

## Research Article

**Bryozoa (Cheilostomata, Ctenostomata, and Cyclostomata) in Galapagos Island fouling communities**Linda D. McCann<sup>1\*</sup>, Megan I. McCuller<sup>2</sup>, James T. Carlton<sup>3</sup>, Inti Keith<sup>4</sup>, Jonathan B. Geller<sup>5</sup> and Gregory M. Ruiz<sup>6</sup><sup>1</sup>Smithsonian Environmental Research Center, Romberg Tiburon Center, 3152 Paradise Drive, Tiburon, California 94920, USA<sup>2</sup>North Carolina Museum of Natural Sciences Research Lab, 1671 Gold Star Drive, Raleigh, North Carolina 27699, USA<sup>3</sup>Williams College - Mystic Seaport Maritime Studies Program, 75 Greenmanville Ave., Mystic, Connecticut 96355, USA<sup>4</sup>Charles Darwin Research Station, Marine Science Department, Puerto Ayora, Santa Cruz Island, Galápagos, Ecuador<sup>5</sup>Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA<sup>6</sup>Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USAAuthor e-mails: [mccannl@si.edu](mailto:mccannl@si.edu) (LDM), [megan.mcculler@naturalsciences.org](mailto:megan.mcculler@naturalsciences.org) (MIM), [james.t.carlton@williams.edu](mailto:james.t.carlton@williams.edu) (JTC), [inti.keith@fcdarwin.org.ec](mailto:inti.keith@fcdarwin.org.ec) (IK), [geller@mml.calstate.edu](mailto:geller@mml.calstate.edu) (JBG), [ruizg@si.edu](mailto:ruizg@si.edu) (GMR)

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**OPEN ACCESS****Abstract**

Bryozoans have been infrequently studied in the Galapagos Islands, and even less so in nearshore biofouling assemblages. Based on surveys of Galapagos fouling communities in 2015 and 2016, we report 18 bryozoan species. At least 10 species are new records for the Galapagos, including *Amathia* sp. 1 (*Bowerbankia* group), *Beania klugei* Cook, 1968, *Bugulina stolonifera* (Ryland, 1960), *Caulibugula* cf. *dendrograpta* (Waters, 1913), *Celleporaria inaudita* Tilbrook, Hayward and Gordon, 2001, *Hippopodina tahitiensis* (Leca and d'Hondt, 1993), *Nolella stipata* Gosse, 1855, *Schizoporella pungens* (Canu and Bassler, 1928), *Sundanella* sp. and *Watersipora subtorquata* (d'Orbigny, 1852) *sensu* Vieira et al. 2014a. More than half of these are considered likely ship-borne introductions. *Schizoporella pungens* was the most abundant bryozoan. Continuing explorations of Galapagos biofouling communities will likely reveal additional introduced and native bryozoan species.

**Key words:** Santa Cruz Island, Baltra Island, introduced species, biofouling, cryptogenic species**Introduction**

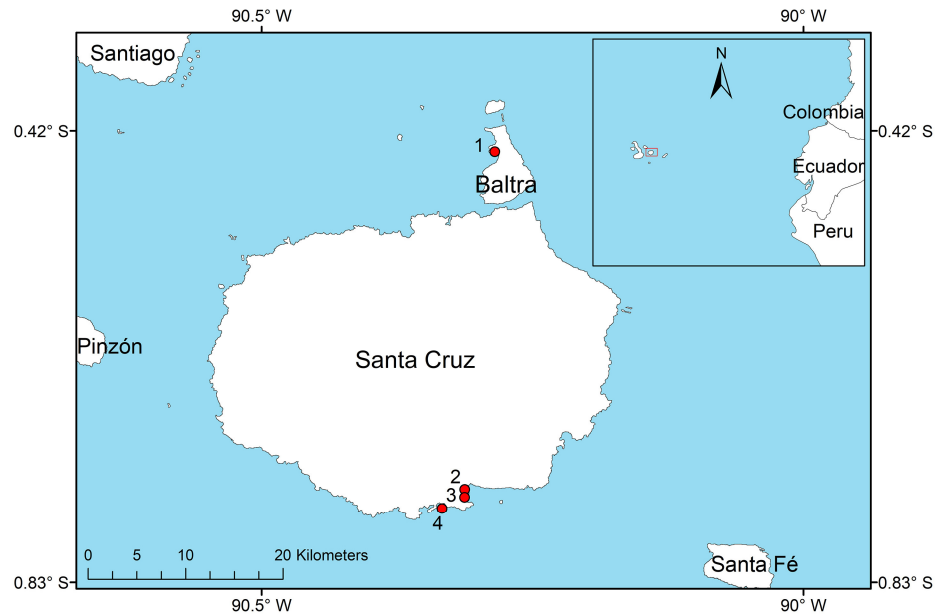
Despite its designation as a World Heritage Site, many small marine invertebrates of the Galapagos Islands, including the Bryozoa, remain largely understudied, particularly in near-shore biofouling assemblages. Banta and Redden (1990) summarized previously published work on Galapagos bryozoans, providing an annotated list of the 184 known species from 41 sites across the Archipelago. Three expeditions constitute the majority of known collections: the *Albatross* cruises of 1888 and 1891 (Canu and Bassler 1930), the *St. George* cruise of 1924 (Hastings 1930), and the *Velero III* Allan Hancock Foundation expeditions from 1932 to 1938 (Osburn 1950, 1952, 1953; Osburn and Soule 1953; Soule 1959, 1961,

1963). To these, Banta and Redden (1990) added seven species collected in July 1980 at “snorkel depth near boat docks” in Academy Bay on Santa Cruz Island. Witman and Smith (2003) reported eight species of bryozoans (*Crisia* sp., *Parasmittina* sp., *Caberea* sp. (as *Cabarea* sp.), *Bugula* (now *Bugulina*) *californica* Robertson, 1905, *Bugula* sp., *Cycloperiella rosacea* Osburn, 1947 (now *Cosciniopsis violacea* (Canu and Bassler, 1928)), *Lichenopora intricata* (Busk, 1856), and an unidentified species) collected in 1999–2000 from Rocas Gordon islet adjacent to Santa Cruz Island. Of these, *L. intricata* (previously known from California to Mexico (Osburn 1953) and possibly south to Panama (Powell 1971)), represented a new record for the Islands; it was also reported, based upon 2000–2001 collections, by Bustamante et al. (2002). Since 2000, several new cheilostome species have been described from the Galapagos, including *Microporella galapagensis* (as *Microporelloides galapagensis* Soule, Chaney and Morris, 2003) from Santa Cruz Island (Soule et al. 2003), *Cradoscrupocellaria galapagensis* Vieira, Spencer Jones and Taylor, 2013, and *C. hastingsae* Vieira, Spencer Jones and Taylor, 2013 from Santiago (James) and Isabela Islands.

Our work on Galapagos bryozoans began in 2015 as part of a larger study on marine bioinvasions in the Archipelago (Carlton et al. 2019). On the first author’s (LDM) first visit in February 2015, the weedy fouling species *Amathia verticillata* (delle Chiaje, 1822), commonly known as “Zoobotryon”, was discovered draping in long tendrils from the limbs of red mangrove trees in Tortuga Bay (McCann et al. 2015). The present study reports additional records of bryozoans in Galapagos biofouling communities based upon collections in 2015 and 2016.

## Materials and methods

The present collections of Galapagos species were made from bryozoan communities on natural (mangroves) and anthropogenic (docks, settlement panels) substrates. In February 2015 limited collections were conducted for intertidal species at one site in Tortuga Bay, Santa Cruz Island (mangrove roots, rock and sand habitat at low tide) and biofouling species at one site on Baltra island (floating dock) and Academy Bay, Santa Cruz Island (pilings and dock). Settlement panels were deployed at three sites: (1) the passenger docks in downtown Puerto Ayora, Academy Bay, Santa Cruz Island (latitude  $-0.747789$ ; longitude  $-90.312494$ ), (2) a private dock in adjacent Franklin’s Bay ( $-0.7552$ ;  $-90.312656$ ), also on Santa Cruz Island, and (3) an Ecuadorian Navy floating dock on Baltra Island ( $-0.435978$ ;  $-90.284803$ ) (Figure 1). The panels consisted of  $14 \times 14$  cm, 0.5 cm thick, grey polyvinyl chloride (PVC) plates suspended horizontally at one meter depth. A set of panels deployed in February 2015 and another in January 2016 were retrieved 14 and 3 months later, respectively, in April 2016, and brought to the Marine Biological Laboratory of the Charles Darwin



**Figure 1.** Location of Galapagos Islands off Ecuador (inset). Study sites: (1) Baltra Island, (2) Academy Bay, (3) Franklin's Bay, and (4) Tortuga Bay, Santa Cruz Island.

Research Station, in Puerto Ayora, for analysis. Plates were examined while the biofouling community was still alive (Supplementary material Table S1).

Hard-bodied bryozoans were preserved in 95% ethanol, while soft-bodied species were placed into 10% formalin and seawater (later transferred to 70% ethanol for storage) and 95% ethanol for genetic analysis. Where possible, paired morphological and molecular samples were collected for each species from each locality, and vouchers were deposited in the Smithsonian Environmental Research Center (SERC) specimen library in Edgewater, Maryland. Samples were examined under a stereo microscope and measurements were made on three to six different colonies for each species (except for those species for which we only found one or two colonies; the total number of measurements for all colonies (N) is indicated with each description). Zooid measurements were made with an ocular micrometer on a Wild M8 stereo microscope (Leica Microsystems, Wetzlar, Germany) at 50<sup>x</sup> with 16<sup>x</sup> oculars. Specimens were photographed by light microscopy with a Canon Rebel T5i (Canon U.S.A., Inc., Melville, New York, USA). A subset of the best samples (colonies with reproductive structures, avicularia, and other defining features) were selected for scanning electron microscopy (SEM). Specimens were cleaned in sodium hypochlorite solution, rinsed in tap water, air dried, and coated with Au-Pd using an Anatech USA Hummer 6.6 Sputtering System at 15mA (Anatech USA, Hayward, California, USA) and viewed under a JEOL JSM-7100FLV field emission scanning electron microscope (JEOL USA Inc., Peabody, Massachusetts, USA) at 5.0 kV accelerating voltage.

Large colonies of several species were chosen for combined molecular and morphological analysis, with half the colony going to each (Table S2). DNA was extracted from ~ 25 mg colony subsamples using the DNEasy

blood and tissue kit (Qiagen, Catalog No. 69504) following the manufacturer's protocol. A 654 bp fragment of the cytochrome *c* oxidase subunit I (COI) mitochondrial gene was amplified by polymerase chain reaction (PCR) using primers and methods described by Geller et al. (2013). For two specimens, a primer from Leray et al. (2013) was used to produce a shorter amplicon. PCR products were purified using Agencourt AMPure beads (Beckman Coulter, Catalog No. A63880) according to the manufacturer's protocol and sent to Elim Biopharmaceuticals (Hayward, California, USA) for dideoxy chain termination sequencing. Forward and reverse sequences were assembled and primer sequencers removed using Geneious 10.1 (Biomatters, Auckland, New Zealand).

In addition, one of the authors (JTC) provided bryozoan specimens that he collected in April 1987 from the hull fouling community of a local resident fishing vessel, coincidentally named the *Albatross*, in Academy Bay, Santa Cruz Island; *Watersipora* from this material is incorporated in the present study. We agree with the taxonomic revision of *Watersipora subtorquata* outlined in Vieira et al. (2014a) and hereafter refer to the species as *Watersipora subtorquata*. The first author (LDM) also obtained specimens of *Watersipora* from the 1934 Allan Hancock Expedition to the Galapagos from the Santa Barbara Museum of Natural History. In May 2011, LDM examined, for comparative purposes, a collection of bryozoans made by A. Herrera in 1985 at Boy Scout Beach (8.916667; -79.533333), on Naos Island, Panama City, on the Pacific coast of Panama. The collection is housed at the Smithsonian Tropical Research Institute in Panama City.

All measurements are in millimeters and abbreviations are as follows: Lz, zooid length; Wz, zooid width; Lav, avicularium length; Wav, avicularium width; Llav, lateral avicularium length; Wlav, lateral avicularium width; Lfav, frontal avicularium length; Wfav, frontal avicularium width; Lor, orifice length; Wor, orifice width; Lop, opesia length; Wop, opesia length; Lsc, scutum length; Wsc, scutum width; Ws, stolon width; Lov, ovicell length; Wov, ovicell width; Lv, vibraculum length.

For systematic accounts we use the classification system of the "Bryozoan Home Page", <http://bryozoa.net/> (Bock 2018).

## Results

Sixteen bryozoan species were identified from settlement panels. Two additional species were identified from intertidal collections only, in Tortuga Bay and Academy Bay on Santa Cruz Island (Table 1), for a total of 18 species (Table S2). Six species were found in both intertidal collections and on panels including *Cradoscrupocellaria* sp., *Celleporaria inaudata*, *Schizoporella pungens*, *Bugulina stolonifera*, *Watersipora subtorquata*, and *Amathia verticillata*. The majority of species (11) are Cheilostomata, with the remaining 5 and 2 species being Ctenostomata and Cyclostomata, respectively. Nine species were rare, being recorded only once



**Table 1.** Galapagos bryozoans treated here, in alphabetical order and by site (SC = Santa Cruz Island). Species with an \* are new records for the Galapagos. New records for specific sites in the Archipelago for previously reported species are also indicated with an \* under the specific site column. Species that may have been reported previously under another name are not indicated as new records. Tortuga Bay records and those in italics for other sites are from intertidal collections only. Abundance: A = abundant (> 5 plates), M = common (3–5 plates), R = rare (1–2 plates). Status: C, Cryptogenic; I, introduced; – undetermined.

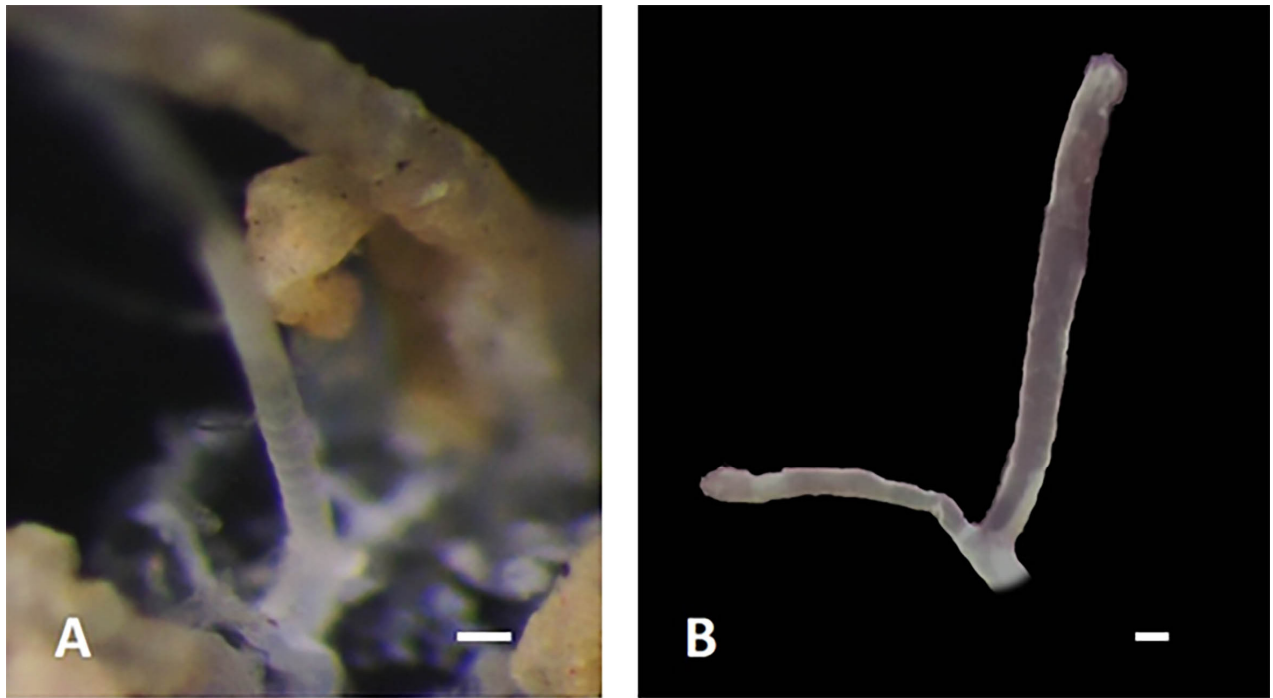
Taxa	Baltra Island	Academy Bay, SC	Franklin's Bay, SC	Tortuga Bay, SC	Status
<i>Aetea curta</i>	R				C
<i>Amathia</i> sp. 1 ( <i>Bowerbankia</i> )*	R	R			–
<i>Amathia</i> sp. 2		M	R		–
<i>Amathia verticillata</i>	M*	R*	M	<i>A</i>	I
<i>Beania klugei</i> *				<i>R</i>	I
<i>Bugula neritina</i>	R				I
<i>Bugulina stolonifera</i> *	<i>R</i>		R		I
<i>Caulibugula</i> cf. <i>dendrograpta</i> *		A			I
<i>Celleporaria inaudita</i> *	R	A	A	<i>R</i>	I
<i>Cradoscrupocellaria</i> sp.		<i>R</i>	<i>R</i> *		–
<i>Crisia</i> sp.		<i>R</i>			–
<i>Hippopodina tahitiensis</i> *	A		A		I
<i>Nolella stipata</i> *	M		M		C
<i>Patinella</i> sp.		R			–
<i>Savignyella lafontii</i>	A*		A*		C
<i>Schizoporella pungens</i> *	A	A	R	<i>A</i>	I
<i>Sundanella</i> sp.*			R		–
<i>Watersipora subtorquata</i> *	M	M	M	<i>M</i>	I
Total Number of Taxa	11	10	11	5	18

or twice (*Sundanella* sp., *Amathia* sp. 1, *Cradoscrupocellaria* sp., *Bugulina stolonifera*, *Bugula neritina* (Linnaeus, 1758), *Aetea curta*, and *Patinella* sp. from panels, and *Crisia* sp. and *Beania klugei* from the intertidal collections).

