REDESCRIPTION AND REVISION OF SOME RED-PIGMENTED *BUGULA* SPECIES

JUDITH E. WINSTON[1] AND ROBERT M. WOOLLACOTT[2]

ABSTRACT. In this study, we describe or redescribe nine species of red-pigmented aviculiferous *Bugula* and compare them with the type species of the genus, *Bugula neritina* (L.). The names *Bugula robusta* MacGillivray and *Bugula minima* (Waters) have both been used (often interchangeably) for red-pigmented aviculiferous *Bugula* specimens collected from localities ranging from Tasmania to the Red Sea. Our analysis indicates, however, that *Bugula robusta* is a cool-water species whose distribution appears to be limited to the southern Australian region, whereas *Bugula minima* is a warm-water species distributed from the Red Sea to the Indo-Pacific. These, as well as some of the other species for which these names have been used by various authors, are described and illustrated here from museum material. *Bugula providensis, Bugula miniatella, Bugula ceylonensis, Bugula robustoides, Bugula solorensis,* and *Bugula paternostrae* are described as new. The descriptions of *Bugula robusta, Bugula minima,* and *Bugula crosslandi* are revised.

INTRODUCTION

We began this project out of necessity. One of us (RMW) was studying the development of *Bugula neritina*, and during the project, another red-pigmented *Bugula* species, this one with avicularia, was found at Coconut Island, Oahu, Hawaii. Its development was studied as well. The Hawaiian aviculiferous species appeared most similar to either *Bugula minima* (Waters) 1909 from the Red Sea or *Bugula robusta* MacGillivray 1869 from Victoria, Australia, but the descriptions of the two species in the literature were so inconsistent that it was impossible to determine whether the Hawaiian material belonged to either species. Winston, meanwhile, was studying western Atlantic and Caribbean collections and was concerned because the *Bugula* species that Osburn (1914) and authors who followed him had recognized as *Bugula minima* (Waters) did not closely resemble the one available illustration of a Red Sea specimen. To resolve these related problems, we decided to look at as much material as we could locate under those two names in museum collections, including type material if possible. Many of the specimens we examined for this project consisted of a few branches or branch fragments mounted as whole mounts in resin on slides. Those specimens could not be used for study by scanning electron microscopy (SEM). Measurements and light photomicrographs were also difficult because of the limited transparency of the old slide preparations. Despite these difficulties, it soon became apparent that the two names had been used by a number of authors from localities around the world for material that, by modern standards, belongs to several distinct taxa. In this paper, we attempt to clarify the situation by redescribing and illustrating *B. minima* and *B. robusta* and describing as new species some of the other specimens that had been synonymized under one of those names.

Taxonomic History

Bugula neritina, type species of the genus *Bugula*, was one of the earliest bryozoans described (Linnaeus, 1758). Late 18th and 19th century marine expeditions

---

[1] Virginia Museum of Natural History, 21 Starling Avenue, Martinsville, Virginia 24112.

[2] Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138.

Bull. Mus. Comp. Zool., 159(3): 179–212, September, 2008

and surveys discovered the species at many warm-temperate and tropical localities around the world. For example, in her *Synonymic Catalogue of Marine Bryozoa*, Eliza Jelly (1889) listed 30 references to the species. No doubt its distinctive dark red coloration, large, tufted, seaweedlike colony form, and apparent preference for shallow water were partially responsible for the abundance of records. However, its eurytopic physiology and fouling habit might also have favored its early anthropogenic introduction to many areas.

Despite its status as type species of the genus *Bugula*, *Bugula neritina* differs from other known members of the genus in lacking the pedunculate, bird's head avicularia characteristic of the group. Early bryozoan taxonomists did not recognize the significance of this difference. When Arthur Waters in his publication on bryozoans from the Red Sea (1909) described a red-colored *Bugula* with avicularia, he considered it merely a new variety of *neritina.* In his synonymy of variety *minima*, he included material from Australia and Manaar (Gulf of Ceylon), as well as the Red Sea. He listed specimens from geographically distant localities: Ball's Head, New South Wales; Mersa Makdah, Khor Dongola, and Agig Suraya, Red Sea; and Prison Island, Zanzibar Channel (Indian Ocean). Waters gave no indication that he considered any one specimen or locality more important than the others, although he illustrated material only from two of the Red Sea localities: Khor Dongola and Nersa [sic] Makdah.

Waters was followed by the influential bryozoan taxonomist Sidney F. Harmer of the British Museum, who carried out his work during the early part of the 20th century, a period when biologists had begun to realize the importance of variation within populations. Harmer considered bryozoan species capable of possessing a wide range of intraspecific variation in zooid morphology and size. As a consequence, in the three volumes of the *Polyzoa of the Siboga Expedition*, he often synonymized what are now recognized as several different species under a single name. In *Part II, Cheilostomata Anasca* (1926), Harmer placed all specimens of Waters' variety *minima*, as well as material from localities ranging from the Red Sea to the Java Sea, in synonymy under *Bugula robusta*, a species originally described in 1869 from Victoria, Australia, by P. H. MacGillivray. Harmer included all of the Siboga specimens he examined in *B. robusta*, although his illustrations and discussion indicate a large amount of variation even within that geographically more restricted collection.

In her 1939 paper "Notes on some cellularine Polyzoa," Anna B. Hastings, also of the British Museum, followed Harmer in considering Waters' material from Zanzibar to be *B. robusta*, going so far as to put additional labels to that effect on the backs of the slides she examined. She raised *B. minima* to specific level, making its type the Crossland-Waters specimen from Mersa Makdah, then housed in the University of Liverpool Museum. She also described a new species, *Bugula crosslandi* Hastings, 1939. Its type was a British Museum specimen from Abu Shaar, Red Sea, collected by Crossland, but in her synonymy and discussion, she also claimed one of Waters' Red Sea specimens (Waters' Khor Dongola specimen from the University of Liverpool Museum) and specimens from the Pacific coast of Panama as belonging to *B. minima.*

Working in both the tropical western Atlantic and eastern Pacific, Harmer's contemporary, Raymond C. Osburn, who shared Harmer's view of the degree of variation possible within bryozoan species, used the name *Bugula minima* for all red *Bugula* with avicularia that he found in collections from the Tortugas, Florida (1914), Puerto Rico (1940), and the Pacific coast of Costa Rica and the Gulf of Panama (1950).

METHODS

We examined specimens from the Bishop Museum, Honolulu, Hawaii; the Natural History Museum, London, England (British Museum); the Manchester Museum, Manchester, England; the Museum Victoria, Australia (old Royal Museum of Victoria); The Natural Museum of Natural History, Smithsonian Institution, Washington, D.C.; The Allan Hancock Foundation Bryozoan Collection, Santa Barbara Museum of Natural History, Santa Barbara, California; the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; and the Virginia Museum of Natural History, Martinsville, Virginia.

For morphometric comparison, the following measurements were made on selected colonies: zooid length (LZ); zooid width (WZ) measured at maximum width of zooid, usually at or near distal end; opesia length (Lopes) and opesia width (Wopes), the greatest length and width of the membranous area of the frontal wall; orifice length (LO, if possible); orifice width (WO); ovicell length (LOv); ovicell width (WOv, if ovicells present); avicularium length (Lav); and avicularium width (Wav). All measurements were made with the use of a Wild stereomicroscope with 20× oculars at 100× magnification. We also included the ratio of avicularian length to zooid width (Lav/WZ) suggested by Ryland (1960) as potentially useful in distinguishing *Bugula* taxa. For species with more than one size class of avicularia, the length of the large avicularia was used in determining this ratio. Table 1 gives the morphometric results for the colonies studied.

We also photographed colonies to show branch bifurcation type and morphology of zooids, ovicells, and avicularia. Because much of the material consisted of whole mount slide preparations, photography and measurement were sometimes difficult. For example, because of opacity of some of the old slides, measurement of zooid length had to be done from the frontal side, rather than the basal side as has been recommended for *Bugula* (Hayward and Ryland, 1998). For consistency, all measurements included in this study were taken from the frontal surface. Material of some species was available for SEM study. Those specimens are illustrated by SEM images, as well as light micrographs.

RESULTS

Cheilostome Morphology

Members of the order Cheilostomata are the dominant group of bryozoans in Recent seas. They are characterized by tubular to box-shaped zooids with variously calcified walls and an operculum, a hinged flap, usually with chitinous thickening, opening on the frontal surface for protrusion of the lophophore. They are also characterized by widespread occurrence of polymorphism, the development of various types of specialized heterozooids, in addition to the feeding autozooids.

Morphology of *Bugula* Species

Members of the genus *Bugula* produce erect branching colonies from an upright ancestrula. Colonies are attached by tubular rhizoids, kenozooidal heterozooids that develop from pore plates in frontal, lateral, and basal surfaces of autozooids and grow toward the substratum to anchor the colony. The branches are formed by two or more series of zooids that are wide distally and narrow proximally in shape, in frontal view looking subtriangular and in basal view showing forked proximal ends. Basal and lateral walls are lightly calcified, but most of the frontal wall is membranous, giving colony branches considerable flexibility. Unlike most other cheilostomes, the orifice is closed by a membranous flap rather than a reinforced operculum. The width of the opening may be visible on closed zooids, but its length usually cannot be determined accurately. Some species have spines on the distal angles of the zooids. At least some of the spines may be jointed, and therefore kenozooidal. Almost all species have motile pedunculate bird's head avicularia (Figs. 1A–C). The body of the avicularium zooid makes up the

TABLE 1. MORPHOMETRIC DATA FOR RED *BUGULA* SPECIES STUDIED.

Character measured (mm)	*B. neritina*	*B. minima*				*B. providensis*	*B. miniatella*	*B. crosslandi*	*B. ceylonensis*
	Hawaii[1]	Red Sea[2]	Hawaii (MCZ)[3]	Hawaii (BM)[4]	East Africa[5]	Seychelles[6]	Tortugas, Florida[7]	Red Sea[8]	Sri Lanka[9]
LZ	18	6	6	12	6	6	6	12	6
Mean	0.72	0.56	0.66	0.57	0.61	0.68	0.58	0.51	0.53
SD	0.03	0.06	0.04	0.06	0.09	0.07	0.05	0.04	0.03
Range	0.68–0.76	0.49–0.67	0.61–0.72	0.52–0.75	0.51–0.76	0.57–0.74	0.53–0.66	0.44–0.57	0.49–0.57
WZ	18	6	6	12	6	6	6	12	6
Mean	0.21	0.20	0.21	0.20	0.20	0.19	0.18	0.17	0.20
SD	0.002	0.001	0.01	0.01	0.02	0.02	0.02	0.02	0.02
Range	0.18–0.23	0.19–0.21	0.19–0.23	0.17–0.20	0.20–0.23	0.15–0.21	0.15–0.19	0.15–0.18	0.17–0.21
LO	—	—	—	—	—	—	6	2	—
Mean	—	—	—	—	—	—	0.07	0.05	—
SD	—	—	—	—	—	—	0.01	0.01	—
Range	—	—	—	—	—	—	0.06–0.10	0.05–0.06	—
WO	—	6	6	12	6	6	6	12	6
Mean	—	0.12	0.13	0.11	0.13	0.11	0.11	0.09	0.13
SD	—	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01
Range	—	0.11–0.13	0.11–0.15	0.10–0.13	0.11–0.13	0.10–0.13	0.10–0.13	0.07–0.11	0.11–0.13
Lopes	—	6	6	12	6	6	—[10]	12	6
Mean	—	0.43	0.50	0.52	0.51	0.51	—	0.37	0.43
SD	—	0.04	0.05	0.06	0.06	0.08	—	0.01	0.03
Range	—	0.38–0.48	0.42–0.57	0.46–0.64	0.46–0.59	0.40–0.57	—	0.35–0.39	0.42–0.49
Wopes	—	6	6	12	6	6	—[10]	12	6
Mean	—	0.15	0.16	0.17	0.15	0.16	—	0.15	0.17
SD	—	0.02	0.02	0.01	0.01	0.02	—	0.01	0.01
Range	—	0.13–0.17	0.13–0.17	0.15–0.18	0.13–0.17	0.13–0.17	—	0.13–0.18	0.15–0.19
LOv	18	2	6	6	6	6	6	12	5
Mean	0.21	0.20	0.24	0.20	0.23	0.20	0.19	0.17	0.22
SD	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01
Range	0.18–0.23	0.19–0.21	0.23–0.25	0.19–0.22	0.209–0.238	0.171–0.228	0.171–0.190	0.147–0.184	0.21–0.23
WOv	18	2	6	6	6	6	6	12	5
Mean	0.29	0.23	0.26	0.21	0.25	0.24	0.21	0.20	0.26
SD	0.02	—	0.01	0.02	0.01	0.01	0.01	0.01	0.02
Range	0.27–0.32	0.23	0.25–0.26	0.18–0.23	0.24–0.27	0.3–0.25	0.19–0.23	0.18–0.22	0.25–0.29
Lav1	—	6	6	12	6	6	6	12	6
Mean	—	0.24	0.28	0.22	0.24	0.27	0.22	0.15	0.26
SD	—	0.02	0.03	0.02	0.03	0.02	0.02	0.01	0.02
Range	—	0.21–0.257	0.25–0.32	0.18–0.25	0.21–0.29	0.25–0.29	0.19–0.25	0.13–0.17	0.23–0.29
Wav1	—	6	6	12	6	6	6	12	6
Mean	—	0.10	0.12	0.10	0.10	0.11	0.09	0.08	0.14
SD	—	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Range	—	0.09–0.11	0.11–0.14	0.09–0.13	0.08–0.11	0.95–0.11	0.08–0.10	0.07–0.09	0.11–0.15
Lav2	—	6	5	10	4	—	—	—	
Mean	—	0.46	0.52	0.46	0.39	—	—	—	
SD	—	0.06	0.10	0.06	0.07	—	—	—	
Range	—	0.380–0.532	0.399–0.665	0.294–0.515	0.323–0.475	—	—	—	
Wav2	—	5	6	10	4	—	—	—	
Mean	—	0.16	0.2	0.15	0.16	—	—	—	
SD	—	0.02	0.01	0.02	0.03	—	—	—	
Range	—	0.13–0.19	0.19–0.21	0.11–0.18	0.13–0.19	—	—	—	
Lav/WZ ratio	—	2.3	2.5	2.4	2.0	1.4	1.2	0.9	1.3

"head." Its distal edge is elongated into the rostrum, the upper "beak" of the bird's head shape. The lower "beak" is the mandible of the avicularium, homologous to the operculum of the autozooid. Most of the body cavity of the avicularium is filled by muscles, but a long-bristled polypide rudiment, or setiferous organ, is protruded through a central orifice in the frontal membrane. The base of the avicularium is attenuated into a peduncle, which is attached through a pore to a peduncle cush-

TABLE 1. EXTENDED.

