculpta (Hincks, 1882)	+		

	Collected by:		
Family Microporellidae	This Study	Bilderback (unpublished data)	McCauley (1972)
Fenestruloides n. sp.	+		
Fenestruloides blaggae (Soule, Soule, & Chaney, 1995)		+	
Microporella catalinensis (Soule, Soule, & Chaney, 1995)		+	
Microporella infundibulipora (Soule, Soule, & Chaney, 1995)		+	
Microporella planata (Soule, Soule, & Chaney, 1995)	+		
Microporella setiformis (O’Donoghue & O’Donoghue, 1923)		+	
Microporella vibraculifera (Hincks, 1883)	+		
Family Myriaporidae			
Myriapora coarctata (M. Sars, 1863)	+		+
Myriozoum tenue (O'Donoghue &O'Donoghue, 1923)	+		+
Family Phidoloporidae			
Phidolopora pacifica (Robertson, 1908)	+		
Rhynchozoon rostratum (Busk, 1855)	+	+	
Family Romancheinidae			
Escharella rugosa (Soule, Soule, & Chaney, 1995)		+	
Escharella rylandi (Soule, Soule, & Chaney, 1995)		+	
Family Schizoporellidae			
Schizoporella unicornis (Johnston in Wood, 1844)	+		
Family Smittinidae			
Dengordonia uniporosa (Soule, Souley, & Chaney, 1995)	+	+	
Parasmittina collifera (Robertson, 1908)	+	+	
Pleurocodonellina longirostrata (Hincks, 1883)	+		

	Collected by:		
Family Smittinidae (cont.)	This Study	Bilderback (unpublished data)	McCauley (1972)
Smittina ovirotula (Soule, Soule, & Chaney, 1995)		+	
Smittoidea prolifica (Osburn, 1952)	+		
Family Teuchoporidae			
Lagenicella neosocialis (Dick & Ross, 1988)		+	
Lagenicella punctulata (Gabb & Horn, 1862)	+		+
Family Trypostegidae			
Trypostega claviculata (Hincks, 1884)	+		
Family Umbonulidae			
Rhamphostomella costata (Lorenz, 1886)		+	
Family Watersiporidae			
Dakaria dawsoni (Hincks, 1883)	+	+	
Order Ctenostomatida			
Family Alcyonidiidae			
Alcyonidium parasiticum (Fleming, 1828)		+	
Family Flusterllidridae			
Flustrellidra spinifera (O'Donoghue & O'Donoghue, 1923)		+	
Class Stenolaemata			
Order Cyclostomatida			
Suborder Articulina			
Family Crisiidae			
Crisia maxima (Robertson, 1910)	+	+	
Crisia occidentalis (Trask, 1857)		+	
Filicrisia franciscana (Robertson, 1910)		+	

	Collected by:		
	This Study	Bilderback (unpublished data)	McCauley (1972)
Suborder Cerioporina			
Family Heteroporidae			
Heteropora pacifica (Borg, 1933)		+	
Family Tretocycloeciidae			
Tetrocycloecia magna (O'Donoghue & O'Donoghue, 1923)	+		
Suborder Cyclostomatida incertae sedis			
Diaperoforma californica (d'Orbigny, 1852)	+	+	
Suborder Fasciculina			
Family Frondiporidae			
Filifascigera fasciculata (Hincks, 1880)	+		
Suborder Rectangulata			
Family Lichenoporidae			
Disporella separate (Osburn, 1953)		+	
Patinella verrucaria (O. Fabricius, 1780)	+		
Suborder Tubuliporina			
FamilyTubuliporidae			
Tubulipora pacifica (Robertson, 1910)		+	
Family Plagiociidae			
Plagioecia patina (Lamarck, 1816)	+	+	
Family Stomatoporidae			
Stomatopora I	+		
Stomatopora granulata (Milne-Edwards, 1838)	+		

Figure 2: Character analysis of a putative new species of *Fenestruloides* as compared with its sister taxa, *Fenestruloides morrisae* and *Fenestruloides umbonata* (Soule, Soule, and Chaney 1995).

Character	***Fenestruloides n. sp.***	***Fenestruloides morrisae***	***Fenestruloides umbonata***
Zoid length and range	577.6 ± 47.5 µm 510-700 µm	- 620-740 µm	- 670-700 µm
Zooid width and range	528.4 ± 55.5 µm 430-620 µm	- 500-650 µm	- 600 µm
Zooid L/W ratio	1.13-1.18	1.14-1.24	1.12-1.17
Zooid with gymnocyst rim	+	-	-
Frontal pore number on zooid without ovicell	87-94	61-77	~99
Frontal pore diameter	23.1± 2.4 µm	20-25 µm	20-25 µm
Number of frontal pore rows between aperture proximal rim and ascopore	2-(3)	2-4	3+
Number of marginal rows of frontal pores	3-5	3-6	3
Ascopore length	16.4±3.7 µm	50 µm	30-40 µm
Ascopore width	35.9±3.3 µm	60-80 µm	60-70 µm
Ascopore L/W ratio	0.46	0.63-0.83	0.50-0.57
Ascopore width/frontal pore diameter ratio	1.49-1.60	3.89	2.43-2.55
Ascopore opening	wide (5.4±1.0 µm), between uvulate process & rim	narrow (3.7 µm), between uvulate process & rim	narrow (3.1 µm), almost closed, between uvulate process and rim
Ascopore denticulation	weakly denticulate	strongly denticulate	strongly denticulate
Ascopore with rim	-	+	+

Table 2: Continued

Character	*Fenestruloides* *n. sp.*	*Fenestruloides* *morrisae*	*Fenestruloides* *umbonata*
Avicularium	-	-	rare
Umbo	-	-	+
Aperture length and range	126.9±7.8 µm 117-138 µm	120-130 µm	150 µm
Aperture width and range	156.5± 7.4 µm 147-167 µm	120-140 µm	180-210 µm
Aperture L/W ratio	0.80-0.83	0.92-1.0	0.71-0.83
Aperture spines	2-3	3-4	1-2
Ovicell	Inflated, 20 ridged with chevron at proximal margin	Flattened, smooth, imperforate except 1-2 closed pores	Inflated, rugose with crossed ribs at proximal margin
Ovicell rimmed by gymnocyst	+	-	+
Ovicell length	386.6±158.1 µm	215.6 µm	196.5 µm
Ovicell width	342.3±21.1 µm	292.5 µm	211.5 µm
Ovicell L/W ratio	1.12	0.74	0.93

Glossary of Terms

Bottom Trawling: A method of fishing where a net is trawled (dragged) along the ocean floor.

Disjunct Population: A population that is geographically isolated from other populations of that species.

Dredge: A type of subtidal collection method where a net or box is dragged along the sea floor to collect samples.

Ecosystem Based Management (EBM): A management practice which strives to include all ecologically important species and functions rather than a few select species.

Functional Extinction: A species that is not physically absent from an ecosystem, but is no longer able to fulfill its ecological role.

Marine Detritus: Small, undissolved bits of organic matter.

Marine Reserve: A protected area in which no extractive activities are permitted (with the occasional exception of scientific studies).

Ocean Acidification: Refers to the decreasing pH of the world's oceans; caused by the uptake of atmospheric carbon dioxide (CO_2).

Operational Taxonomic Unit (OTU): A sampling technique where organisms are grouped into units based on taxonomic relationships. These groups are later used as units of analysis.

Paleozoic Era: From 544 million to 230 million years ago.

Phytoplankton: Microscopic, free-floating marine algae.

Rarefaction Curve: An analytical technique to assess **species richness** through sampling. Theoretically, as more samples are conducted, fewer new species will be collected and the curve will begin to asymptote. Once this happens a site's species richness can be estimated.

Redundant Species: Species which share one or more ecological function.

SEM: Acronym for a scanning electron microscope.

Sessile: Refers to animals that typically do not move (i.e. barnacles, muscles, etc.)

Size Refuge: Refers to the theory that if an organism (or colony) grows large enough, it will no longer be suitable prey for predators. Also can refer to refuge from damage or competition.

Source Population: Populations that provide large amounts of larvae that then dispurse (ant. Sink population).

Species Richness: A measure of the absolute number of species. Ecosystems with five species have less species richness than an ecosystem with ten different species.

Subtidal: The area of the ocean that is below the low-tide line and rarely (if ever) exposed.

Suspension Feeder: Animals that feed by collecting food (in the form of **marine detritus** or holoplankton) which is suspended in the water column.

Glossary of Taxonomy

Adventitious Avicularium: A type of **avicularium** located on the surface of a zooid.

Ancestrula: The founding **zooid** of a colony formed by larval metamorphosis; gives rise to all other zooids of a colony via asexual budding.

Androzooid: A male **zooid**.

Aperture: Opening in body wall through which **lophophore** is extended.

Areolar Pore: A marginal pore in the frontal wall in ascophorans

Ascopore: The calcified opening of the **ascus** in ascophoran cheilostomes.

Ascus: A flexible sac proximal to aperture in ascophoran cheilostomes, opened by calcified **ascopore**; functions hydrostatically in the extension and retraction of lophophore.

Autozooid: A feeding **zooid**.

Avicularium (pl. avicularia): A type of **heterozooid** with a reduced **polypide** but strong muscles used to operate a modified **operculum**; used for colony defense to prevent overgrowth.

Cancellus (pl. cancelli): In some cyclostomes, a calcified tube (either extrazooidal or of a **kenozooid**); often enclose **zooids**; horizontal laminae may close cancelli leading to secondary calcification (as in *Tetrocycloecia*).

Colony Form: The general shape, morphology, and budding pattern of a colony

Condyle: One of a pair of **denticles** on which **operculum** hinges.

Cryptocyst: In some anascan cheilostomes, a calcified frontal shelf separated from the frontal membrane by a ceolom.

Dentical: A general term for suboral teeth in an aperture.

Distal: Referring to the side furthest from the **ancestrula**, typically end of the **zooid** bearing the **aperture**.

Fenestrate: A net-like or lacy colony form, as in *Phidolopora* (syn. Reticulate)

Frontal Budding: Budding of **zooids** from the **frontal wall** in gymnolaemates; produces multilaminate colonies.

Frontal Wall: A calcified body wall connecting **lateral** and **transverse walls**; pertaining to the **aperture**-bearing side of the colony.

Funicular tissue: Tissue connecting the **polypide** of a **zooid** with those of its neighbors; spans **zooecia** via communication pores; involved in the transport of nutrients and messages among members of a colony.

Gonozooid: A brood chamber in stenolaemates; a type of **heterozooid**.

Gymnocyst Rim: Where **gymnocyst** and outer cuticle join; a narrow, flat shelf along the edge of the gymnocyst.

Gymnocyst: In anascan cheilostomes, the calcified **frontal wall** touching the outer cuticle.

Heterozooid: A specialized **zooid** (ant. **autozooid**); see **androzooid, avicularium, gonozooid, kenozooid, ovicell, vibraculum.**

Internode: Section bearing **autozooids** in erect, articulated colonies.

Interzooecial avicularium: A type of **avicularium** located between **zooids**; typically smaller than and communicates with neighboring zooids.

Kenozooid: A **heterozooid** lacking a **polypide** and usually an **aperture** and muscles; serves as a spacer (structural support) for a colony or a modified anchoring device.

Lateral Wall: Vertical walls between adjacent rows of cheilostomes; aligned with direction of colony growth.

Lophophore: A cone-shaped ring of ciliated tentacles surrounding the mouth of a **zooid**; used for feeding.

Lyrula: Subopercular **dentical**, often anvil-shaped, on aperture's proximal side.

Multiserial: Colony form in which zooids are budded **distally** in multiple rows (*Dendrobeania*).

Ooeciostome: The **gonozooid's** aperture in stenolaemates through which larvae are released; shape typically unique to species.

Operculum: A generally uncalcified flap covering the **aperture**; hinges on **condyles**.

Ovicell: The brood chamber in cheilostomes; often globular in shape.

Penduncualte Avicularium: Referers to a stalked **avicularium**, as in *Dendrobeania*.

Peristome: A calcified collar or tubular prolongation around the **aperture** in some cyclostomes.

Polypide: The tissues and organs of a **zooid** that are periodically broken down and replace; includes tentacles, tentacle sheath, musculature, and nerve ganglion.

Reticulate: A net-like or lacy colony form, as in *Phidolopora* (syn. Fenestrate).

Scutum: In anascans, a flattened, shield-like spine overhanging the zooid's frontal membrane.

Sinus: A slit or notch on an **aperture's** proximal edge in some cheliostomes.

Transverse Wall: In gymnolaemates, a vertical wall separating a zooid from its proximal and distal neighbors.

Umbo (pl. umbones): a raised, knob-like protrusion on a zooid's **frontal wall**; often proximal to aperture or on ovicell.

Uniserial: Colony form in which **zooids** are budded distally in a single row, as in *Stomatopora*.

Vibraculum (pl. vibracula): A modified **avicularium** mandible with a long, whip-like structure; unique to cheilostomes.

Zooecium (pl. zooecium): The skeletal remains of a **zooid**.

Zooid: A general term for any individual (member) of a colony, formed by asexual budding; specific types are referred to by a number of prefixes (see **androzooid**, **autozooid**, **gonozooid**, **heterozooid**, and **kenozooid**).

Appendix A

Scanning electron micrographs of bryozoans collected by this study

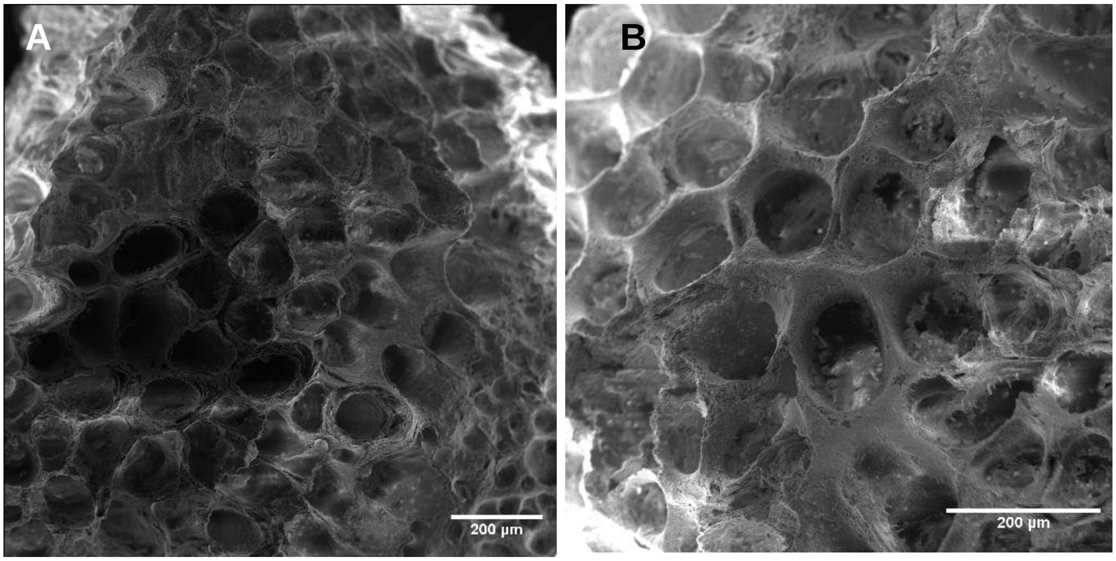

Plate 1: *Alderina brevispina*. A. View of a partial colony. Frontal membranes have been removed. B. View showing minute spines on zooids' lateral walls.

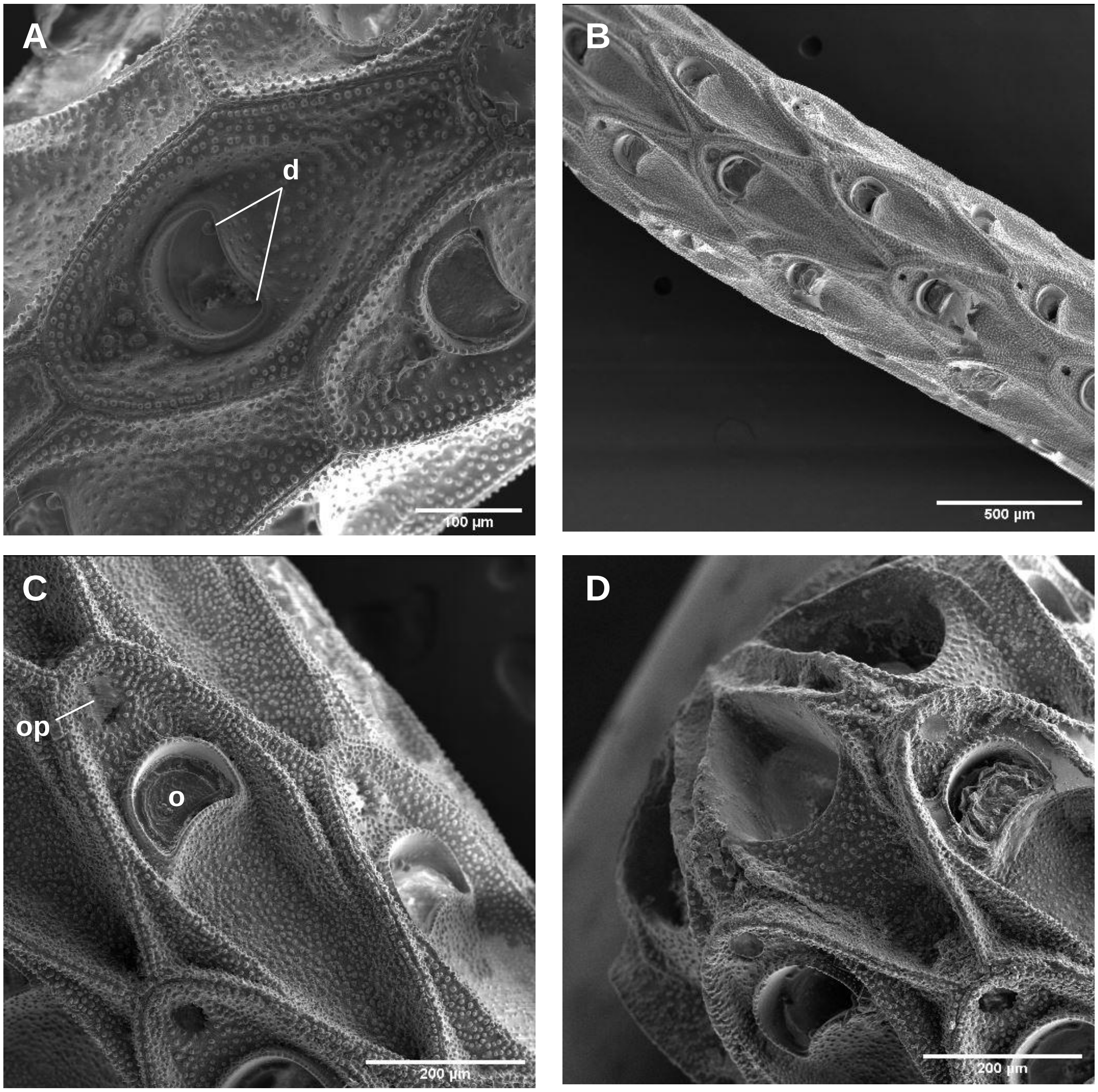

Plate 2: *Cellaria diffusa*. A. Diamond-shaped zooid showing a pair of denticles (d) on the proximal edge of the aperture. Distal rim to lower left. B. Part of an internode with ovicell pores visible distal to zooid apertures. C. Diamond-shaped zooid, showing operculum (o) and partially covered ovicell pore (op). D. Distal end of a branch showing newly forming zooids.