Species composition varied among sites. *Schizoporella pungens* was the most abundant bryozoans and was found at all 4 sites. *Watersipora subtorquata* and *Amathia verticillata* also occurred at all sites. Many species occurred on up to 50% of plates (common in Table 1) or > 50% of plates (abundant in Table 1). However, 39% of species were found at only 1 site (Table 1). Ten of the 18 species are new records for the Galapagos, including *Amathia* sp. 1 (*Bowerbankia* group), *Beania klugei* Cook, 1968, *Bugulina stolonifera*, *Caulibugula* cf. *dendrograpta* (Waters, 1913), *Celleporaria inaudita*, *Hippopodina tahitiensis* (Leca and d'Hondt, 1993), *Nolella stipata* Gosse, 1855, *Schizoporella pungens*, *Sundanella* sp., and *Watersipora subtorquata*. Up to five taxa may prove to be new species: *Amathia* sp. 1, *Amathia* sp. 2, *Patinella* sp., and possibly *Sundanella* sp. and *Cradoscrupocellaria* sp. One species, *Aetea curta*, may represent a prior record reported earlier as *A. ligulata* Busk, 1852.

### Systematic Account

Synonymies are generally limited to records in the north eastern Pacific Ocean, and those that include adequate descriptions and illustrations.



**Figure 2.** A–B. *Aetea curta*, SERC 232861i, Baltra Island, Galapagos: A. zooid showing coarse annulations on the base of the stem; B. different zooid showing terminal open end nearly as long as the basal stem section. All scales = 100  $\mu$ m. Photos by L. McCann.

Class Gymnolaemata Allman, 1856

Order Cheilostomata Busk, 1852

Suborder Inovicellina Jullien, 1888

Superfamily Aeteoidea Smitt, 1867

Family Aeteidae Smitt, 1867

Genus *Aetea* Lamouroux, 1812

***Aetea curta* Jullien, 1888**

(Figure 2A, B)

*Aetea curta* – Jullien 1888, 26; Hastings 1943, 473–475, Figs. 58A–B, Pl. 13, Fig. 1; Vieira et al. 2016, 63–64, Figs. 4–5.

*Aetea ligulata* – Osburn 1950, 13–14, Pl 1, Fig. 4; Tilbrook et al. 2001, 37, Fig. 2A; Taylor and Tan 2015, 5–6, Figs. 2A–F.

not *Aetea ligulata sensu* Busk 1852.

**Material:** SERC 232861i, Baltra Island, collected April 2016.

**Description:** Zooids shiny white, with creeping basal portion rising into an erect tube; zooid stolonial, basal portion irregularly shaped, generally the same width as or narrower than the erect stalk; zooid tubular portion straight or slightly bent with coarse, wide rings (Figure 2A) proximally, distal head slightly wider, spoon-shaped; frontal membrane occupying approximately 45% the length of the stalk (Figure 2B); aperture terminal; no spines or tubercles seen; zooids variable in length.  $Lz = 0.962 \pm 0.324$ ,  $Wz = 0.074 \pm 0.037$ , (N = 4).

**Remarks:** Material limited to four zooids. Four species of *Aetea* have been previously reported from the Galapagos: *A. anguina* (Linnaeus, 1758), *A. ligulata*, *A. recta* Hincks, 1861 [now *A. sica* (Couch, 1844)], and *A. truncata* (Landsborough, 1852). Unlike *A. anguina* and *A. sica*, both with a finely annulated stalk, our Galapagos specimens possess a tubular stalk with coarse, wide, rings, matching well the original description of Jullien (1888) and Hastings' redescription (1943) of *A. curta*. We address *A. truncata* and *A. ligulata* below.

**Distribution:** *Aetea curta* was originally described from the Straits of Magellan (Jullien 1888) and is reported here for the first time from the Galapagos. Hastings (1943) indicated that her material from Pacific Panama, originally identified as *A. truncata*, was likely *A. curta* and suggested that specimens from Ascension Island in the mid-Atlantic may also be this species. However, a similar species, *A. ligulata*, described from the coast of Patagonia and Straits of Magellan, is widely recorded from both the Pacific Ocean (including Bartolomé, Isabela, and San Cristobal Islands, Galapagos; Colombia; and the Gulf of Panama) and the Atlantic Ocean (Osburn 1940, 1950). Hastings (1943) further suggested that *A. curta* and *A. ligulata* may be the same species, although she did not synonymize them. Although Osburn (1940, 1950) named his Galapagos material *A. ligulata*, Soule et al. (1995) pointed out that Osburn's species is annulated, while in the original description of *A. ligulata*, Busk (1852) specifically notes that the "surface [is] not ringed" (but this is contradicted in Busk's own figure). Unfortunately, Busk's type specimen is missing, so that the contradiction between his description and figure cannot be resolved. Vieira et al. (2016) suggested that Busk's *A. ligulata* may be a synonym of either *A. fuegensis* (Jullien, 1888), another Patagonian species, or of *A. curta*. The other species described from the Eastern Pacific, *A. paraligulata* Soule, Soule and Chaney, 1995 has a distinctive constriction at the base of the aperture, also apparent in the original figure of *A. ligulata* (Busk 1852, plate 42), but not present in Osburn's figure of *A. ligulata*, nor in figures or descriptions of *A. curta*. Osburn (1950) does not give measurements, but Galapagos material appears to be closest to *A. curta*, based on the lack of constriction below the distal "head", similar proportion of spoon head to basal stalk, and appearance of coarse rings on the basal stalk.

The figure in Tilbrook et al. (2001) of *A. ligulata* from Vanuatu appears to indicate the same species as our Galapagos material. In addition to the Pacific sites, *A. curta* is reported from many sites in the western Atlantic, as far north as the Caribbean in Belize (Vieira et al. 2016). Either *A. curta* is a species complex or has been introduced from one ocean to the other. The latter possibility leads us to our designating it as cryptogenic in the Galapagos fauna at this time.

Suborder Flustrina Smitt, 1868

Superfamily Buguloidea Gray, 1848

Family Beaniidae Canu and Bassler, 1927

Genus *Beania* Johnston, 1840

***Beania klugei* Cook, 1968**

(Figure 3A)

*Beania klugei* – Cook 1968, 164, Fig. 2A–B; Tilbrook et al. 2001, 46; Vieira et al. 2010, 6–7, Figs. 7–8, 20, Table 1.

*Beania intermedia* – Hastings 1930, 705.

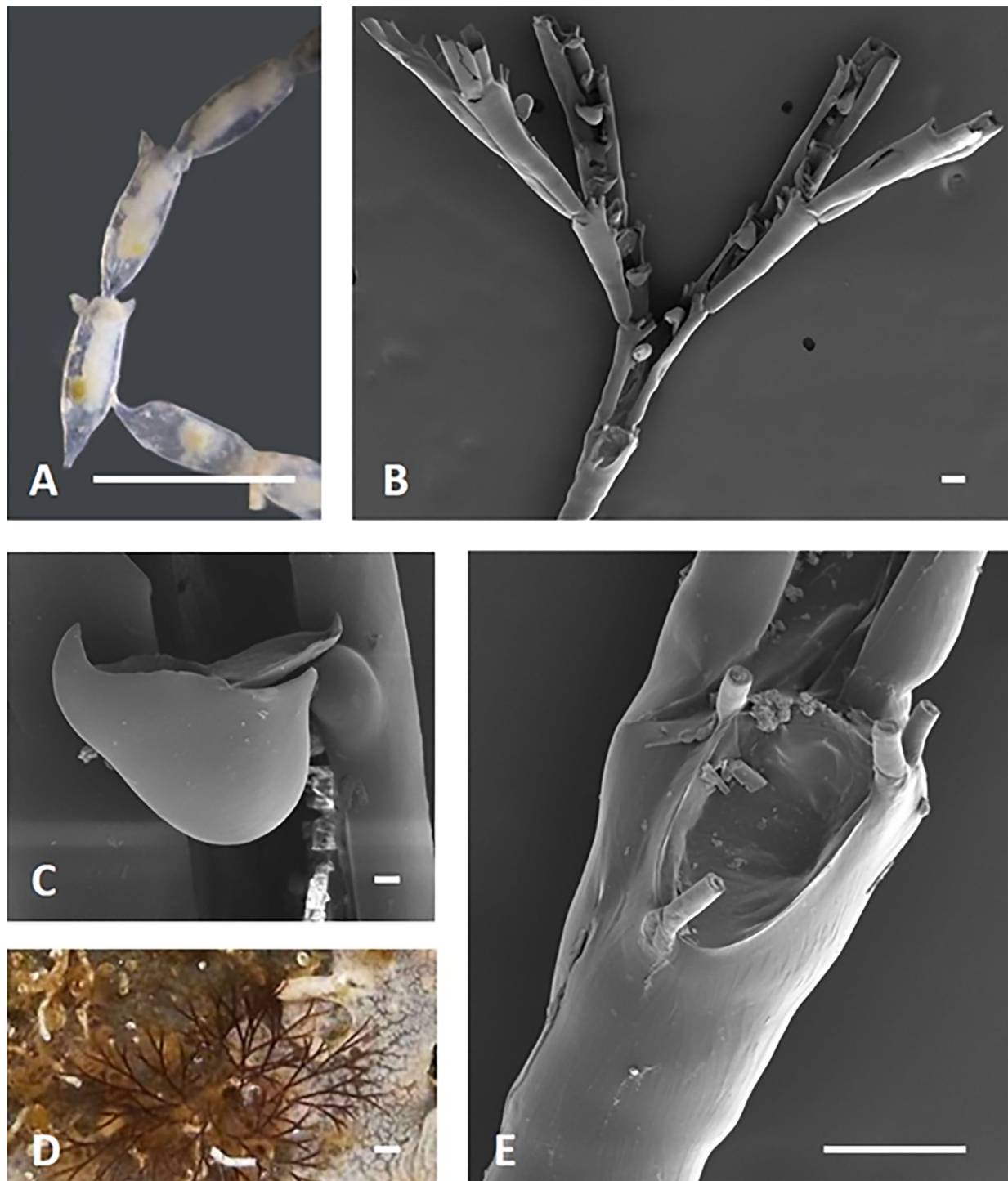
**Material:** SERC 2138114, colony on mangrove roots, Tortuga Bay, Santa Cruz Island, collected February 2015.

**Description:** Zooids tan colored and boat-shaped, uniserial; proximal ends with very short, narrow connective tubes; new zooids arise below midline on either side or from distal end of zooid; avicularia paired distolaterally, small, with tiny rounded projections distally (Figure 3A); no marginal spines; polypide and ovicell not seen.  $Lz = 0.855 \pm 0.056$ ,  $Wz = 0.286 \pm 0.021$ ,  $Lav = 0.125 \pm 0.019$ ,  $Wav = 0.102 \pm 0.008$ , (N = 5).

**Remarks:** Specimen examined was unattached to substrate. The specimen is similar to descriptions of the species by Vieira et al. (2010) from Atlantic Brazil. This is the first record from the Galapagos Islands.

**Distribution:** Several species of *Beania* have been reported from the Northeast Pacific Ocean (Osburn 1950), none of which corresponds with the present material. Two species had been included under the name *B. intermedia* (Hincks, 1881) until Cook (1968) clarified the characters of *B. intermedia* and erected the name *B. klugei* (based upon material from West Africa) for the *Beania* without spines and with the above characters. Incorporating older records prior to its description as a new species, *B. klugei* has now been reported from along or off the African coast (St. Helena, Cape Verde Island, Sierra Leone; Fransen 1986) as well as from the Western Atlantic from North Carolina to Florida, USA, the Caribbean, the Gulf of Mexico (Winston 1982; Fransen 1986), and more recently from Colombia (Montoya-Cadavid et al. 2007) and Brazil (Vieira et al. 2008). Outside the Atlantic, records include the Red Sea (Fransen 1986; Ostrovsky et al. 2011) and Indian Ocean (Satyanarayana Rao and Ganapati 1974), the South China Sea (Liu et al. 2001), and Vanuatu (Tilbrook et al. 2001). A record from Australia (Hayward and Ryland 1995) was attributed by Tilbrook et al. (2001) to *B. cookae* Tilbrook, Hayward, and Gordon, 2001, a species with more domed avicularia and slightly larger than *B. klugei*. Prior to the present report, the sole Eastern Pacific records were from Coiba Island, Panama (Hastings 1930; as *B. intermedia*) and Panama City (Fransen 1986).

Thus *B. klugei* occurs from the south coast of the United States through the Caribbean and Gulf of Mexico to Brazil, while in the Eastern Atlantic it occurs in a restricted range from Sierra Leone to Cape Verde Island.



**Figure 3.** A. *Beania klugei*, zooids showing branching pattern, SERC 2138114, Galapagos; B–C, E. *Bugulina stolonifera*, SERC 232836, Galapagos: B. colony morphology; C. close-up of avicularia, scale = 10  $\mu\text{m}$ . D. *Bugula neritina* colony on plate, SERC 310275, Galapagos, scale = 2.5 mm; E. *Bugulina stolonifera*, first zooid. All other scales = 100  $\mu\text{m}$ . Photos by L. McCann and SEMs by M. McCuller.

Indo-Pacific localities are few and widely scattered from the Red Sea to the South China Sea. Its very broad distribution in the Western Atlantic may suggest that it was introduced to the Indo-Pacific; its isolation in the tropical Eastern Pacific suggests that it was likely introduced to Panama and the Galapagos Islands, but whether from the Caribbean or the Indo-West Pacific remains unknown.



Family Bugulidae Gray, 1848

Genus *Bugula* Oken, 1815

***Bugula neritina* (Linnaeus, 1758)**

(Figure 3D)

*Sertularia neritina* – Linnaeus 1758, 815.

*Bugula neritina* – Robertson 1905, 266, Pl 9, Fig. 47; Hastings 1930, 704; Osburn 1950, 154–155, Pl 23, Fig. 3, Pl 24, Fig. 3.

**Material:** SERC 310275 Baltra Island, collected April 2016.

**Description:** Colonies branching erect, purplish red, biserial, approximately 3 cm tall × 4 cm wide; zooids long and slender at colony base, becoming shorter near distal branch ends; zooid distal corners pointed; avicularia and spines absent; ovicells large and globular, attached at the inner edge of distal edge of the zooids. See Winston and Woollacott (2008) for a more detailed description of this species.  $Lz = 0.654 \pm 0.079$ ,  $Wz = 0.285 \pm 0.020$ , (N = 8).

**Remarks:** We only found one colony on our panels SERC 31075, at the busy harbor of Baltra Island collected April 2016.

**Distribution:** *Bugula neritina* is a species complex (McGovern and Hellberg 2003; Fehlaue-Ale et al. 2013), although the clades characterized to date have not been assigned species names. As Fehlaue-Ale et al. (2013) noted, “Type S is considered widespread in tropical, subtropical, and temperate regions due to anthropogenic transport”. The Baltra site contained many introduced fouling bryozoan species (Table 1); similarly, specimens were collected near boat docks in 1980 in Academy Bay, Santa Cruz Island (Banta and Redden 1990; Banta 1991). While we do not yet have genetic data for Galapagos *B. neritina* harbor populations to confirm that they are Type S, it seems probable that they may represent the same clade found in warm-water ports worldwide. We thus provisionally treat these harbor populations as introduced, as we have no basis to presume that they would be an exception to this pattern. Powell (1971) reported what we regard as probable introduced populations of *B. neritina* from Pacific Panama. Hewitt et al. (2004) and Carlton and Eldredge (2009) regard *B. neritina* as introduced to Australia and the Hawaiian Archipelago respectively. Cryptic species within *B. neritina* have been genetically characterized in the Western Atlantic, in California, Australia, and elsewhere, but not yet in the Tropical Eastern Pacific. It would thus be of interest to re-examine both morphologically and genetically Hasting’s 1924 collections of *Bugula* “*neritina*” from non-harbor habitats of Santiago, Floreana, and Isabela Islands.

Genus *Bugulina* Gray, 1848

***Bugulina stolonifera* (Ryland, 1960)**

(Figure 3B, C, E)

*Bugulina stolonifera* – Ryland 1960, 78–80, Figs. 1 B, 2 G, 6 A–E; Hayward and Ryland 1998, 228–229, Fig. 72 A–D.

*Bugulina stolonifera* – Fehlaue-Ale et al. 2015, 334–337.

**Material:** SERC 232836, Franklin's Bay, Santa Cruz Island, and 310273 Baltra Island, collected April 2016.

**Description:** Colonies erect, tan, biserial, branching pattern Type 3, sometimes Type 4 (Ryland 1960, Figure 1); zooids arising from a stolon, sometimes with a long kenozooid to start; zooids with two outer (very rarely three) and one inner distal spines (2:1), the spine pattern occasionally 2:2 before branching; opesia occupies approximately  $\frac{3}{4}$  of the frontal surface; pedunculate avicularia on zooid outer lateral edge, often above the midline, rostrum rounded, head elongated with flat abfrontal margin; ovicell globular, wider than long; ancestrula with 5 spines: 2 distal pairs and 1 medial at the base of an oval membranous frontal area.  $Lz = 0.560 \pm 0.064$ ,  $Wz = 0.145 \pm 0.017$ ,  $Lav = 0.165 \pm 0.019$ ,  $Wav = 0.137 \pm 0.008$ , ( $N = 5$ );  $Lov = 0.156 \pm 0.004$ ,  $Wov = 0.164 \pm 0.009$ , ( $N = 3$ ).

