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Taxonomic review of the family Colatooeciidae Winston, 2005 (Bryozoa, Cheilostomata), with description of seven new species

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Abstract

Colatooeciidae includes the genera *Colatooecia*, *Cigclisula* and *Trematooecia*. While *Colatooecia* is considered a well-defined genus, the differences between *Cigclisula* and *Trematooecia* are poorly defined. This taxonomic review was undertaken to understand the morphological differences between *Cigclisula* and *Trematooecia*. The type species of *Cigclisula* is redescribed and the type species of *Trematooecia* is designated and redescribed. Diagnostic characters of both genera are redefined. Six new species of *Cigclisula* and one of *Trematooecia* are described: *Cigclisula australis* n. sp., *Cigclisula buski* n. sp., *Cigclisula fistulosa* n. sp., *Cigclisula osburni* n. sp., *Cigclisula perforata* n. sp., *Cigclisula winstonae* n. sp. and *Trematooecia rotunda* n. sp. Four species previously assigned to *Cigclisula* are transferred to *Trematooecia*: *Trematooecia arborescens* (Canu & Bassler, 1928) n. comb., *Trematooecia gemmea* (Winston & Woollacott, 2009) n. comb., *Trematooecia hexagonalis* (Canu & Bassler, 1930), and *Trematooecia verticalis* (Maplestone, 1910) n. comb. Two species previously assigned to *Trematooecia* are transferred to *Cigclisula*: *Cigclisula turrita* (Smitt, 1873) and *Cigclisula psammophila* (Winston & Håkansson, 1986) n. comb.

Key words: bryozoans, *Colatooecia*, *Cigclisula*, *Trematooecia*, new species, new combinations, redescription

Introduction

The family Colatooeciidae and genus *Colatooecia* were erected by Winston (2005) to accommodate the problematic species *Porina serrulata* Smitt (1873). According to Winston (2005), this species has a unique combination of characters: presence of a spiramen, thick porous frontal calcification, avicularia with complete calcified pivotal bar and ectooecium with median membranous area (looks like a fenestra when cuticular parts are removed). Based on characters of the frontal wall calcification, avicularia and ooecia, Vieira *et al.* (2010a) suggested that *Cigclisula* Canu & Bassler, 1927 and *Trematooecia* Osburn, 1940, which had been placed in different families, belonged to Colatooeciidae.

While *Colatooecia* is considered a well-defined genus, the taxonomy of *Cigclisula* and *Trematooecia* is very intricate and confused (Vieira *et al.* 2010a). When Canu and Bassler (1927) erected *Cigclisula*, they stated that the main character was the ectooecium perforated by large pseudopores. However, species having the ectooecium with merely a frontal circular or slit-like membranous area have been also assigned to *Cigclisula* (e.g. Maplestone 1910; Winston & Woollacott 2009; Vieira *et al.* 2010a). *Trematooecia* was erected by Osburn (1940), based on specimens attributed to *Lepralia turrita* Smitt, 1873 from the Caribbean. Maturo (1968), Banta & Carson (1977) and Winston (2005), however, suggested that these specimens were not conspecific with Smitt's species. Unaware of Osburn's genus, Harmer (1957) posthumously included *L. turrita* in *Cigclisula*; Maturo (1968) and Banta & Carson (1977) suggested that *Trematooecia* was a synonym of *Cigclisula*, whereas other authors (e.g. Winston 2005; Winston & Woollacott 2009; Vieira *et al.* 2010a) choose to keep the genera separate. Over the years, many species from the Atlantic and Pacific have been described and assigned either to *Cigclisula* or *Trematooecia*, but no clear morphological distinction of these genera has been published yet.

In this paper we redescribe the type species of *Cigclisula* and designate and redescribe the type species of *Trematooecia*, providing morphological diagnoses that discriminate between both genera. Based on the characters that we interpret as diagnostic, we describe and illustrate six new species of *Cigclisula* and one of *Trematooecia* and propose six new combinations. Remarks and descriptions are provided for other species.

Material and methods

Type and non-type specimens analyzed in this study are registered in the Natural History Museum (NHMUK), London, UK; National Museum of Natural History (USNM), Smithsonian Institution, Washington DC, USA; Museum of Comparative Zoology (MCZ), Harvard University, Massachusetts, USA; Musée Zoologique of Strasbourg (MZS), Strasbourg, France; Museum Victoria (NMV), Melbourne, Australia; Museu de Zoologia da Universidade Federal da Bahia (UFBA), Salvador, Brazil; and Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil.

Colonies were first examined under a stereomicroscope and selected specimens were studied using scanning electron microscopy (SEM). Measurements (Fig. 1) were made from digital SEM images using the software ImageJ®. Abbreviations (for skeletal characters): zooid length (Lz), zooid width (lz), diameter of frontal pseudopores (Dp); orifice length (Lo), orifice width (lo), suboral avicularium length (Lavs), suboral avicularium width (lavs), interzooidal avicularium length (Lavi), interzooidal avicularium width (lavi), frontal avicularium length (Lavf), frontal avicularium width (lavf), ooecium length (Lov), ooecium width (lov), ooecium fenestra length (Lovf), ooecium fenestra width (lovf), ooecium frontal pseudopore diameter (Dovp).

Systematic account

Order Cheilostomata Busk, 1852

Suborder Neocheilostomina d'Hondt, 1985

Superfamily Celleporoidea Johnston, 1838

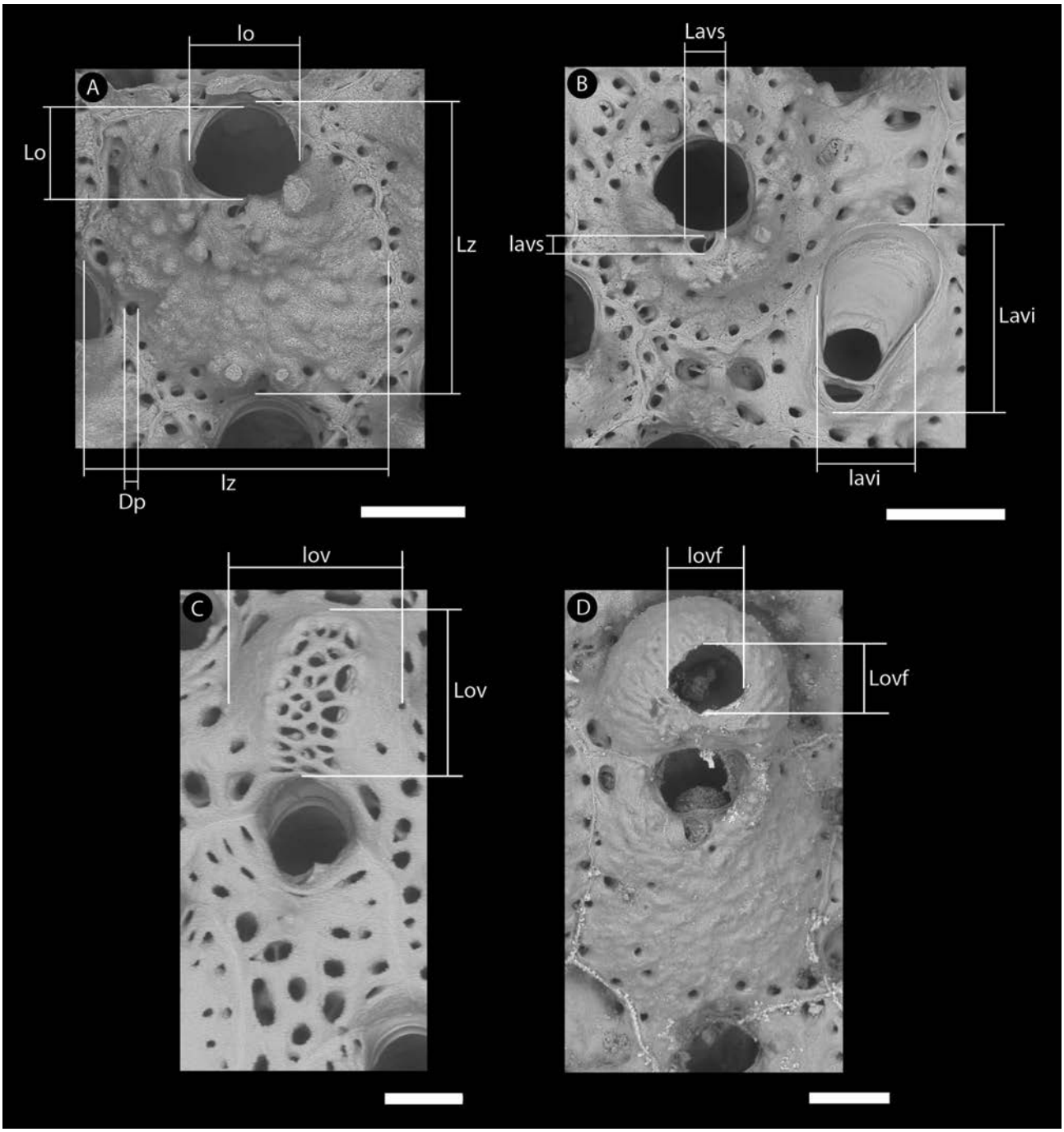

FIGURE 1. Morphometric characters of Colatooeciidae. **A,** zooid length (Lz), zooid width (lz), diameter of frontal pores (Dp); orifice length (Lo), orifice width (lo); **B,** suboral avicularium length (Lavs), suboral avicularium width (lavs), interzooidal avicularium length (Lavi), interzooidal avicularium width (lavi); **C,** ooecium length (Lov), ooecium width (lov); **D,** ooecium fenestra length (Lovf), ooecium fenestra width (lovf). Scale bars = 200 μm.

Family Colatooeciidae Winston, 2005

Type genus. *Colatooecia* Winston, 2005; type species *Porina serrulata* Smitt, 1873, by original designation.

Diagnosis (revised). Colony encrusting, uni- to multilaminar or erect and bilaminar. Frontal shield perforated by pseudopores, thickening as zooids and colonies age. Spiramen may be present, conspicuous in developing zooids, joining with the peristome and immersed in frontal shield in completely calcified zooids. Primary orifice transversely D-shaped to rounded, secondary orifice level with frontal-shield surface, with or without tubercles.

Condyles present or absent. Spines absent. Interzooidal and adventitious avicularia sometimes present. Ooecium not closed by operculum, recumbent on distal zooid, soon becoming embedded in its secondary calcification; entooecium largely calcified, with membranous frontal area; ectooecium smooth, calcified, with single membranous area or with longitudinal band of pseudopores.

Remarks. The family was erected to accommodate *Colatooecia* Winston, 2005, but Vieira *et al*. (2010a) also included *Trematooecia* and *Cigclisula* owing to characteristics of the frontal shield and ooecia. Both genera were previously placed in different families such as Stomatochetosellidae Canu & Bassler, 1917 (Canu & Bassler 1927; Harmer 1957; Hayward & Ryland 1995) and Hippoporidridae Vigneaux, 1949 (Tilbrook 2006; Ayari *et al.* 2008), from which both differ mostly in features of the ooecium (for additional information see Vieira *et al.* 2010a).

Genus *Colatooecia* Winston, 2005

Type species. *Porina serrulata* Smitt, 1873, by original designation.

Diagnosis. Colony rigid, erect and branching. Frontal wall evenly perforated by large pseudopores, frontal surface thickening with increasing calcification. Spiramen conspicuous in young zooids, joining with peristome and immersed in frontal wall with increasing calcification and in completely calcified zooids. Primary orifice oval, becoming obscured by the secondary orifice. Adventitious avicularia with complete crossbars. Ooecium embedded in frontal surface, ectooecium with central membranous area (looks like a fenestra when cuticular parts are removed); entooecium bridged by a sieve of delicate costae which interdigitate at the mid-point of the ooecium.

Colatooecia serrulata (Smitt, 1873)

(Fig. 2, Table 1)

Porina serrulata Smitt, 1873: 27, pl. 5, figs 116–125. [W of Tortugas and Florida]
Cigclisula serrulata: Canu & Bassler 1928a: 125, pl. 20, figs 1–14, text-fig. 24. [Fowey Light, Miami, Florida]
Spiroporina? *serrulata*: Cheetham & Sandberg 1964: 1027, text-figs 26–27. [Gulf of Mexico]
Colatooecia serrulata: Winston 2005: 93, figs 257–261. [W of Tortugas and Florida]

Material examined. USNM 7476, *Cigclisula serrulata*, F. Canu & R.S. Bassler det., 1928a, Fowey Light, 15 miles (24.1 km) South of Miami, Florida.