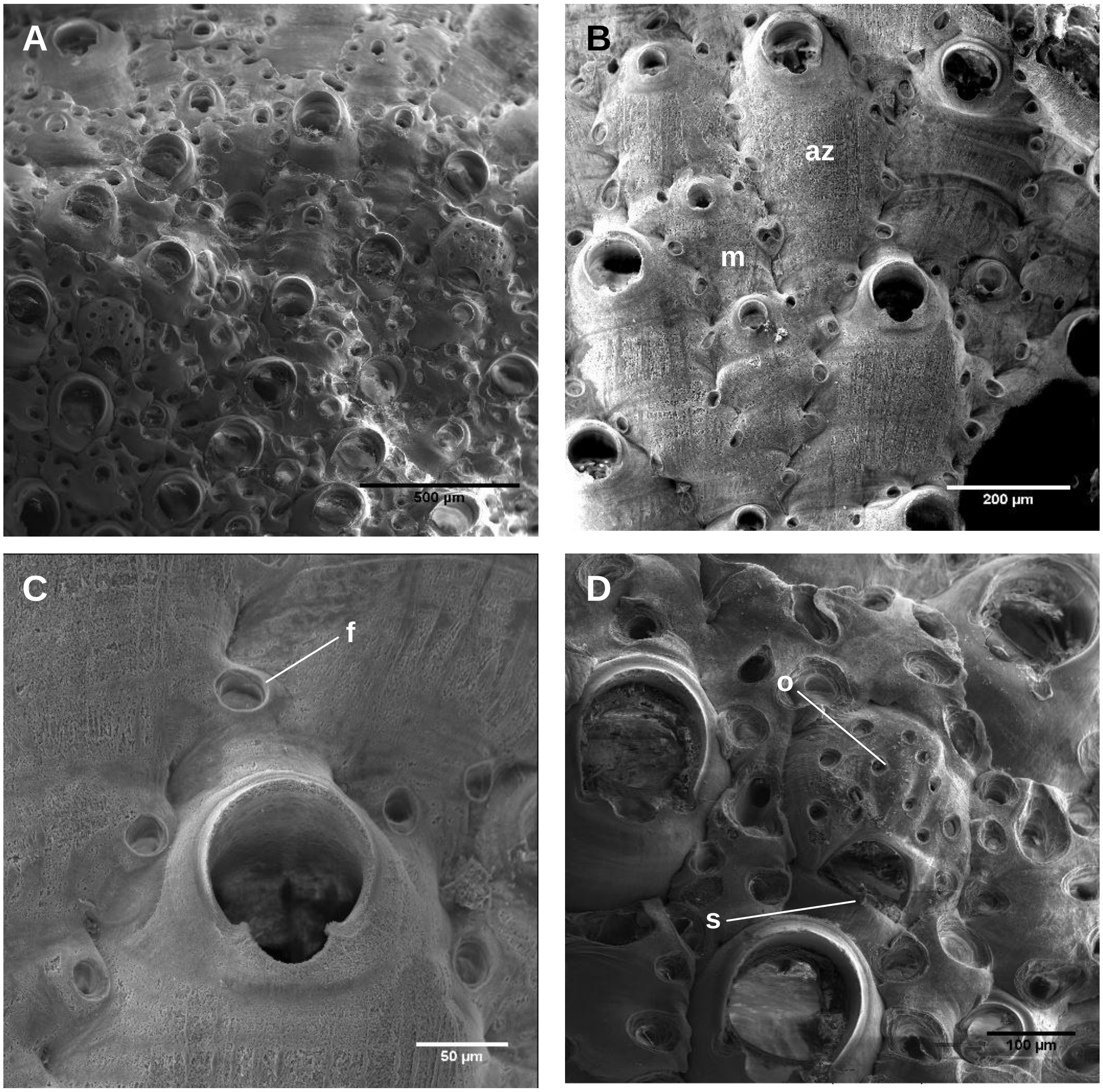

Plate 3: *Celleporella hyalina.* A. Colony with large autozooids surrounded by smaller male zooids. B. Autozooids (az) surrounding smaller male zooids (m). C. Detail of autozooid aperture and flaring fenestraea (f) at zooid margin. D. Detail of ovicell (o) with a shallower, wider sinus (s) than surrounding zooids.

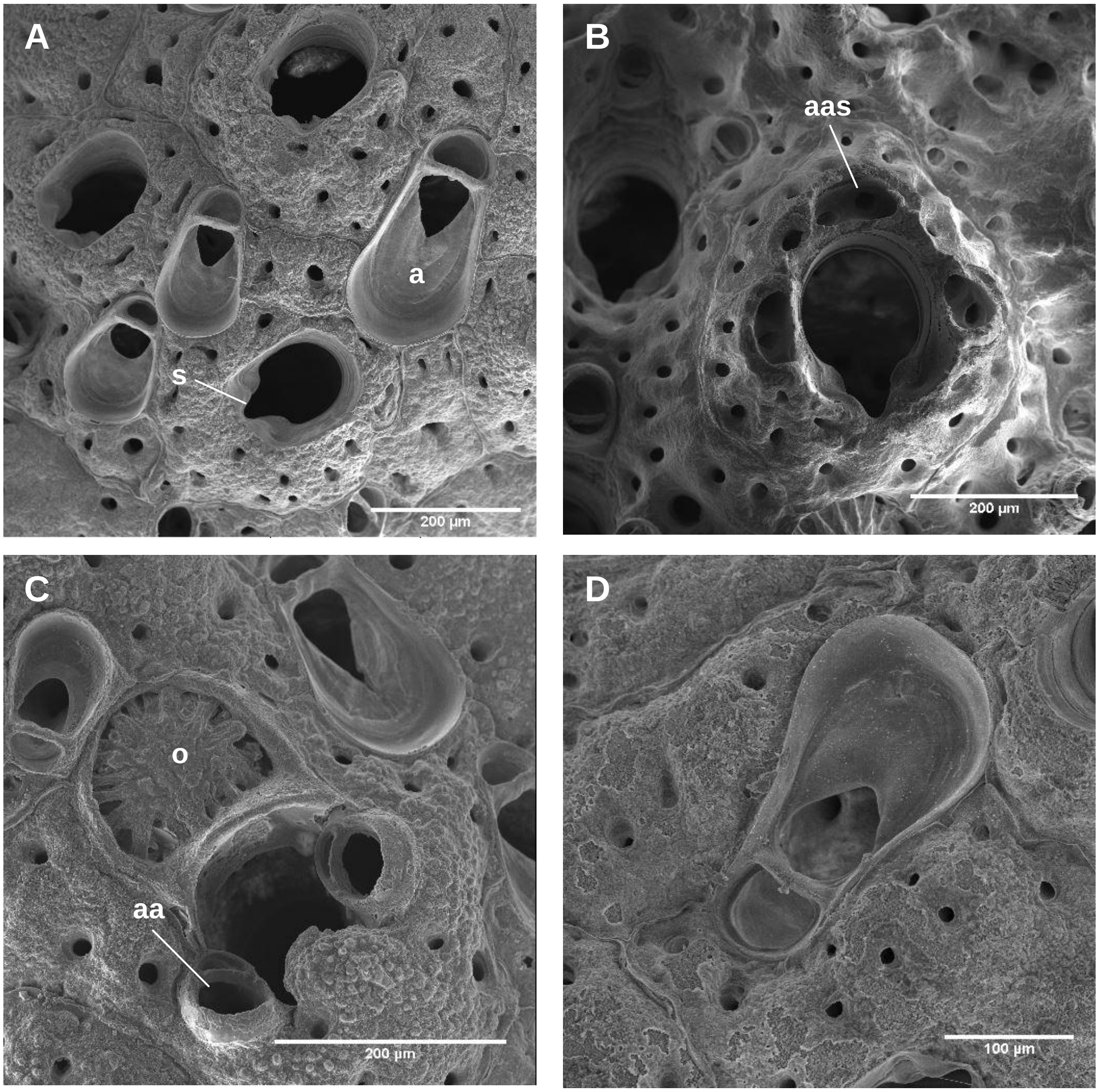

Plate 4: *Celleporina robertsoniae*. A. Zooids with deep sinus (s) and no avicularia around aperture. Large, spatulate interzooecial avicularia (a). B. Zooid with three adventitious avicularia scars (aas). C. Ovicell (o) with three adventitious avicularia (aa). D. Detail of large, spatulate interzooecial avicularium.

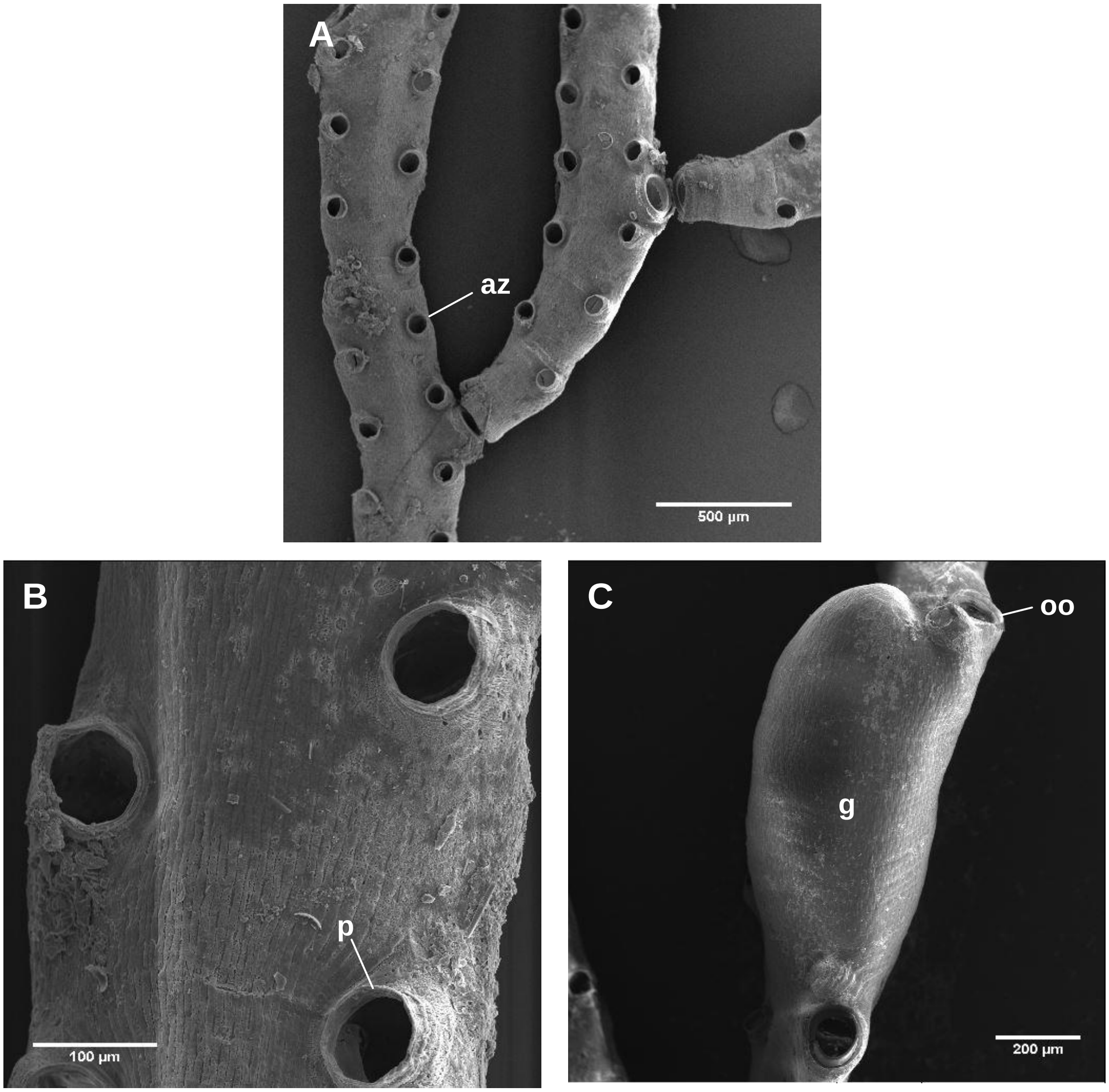

Plate 5: *Crisia maxima*. A. Colony form showing many autozooids (az) and internodes. B. Detail of autozooids and raised peristomes (p). C. Detail of gonozooid (g) and ooeciostome (oo).

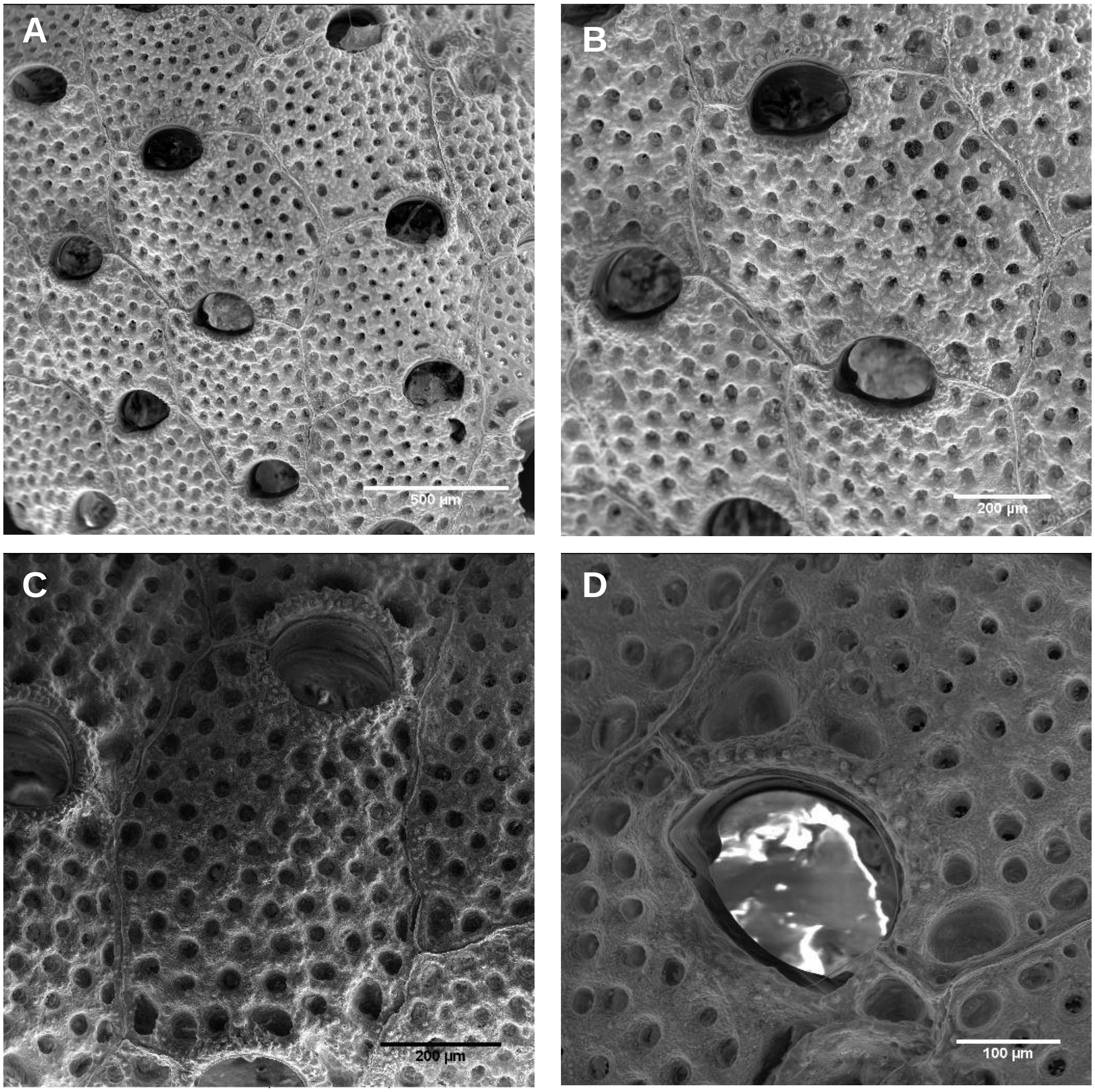

Plate 6: *Dakaria dawsoni*. A. Colony form, reticulate frontal wall of zooids, D-shaped or oval apertures. B-C. Enlarged, zooids with granules and pores. D. Detail of aperture, juncture in transverse walls on either side of aperture.