**Remarks:** Only two Galapagos specimens are in hand for *B. stolonifera*. It has not been previously reported from the Galapagos Islands. The species has often been confused with *Bugulina californica* (Robertson, 1905) which was previously reported from Galapagos. The two species differ in colony shape: *B. californica* forming a spiral and *B. stolonifera* forming tufts; in addition, *B. californica* develops multiserial branches in the distal part of colonies, not seen in *B. stolonifera*. Soule et al. (1995) also noted that *B. californica* has large ( $Lav = 0.18\text{--}0.21$  mm) "bird's head" avicularia occurring on both the inner and outer wall of the zooids at the bifurcations, whereas those in *B. stolonifera* are smaller and only on the outer wall where branches divide. Previous records of *B. californica* from harbors on the North American Pacific Coast are generally thought to be attributable to *B. stolonifera* (Cohen and Carlton 1995). Our work in California suggests that the latter species is widespread in harbors, while we have only documented *B. californica* from a few higher flow locations (Ruiz et al., *unpublished*), not generally in harbors, similar to Soule et al.'s (1995) description of its tendency to be found on outer coasts in areas subject to higher water flow. Thus, the record of *B. californica* from the Galapagos (Osburn 1950) from 32 fms (58.5 m) off San Cristobal Island likely represents either that species or an undescribed deeper-water tropical sibling.

*Bugulina avicularia* (Linnaeus, 1758), another species at times confused with *B. stolonifera*, is the only straw-colored species in the group previously reported from the Galapagos. It differs from *B. stolonifera* in the ancestrular spine pattern, the spiraling colony form, and having avicularia that are larger than the width of the zooid (Hayward and Ryland 1998).

**Distribution:** The recognition of this species as a global invader was delayed by its not having been described until 1960, a situation compounded by its type locality being in a non-native region (Ryland 1960; Ryland et al. 2011). Prior to 1960, *B. stolonifera* was typically identified as *B. avicularia* or

*B. californica*. *Bugulina stolonifera* is native to the Northwestern Atlantic Ocean, ranging from Maine to the Gulf of Mexico. It is a member of a clade restricted to the North Atlantic and Mediterranean (Fehlauer-Ale et al. 2015); *B. stolonifera* is well documented as non-native to Europe and to the Pacific Ocean, and the oldest records by far are on the North American Atlantic coast. This said, its reported very broad range from cold temperate to tropical waters, along with its broad morphological variability (L. McCann, *personal observations*), may suggest a species complex. In addition to being introduced to Europe, including the Mediterranean, as well as to West Africa, it has been carried via shipping to the Indo-Pacific, including the Indian Ocean, New Zealand, Australia, China and Japan, as well as to the Pacific coast of North America.

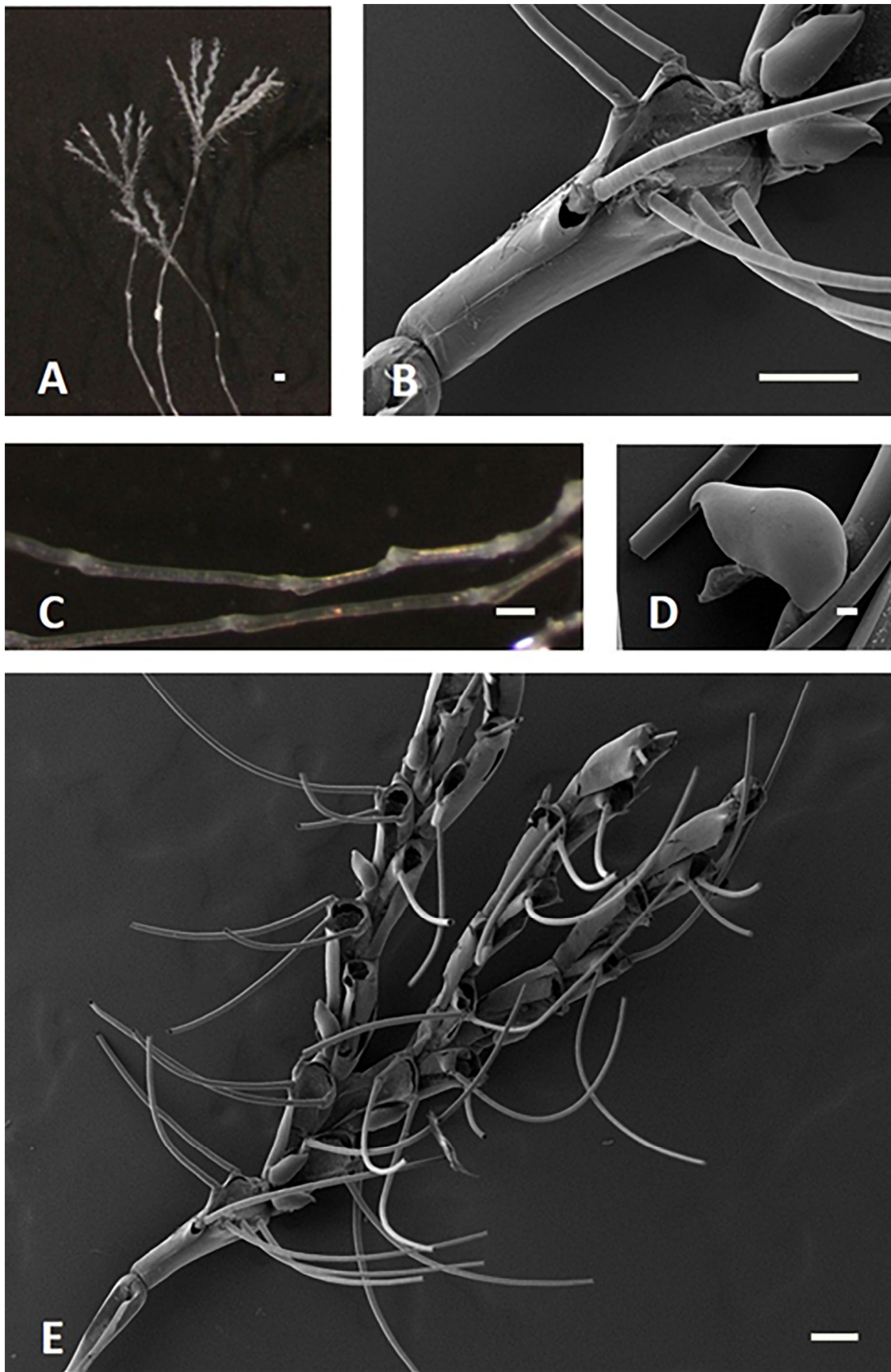
Genus *Caulibugula* Verrill, 1900

***Caulibugula* cf. *dendrograpta* (Waters, 1913)**

(Figure 4A–E)

**Material:** SERC 232740, 310195, 234083, 234093, 310413 (Genbank #MK359643), 310419i, 232756, 232770, 232774, 234090i2, 233024, 233065, 233051, 233007 from Academy Bay, Santa Cruz Island, collected April 2016; *C. armata* Verrill, 1900, SERC 15277 Indian River, Florida, USA (identification by Judith Winston) collected August 2005. Also examined *C. armata*, SERC 19398 Honolulu, Hawaii, USA (LDM determination), collected July 2006.

**Description:** Colony pale, up to 1.5 cm tall, with autozooids originating from a stalk of 5–13 kenozooidal segments; kenozooidal segments with swollen nodes, not ringed, ranging from 0.462–1.369 mm in length and 0.077–0.092 mm in width, usually with a shorter node before branching; 2 branching patterns observed: two new branches arise from a node, one proximally to the other, or one branch arises from the end plate on the previous kenozooid at the base of the node and the other at the top of the short node; bifurcation Type 4; zooids with distal spines: 0–2 jointed (usually 2) outer, 1 inner, strongly curved inward, up to 2 times longer than zooids; pedunculate avicularia infrequent, always at outer base of zooid; first or proximal zooid slightly elongated, frontal membrane oval, usually surrounded by 6 jointed spines: 2 on the left side, 1 proximally and 3 on the right side; 2 more zooids arise from the proximal zooid, one on each side, each with an outer avicularium; from each of these zooids a biserial pair of zooids forms, branches facing out and away from one another forming a “cup-shaped fan” 3.85–4.31 mm in length; ovicell broader than tall, attached to the mid to inner edge of zooid; rhizoids digitiform, arising near the base, extending from first few nodes of stem, but rarely observed;  $Lz = 0.338 \pm 0.039$ ,  $Wz = 0.123 \pm 0.017$ , ( $N = 10$ );  $Lav = 0.117 \pm 0.008$ , ( $N = 5$ );  $Lov = 0.100 \pm 0.011$ ,  $Wov = 0.131 \pm 0.033$ , ( $N = 2$ ).



**Figure 4.** A–E. *Caulibugula* cf. *dendographta*, Academy Bay, Galapagos: A. colonies connected by rhizomes, SERC310419; B. close-up primary zooid, SERC 310413; C. zooid stems showing nodes of variable lengths, SERC310419; D. avicularia, SERC 310413, scale = 10  $\mu$ m; E. colony showing zooids facing outward, SERC 310413. All other scales = 100  $\mu$ m. Photos by L. McCann and SEMs by M. McCuller.



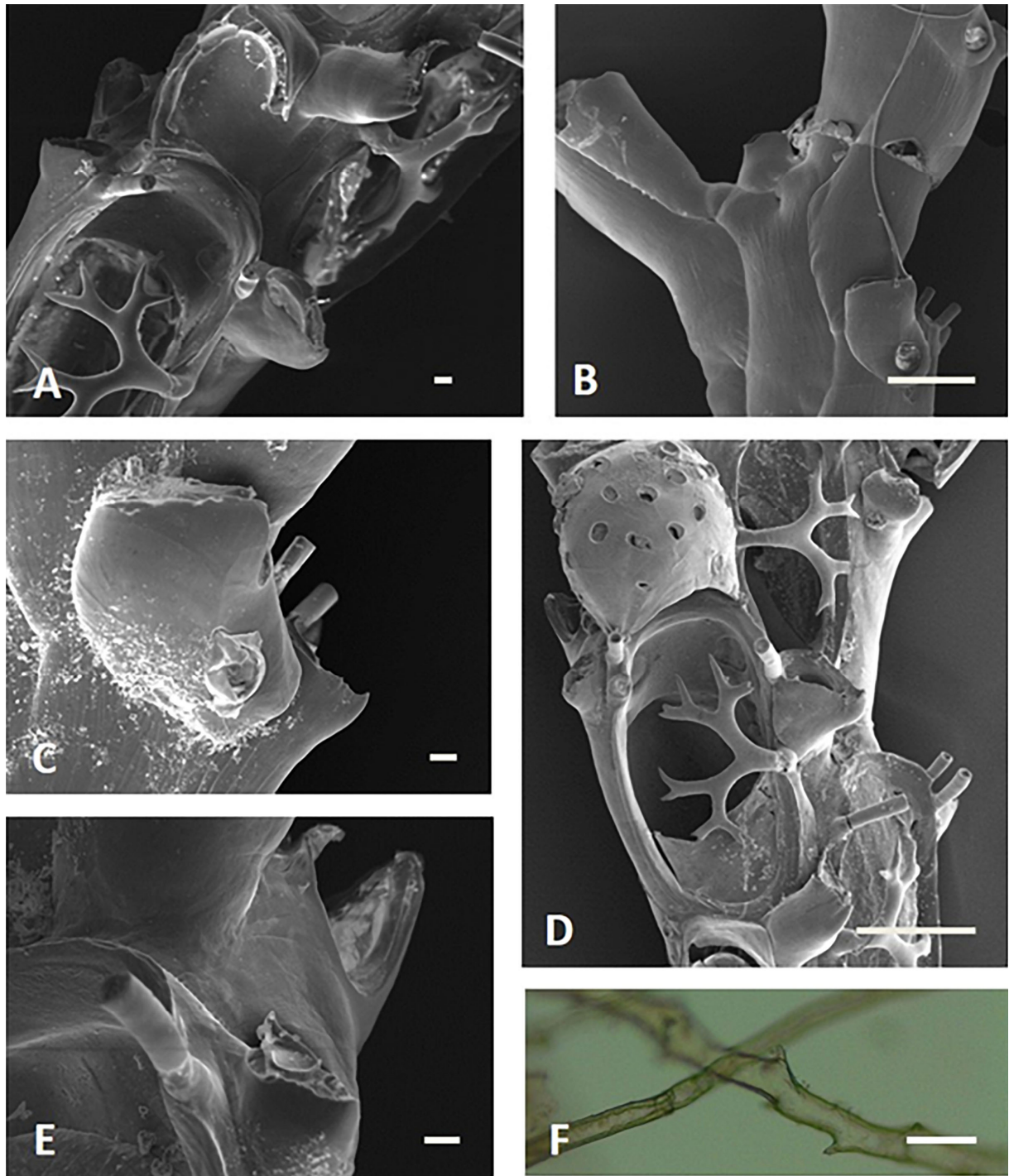
**Remarks:** Specimens examined were small, young colonies, with few secondary branches. Only 2 colonies were reproductive. Our material most closely resembles *Caulibugula dendrograpta* and *C. armata*. Verrill (1900) described *C. armata* as having annulations at the base of each branch, which is not seen in Galapagos specimens. Since Verrill's original description of *C. armata* is very vague, we use the assessment of the type by Maturo (1966). Marcus (1938) attempted to delineate the characters that separate *C. armata* from *C. dendrograpta*, but Maturo (1966) suggested that Marcus' species was actually *C. dendrograpta*. Despite this confusion, the original description of *C. dendrograpta* in Waters (1913) is fairly detailed, although there are no measurements.

Galapagos material exhibit the following differences from *C. dendrograpta*: the number of lateral spines in the proximal zooid varies from 1–3 on each side, whereas *C. dendrograpta* has 8 spines (“5 on one side and 3 on the other,” Waters 1913, p. 470), zooids face outward in the fan cup as opposed to inward in *C. dendrograpta*, and lateral avicularia are positioned at the base of the zooids, while those in *C. dendrograpta* were observed to migrate up the zooid, positioned near the tip of the zooid in older zooids. Both Waters (1913) and Maturo (1966) mention the changing position of the avicularia that characterizes *C. dendrograpta*. Ovicells in Galapagos specimens are also more oblong than globular, as figured in Waters' original description of *C. dendrograpta* (1913, plate 16, Fig. 4). In Galapagos material, zooids are generally shorter and avicularia slightly longer than those described by Maturo (1966) for *C. dendrograpta*.

**Distribution:** *Caulibugula dendrograpta* was described from Zanzibar in the Western Indian Ocean, and at the same time noted from Port Phillip, Melbourne, Australia (Waters 1913). It was further reported from Indonesia, New Guinea, the Philippines, and the South China Sea (Liu 1985; Fransen 1986; Tilbrook 2006). It is regarded as an introduction to the Hawaiian Islands (Zabin 1999; Carlton and Eldredge 2009). It further occurs in both the Eastern Atlantic (Sierra Leone and Cape Verde Islands; Fransen 1986) and the Western Atlantic (North Carolina to Florida, the Caribbean, and Brazil; Osburn 1914; Maturo 1966; Fransen 1986).

Krutwa (2014) reported “*Caulibugula* spp.” from 2009–2011 collections in sublittoral rocky reef habitats off Floreana Island in her doctoral dissertation. While we have yet to confirm that our material is *C. dendrograpta*, the absence of any report of this genus in the Galapagos over more than 115 years of bryozoan collections and research in the Tropical Eastern Pacific, leads us to consider that this species has likely been introduced from the Indo-West Pacific. Its presence in shallow sublittoral rocky reef habitats is in concert with the presence of other introduced species in non-harbor environments in the Galapagos Islands (Carlton et al. 2019).





**Figure 5.** A–F. *Cradoscrupocellaria* sp., SERC 310423, Franklin’s Bay, Santa Cruz Island, Galapagos: A. two types of frontal avicularia; B. vibracula and axial zooid; C. close-up of vibracular chamber and lateral avicularia; D. ventral view showing large branching scutum and ovicell; E. close-up of lateral and large frontal avicularia; F. hooked and non-hooked radicle. Scale A, C, E = 10  $\mu$ m, B, D, F = 100  $\mu$ m. Photos and SEMs by M. McCuller.

Family Candidae d’Orbigny, 1851

Genus *Cradoscrupocellaria* Vieira, Spencer Jones and Winston, 2013

***Cradoscrupocellaria* sp.**

(Figure 5A–F)

**Material:** SERC 310423, Franklin’s Bay, and SERC 184064, Academy Bay, Santa Cruz Island, collected April 2016.

**Description:** Colony erect, jointed, branching with 7–17 zooids per node, but usually 9 or 11; zooids slender at base, widening distally, with 1 inner and 1–3 (rarely 3, often 2 on non-ovicellate zooids) unbranched outer distal spines; scutum attached medially and present in nearly all zooids, narrow, branching 3 times, forming 7–13 slender, pointed tips which are sometimes forked; lateral avicularium small, at distal outer margin; frontal avicularia dimorphic, most small, often raised and below the opesia oriented transversely, but sometimes larger avicularia present on basal lateral edge of opesia directed forward, with hooked rostrum variable in size; cryptocyst present, narrow; opesia rectangular with rounded corners, occupying 2/3rds of the frontal wall; vibraculum chamber slightly rounded at base and straight, transverse at the top; one axial vibraculum, 3 axial spines; rhizoids often smooth but sometimes with hooks part of their length (Figure 5F), extending perpendicularly from basal side of branches; ovicell irregularly porous.  $Lz = 0.441 \pm 0.048$ , (N = 9);  $Wz = 0.183 \pm 0.021$ , (N = 14);  $Lop = 0.300 \pm 0.027$ , (N = 12);  $Lov = 0.185 \pm 0.013$ ,  $Wov = 0.171 \pm 0.018$ ,  $Lsc = 0.115 \pm 0.016$ ,  $Wsc = 0.145 \pm 0.024$ ,  $Llav = 0.051 \pm 0.012$ ,  $Wlav = 0.063 \pm 0.010$ , (N = 9);  $Lfav = 0.161 \pm 0.008$ ,  $Wfav = 0.120 \pm 0.026$ ,  $Lv = 0.090 \pm 0.004$ ,  $Wv = 0.090 \pm 0.008$ , (N = 6).