Character measured (mm)	*B robusta*		*B. robustoides*		*B. solorensis*			*B. paternostrae*	
	Victoria, Australia[11]	Tasmania, Australia[12]	New South Wales, Australia[13]	New South Wales, Australia[14]	Zanzibar Channel[15]	Solor Island, Indonesia[16]	American Samoa[17]	Talaud Island, Indonesia[18]	Paternoster Island, Indonesia[19]
LZ	18	18	12	6	12	6	6	6	6
Mean	0.78	0.77	0.73	0.78	0.61	0.70	0.75	0.70	0.72
SD	0.03	0.05	0.04	0.03	0.05	0.05	0.02	0.03	0.02
Range	0.77–0.86	0.66–0.90	0.67–0.80	0.76–0.82	0.55–0.72	0.63–0.76	0.72–0.77	0.67–0.74	0.69–0.74
WZ	18	18	12	6	12	6	6	6	6
Mean	0.37	0.37	0.27	0.33	0.29	0.26	0.26	0.37	0.29
SD	0.05	0.06	0.02	0.03	0.01	0.02	0.03	0.04	0.02
Range	0.29–0.49	0.24–0.52	0.23–0.32	0.30–0.38	0.26–0.31	0.25–0.29	0.22–0.31	0.32–0.42	0.26–0.32
LO	18	18	6	6	—	—	6	6	1
Mean	0.08	0.08	0.07	0.07	—	—	0.07	0.29	0.07
SD	0.01	0.01	0.01	0.02	—	—	0.01	0.01	—
Range	0.07–0.10	0.07–0.11	0.06–0.09	0.06–0.10	—	—	0.06–0.08	0.29–0.30	—
WO	18	18	12	6	11	6	6	6	6
Mean	0.16	0.18	0.31	0.14	0.15	0.13	0.13	0.24	0.16
SD	0.02	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.03
Range	0.13–0.19	0.15–0.24	0.11–0.17	0.13–0.15	0.13–0.28	0.114–0.13	0.11–0.15	0.22–0.25	0.13–0.20
Lopes	18	18	12	6	12	6	6	6	6
Mean	0.56	0.62	0.61	0.57	0.52	0.52	0.63	0.50	0.56
SD	0.04	0.08	0.05	0.03	0.05	0.05	0.01	0.02	0.03
Range	0.48–0.67	0.53–0.74	0.51–0.67	0.53–0.61	0.13–0.18	0.48–0.57	0.61–0.66	0.48–53	0.54–0.61
Wopes	18	18	12	6	12	6	6	6	6
Mean	0.24	0.28	0.21	0.23	0.24	0.22	0.22	0.30	0.23
SD	0.04	0.04	0.02	0.03	0.02	0.03	0.02	0.05	0.03
Range	0.17–0.34	0.22–0.36	0.19–0.24	0.19–0.26	0.22–0.28	0.25	0.18–0.24	0.23–0.34	0.19–0.26
LOv	8	—	12	6	6	6	6	—	6
Mean	0.34	—	0.31	0.27	0.25	0.24	0.23	—	0.244
SD	0.03	—	0.02	0.02	0.02	0.02	0.01	—	0.03
Range	0.30–0.40	—	0.29–0.34	0.25–0.29	0.24–0.28	0.21–0.27	0.20–0.24	—	0.20–0.28
WOv	8	—	12	6	6	6	6	—	6
Mean	0.32	—	0.30	0.29	0.25	0.26	0.25	—	0.23
SD	0.04	—	0.02	0.01	0.02	0.02	0.01	—	0.04
Range	0.27–0.36	—	0.27–0.32	0.29–0.30	0.22–0.26	0.25–0.29	0.24–26	—	0.17–028
Lav1	13	18	12	6	12	6	6	6	6
Mean	0.43	0.40	0.33	0.33	0.37	0.38	0.33	0.27	0.29
SD	0.03	0.04	0.03	0.03	0.02	0.05	0.03	0.02	0.02
Range	0.38–0.44	0.28–0.46	0.29–0.38	0.29–0.36	0.33–0.40	0.32–0.47	0.28–0.35	0.25–0.29	0.28–0.32
Wav1	12	18	12	6	12	6	6	6	6
Mean	0.24	0.21	0.19	0.21	0.16	0.15	0.12	0.14	0.150
SD	0.01	0.02	0.02	0.01	0.02	0.01	0.01	0.01	0.02
Range	0.23–0.27	0.18–0.25	0.17–0.23	0.19–0.23	0.13–0.18	0.11–0.13	0.10–13	0.23–0.34	0.13–0.32
Lav/WZ ratio	1.2	1.1	1.3	1.2	1.3	1.5	1.3	0.73	1.0

[1] MCZ 100106. Waikiki Yacht Club, Oahu, Hawaii.
[2] NHM 1937.9.28.37. Ghardaqa, Red Sea.
[3] MCZ 100107. Coconut Island, Oahu, Hawaii.
[4] BKBM K1019. Barber's Point Harbor; K843. Honolulu Harbor, Oahu, Hawaii.
[5] NHM 1939.4.18.2. Dar-es-Salaam, Tanzania, Indian Ocean.
[6] NHM 1936.12.30.166. Providence Island, Seychelles, Indian Ocean.
[7] NMNH 208837 (need catalog number). Tortugas, Florida.
[8] NHM 1937.9.28.35. Abu Shaar, Red Sea.
[9] NHM 1899.7.1.4608. Ceylon.
[10] Could not see to measure in cleared, whole-mount specimen.
[11] MV F 91987 (63486). Victoria, Western Port; 63489. Victoria, location unknown; NHM 97.5.1.378.
[12] MV F 133121–133123. Tasmania, Australia.
[13] NHM 1888.1.2.2. Port Jackson, New South Wales, Australia.
[14] NHM 1883.11.29.24. Port Jackson, New South Wales, Australia.
[15] MM 1299. Zanzibar Channel, Zanzibar, Indian Ocean.
[16] NHM 1928.3.6.267. Solor Island, Indonesia.
[17] BKBM K1046. American Samoa.
[18] NHM 1928.3.6.268.
[19] NHM 1979.1.8.1. Paternoster Island, Indonesia.

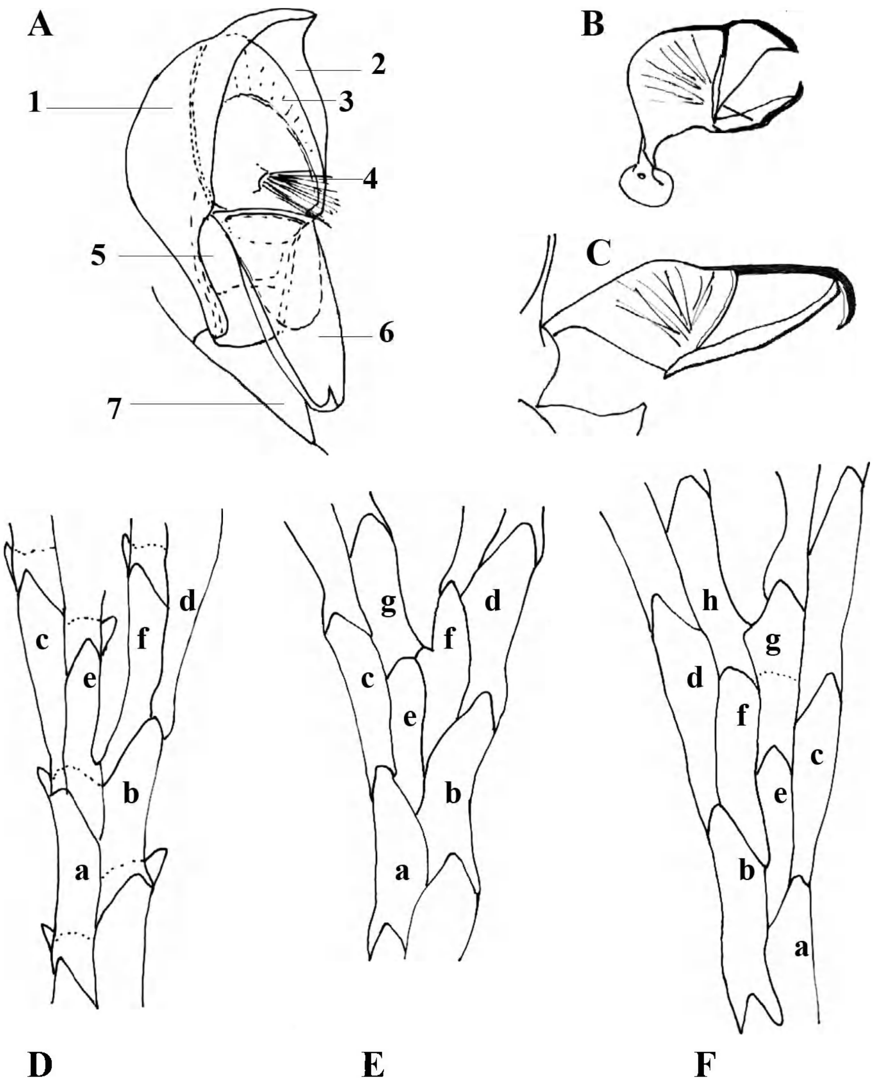

Figure 1. A. Structure of a pedunculate or "bird's head" avicularium: 1. Body of avicularian zooid = "head." 2. Rostrum of zooid = "beak." 3. Cryptocyst of avicularian zooid. 4. Sensory bristles of polypide rudiment. 5. Peduncle, elongate proximal portion of avicularian zooid. 6. Mandible = lower part of "beak." 7. Peduncle cushion. B. Round-headed avicularium in profile (A and B redrawn from Kauffmann, 1971). C. Elongate sway-backed avicularium in profile. D. Harmer's bifurcation type 3 in basal view. E. Bifurcation type 4 in basal view. F. Bifurcation type 5 in basal view (D, E, and F redrawn from Ryland, 1960).

ion, which is part of the wall of the supporting autozooid. Ovicells are hyperstomial, crescentic to globular, or helmet-shaped.

In biserial species such as those discussed here, patterns of branch bifurcation are usually one of three types: types 3, 4, and 5 of Harmer (1926) (Figs. 1D–F).

TAXONOMIC SECTION

Order Cheilostomata
Suborder Neocheilostomina d'Hondt, 1985 (part)
Infraorder Flustrina Smitt, 1868 (part)
Superfamily Buguloidea Gray, 1848
Family Bugulidae Gray, 1848

Genus *Bugula* Oken, 1815

Bugula neritina group

Bugula neritina (Linnaeus, 1758)

Figures 2, 3

Sertularia neritina Linnaeus, 1758: 815.

Bugula neritina Robertson, 1905: 266, pl. 9, fig. 47; pl. 16, fig. 97. Hastings, 1930: 704. Osburn, 1950: 154, pl. 23, fig. 3; pl. 24, fig. 3. Ryland and Hayward, 1977: 162, fig. 78. Winston, 1982: 129, fig. 52. Hayward, 1988: 289. Gordon and Mawatari, 1992: 21, pls. 2G, 5F. Hayward and Ryland, 1998: 220, fig. 68. Liu et al., 2001: 466, pl. 22, figs. 1, 2. Seo, 2005: 330, pls. 47–49. Tilbrook, 2006: 39, pl. 5C.

Description. Colonies consisting of erect, biserial, wine-red to red-brown branches, forming tufts up to 10 cm in length in some habitats. Large, about 0.72 mm in length, elongate zooids, about 0.21 mm wide distally, and tapering proximally, with frontal membrane covering almost entire frontal wall. Zooids with no distal spines, but with sharply pointed distal corners. Polypides large, red-pigmented, the mean tentacle number (of Florida specimens) 23, mean lophophore diameter 0.76 mm. No avicularia. Ovicells large and globular, attached to distal corners of zooids and oriented at a slight angle to branch axis. Reddish brown when filled with brooded embryos, becoming more calcified and pearly white in color as they age.

Diagnosis. No avicularia. Zooids large, colonies becoming large, ovicells globular.

Notes. Bugula neritina is likely the most widely studied of all bryozoans, having been the focus of investigations ranging from biogeographic occurrence, invasive biology, embryonic development, larval biology, and settlement and growth to inter- and intraspecific interactions. As is known to occur in all species of *Bugula* examined to date and is documented also in certain other cheilostomes, *B. neritina* possesses an extraembryonic nutrition system. A specialized lining of the ovicells is modified for the manufacture and transport of nutrients across the extracellular barrier of the ovicell lining to the developing embryo that resides within the lumen of the brood chamber (Woollacott and Zimmer, 1972, 1975). During development from egg to larva, an approximately 500-fold increase in volume occurs (Woollacott and Zimmer, 1975). Because the larva lacks a digestive tract, persistent blastocoel, or coelomic cavities, this increase in volume represents a direct increase in mass. The functional significance resides, in part, in increased provisioning of nutrients supporting duration of the larval swimming period, for transformations at metamorphosis until an ancestrula capable of feeding has developed, and for production of an ancestrula that is generally larger than observed in related species. Wendt (1996, 1998, 2000) has studied in detail the energetics of swimming and metamorphosis in this species.

Bugula neritina is of medical interest because of the activities of one of the natural products isolated from this species: bryostatin-1, a cyclic macrolactone (Pettit et al., 1982). This substance has been linked with action against a number of cancers by enhancing effectiveness of other anticancer drugs and reversing multidrug resistance, activation of T cells, immunomodulation and stimulation of hematopoietic progenitor cells, and possessing possible antidepressant and memory-enhancing effects (Kijoa and Sawangwong, 2004; Paul et al., 2007; Sharp et al., 2007a). Davidson and coworkers (2001) localized the site of its synthesis to symbiotic bacteria occurring in association with *B. neritina.* Woollacott (1980) described, on the basis of anatomy, the presence of bacteria in the pallial sinus of *B. neritina* larvae and noted that these bacteria are released like a cloud around the larva at the onset of metamorphosis, potentially providing a route for intraspecific vertical transmission as well as having roles in other possible intra- and interspecific interactions. Furthermore, Woollacott reported that whereas bacteria were also found in *B. simplex* larvae, they were not observed in larvae of *B. turrita*, a species that arises

Figure 2. *Bugula neritina*. Oahu, Hawaii. MCZ 100106. SEM images. A. Ovicelled branches. Scale bar = 200 μm. B. Branch of colony showing ovicelled and nonovicelled zooids. Scale bar = 200 μm. C. Basal side of branch showing bifurcation pattern. Scale bar = 200 μm. D. Two ovicells and adjacent nonovicelled zooid. Note small spiny projections on distal edges of zooids, but no jointed spines such as occur in many *Bugula* species. Scale bar = 100 μm.

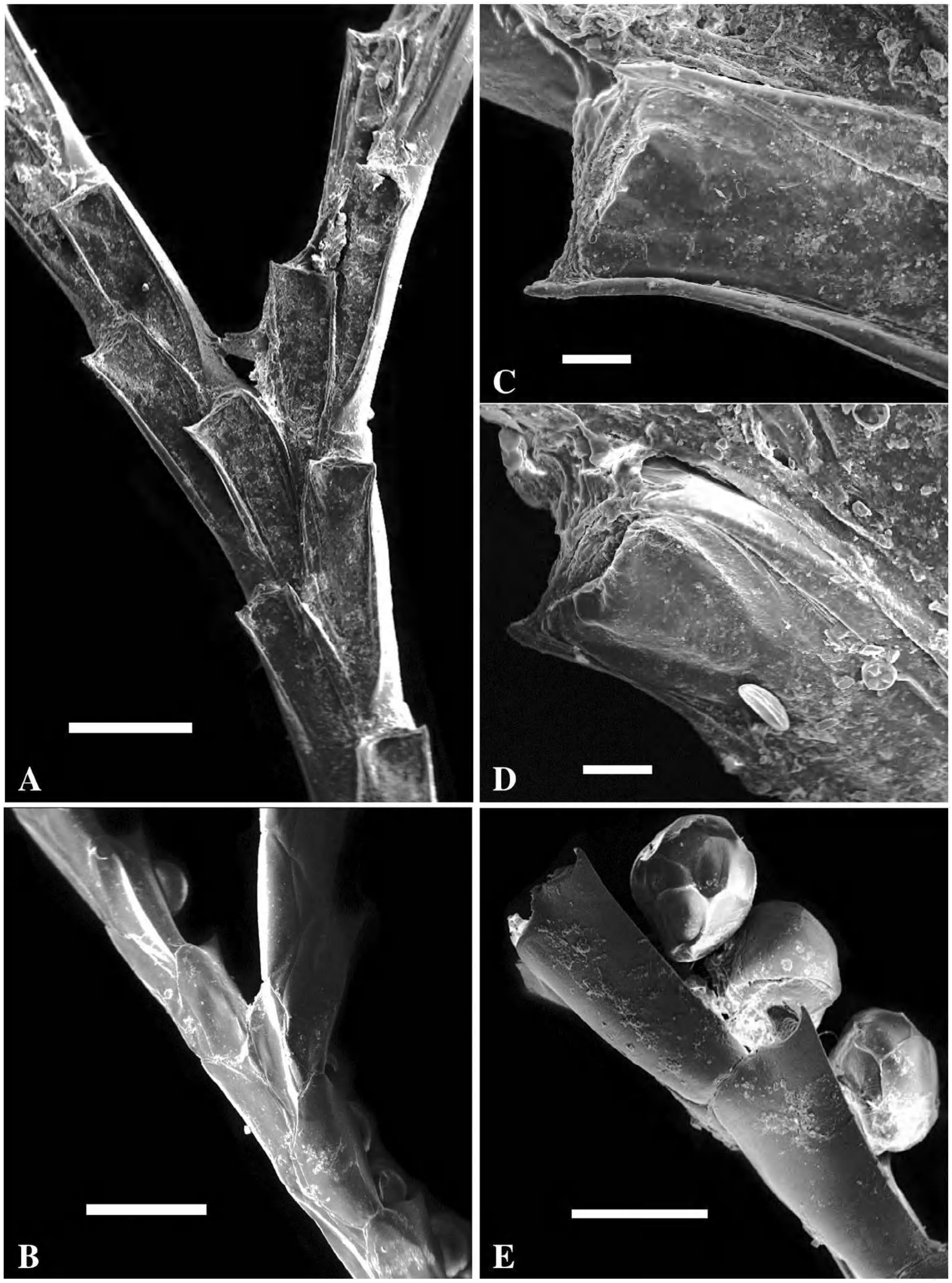

Figure 3. *Bugula neritina*. Bogue Sound, North Carolina, Atlantic Ocean. VMNH 210. SEM images. A. Front view of branch bifurcation. Scale bar = 400 μm. B. Back view of branches showing bifurcation pattern. Scale bar = 400 μm. C. Orifice, showing its liplike structure. Scale bar = 60 μm. D. A second, slightly gaping, orifice. Scale bar = 60 μm. E. Three ovicells at a branch tip, viewed from reverse side of branch. Scale bar = 200 μm.

in seasonal successional series after *B. simplex.* Woollacott and Zimmer (1975) also illustrated bacteria in association with the funicular cords of the autozooids in *B. neritina.* Koty Sharp and coworkers (2007b) provide a detailed account of localization of bryostatins through the life cycle of *B. neritina.*

A functional role for bryostatin in the life cycle of *B. neritina* is now well established (Lindquist and Hay, 1996; Lopanik et al., 2004, 2006; Sharp et al., 2007b). Bryostatins are unpalatable to certain species of fish and, thereby, deter predation on *B. neritina* larvae. High concentrations of bryostatins also exist in tissues of zooids near the distal tips of branches, which might reduce predation on these growing regions of colonies.