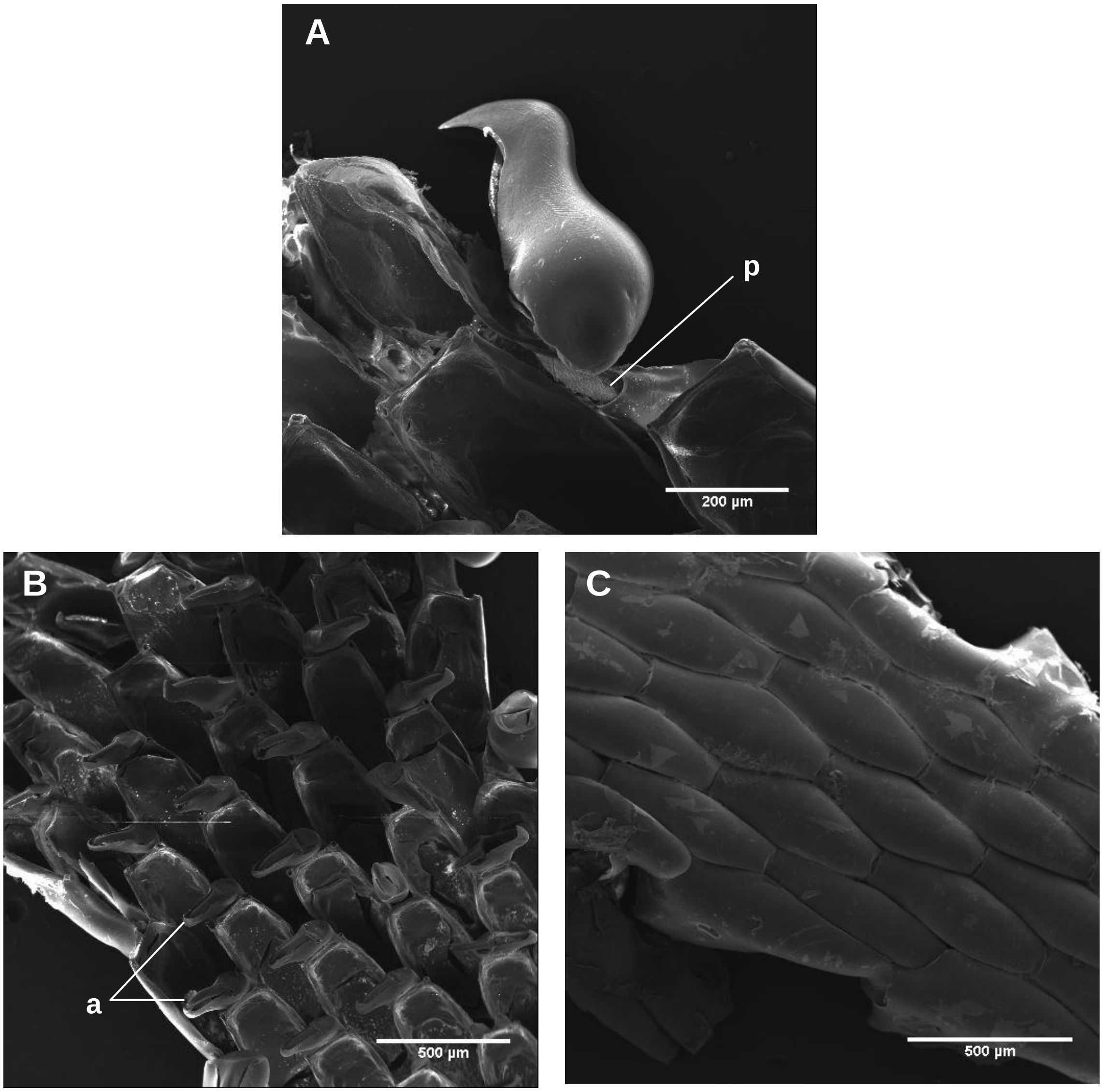

Plate 7: *Dendrobeania curviostrata*. A. Detail of giant, hooked interzooecial penduculate avicularium on outer margin, note pedestal (p). B. Colony branch with giant, hooked avicularia on dorsal end of zooids (a), spine scars on zooids' distal corners. C. Ventral side of colony, straight distal and ventral walls, curved lateral walls.

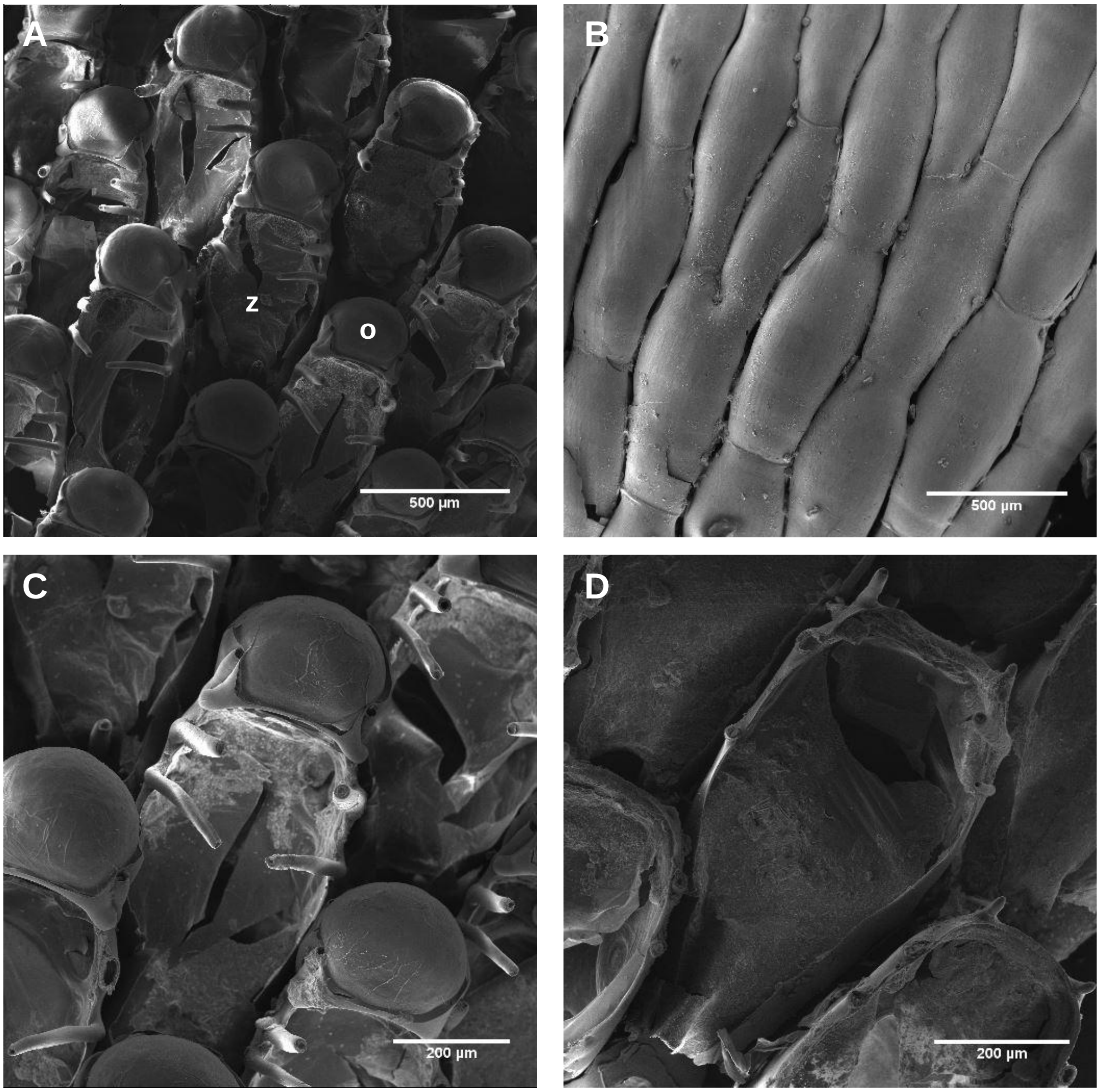

Plate 8: *Dendrobeania laxa*. A. Colony frond with ovicells (o) and autozooids (z). B. Ventral side of colony, straight distal and ventral walls, curved lateral walls. C. Detail of zooid and ovicell; note the wrinkled surface of ovicells and long spines curving over frontal wall. D. Enlarged zooid with basal portions of spines.

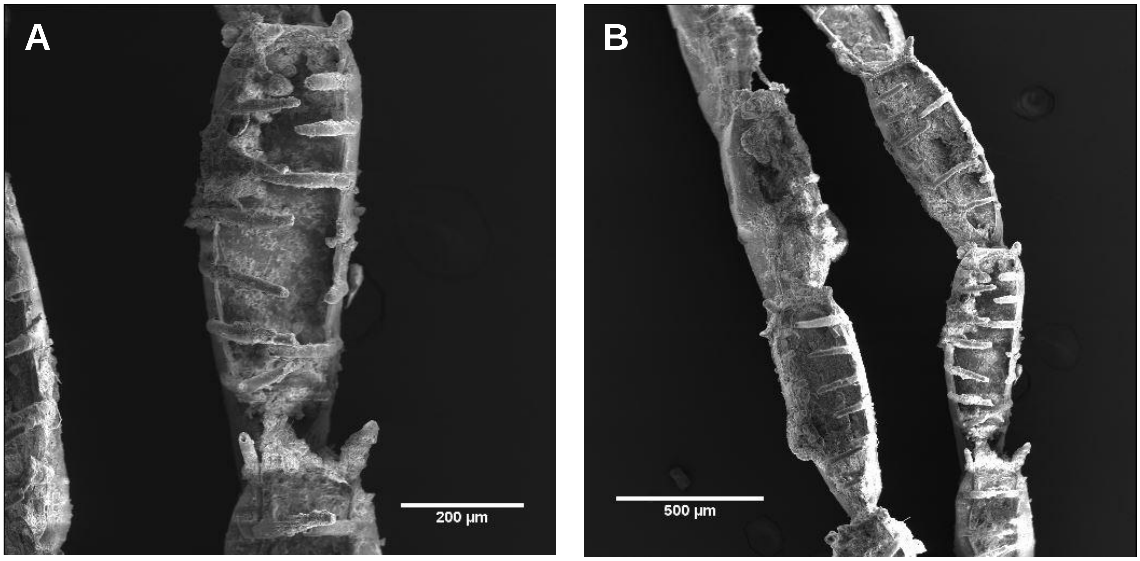

Plate 9: *Dendrobeania longispinosa*. A. Zooid, long spines curving over zooid's front; frontal membrane removed.   B. Columns of zooids; colony branches often composed of zooids in serial, six or more rows.

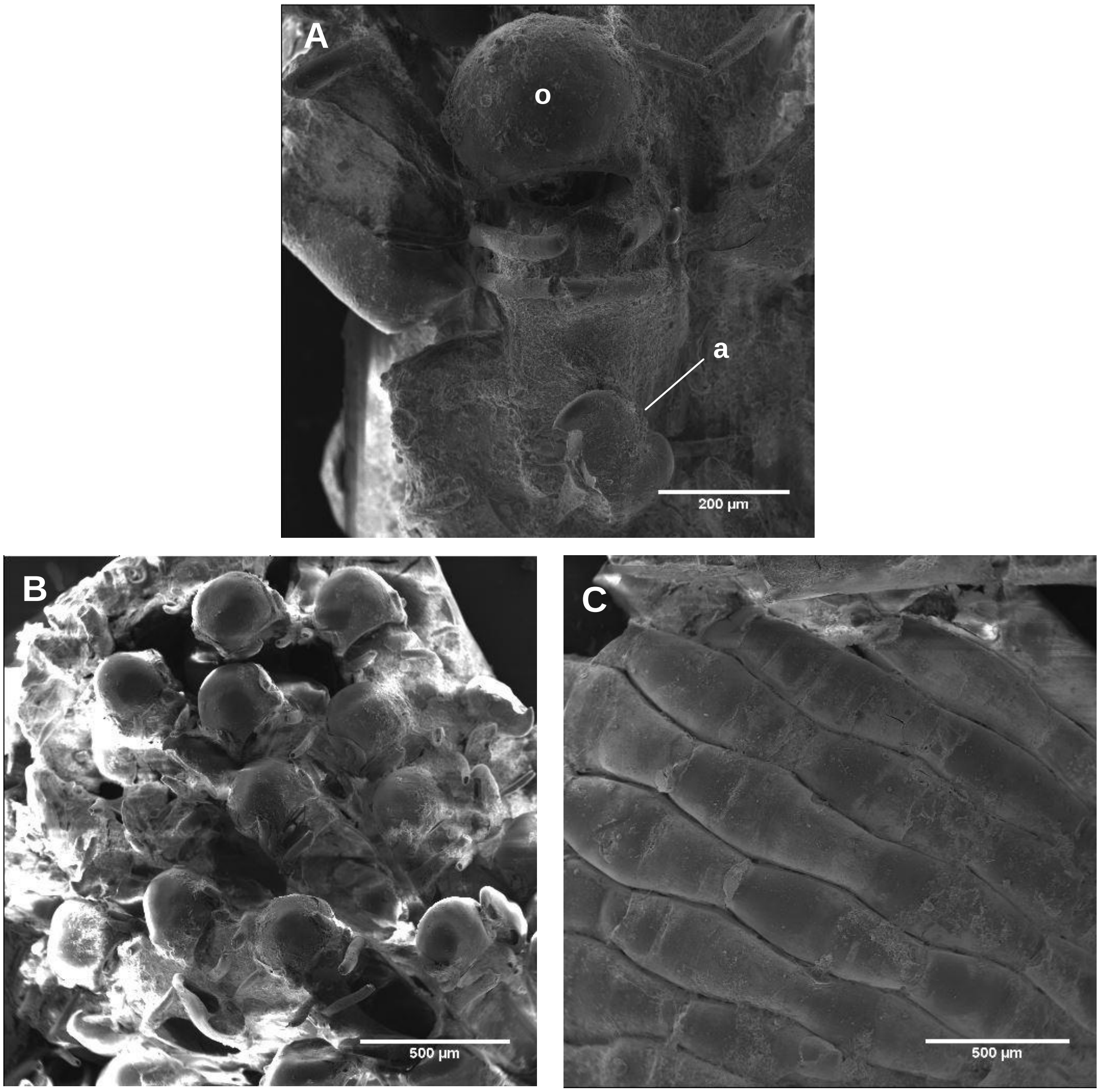

Plate 10: *Dendrobeania murrayana*. A. Detail of uncleaned ovicell (o) and giant, hooked avicularium (a). B. Colony frond; note the long spines curving over the frontal. C. Ventral side of colony, straight distal and ventral walls, curved lateral walls.

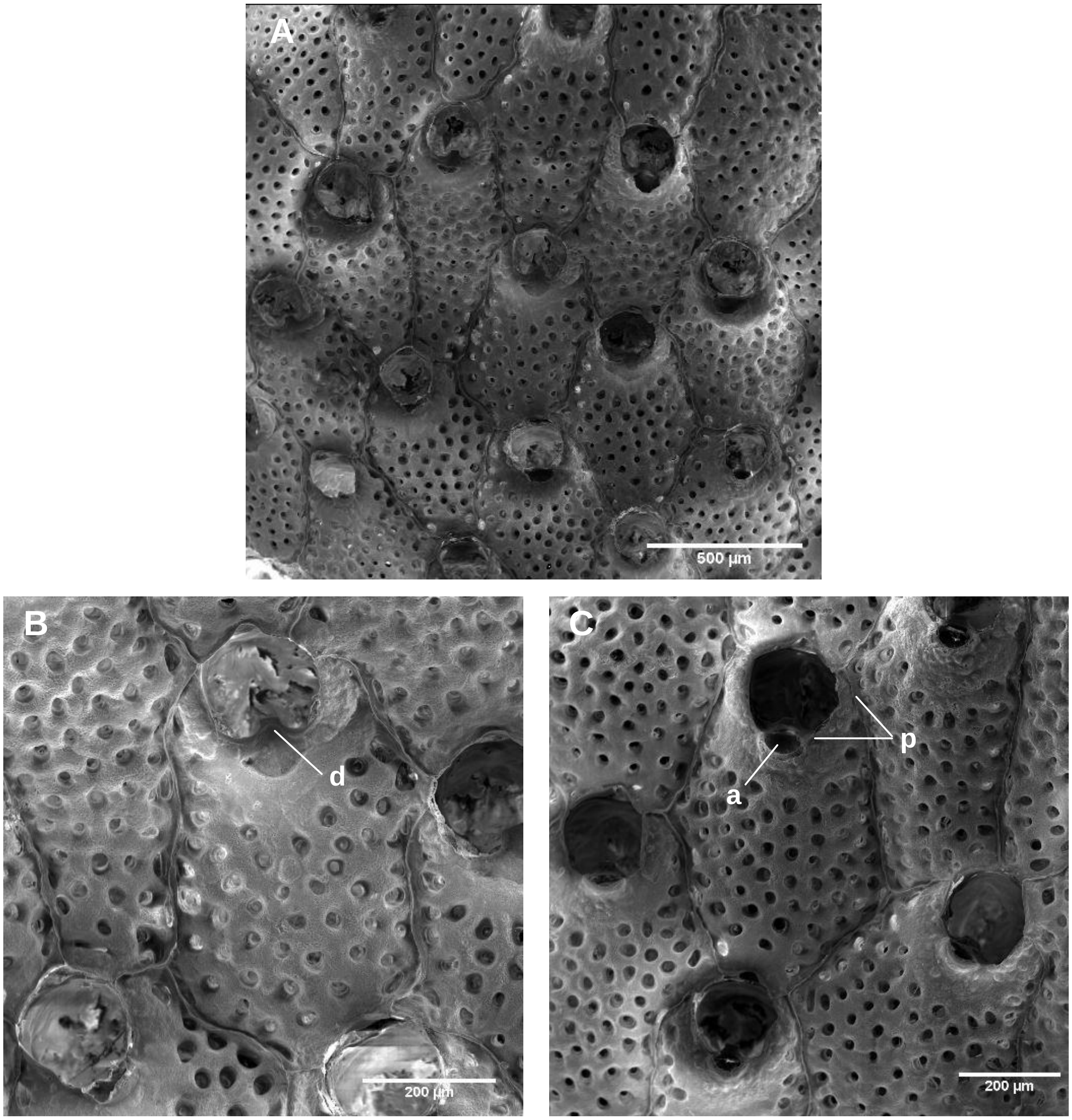

Plate 11: *Dengordonia uniporosa*. A. Colony overview, frontal pores on zooids. B. Enlarged zooid, narrow anvail-shaped lyrula denticle (d). C. Zooids with avicularium (a) embedded within peristome (p).

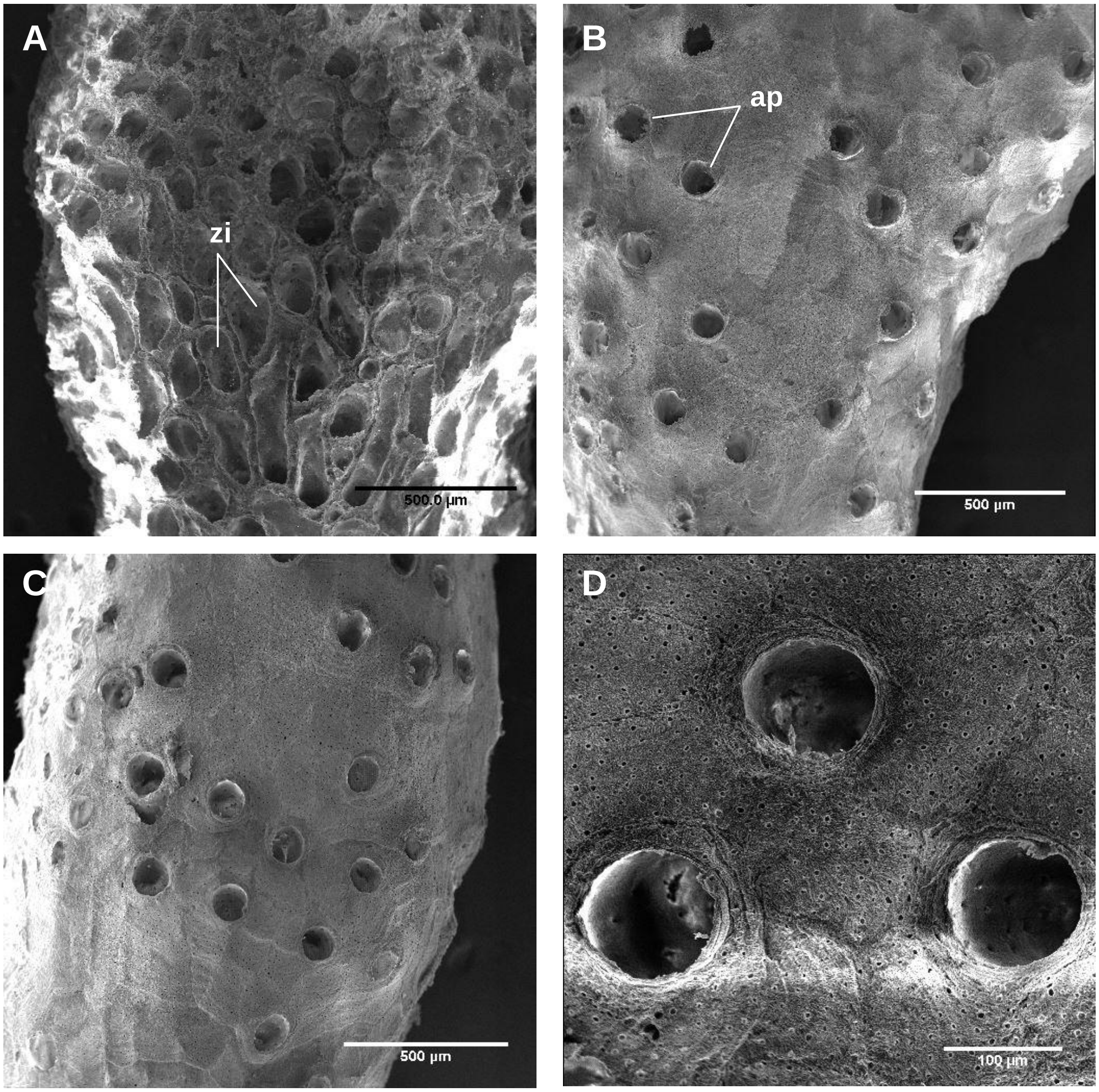

Plate 12: *Diaperoforma californica*. A. Colony overview with frontal walls removed to show zooid interior (zi). B-C. Colony overview, zooid apertures (ap). D. Enlarged apertures and frontal walls.