Description. Colony erect, bilaminar, branching. Zooids hexagonal at growing edge, becoming irregular with development, longer than wide, limited by slightly raised walls. Frontal shield heavily calcified, with 22–36 regularly spaced pseudopores. Primary orifice small relative to frontal shield, almost rounded, wider than long, lacking condyles. Secondary orifice subcircular, with smooth peristome that becomes embedded in frontal surface with colony development. Often 1, rarely 2, rounded adventitious avicularia placed at zooidal margins near primary orifice and sometimes at proximal border of ectooecium. Frontal avicularia with large rostrum, rectangular, longer than wide, with rounded proximal and straight distal edge; calcified palate occupies half rostral length; opesia trifoliate proximally, quadrangular distally. Interzooidal avicularia placed at margins of colony, as long as zooids, rostrum straight, spatulate, longer than wide, proximal edge rounded and distal edge deep, concave; calcified palate occupies more than half rostral length, its foramen somewhat trifoliate owing to a ligula; avicularian opesia smaller, quadrangular. Ooecium immersed; ectooecium with central membranous area; entooecium bridged by sieve of delicate costae that interdigitate at mid-point of ooecium.

Remarks. *Colatooecia* is monotypic. The type species *Colatooecia serrulata* was previously included in *Porina* (Smitt 1873), *Cigclisula* (Canu & Bassler 1928) and, doubtfully, *Spiroporina* (Cheetham & Sandberg 1964) (see Winston 2005). Cheetham & Sandberg (1964) pointed out that the species could not be placed easily in any known genus; Winston (2005) introduced *Colatooecia* for it based on the appearance of the frontal calcification and the distinctive costate ooecium.

The combination of a spiramen, thick porous frontal calcification, ectooecium with an elongate membranous area, two rows of tiny entooecial costae and rectangular frontal avicularia with distal trifoliate and proximal quadrate openings in *C. serrulata* is unique in the family.

Distribution. Northwestern Atlantic: Cape Hatteras to Florida and Gulf of Mexico (Winston 2005).

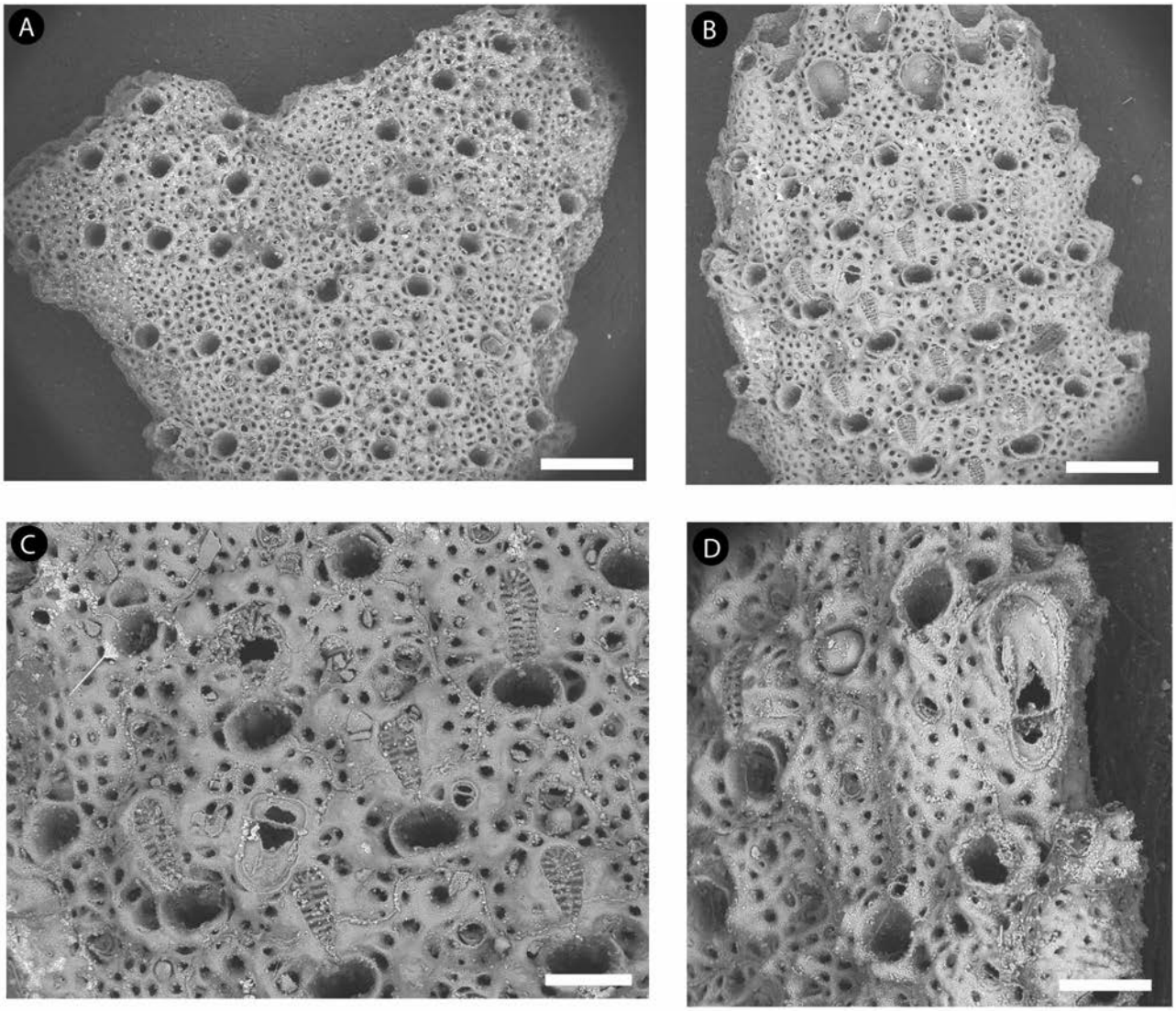

FIGURE 2. *Colatooecia serrulata* (Smitt, 1873). **A–D,** USNM 7476, Florida. **A,** erect bilaminar colony. **B,** ovicelled zooids. **C,** close-up of ovicelled zooids and rectangular frontal avicularia. **D,** close-up of shoe-shaped interzooidal avicularium. Scale bars: A, B = 500 μm; C, D = 200 μm.

TABLE 1. Morphometric data for Colatooeciidae species studied (in mm).

	Colatooecia serrulata	***Cigclisula occlusa***		
	Florida[1]	Philippines[2]	Philippines[3]	Philippines[4]
Lz	10	10	10	10
Mean (SD)	0.557 (0.125)	0.593 (0.059)	0.553 (0.084)	0.752 (0.079)
Range	0.422–0.740	0.468–0.635	0.497–0.761	0.646–0.861
lz	10	10	10	10
Mean (SD)	0.299 (0.039)	0.375 (0.058)	0.385 (0.037)	0.515 (0.052)
Range	0.227–0.351	0.312–0498	0.340–0.453	0.438–0.605
Dp	10	10	10	10
Mean (SD)	0.017 (0.003)	0.027 (0.006)	0.025 (0.008)	0.022 (0.007)
Range	0.011–0.022	0.019–0.041	0.010–0.036	0.012–0.040
Lo	10	10	10	10

.....continued on the next page

TABLE 1. (Continued)

	Colatooecia serrulata	*Cigclisula occlusa*		
	Florida[1]	Philippines[2]	Philippines[3]	Philippines[4]
Mean (SD)	0.091 (0.011)	0.152 (0.010)	0.165 (0.009)	0.185 (0.011)
Range	0.076–0.112	0.134–0.168	0.148–0.176	0.164–0.202
lo	10	10	10	10
Mean (SD)	0.119 (0.014)	0.161 (0.006)	0.151 (0.017)	0.180 (0.009)
Range	0.100–0.143	0.148–0.168	0.115–0.168	0.172–0.203
Lavs	-	10	10	10
Mean (SD)	-	0.108 (0.026)	0.069 (0.019)	0.076 (0.017)
Range	-	0.055–0.121	0.069–0.108	0.051–0.097
lavs	-	10	10	10
Mean (SD)	-	0.056 (0.015)	0.046 (0.019)	0.047 (0.013)
Range	-	0.030–0.074	0.028–0.085	0.033–0.077
Lavi	10	1	3	4
Mean (SD)	0.223 (0.016)	0.541	0.332 (0.024)	0.512 (0.134)
Range	0.204–0.238	-	0.290–0.335	0.316–0.609
lavi	10	1	3	4
Mean (SD)	0.168 (0.040)	0.152	0.115 (0.021)	0.174 (0.068)
Range	0.131–0.205	-	0.082–0.121	0.086–0.253
Lavf	10	10	10	6
Mean (SD)	0.061 (0.006)	0.047 (0.007)	0.035 (0.006)	0.052 (0.007)
Range	0.054–0.075	0.038–0.057	0.028–0.051	0.042–0.062
lavf	10	10	10	6
Mean (SD)	0.051 (0.005)	0.029 (0.007)	0.035 (0.003)	0.045 (0.005)
Range	0.045–0.063	0.031–0.040	0.029–0.040	0.039–0.054
Lov	10	4	-	2
Mean (SD)	0.230 (0.016)	0.361 (0.033)	-	0.401 (0.007)
Range	0.204–0.255	0.330–0.407	-	0.396–0.406
lov	10	4	-	2
Mean (SD)	0.218 (0.026)	0.373 (0.012)	-	0.418 (0.058)
Range	0.181–0.255	0.368–0.397	-	0.378–0.458
Dovp	-	15	-	25
Mean (SD)	-	0.028 (0.011)	-	0.077 (0.035)
Range		0.008–0.048	-	0.028–0.175

[1] USNM 7476, Miami, Florida. [2] NHMUK 1944.1.8.284, Samboangan, Philippines. [3] NHMUK 1887.12.9.588, Samboangan, Philippines. [4] USNM 8039, Tinakta Island, Philippines.

Genus *Cigclisula* Canu & Bassler, 1927

Type species. *Escharoides occlusa* Busk, 1884, by original designation.

Diagnosis (revised). Colony encrusting, uni to multilaminar, or erect and bilaminar. Autozooids oblong to hexagonal, heavily calcified. Frontal shield with frontal pseudopores and marginal areolar pores. Primary orifice

transversely D-shaped, hoof-shaped or subelliptical. Secondary orifice formed by raised and rounded tubercles that often obscure the primary orifice. Suboral avicularium often present, seated low near the primary orifice. Interzooidal and frontal avicularia with complete crossbars. Ooecium not closed by operculum, coarse surface calcification, ectooecium with longitudinal band of pseudopores.

Remarks. When Canu & Bassler (1927) erected *Cigclisula*, they stated that "the ovicell is hyperstomial, opening in the peristome, never closed by the operculum, with the frontal perforated by very large pores". Nevertheless, species in which the ectooecium has a frontal circular or slit-like membranous area, typical of *Trematooecia* (see remarks under *Trematooecia*), have frequently been attributed to *Cigclisula*. *Cigclisula* and *Trematooecia* share morphological characters that can lead to cross-identification: colonies can be encrusting and multilaminar with globose zooids or erect and bilaminar; marginal and frontal pseudopores are common; the primary orifice may or may not have condyles; the secondary orifice is frequently surrounded by tubercles; suboral and interzooidal avicularia can be present. Because of these overlapping characters Harmer (1957), Maturo (1968) and Banta & Carson (1977) included in *Cigclisula* species that have been attributed to *Trematooecia*. The type species of these genera are, respectively, *Escharoides occlusa* Busk, 1884 and *Holoporella aviculifera* Canu & Bassler, 1923 (misidentified as *Trematooecia turrita* by Osburn, 1940). Our analysis of the type species has determined that their ooecia are morphologically distinct. Whereas *Cigclisula occlusa* has an ectooecium with a longitudinal band of irregular pseudopores, *Trematooecia aviculifera* has an ectooecium with a circular membranous window. On this basis, at least, it seems appropriate to maintain both genera.