In this paper we have illustrated both Pacific and Atlantic material and presented a morphological description applicable to populations worldwide on the basis of the traditional view of *B. neritina* as a widespread, warm-water, fouling species. However, analysis of bryostatins found in populations from different localities or depths show variation in the kinds and amounts of several bryostatin compounds present, indicating that *B. neritina* could be a cryptic species complex, rather than a single species (Davidson and Haygood, 1999; McGovern and Hellberg, 2003).

Note that the synonymy given above is not a complete synonymy for *B. neritina* (which would take several pages). The references cited emphasize Indo-Pacific records or refer to additional taxonomic citations in their synonymies of the species.

Distribution. Bugula neritina sensu lato is one of the most widespread fouling bryozoans, occurring in tropical to temperate waters on both natural and artificial substrata.

Specimens Examined. MCZ 100106. *Bugula neritina*, floating docks, Waikiki Yacht Club, Ali Wai Basin, Oahu, Hawaii, 30 June 1992, R. M. Woollacott coll. MCZ 100108. *Bugula neritina*, Amelia Island, Florida, 1861, S. H. Scudder coll. MCZ 100109. *Bugula neritina*, Amelia Island, Florida, 1861, S. H. Scudder coll. MCZ 100110. *Bugula neritina*, Mussel Point, California, 36°37′20″N, 121°54′15″W, A. E. Blagg coll., 4 Apr. 1938. VMNH 210.00. *Bugula neritina*, Bogue Sound, Island Harbor Marina, Emerald Isle, North Carolina, Lynn Pritchett coll., 29 Aug. 1993. VMNH 701.00. *Bugula neritina*, Walton Rocks, South Hutchinson Island, St. Lucie County, Florida, 19 Feb. 1999, J. E. Winston coll. VMNH 852.00. *Bugula neritina*, south end of Wrightsville Beach, New Hanover County, North Carolina, 16 June 1999, J. E. Winston coll. VMNH 1683.00. *Bugula neritina*, Ocean Isle Beach, Ocean Isle, Brunswick Co., North Carolina (beach drift), 5 May 2000, C. Carter coll. VMNH 2563.00. *Bugula neritina*, Folly Beach, Charleston Co., South Carolina, 13 Apr. 1995, J. E. Winston coll.

Bugula minima group

Bugula minima (Waters, 1909)

Figures 4–7

Bugula neritina var. *minima* part Waters, 1909: 136, pl. 11, figs. 6, 7; Waters, 1913: 471.
Bugula neritina (L.), forma *minima* Waters part Marcus 1921: 1 (not fig. 1).
Bugula robusta part Harmer, 1926: 435, not *Bugula robusta* Macgillivray, 1869.
Bugula minima part Hastings, 1939: 334, text-figs. 276A, B, C.

Neotype. Bugula minima Waters Hastings. Seaward edge, outer reefs, Ghardaqa, Red Sea, LWS. 1933. Dr. C. Crossland. NHM 1937.9.28.37.

Description. Colony erect, biserial, long-branched feathery tufts. Branching pattern of Harmer's type 4. Color red-brown when living, pigmentation very similar to that of *B. neritina*; brown pigment remaining in both dry- and wet-preserved specimens. Zooids elongate, about 0.56–0.66 mm long, widest distally (about 0.20 mm) and tapering proximally, outer lateral walls straight. Outer distal corners pointed, inner distal edges angular to rounded. Lightly calcified, with frontal opesial membrane covering most of the frontal wall. Avicu-

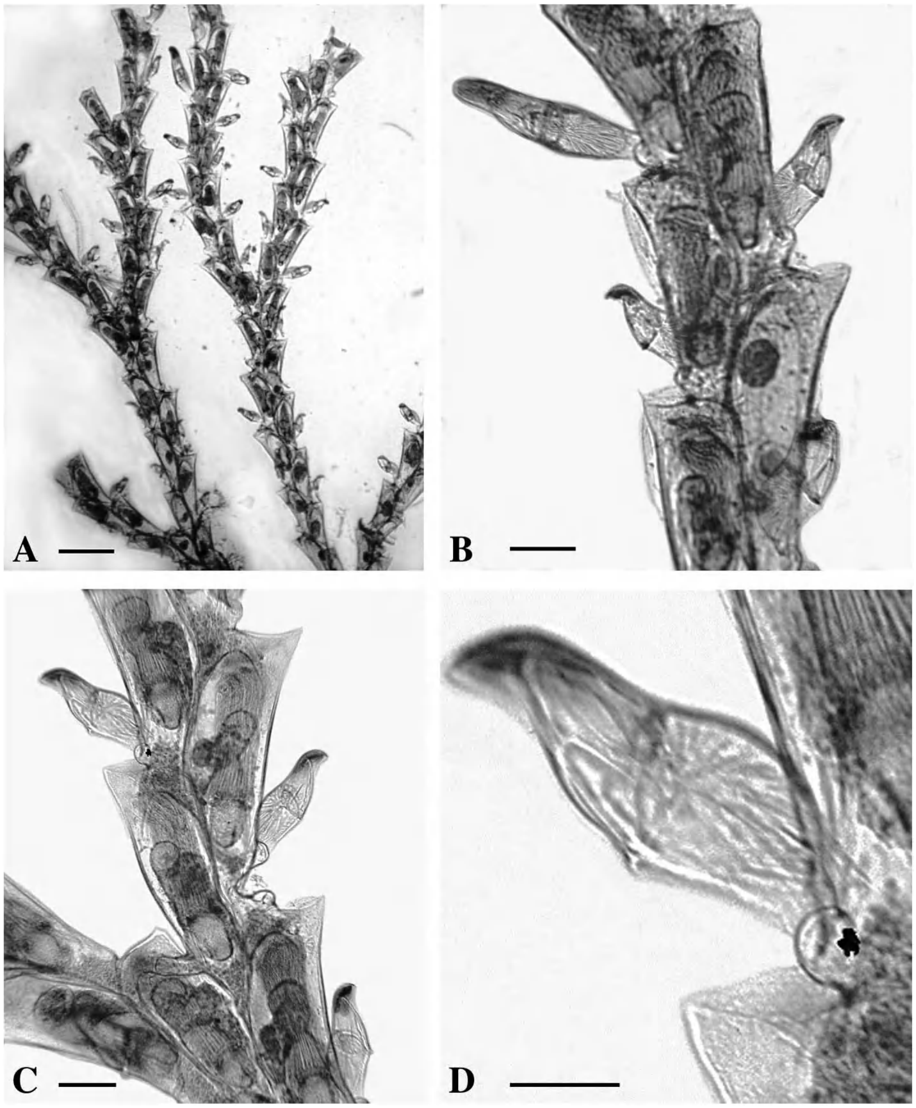

Figure 4. *Bugula minima.* Neotype. Light micrograph of whole mount on glass slide. Ghardaqa, Red Sea. NHM 1937.9.28.37. A. Colony branches, note small and large avicularia. Scale bar = 1 mm. B. Portion of branch showing several zooids with small and large avicularia. Scale bar = 100 μm. C. Back of branch showing bifurcation pattern. Scale bar = 100 μm. D. Close-up of an avicularium; note elongate head and dark pigmented tips of the elongate beak. Scale bar = 50 μm.

laria dimorphic, varying in size and shape. The smaller avicularia have rounded body and rostrum, but distinct, dorsally sway-backed appearance because of the curvature of both. The larger avicularia have a more elongated, sway-backed profile, with a diagonal line of cryptocyst demarcating the two sections. The inner body portion is elongate and shallowly convex dorsally; the outer portion a shorter, higher convexity with sharply down-curved beak, deeply pigmented at its tip. Avicularia are attached to a short peduncle cushion, which is positioned proximally on the outer side

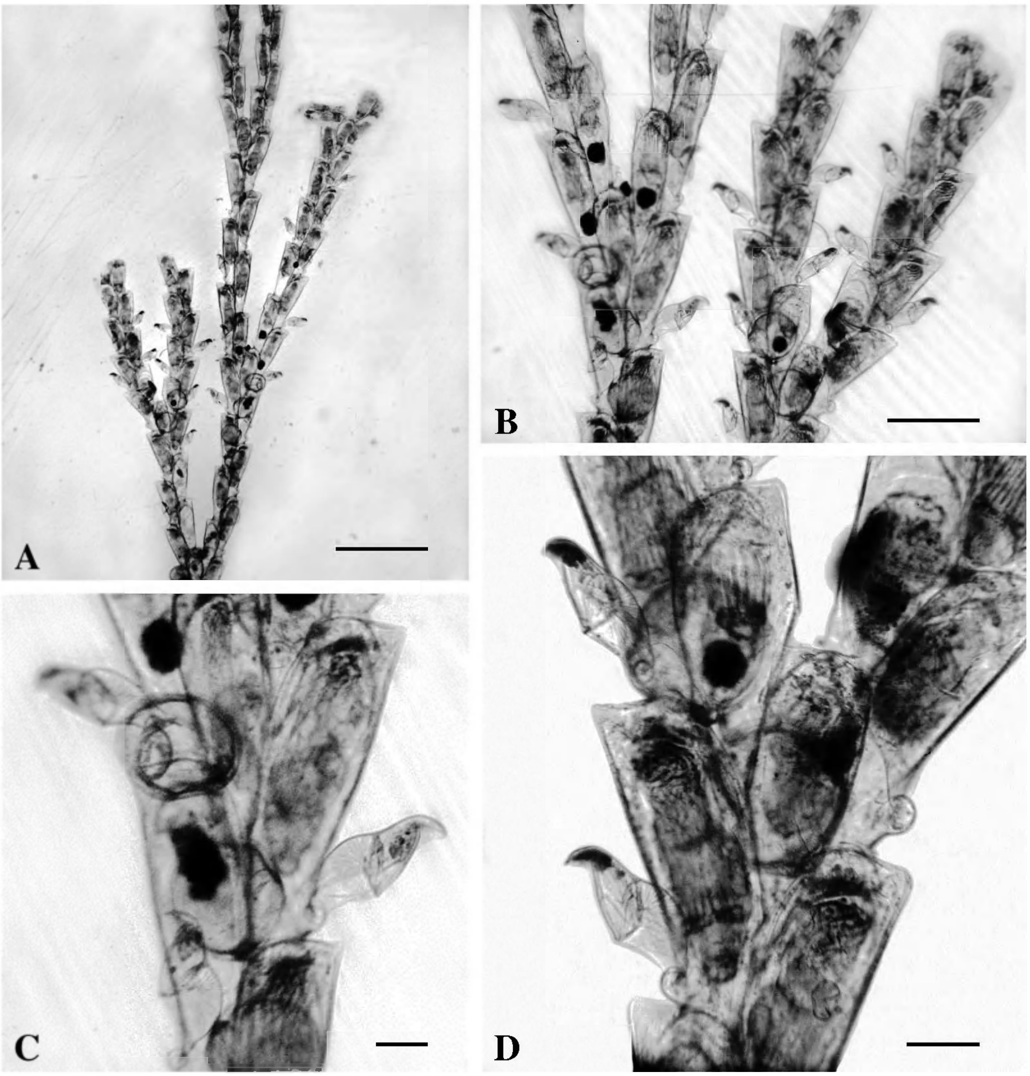

Figure 5. *Bugula minima.* Specimen from Dar-es-Salaam, Tanzania, Africa, Indian Ocean. NHM 1939.4.18.2. Light micrograph of whole mount on slide. A. Portion of branching colony fragment. Scale bar = 1 mm. B. Close-up of branches showing small and large avicularia; note elongate sway-backed shape and dark pigmented beak tip. Scale bar = 500 μm. C. Branch viewed from reverse side, showing zooids, one ovicell, and three avicularia. Scale bar = 100 μm. D. View of reverse side of colony showing bifurcation pattern. Scale bar = 100 μm.

of the zooid at about the level of the proximal edge of the frontal membrane. Ovicells are globular, attached at the inner distal angle of zooids, and oriented more or less horizontally. As they mature, they develop a broad, thickened outer band. Brown embryos could still be seen in the slide preparations examined.

Diagnosis. Colonies and zooids large, ovicells globular, avicularia dimorphic, both small and large avicularia sway-backed, large avicularia very elongate, attached by short peduncles to outer sides of zooids at the level of the base of the frontal membrane.

Notes. One of our goals was to find the

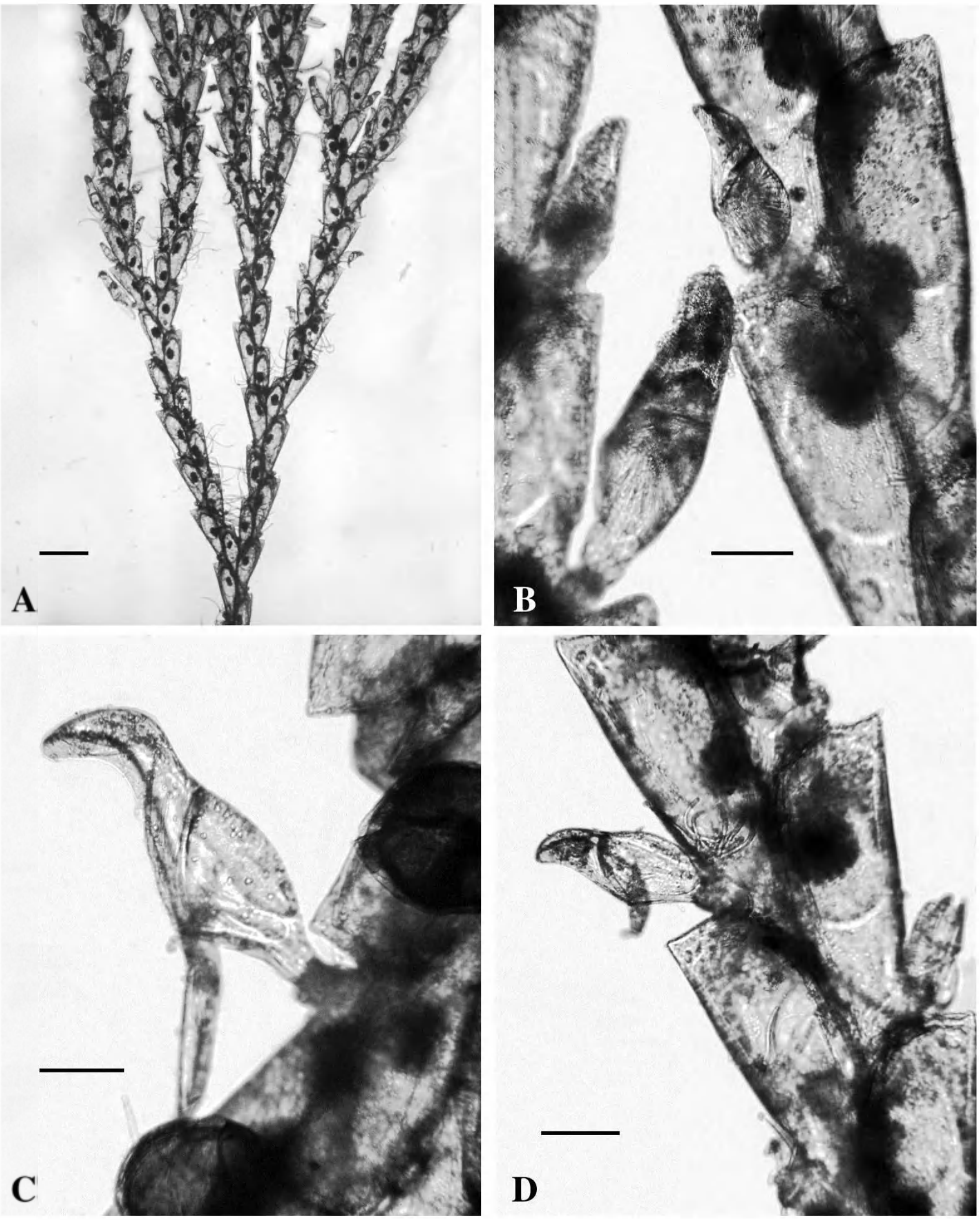

Figure 6. *Bugula minima*. Oahu, Hawaii. MCZ 100107. Light micrograph of wet-preserved specimen. A. Colony branches. Scale bar = 500 μm. B. Close-up of branches showing zooids and a large avicularium. Scale bar = 100 μm. C. Large avicularium with open mandible. Scale bar = 100 μm. D. Zooids and small avicularium. Scale bar = 100 μm.