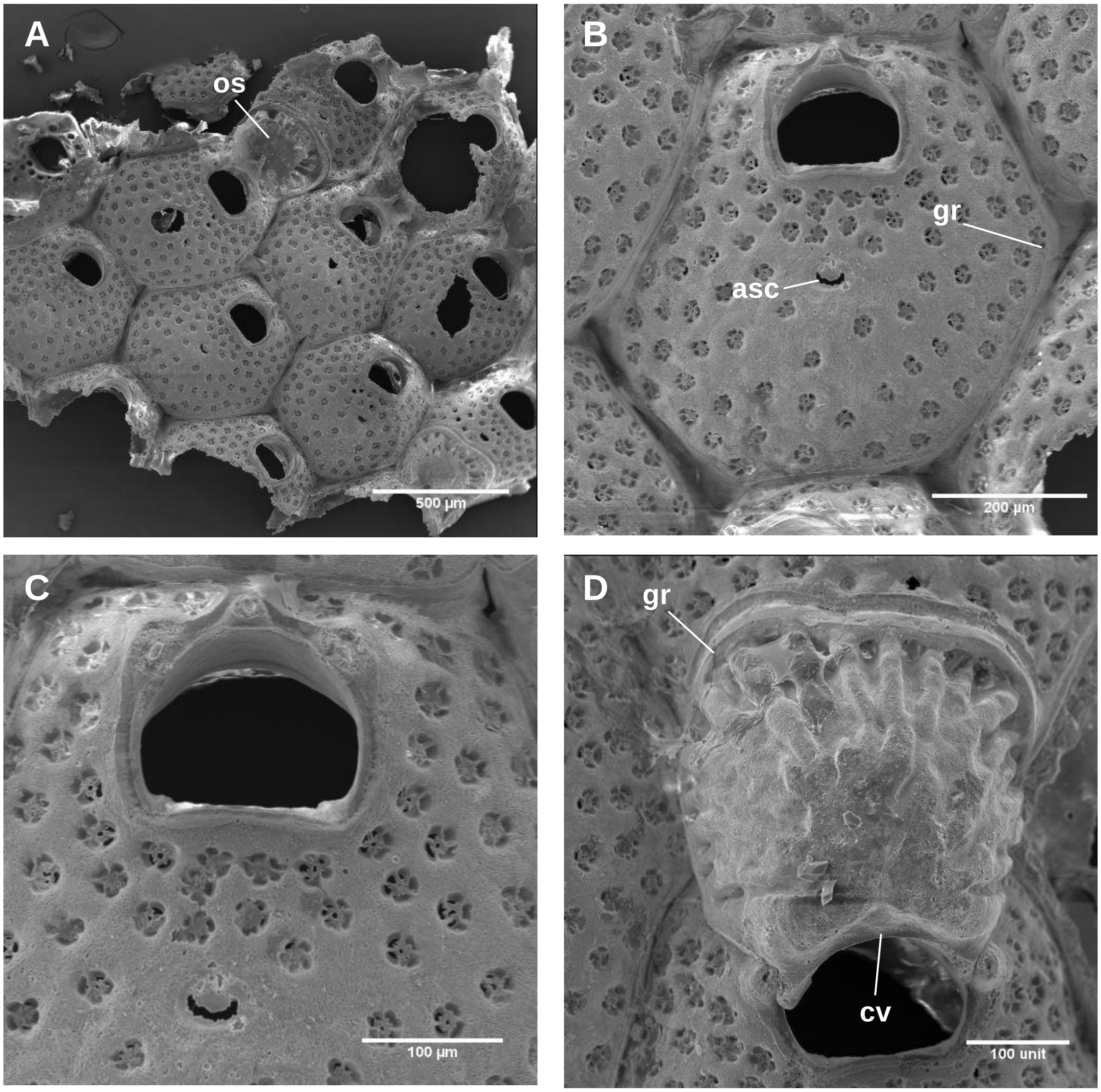

Plate 13: *Fenestruloides n. sp.*. A. Colony view, frontal pores, D-shaped aperture with 2-3 distal spines, ovicell scars (os). B. Enlarged zooid showing narrow ascopore (asc), distribution of frontal pores, and gymnocyst rim (gr). C. Enlarged aperture; weakly denticulate ascopore, three spine scars distal to aperture, 2-3 rows of frontal pores between aperture and ascopore. D. Detail of ovicell showing gymnocyst rim (gr), chevron (cv) at proximal margin, and ovicell ridges; ovicell imperforate with marginal pores, two spines on proximal corners.

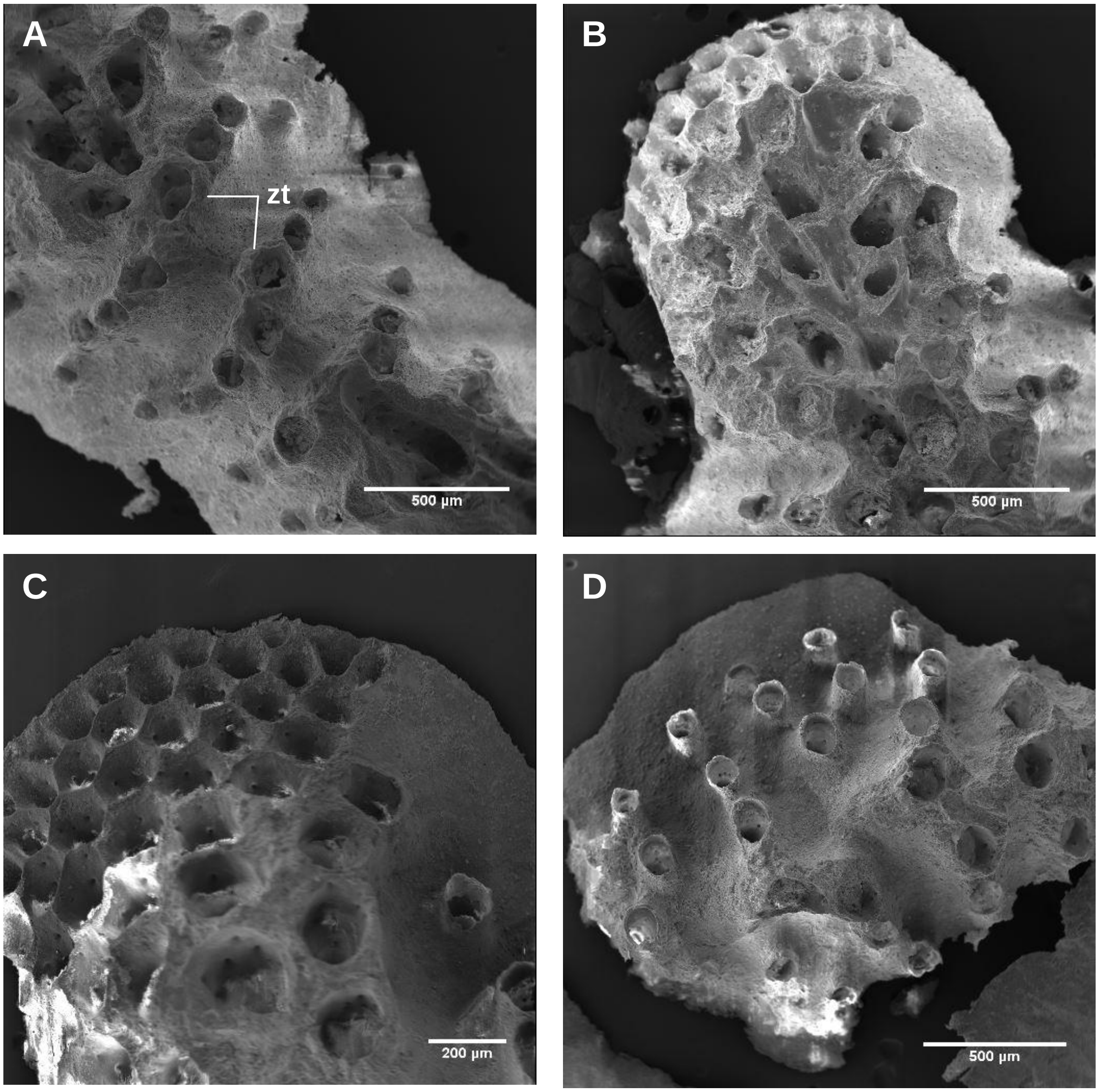

Plate 14: *Filifascigera fasciculata*. A. Colony overview showing bunched zooecial tubes (zt); constant basal width. B. Distal branch end, wider than established branches. C-D. Distal branch end, showing developing zooids and zooecial tubes.

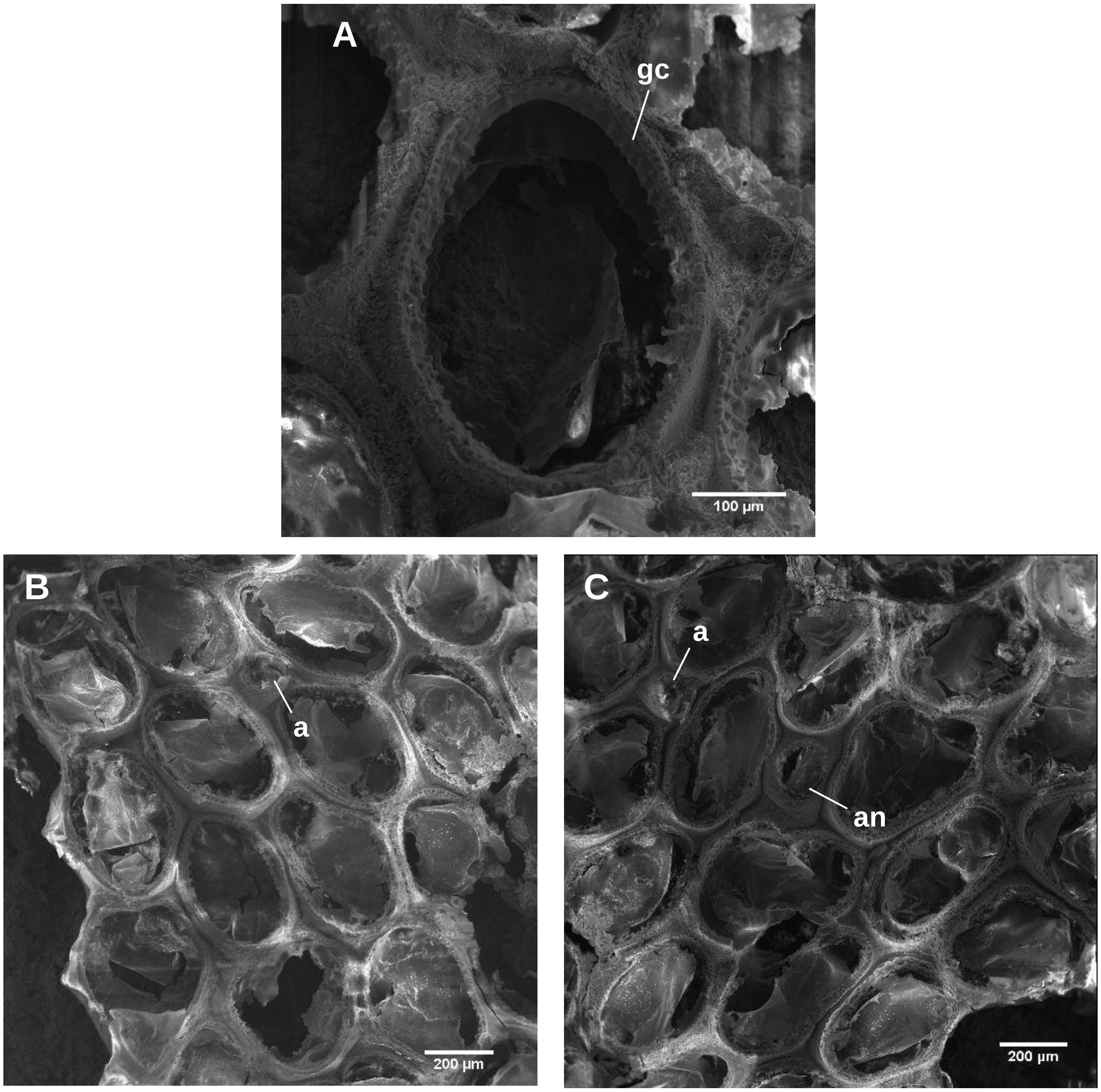

Plate 15: *Hincksina alba*. A. Enlarged zooid showing granular cryptocyst (gc). B-C. Colony overview showing interzooecial avicularia (a) ancestrula (an); note generally oval-shaped zooids.

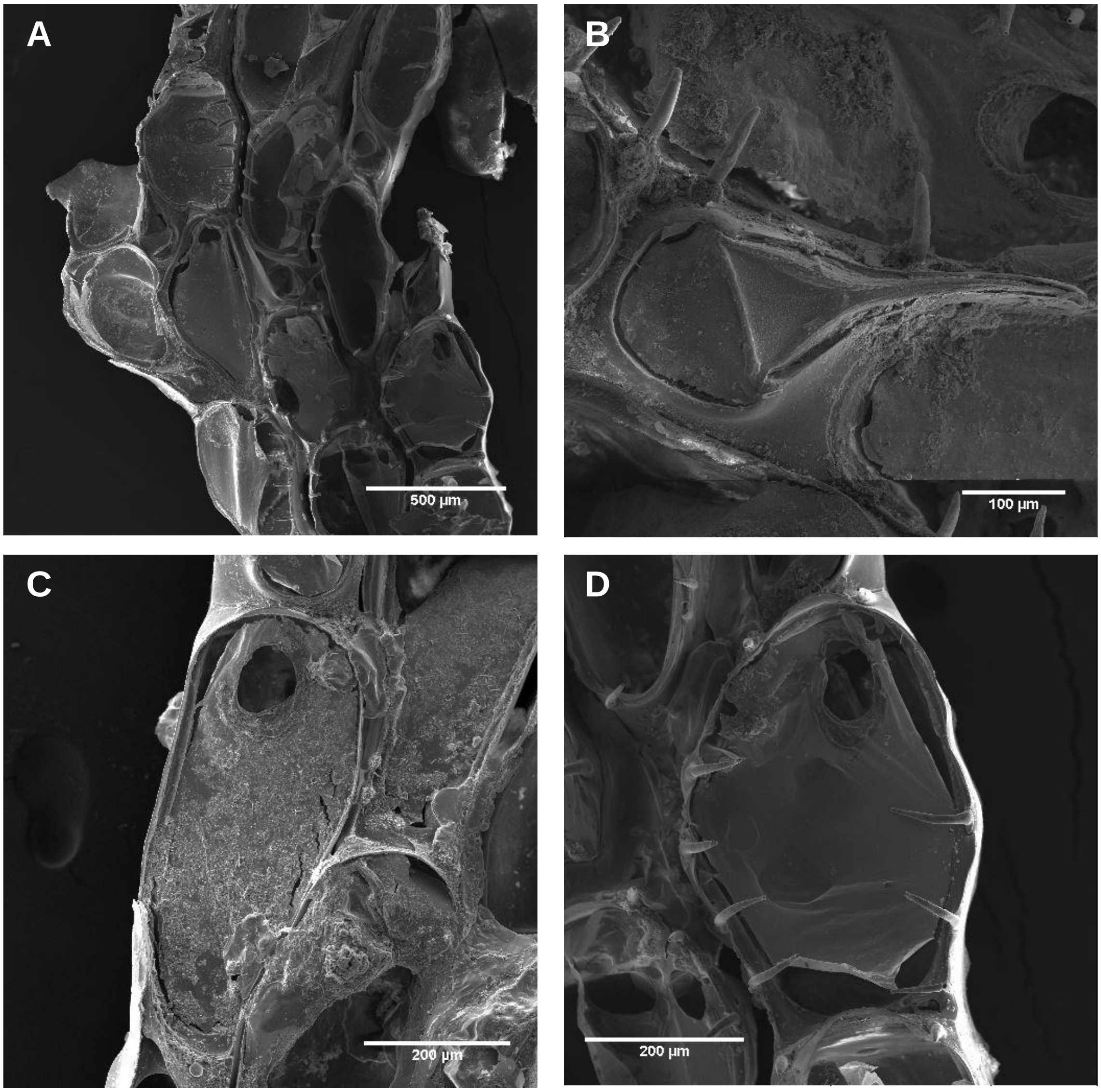

Plate 16: *Hincksina pallida*. A. Colony view with oval zooids; some missing frontal membrane. B. Interzooecial avicularium between transverse walls. C-D. Enlarged zooids. C. Uncleaned spineless zooid. D. Cleaned spiny zooid.