**Remarks:** *Cradoscrupocellaria bertholletii* (Audouin, 1826) has been reported extensively worldwide (including in the Galapagos) and exhibits a great deal of variability in characters over this range. Vieira et al. (2013) redescribed the species to try to resolve some of the taxonomic issues, erecting several new species. Hastings' (1930) Galapagos nominal *C. bertholletii* (as *Scrupocellaria bertholletii*) specimens were separated into 2 species: *C. galapagensis* and *C. hastingsae* (Vieira et al. 2013). The Eastern Pacific variant, *C. bertholletii tenuirostris* (Osburn 1950), was elevated to species rank based on its elongate frontal avicularia and more highly branched scutum (Vieira et al. 2013). Our specimens are similar to *C. tenuirostris*, but they do not have the unique, elongate frontal avicularia. Our zooids are also narrower and in mature colonies there are more zooids per node. The other species in the Galapagos can be distinguished from our material as follows: *Cradoscrupocellaria galapagensis* has more distal spines, a longer scutum with more points, and zooids are shorter and slightly wider, while *C. hastingsae* differs in having wider zooids, a more strongly hooked rostrum in the large frontal avicularia, and the scutum is rarely trifurcate and often lacking. Our material is also similar to a species in Pacific Panama, *C. osburni*, but that species has 6–7 distal spines and 6 axial spines, while the Galapagos specimens have at most 4 distal spines and 1 axial spine. *Cradoscrupocellaria gorgonensis* Vieira, Spencer Jones and Winston, 2013, from Gorgona Island, Colombia, has more distal spines and the scutum only bifurcates twice. None of these species has hooked rhizoids.

Our specimens appear to be most similar to *C. atlantica* Vieira, Spencer Jones and Winston, 2013 (from Brazil and Florida) with the only difference being more zooids per internode in mature colonies, occasional presence of hooked rhizoids, and the number of distal spines: 2–4 in Galapagos material and 4–5 in *C. atlantica*. All of these characters can be variable within a colony and the hooked rhizoids were seen only once, and only on a small section of otherwise smooth rhizoids. Genetic analysis may further help to distinguish these species.

**Distribution:** Previous records of *C. bertholletii* from the Galapagos have been reexamined by Vieira et al. (2013) and were determined to be other species as noted above. Vieira et al. (2013) restricts *C. bertholletii* to the Atlantic-Mediterranean region and New Zealand, making it unlikely that, even if all of Osburn’s material was not re-examined, *C. bertholletii* was ever present. Regardless, this is the first record of a “*bertholletii*”-like cradoscrupocellarid from Santa Cruz Island. The records of *C. bertholletii* reported by Powell (1971) from Panama are likely to be re-assigned to one or more of the above species as well. We are also re-examining additional material from ongoing Panama biofouling studies (Ruiz et al., *unpublished*).

If the Galapagos species is, in fact, *C. atlantica*, this would extend its range to the Pacific Ocean.

Superfamily Schizoporelloidea Jullien, 1883

Family Hippopodinidae Levinsen, 1909

Genus *Hippopodina* Levinsen, 1909

***Hippopodina tahitiensis* (Leca and d’Hondt, 1993)**

(Figure 6A–C)

*Hippopetraliella tahitiensis* – Leca and d’Hondt 1993, 401–409, Pl 1, Figs. 1–8, Table 1.

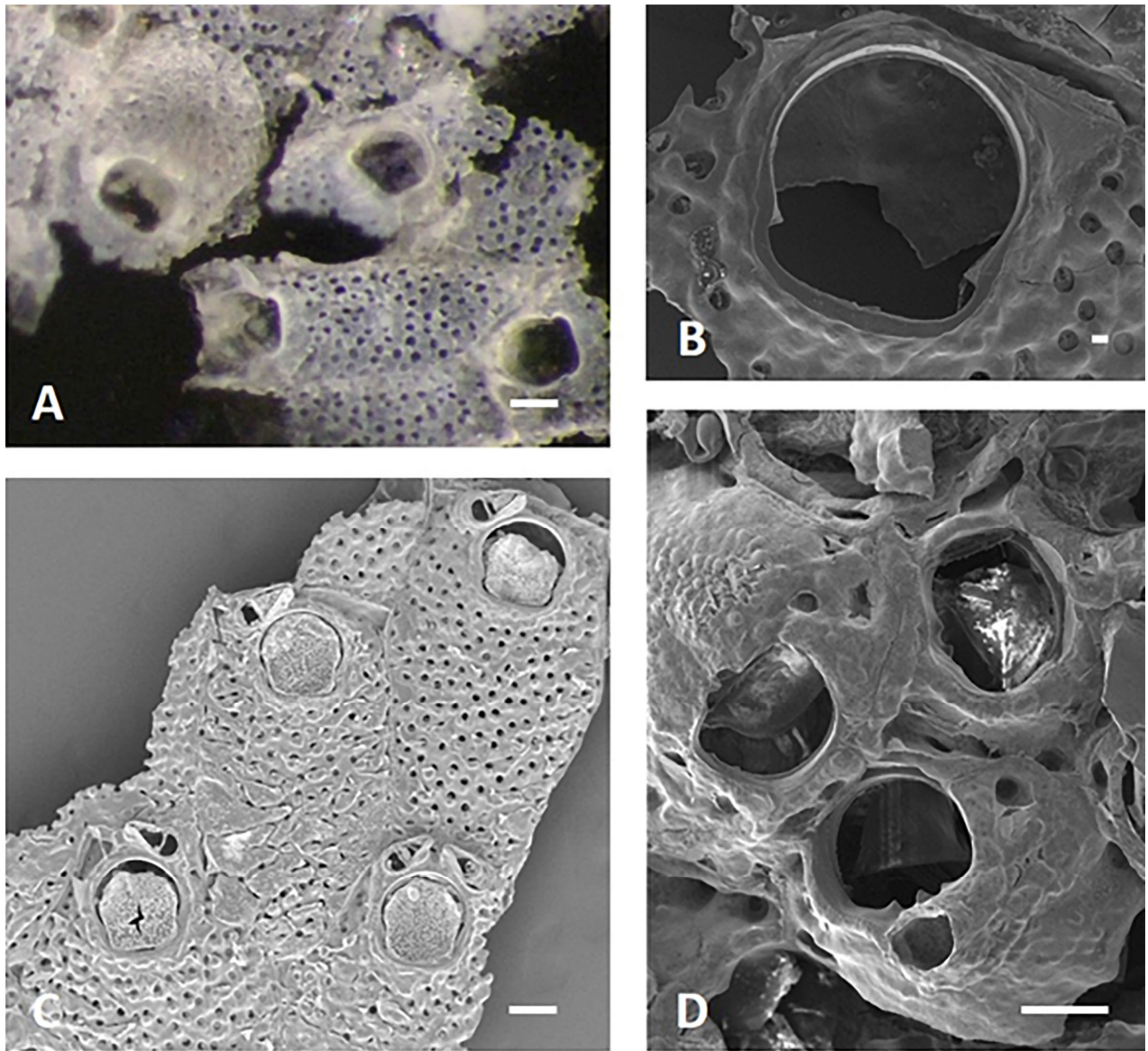
*Hippopodina viriosa* – Tilbrook 1999, 455, Fig. 2 b, d, f; Tilbrook et al. 2001, 90, Fig. 18 C.

**Material:** SERC 234219, 311591 (Genbank #MK359649), 232878, 310427 Baltra Island, 232905 Franklin’s Bay, Santa Cruz Island, collected April 2016; SERC 138269 Taboguilla Island, Pacific Panama, collected September 2008.

**Description:** Zooids encrusting, rectangular, frontal wall covered with small pseudopores approximately 0.015 mm wide; primary orifice hoof shaped, rounded distally, slightly narrower proximal margin, generally straight; lateral condyles present; avicularia short and stout, usually single but occasionally paired or lacking, typically placed above and distolaterally to the midline of the orifice, directed medially; ovicells flat and embedded, evenly perforated with irregularly-sized pseudopores; ancestrula not observed.  $Lz = 0.763 \pm 0.0953$ ,  $Wz = 0.496 \pm 0.063$ ,  $Lor = 0.215 \pm 0.015$ ,  $Wor = 0.199 \pm 0.012$ , (N = 8);  $Lav = 0.137 \pm 0.008$ ,  $Wav = 0.065 \pm 0.004$ , (N = 5).

**Remarks:** This species is very similar to *H. irrikiensis* Tilbrook, 1999, which also occurs in the Pacific (Tilbrook 2006; Ruiz et al., *unpublished*), but the latter has a triad ancestrula, a more oval shaped orifice with a concave





**Figure 6.** A–C. *Hippopodina tahitiensis*, SERC 234219, Baltra Island, Galapagos: A. zooid with ovicell in upper left; B. orifice; C. zooids with 2 avicularia. D. *Celleporaria inaudita*, zooids showing variability in orifice and sinus, SERC 310197, Academy Bay, Galapagos. All scales = 100  $\mu$ m. Photo by L. McCann and SEMs by M. McCuller.

border, and longer, narrower avicularia. The specimens in Galapagos match the original description of *H. tahitiensis* well, although the avicularia and orifice on Galapagos specimens are slightly wider and we were not able to verify the form of the ancestrula.

**Distribution:** *Hippopodina tahitiensis* was described from French Polynesia; since then, through re-assignments of records formerly under the name *H. feegeensis* (MacGillivray, 1891) and synonymies, it has been widely reported throughout the Indo-Pacific region as far north as Japan (Tilbrook 1999, 2006), including being regarded as introduced to the Hawaiian Islands (Carlton and Eldredge 2009). While Tilbrook (2006) assigned earlier records in Hawaii by Soule and Soule (1968, as *H. feegeensis*) to this species, we note that their description and figure present characters, such as dimorphism in the orifice of ovicelled zooids and long avicularia that

“may touch distally behind aperture”, which are not attributed to *H. tahitiensis*. Nevertheless, material assignable to *H. tahitiensis* is found in Hawaii (Carlton and Eldredge 2009; Ruiz et al., *unpublished*).

The present material represents the first published record of this species in the Eastern Pacific Ocean, although ongoing biofouling studies have recently also documented this species on the Pacific coast of Panama (Ruiz et al., *unpublished*). *Hippopodina tahitiensis* ranges widely throughout the Indo-West Pacific Ocean, which we take to be the native region. It has also been reported from the Western Atlantic (Colombia, the West Indies, and Brazil (Tilbrook 1999, 2006)) where we regard it as introduced. Given its fouling nature and the presence of additional outlier populations in the Hawaiian Islands (Carlton and Eldredge 2009), we regard it as likely introduced to the Tropical Eastern Pacific as well.

Superfamily Lepralielloidea Vigneaux, 1949

Family Lepraliellidae Vigneaux, 1949

Genus *Celleporaria* Lamouroux, 1821

***Celleporaria inaudita* Tilbrook, Hayward and Gordon, 2001**

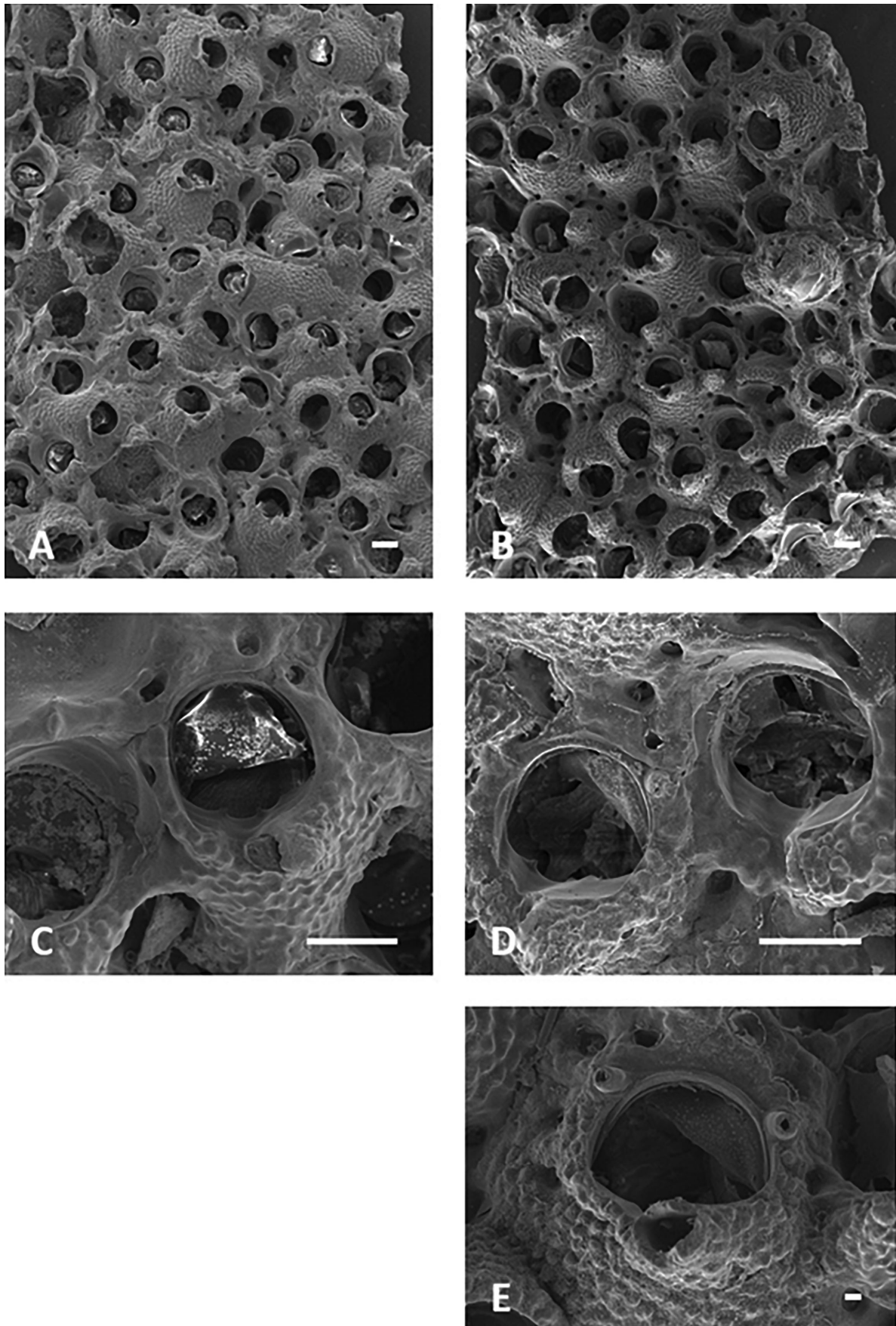
(Figures 6D, 7A–E, 8A–D)

*Celleporaria inaudita* – Tilbrook et al. 2001, 72–73, Fig. 13 D–F.

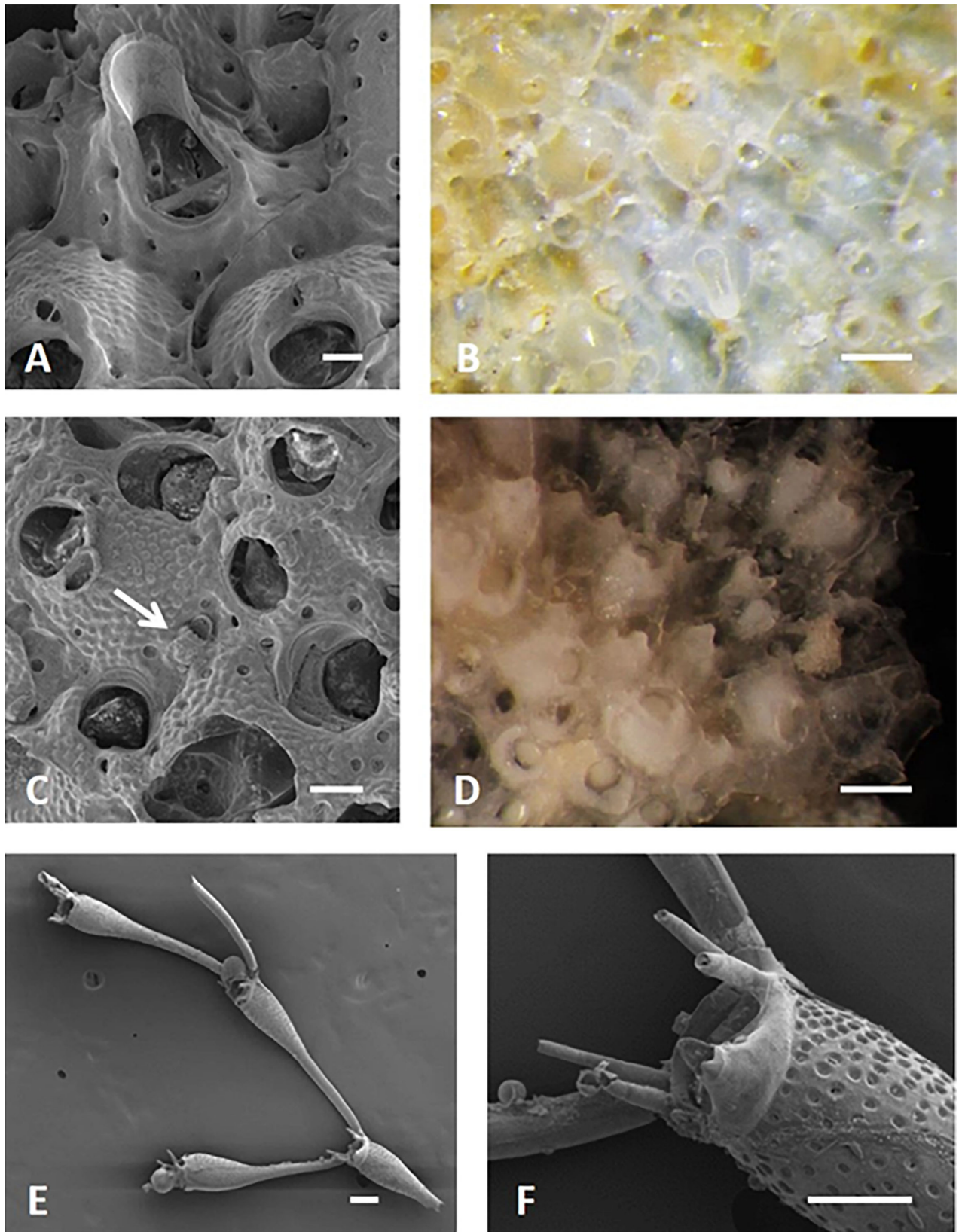
**Material:** SERC 158518, 232791, 232733, 234095, 234079, 310419 (Genbank #MK359647), 310412 (Genbank #MK359646), 310197 (Genbank #MK359644), 232771, 233030, 310262 (Genbank #MK359645), 233066, 233047, 234092 (Genbank #MK359648), Academy Bay, collected April 2016; SERC 158507 Tortuga Bay, collected February 2015; SERC 232814, 311826, 233111, 311925, 232837, 232901 Franklin’s Bay, Santa Cruz Island; SERC 234196 Baltra Island, collected April 2016; also SERC 2614 collected in February 2015 from Baltra Island dock biofouling.