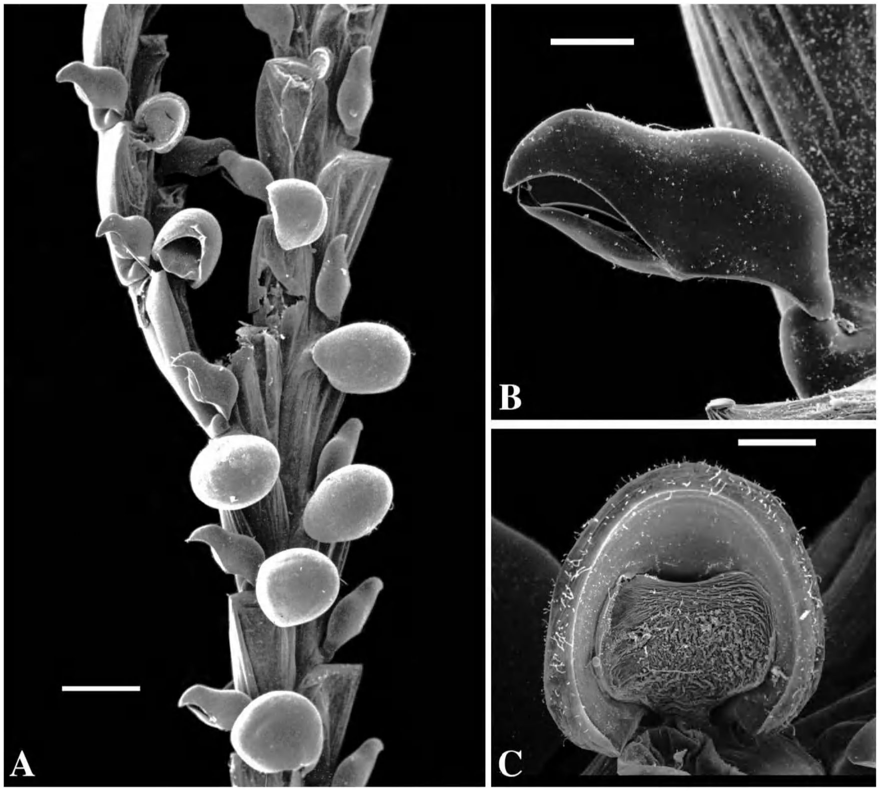

Figure 7. *Bugula minima.* Oahu, Hawaii. MCZ 100107. SEM images. A. Ovicelled colony branch showing zooids and avicularia. Scale bar = 200 μm. B. One of the elongate avicularia in side view. Scale bar = 50 μm. C. Developing ovicell. Scale bar = 25 μm.

original Red Sea and Indian Ocean material studied by Waters. Bryozoologists had believed for years that all of Waters' specimens, including type material, had been lost in bombing during World War II, but this was not the case. Thanks to the assistance of Henry McGhie and Rebecca Smith at the Manchester Museum, we were able to obtain three slides of Waters' material from Zanzibar. However, it did not include any type material. Hastings (1939) had designated a specimen she had borrowed from the Liverpool University Zoology Museum (Mersa Makdah, Red Sea, 5 fathoms, Waters) the type of *B. minima.* Thanks to Ian Wallace at the Liverpool Museum, we learned that the specimens from the Crossland collection, including the *B. minima* type, apparently remained in the Zoology Museum until the early 1960s when the university discarded its collections. A copy of a typed list of material that was in the University Museum's collection 1938/1939, created by Kathleen Carpenter and received from Ian Wallace, lists five slides of *B. minima.* Becaue the type of *B. minima* designated by Hastings no longer exists and we know of no topotypic specimens, we here designate the British Museum specimen from el-Ghardaqa, Red Sea, Egypt (NHM 1937.9.28.37), as neotype. As Figure 5 shows, one other specimen she listed as *B. minima,* NHM 1939.4.18.2 from Dar-es-Salaam (on the opposite side of the Zanzibar channel from Waters' location), clearly belongs in *B. minima.* Other specimens she included in *minima,* those from Providence Island and Ceylon, represent two different unnamed species and will be described below.

The Hawaiian specimens collected by Woollacott are very similar in zooid size to *B. minima* specimens from the Red Sea and East Africa–Zanzibar Indian Ocean localities and are included here (Figs. 6, 7). The avicularia of the Hawaiian colonies show a more extreme range in size: the large ones are larger, the outer lateral edges of zooids straighter than those of the Red Sea specimen, in particular, and the peduncles of the avicularia might be slightly more proximally attached. Several Honolulu-area specimens loaned by the Bishop Museum (see Specimens Examined) also match the MCZ Hawaiian *B. minima*.

Distribution. Red Sea, Indian Ocean, Hawaii.

Specimens Examined. NHM 1937.9.28.37. *Bugula minima*, Waters Hastings, Seaward edge, outer reefs, Ghardaqa, Red Sea, LWS, 1933, Dr. C. Crossland. MM 1299. *Bugula neritina* var. *minima*, Ras Orowamnibe, Zanzibar Channel, 10 fathoms. Crossland Exp. 515 (E. collection A. W. Waters). MM 1300. *Bugula neritina* var. *minima*, mandibles, Prison Island, Zanzibar Channel, 8 fathoms. Crossland Exp. 505 (E. collection A. W. Waters). MM 1301. *Bugula neritina* var. *minima*, Prison Island, Zanzibar Channel, 8 fathoms. Crossland Exp. 505 (E. collection A. W. Waters). NHM 1939.4.18.2. *Bugula neritina* var. *minima*, Waters, Daressalam Stuhlmann Berlin Museum Part of 1944 [slide with whole mount, two cover slips, one has just a few avicularia under it], from Dar-es-Salaam, Tanzania (east Africa, Indian Ocean). MCZ. 100107. *Bugula minima*, Coconut Island, Oahu, Hawaii, Woollacott and Zimmer coll., 21 and 24 July 1995. BPBM K832. *Bugula robusta*, Oahu, Honolulu Harbor, Station 5. BPBM K843. *Bugula robusta*, Oahu, Honolulu Harbor, Station 8. BPBM K832. *Bugula robusta*, Oahu, Honolulu Harbor, Station 11. BPBM K1019. *Bugula robusta*, Oahu, Barbers Point Harbor Station 30.

Bugula providensis new species
Figure 8

Bugula neritina var. *minima* Thornely, 1912: 141.
Bugula minima (part) Hastings, 1939: 334.

Holotype. NHM.1936.12.30.166. *Bugula neritina* var. *minima.* Miss L. R. Thornely. Providence Is. 50–78f.

Etymology. Named after the location where the specimen was collected, near Providence Island, 9°14′S, 51°03′E, one of the Farquar group in the Outer Islands of the Seychelles, Indian Ocean.

Description. Colony composed of erect biserial branches, brownish red in color. Zooids elongate (about 0.68 mm long by 0.19 mm wide), sub-triangular, without spines. Avicularia are large and sway-backed, with long strongly hooked beaks, similar in shape to those of *B. minima*, but all similar in size, about 0.27 mm long by 0.11 mm wide, comparable in size to the large avicularia of *B. minima*, but differing in their position and orientation. The peduncle of the avicularium is attached to a peduncle cushion at the proximal edge of the zooid, almost on the outer lateral wall, not at the very base of the zooid, but up about the width of the pedicel from its proximal margin. Avicularia are oriented with beaks tilted diagonally outward, so that they stand out on either side of a branch in an evenly spaced feathery series. Ovicells are flattened, more ovoid than round. They are attached to inner distal corners of zooids and appear to droop and fill out as they mature.

Diagnosis. Avicularia monomorphic, sway-backed, elongate, similar to large avicularia of *B. minima* but with their attachment point on peduncle cushion about a peduncle width up from the proximal margin, close to lateral wall. Avicularia oriented diagonally, projecting featherlike from the branches.

Notes. This appears to be another species in the *minima* group. In addition to the sway-backed shape of the avicularia, the colony branches are delicate and flexible, like those of other *minima* species,

Figure 8. *Bugula providensis* new species. Light micrograph of holotype. NHM 1936.12.30.166. A. Branches of colony. Scale bar = 2 mm. B. Detached sway-backed avicularium. Scale bar = 200 μm. C. Basal view of branch showing bifurcation. Scale bar = 500 μm. D. Portion of branch to show ovicells and position of avicularia. Scale bar = 200 μm. E. Close-up of autozooids and avicularia. Scale bar = 200 μm.

rather than sturdy, as in those of the *robusta* group. Although only one specimen we examined belonged to this species, its morphology, especially the orientation of the avicularia, was distinct from all others. Thornely believed it to be Waters' "var. *minima*," apparently partly because the colonies of the specimens she examined were small, "1/2 inch in height growing on seaweed," and like many who followed, she interpreted Waters' name as meaning miniature in colony size. Hastings (1939) also considered Thornely's material to be *B. minima*.

Specimens Examined. *Bugula neritina* var. *minima*, Miss L. R. Thornely. Providence Is., 50–78f. NHM.1936.12.30.166. [Name crossed out and with second name pasted on label] *Bugula minima* Waters.

Distribution. Providence Island, Indian Ocean.

Bugula miniatella new species
Figure 9

Bugula neritina var. *minima* Osburn, 1914: 187. Not Waters, 1909: 136.

Holotype. *Bugula minima* Waters. USNM 537252. Tortugas, Florida, 8 fathoms, R. C. Osburn coll.

Etymology. Diminutive of *miniata*, Latin *miniatus*, bright red.

Description. Colony small, composed of erect biserial branches 1–2 cm in length, brownish red in color. Zooids elongate, about 0.58 mm long by 0.18 mm wide, sub-triangular, widest at distal end, tapering proximally. Both distal edges sharply pointed, although the points on outer sides of zooids may be more exaggerated. Zooids delicate, frontal membrane covering most of frontal wall. Avicularia all similar in size and shape, sway-backed and somewhat elongated, but with head and beak portions about equal in length. They are attached on a very short peduncle at the outer side of the proximal wall of the zooids, and tilted at a 45°–60° angle outward from the branches. Ovicells are almost spherical, 0.19 mm long by 0.02 mm wide, attached to inner edge of zooid, and with bottom margin parallel to distal edge of zooid. Ovicells developing on very short branches.

Diagnosis. Zooid size comparable to that of other red-pigmented species, but size of mature reproductive colonies very small. Ovicells spherical. Avicularia small, monomorphic, sway-backed, and somewhat elongate, attached at outer edges of proximal margins of zooids.

Notes. Osburn's description indicates that he found only one colony in his Tortugas collection, so the two slides in the NMNH are parts of a single holotype. The monomorphic avicularia are not as sway-backed as those of the Red Sea–Indo-Pacific *B. minima*, but the head section is not as rounded as that of *B. robusta* and most other *Bugula* species, making the avicularia more like those of *B. minima* in shape, but with a less elongate beak portion. Waters called his Red Sea species *B. minima* because the zooids were smaller in size than those of *B. neritina*. However, in the case of western Atlantic specimens, Osburn and others who followed him apparently took the name to mean small in colony size as well. This species is found on algae, sea grasses, and other ephemeral substrata. It attains only a small size and produces abundant ovicells along its short branches, indicating that it reproduces early in astogeny, in contrast to *B. minima*, which has a colony size comparable to that of *B. neritina*, but slightly smaller zooids.

Specimens Examined. *Bugula minima* Waters. USNM 537252. Tortugas, Florida, 8 fathoms, R. C. Osburn coll. [2 whole mounts on slides, taken from a single colony].

Distribution. Florida to the Caribbean.

Bugula crosslandi Hastings, 1939
Figure 10

Bugula neritina var. *minima* part Waters, 1909: 136, pl. 11, figs. 4, 5.
Bugula crosslandi part Hastings, 1939: 337 (text-fig. 276D; not text-fig. 277A).

Holotype. NHM 1937.9.28.35. Abu

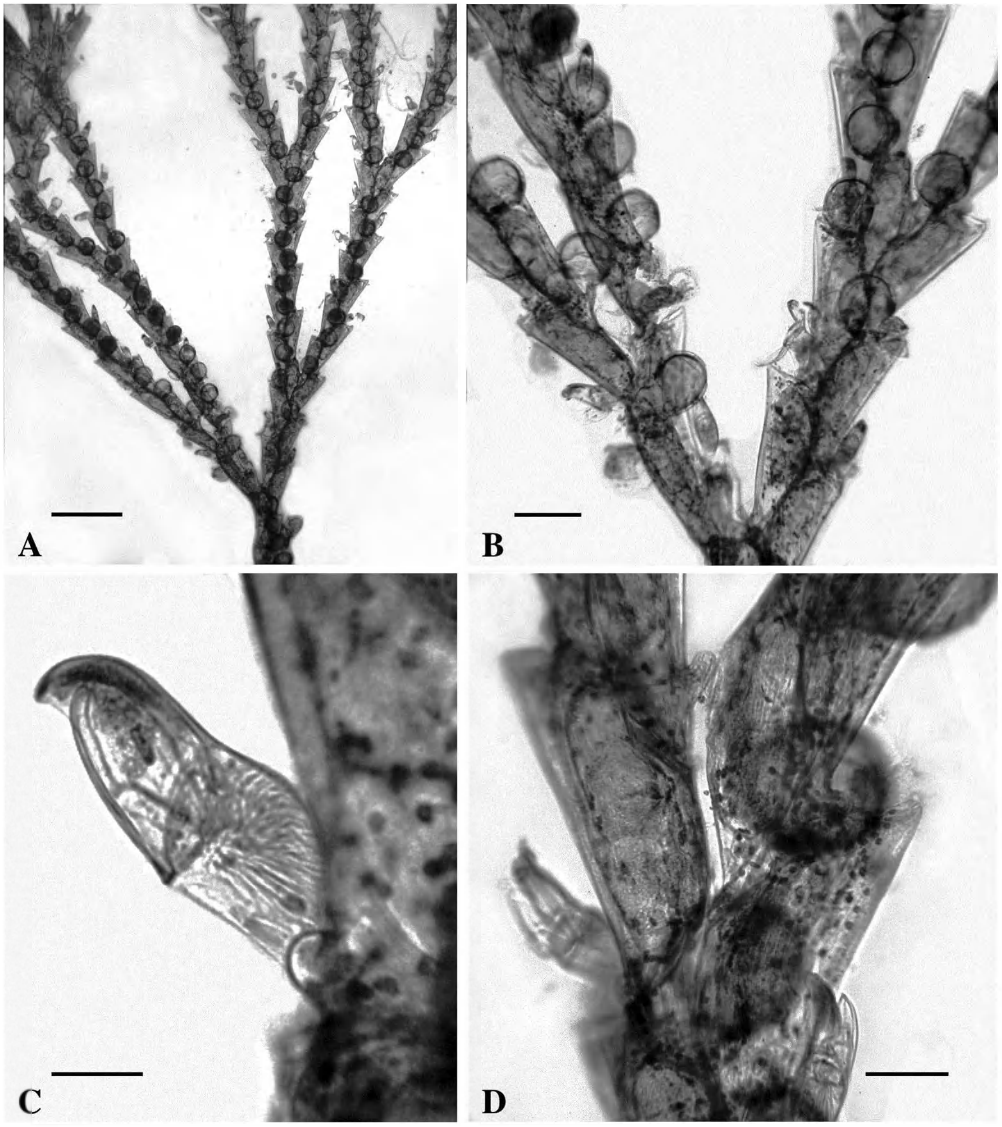

Figure 9. *Bugula miniatella* new species. Holotype. NMNH 208837. Tortugas, Florida. Light micrograph of whole mount on glass slide. A. Branches of colony fragment. Scale bar = 1 mm. B. Closer view of branches showing zooids with ovoid to spherical ovicells and sway-backed avicularia. Scale bar = 250 µm. C. Close-up of branch; note elongate sway-backed avicularium with pigmented beak tip. Scale bar = 50 µm. D. Back view of branches showing bifurcation pattern. Scale bar = 100 µm.