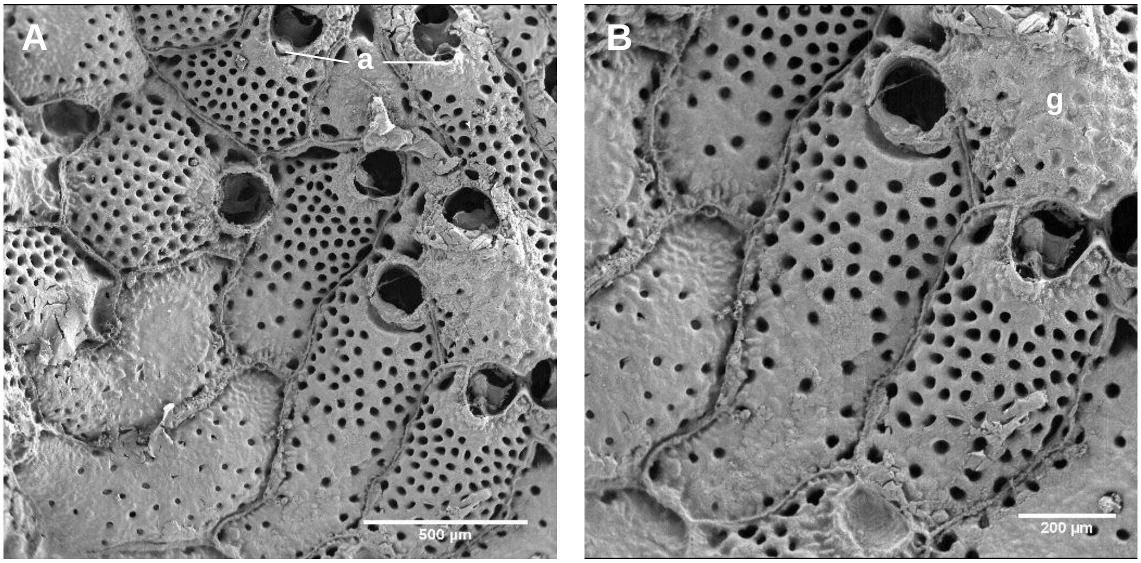

Plate 17: *Hippoporina insculpta*. A. Colony view with avicularium (a) proximal to aperture. B. Enlarged, showing frontal pores and partially removed gymnocyst (g).

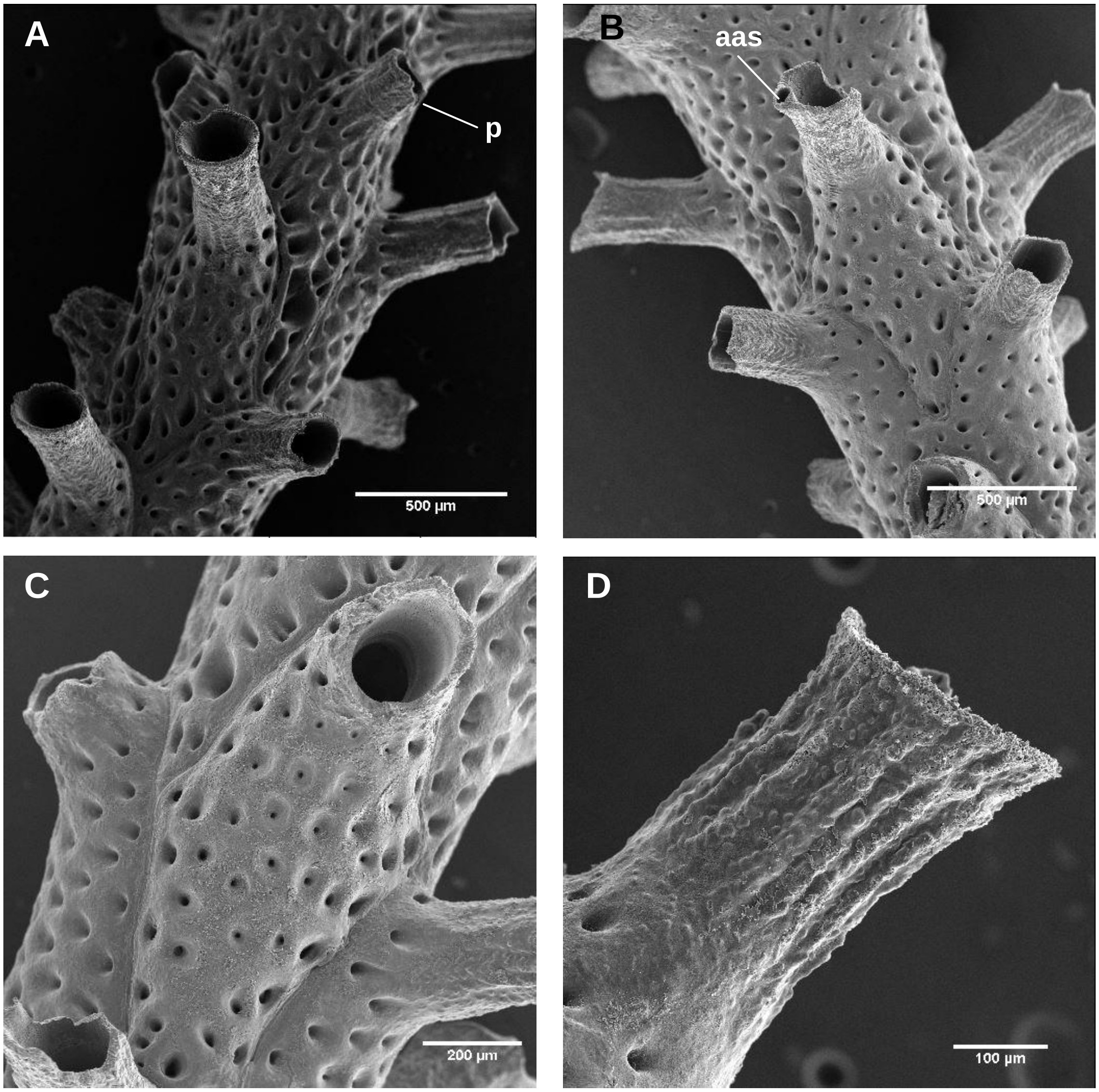

Plate 18: *Lagenicella punctulata*. A-B. Branching, erect colony with porous frontal walls and spine-like peristomes (p). B. Adventitious avicularium scar (aas) on peristome tip. C. Enlarged zooid, showing reticulate, porous frontal wall and broken peristome. D. Enlarged side-view of peristome resembling fused spines and showing the fluted tip.

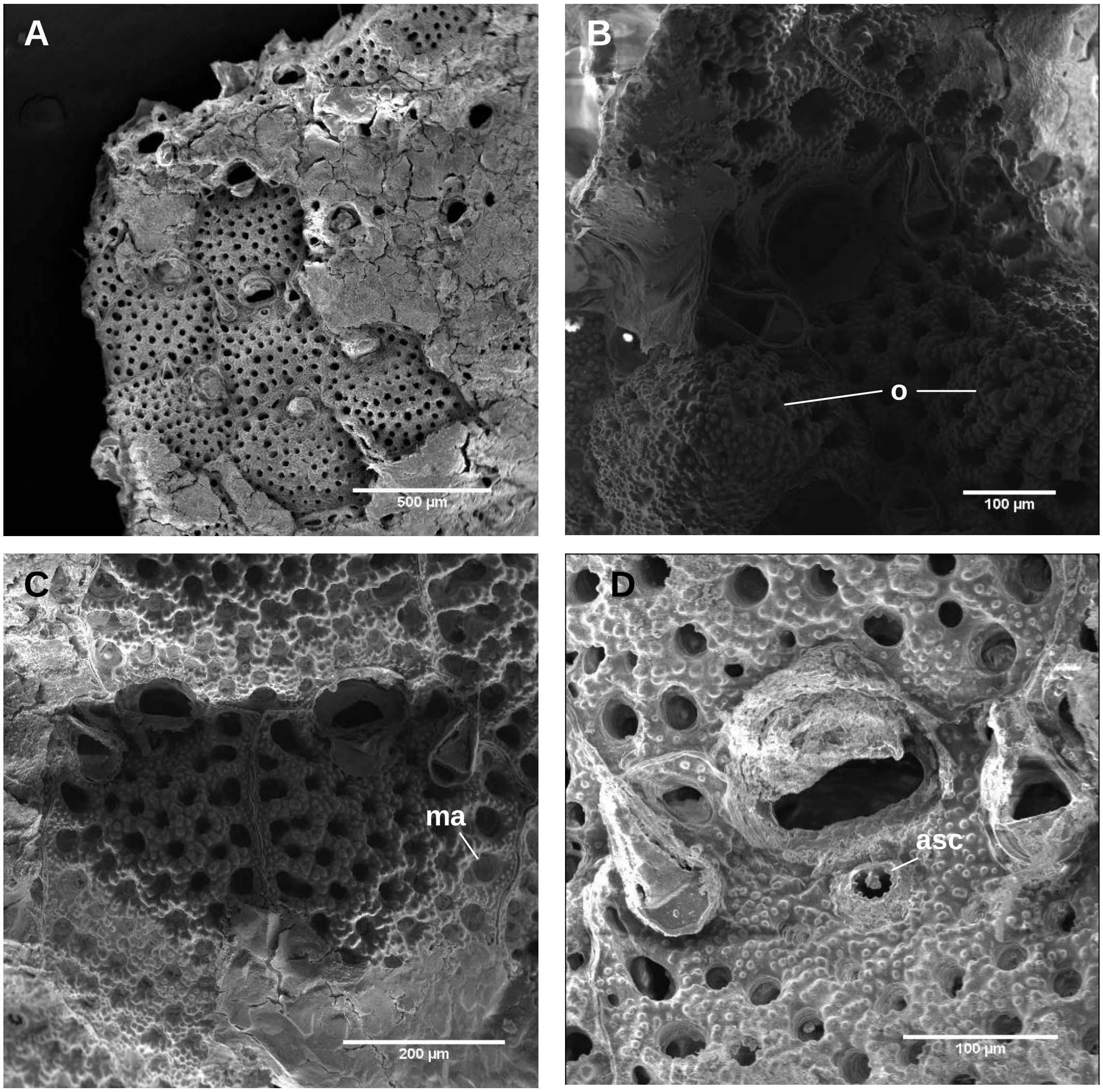

Plate 19: *Microporella planata*. A. Overview showing several cleaned zooids and numerous uncleaned zooids. B-C. Enlarged zooids, showing interstitial avicularia (paired or unpaired) and granulate, porous surface; marginal areolae (ma). B. Porous ovicell (o); imperforate top with ribbed, porous sides. D. Enlarged D-shaped aperture, showing parired avicularia, ascopore (asc), and granular texture.

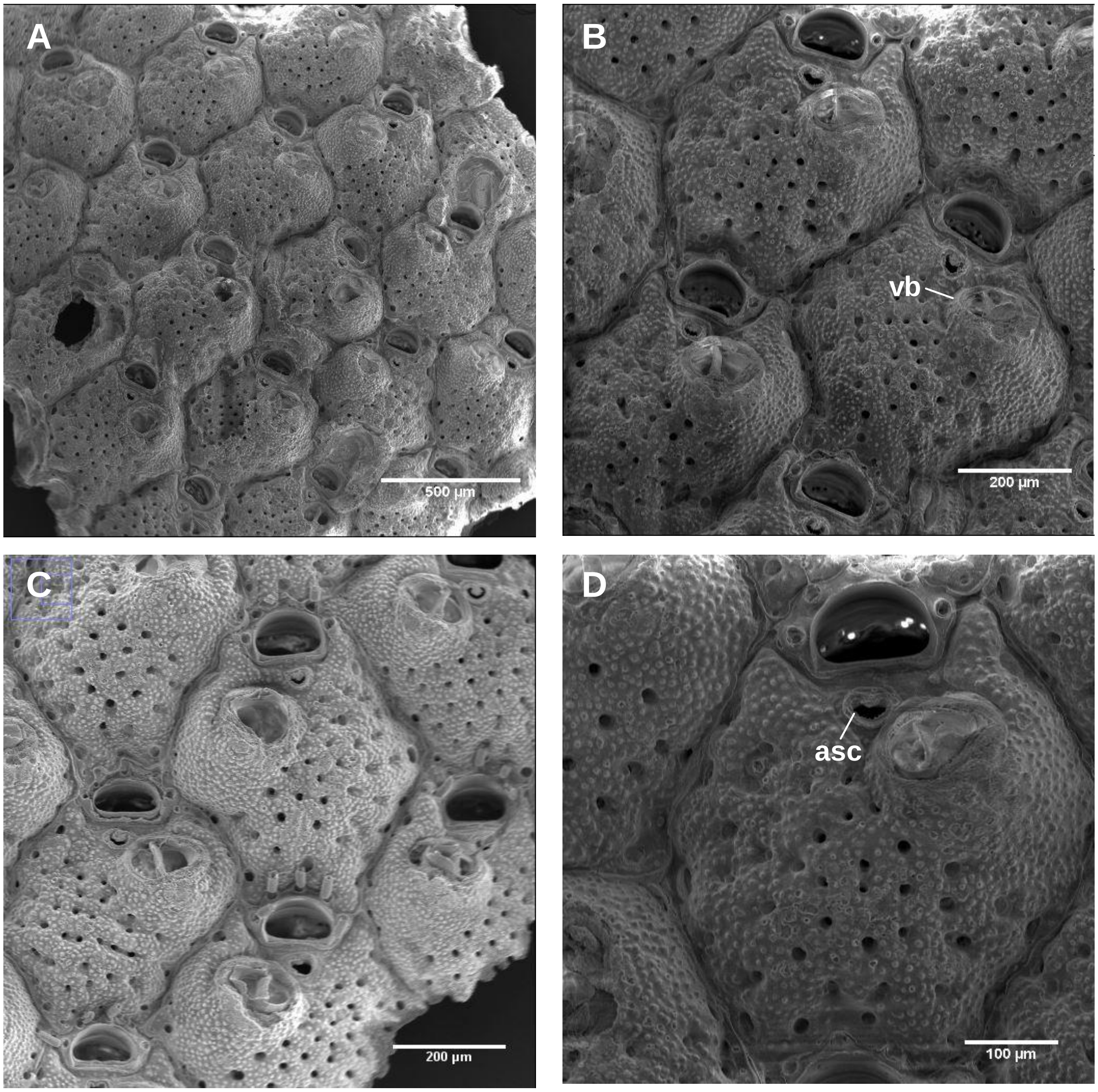

Plate 20: *Microporella vibriculifera*. A. Overview of numerous zooids. B-C. Enlarged zooids, showing granulate, porous frontal wall, 4-5 spines on distal end of aperture, and vibracular base (vb). D. Enlarged view of frontal wall, ascopore (asc), and vibracular base (vibracular whips were removed during cleaning).

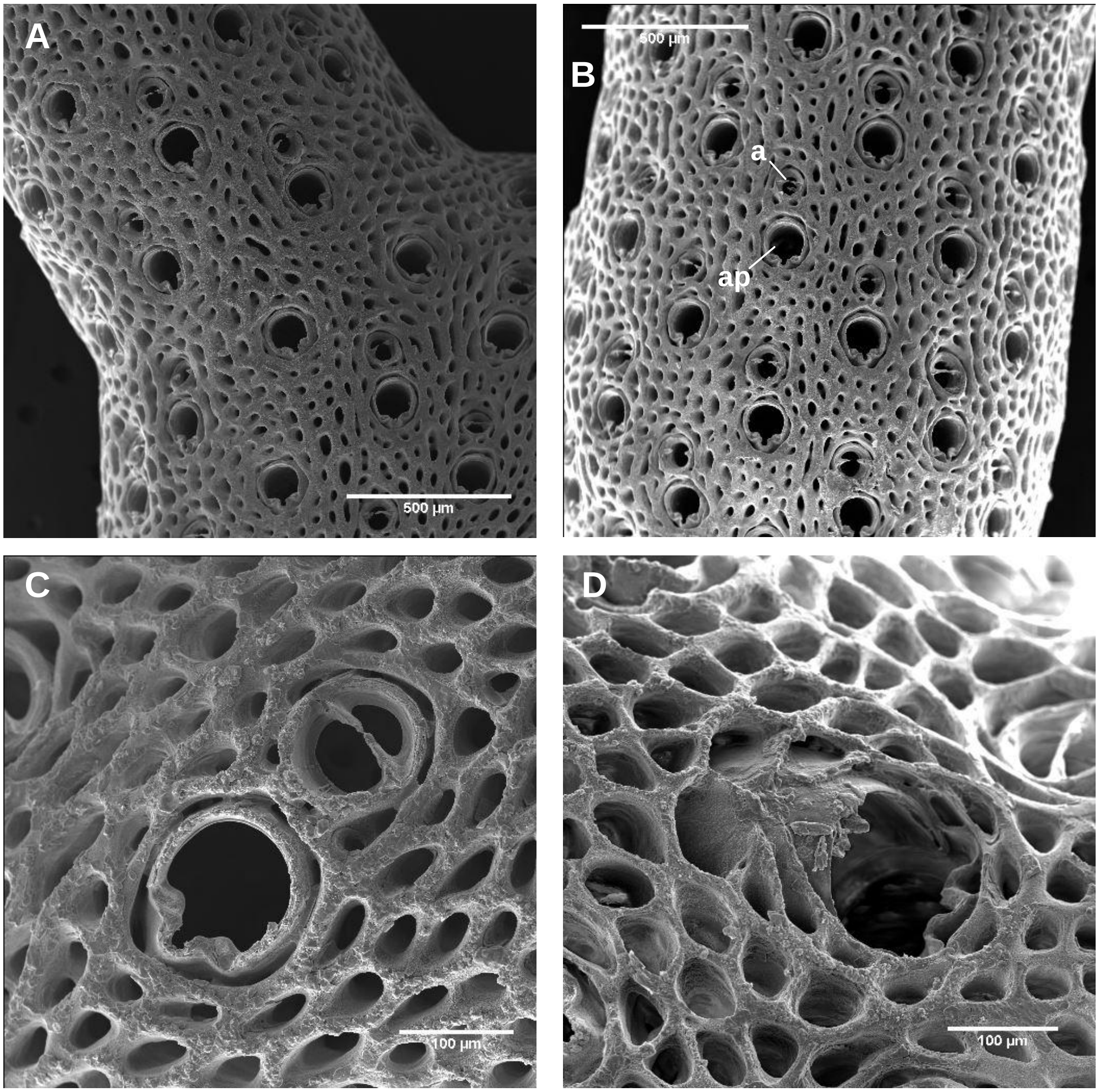

Plate 21: *Myriapora coarcata*. A-B. Colony form showing numerous zooids and avicularia. A. Showing branch division. B. Showing large avicularia (a) on midline, distal to zooid apertures (ap). C. Enlarged aperture and large aviculariaum. D. Detail of ovicell.