Accordingly, at least two species previously assigned to *Trematooecia* are reassigned to *Cigclisula*, viz *Cigclisula turrita* (Smitt, 1873) and *Cigclisula psammophila* (Winston & Håkansson, 1986) n. comb. *Porella rogickae* Soule, 1961 was assigned to *Cigclisula* by Bock (2014), following Banta & Carson (1977), who considered it related to *Trematooecia aviculifera* (as *Cigclisula*). Soule's treatment may be correct, however, as *P. rogickae* has a primary orifice with a transversely narrow lyrula and imperforate ooecium, typical of *Porella* Gray, 1848 and different from *Cigclisula*, which has a semicircular to elliptical primary orifice and ooecium perforated by irregular pseudopores.

Cigclisula occlusa (Busk, 1884)

(Figs 3–5, Table 1)

Escharoides occlusa Busk, 1884: 150 (in part), pl. 21, fig. 8 (part). [Zamboanga, Philippines; not specimen from Cape York, Australia]
Lepralia occlusa: Waters 1888: 26, pl. 3, figs 32–34. [Zamboanga, Philippines]
Lepralia occlusa: Waters 1909: 152 (in part), pl. 13, fig. 15; pl. 14, figs 1–9, 13 (?in part). [Zamboanga, Philippines]
? *Escharoides occlusa*: Waters 1913: 519. [Zanzibar, Indian Ocean]
? *Escharoides occlusa*: Robertson 1921: 56. [Straits of Malacca, Indian Ocean]
? *Myriozoum occlusum*: Marcus 1923: 435, pl. 25, figs 8 a, b. [Aru Islands, Indonesia]
Cigclisula occlusa: Canu & Bassler 1929: 291, pl. 31, figs 3–10. [Philippines]
Cigclisula occlusa: Harmer 1957: 1057, pl. 69, figs 16–18. [Philippines]

Material examined. *Lectotype:* NHMUK 1944.1.8.284 [dry specimens; figured by Busk 1884, pl. 21, fig. 8 (part)], *Escharoides occlusa*, G. Busk coll., Challenger Expedition, Samboanga, Philippines, 10 ftm (18.29 m). *Paralectotypes:* NHMUK 1887.12.9.588 [two dried specimens; figured by Busk, pl. 21, fig. 8]; NHMUK 1887.12.9.594 [large dry colony]; NHMUK 1899.7.1.2138 [balsam slide]; NHMUK 1899.7.1.2138 [balsam slide]; NHMUK 1899.7.1.2141 [balsam slide]; NHMUK 1887.12.9.589 [balsam slide], *Escharoides occlusa*, G. Busk coll., Challenger Expedition, Samboanga, Philippines, 10 fths (18.29 m). NHMUK 1887.12.9.590 [dry slide]; NHMUK 1887.12.9.592 [dry]; NHMUK 1887.12.9.592 part [dry slide]; *Escharoides occlusa*, G. Busk coll., Challenger Expedition, Stn 148, off Possession Island, 24°47' S, 51°37' E, South Indian Ocean, 210 ftm (384 m). *Additional specimens:* USNM 8039, *Cigclisula occlusa* (Busk), Canu & Bassler 1929, Albatross Stn D5158, Tinakta Island, Tawi Group, Philippines, 22 m. USNM 8037, *Cigclisula occlusa* (Busk), Albatross Stn D5137, Jolo Light, Jolo Island, Philippines, 36.6 m.

Description. Colony erect, bilaminar, branching. Zooids hexagonal, longer than wide, limited by slightly raised lateral walls. Frontal shield heavily calcified, smooth-textured, uniformly punctured by 24–40 pseudopores. Primary orifice small relative to frontal shield, somewhat hoof-shaped, as long as wide, sunken, with arcuate anter

and concave poster delimited by 2 down-curved condyles at about one-third orifice length. Secondary orifice raised, non-tubercular, almost circular. Suboral avicularium elliptical, laterally placed and distally directed, of 2 sizes, 1 small (0.055–0.121 mm long), the other double-sized, commonly on zooids in the center of branches. Frontal avicularia small, rare, elliptical, 1–2 per zooid, placed at zooidal margins, sometimes around ooecial margin. Interzooidal avicularia longer than wide, with broadly spatulate mandible; rostrum with rounded proximal edge, median constriction distinct and distal edge concave; calcified palate occupying more than half rostral length, with acutely triangular foramen. Ooecium subglobose, not very prominent, becoming immersed in secondary cacification; ectooecium with longitudinal band of 11–29 irregular pseudopores.

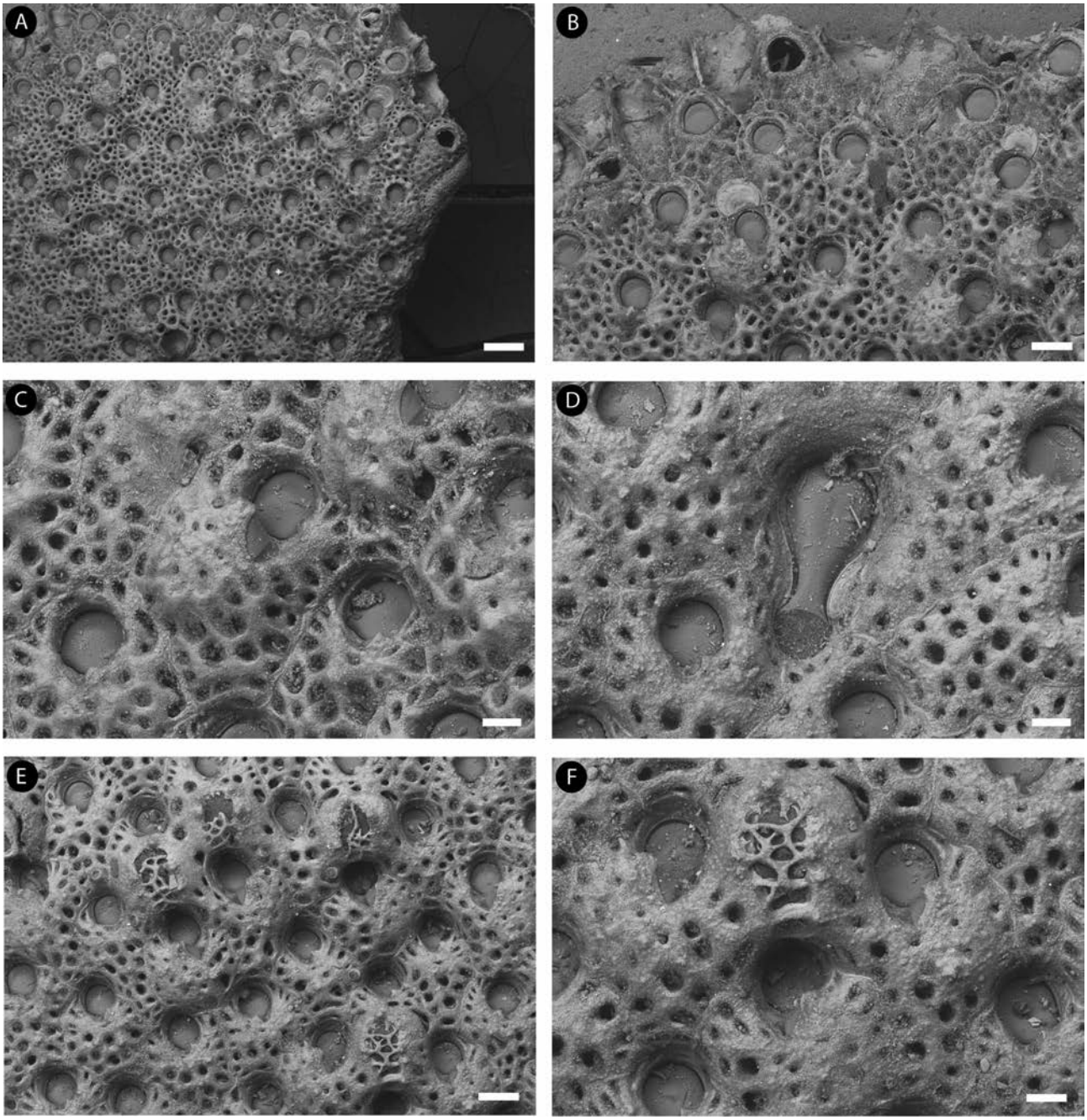

FIGURE 3. *Cigclisula occlusa* (Busk, 1884). **A–F,** NHMUK 1944.1.8.284, lectotype, Philippines. **A,** erect bilaminar colony. **B,** group of zooids at growing edge. **C,** close-up of zooid with suboral avicularium. **D,** close-up of spatulate interzooidal avicularium. **E,** ovicelled zooids. **F,** close-up of ovicelled zooid. Scale bars: A = 400 µm; B, E = 200 µm, C, D, F = 100 µm.

Remarks. Waters (1913) suggested that a new genus was needed to accommodate *Escharoides occlusa* Busk, 1884 owing the morphology of ooecia and avicularia, but did not name one. Subsequently, Canu & Bassler (1927)

designated it as the type species of *Cigclisula*, characterized by the non-cleithral ooecium with a grating-like surface (longitudinal band of pseudopores). Whereas the grating-like surface of *Colatooecia* is an entooecium covered by a membranous ectooecial area, in *Cigclisula* it is a pseudoporous ectooecium.

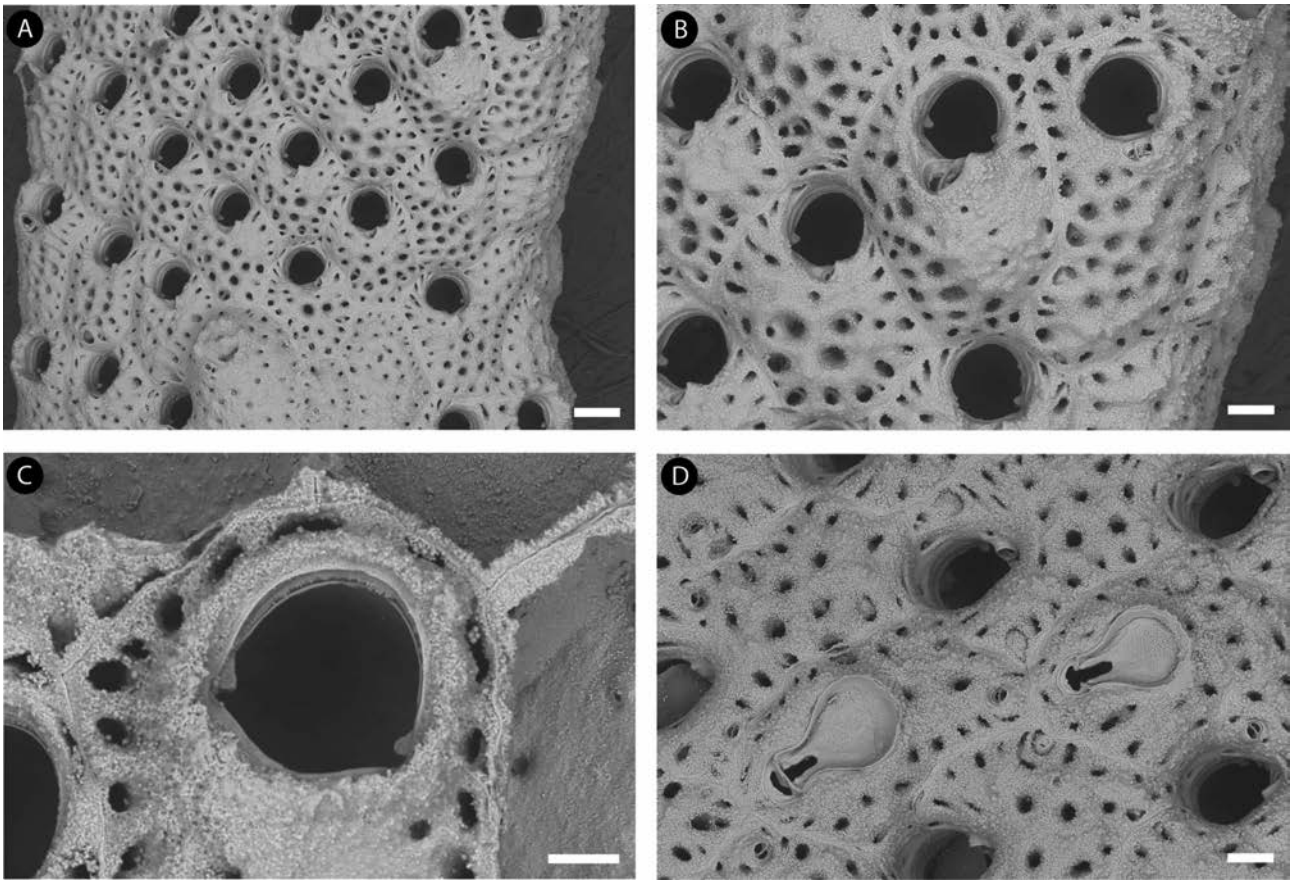

FIGURE 4. *Cigclisula occlusa* (Busk, 1884). **A–D,** NHMUK 1887.12.9.592 part, paralectotype, Philippines. **A,** group of zooids. **B,** close-up of zooids and suboral avicularium. **C,** primary orifice. **D,** spatulate interzooidal avicularia. Scale bars: A = 200 μm; B, D = 100 μm, C = 60 μm.