Shaar, Red Sea, ½ to 1 fathom, 20 May 1933 (Dr. C. Crossland).

Description. Colony made up of short, delicate, biserial branches, light reddish brown in color, with type 4 branching, and long attachment rhizoids. Zooids elongate, about 0.51 mm long and 0.17 mm wide, widest distally, tapering proximally, then widening slightly at bases. Outer distal corners of zooids sharp-edged, but not extremely pointed, frontal membrane covering at least 75% of the frontal surface.

Avicularia small, monomorphic, attached on a short peduncle cushion at outer side of proximal gymnocyst, below proximal end of frontal membrane, but above proximal end of zooid. Avicularia with a rounded head and a narrow hooked beak. Ovicells attached at an angle to inner distal corner of zooids, subspherical, with a thickened band around the proximal margin.

Diagnosis. Colony size small, similar in size to that of *Bugula miniatella*, but avicularia round headed, with narrow hooked beaks and short peduncles inserted above the proximal margins of outer edges of zooids.

Notes. Osburn (1950) considered his material to belong to *B. minima*. However, the eastern Pacific material we examined appears to belong to Hastings "*Bugula crosslandi*," as illustrated by the specimen from Gorgona, Panama (text-fig. 277A of Hastings [1939] and p. 704, pl. II, fig. 6), but not with her type material from the Red Sea. As Hastings (1939) noted in her remarks on *crosslandi*, eastern Pacific specimens differ from the type material of *crosslandi* from the Red Sea in having smaller and more slender avicularia. The eastern Pacific species is similar to Tortugas *miniatella*, as well as Red Sea *crosslandi*, in its small size at maturity, but probably should be named separately.

Specimens Examined. Red Sea Material. Because the Waters material from Khor Dongola that Hastings illustrated (her text-fig. 276D) was part of the Liverpool University Zoology Museum collection, which no longer exists, the only Red Sea material available for our examination was the type specimen, NHM 1937.9.28.35 *Bugula crosslandi* Hastings [originally labeled *Bugula neritina* var. *minima* Wat.], Abu Shaar, Red Sea, ½–1 fathom, Dr. C. Crossland. The material consists of two microscope slides and one jar of wet material (apparently that from which slides were made). **Eastern Pacific material.** Allan Hancock Foundation. *Bugula minima* (Waters). RCO. Cocos Island, Costa Rica, Hancock STA 779-38. "Drawn." *Bugula minima* (Waters). STA. 95. Panama. Galtsoff coll. (a good colony with ovicells). *Bugula minima* (Waters). Baja. Off S. end Tiburon. Allan Hancock Foundation. STA 1631 (clump with rootlets, and short branches with ovicells).

Distribution. Red Sea.

Bugula robusta group

Bugula robusta MacGillivray, 1869
Figures 11, 12

Bugula robusta MacGillivray, 1869: 129; MacGillivray in McCoy, 1881: 29, pl. 78, fig. 1.

Holotype. Bugula robusta MacGillivray, 1869. MV F 45556. Victoria, loc. unknown.

Description. Colonies composed of erect, biserial branches, purple when living, gray-brown when dry. Large zooids, about 0.78 mm long by 0.37 mm wide, with more strongly calcified lateral walls than those of other species studied here, their edges appearing whitish and thickened, especially on distal rims and in basal view. Zooids have inner distal edges rounded, outer distal edges tapering to a blunt conical point. Zooid shape broadly triangular, ratio of greatest length to width about 2:1. Orifice D-shaped with chitinous reinforcement, more noticeable than those of other *Bugula* species; golden yellow in color. Frontal membrane shorter proportionally than in other species. Avicularia have large rounded heads and short, narrow, down-curved beaks. They are attached to short peduncle cushions located on the outer proximal edges of the zooids. Ovicells slightly greater in length than width, attached at an angle to distal corner of zooids.

Diagnosis. Living colonies purple, walls white rimmed, well-calcified, with D-shaped operculum. Avicularia not elongated, with round heads and short beaks, attached on a short peduncle to outer proximal edges of zooids. Ovicells slightly longer than wide.

Notes. The specimens from Victoria match MacGillivray's original description

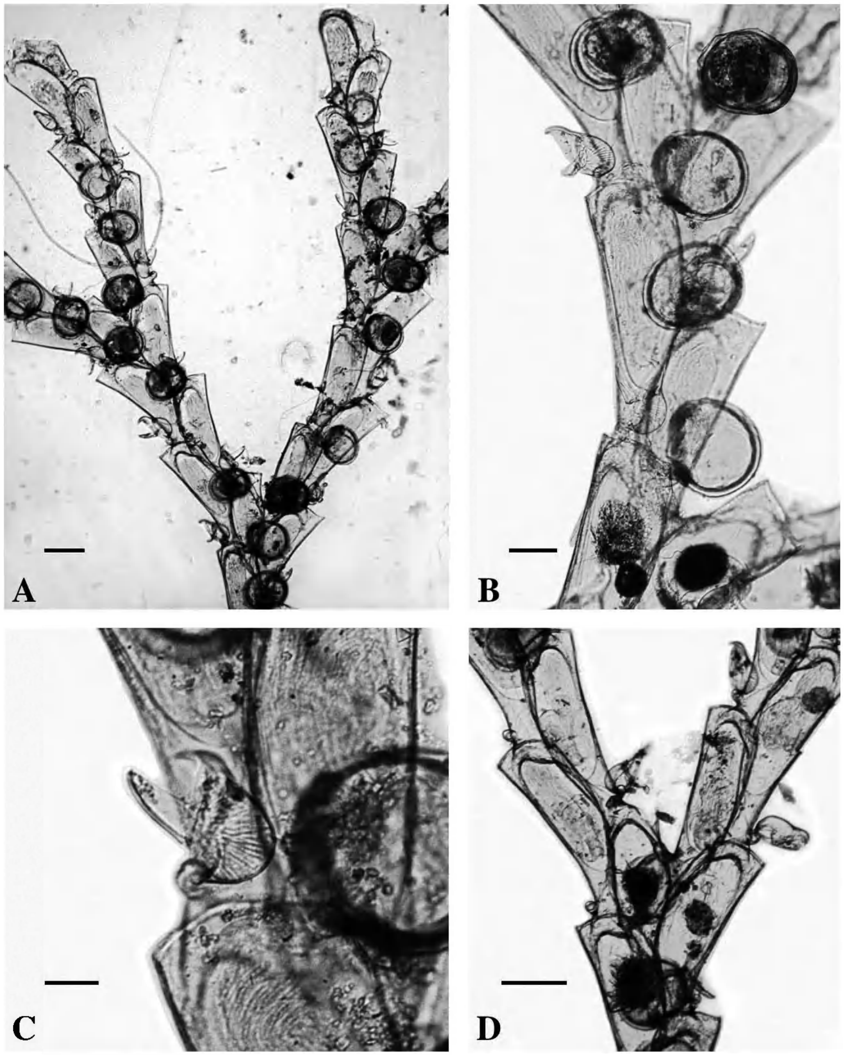

Figure 10. *Bugula crosslandi.* Holotype. NHM 1937.9.28.35. Abu Shaar, Red Sea. Light micrograph of whole mount on slide. A. Ovicelled branches of colony. Scale bar = 200 μm. B. Branch showing several zooids with ovicells and avicularia. Scale bar = 100 μm. C. Close-up showing one round-headed avicularium with open mandible. Scale bar = 50 μm. D. Reverse side of branch showing bifurcation pattern and position of several avicularia. Scale bar = 200 μm.

and his illustration in the *Prodromus.* Like most workers at the time, MacGillivray did not designate types. However, collections staff at Museum Victoria have identified one specimen as that likely to have been used in the original description. The putative type specimen is heavily encrusted with white calcareous material, some distal edges are also thickened by calcification, as is apparent in the illustration of *B. robusta* in plate 78, figure 1, of McCoy's *Prodromus of the Zoology of Victoria* (1881). Some question remains about the coloration of the species in life. MacGillivray states that it is of "greyish brown" color, not red or purple. This is true for dry material, but an underwater photograph of a living South Australian colony

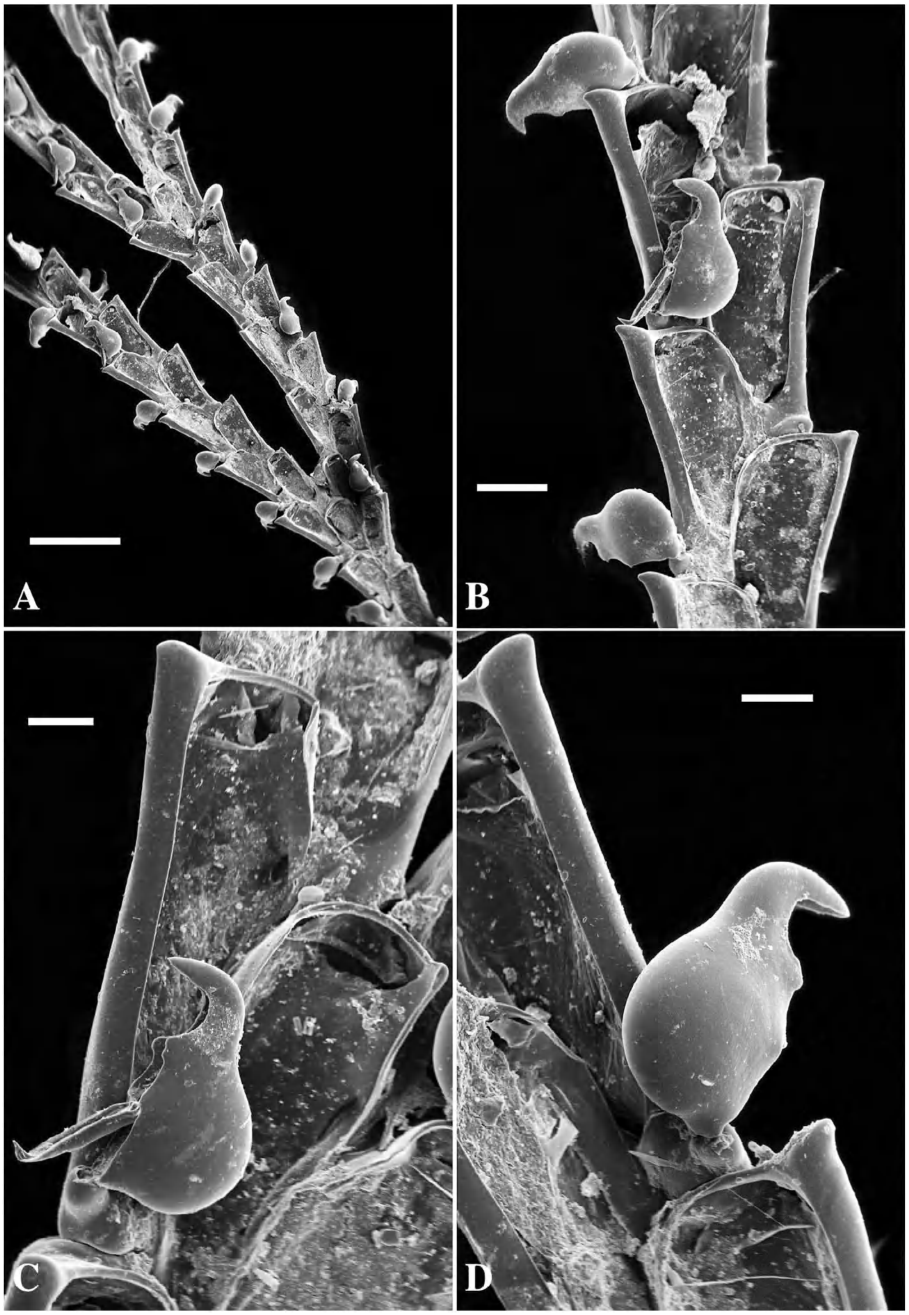

Figure 11. *Bugula robusta.* Tasmania, Australia. MV F 133123. SEM images. A. Colony branches. Scale bar = 1 mm. B. Branch showing zooids and avicularia; note opercula with reinforced rims and thick calcified walls of zooids. Scale bar = 200 µm. C. Two zooids and round-headed avicularium with sharply hooked beak tip and open mandible. Scale bar = 100 µm. D. Second avicularium with closed mandible, note strongly calcified outer walls of zooid. Scale bar = 100 µm.

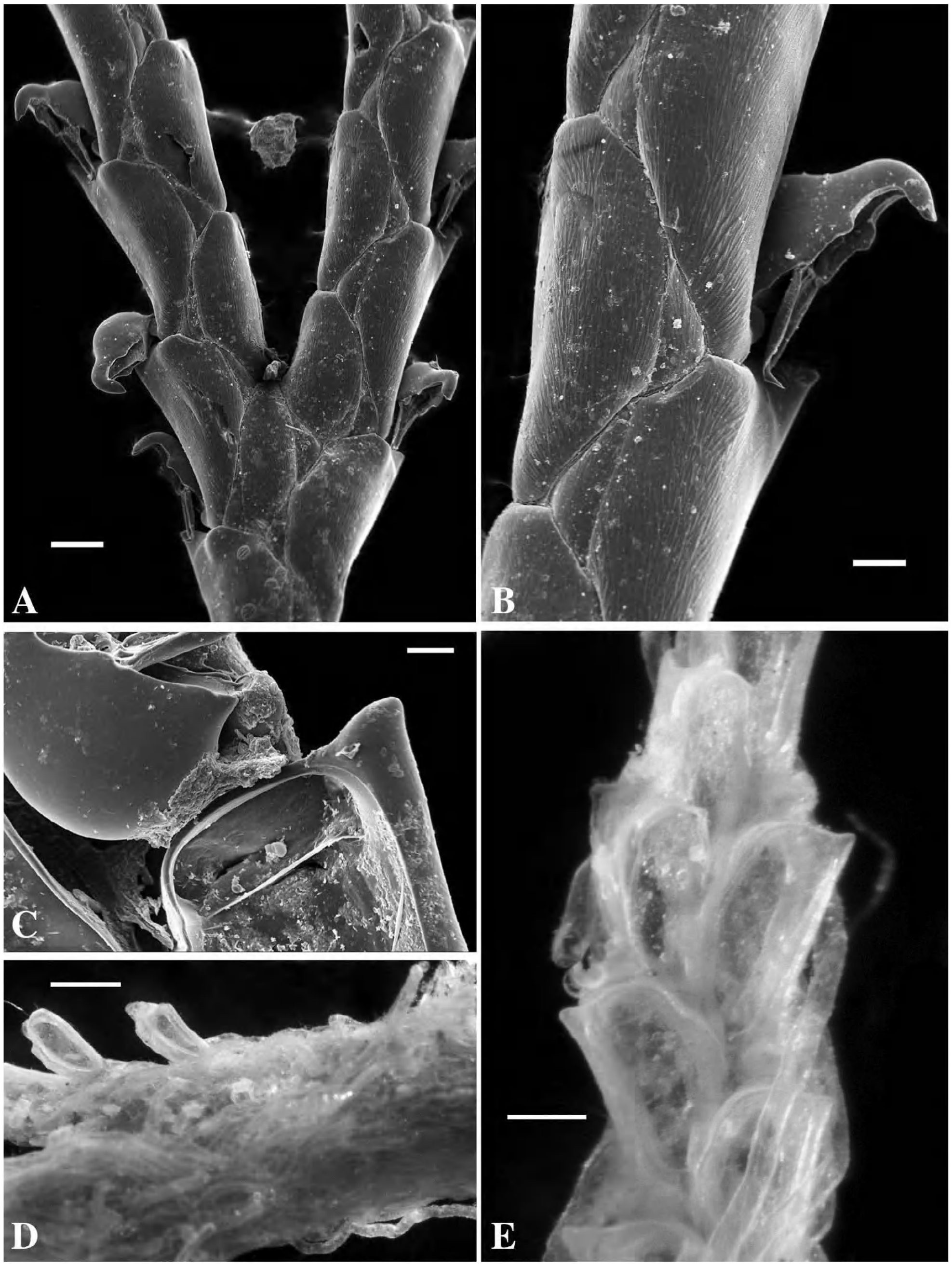

Figure 12. *Bugula robusta*. Tasmania. SEM and light microscope images. SEM: A. Abfrontal side of branch, showing bifurcation pattern. Scale bar = 200 μm. B. Close-up of abfrontal side of branch, showing zig-zag patterning of adjoining walls. Scale bar = 100 μm. C. Close-up of operculum of one zooid and position of peduncle of distal zooid on its outer proximal frontal wall. Scale bar = 50 μm. Light micrographs: D. Back view of radicles and zooids near base of a colony. Scale bar = 100 μm. E. Another view of colony base showing thick bundle of attachment radicles. Scale bar = 100 μm.

by Karen Gowlett-Holmes (1999) shows it to have robust, curving, purple and orange-brown branches with distinct white rims. The distribution of actual *B. robusta* appears to be limited to cool-water habitats in southern Australia and Tasmania. Tropical records of the species are highly suspect, although completely understandable given that Harmer lumped many specimens from different localities under the *Bugula robusta* name in his 1926 Siboga Expedition report and illustrated at least three different species, none of them *B. robusta*, as that species.