**Description:** Colony encrusting, uni- to multilaminar; zooids pale pink to peach colored in life (Figure 8B) and retaining slight tan color in preserved material; frontal wall nodular with distinctive widely-spaced marginal pores, usually obscured by secondary calcification and frontal budding; sub-oral avicularia with serrated edge, often raised into a point; primary orifice the same size as, or slightly wider than, long, with 0 to 3 shallow sinuses and area between sinuses pointed or blunt, rarely tooth like, one cusp almost always much larger than the other; oral spines rare, commonly present on growing edge (see detailed remarks below); adventitious avicularia scattered, large but size variable, serrated edge sometimes present, widest at the crossbar and rounded distally, mandible strongly chitinized; ovicells nodular, broadly open, cap-like, ova pale purple.  $Lz = 0.448 \pm 0.093$ ,  $Wz = 0.320 \pm 0.072$ , ( $N = 28$ );  $Lor = 0.133 \pm 0.013$ ,  $Wor = 0.153 \pm 0.017$ , ( $N = 19$ );  $Lav = 0.268 \pm 0.082$ ,  $Wav = 0.180 \pm 0.024$ , ( $N = 14$ );  $Lov = 0.213 \pm 0.031$ ,  $Wov = 0.244 \pm 0.022$ , ( $N = 3$ ).





**Figure 7.** A–E. *Celleporaria inaudita*, Galapagos: A. view of whole colony, SERC 311826; B. view of another colony, SERC 234079; C. zooid with 2 irregular sinuses, SERC 310419; D. orifice with 2 irregular sinuses and possible spine scar middle, SERC 234079; E. close-up of orifice showing spines, SERC 234079 scale = 10  $\mu\text{m}$ . All other scales = 100  $\mu\text{m}$ . SEMs by M. McCuller.



**Figure 8.** A–D. *Celleporaria inaudita*, Galapagos: A. adventitious avicularia, SERC 311826; B. live colony, SERC 311925; C. close-up of zooid with proximal frontal avicularia (arrow), SERC 310419; D. zooids showing suboral avicularia raised into an umbo and open ovicells lower left, SERC 234079. E–F. *Savignyella lafontii*, colony and close-up, SERC 232827, Galapagos. Scale: B and D = 500  $\mu$ m. All other scales = 100  $\mu$ m. Photos by L. McCann and SEMs by M. McCuller.



**Remarks:** A common fouling species. It was often quite abundant in our study, dominating space on panels. It is very similar to the Caribbean species *Celleporaria sherryae* Winston, 2005, except for the presence of spines around the orifice, and in having slightly shorter zooids. However material of *C. sherryae* was limited in the original description (Winston 2005) and only one of 6 images shows spines (pg 53, Figure 142), so it is difficult to assess how variable the presence and number of spines may be in this species. Winston (2005) indicated that *C. sherryae* has up to 4 or more spines and Harmelin (2014) noted that the oral spines were typically 4, but occasionally up to 5–6, or only 2 when the distal spines were submerged in secondary calcification (see also Lezzi et al. 2015, Table 1). Material from Pacific Panama identified as *C. sherryae* (Ruiz et al., *unpublished*) by the first author (LDM) exhibits spines on the growing edge in some zooids, but are not present on most zooids in older, multi-laminar colonies, nor are there scars discernable under the dissecting microscope (see also Harmer 1957, p. 34). The same is true of Galapagos material, as when spines were present in colonies, they were extremely rare and variable in number, further suggesting that using spines for diagnostic purposes may be difficult in mature colonies.

In one zooid of one colony (Figure 8C and SERC 310419), we observed a small proximo-laterally placed avicularium that otherwise looked much like the suboral avicularia. This is not mentioned in descriptions of *C. sherryae* or *C. inaudita* and was seen only once, despite our examination of many colonies. The presence and form of the sinus (Figures 6D; 7C, D; 8A, C) was quite variable within a colony, ranging from 0–3 sinuses of various shapes and sizes (also see Souto et al. 2016, Fig. 2E–H). Also notable was the variation in the size of the orifice and its relative proportions. Colonies with and without spines were very similar in size and, although spineless zooids within colonies were slightly longer and wider on average, this variability was within the standard deviation of the measurements. In general, Galapagos material is slightly smaller than measurements of either *C. inaudita* or *C. sherryae* from the literature (Tilbrook et al. 2001; Winston 2005). For now, we chose to be conservative and include our material under the older name from the Pacific, *C. inaudita*, and await further genetic and morphological work to determine if this actually represents more than one species.

Five other *Celleporaria* have been reported from the Galapagos previously: *C. hancocki* (Osburn, 1952), *C. albirostris* (Smitt, 1873), *C. brunnea* (Hincks, 1884), *C. quadrispinosa* Canu and Bassler, 1930 and *C. peristomata* (Osburn, 1952). *Celleporaria inaudita* can be differentiated from *C. albirostris*, *C. peristomata* and *C. hancocki* by their lack of any kind of orificial sinus; the last species also has giant interzoecial avicularia. *Celleporaria brunnea* has a single distinctive sinus, brown tissue and anvil-shaped adventitious avicularia. This is the first record of *C. inaudita* in the Galapagos Islands.

**Distribution:** *Celleporaria inaudita* was described from Vanuatu in Melanesia (Tilbrook et al. 2001) where it was also common. It has since been reported as far east as the Red Sea (Ostrovsky et al. 2011) and as far north as the South China Sea (as *C. paratridenticulata* Liu et al. 2001, synonymized by Tilbrook 2006). Newly reported as invading the Eastern Atlantic Ocean, it was first detected in 2013 in Madeira (Souto et al. 2016). Given its primarily Indo-West Pacific distribution and its absence in any of the previous surveys from the Galapagos, despite its great abundance in our surveys, we suggest it is likely introduced to the Galapagos marine fauna.

Superfamily Catenicelloidea Busk, 1852

Family Savignyellidae Levinsen, 1909

Genus *Savignyella* Levinsen, 1909

***Savignyella lafontii* (Audouin, 1826)**

(Figure 8E, F)

*Eucratea lafontii* – Audouin 1826, 242.

*Catenaria lafontii* – Hastings 1930, 732.

*Savignyella lafonti* – Osburn 1952, 288, Pl 31, Fig. 3

**Material:** SERC 232845, 234220, 234176, 232888, 121854 Baltra Island; SERC 234145, 234146, 232827 Franklin’s Bay, Santa Cruz Island, collected April 2016.

**Description:** Colony erect, branching in uniserial chains, pale brown to brick colored in life; branches jointed; zooids tear-drop shaped, thin tubes proximally, becoming inflated and porous distally; peristome raised, with 4 spines; suboral avicularium sometimes present; ovicells porous.  $Lz = 1.218 \pm 0.158$ ,  $Wz = 0.231 \pm 0.707$ , (N = 5).

**Remarks:** A distinctive species and the only member of the genus.

**Distribution:** Reported worldwide in warm oceans, a distribution highly suggestive of either a cryptic species complex requiring genetic elucidation or of a widely-distributed introduced species of as-yet unknown provenance. Common at Baltra Island and occasionally seen in Franklin’s Bay on Santa Cruz Island. It was previously reported from the Galapagos from Tagus Cove, Isabela (Albemarle) Island based upon Hancock dredgings in 1933. Elsewhere in the Eastern Pacific it is known from Panama, Colombia, and southern California (Osburn 1953 and references therein). It is regarded as a weedy, introduced harbor species in the Hawaiian Islands (Carlton and Eldredge 2009), Australia (Wyatt et al. 2005), and elsewhere. While we believe that it is very unlikely to be native to the tropical Eastern Pacific, the possibility of a species complex being present in the Islands leads us to regard it as a cryptogenic species.

Superfamily Schizoporelloidea Jullien, 1883

Family Schizoporellidae Jullien, 1883

Genus *Schizoporella* Hincks, 1877

***Schizoporella pungens* (Canu and Bassler, 1928)**

(Figures 9A–F; 10E, F)

*Schizopodrella pungens* – Canu and Bassler 1928, 94–95, Pl 27, Figs. 5–12, 15 a–c.

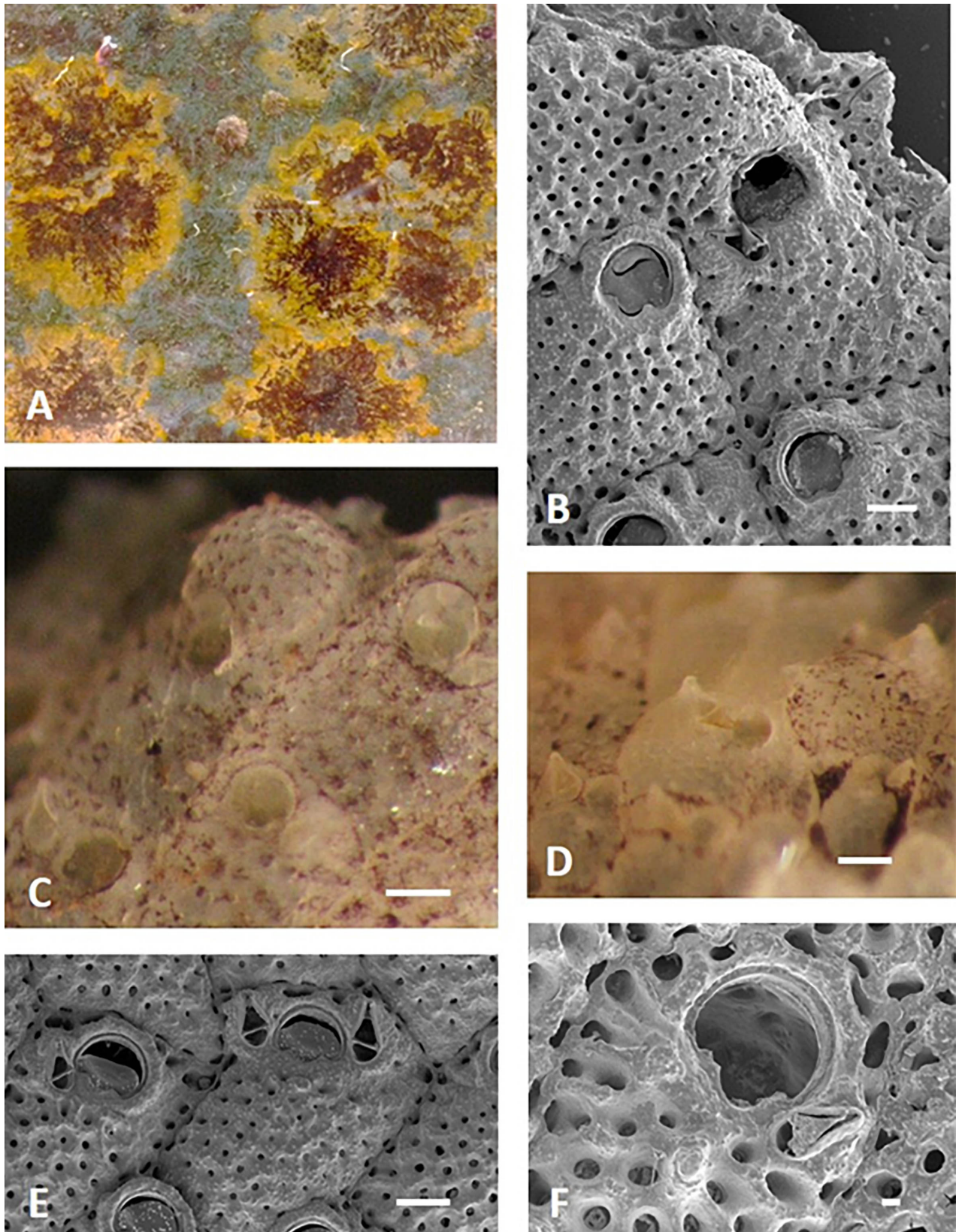
*Schizoporella pungens* – Winston 2004, 8–9, Fig. 7; Winston 2005, 67–68, Figs. 179–186.

**Material:** SERC 2560 (Genbank #MK359651), 2610, 2632 (Genbank #MK35950), 15806 Tortuga Bay, collected February 2015 and SERC 232745, 310420 (Genbank #MK359653), 234094, 234073, 232846, 234053, 311588, 311589 (Genbank #MK359655), 233063, 233037, Academy Bay, and SERC 232902 Franklin’s Bay, Santa Cruz Island; SERC 233076, 234174, 232892, 232883, 310428 (Genbank #MK359654), 309426, 311920 (Genbank #MK359656), Baltra Island, collected April 2016. SERC 180935 Bermuda, collected October 2013, (identification by Judith Winston). Also examined were *Schizoporella errata* bryoliths from San Francisco Bay, CA, USA.

**Description:** Colony encrusting, extensive, unilaminar, color distinctive, pigmented with varying degrees of dark purple “star bursts” in older zooids, sometimes becoming solid purple, “chains” of zooids with little or no pigment randomly scattered throughout the colony, color orange at the growing edges; zooids usually almost square, but can be quite variable in shape and size, separated by furrows and ridges; one avicularium, rarely two, present next to and slightly below the orifice, orientation always greater than 45° from the midline, pointing distolaterally, to occasionally laterally, rarely proximo-laterally, sometimes elevated and enlarged, distinctly hooked at the tip, rostrum sometimes curved; becoming hyperstomial in older colonies; frontal wall covered with approximately 40 small pseudopores (N = 5) varying in size from 0.015–0.031 mm; orifice slightly longer than wide with a narrow, U-shaped sinus variable in width (N = 11, 0.0462–0.0923 mm); condyles prominent, rounded, directed laterally or slightly distally; no spines present; peristome granular and slightly raised in older colonies; ovicells slightly flattened globes, no lateral ridges, perforated by tiny evenly-spaced pseudopores, sometimes with a very slight central umbo, becoming embedded in older colonies; ancestrula slightly smaller than other zooids, with 8 spines around orifice. Standard measurements are compared with *S. errata* (Waters, 1878) in Table 2.

**Remarks:** The taxonomy of this group still requires extensive work. *Schizoporella pungens*, originally described from the Gulf of Mexico (Canu and Bassler 1928, as *Schizopodrella pungens*), has often been confused with *S. errata*, described from the Mediterranean. These species are part of a complex of related species, including *S. serialis* (Heller, 1867) and *S. isabelleana* (d’Orbigny, 1842) (both synonymized with *S. pungens* (Winston 2005)), *S. violacea* (Canu and Bassler, 1930) (synonymized with *S. errata* (Hayward





**Figure 9.** A–F. *Schizoporella pungens*, Santa Cruz Island, Galapagos: A. several colonies up to 5.5 cm across on a plate from Franklin’s Bay; B–E. SERC 311589; B. zooid showing hyperstomial ovicell; C. ovicell with slight umbo in center; D. lateral view of avicularia; E. orifice and avicularia; F. close-up of zooid, SERC 310420. Scale B–E =100  $\mu$ m, F=10  $\mu$ m. Photos by L. McCann and SEMs by M. McCuller.

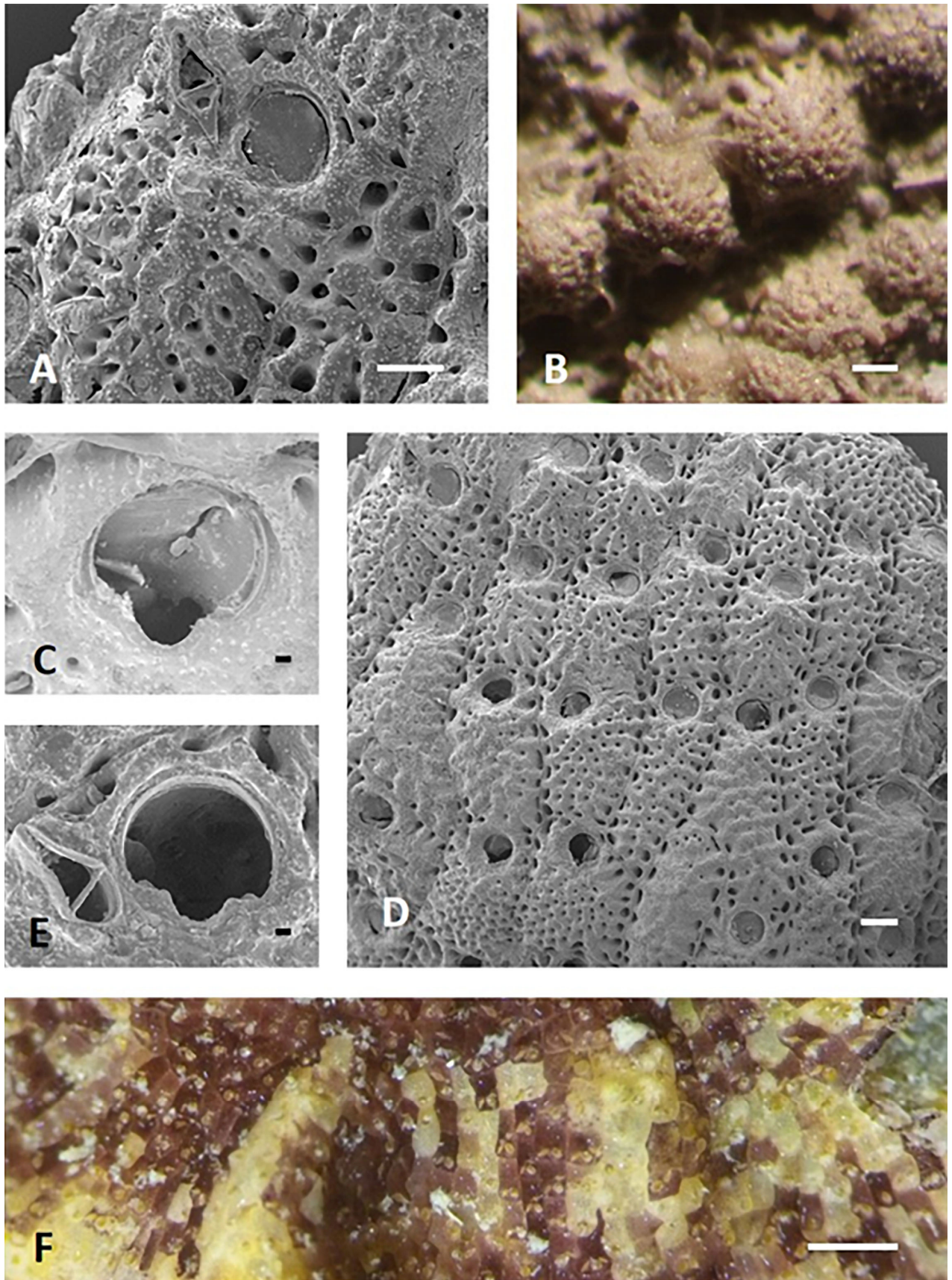
**Table 2.** *Schizoporella* measurements. *Schizoporella pungens*, including Galapagos material from this study (5 colonies measured for all characters except ovicells which were measured on 2 colonies); type material from Florida (Canu and Bassler 1928); additional material from Florida (Winston 2005); *Schizoporella errata*, from San Francisco Bay, California (5 colonies measured for all characters except ovicells and avicularia which were measured on 4 and 2 colonies respectively), and the topotype from Bay of Naples, Italy (Tompsett et al. 2009). Blank fields indicate no data are available.