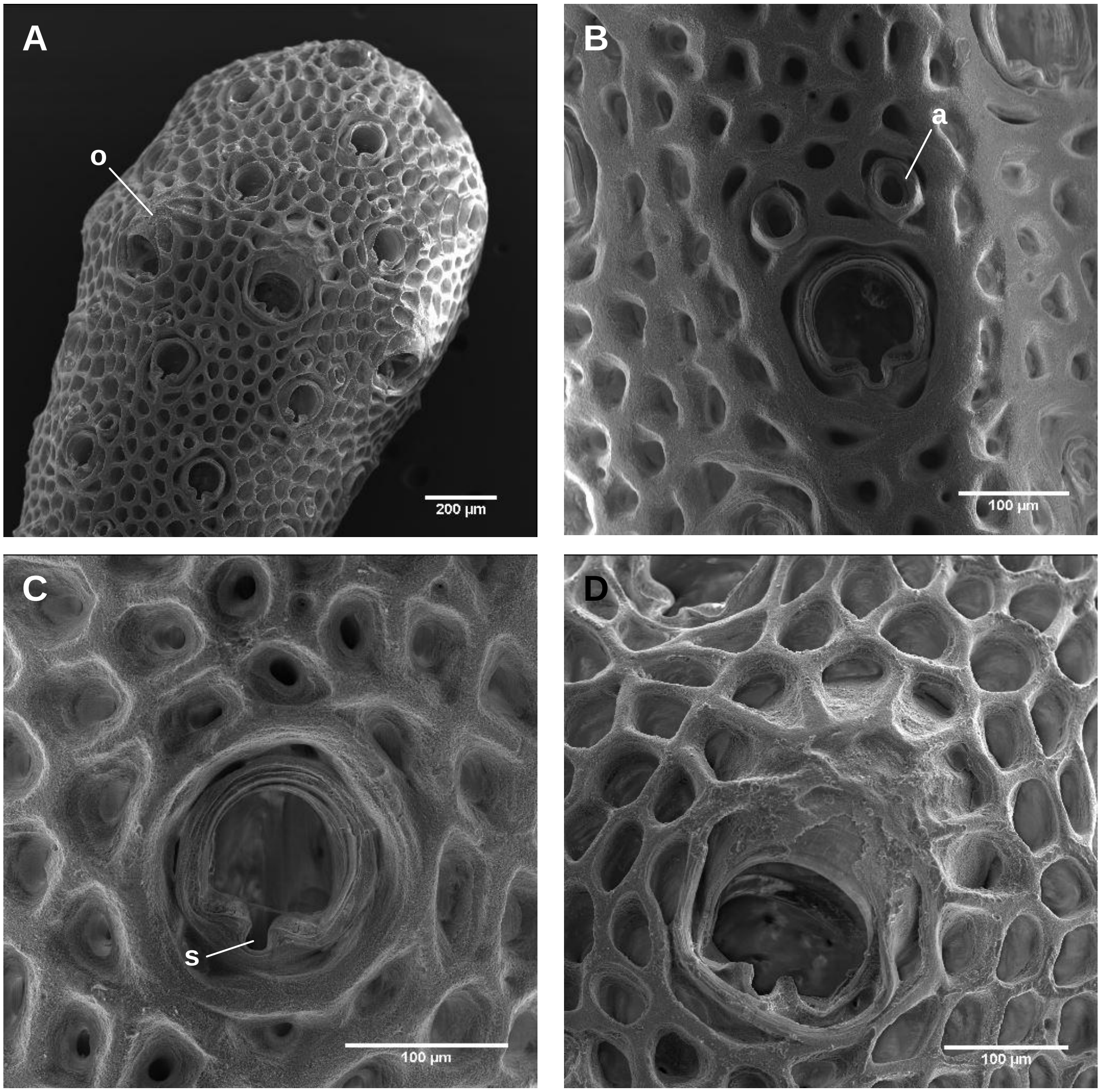

Plate 22: *Myriozoum tenue*. A. Distal tip of colony branch showing zooids with paired avicularia; ring of ovicells (o) just proximal to distal tip. B. Enlarged zooid with paired, avicularia (a). C. Zooid with no avicularia, showing deep, pinched sinus (s). D. Detail of ovicell; note shallower, wider sinus.

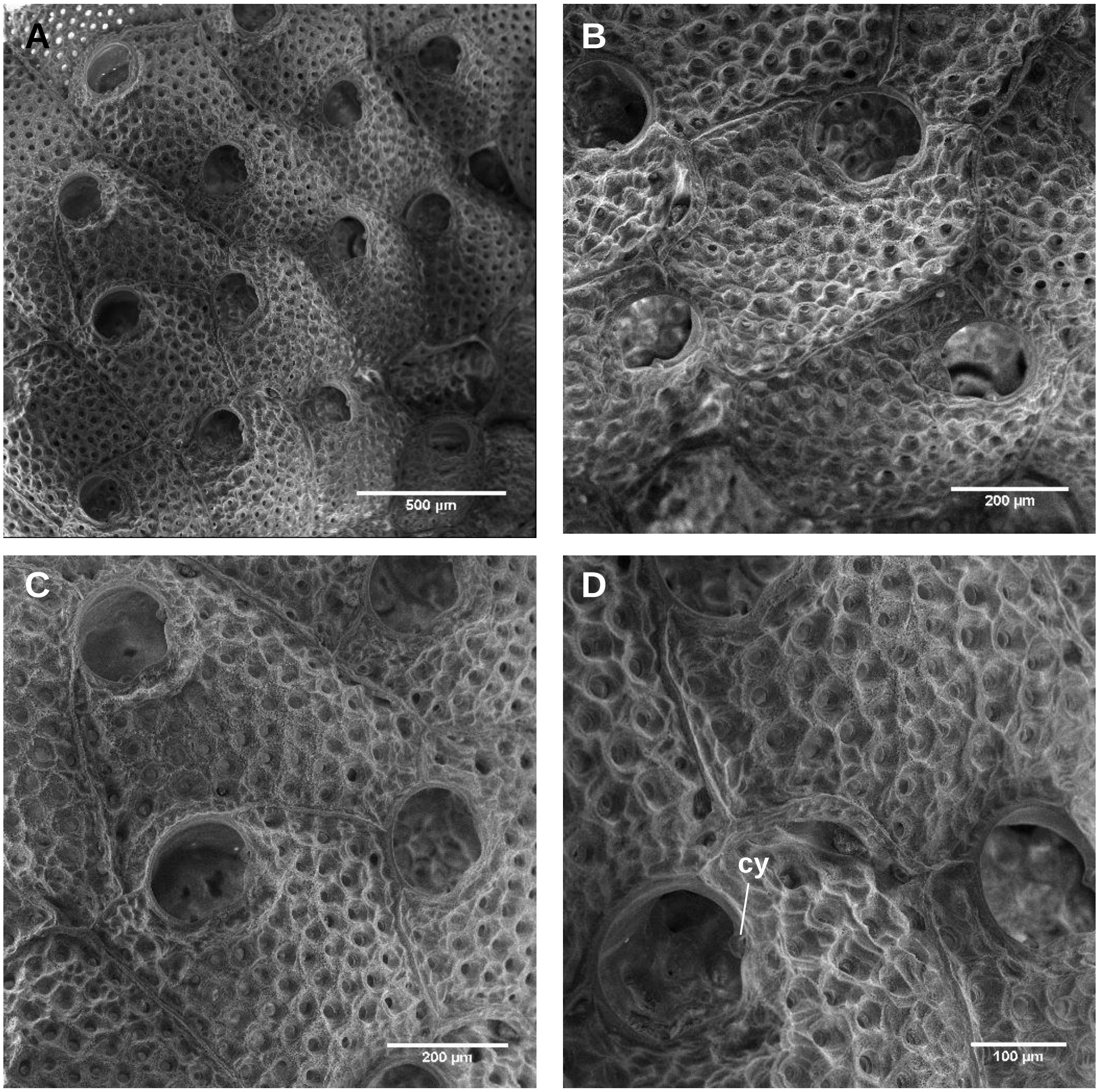

Plate 23: *Neodakaria islandica*. A. Colony view. B-C. Enlarged zooids, showing shallow sinus, and cupped, porous frontal wall. D. Details of aperture showing cupped frontal wall, shallow sinus, depressed area immediately proximal, and knob-like condyles (cy).

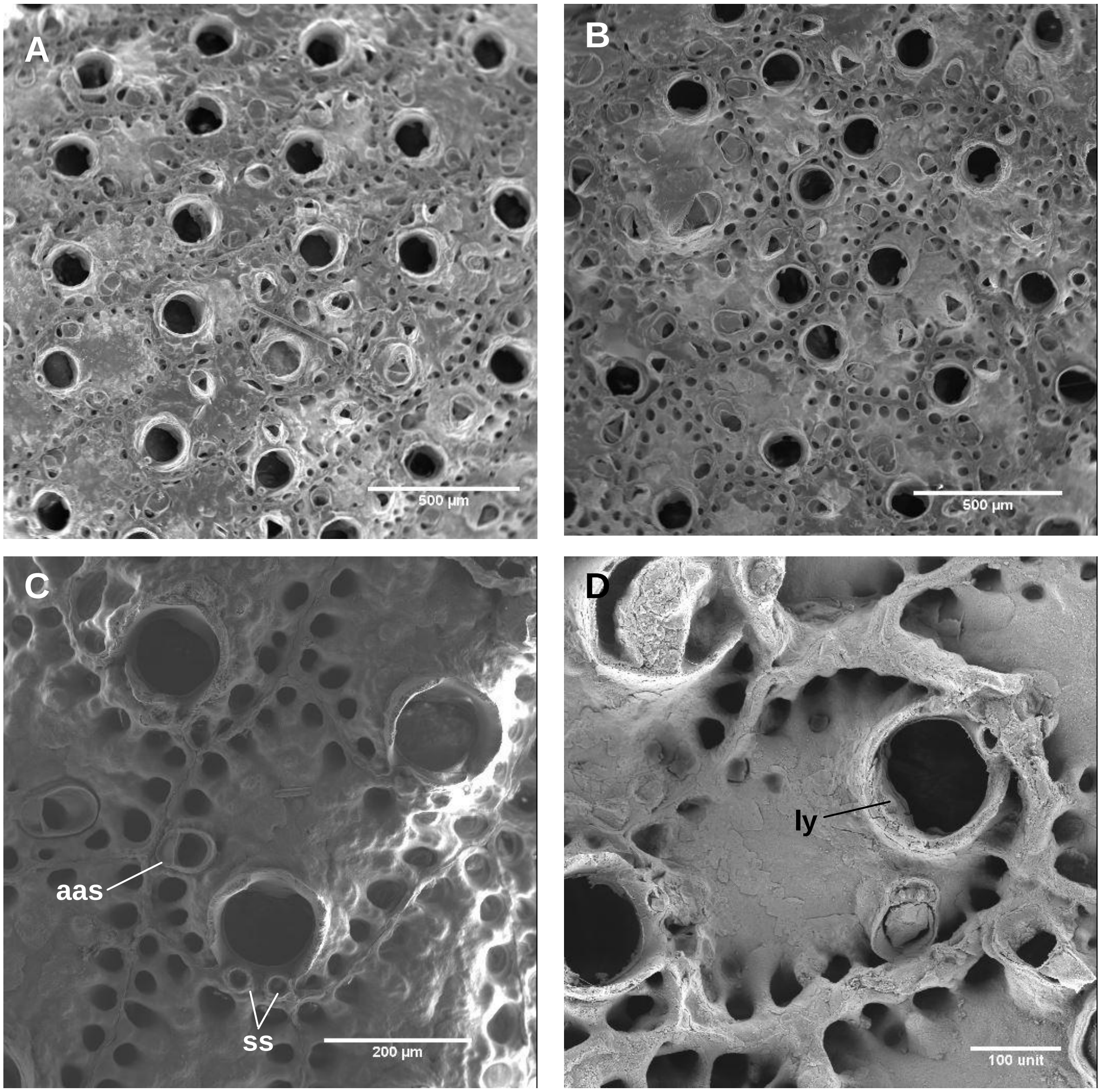

Plate 24: *Parasmittina collifera*. A-B. Colony view showing zooids oriented in various directions. C. Enlarged view of zooids (distal end down) showing two spine scars (ss) distal to aperture, adventitious avicularia scars (aas), and large marginal pores. D. Same, showing a zooid with a single spine scar and a shallow lyrula (ly).

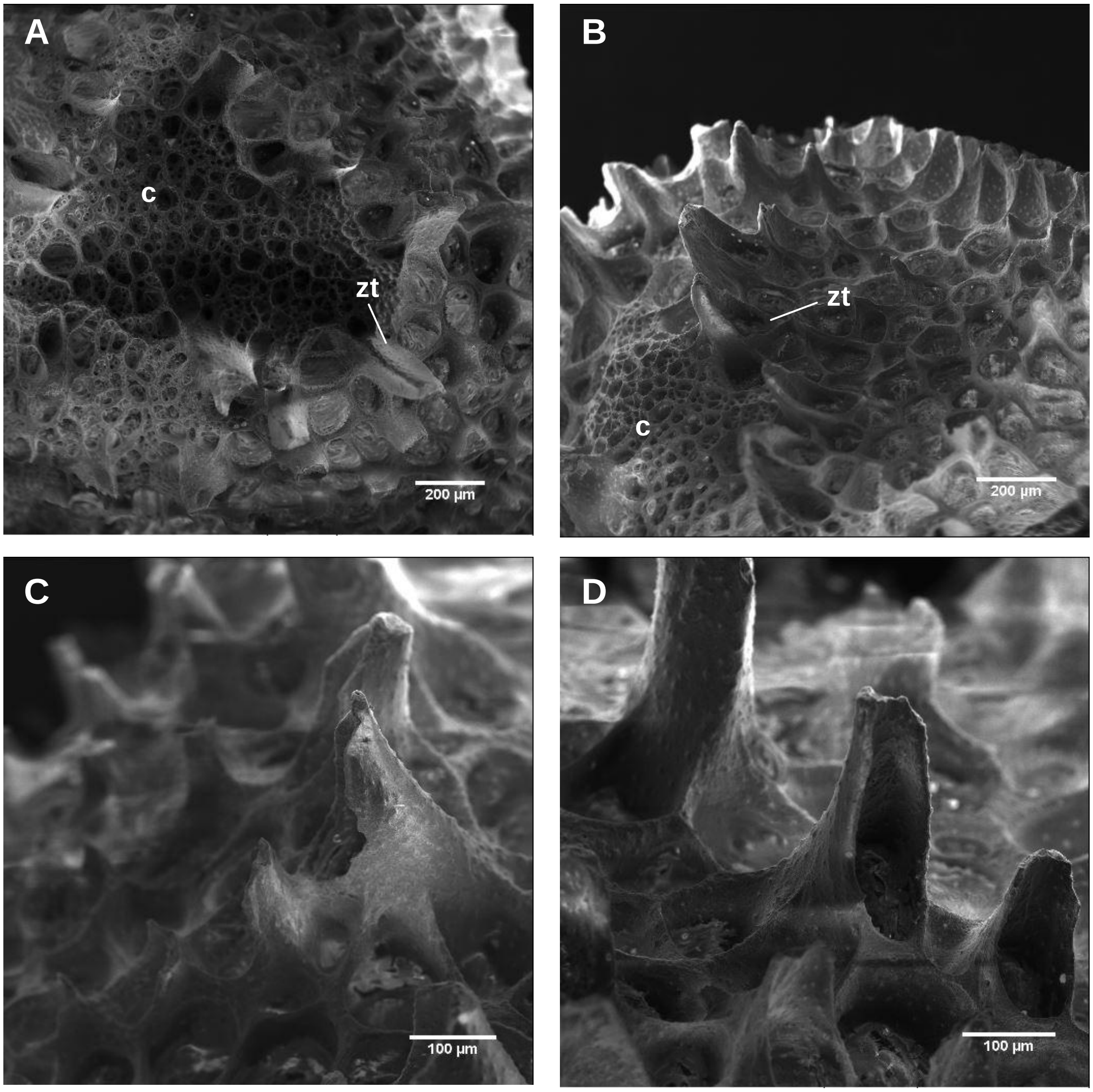

Plate 25: *Patinella verrucaria*. A-B. Colony view showing zooecial tubes (zt) and cancelli (c). C-D. Side-view of zooecial tubes showing asymmetric structure and variability in height.

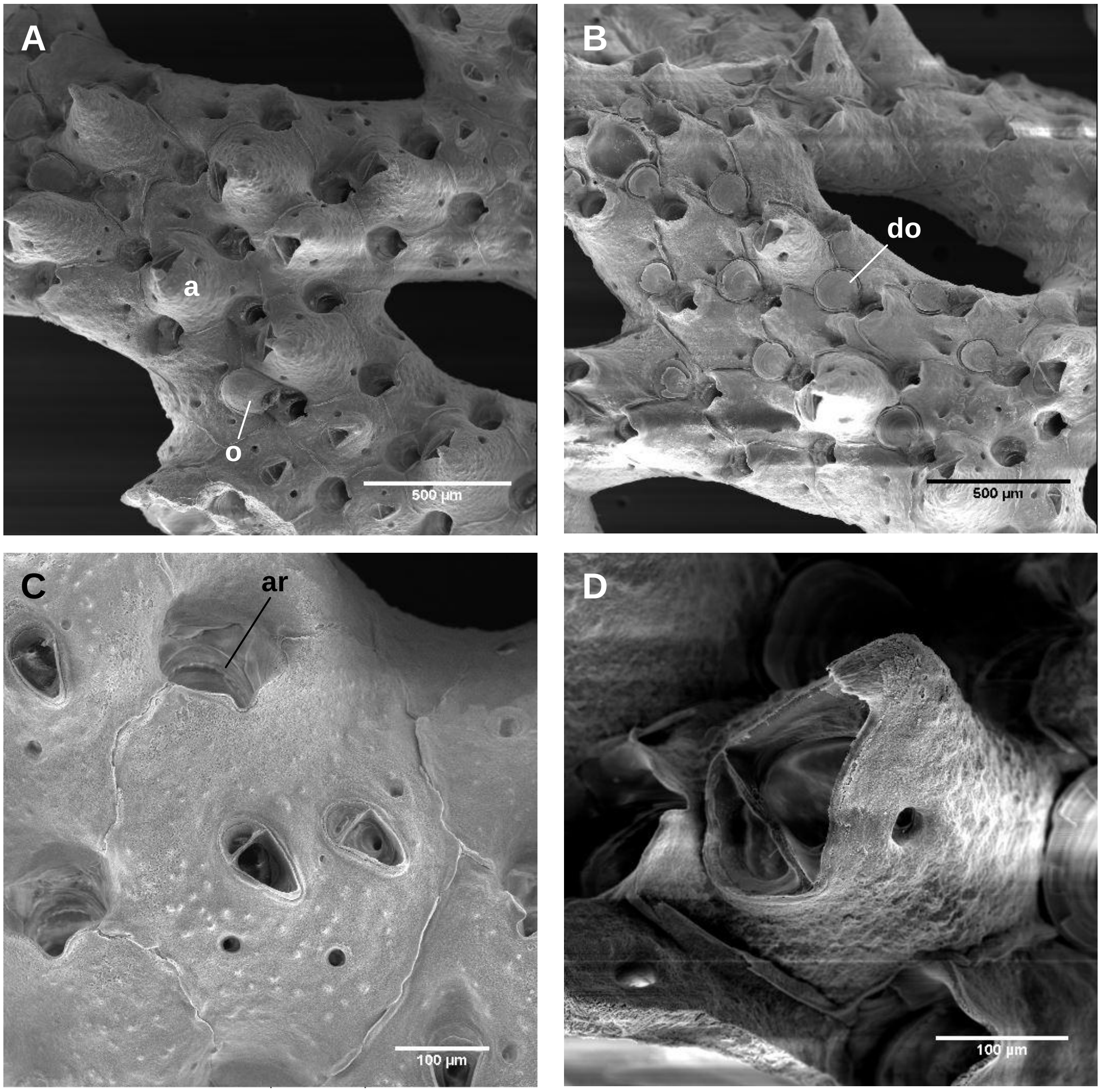

Plate 26: *Phidolopora pacifica*. A. Colony view showing fenestrate morphology, an ovicell (o), giant interzooecial avicularia (a), and numerous zooids. B. Colony view showing numerous developing ovicells (do) and intezooecial avicularia. C. Detail of zooid showing beaded apertural rim (ar), adventitious avicularia, and few frontal pores. D. Detail of large interstitial avicularium.