Specimens Examined. Bugula robusta MacGillivray, 1869. MV F 45556. Loc. unknown. Vic., one microslide? Holotype. (five branches, avicularia, no ovicells). *Bugula robusta* MacGillivray, 1869. MV F 91986. Loc. unknown, Vic., one microslide. J. Bracebridge Wilson. (two fragments, encrusted, avic., no ovicells). *Bugula robusta* (M under the *Bugula robusta* name) MacGillivray, 1869. MV F 91987. Loc. Western Port, Vic., one microslide. J. B. Wilson MacGillivray coll. *Bugula robusta* MacGillivray, 1869. MV F 91988. Loc. Port Phillip Heads, Vic., one microslide. (one large and two smaller fragments, very debris-encrusted; avicularia gone, no ovicells). *Bugula robusta* MacGillivray, 1869. MV F 91989. Loc. Port Phillip Heads, Vic., one microslide also one large and some smaller fragments. MV F 133121. *Bugula robusta.* Australia, Tasmania, near Burial Point, Southport, 43°25′S, 146°58′E, A. Blackman coll., 1983. Identified by Phillip E. Bock, 1 May 2007. MV F 133122. *Bugula robusta.* Australia, Tasmania, near Tinderbox, d'Entrecasteaux Channel, 4303′S, 147°19′E. A. Blackman coll., 1983. Identified by Phillip E. Bock, 1 May 2007. MV F 133123. *Bugula robusta.* Australia, Tasmania, *Bugula robusta*, Australia, Tasmania, Spring Beach, Orford, 42°34′S, 147°54′E, A. Blackman coll., 1983. Identified by Phillip E. Bock, 1 May 2007.

Distribution. Victoria, South Australia and Tasmania, Australia.

Bugula ceylonensis new species

Figure 13

Holotype. Bugula minima. NHM, Busk Collection, 1899.7.1.4608. Ceylon, 7–10 fathoms. Holdsworth.

Etymology. Named after the location where the type specimen was collected, then known as Ceylon, now Sri Lanka.

Description. Colony erect, consisting of robust biserial branches, brown-pigmented when dry. Zooids broadly sub-triangular in appearance, shorter than those of preceding species, about 0.53 mm long by 0.20 mm wide. Frontal membrane extending almost to base of zooid. In dry specimens, the basal and lateral walls curve strongly around the frontal membrane. Avicularia are large, round-headed, all of similar size, and positioned in a central proximal location on a knoblike peduncle cushion. Ovicells smaller and more hemispherical than those of *B. minima*, attached at a sharp angle to the inner distal corner of zooids.

Diagnosis. Zooids shorter than those of *B. robusta.* Avicularia monomorphic, large, round headed, attached at a centro-proximal position on a knoblike peduncle. Ovicells almost hemispherical.

Notes. This specimen was included by Hastings (1939) in *B. minima*, although it lacked two types of avicularia. The position of the avicularia, as well as the sizes and shapes of zooids and ovicells also differ from those of *B. minima.* Thornely (1905: 109) lists a *B. neritina* with avicularia from Ceylon but gives no illustration and a very minimal description.

Specimens Examined. Bugula minima. NHM, Busk Collection, 1899.7.1.4608. Ceylon, 7–10 fathoms. Holdsworth [originally labeled *Bugula robusta*; the *robusta* is crossed out and a separate label with *Bugula minima* is pasted on the slide].

Distribution. Sri Lanka (Ceylon).

Bugula robustoides new species

Figure 14

Holotype. NHM 1879.5.27.1. *Bugula robusta* Port Jackson, Sydney Harbor, New South Wales, Australia.

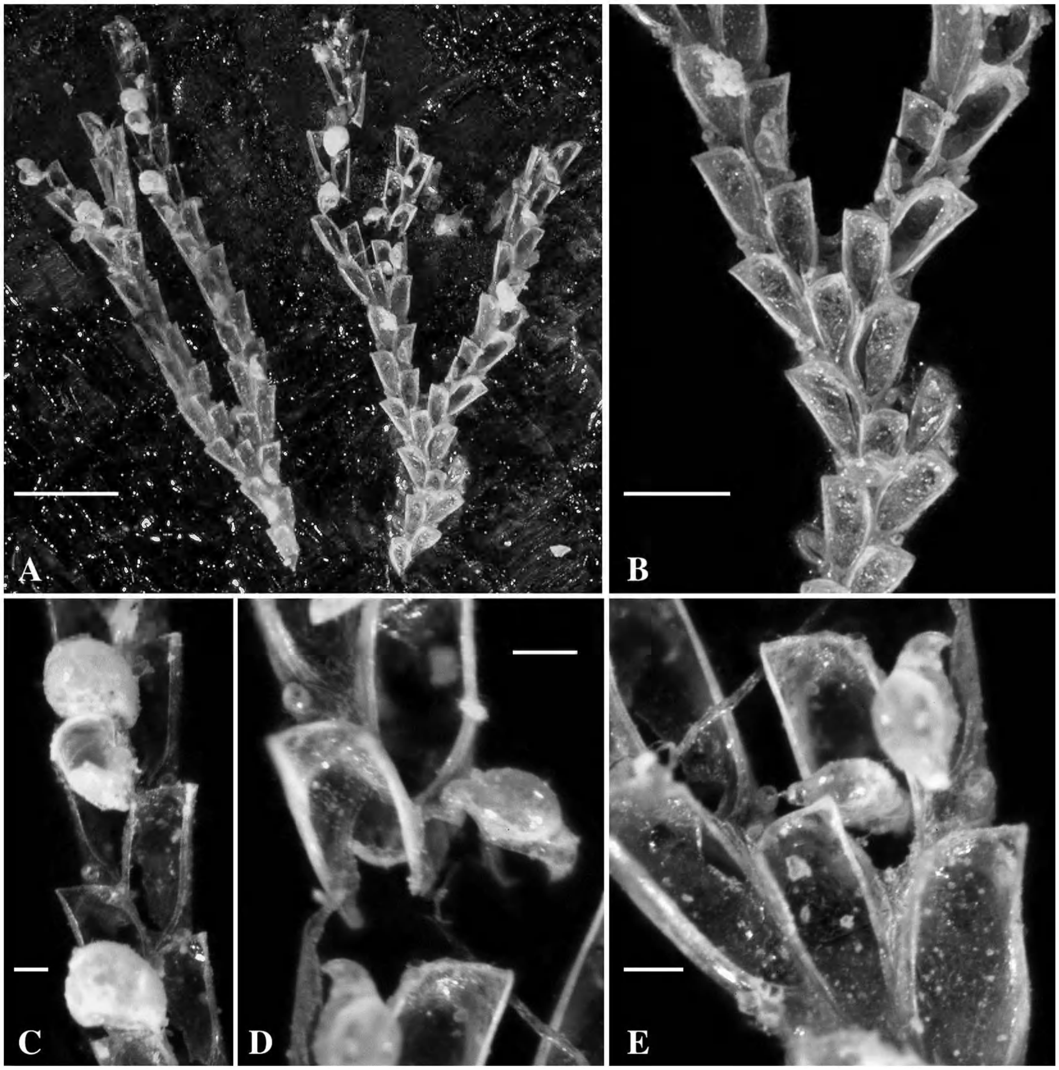

Figure 13. *Bugula ceylonensis* new species. Holotype. NHM 1899.7.1.4608. Ceylon. Light micrograph of dried colony glued on wooden slide. A. The two branch fragments of the holotype specimen. Scale bar = 1 mm. B. Front view of bifurcation; note zooid shape. Scale bar = 200 μm. C. Ovicelled zooids. Scale bar = 100 μm. D. Round-headed avicularium with open mandible. Scale bar = 100 μm. E. Zooids and two more avicularia. Scale bar = 100 μm.

Etymology. From the Latin ending *-oides*, like, resembling = *robusta*-like.

Description. Colony consisting of erect, biserial branches, brownish red in color. Zooids large, elongate, about 0.73–0.78 mm in length by 0.27–0.33 mm in width, widest distally, tapering somewhat proximally, but more rectangular in shape than those of other species described here. Outer distal angle of zooids sharply pointed, inner edge may be rounded or slightly pointed. Frontal membrane taking up more than three-quarters of frontal wall, but nonmembranous walls well chitinized and clearly visible in transmitted light. Orifice shape faintly visible, but no distinct

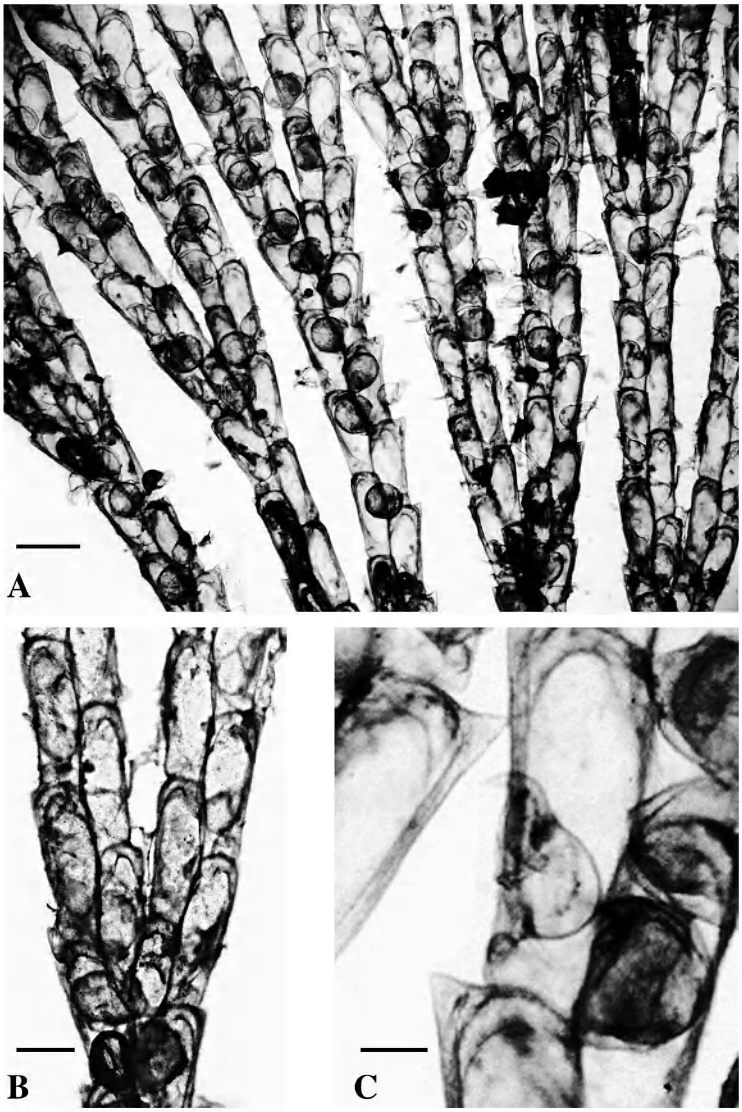

Figure 14. *Bugula robustoides* new species. Holotype. NHM 1879.5.27.1. Port Jackson, Sydney Harbor, New South Wales, Australia. Light micrographs of whole mount on slide. A. Colony branches, showing narrow, almost rectangular shape of zooids and numerous ovoid to spherical ovicells. Scale bar = 500 μm. B. Abfrontal view of branches, showing bifurcation pattern. Scale bar = 250 μm. C. Close-up of round-headed avicularium; note position of attachment. Scale bar = 100 μm.

operculum occurs. Avicularia monomorphic, of a more typical bird's head type, with a large rounded head region and a short down-curved beak and mandible. They are attached on a short round peduncle to the outer lateral margin of the zooids, a short distance above the proximal margin at the edge of the proximal end of the frontal membrane. Ovicells cup-shaped to globular, attached at the inner side of the distal margin of the zooid at an angle.

Diagnosis. The species differs from the Victorian *B. robusta* described by Mac-

Gillivray in coloration, more elongate subtriangular zooid shape, lower degree of calcification, more spherical ovicell shape, and lack of a well-chitinized operculum.

Notes. The New South Wales, Australia, specimens and specimens from Holothuria Bank, North West Australia, are considered to belong to this species, which might be found to be more widespread in the Indo-Pacific.

Specimens Examined. USNM 9485. *Bugula robusta.* Port Jackson (apparently from an exchange with NHM, originally part of NHM 1883.11.29.24). NHM 1879.5.27.1. *Bugula robusta.* Port Jackson. New South Wales, Australia. NHM 1883.11.29.24. *Bugula robusta.* Port Jackson, New South Wales, Australia. NHM 1892.1.28.60. *Bugula robusta* MacG., Holothuria Bank, North West Australia, [3°35′S, 126°E], 24–34 fathoms.

Distribution. Australia and perhaps other Indo–West Pacific localities.

Bugula solorensis new species
Figures 15–17

Bugula robusta part Harmer, 1926: 435, pl. XXXII, figure 2 only.

Holotype. NHM 1928.3.6.267. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 61. Reef. Lamakwera, Solor Id., E of Flores. Monograph xxviii, p. 435, no. 287A2.

Etymology. Named after the island where it was collected during the Siboga Expedition.

Description. Colony composed of erect, biserially branching tufts, dried specimens brown in color. Zooids elongate, about 0.61–75 mm long, slightly narrowed distally, their greatest width about 0.26–0.29 mm around the mid-region of the zooids, at which point they narrow sharply to the proximal ends. Distal rim of zooids with rounded inner corners and sharply pointed outer corners. Avicularia have round heads and long, very narrow beaks, hooked only at the extreme tips. Slight variations in avicularian size occur, but avicularia are not clearly dimorphic. The peduncle is long and inserted at the base of the opesia close to the outer proximal edge of the zooid. Ovicells broader at proximal edge, cup-shaped, with a broad proximal band, and attached at an angle to inner distal rim.

Diagnosis. Zooids elongate, greatest width at mid-section, then sharply tapering. Avicularia somewhat variable in size, with round heads and long, narrow beaks, hooked at very tips. Ovicells cup-shaped.

Notes. This specimen is the one illustrated as figure 1, pl. XXXII, of Harmer (1926).

Specimens Examined. Bugula robusta MacGillivray, Siboga Expeditie Malay Archipelago Stat: 61. Reef. Lamakwera, Solor Id., E of Flores. 1928.3.6.267. Monograph xxviii, p. 435, No. 287A2. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 313, 0–36 M 1928.3.6.274. Monograph xxviii, p. 435, No. 553A. *Bugula neritina* var. *minima.* Ras Orowamnibe, Zanzibar Channel, 10 fathoms. Crossland Expedition. 515. Manchester Museum 1299 [and on small label] E. A. W. Waters coll. H.1186. *Bugula robusta.* Tutuila, main dock, PPH, sta. 4, coll. 17 May 2007. BPBM K1046.

Distribution. Zanzibar. Reef off Solor Island, east of Flores, in Lesser Sunda Islands of Indonesia, American Samoa.

Bugula paternostrae new species
Figure 18

Bugula robusta part Harmer, 1926: 435, pl. XXXII, figures 1, 5, 6.

Holotype. NHM 1979.1.8.1. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 315 [Paternoster Island], N of Sumbawa, 0–36 m. Monograph xxviii, p. 435, No. 251C. 1928.3.6.268.

Etymology. Named for Paternoster Island, north of Sumbawa, Indonesia, where the holotype was collected.

Description. Colony composed of erect biserial branches. Zooids more triangular than those of other species studied here, giving branches a saw-toothed appearance.