<i>Schizoporella pungens</i>								
Santa Cruz Island, Galapagos								
This study	Lz	Wz	Lor	Wor	Lav	Wav	Lov	Wov
N	30	30	30	30	22	22	9	9
Mean	0.487	0.326	0.137	0.138	0.141	0.068	0.254	0.281
St Dev	0.095	0.078	0.013	0.013	0.037	0.019	0.048	0.043
Range	0.308–0.677	0.200–0.477	0.108–0.154	0.108–0.161	0.077–0.246	0.038–0.108	0.231–0.354	0.231–0.400
Florida, USA (cotypes)								
Canu and Bassler 1928	Lz	Wz	Lor	Wor	Lav	Wav	Lov	Wov
Range	0.60–0.75	0.30–0.40	0.14–0.15	0.12				
Florida, USA								
Winston 2005	Lz	Wz	Lor	Wor	Lav	Wav	Lov	Wov
N	6	6	6	6	6	6		
Mean	0.6	0.48	0.13	0.15	0.13	0.06		
St Dev	0.03	0.09	0.01	0.01	0.05	0.02		
Range	0.576–0.648	0.378–0.63	0.117–0.144	0.126–0.162	0.09–0.216	0.036–0.09		
<i>Schizoporella errata</i> bryoliths								
San Francisco Bay, California, USA								
This study	Lz	Wz	Lor	Wor	Lav	Wav	Lov	Wov
N	25	25	25	25	7	7	15	15
Mean	0.554	0.371	0.134	0.142	0.147	0.064	0.317	0.359
St Dev	0.074	0.079	0.031	0.033	0.020	0.023	0.039	0.048
Range	0.446–0.738	0.261–0.554	0.115–0.185	0.123–0.185	0.123–0.169	0.054–0.107	0.231–0.369	0.261–0.431
Italy, Mediterranean								
(topotype) Tompsett et al. 2009								
	Lz	Wz	Lor	Wor	Lav	Wav	Lov	Wov
N	31	31	25	26	10			
Mean	0.494	0.371	0.147	0.154	0.137			
St Dev	0.043	0.071	0.011	0.015	0.019			
Range	0.381–0.558	0.263–0.508	0.125–0.172	0.125–0.181				

and Ryland 1999)), *S. pseudoerrata* Soule, Soule and Chaney, 1995 (likely synonymous with *S. errata* (Matthew Dick, *personal communication*)), *S. erratoidea* Liu, Xueming and Jianghu, 2001, *S. variabilis* (Leidy, 1855), and possibly *S. mazatlantica* (Busk, 1856) if the latter is a valid species. There is a great degree of character overlap and inconsistencies in literature descriptions of all of these species.

In our Galapagos material, many of the characters are extremely variable within a single colony (Lz, Wz, Lav, Wav, width of the sinus, and orientation and size of the avicularia, for example). Winston (2004) suggested that the ancestrula, presence of ridging on the ovicells, and budding pattern may be of use in morphologically distinguishing the species. Although in both *S. errata* and *S. pungens* the ancestrula has 8 spines, Winston (2005) indicated that they “differ slightly, in terms of orifice shape and position of the spines.” Unfortunately, we had only one colony with an





**Figure 10.** A–D. *Schizoporella errata* bryolith, San Francisco Bay, California, USA and E, F. *Schizoporella pungens*, SERC 310420, Academy Bay, Santa Cruz Island, Galapagos: A. mature colony avicularia and orifice; B. ovicells with side ridges; C. orifice; D. view of colony; E. orifice and avicularia; F. live colony on plate showing “ladders” of unpigmented zooids. Scale C and E = 10  $\mu$ m, A, B, D and F = 100  $\mu$ m. Photos by L. McCann and SEMs by M. McCuller.

ancestrula in Galapagos material. Our specimens from Panama do have a wider, shorter orifice in the ancestrula than that pictured for *S. errata* in Hayward and Ryland (1999) (there are no ancestrulae in the lectotype and associated material of *S. errata*, according to Tompsett et al. (2009), and thus we refer for comparison to page 213, figure 86C, in Hayward and Ryland (1999)). Winston (2005) also states that *S. pungens* has a shorter and broader orifice than *S. errata*. The co-types of Canu and Bassler (1928) have an orifice narrower in width than length, but unfortunately we have no record of how many measurements this represents nor the standard deviation.

Although very few colonies had ovicells, none of the Galapagos material exhibited “prominent” lateral ridges on the ovicells. Both *S. errata* and *S. pungens* have been described as having lateral ridging on the ovicells. Hayward and Ryland (1999, fig. 86B) and Ryland et al. (2014, fig.10C) illustrate ridging on *S. errata*, and we have seen pronounced lateral ridges on some ovicells in bryolith specimens from San Francisco Bay (Figure 10A–D) that were morphologically and genetically identified as *S. errata* (Zabin et al. 2010). Winston (2005) noted ovicell ridges for *S. pungens* only “in early stages.” Tompsett et al. (2009) describes the ovicell as unridged in the topotype of *S. errata*, but his figure (Fig. 4E) is not clear on this point; there were no ovicellate zooids in the type material. Canu and Bassler (1928) did not report ovicell ridging in their original description of *S. pungens*, simply describing the ovicell as “large, globular and porous.” Thus, this character remains unclear as a distinction between the two species.

COI analysis of six different specimens collected from all 4 sites in the Galapagos during both years did not match any record in Genbank at a 95% threshold (including material identified as *S. errata* from both Australia and San Francisco Bay, CA), a degree of similarity often used for assigning species identity when using the COI gene as a marker. Morphological examination of *S. errata* from San Francisco Bay (Figure 10A–D) also suggests that the Galapagos species is different, both in individual zooid morphology and in growth characteristics of the whole colony (Table 2). *Schizoporella pungens* usually forms large, single or multilayered, sometimes “massive” (Winston 2004) crusts rather than the free form, mounded bryoliths that often characterize *S. errata* (Ferdeghini et al. 2000; Zabin et al. 2010).

Earlier surveys in Pacific Panama (Hastings 1930; Powell 1971; collections by A. Herrera in 1985 [see Methods]) and the Galapagos (Hastings 1930; Osburn 1952) found no *Schizoporella* in this species group. *Schizoporella pungens* has only recently (2008) been documented in Pacific Panama, near the Panama Canal mouth (Ruiz et al., *unpublished*), presumably having arrived as ship hull fouling from the Caribbean, where *S. pungens* is extremely abundant. Fossil material of a similar morphology is present in



Pliocene material from Jamaica (Taylor and Foster 1998, as *S. errata*), but not in Europe or the Pacific. For these reasons we have chosen to use the Caribbean name while awaiting a comprehensive genetic and morphological analysis of this and related material.

**Distribution:** In addition to the Galapagos, the first author (LDM) has examined material from the Hawaiian Islands, Pacific (as noted above) and Atlantic Panama, all of which appear to be *S. pungens*. This material, too, awaits further integrated taxonomic work combining morphological and molecular analyses.

Superfamily Smittinoidea Levinsen, 1909

Family Watersiporidae Vigneaux, 1949

Genus Watersipora Neviani, 1896

***Watersipora subtorquata* [d'Orbigny, 1852] sensu Vieira et al. 2014a**

(Figure 11A–C)

*Escharina torquata* – d'Orbigny 1852, Pl 4, Figs. 2–3.

*Watersipora cucullata* – Hastings 1930, in part, 729–730, plate XV, Figs. 102–104; Osburn 1950, in part, 472–473, Pl 56, Figs. 1 and 4

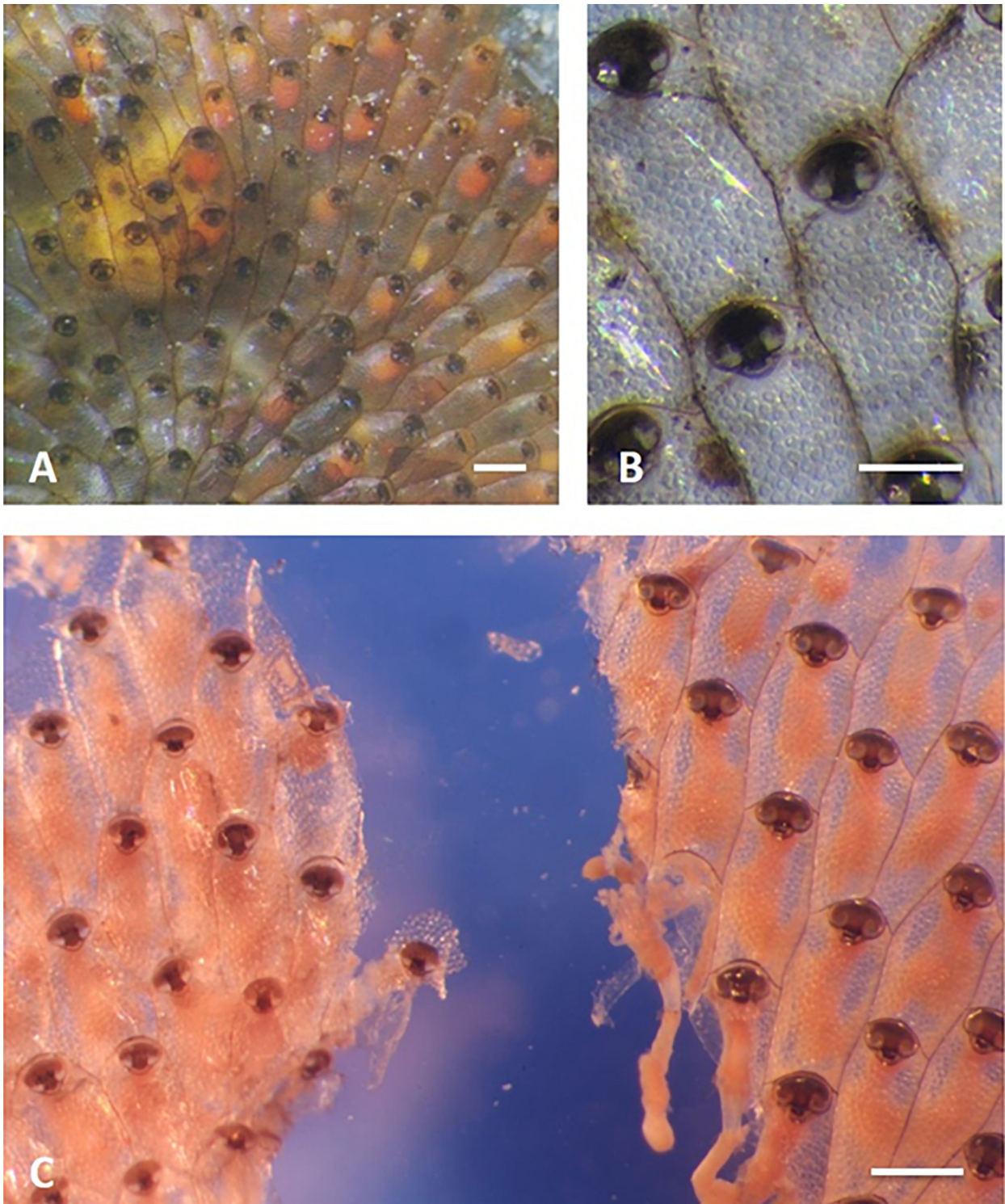
*Watersipora subovoidea* – Ryland et al. 2009, 54–55, Fig. 4 c–d, g–h, Table 1–2.

*Watersipora subtorquata* – Vieira et al. 2014a, 155–162, Figs. 1–5, 12–15, 18–24.

**Material:** SERC 234068 Academy Bay, SERC 232903, 233132, 234147 Franklin's Bay, Santa Cruz Island collected April 2016; SERC 2541, 2554, 2555, 2610 Tortuga Bay, Santa Cruz Island, collected February 2015; SERC 232847, 310268 (Genbank #MK359659), 311822, 311921, 311922 (Genbank #MK359661), 234187, 232855, 232856 (Genbank #MK359658), 310424 (Genbank #MK359660), Baltra Island, collected April 2016. Specimens are also in hand from Academy Bay, Santa Cruz, collected (JTC) April 1987 from hull fouling on a resident fishing vessel, *Albatross*. In addition, we have examined *Watersipora* specimens from Santiago Island (Santa Barbara Museum of Natural History (SBMNH 620190) and Floreana Island (SBMNH 620191) collected by the *Velero* 1934 Hancock Expeditions and previously identified as *Watersipora cucullata* by R. Osburn.

**Description:** *Watersipora subtorquata* was redescribed in detail by Vieira et al. (2014a) and we follow this assessment.  $Lz = 0.877 \pm 0.159$ ,  $Wz = 0.411 \pm 0.051$ ,  $Lor = 0.212 \pm 0.010$ ,  $Wor = 0.240 \pm 0.014$ , sinus width =  $0.122 \pm 0.022$ , sinus length =  $0.043 \pm 0.008$ , (N = 15).

**Remarks:** Most records in the literature for *Watersipora subtorquata* have been found to be other species. Only 1 species, found commonly, of *Watersipora* was present in the fouling community on Santa Cruz Island, *W. subtorquata*. While the peristome in our specimens is only slightly raised, the major character separating our material from congeners previously recorded from the Galapagos is the absence of a latero-oral intrazoooidal septula. Previous records of *Watersipora* in the Galapagos include *W. nigra* (Canu and Bassler, 1930), described as a new species based



**Figure 11.** A–B. *Watersipora subtorquata sensu* Vieira et al. 2014a, Franklin’s Bay, Santa Cruz Island, Galapagos: A. live colony on plate showing pale color and pinkish embryos; B. close-up of orifice showing lucidae, SERC 232903. C. comparison of *W. subtorquata* from Galapagos (on left), SERC 311922, with *W. subatra*, California, USA (on right), SERC 180315, Ethanol preserved colonies. Scale = 400  $\mu$ m. Photos by L. McCann.