Busk (1884) described *Escharoides occlusa* using specimens from Zamboanga (Philippines), Possession Island (South Indian Ocean) and Cape York (Australia). Examination of these specimens has revealed differences among colonies from these localities, leading to the recognition of two new species from Australia. Specimens from the Philippines have a smooth frontal shield and ooecia whereas specimens from Australia have a minutely tubercular frontal shield and ooecia (*Cigclisula australis* n. sp.), with small protuberances in *Cigclisula buski* n. sp. *Cigclisula occlusa*, *C. australis* n. sp. and *C. buski* n. sp. have two sizes of interzooidal avicularia that differ in the shape of the opesia—acutely triangular in *C. occlusa*; both triangular (larger interzooidal avicularia) and oval (smaller interzooidal avicularia) in *C. australis* n. sp.; oval in *C. buski* n. sp. The ectooecium in *C. occlusa* has 11–29 pseudopores; that in *C. australis* n. sp. is less porous, with 7–18 pseudopores; in *C. buski* n. sp. there are 38–50 pseudopores. Additionally, zooids, frontal pseudopores and suboral avicularia are larger in *C. occlusa* than in *C. australis* n. sp. and *C. buski* n. sp. (see remarks under *C. australis* n. sp. and *C. buski* n. sp.). It is not possible to recognize diagnostic characters in the original Busk (1884) illustrations and the provenance of the illustrated specimens is unknown, therefore we cannot say if they truly belong to *C. occlusa*, *C. australis* n. sp. or *C. buski* n. sp.

Over time, many specimens assigned to *C. occlusa* were registered from different localities, including Zanzibar (Waters 1909, 1913), the Malay Archipelago (Robertson 1921) and the Indian Ocean and Red Sea (Waters 1909; Dumont 1981). Specimens from Zanzibar described by Waters (1909, 1913) have two large spatulate avicularia on the margin of the colony and semicircular avicularia scattered over the zooids. Specimens from the Red Sea (Waters 1909) have a semicircular avicularium placed at the proximal end of the zooid. Busk's specimens of *C. occlusa, C. australis* n. sp. and *C. buski* n. sp. have single large interzooidal avicularia commonly placed at colony margins and elliptical avicularia placed at zooidal margins. Robertson (1921) did not describe specimens

from the Malay Archipelago and referred to Waters's (1909) description. Dumont (1981) also did not describe specimens from the Red Sea and, pending examination of these specimens, as well as specimens from the Indian Ocean, it is not possible to say if they belong to *C. occlusa*, *C. australis* n. sp., *C. buski* n. sp. or other species.

Cigclisula occlusa is characterized by two sizes of suboral avicularia, interzooidal avicularia with a spatulate rostrum and triangular opesia and a subglobose slightly prominent ooecium having an ectooecium with a longitudinal band of 11–29 pseudopores.

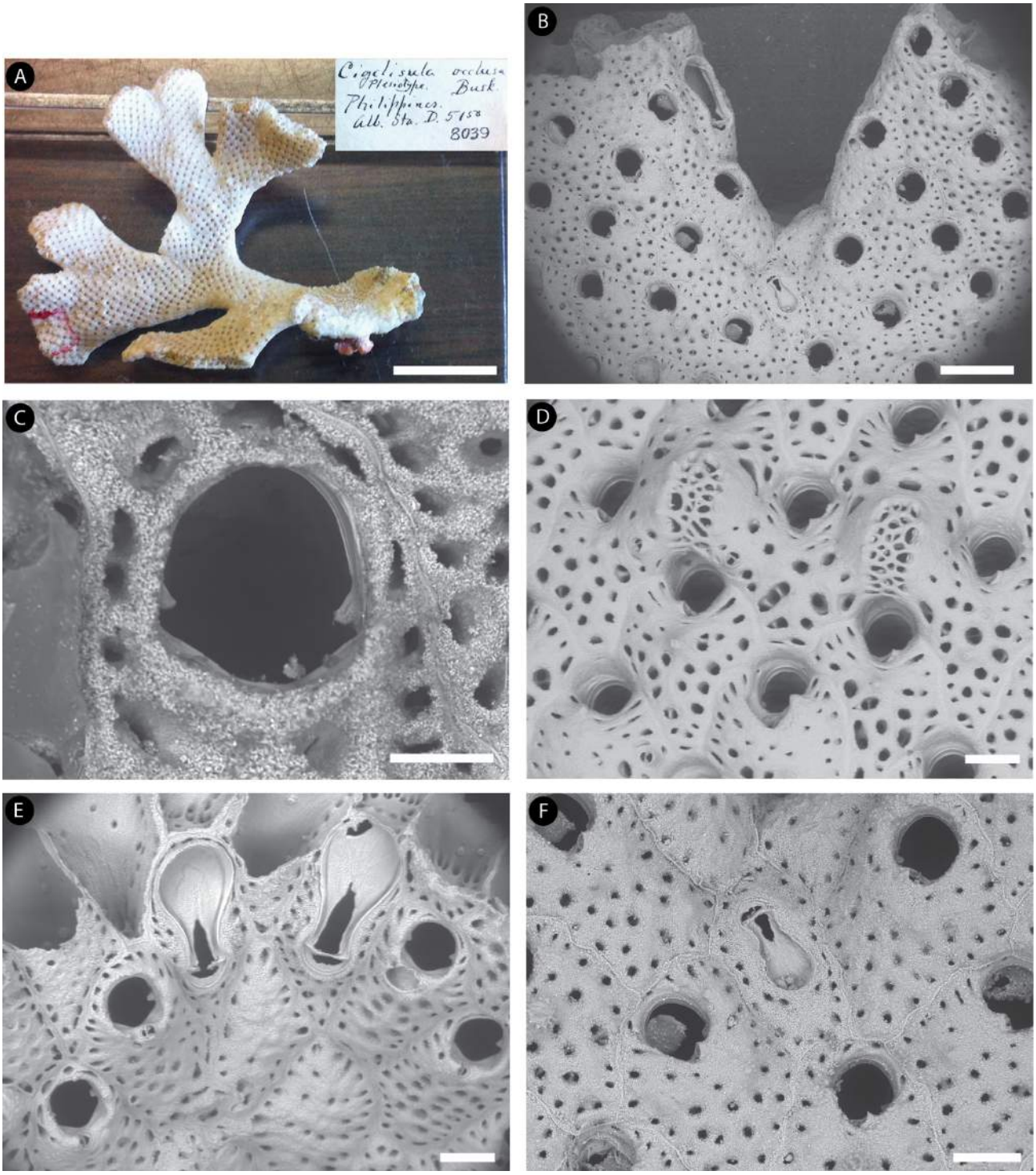

FIGURE 5. *Cigclisula occlusa* (Busk, 1884). **A–D,** USNM 8039, Philippines; **E–F,** USNM 8037, Philippines. **A,** entire erect colony. **B,** zooids at bifurcation of erect bilaminar colony. **C,** primary orifice. **D,** ovicelled zooids. **E,** zooids at growing edge of branch and spatulate interzooidal avicularia. **F,** zooids and small spatulate interzooidal avicularium. Scale bars: A = 1 cm; B = 500 μm; C = 100 μm; D, E, F = 200 μm.

Cigclisula occlusa resembles *Cigclisula cautium* Hastings, 1932, *Cigclisula fissurata* (Ortmann, 1890) and *Cigclisula fruticosa* Hayward & Ryland, 1995 in having erect bilaminar colonies. *Cigclisula occlusa* differs from *C. cautium* in having a shorter zooid size, two sizes of suboral avicularium (one size only in *C. cautium*) and more ectooecial pseudopores (11–29 in *C. occlusa,* 6–7 in *C. cautium*). Differences from *C. fissurata* include the distribution of frontal pseudopores (uniform in *C. occlusa,* marginal in *C. fissurata*), interzooidal and frontal avicularia (present in *C. occlusa,* absent in *C. fissurata*) and number of ectooecial pseudopores (11–29 in *C. occlusa,* 2–5 in *C. cautium*). Differences from *C. fruticosa* include the elliptical primary orifice and non-tubercular secondary orifice of *C. occlusa* and the number of ectooecial pseudopores, about 6 in *C. fruticosa*.

Distribution. Indo-Pacific: Philippines.

***Cigclisula areolata* (Kirkpatrick, 1890)**
(Fig. 6, Table 2)

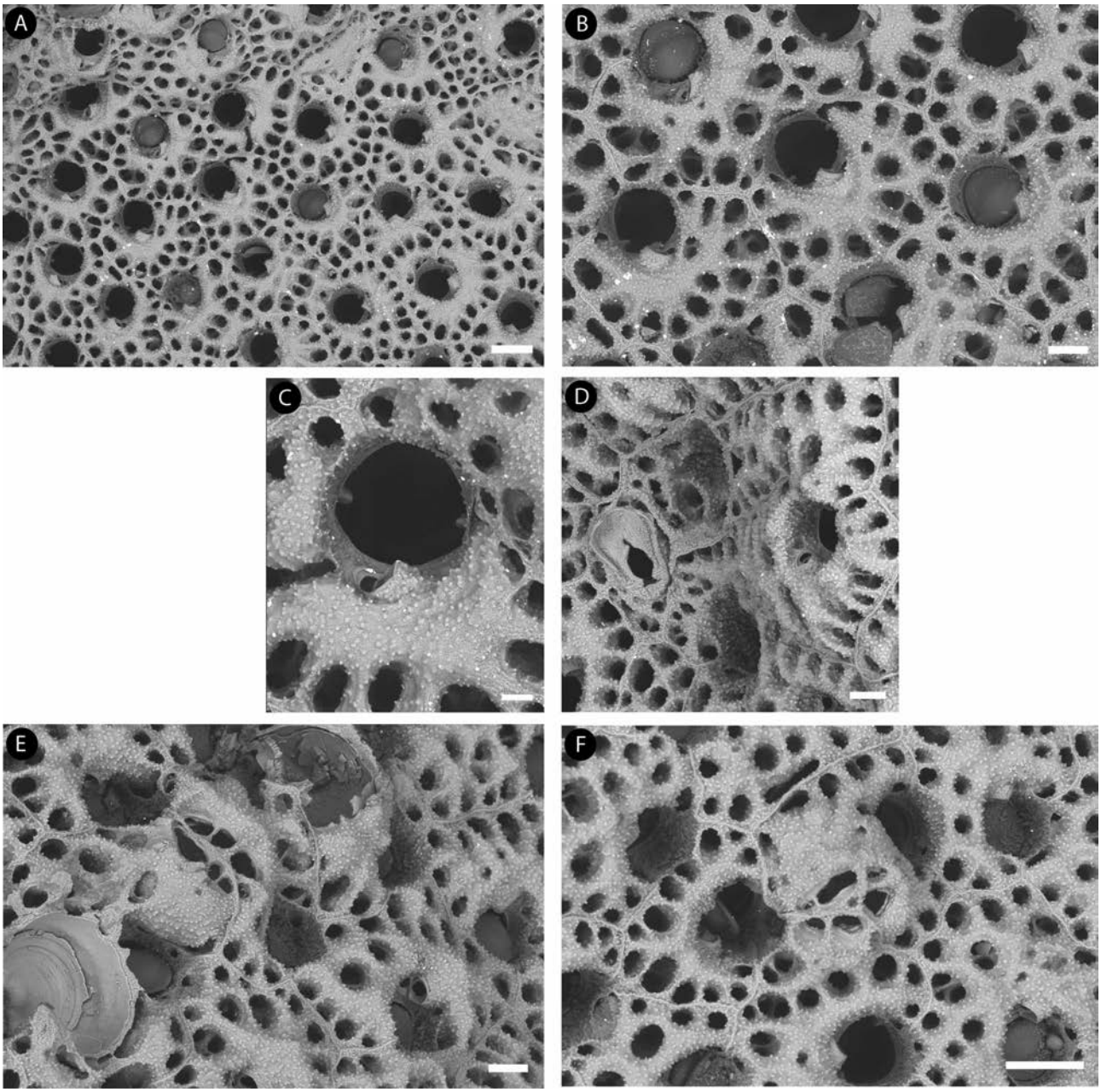

FIGURE 6. *Cigclisula areolata* (Kirkpatrick, 1890). **A–F,** NHMUK 2014.8.6.1, lectotype, Australia. **A,** group of zooids. **B,** close-up of zooids and suboral avicularia. **C,** primary orifice and suboral avicularium. **D,** close-up of spatulate interzooidal avicularium. **E, F,** ovicelled zooids. Scale bars: A, F = 200 µm, B, D, E = 100 µm; C = 40 µm.