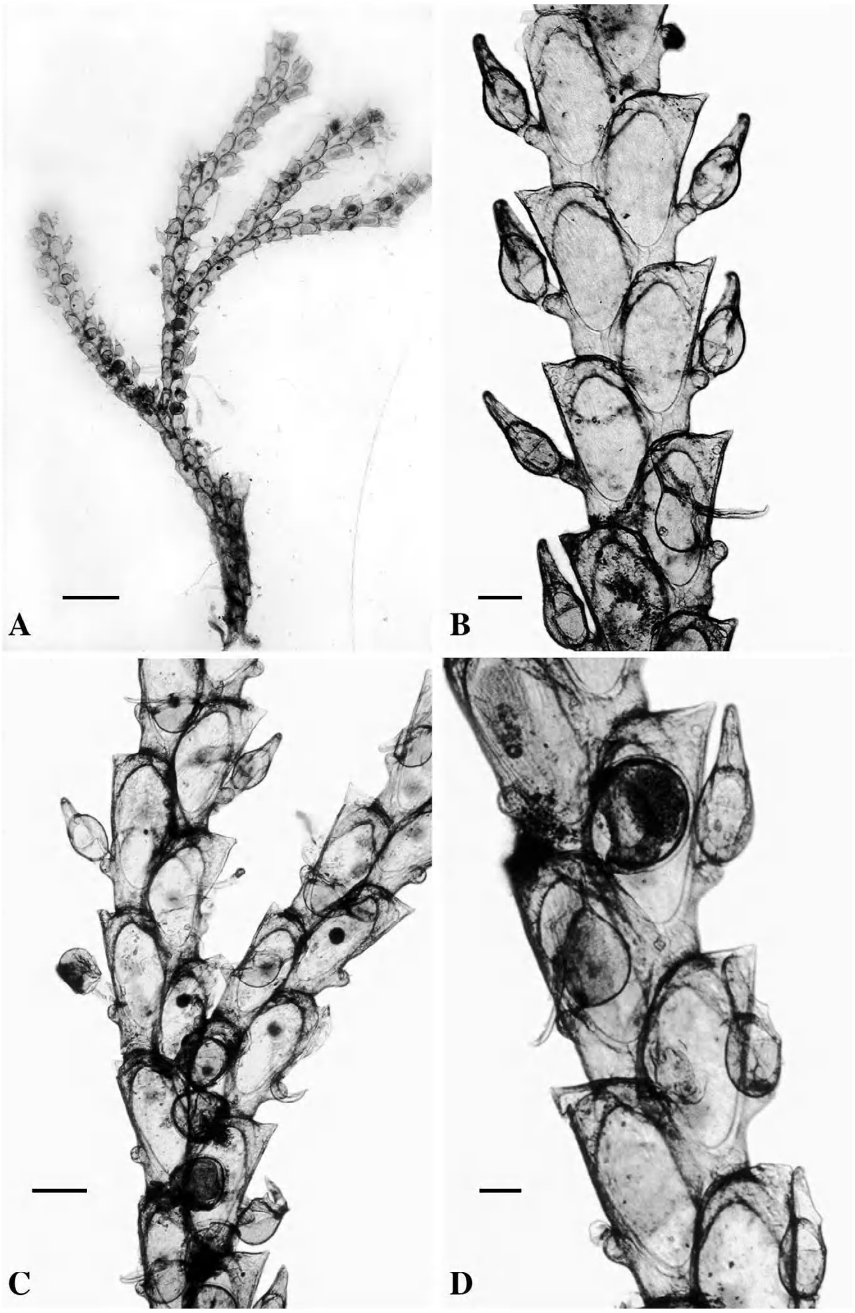

Figure 15. *Bugula solorensis* new species. Waters' Zanzibar specimen. Light micrographs of whole mount on slide. A. View of branches of colony fragment. Scale bar = 1 mm. B. Colony branch showing more triangular shape of zooids, with scalloped distal rim, and long peduncles of round-headed avicularia, with elongate beaks. Scale bar = 100 μm. C. Abfrontal view of branch, showing bifurcation pattern. Scale bar = 250 μm. D. Close-up of several zooids, showing orientation and shape of ovicell and avicularia. Scale bar = 100 μm.

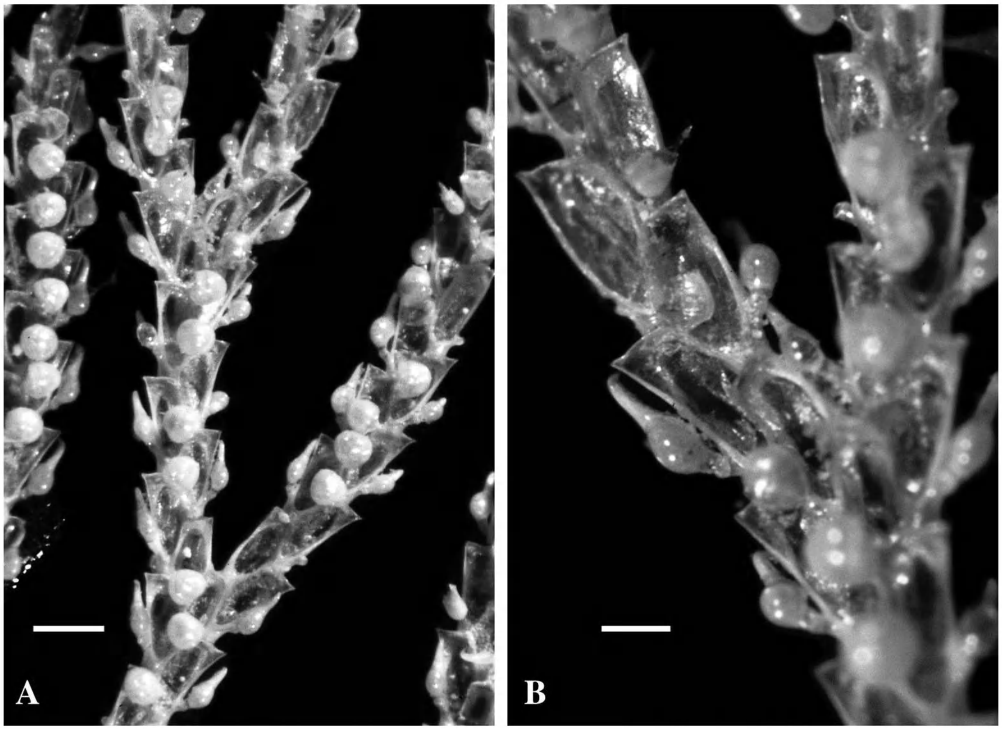

Figure 16. *Bugula solorensis* n. sp. NHM 1928.3.6.267. Solor Island specimen. Light micrograph of dry specimen on wooden slide. A. Colony branches; note feathery appearance due to position of long-beaked avicularia and shape and position of ovicells. Scale bar = 500 μm. B. Closer view of bifurcation area. Scale bar = 250 μm.

Distal rim of zooids convex to wide and scalloped, diagonally oriented to branch direction, with outer distal points short and sharp, becoming thickened and more heavily calcified with age. Frontal membrane occupies about three-quarters of the frontal wall, but other walls appear more calcified than those of any other species studied here except *B. robusta.* Avicularium round-headed and short-beaked, the peduncle attached about two-thirds of the way down the outer lateral wall of the zooid, but because of its length, the head of the avicularium has a position about halfway up the side. Ovicells higher than wide, cap- to helmet-shaped and attached to inner distal edge of zooids at an oblique angle.

Diagnosis. Zooids triangular, about 0.70–0.72 mm long by 0.29–0.37 mm wide. Distal rim of inner zooid on branch becoming wide and scalloped. Outer distal edge becoming heavily calcified in older zooids. Avicularia monomorphic, round-headed and short-beaked, on long peduncle and peduncle cushions attached about ⅔ of the way down the outer sides of zooids. Ovicells cap- to helmet-shaped.

Notes. In the strong degree of calcification of zooid walls (of older parts of colony) and more triangular zooid shape, both this species and *B. robusta* show similarities with *Halophila* species.

Specimens Examined. NHM 1979.1.8.1. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 315 [Paternoster Island, N of Sumbawa, 0–36 m. Monograph xxviii, p. 435, N. 251C. 1928.3.6.268. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 133, 0–36 m Lirung, Talaut Island, S of Mindanao. 1928.3.6.268.

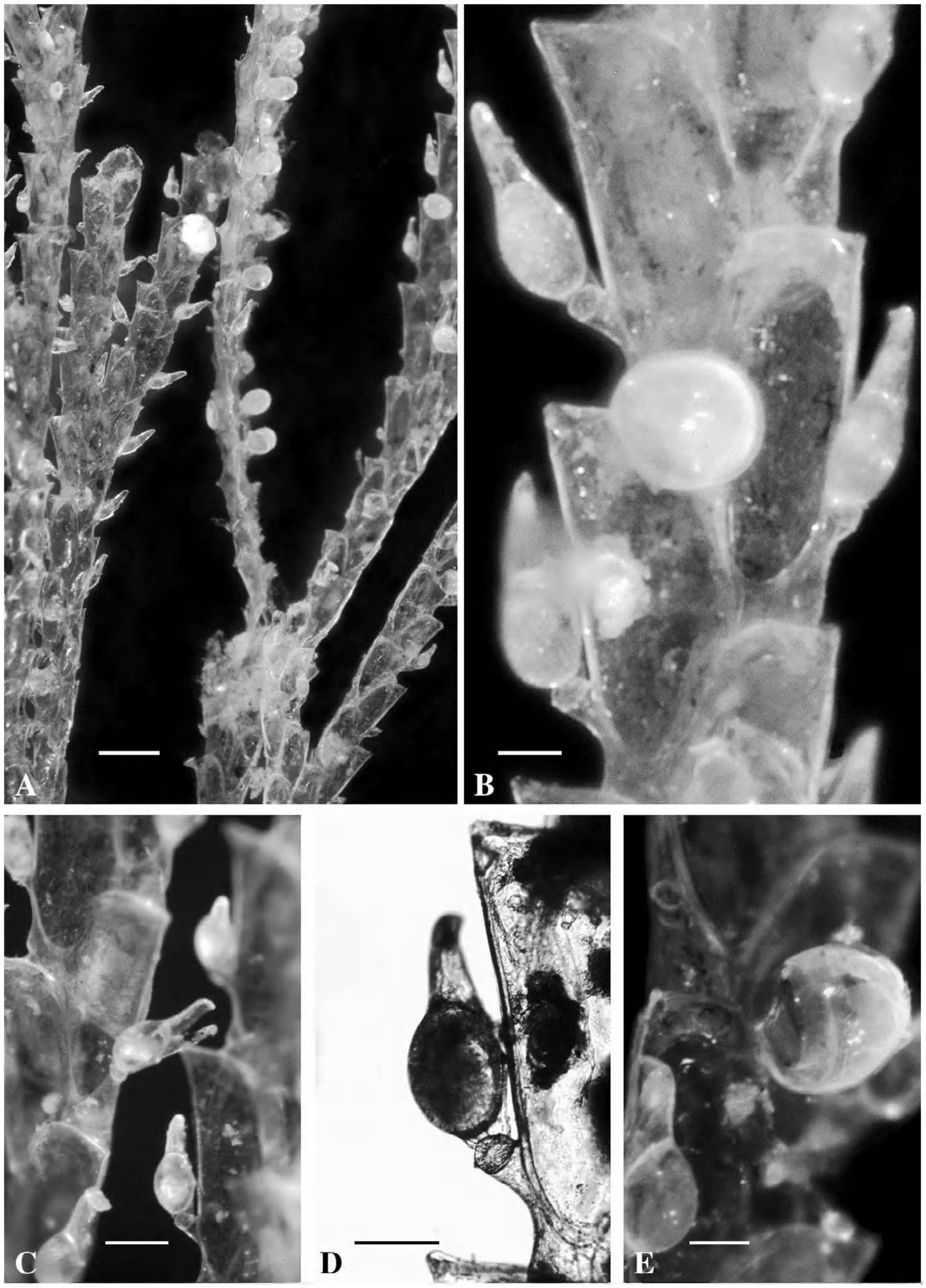

Figure 17. *Bugula solorensis* n. sp. BPBM K 1046. American Samoa. Light micrograph of wet-preserved specimen. A. Colony branches; note large diagonally oriented ovicells and feathery appearance caused by arrangement of avicularia. Scale bar = 500 μm. B. Zooids, ovicells and avicularia, note columnar peduncles of avicularia. Scale bar = 100 μm. C. Avicularia showing elongate beak, hooked at tip, and an open mandible. Scale bar = 100 μm. D. One elongated avicularium in profile. Scale bar = 100 μm. E. Close-up of cup-shaped, banded ovicell. Scale bar = 100 μm.

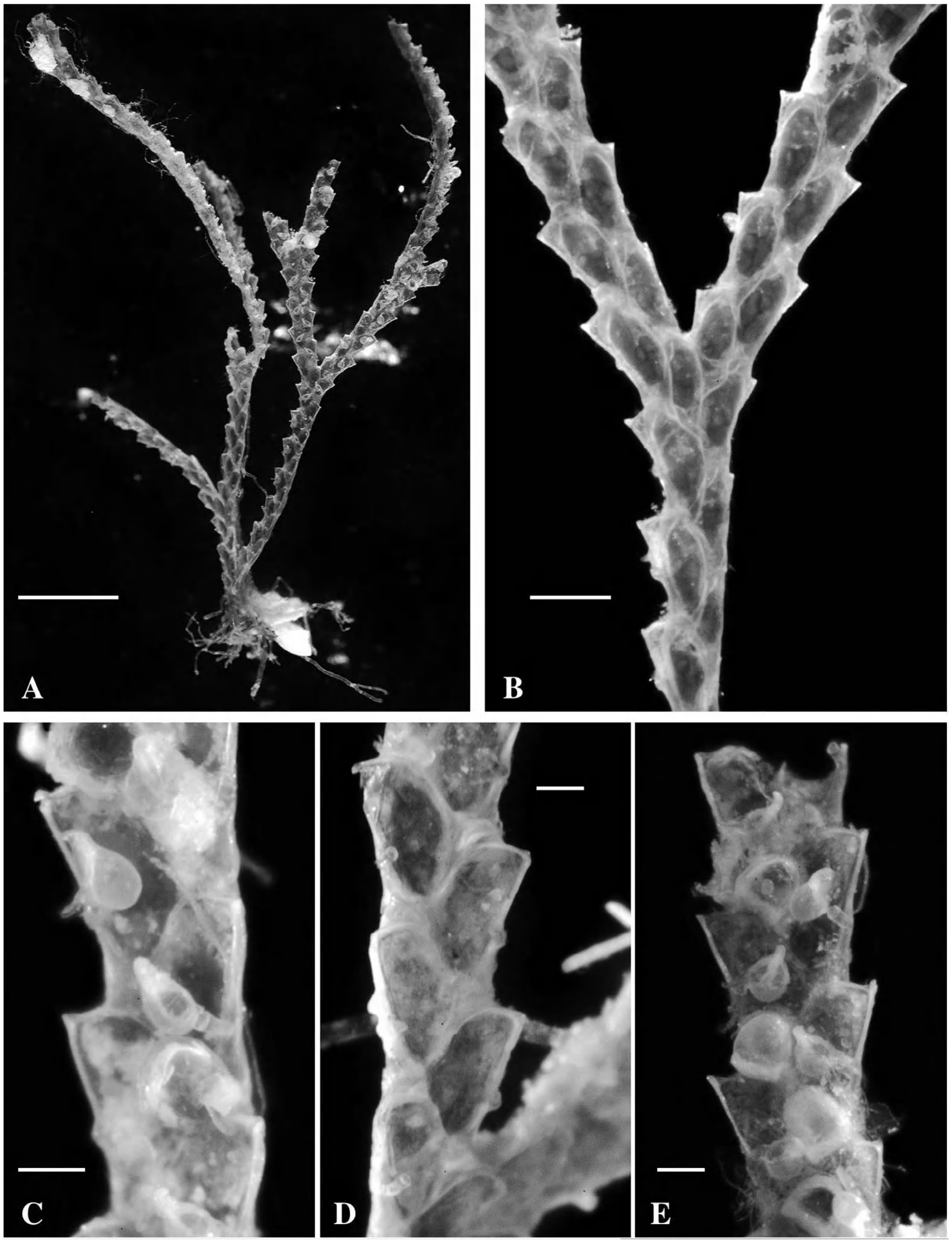

Figure 18. *Bugula paternostrae* new species. Holotype. NHM 1979.1.8.1. *Bugula robusta*, Paternoster Island, Indonesia. A. Branching colony with radicles at base. Scale bar = 2 mm. B. Back view of branch bifurcation. Scale bar = 500 μm. C. Frontal surface of branch showing round-headed avicularia on medium-length peduncle. Scale bar = 200 μm. D. Zooids from older part of colony showing scalloped distal rim. Scale bar = 200 μm. E. Area near growing tip showing cup- to hood-shaped ovicells. Scale bar = 200 μm.