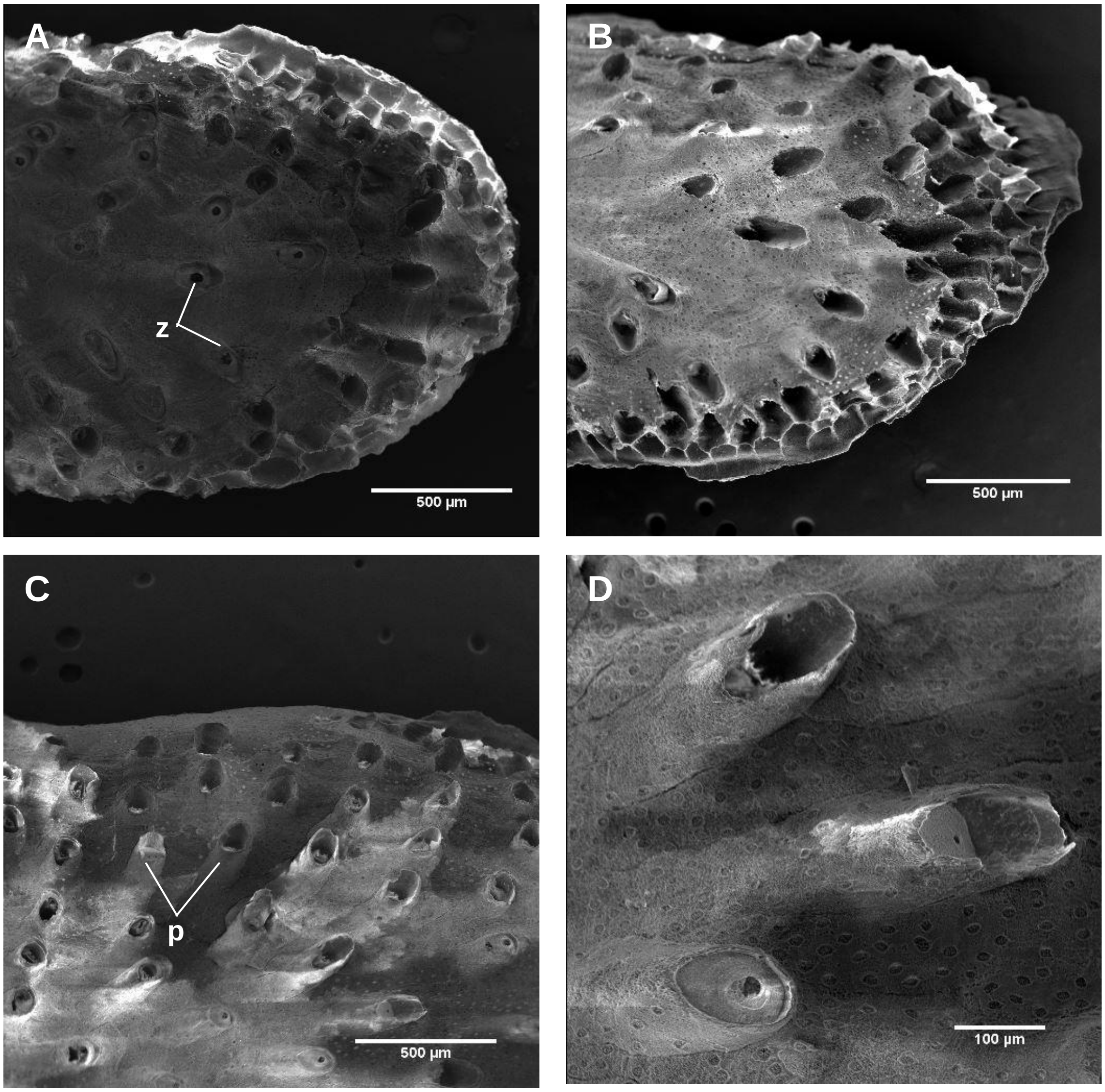

Plate 27: *Plagioecia patina*. A-B. Colony view showing pancake-shaped morphology and numerous zooids (z). C. Side view of colony, showing short peristomes (p). D. Detail of peristomes showing elliptical and rounded apertures and pocked surface of colony.

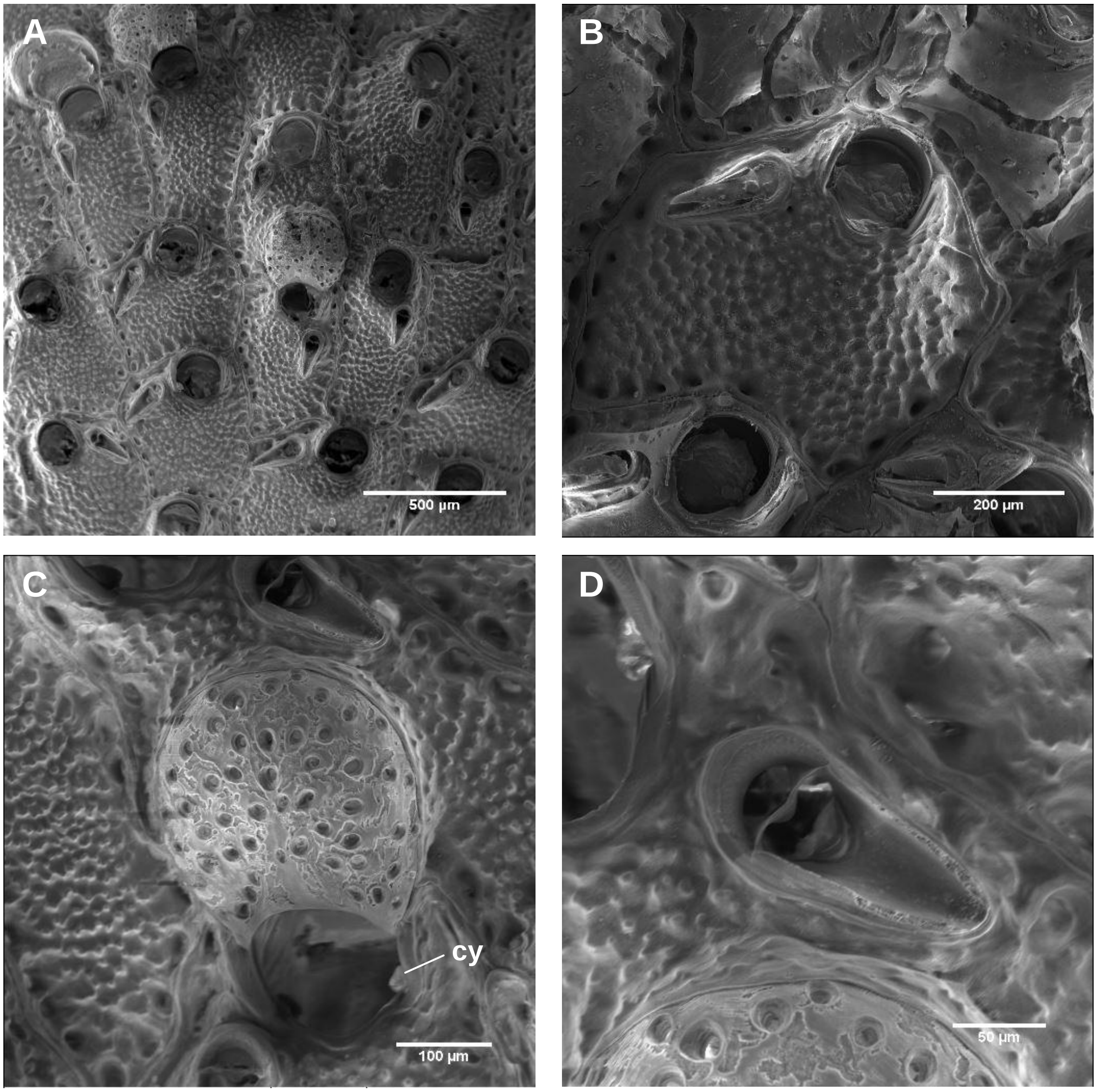

Plate 28: *Pleurocodonellina longirostrata*. A. Colony view; note ovicells in center and in top-left and suboral avicularia. B. Enlarged zooid, showing cupped, imperforate frontal wall, marginal areolar pores, adventitious avicularium, and wide, shallow sinus. C. Detail of ovicell with large condyles (cy). D. Detail of adventitious avicularia showing chevron-shaped hinge bar.

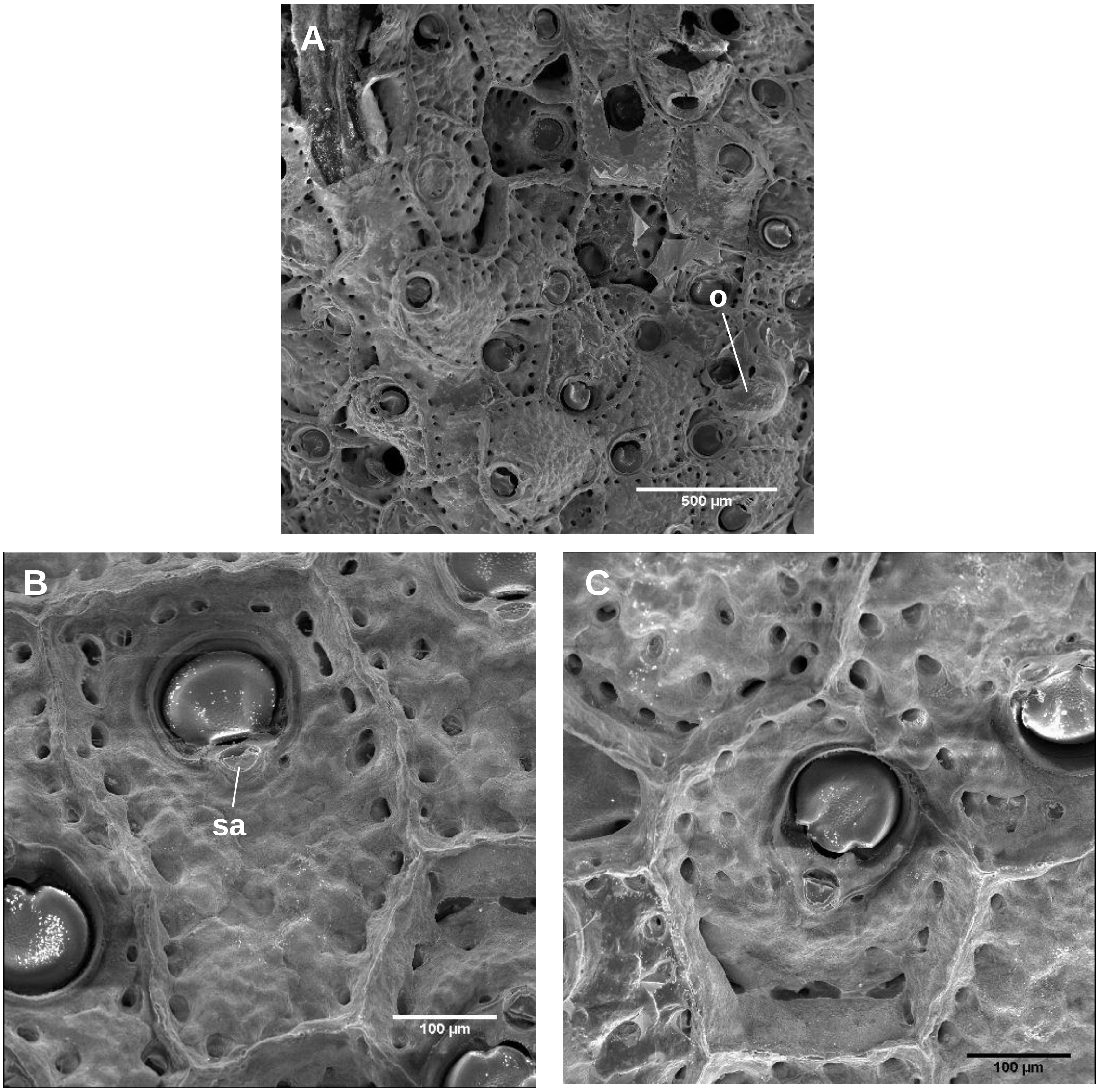

Plate 29: *Porella columbiana*. A. Colony view showing arrangement of zooids and an ovicell (o). B-C. Enlarged zooids with marginal areolar pores and suboral avicularium (sa).

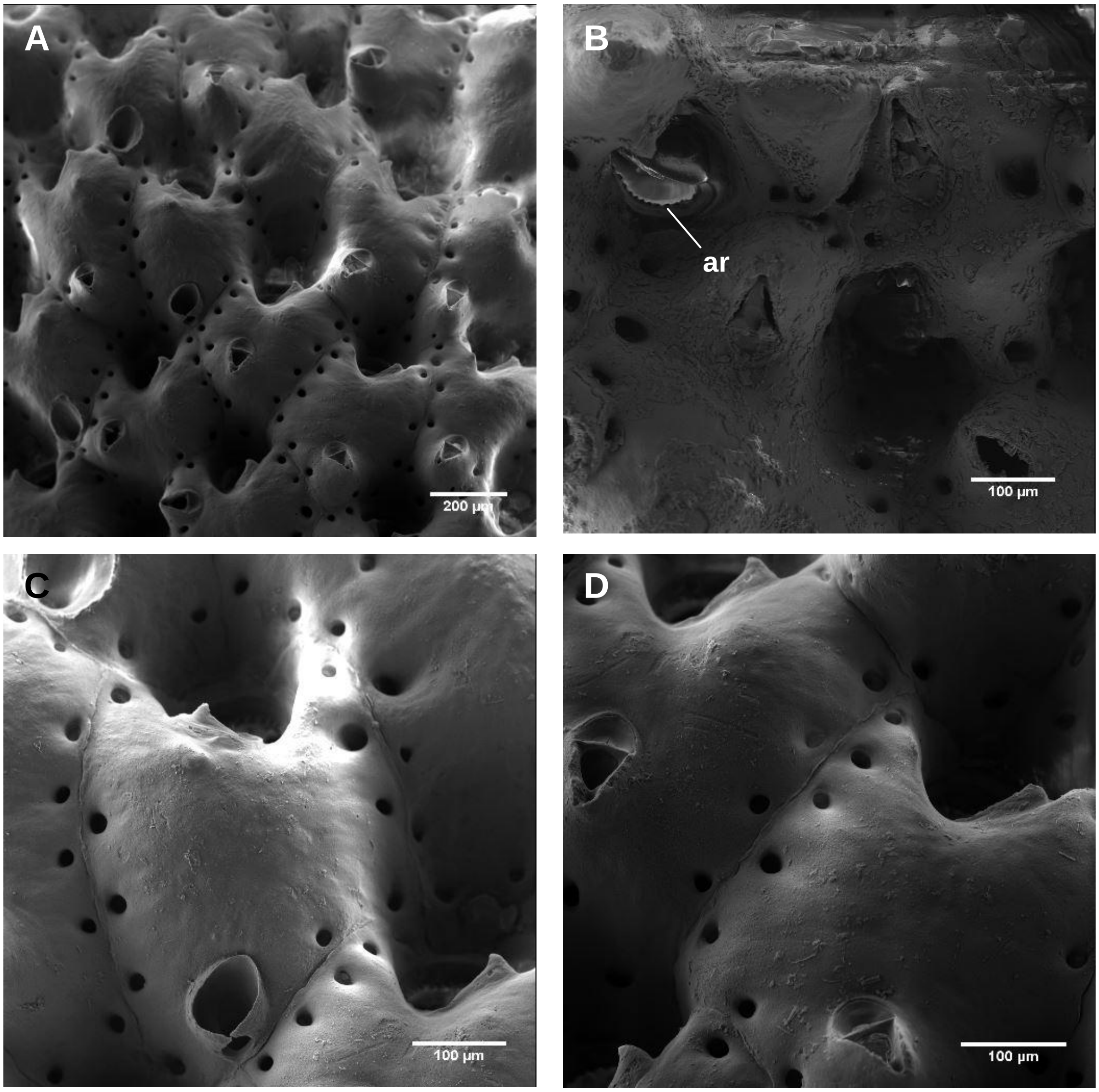

Plate 30: *Rhynchozoon rostratum*. A. Colony view showing zooid arrangement and adventitious avicularia. B. Enlarged aperture showing beaded aperture rim (ar). C. Detail of marginal areolar pores. D. Enlarged adventitious avicularia.