Lepralia occlusa var. *areolata* Kirkpatrick, 1890: 618, pl. 16, figs 7, 7a. [Australia]
Porella areolata: Livingstone 1926: 91 (in part, encrusting specimens). [Great Barrier Reef, Australia]
Cigclisula areolata: Hastings 1932: 434. [Great Barrier Reef, Australia]
Not *Porella areolata*: Ortmann 1890: 42, pl. 3, fig 20. [Japan]

Material examined. *Lectotype:* NHMUK 2014.8.6.1, *Lepralia occlusa* var. *areolata*, Kirkpatrick det., Murray Island, Torres Straits, A.C. Haddon, 15–20 ftm (27.4–36.6 m). *Paralectotypes:* NHMUK 1890.3.24.60; NHMUK 1890.11.22.3 (two balsam slide); NHMUK 1999.3.9.6, same data as Lectotype.

Description. Colony encrusting, uni- to multilaminar. Zooids polygonal, as long as wide, delimited by distinct grooves. Frontal shield heavily calcified, minutely tubercular, marginally punctured by 1–2 rows of 12–24 large pseudopores. Primary orifice large relative to frontal shield, centered, transversely D-shaped, wider than long, sunken, with arch-shaped anter and concave poster, separated by 2 midlateral down-curved condyles. Secondary orifice non-tubercular, slightly raised. Suboral elliptical avicularium laterally directed. Frontal avicularia absent. Interzooidal avicularia smaller than zooids, longer than wide, rostrum obovate, proximal edge rounded and distal edge deep concave, calcified palate occupies more than half of rostrum, foramen trifoliate proximal and oval distally. Ooecium subglobose, minutely granular, inclined toward zooid surface; ectooecium with longitudinal band of 6–7 large irregular pseudopores.

Remarks. The species was described by Kirkpatrick (1890) as a variety of *Lepralia occlusa* (= *Cigclisula occlusa*), but later authors considered it to be distinct (Hastings 1932). There are some differences between *C. areolata* and *C. occlusa*: *C. areolata* has encrusting colonies, a transversely D-shaped orifice, no frontal avicularia and interzooidal obovate avicularia, while *C. occlusa* has erect colonies, a longer-than-wide orifice (Hastings 1932), small frontal avicularia placed at zooidal margins and interzooidal spatulate avicularia.

According to Hastings (1932), *C. areolata* is distinguished from the Japanese species described by Ortmann (1890) as *Porella areolata* in the colony form (erect in *C. areolata*, encrusting in the Japanese specimens) and primary orifice (transversely D-shaped in *C. areolata*, elliptical in Japanese specimens). Ortmann (1890) gave only a short description with a single uninformative illustration of *P. areolata*, so the specimens studied by him should be reexamined to determine their identity.

Livingstone (1926) described both encrusting and erect colonies in *C. areolata*. These two colony forms, however, were reassigned by Hastings (1932) to two distinct species of *Cigclisula*: *C. areolata*, with encrusting colonies and *C. cautium* with erect bilaminar colonies. Other differences include (i) zooid size (larger in *C. cautium*), (ii) shape and size of primary orifice (transversely D-shaped and longer in *C. areolata*, elliptical and smaller in *C. cautium*), and (iii) frontal avicularia in *C. cautium* (absent in *C. areolata*).

Cigclisula areolata is distinguished from all congeners by the presence of interzooidal avicularia having the rostrum obovate with the foramen trifoliate proximal and oval distally.

Distribution. Pacific: Australia (Queensland).

TABLE 2. Morphometric data for *Cigclisula* species studied (in mm).

	C. areolata	***C. cautium***		***C. fissurata***	***C. porosa***
	Australia[1]	Australia[2]	Australia[3]	Japan[4]	Galápagos[5]
Lz	10	10	10	10	10
Mean (SD)	0.439 (0.004)	0.630 (0.052)	0.666 (0.034)	0.818 (0.012)	0.639 (0.067)
Range	0.314–0.479	0.594–0.782	0.597–0.721	0.523–0.940	0.551–0.749
lz	10	10	10	10	10
Mean (SD)	0.475 (0.045)	0.316 (0.031)	0.399 (0.040)	0.463 (0.047)	0.501 (0.068)
Range	0.373–0.524	0.291–0.385	0.307–0.450	0.393–0.538	0.365–0.580
Dp	10	10	10	10	10
Mean (SD)	0.034 (0.011)	0.032 (0.006)	0.033 (0.008)	0.016 (0.004)	0.024 (0.006)
Range	0.025–0.064	0.021–0.042	0.021–0.048	0.010–0.025	0.015–0.032
Lo	10	10	10	-	10

.....continued on the next page

TABLE 2. (Continued)

	C. areolata	*C. cautium*		*C. fissurata*	*C. porosa*
	Australia[1]	Australia[2]	Australia[3]	Japan[4]	Galápagos[5]
Mean (SD)	0.153 (0.005)	0.117 (0.002)	0.126 (0.009)	-	0.208 (0.012)
Range	0.138–0.158	0.102–0.172	0.116–0.144	-	0.180–0.225
lo	10	10	10	-	10
Mean (SD)	0.160 (0.008)	0.124 (0.010)	0.129 (0.005)	-	0.203 (0.017)
Range	0.141–0.169	0.109–0.142	0.118–0.135	-	0.173–0.228
Lavs	10	5	10	-	-
Mean (SD)	0.072 (0.014)	0.053 (0.003)	0.074 (0.009)	-	-
Range	0.040–0.082	0.044–0.054	0.059–0.087	-	-
lavs	10	5	10	-	-
Mean (SD)	0.043 (0.007)	0.037 (0.003)	0.040 (0.004)	-	-
Range	0.028–0.056	0.033–0.043	0.034–0.049	-	-
Lavi	1	3	1	-	-
Mean (SD)	0.270	0.455 (0.011)	0.514	-	-
Range	-	0.318–0.541	-	-	-
lavi	1	3	1	-	-
Mean (SD)	0.149	0.0130 (0.013)	0.125	-	-
Range	-	0.109–0.135	-	-	-
Lavf	-	10	10	-	2
Mean (SD)	-	0.046 (0.007)	0.053 (0.004)	-	0.075 (0.010)
Range	-	0.031–0.060	0.047–0.060	-	0.068–0.082
lavf	-	10	10	-	2
Mean (SD)	-	0.043 (0.007)	0.046 (0.003)	-	0.072 (0.003)
Range	-	0.031–0.060	0.042–0.054	-	0.070–0.075
Lov	2	2	-	5	2
Mean (SD)	0.360 (0.007)	0.386 (0.051)	-	0.451 (0.030)	0.319 (0.013)
Range	0.359–0.360	0.349–0.423	-	0.416–0.496	0.309–0.328
lov	2	2	-	5	2
Mean (SD)	0.419 (0.011)	0.394 (0.016)	-	0.410 (0.046)	0.547 (0.067)
Range	0.411–0.427	0.382–0.406	-	0.380–0.500	0.499–0.594
Dovp	10	8	-	-	25
Mean (SD)	0.036 (0.008)	0.046 (0.012)	-	-	0.019 (0.006)
Range	0.023–0.048	0.028–0.065	-	-	0.012–0.035

[1] NHMUK 2014.8.6.1, Murray Island, Torres Straits. [2] NHMUK 1932.4.20.54, Queensland, Australia. [3] USNM 9574, Queensland, Australia. [4] MZS 68.1–2, Japan. [5] USNM 8514, Galápagos Islands.

Cigclisula cautium Hastings, 1932

(Figs 7–8, Table 2)

Porella areolata: Livingstone 1926: 92 (in part, erect specimens), pl. 8, figs 2–4. [Great Barrier Reef, Australia; Japan]
Cigclisula cautium Hastings, 1932: 435, text-fig. 13A–C. [Great Barrier Reef, Australia]

Material examined. *Holotype:* NHMUK 1932.4.20.54 (one dry and two balsam slides), *Cigclisula cautium*, A.B. Hastings det., Great Barrier Reef Expedition, Station XIV, 0.5 n. mile (0.9 km) SE of Lizard Island, Queensland, Australia, 35 m. *Paratype*: USNM 9574, *Cigclisula cautium*, A. B. Hastings det., 1932, Great Barrier Reef Expedition, Station XIV, 0.5 n. mile (0.9 km) SE of Lizard Island, Queensland, Australia, 35 m.

Description. Colony erect, bilaminar, branching. Zooids hexagonal, longer than wide, delimited by slightly raised lateral walls. Frontal shield heavily calcified, with small protuberances, uniformly punctured by 14–24 pseudopores. Primary orifice small relative to frontal shield, subelliptical, as long as wide, sunken, with arch-shaped anter and concave poster, separated by 2 proximolateral down-curved condyles. Secondary orifice raised, non-tubercular, subcircular. Suboral avicularium elliptical, laterally placed, distally directed. Frontal avicularia small, elliptical, 1–2 per zooid, placed at zooidal margins. Interzooidal avicularia longer than wide; rostrum spatulate with rounded proximal edge, median constriction distinct and distal edge concave; calcified palate occupying more than half of the rostrum length, with oval foramen. Ooecium subglobose, slightly prominent; ectooecium with longitudinal band of 6–7 irregular pseudopores.