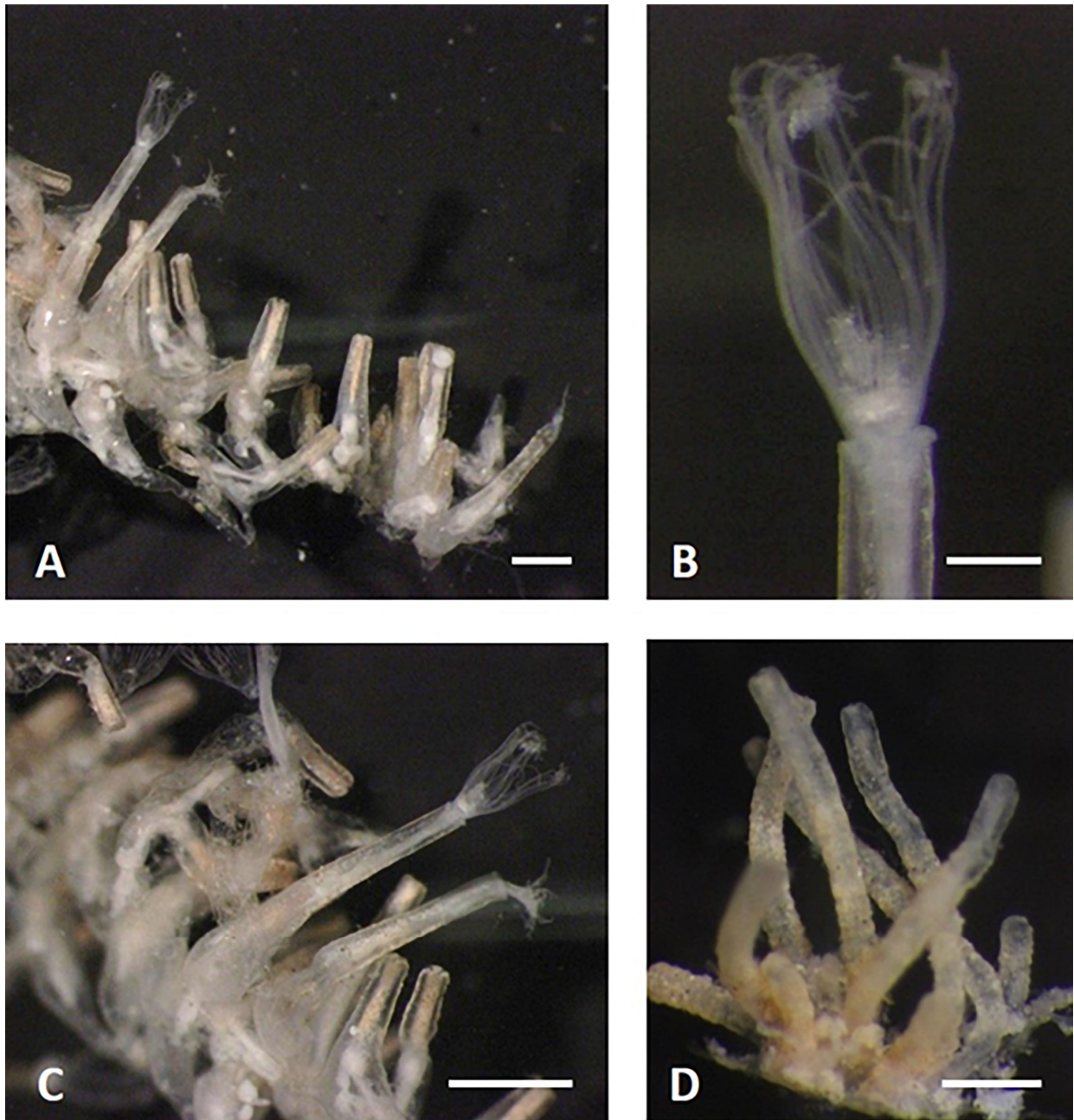
upon specimens collected by the *Albatross* in 1888 in deeper water (73 m) off Espanola Island and *W. cucullata* (Busk, 1854) of Hastings (1930), from Colombia (Gorgona) and the Galapagos. Hastings’ material, based on 1924 collections, were from open-ocean habitats, including a rocky shelf-cave habitat on Isabela Island and dredgings on mixed bottoms in 9 to 22 m on

both Isabela and Santiago Islands. Osburn (1952) also recorded *W. cucullata* in the Galapagos from the 1930s Hancock Expeditions, indicating that specimens had been obtained from many (but an unstated number) of stations from the Galapagos to the Gulf of Mexico.

Both Hastings (1930) and Osburn (1952) use the name *W. cucullata*, which has been widely confused with *W. subtorquata*. Both authors also illustrate a range of characteristics in their figures, suggesting the presence of multiple species in their collections, some of which are likely *W. subtorquata sensu* Vieira et al. 2014a, but none of those figured from Galapagos localities appear to be this species (Hastings 1930, Pl. XV, figure 102; Osburn 1952, Pl. 56, figure 4). The first author (LDM) examined two of the four 1934 *Velero* samples identified as *W. cucullata* in Osburn's collections from the Hancock Expeditions, housed at the Santa Barbara Museum of Natural History. The species-level resolution of Osburn's material remains uncertain, but the specimens are not *W. subtorquata*. The other two specimens are missing (P. Valentich-Scott, *personal communication*, 2018). It seems probable that previous collections of *Watersipora* in the Islands represent other species, and we therefore regard *W. subtorquata* as an introduction. *W. Banta* (in Banta and Redden 1990) did not find *Watersipora* in his harbor collections from Academy Bay in 1980, but biofouling retrieved by one of us (JTC) in April 1987 from a local fishing vessel in Academy Bay, Santa Cruz Island, contains *Watersipora subtorquata* as conceptualized by Vieira et al. (2014a) and as identified here. Our Galapagos material matches genetically material in Genbank from Florida under the former name, *W. subovoidea* (now *W. subtorquata*), as well as additional material verified by the first author, at greater than a 95% threshold.

**Distribution:** Given the degree of confusion around the various *Watersipora* species in the literature, we base all of our distributional information on our own examination of specimens (Galapagos, Florida, Hawaii, and California; Ruiz et al., *unpublished*), literature that contains clear characters attributable to this species, and specimens examined by Vieira et al. (2014a). Based on this, *W. subtorquata* is reported in the Atlantic from Brazil, Florida, Bermuda, the Virgin Islands, Venezuela, Colombia, Ghana, Senegal, and South Africa; in the Mediterranean from Egypt, Italy, Israel, the Aegean Sea, Morocco, Malta, and Suez; in the Indian Ocean from the Red and Arabian Seas, and in the Pacific Ocean from eastern Australia, New Caledonia, California, the South China Sea, and Hawaii, where it was present (identifications by LDM) in two recent surveys on O'ahu (2006 and 2015). Although Soule and Soule (1968) placed it in synonymy with *W. edmondsoni*, molecular analysis of material identified as *W. edmondsoni* from Hawaii by Mackie et al. (2012) suggests that at least some of the material identified as such is a different species. There is likely more than one species under this name present in Hawaii (Soule and Soule 1975; Vieira et al. 2014a). The present material represents the first published record for the Eastern Pacific Ocean.





**Figure 12.** A–C. *Sundanella* sp., SERC 311913, Galapagos: A. showing embryos being expelled from zooid third from right; B. view of tentacular crown, scale = 250  $\mu$ m; C. several zooids in the colony. D. *Nolella stipata*, SERC 233117. Both from Franklin’s Bay, Santa Cruz Island, Galapagos. Scale A, C and D = 500  $\mu$ m. Photos by L. McCann.

Class Gymnolaemata Allman, 1856  
 Order Ctenostomata Busk, 1852  
 Suborder Victorellina Jebram, 1973  
 Superfamily Victorelloidea Hincks, 1880  
 Family Nolellidae Harmer, 1915  
 Genus *Nolella* Gosse, 1855

***Nolella stipata* Gosse, 1855**  
 (Figure 12D)

*Nolella stipata* – Gosse 1855, 35–36, plate IV, Fig. 29; Vieira et al. 2014b, 499–451, Fig. 40–42, Table 2.



**Material:** SERC 232891, 232873, 232861 Baltra Island; SERC 233117, 234234, Franklin’s Bay, Santa Cruz Island, collected April 2016. Also examined was *Nolella stipata* SERC 185189 from Bermuda (identification Judith Winston, collected October 2013).

**Description:** Zooids narrow, tubular, covered with fine sediment, width uniform, sometimes slightly narrowing at the tip, connected by very thin stolons 0.03–0.046 mm in width; orifice circular; zooids unbranched, sometimes 1–3 tiny basal prolongations present; lophophore campanulate, with approximately 16–18 tentacles; embryos not observed.  $Lz = 1.355 \pm 0.521$ ,  $Wz = 0.185 \pm 0.033$  (N = 8).

**Remarks:** Our specimens are a bit shorter on average (although the length was quite variable), than those recorded by Vieira et al. (2014b) from Brazil, but otherwise match the description of *N. stipata*. Although there are differences in the size and degree of prolongation of basal projections in *N. stipata* and *N. dilatata* (Hincks, 1860), Maturo (1957) synonymized these species, suggesting that they represent ecological variants, while Vieira et al. (2014b) suggest that they are viable species. The primary difference in the two species, as defined by Hincks (1860), appears to be the presence of “flattened spinous projections” on the stolonal base of the zooids described for *N. dilatata* (Pl XXX, figure 7). Galapagos specimens have no spinous projections, consistent with the original description of *N. stipata* (Gosse 1855).

**Distribution:** Several species in the genus have been confused or synonymized with *N. stipata* in the literature. *Nolella stipata* was reported in the Puritan Expedition (Soule 1963) from western Mexico in Baja California at three island localities. Osburn (1953) reported it from the Gulf of California from San Francisco Island, while other authors recorded it as far north as the Queen Charlotte Islands. In recent biofouling studies we have documented the species from Hawaii (Ruiz et al., *unpublished*), Pacific Panama, Coos Bay (South Slough), Oregon USA, and possibly from San Francisco Bay, California USA (Ruiz et al., *unpublished*). It has also been reported as widespread in the western Atlantic by Maturo (1957) (who also did not distinguish *N. stipata* and *N. dilatata*) and south to Brazil (Vieira et al. 2014b). This is the first record for the species in the Galapagos. As with *Savignyella lafonti*, we consider this species to be cryptogenic, as it likely involves a combination of both a species complex and one or more clades dispersed for centuries by shipping.

Family Sundanellidae Jebram, 1973

Genus *Sundanella* Braem, 1939

***Sundanella* sp.**

(Figure 12A–C)

**Material:** One sample only, SERC 311913 (Genbank # MK359657), Franklin’s Bay, Santa Cruz Island, collected April 2016.

**Description:** Zooids yellowish-beige, large and transparent, budding directly from each other; new zooids arising from often widened proximal portion; polypides large, lophophore campanulate, with between 20 and 32 tentacles; lophophore 0.738–1.0 mm tall and 0.354–0.369 mm wide (N = 5); Lz =  $1.490 \pm 0.381$ , Wz =  $0.440 \pm 0.080$ , (N = 8).

**Remarks:** There are currently only 2 species in the genus. *Sundanella sibogae* (Harmer, 1915), described from Indonesia from depths ranging to 30 m, has zooids up to 3.1 mm in length. *Sundanella rosea* Vieira et al., 2014b, from the shallow waters of Brazil, has zooids up to 5 mm in length, is slightly narrower than the Galapagos specimen, and is characterized by having large pink eggs. We did not note the color of the eggs in our specimens in life (Figure 12A), but they are white to beige in preserved material.

**Distribution:** This is a new record for the genus for the Galapagos. Even given our having only one sample, it seems likely it represents an undescribed species.

Suborder Vesicularina Hincks, 1880

Superfamily Vesicularioidea Hincks, 1880

Family Vesiculariidae Hincks, 1880

Genus *Amathia* Lamaroux, 1812

#### ***Amathia* (*Bowerbankia* group) sp. 1**

**Material:** SERC 234090i from Academy Bay, Santa Cruz Island; SERC 234227, 232873i from Baltra Island, collected April 2016.

**Description:** Zooids very transparent, of variable length, tubular, slightly wider at base; 12–14 equal-length tentacles, long, approximately 0.846 mm (N = 2 lophophores); color of embryos not observed; stolons wide relative to zooid width (approximately  $\frac{3}{4}$  zooid width), zooids attached alternately. Lz =  $0.927 \pm 0.421$  (N = 10); Wz =  $0.208 \pm 0.068$ , Ws =  $0.122 \pm 0.040$  (N = 24).

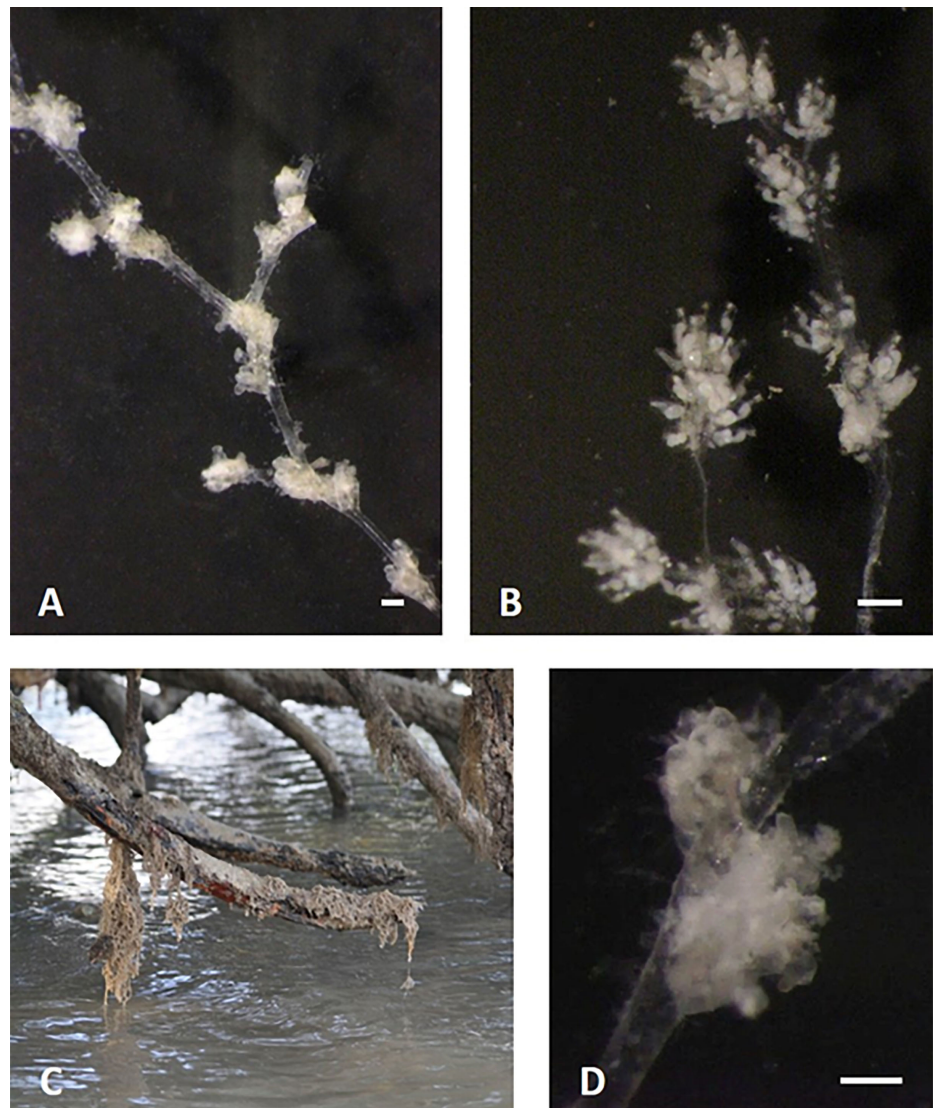
**Remarks:** The Galapagos material was limited, represented by only three tiny specimens. The tentacle number does not fit the description of any species currently known. More material would be necessary to determine its affinities, but this is likely a new species.

**Distribution:** This is the first record for the “*Bowerbankia*” group of *Amathia* from the Archipelago.

#### ***Amathia* sp. 2**

(Figure 13A, D)

**Material:** SERC 232737, 234090, 234100, 310418, 310194, 232779, 233056, 233010, 233071, 234287 from Academy Bay and SERC 233096 from Franklin’s Bay, Santa Cruz Island, collected April 2016. Also examined *Amathia vidovici* (Heller, 1867) SERC 123640 Biscayne Bay, Florida, USA



**Figure 13.** A, D. *Amathia* sp. 2, SERC 234090 and B–C. *Amathia verticillata*, SERC 233125, Galapagos: A. *Amathia* sp. 2, view of colony branches; B. *Amathia verticillata*, view of colony branches; C. another colony attached to mangrove roots in Tortuga Bay, Santa Cruz Island, Galapagos; D. *Amathia* sp. 2, view of one cluster of  $\geq 9$  pairs of zooids. A, B, and D scale = 300  $\mu\text{m}$ . Photos by L. McCann.

collected August 2004, and *Amathia dichotoma* (Verrill, 1873) SERC 302534 Morro Bay, California, USA, collected August 2013, SERC 192512 Mission Bay San Diego, California, USA (identifications of material from other sites by Judith Winston, collected July 2013).

**Description:** Colony erect, delicate, regularly dichotomously branched, generally with one branch being wider, color pale beige, transparent; pigment spots not observed; zooids approximately the same length although sometimes those in the middle of the cluster are longer, arranged in biserial clusters (no single zooids on the ends) of 8–13 zooids, 1–2 per node, making a complete spiral around the stolon; zooid clusters occupy the latter half of the stolon just at the branching node, sometimes with an additional cluster midway up the node, never greater than 50% of the stolon internode is bare, usually less; spiral pattern of clusters follows the

maternal direction and can be clockwise or counterclockwise; zooids connate part of their length, but amount of zooid joined is variable, ranging from 10 to 95% of the total zooid length; rhizoids not observed.  $Lz = 0.327 \pm 0.073$ , (N = 8);  $Wz = 0.120 \pm 0.013$ , (N = 25);  $Ws = 0.186 \pm 0.061$  (N = 8).

**Remarks:** Much of our material was fouled, making measurements difficult. The current material cannot definitively be placed into any of the known species. Trichotomous branching, a rare feature in the genus, was observed on a single colony at one junction. *A. rudis* Kubanin, 1992 is similar, but the zooids are generally longer and wider and the trichotomous branching is more common than in our Galapagos material.

**Distribution:** Osburn (1953) recorded *Amathia vidovici* from the Galapagos from 20 unspecified stations from the Hancock Expedition, but Banta (1991) did not find any ctenostomes in his 1980 collection on Santa Cruz Island. Although the material we examined does exhibit some “*vidovici*”-like characteristics, it does not clearly fall into this species, as it has a larger number of zooid pairs per cluster, a wider stolon, and less bare space on the internodes. It also cannot be identified as *A. distans* Busk, 1886 or *A. brasiliensis* Busk, 1886 based on existing descriptions, although it shares affinities with these species as well. Unfortunately, some descriptions also contradict one another and many of the original descriptions are very vague, including the description of *A. vidovici*; lacking a type specimen (Hayward and McKinney 2002), the latter species is problematic. In Gordon and Spencer-Jones (2013), which covers almost all of the valid species in the genus, Galapagos material keys out to *A. brasiliensis*, but in this species the zooids are not connate, rarely one-third of the zooid being attached, whereas in the Galapagos material this character is quite variable and zooids are often more connate, sometimes nearly to the tips of the zooids. Additionally, in the original description of *A. brasiliensis*, Busk (1886) states that in the younger internodes the spiral “occupies only the upper part, but in the older nearly their entire length” is taken up by the cluster of zooids, which is not the case in Galapagos material. Zooids of *Amathia brasiliensis* are also longer on average and have distinctive pigmentation which was not observed in Galapagos specimens, although we did not examine live material for this character. Southern California material from recent settlement plate surveys has been identified as *A. dichotoma* (identifications by Judith Winston; Ruiz et al., *unpublished*), but this species has fewer zooids per cluster, is stiffer, and the cluster does not make a full spiral around the stolon, characteristics not found in the Galapagos material. Given all of these distinctions, it seems likely that this is an undescribed species.