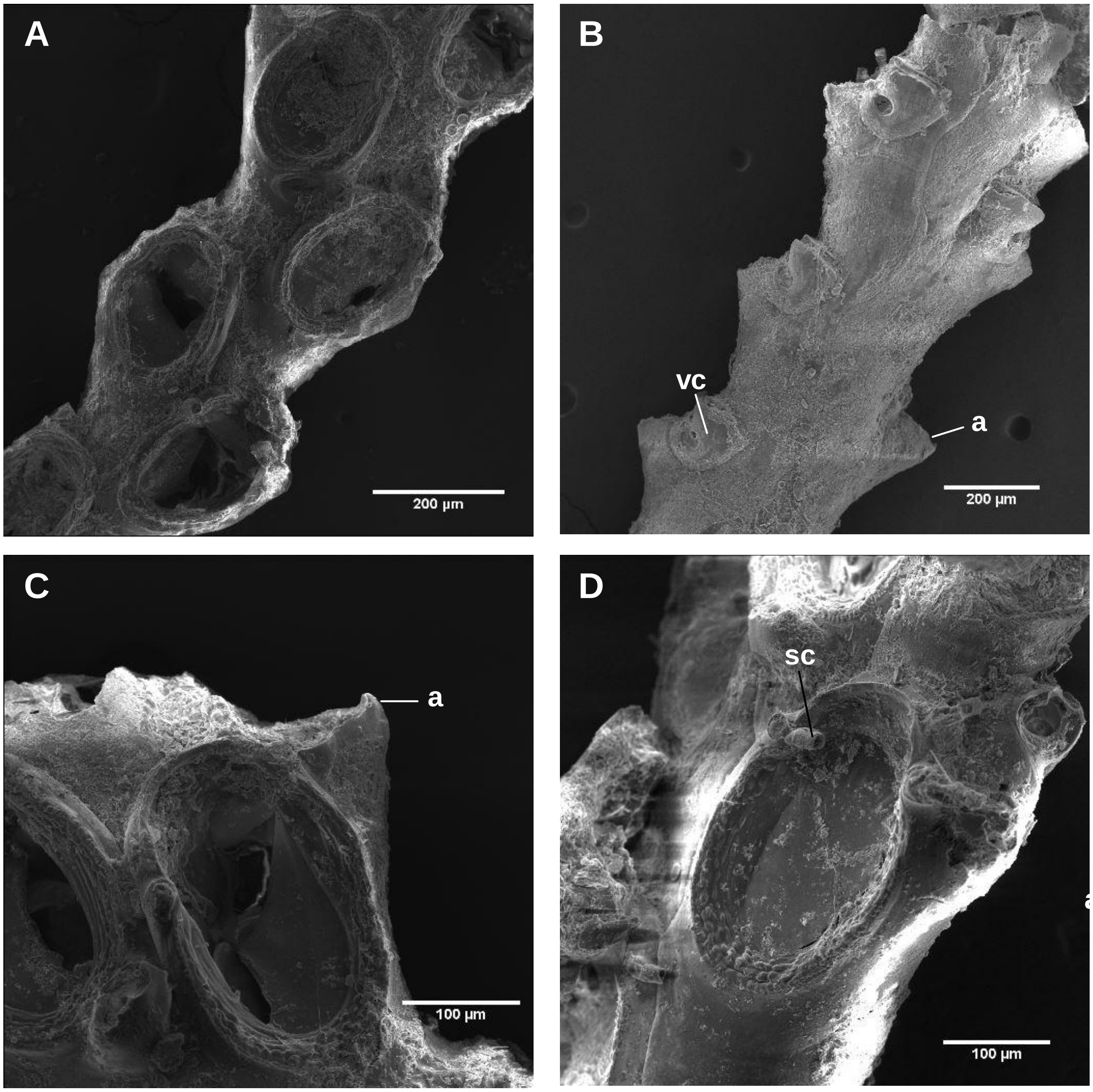

Plate 31: *Scrupocellaria varians*. A. Colony view showing zooid arrangement. B. Dorsal surface showing vibracular chambers (vc) and marginal avicularia (a). C. Enlarged zooid and marginal avicularium. D Enlarged zooid with remnants of scutum (sc), and marginal avicularium (a).

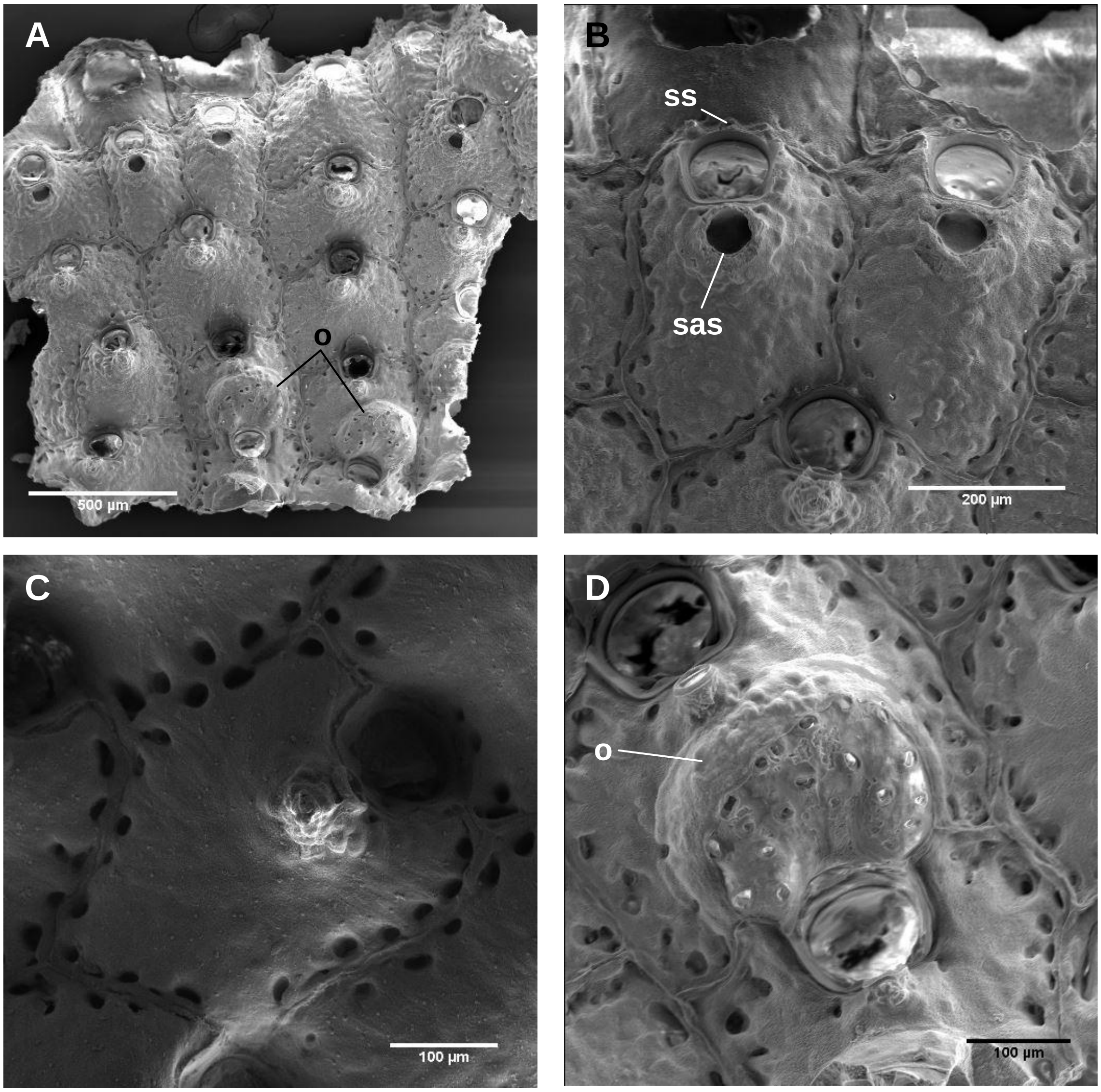

Plate 32: *Smittoidea prolifica*. A. Colony view showing organization of zooids and ovicells (o). B-C. Close-up of zooids. B. Close up of two zooids showing spine scars (ss) and suboral avicularium scars (sas). C. Close-up of a zooid showing suboral avucularium. D. Detail of ovicell (o).

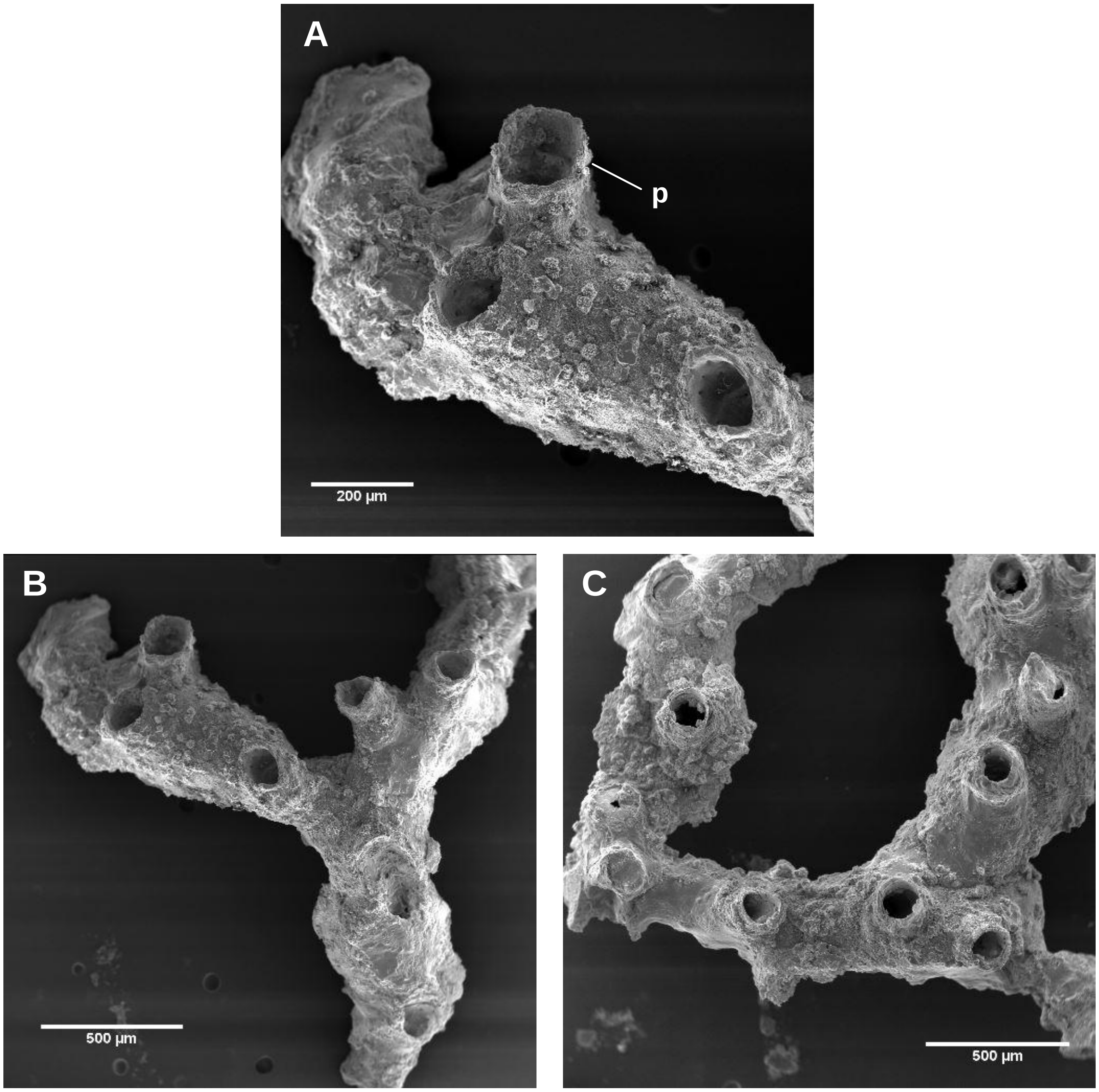

Plate 33: *Stomatopora granulata*. A. Enlarged zooid showing granular surface and peristomes (p). B-C. Colony views showing stolonate form and branching pattern.

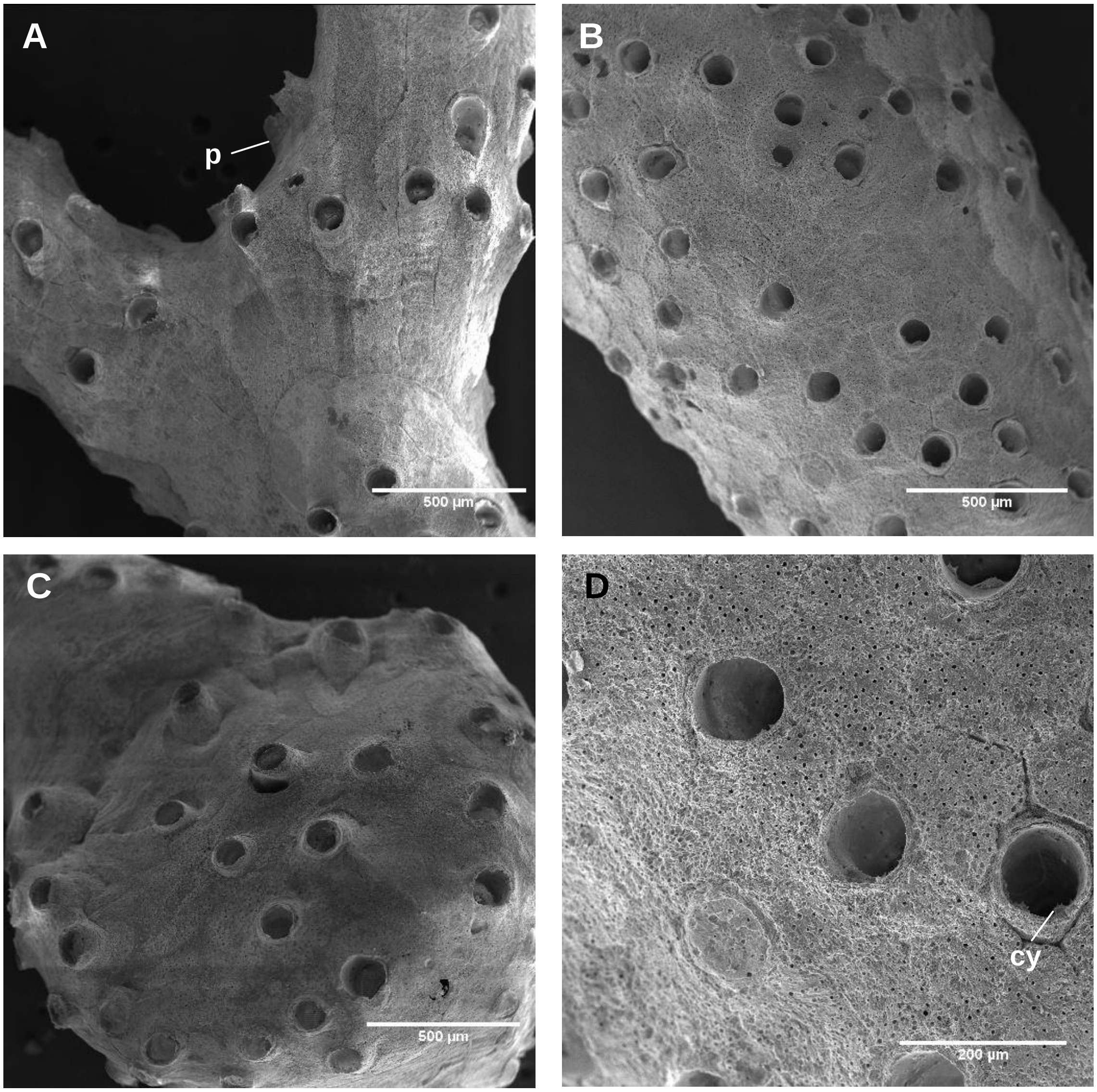

Plate 34: *Tetrocycloecia magna*. A-C. Colony view, showing zooid arrangement and subtle peristomes (p). C. Distal branch end. D. Detail of zooids showing condyls (cy) and imperforate frontal walls.

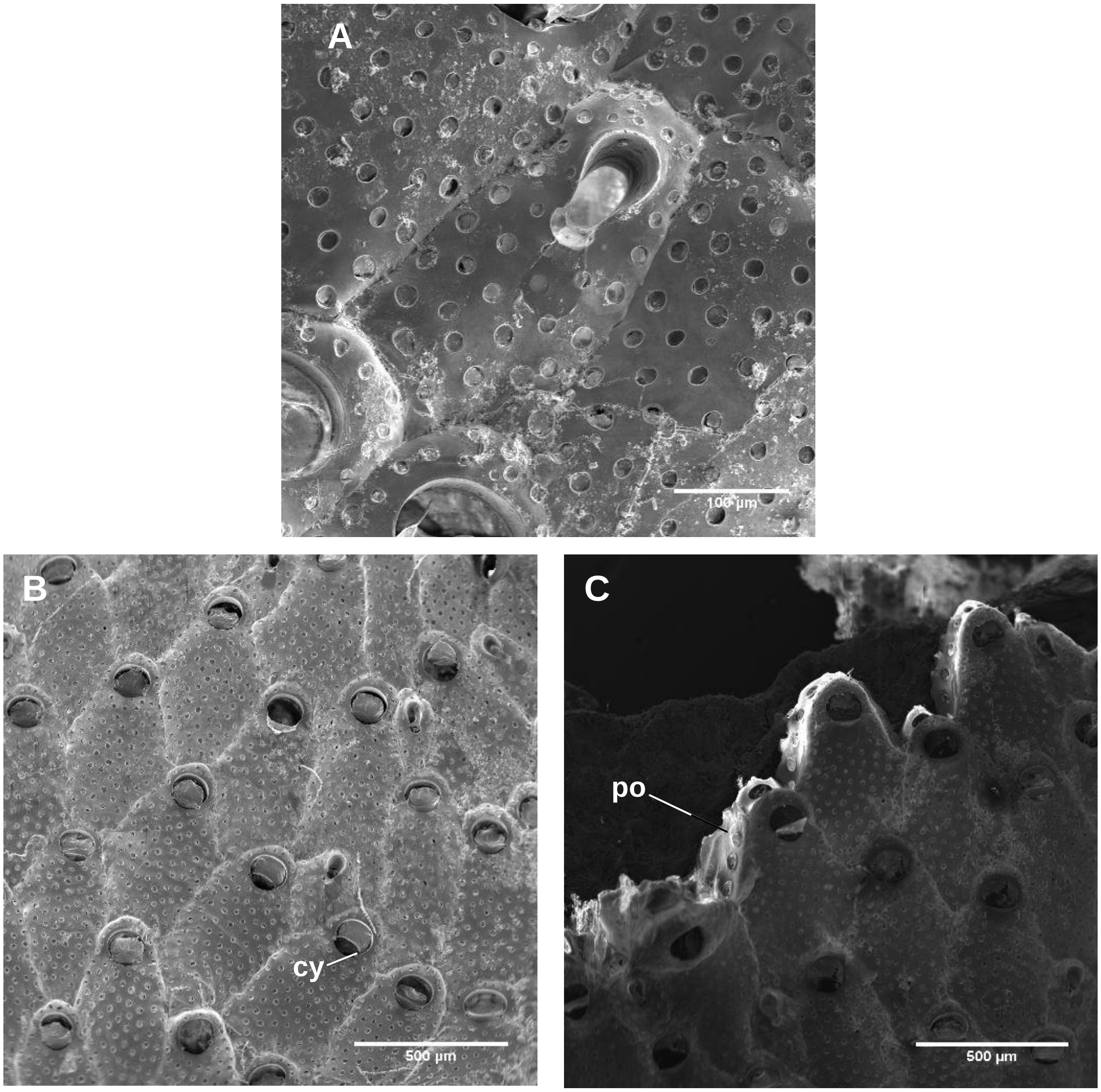

Plate 35: *Trypostega claviculata*. A. Detail of small, interzooecial keyhole shaped avicularium, and widely spaced frontal pores. B. Colony with a row of pores distal to aperture and thin condyles (cy). C. View of colony's side showing pores (po) for transport between zooids.

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