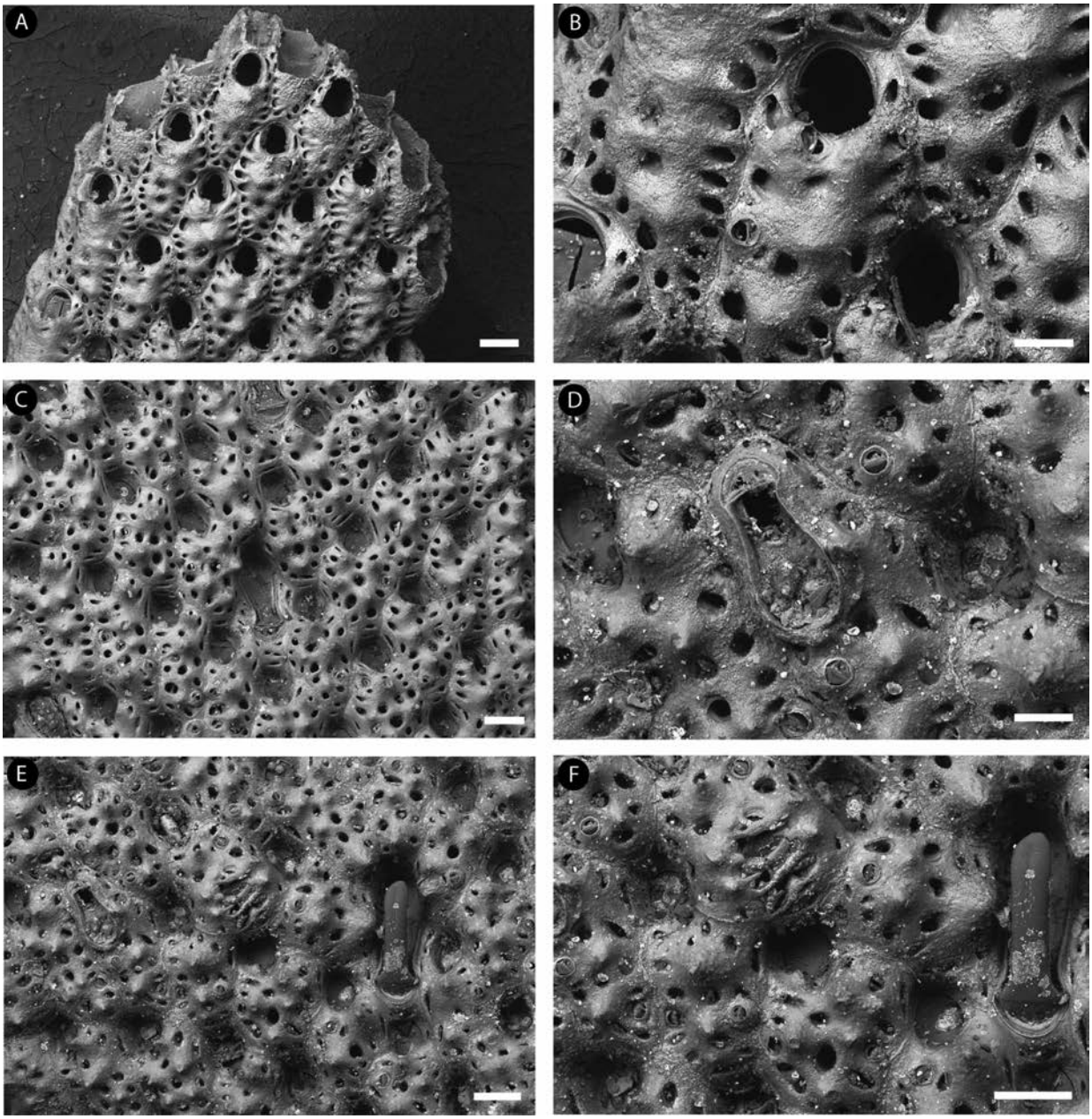

FIGURE 7. *Cigclisula cautium* Hastings, 1932. **A–F,** NHMUK 1932.4.20.54, holotype, Australia. **A,** zooids at growing edge of branch. **B,** close-up of zooid with suboral avicularium and elliptical frontal avicularia. **C,** group of zooids and foot-shaped interzooidal avicularium. **D,** spatulate interzooidal avicularium. **E,** ovicelled zooids and interzooidal avicularia. **F,** close-up of ovicelled zooids and interzooidal avicularia. Scale bars: A, C E, F = 200 μm; B, D = 100 μm.

Remarks. *Cigclisula cautium* is characterized by a frontal shield with small protuberances, interzooidal avicularia with a spatulate rostrum and oval opesia, and ectooecium with a longitudinal band of 6–7 irregular pseudopores.

Cigclisula cautium resembles *C. occlusa*, *C. fissurata* and *C. fruticosa* in having erect, bilaminar colonies. It differs from *C. occlusa* in zooid size (longer in *C. cautium*), a suboral avicularium of only one size (two distinct sizes in *C. occlusa*) and the number of ectooecial pseudopores (6–7 in *C. cautium*, 11–29 in *C. occlusa*). *Cigclisula fissurata* differs in the distribution of frontal pseudopores (uniform in *C. cautium*, marginal in *C. fissurata*), interzooidal and frontal avicularia (present in *C. cautium*, absent in *C. fissurata*) and number of ectooecial pseudopores (6–7 in *C. cautium*, 2–5 in *C. fissurata*). *Cigclisula fruticosa* differs in the distribution of frontal pseudopores (uniform in *C. cautium*, irregular in *C. fruticosa*), orifice shape (subelliptical primary orifice and non-tubercular secondary orifice of *C. cautium*) and the number of ectooecial pseudopores, about 6 in *C. fruticosa*.

Distribution. Pacific: Australia (Queensland) and Japan (Tsushima Island; see Hastings 1932).

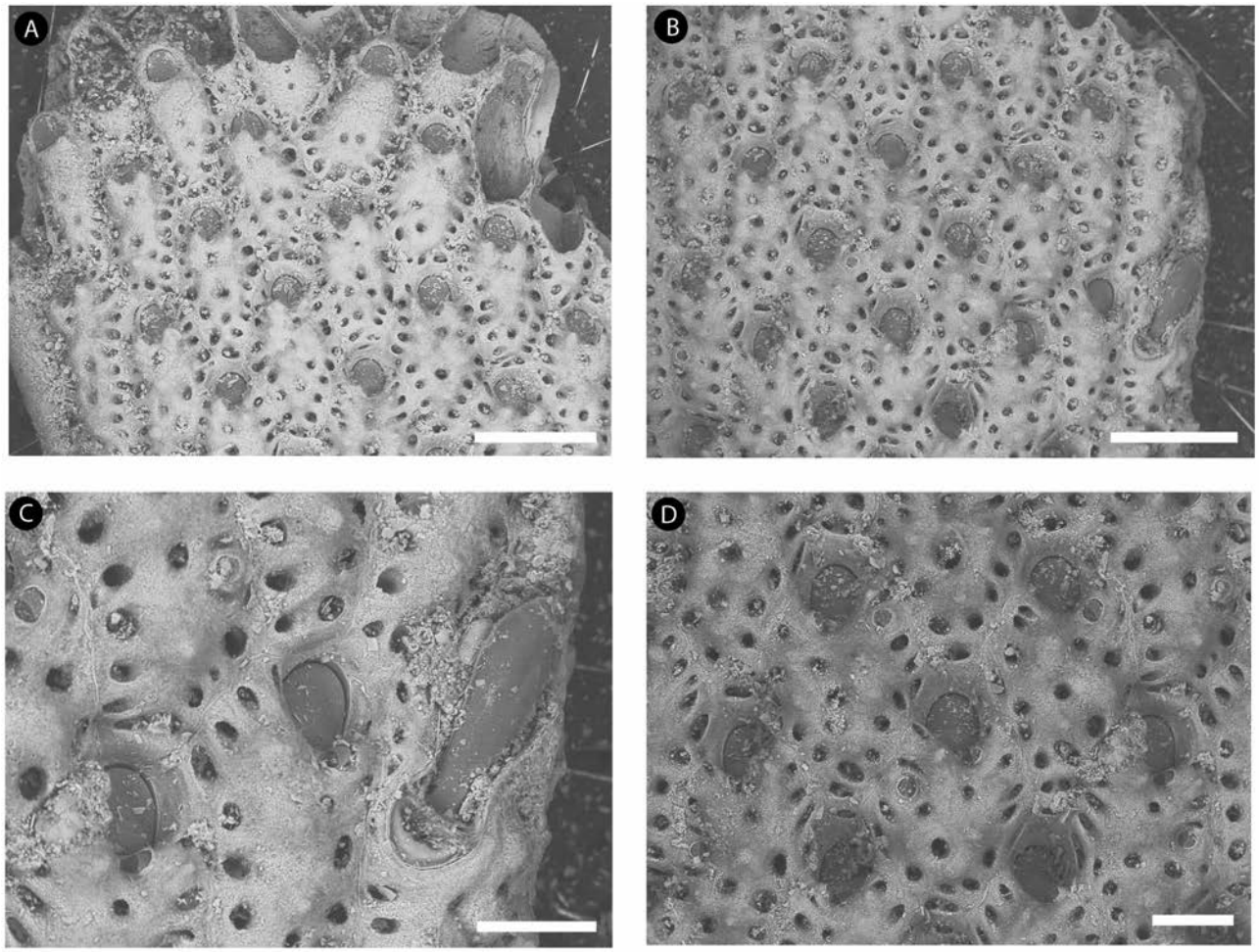

FIGURE 8. *Cigclisula cautium* Hastings, 1932. **A–D,** USNM 9574, paratype, Australia. **A,** zooids at growing edge of branch. **B,** group of zooids and spatulate interzooidal avicularium. **C,** orifices and spatulate interzooidal avicularium. **D,** group of zooids with small, elliptical frontal avicularia. Scale bars: A, B = 500 μm; C, D = 200 μm.

Cigclisula fissurata (Ortmann, 1890)

(Fig. 9, Table 2)

Porella fissurata Ortmann, 1890: 41, pl. 3, fig 14. [Japan]
?*Porella fissurata*: Livingstone 1926: 92, pl. 8, figs 5–7. [Australia]

Material examined. *Syntypes:* MZS 68.1–2, *Porella fissurata*, A. Ortmann det., collected 1882, Sagami Bay, Japan.

Description. Colony erect, bilaminar, branching. Zooids hexagonal, longer than wide, limited by slightly

raised lateral walls. Frontal shield heavily calcified, minutely tubercular, marginally punctured by 12–28 pseudopores. Primary orifice small relative to frontal shield, subelliptical, sunken. Secondary orifice raised, non-tubercular, subcircular. Suboral avicularium elliptical, laterally placed, distally directed. Frontal and interzooidal avicularia absent. Ooecium subglobose, slightly prominent; ectooecium with longitudinal band of 2–5 irregular pseudopores.

Remarks. Owing to the presence of a suboral avicularium, this species was originally assigned to *Porella*. Species of *Porella*, however, have an imperforate ectooecium whereas that in *C. fissurata* has a longitudinal band of 2–5 irregular pseudopores. Thus, as suggested by Hastings (1932) and Harmer (1957), this species is better assigned to *Cigclisula*.

Cigclisula fissurata is distinguished from all congeners by the absence of frontal and interzooidal avicularia. Purported *Porella fissurata* from Australia (Livingstone 1926) requires reinvestigation.

Distribution. Pacific: Japan.

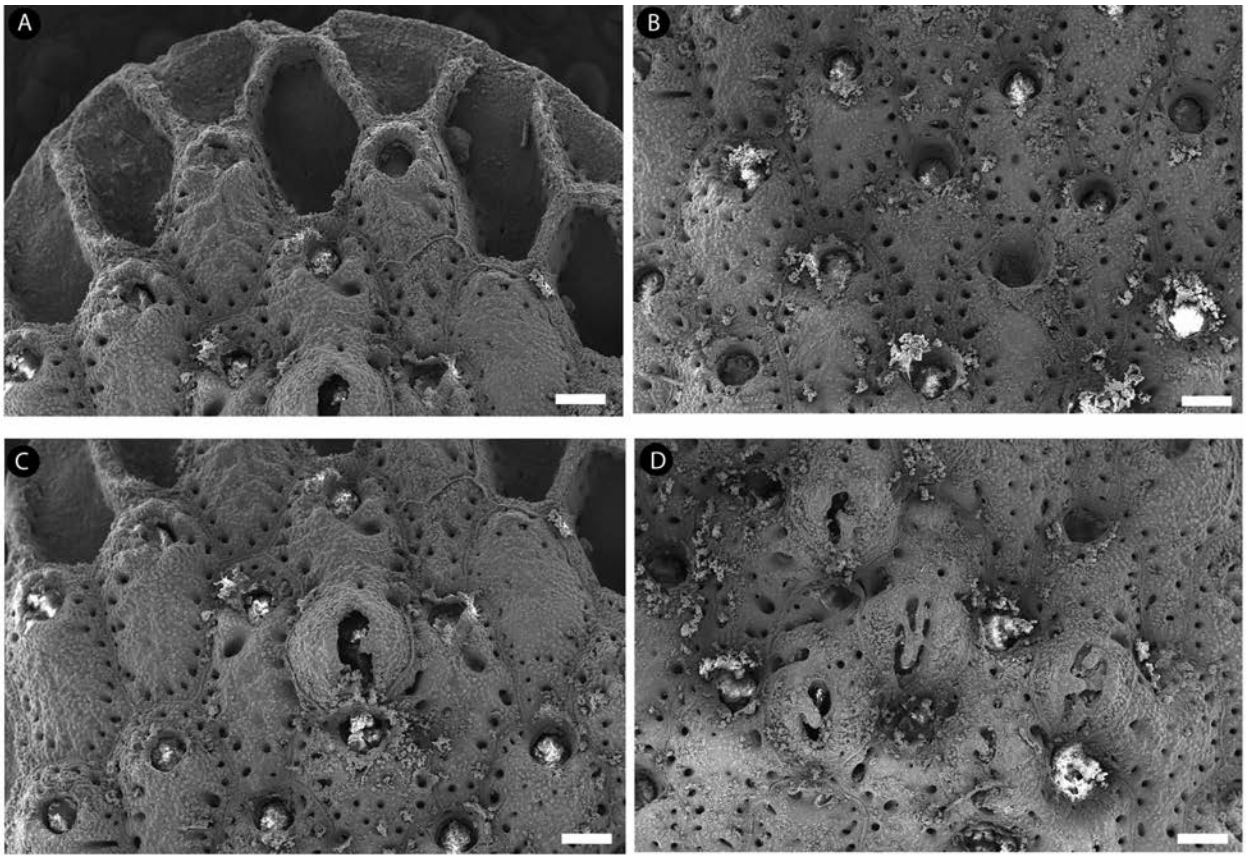

FIGURE 9. *Cigclisula fissurata* (Ortmann, 1890). **A–D**, MZS 68.1–2, syntype, Japan. **A,** zooids at growing edge of branch. **B,** group of zooids. **C,** single broken ovicell. **D,** ovicelled zooids. Scale bars = 200 µm .