### ***Amathia verticillata* (delle Chiaje, 1822)**

(Figure 13B–C)

*Hydra verticillata* – delle Chiaje 1828, 203; 1822, Pl 47, Figs. 1–2.

*Zoobotryon verticillatum* – Osburn 1953, 742–743, Pl. 79, Fig. 3; Vieira et al. 2014b, 518–520, Figs. 98–101.

*Amathia verticillata* – Waeschenbach et al. 2015, 10; McCann et al. 2015, 255–260.

**Material:** SERC 233010 Academy Bay, SERC 234144, 233096, 233125, 234144, 233096 Franklin’s Bay, Santa Cruz Island; SERC 23084 Baltra Island, and additional material from Tortuga Bay, collected in February 2015 and April 2016.

**Description:** Colony of long, large, spaghetti-like branches with short zooids in straight, non-spiraling rows of 2–10 transparent zooids; up to 0.5 m long.  $Lz = 0.407 \pm 0.133$ , (N = 19);  $Wz = 0.206 \pm 0.028$ , (N = 14);  $Ws = 0.421 \pm 0.082$  (N = 13).

**Remarks:** A very distinctive and easily identified species looking a bit like cellophane noodles or sauerkraut. We found this species in the Galapagos for the first time in surveys on Santa Cruz Island in 2015 (McCann et al. 2015) (Figure 13C). In 2016, the species was still present in Tortuga Bay. We also found it in 2016 at Baltra Island and on the north side of Santa Cruz Island, in an area not surveyed the previous year. It appears to be able to proliferate in both tropical and temperate climates.

**Distribution:** First reported from the Atlantic coast of Brazil two centuries ago, the known distribution of the species continues to expand, likely through ship hull fouling (Tilbrook 2012; McCann et al. 2015; Xiong et al. 2017). It is a major fouling species worldwide and has previously been reported from the central Pacific from Palmyra Atoll (Knapp et al. 2011) and the Hawaiian Archipelago out to Midway (Carlton and Eldredge 2009). In the Eastern Pacific Ocean it is known from California (Cohen and Carlton 1995; San Diego to San Francisco, Ruiz et al., *unpublished*), the Gulf of California (Banta 1980), and mainland Ecuador as well (McCann et al. 2015). The 2015 collections represented the first time the species had been reported from the Galapagos.

Class Stenolaemata Borg, 1926

Order Cyclostomata Busk, 1852

Suborder Articulina d’Orbigny, 1826

Family Crisiidae Johnston, 1838

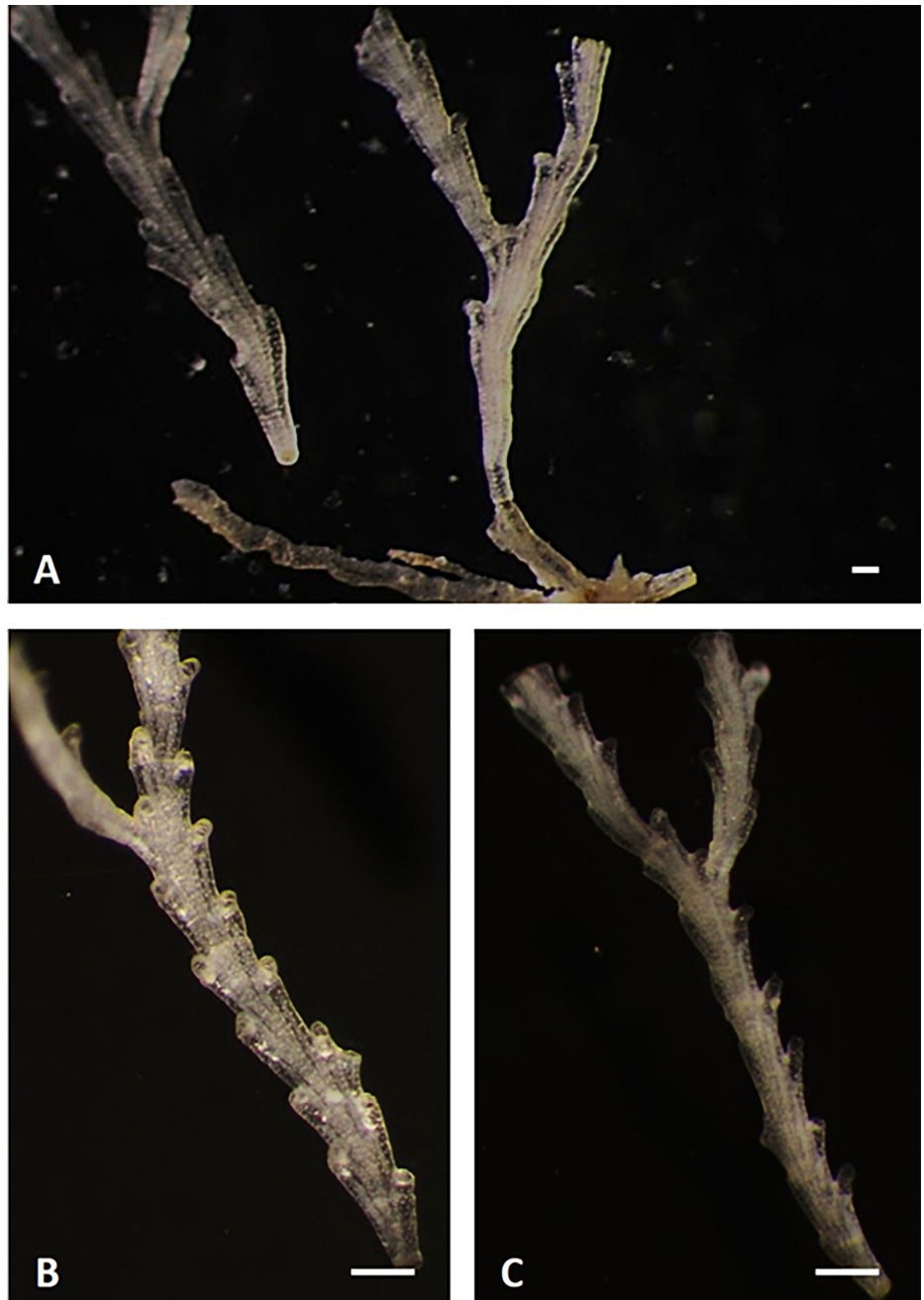
Genus *Crisia* Lamouroux, 1812

### ***Crisia* sp.**

(Figure 14A–C)

**Material:** SERC 2617, Academy Bay, Santa Cruz Island, collected February 2015.

**Description:** Colony erect, delicate, with 9–19 zooids per internode; internodes ranging from 0.09228–0.13842 mm wide; internode joints pale



**Figure 14.** A–C. *Crisia* sp., SERC 2617, Tortuga Bay, Santa Cruz Island, Galapagos: A. colony showing base; B. dorsal view; C. ventral view of same. Scale = 250  $\mu$ m. Photos by L. McCann.

to golden in longer branches; branches angled from 10–45°; zooids long, sometimes extending full length of internode, zooid tubes protruding slightly frontally, opening round; internodes without keel; gonozooids not observed.  $Wor = 0.070 \pm 0.008$ , Node length =  $2.179 \pm 0.240$ , (N = 6).

**Remarks:** Our only 1 small, non-reproductive piece makes it impossible to take this identification further, as gonozooids are defining characters for differentiating species in the cyclostomes. However, some comparisons can be made to species previously reported from the Islands. Three *Crisia* species have been reported from the Galapagos, including *Crisia maxima* Robertson, 1910, *Crisia occidentalis* Trask, 1857 and *C. serrulata* Osburn,

1953, all of which are found from British Columbia southward down the coast of the Americas (Osburn 1953). *Crisia maxima* has dark brown joints, *Crisia occidentalis* has 5–12 zooids per internode and zooids are often pointed on the outer ends, and *C. serrulata* has 12–30 zooids per internode and the zooids are merged almost to their tips. The Galapagos material exhibits none of these combinations of characters, suggesting that it may be another species not previously recorded in the Galapagos.

Suborder Rectangulata Waters, 1887

Family Lichenoporidae Smitt, 1867

Genus *Patinella* Gray, 1848

***Patinella* sp.**

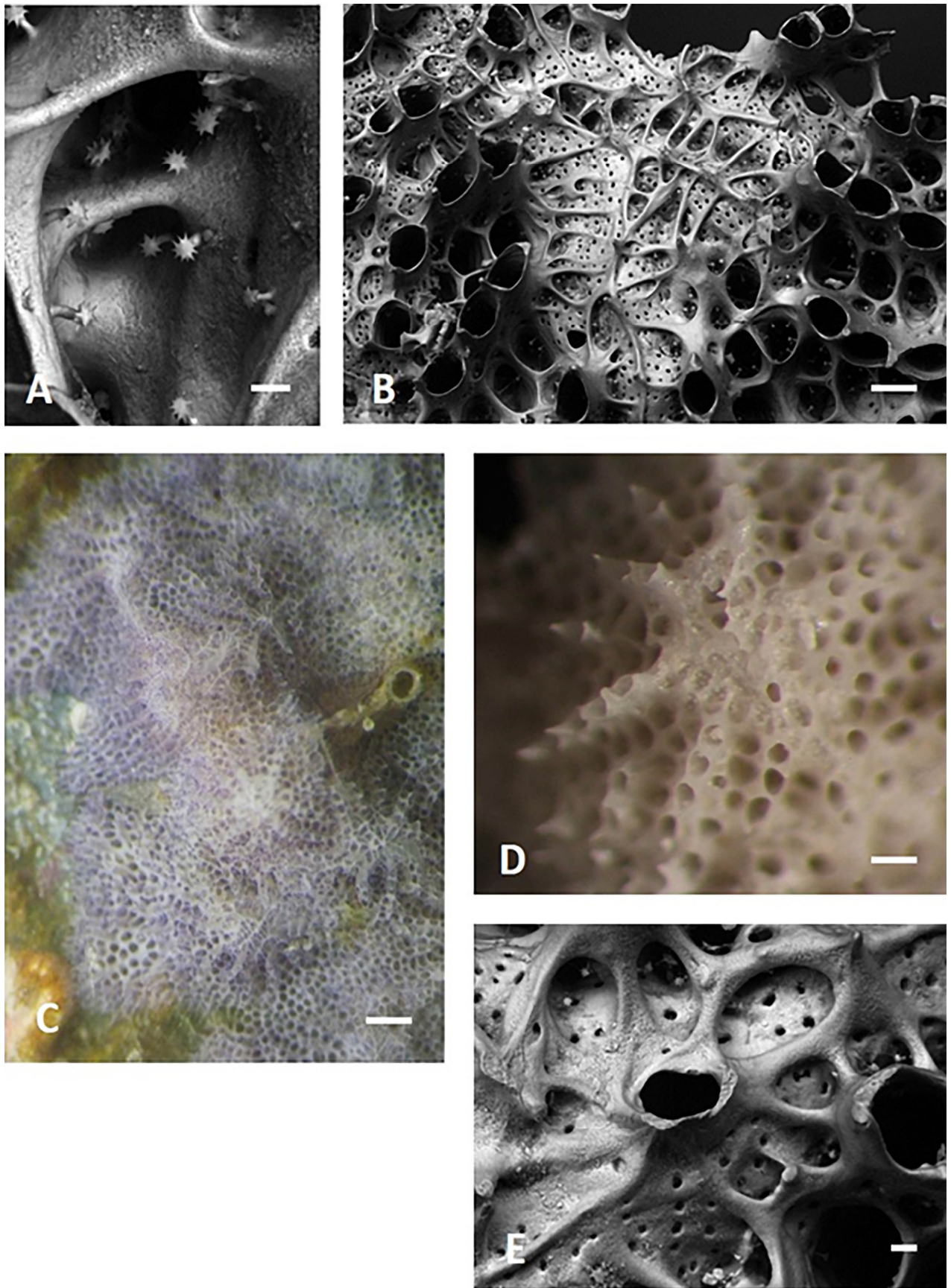
(Figure 15A–E)

**Material:** SERC 234256, 234257, 234258, from Academy Bay, Santa Cruz Island, collected April 2016.

**Description:** Four colonies, 5–20 mm across; colonies adnate, adhering closely to the substrate except at growing edges which are curled upward, with purple pigment spots, whole colony appearing light violet in color, but becoming bright white in ethanol; multiple maculae, sunken in smaller colonies, but with raised central oval area in larger colonies; maculae sometimes round, sometimes forming a long, narrow ridge, located throughout the colony; peristomes truncate, round to oval, the aperture wider in the direction of the radii, relatively short and connate with inside edge usually raised into a point, rarely raised to points on opposing sides; peristomes uniserial, with four to seven peristomes in sometimes straight, sometimes meandering lines, radiating out from maculae to create a star-like pattern; kenozooidal openings bigger than peristomal openings, irregular in shape with 1–2 rows between radii, often with pinhead spinules (9–11); alveoli open, without “iris-like” closures, but often closed by a porous membrane and crested with narrow ridges running their length; brood chamber pore plate sometimes visible through the kenozooidal openings (Figure 15E); budding not observed.  $Wz = 0.077–0.085$ ,  $Wkz = 0.077–0.153$  mm, (N = 10).

**Remarks:** The distinctions between the *Patinella* and *Disporella* Gray, 1848, are not entirely clear. Galapagos colonies are provisionally identified as members of the genus *Patinella* based on the irregularly shaped alveoli, the partly divided secondary alveoli (Figure 15B), and the possible presence of raised ooeciopores (Figure 15E), until a more detailed analysis can be done. Our specimens have many maculae of different shapes and the number of pinhead spicules was quite variable (Figure 15A), both characters that have been used to help distinguish species. All the species currently placed in *Patinella* were first described from the Atlantic and Mediterranean, but this group needs revision to clarify species relationships and generic assignments.





**Figure 15.** A–E. *Patinella* sp., SERC 234258, Academy Bay, Santa Cruz Island, Galapagos: A. alveoli showing pin head spicules; B. brood chamber; C. another colony with at least 6 raised maculae; D. zooids showing peristomes with single projections; E. possible oeciopore. Scales in  $\mu\text{m}$  A.10 B. 200 C.500 D.150 E. 20. Photos by L. McCann and SEMs by Paul Taylor.



**Distribution:** Several species in the family are recorded from the Galapagos previously, including two similar species, *Disporella ovoidea* (Osburn, 1953), *Patinella radiata* (Audouin, 1826) by Canu and Bassler (1928) and *Lichenopora intricata*. *Disporella ovoidea* can be distinguished from our species by its central, large dominating maculae, while *P. radiata* has more peristomes that radiate out in very regular rows. *Lichenopora intricata* has “rows of cells radiating irregularly” (Busk 1856) and the central area is flat and depressed, while in Galapagos material the peristomes are quite regularly arranged and the central areas are raised and mounded. It seems likely that this is an undescribed species.

## Discussion

Banta (1991) remarked that the collections he made in July 1980 while snorkeling in Academy Bay, “are the only ones I know of made in a Galapagos fouling community”. He noted that the only fouling bryozoan species he found was *Bugula neritina*. Remarkably, the next extensive assessment of these communities was not until the present collections in 2015–2016. The limited collections made by Banta in 1980 and by one of us (JTC) in 1987, combined with the absence of port and harbor collections prior to the 1980s, and in the 35 years since, make it challenging to assess when any of the introduced or cryptogenic species documented here arrived in the Galapagos Islands. Rather, our current work now provides an important baseline for assessing the potential arrival of new introductions.

Of the 18 species treated here, we consider 10 likely to be non-native, three to be cryptogenic, and the remaining five as perhaps native. Of the introduced species, the origins of two (*Bugula neritina* and *Amathia verticillata*) remain unclear. The remaining eight species appear to originate in either the tropical waters of the Western Atlantic or Indo-Pacific Oceans. The latter may have arrived through the Panama Canal, either in vessel hull biofouling (if capable of surviving the passage through the freshwater Gatun Lake) or as colonies taken into ballast tanks on small bits of debris or seaweed (and thus immune to freshwater exposure). However, all but one of the species (*Celleporaria inaudita*) we consider here with possible Atlantic origins have also been introduced elsewhere in the Pacific Ocean, making the precise origins of Galapagos populations unknown, pending global population genetic studies.

Banta (1991) remarked that it was likely that ctenostome bryozoans had been under-reported in the Galapagos relative to other bryozoan orders. He noted that only two species were known at the time: *Amathia vidovici*, which, as discussed above, is a species of uncertain identity, and *Buskia seriata* Soule, 1953 (in Osburn and Soule 1953), the latter apparently not collected in the Islands since 1931. The Galapagos specimens of *A. vidovici*

reported by Osburn and Soule (1953) remain to be re-examined. In 2015, we reported for the first time the presence of “zoobotryon”, *Amathia verticillata* in the Galapagos (McCann et al. 2015). To these species we now add four additional ctenostomes, *Nolella stipata*, *Sundanella* sp., and two as yet undetermined species of *Amathia*. Whether some of these species were historically present, or all represent ship-borne introductions since the last major explorations for Galapagos bryozoans in the 1930s, remains unknown.

We have taken the first steps to generate a genetic database of the fouling species in the islands (Table S2). Unfortunately, many of these species have limited or no representation in molecular data bases at present. Others, such as *Watersipora subtorquata*, are entered in Genbank under incorrect names, further complicating the historical record. More surveys are needed to help clarify both taxonomic affinities and the native or non-native status of these species.

Much work remains to be done on the intertidal and shallow-water bryozoans of the Galapagos Archipelago. Biofouling community explorations remain in place (Carlton et al. 2019), and we have little doubt that these will reveal additional native and introduced species.

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### Supplementary material

The following supplementary material is available for this article:

**Table S1.** Occurrences of bryozoans at sampling locations in the Galápagos Islands in 2015–2016 (as reported herein).

**Table S2.** A list of all Galapagos samples of bryozoans with CO1 data deposited in Genbank.

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