Monograph xxviii, p. 435, N. 102A2. [dry branch on slide]. *Bugula robusta* MacGillivray, Siboga Expeditie Malay Archipelago Stat: 184, 36 m. 2000.9.18.9. Monograph xxviii, p. 435, No. 149b.

Distribution. Indonesia.

DISCUSSION

Despite their long confusion in the literature, *B. minima* and *B. robusta* are not synonymous. They appear to form a least two morphological groups of species or species complexes, all characterized by deep wine-red to red-brown pigmentation. With regard to the taxa whose questionable identities instigated this project, our results have shown that the red aviculiferous Hawaiian *Bugula* studied by Woollacott belongs in the *Bugula minima* group. With the others in that group, the specimens share a dark reddish pigmentation (very like that of *B. neritina*) when alive, a lack of spines, zooids shaped like those of *B. neritina*, an avicularium shape that is "sway-backed" with a long hooked rostrum (unlike the more common *Bugula stolonifera* type with its round body and relatively short rostrum beak), avicularia attached to proximal outer edge of zooids and usually polymorphic in size, ovicells attached at inner distal angle of zooids and oriented obliquely to branches, and relatively light calcification. The Hawaiian material shows a more pronounced avicularian dimorphism than Red Sea material.

Material from the western Atlantic that has been identified as *B. minima* since Osburn's 1914 publication on Tortugas bryozoans is not the *B. minima* of Waters. It is described here and named as *Bugula miniatella. Bugula miniatella* is similar to the Red Sea *B. crosslandi* of Hastings (1939), as well as to her and Osburn's specimens from eastern Pacific localities, in being a "minature" species, with a small mature colony size accompanied by early sexual reproduction. *Bugula crosslandi* is redescribed in accordance with the type specimen from Abu Shaar, in the Red Sea. The eastern Pacific material of Hastings and Osburn, identified by them as *B. minima* and *B. crosslandi*, probably represents a single species. However, its redescription will require further study because there may be some overlap with Caribbean species previously recorded as *B. minima*, but differing in some characters from *B. miniatella*.

In addition to those museum specimens labeled *Bugula robusta* that belong to *B. minima*, this identification has been applied to at least four taxa, all characterized by 1) dark red, purplish, or brown coloration when alive; 2) lack of spines; 3) monomorphic avicularia of the round-headed type; 4) ovicells attached at inner distal angle of zooids; and 5) avicularia attached in a position below the distal half of the outer edges of zooids. The different taxa vary from each other in ovicell shape and size, size of avicularia, position of attachment to peduncle cushion and peduncle length, degree of chitinization and calcification, relative length of frontal membrane, and shape of zooids. The true *B. robusta* of MacGillivray was described from Victoria, Australia, and appears to be a cool-water southern Australian species. Material from tropical waters identified as *B. robusta* is most likely *B. minima* or *B. robustoides* but could also belong to any of the warm-water species described above or to some red-pigmented taxon still undescribed.

The genus *Bugula* can be difficult to study, in that some of the morphometric characters that work to distinguish similar species in other genera and families do not work well in this genus. In contrast to the case in many cheilostomes, zooid length and width are not particularly good characters to use to distinguish between species because the species in the subset of the genus studied here are very similar in zooid size. Characters that have been found useful in the genus, such as coloration, colony size and growth form of colony, number of series of zooids along branches, branch bifurcation patterns, and distal spine patterns (e.g., Ryland, 1960) are not as useful for this limited group of taxa. Although the two species with very small mature colonies could be distinguished from the others, most species were represented only by branch fragments, the complete size of their colonies unknown. All species were pigmented, but dried or wet-preserved specimens do not give an accurate idea of the color of living colonies (e.g., the gray-brown of dried *B. robusta* compared with the deep purple and orange of living colonies). All species were biserial, and most had the same bifurcation pattern (type 4). None had jointed spines, although some had sharp, pointed extensions of the distal edges of zooids.

Zooid shape; ovicell shape and orientation; occurrence of pointed, rounded, or scalloped distal ends on zooids; and degree of skeletonization are useful. Avicularia position and shape, relative proportion of head to beak, and shape and width of each part, however, seem to be the most distinctive characters at the species level. Additionally, the ratio of avicularian length to zooid width originally discussed by Ryland (1960) as a potentially useful character in distinguishing *Bugula* species appears to have value for at least some of the species studied (see Table 1).

The taxonomic and functional significance of the red coloration in the species studied here remains obscure. Only in the case of *B. neritina* have attempts been reported to localize, isolate, and/or identify the pigment. Interest in the red pigment of *B. neritina* extends back to the nineteenth century. Krukenberg (1882) refers to this pigment, "Bugulapur," as a floridine and provides spectra under different solvent regimes. Fürth (1903) supplies a list of its basic chemical properties. Subsequent studies by Villela (1948a,b) report that the red pigment in *B. neritina* is adenochrome-like in its properties and provides a protocol for its isolation along with a more lengthy characterization of its chemistry. The chemical properties of this pigment are discussed apparently most recently by Christophersen (1985) and Christophersen and Anthoni (1986). These authors note that preliminary studies indicate it is a sulfur-containing compound. Villela (1948a,b) observed that the pigment is most evident in distal zooids on branches of colonies and also in association with brown bodies. Woollacott and Zimmer (1971, 1975) provided ultrastructural and light microscopic evidence that the larva the pigment is localized in brick-like stacks of "pigmented cells" that occur in a subepidermal location between adjacent coronal cells and in association with the apical disk. On metamorphosis, some of these pigment-bearing cells form the somatic and splanchnic peritoneum, whereas others are found with the funicular tissue. There is no indication of their functional role in either larval or adult stages.

ACKNOWLEDGMENTS

This study would not have been possible without the willingness of the following institutions and individuals to make material available on loan for examination: Bishop Museum, Honolulu, Hawaii, Holly Bolick, Stephen Coles, Lucius Eldredge; Manchester Museum, Manchester, UK, Henry McGhie, Rebecca Smith; Natural History Museum, London, UK, Mary Spencer-Jones; National Museums Liverpool, Liverpool, UK, Ian Wallace; Museum Victoria, Australia, Christopher Rowley; The Allan Hancock Foundation Collection at the Santa Barbara Museum of Natural History, Santa Barbara, California, Henry Chaney; and The Natural History Museum, Smithsonian Institution, Washington, D.C., Alan Cheetham, Jo Ann Sanner. We thank the following individuals at the Museum of Comparative Zoology, Harvard University, for their respective contributions to this study: Mary Catherine Boyett for managing the loans on receipt and their return; Mary Sears for assistance locating reference materials; Helene Ferranti for offering helpful editorial suggestions. Finally, we are especially grateful to Collin Johnson, also of Harvard University, for his cheerful and skilled assistance with the digital photography and in composing the digital formats of the figures.

LITERATURE CITED

CHRISTOPHERSEN, C. 1985. Secondary metabolites from marine bryozoans: a review. Acta Chemica Scandinavica B, **39:** 517–529.

CHRISTOPHERSEN, C., AND U. ANTHONI. 1986. Organic sulfur compounds from marine organisms. Sulfur Reports, **4:** 365–442.

DAVIDSON, S. K., AND M. HAYGOOD. 1999. Identification of sibling species of the bryozoan *Bugula neritina* that produce different anticancer bryostatins and harbor different strains of the bacterial symbiont "*Candidatus* Endobugula sertula." Biological Bulletin, **196:** 273–280.

FURTH, O. VON. 1903. Vergleichende chemische Physiologie der niederen Tiere. Jena, Germany: Verlag von Gustav Fisher. 670 pp.

GORDON, D. P., AND S. F. MAWATARI. 1992. Atlas of marine-fouling Bryozoa of New Zealand ports and harbours. Miscellaneous Publications New Zealand Oceanographic Institute, **107:** 1–52.

GOWLETT-HOLMES, K. 1999. *Bugula robusta.* Deep Glen Bay, Tasmania, Australia [Internet]. Photo index LA3-B5B-2/13-2D. Available from: http://bryozoa.net/gowlett-holmes/bugurob.html

HARMER, S. F. 1926. Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca. Siboga-Expeditie Reports, **28b:** 181–501.

HASTINGS, A. B. 1930. Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the cruise of the S.Y. 'St. George.' Proceedings of the Zoological Society of London, **1929**(4): 697–740.

———. 1939. Notes on some cellularine Polyzoa (Bryozoa). Novitates Zoologicae, **41:** 321–344.

HAYWARD, P. J. 1988. Mauritian cheilostome Bryozoa. Journal of Zoology, London, **215:** 269–356.

HAYWARD, P. J., AND J. S. RYLAND. 1998. Cheilostomatous Bryozoa. Part I. Aeteoidea–Cribrilinioidea. Synopses of the British Fauna (New Series), No. 10, 2nd ed. 1–366.

JELLY, E. C. 1889. A Synonymic Catalogue of the Recent Marine Bryozoa. London: Dulau & Co., 322 pp.

KAUFFMANN, K. 1971. The form and functions of the avicularia of *Bugula* (Phylum Ectoprocta). Postilla, **151:** 1–26.

KIJOA, A., AND P. SAWANGWONG. 2004. Drugs and cosmetics from the sea. Marine Drugs, **2:** 73–82.

KRUKENBERG, C. FR. W. 1882. Die Pigmente, ihre Eigenschaften, ihre Genese und ihre Metamorphosen bei den wirbellosen Thieren, pp. 23–29, pl. II. *In* Vergleichend-Physiologische Studien. Experimentelle Untersuchungen. 2nd series, 3rd part. Heidelberg, Germany: Carl Winter's Universitätsbuchhandlung.

LINDQUIST, N., AND M. E. HAY. 1996. Palatability and chemical defense of marine invertebrate larvae. Ecological Monographs, **66:** 431–450.

LINNAEUS, C. 1758. Systema Naturae. Vol. 1, 10th ed. Stockholm. pp. 789–821.

LIU, X., X. YIN, AND J. MA. 2001. Biology of Marine Fouling Bryozoans in the Coastal Waters of China. Beijing, China: Science Press. 860 pp. [In Chinese with English summary]

LOPANIK, N., N. LINDQUIST, AND N. TARGETT. 2004. Potent cytotoxins produced by a microbial symbiont protect host larvae from predation. Oecologia, **139:** 131–139.

LOPANIK, N., N. M. TARGETT, AND N. LINDQUIST. 2006. Ontogeny of a symbiont-produced chemical defense in Bugula neritina (Bryozoa). Marine Ecology Progress Series, **327:** 183–191.

MACGILLIVRAY, P. H. 1869. Descriptions of some new genera and species of Australian Polyzoa; to which is added a list of species found in Victoria. Transactions and Proceedings of the Royal Society of Victoria, **9:** 126–148.

———. 1881. Polyzoa, pp. 27–46. *In* F. McCoy (ed.), Natural History of Victoria. Prodromus of the Zoology of Victoria. Decade VI. Melbourne: Government Printer.

MARCUS, E. 1921. Indo-pacifische Bryozoen aus dem Riksmuseum in Stockholm. Archiv für Zoologi, **14**(7): 1–23.

MCCOY, F. (ED). 1878–90. Natural History of Victoria. Prodromus of the Zoology of Victoria, 20 Decades in 2 volumes. Melbourne: Government Printer.

MCGOVERN, T., AND M. HELLBERG. 2003. Cryptic species, cryptic endosymbionts, and geographical variation in chemical defenses in the bryozoan *Bugula neritina.* Molecular Ecology, **12:** 1207–1215.

OSBURN, R. S. 1914. Bryozoa of the Tortugas Islands, Florida. Washington, D.C.: Carnegie Institution Publication 182, pp. 181–222.

———. 1940. Bryozoa of Porto Rico with resume of the West Indian bryozoan fauna. New York Academy of Science, Scientific Survey Porto Rico and Virgin Islands, **16:** 321–486.

———. 1950. Bryozoa of the Pacific coast of North America. Part 1. Cheilostomata Anasca. Allan Hancock Pacific Expedition, **14:** 1–269.

PAUL, V. J., K. E. ARTHUR, R. RITSON-WILLIAMS, C. ROSS, AND K. H. SHARP. 2007. Chemical defenses: from compounds to communities. Biological Bulletin, **213:** 226–251.

PETTIT, G. R., C. L. HERALD, D. L. DOUBEK, D. L. HEATH, E. ARNOLD, AND J. CLARDY. 1982. Isolation and structure of bryostatin 1. Journal of the American Chemical Society, **104:** 6846–6848.

ROBERTSON, A. 1905. Non-incrusting chilostomatous Bryozoa of the west coast of North America. University of California Publications in Zoology, **2:** 235–322.

RYLAND, J. S. 1960. The British Species of *Bugula*

(Polyzoa). Proceedings of the Zoological Society of London, **134:** 65–105.

RYLAND, J. S., AND P. J. HAYWARD. 1977. British Anascan Bryozoans. Linnean Society Synopses of the British Fauna (New Series), **10:** 1–188.

SEO, J. E. 2005. Bryozoa. Illustrated Encyclopedia of the Fauna & Flora of Korea, **40:** 1–596.

SHARP, J. H., M. K. WINSON, AND J. S. PORTER. 2007. Bryozoan metabolites: an ecological perspective. Natural Products Reports, **24:** 659–673.

SHARP, K. H., S. K. DAVIDSON, AND M. G. HAYGOOD. 2007. Localization of '*Candidatus* Endobugula sertula' and the bryostatins throughout the life cycle of the bryozoan *Bugula neritina.* The ISME Journal, **1:** 693–702.

THORNELY, L. R. 1905. Report on the Polyzoa collected by Professor Herdman, at Ceylon, in 1902. *In* Report to the Government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar, by W. A. Herdman, with supplementary reports on the marine biology of Ceylon, by other naturalists. Part 5, pp. 449–450.

———. 1912. The marine Polyzoa of the Indian Ocean, from *H.M.S.* Sealark. Transactions of the Linnean Society of London (Zoology), **15:** 137–157.

TILBROOK, K. J., 2006. Cheilostomatous Bryozoa from the Solomon Islands. Santa Barbara Museum of Natural History Monographs No. 4, pp. 1–385.

VILLELA, G. G. 1948a. Adenochrome-like pigment of the Polyzoa *Bugula neritina* (L). Proceedings of the Society for Experimental Biology and Medicine, **68:** 531–533.

———. 1948b. Biocromos (pigmentos) de invertebrados marinhos 1—Briozoarios. Memórias do Instituto Oswaldo Cruz, **46:** 459–471.

WATERS, A. W. 1909. Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S.; together with collections made in the Red Sea by Dr. R. Hartmeyer. XII. The Bryozoa. Part I. Cheilostomata. Linnean Society of London Journal of Zoology, **31:** 123–181.

———. 1913. The marine fauna of British East Africa and Zanzibar, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S. in the years 1901–1902, Bryozoa–Cheilostomata. Proceedings of the Zoological Society of London, **2:** 458–537.

WENDT, D. E. 1996. Effect of larval swimming duration on success of metamorphosis and size of the ancestrular lophophore in *Bugula neritina* (Bryozoa). Biological Bulletin, **191:** 224–233.

———. 1998. Effect of larval swimming duration on growth and reproduction of *Bugula neritina* (Bryozoa) under field conditions. Biological Bulletin, **195:** 126–135.

———. 2000. Energetics of swimming and metamorphosis in larvae of four species of *Bugula* (Bryozoa). Biological Bulletin, **198:** 346–356.

WINSTON, J. E. 1982. Marine bryozoans (Ectoprocta) of the Indian River area (Florida). Bulletin of the American Museum of Natural History, **173:** 99–176.

WOOLLACOTT, R. M. 1980. Association of bacteria with bryozoan larvae. Marine Biology, **65:** 155–158.

WOOLLACOTT, R. M., AND R. L. ZIMMER. 1971. Attachment and metamorphosis of the Cheilo-ctenostome bryozoan *Bugula neritina* (Linné). Journal of Morphology, **134:** 351–382.

———. 1972. Origin and structure of the brood chamber in *Bugula neritina* (Bryozoa). Marine Biology, **16:** 165–170.

———. 1975. A simplified placenta-like system for the transport of extraembryonic nutrients during embryogenesis of *Bugula neritina* (Bryozoa). Journal of Morphology, **147:** 355–378.