Cigclisula fruticosa Hayward & Ryland, 1995

Cigclisula fruticosa Hayward & Ryland, 1995: 558, figs 11E, 12A, B. [Heron Island, Australia]

Type specimen. NHMUK 1999.12.1.1, Station 89, Western Australia, Dampier Archipelago, approx. 1.85 n. miles (3.4 km) North of Gordon Point, Rosemary Island, 20°27.33' S, 116°34.39' E to 20°27.17' S, 116°32.72' E, 27–28 m, 26 July 1999, J. Taylor & E. Glover col., Western Australian Museum don.

Remarks. *Cigclisula fruticosa* is characterized by strongly convex zooids, a secondary orifice with low blunt processes, dimorphic adventitious avicularia and ectooecia with a longitudinal band of about 6 large pseudopores subdivided in 2–4 small pseudopores (Hayward & Ryland 1995). The species is distinguished from all congeners by the primary orifice having a short U–shaped median sinus and the cribrate pseudopores of the ooecium.

Distribution. Pacific: Australia.

***Cigclisula porosa* (Canu & Bassler, 1930)**
(Fig. 10, Table 2)

Holoporella porosa Canu & Bassler 1930a: 39, pl. 6, figs. 7–8. [Galápagos Islands]
Trematooecia porosa: Osburn, 1952: 503, pl. 60, figs. 8–9. [Gulf of California and Galápagos Islands]

Material examined. *Holotype:* USNM 8514, *Holoporella porosa* F. Canu & R. Bassler det., 1930a, Galápagos Islands, Albatross Station, D.2815, 61 m.

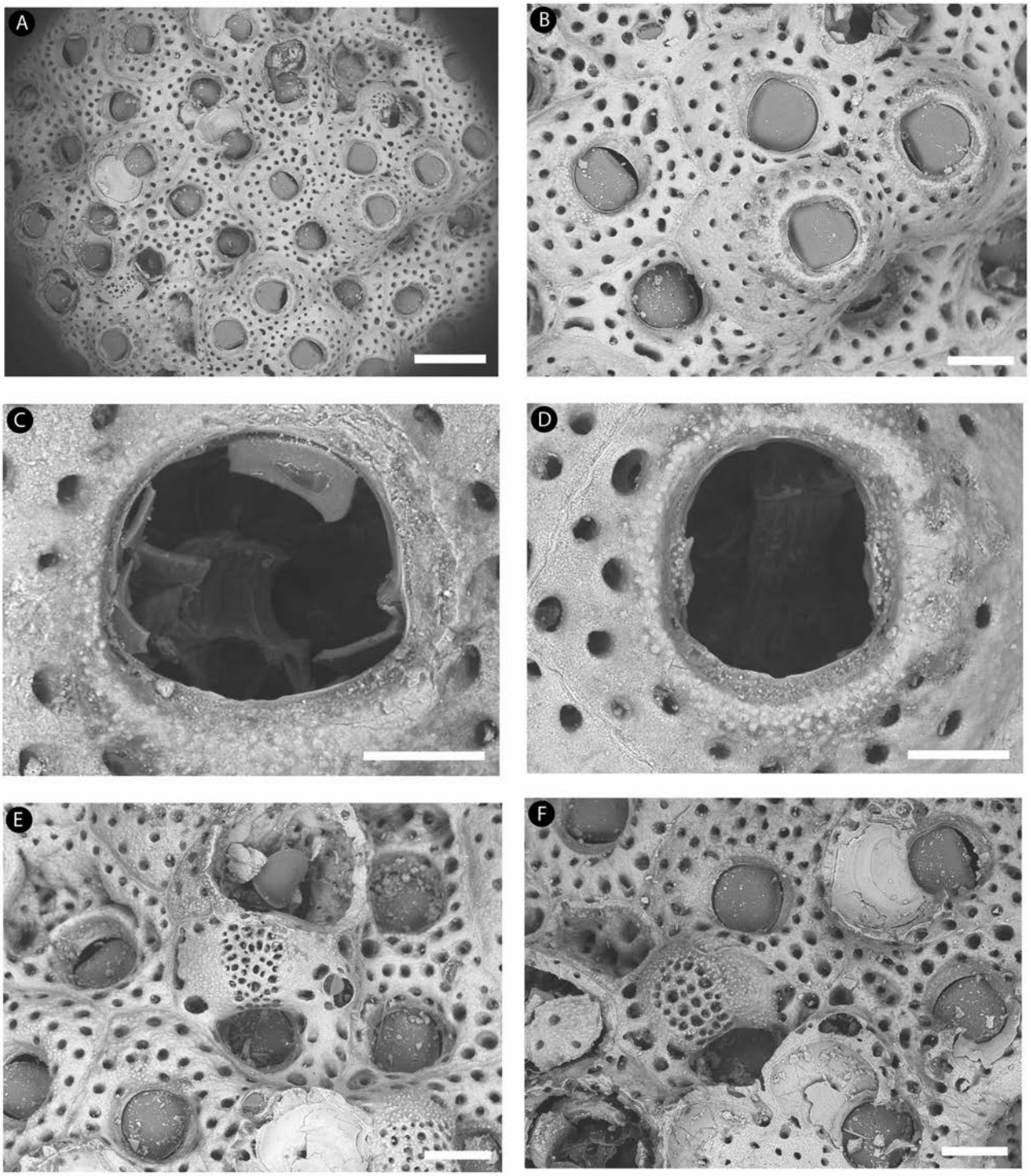

FIGURE 10. *Cigclisula porosa* (Canu & Bassler, 1930). **A–F,** USNM 8514, holotype, Galápagos Islands. **A,** part of encrusting colony. **B,** group of zooids. **C,** primary orifice. **D,** unusually narrow primary orifice. **E, F,** ovicelled zooids and elliptical frontal avicularia. Scale bars: A = 500 µm; B = 200 µm; C, D = 100 µm; E, F = 200 µm.

Description. Colony encrusting, uni- to multilaminar. Zooids hexagonal, becoming polygonal with growth, longer than wide, delimited by distinct grooves. Frontal shield heavily calcified, uniformly punctured by 20–50 pseudopores, minutely granular. Primary orifice large relative to frontal shield, centered, somewhat hoof-shaped, mostly as long as wide, sunken, with arch-shaped anter and concave poster, separated by 2 proximolateral down-curved condyles. Secondary orifice non-tubercular, slightly raised, surrounded by pseudopores. Frontal avicularia small, elliptical, often single (rarely 2 per zooid), placed at zooidal margins. Ooecium subglobose, minutely granular, inclined toward zooid surface; ectooecium with longitudinal band of 33–48 irregular pseudopores.

Remarks. *Cigclisula porosa* was described by Canu & Bassler (1930a) in the same publication as *Trematooecia hexagonalis* (Canu & Bassler, 1930). While the ectooecium of *C. porosa* was described as pseudoporous, Canu & Bassler (1930a) did not recognize ooecia in the holotype of *T. hexagonalis*, but some authors (Osburn 1952; Soule 1961; Soule & Soule 1964) described the ectooecium of this species as pseudoporous, designating these specimens as *T. hexagonalis*. Examination of the holotype of *T. hexagonalis*, however, revealed that the ectooecium has single median membranous area (see remarks under *T. hexagonalis*) contrasting with an irregularly pseudoporous ectooecium, which is distinct in *C. porosa.* Besides the ectooecium and tubercles, other differences between these two species include the diameter of frontal pseudopores, larger in *C. porosa* (0.015–0.032 mm) than in *T. hexagonalis* (0.010–0.018 mm), and the size of frontal avicularia, larger in *C. porosa* (0.068–0.082 mm long, 0.070–0.075 mm wide) than in *T. hexagonalis* (0.028–0.045 mm long, 0.028–0.039 mm wide). Specimens previously reported as *T. hexagonalis* from the Pacific (Osburn 1952; Soule 1961; Soule & Soule 1964) are here reassigned to *Cigclisula osburni* n. sp. (see below).

Cigclisula porosa is characterized by encrusting colonies with the zooidal frontal shield uniformly punctured by 20–50 pseudopores, primary orifice almost rounded with distolateral condyles, secondary orifice non-tubercular, elliptical frontal avicularia and ectooecium with 33–48 irregular pseudopores. This species resembles *C. areolata* in having encrusting colonies, a uniformly punctured frontal shield and non-tubercular secondary orifice, but differs in the the hoof-shaped primary orifice (transversely D-shaped in *C. areolata*) and in the absence of suboral and interzooidal avicularia (present in *C. areolata*).

Distribution. Pacific: Gulf of California and Galápagos Islands.

Cigclisula psammophila (Winston & Håkansson, 1986) n. comb.

Cigclisula cf. *turrita*: Håkansson & Winston 1985: 130, fig. 5B. [South Hutchinson Island, Florida]
Trematooecia psammophila Winston & Håkansson, 1986: 33, figs 76–80. [Capron Shoal, Florida]

Remarks. This species was originally assigned to *Trematooecia* owing to similarities with *Trematooecia turrita* sensu Winston (1984) (= *Cigclisula winstonae* n. sp.; see below). *Cigclisula psammophila* (Winston & Håkansson) n. comb. has encrusting colonies, a secondary orifice with solid tubercles and an ectooecium with a longitudinal band of irregular pseudopores, the latter morphological character a diagnostic feature of *Cigclisula*.

Cigclisula psammophila is distinguished from all congeners by its small size and the absence of avicularia (Winston & Håkansson 1986). Colonies are found encrusting the convex surfaces or borders of sand grains (Håkansson and Winston 1985; Winston and Håkansson 1986).

Distribution. Northwest Atlantic: Florida.

Cigclisula turrita (Smitt, 1873)
(Fig. 11, Table 3)

Lepralia turrita Smitt 1873: 66, pl. 6, figs 226–228. [Florida]
Holoporella turrita: Canu & Bassler 1923: 179, pl. 46, fig. 1. [Pleistocene, Mount Hope, Panama]
? *Holoporella turrita*: Hastings 1930: 732, pl. 7, fig. 73. [Galápagos Islands]
Cigclisula turrita: Harmer 1957: 419 (in part), pl. 69, figs 22, 27. [Puerto Rico]
? *Trematooecia turrita*: Powell 1971: 773. [Panama Canal]
Cigclisula turrita: Banta & Carson 1977: 400, figs 4E, 7. [Costa Rica]
Cigclisula turrita: Winston 1982: 147, fig. 79. [Florida]
Trematooecia turrita: Winston 2005: 105, figs 291–297. [Florida]

Not *Cellepora turrita*: Ridley 1881: 55. [Espírito Santo, Brazil]
Not *Lepralia turrita*: Waters 1913: pl. 73, fig. 10. [Cargados Island, East Africa]
Not *Holoporella turrita*: Osburn 1914: 217. [Tortugas Island, Florida; = *Trematooecia aviculifera* (Canu & Bassler, 1923)]
Not *Holoporella turrita*: Osburn 1927: 131. [Curaçao Island, Caribe; = *Trematooecia aviculifera* (Canu & Bassler, 1923)]
Not *Holoporella turrita*: Canu & Bassler 1928a: 145, text-fig. 33C, D. [Gulf of Mexico; = *Trematooecia aviculifera* (Canu & Bassler, 1923)]
Not *Holoporella turrita*: Canu & Bassler 1929: 420, pl. 59, figs 1–5, text-fig. 164A–C. [Philippines; = *Trematooecia clivulata* Tilbrook, 2006]
Not *Holoporella turrita*: Canu & Bassler 1930b: 74, pl. 5, figs 10–16. [Tunis; = *Trematooecia clivulata* Ayari & Taylor, 2008 *in* Ayari *et al.* 2008]
Not *Trematooecia turrita*: Osburn 1940: 458, pl. 8, fig. 72. [Guanica Harbor, Puerto Rico; Tortugas Island, Florida; Curaçao Island, Caribe; = *Trematooecia aviculifera* (Canu & Bassler, 1923)]
Not *Trematooecia turrita*: Winston 1984: 32, figs 67–68. [Belize; = *Cigclisula winstonae* n. sp.]
Not *Cigclisula* cf. *turrita*: Håkansson & Winston 1985: 130, fig. 5B. [South Hutchinson Island, Florida; = *Cigclisula psammophila* (Winston & Håkansson, 1986)]
Not *Cigclisula turrita*: Zabala & Maluquer 1988: 159, fig. 443. [Mediterranean; ?*Trematooecia clivulata* Ayari & Taylor, 2008]
Not *Trematooecia turrita*: Winston & Wollacott 2009: 285, fig. 33. [Barbados; = *Cigclisula winstonae* n. sp.]

Material examined. *Syntypes*: MCZ # 92, *Lepralia turrita*, F. A. Smitt det., 1873, Florida, April 3, 1869, Cast No. 3, 80m. *Additional specimens:* USNM 68708, *Holoporella turrita*, F. Canu & R.S. Bassler det., 1923, Pleistocene, Mount Hope, Panama. USNM 603762, *Holoporella turrita* (Smitt), Fowey Light, Miami, Florida, 73 m; USNM 603763, *Holoporella turrita* (Smitt), Albatross Station 2639, Straits of Florida, 102 m.

Description. Colony encrusting, uni- to multilaminar, forming small mounds. Zooids squatly vasiform, irregularly polygonal in outline, as long as wide, delimited by distinct grooves. Frontal shield heavily calcified, irregularly punctured by 14–41 pseudopores. Primary orifice centered, deep, longitudinally oval with arcuate anter and concave poster delimited by 2 down-curved condyles at about one-third orifice length. Secondary orifice frequently surrounded by 4–5 (usually 4) truncate tubercles. Suboral avicularium absent. Frontal avicularia small, elliptical, 1–2 per zooid, placed at zooidal proximal margin, between or at ends of tubercles; serrated distal rostral margins. Interzooidal avicularia smaller than zooids, short, rostrum tongue-shaped, longer than wide, proximal edge rectangular and distal edge straight; calcified palate occupies less than half of rostrum; foramen pentagonal. Ooecium subglobose, inclined toward zooid surface, sometimes bearing tubercles and avicularia; ectooecium with longitudinal band of 25–38 irregular pseudopores.

Remarks. Smitt (1873) stated that the ooecium of *Lepralia turrita* was globose and medially perforated by 'pores' (= pseudopores). However, species with different types of ooecium (with a single frontal membranous window) have frequently been identified as *L. turrita* (Waters 1913; Osburn 1914, 1927, 1940; Canu & Bassler 1928a, 1929; Zabala & Maluquer 1988). Harmer (1957) suggested that two ectooecial morphologies occur in the same species: the median slit-like membranous window occurs in young ooecia and pseudopores are found in old ooecia. This condition, however, has never been seen in the same colony and since Harmer (1957) based this observation on different specimens, it is doubtful that he was talking about a single species, but two or more different species.

Osburn (1940) erected *Trematooecia* based on specimens that he named *Trematooecia turrita* and attributed to Smitt's species. His description and the specimens examined, however, all conform to *Trematooecia aviculifera* (Canu & Bassler, 1923) (see remarks under *Trematooecia* and *T. aviculifera*). Despite the presence of solid tubercles around the secondary orifice there are many differences between both species. *Trematooecia aviculifera* has a transversely D-shaped primary orifice lacking condyles, the suboral avicularium is common and frontal avicularia are absent, whereas Smitt's *L. turrita* has a longitudinally oval primary orifice with stout condyles, the suboral avicularium is absent and frontal avicularia are common. The ectooecium, however, comprises the most conspicuous difference between these species: a frontal semicircular window (considered by as diagnostic of *Trematooecia*) in *T. aviculifera* and a longitudinal band of irregular pseudopores (considered by us as diagnostic of *Cigclisula*) in *C. turrita*. Our conclusion is that Smitt's *L. turrita* is better placed in *Cigclisula*.

Over the years, many specimens from different localities including Brazil (Ridley 1881), Galápagos (Hastings 1930) and the Panama Canal (Powell 1971) have been attributed to *L. turrita* Smitt; only reexamination of these will determine their taxonomic position. The single specimen reported by Ridley (1881) differs from *C. turrita* in colonial morphology (erect and branched in Ridley's specimen, encrusting in *C. turrita*), number of peristomial tubercles (2–4 in Ridley's specimen, 4–5 in *C. turrita*), presence of avicularia on the tubercles and around the

secondary orifice (present in Ridley's specimen, lacking in *C. turrita*), and shape of interzooidal avicularia (spatulate in Ridley's specimen, linguiform in *C. turrita*). Part of the material reported by Ridley (1881) may be conspecific with a specimen from Cabo Frio, Brazil (Winston *et al*. in press). Specimens studied by Hastings (1930) differ from *C. turrita* in the presence interzooidal avicularia (absent in Hastings's specimens and present in *C. turrita*) and morphology of oooecia (immersed in Hastings's specimens, prominent and inclined toward the zooid surface in *C. turrita*). Specimens reported by Powell (1971) were not described or illustrated, but he made reference to Hastings specimens that, as discussed above, are distinct from those of Smitt's *L. turrita*.

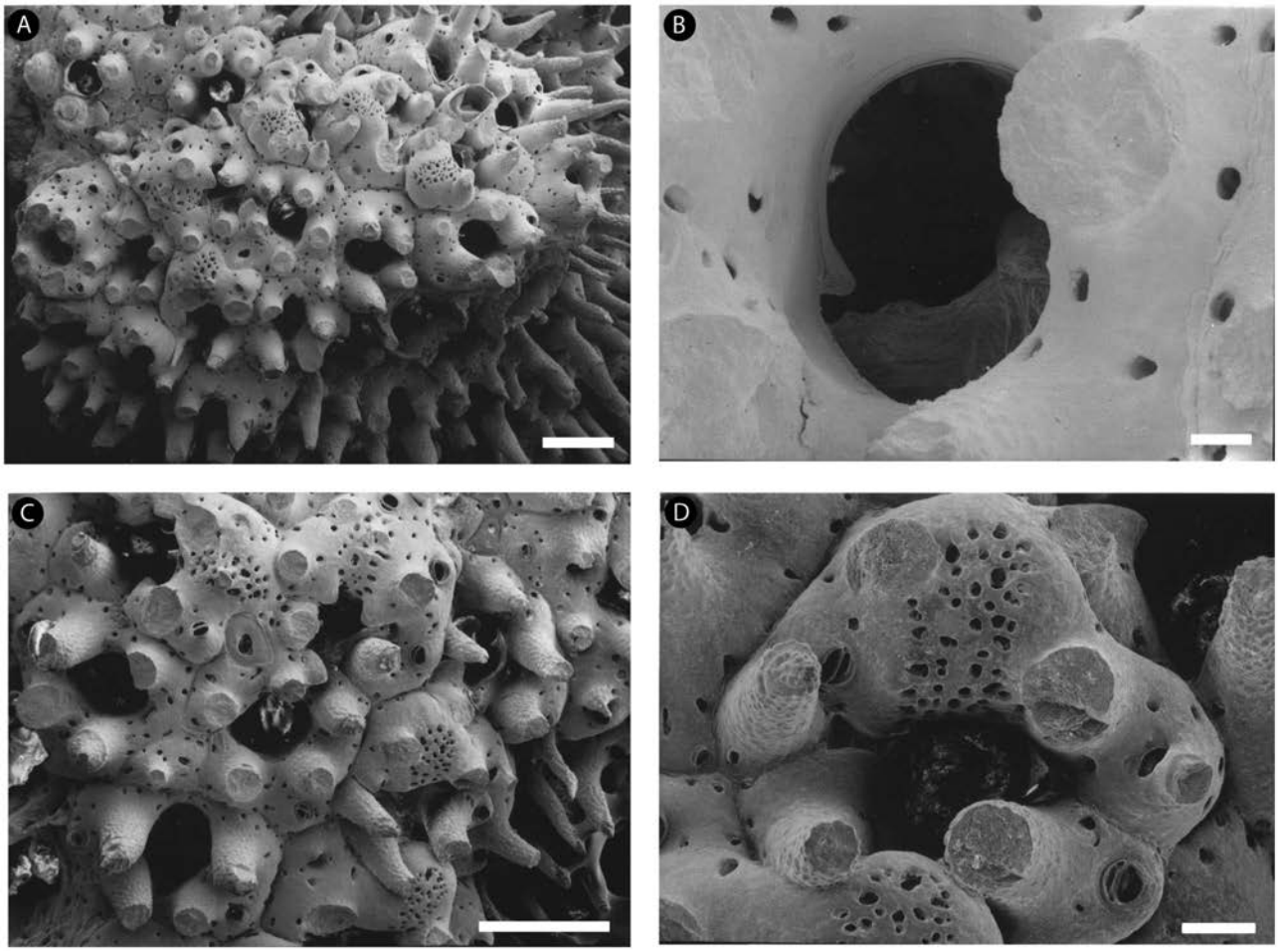

FIGURE 11. *Cigclisula turrita* (Smitt, 1873). **A–D,** MCZ # 92, syntype, Florida. **A,** part of encrusting colony. **B,** primary orifice. **C,** group of ovicelled zooids and elliptical frontal avicularia. **D,** ovicelled zooid and elliptical frontal avicularia. Scale bars: A, B = 400 μm; C = 40 μm; D = 100 μm.

Cigclisula turrita is characterized by the presence of 4–5 solid tubercles around the secondary orifice, interzooidal avicularia with linguiform rostrum and subglobose ooecia. Two other species of *Cigclisula* have encrusting colonies and subglobose ooecia: *C. areolata* and *C. porosa*. *Cigclisula turrita* differs from *C. areolata* in the irregularly punctured frontal shield (that of *C. areolata* is uniformly punctured), longitudinally oval primary orifice (transversely D-shaped in *C. areolata*), presence of tubercles around the secondary orifice (absent in *C. areolata*), absence of suboral avicularia (present in *C. areolata*), and presence of frontal avicularia (absent in *C. areolata*). *Cigclisula porosa* differs from *C. turrita* in the uniformly punctured frontal shield (that of *C. turrita* is irregularly punctured), absence of peristomial tubercles (present in *C. turrita*) and absence of interzooidal avicularia (present in *C. turrita*).

Distribution. Pleistocene (Panama) to Recent (Northwest Atlantic: Florida to Costa Rica).

***Cigclisula australis* n. sp.**
(Fig. 12, Table 3)

Escharoides occlusa Busk, 1884: 150 (in part), pl. 21, fig. 8 (?in part). [Cape York, Australia]
Lepralia occlusa: Kirkpatrick 1890: 604, 612 (?in part). [Torres Straits]
Lepralia occlusa: Waters 1909: 152 (in part), pl. 13, fig. 15; pl. 14, figs 1–9, 13 (?in part). [Cape York, Australia]
Cigclisula occlusa: Hastings 1932: p. 43 (in part), text-fig. 13 (?in part). [Australia]
? *Myriozoum occlusum*: Marcus 1921: 20, pl. 1, fig. 8; pl. 2, figs 1–2. [Australia]

Material examined. *Holotype*: USNM 8894, *Escharoides occlusa* Busk, Challenger Expedition, Cape York, Australia.

Diagnosis. Erect *Cigclisula* with minutely tubercular frontal shield; usually 2–3 frontal avicularia; larger interzooidal spatulate avicularia with triangular foramen and smaller interzooidal spatulate avicularia with oval foramen; ooecium minutely tubercular and ectooecium with longitudinal band of 7–18 irregular pseudopores.

TABLE 3. Morphometric data for *Cigclisula* species studied (in mm).

	C. turrita		***C. australis***	***C. buski***	
	Panama[1]	Florida[2]	Australia[3]	Australia[4]	Australia[5]
Lz	5	5	10	10	10
Mean (SD)	0.621 (0.022)	0.646 (0.141)	0.717 (0.075)	0.622 (0.055)	0.849 (0.050)
Range	0.596–0.646	0.454–0.816	0.587–0.797	0.529–0.716	0.828–0.957
lz	5	5	10	10	10
Mean (SD)	0.598 (0.063)	0.667 (0.121)	0.342 (0.064)	0.360 (0.035)	0.408 (0.055)
Range	0.506–0.666	0.552–0.858	0.296–0.490	0.310–0.434	0.325–0.489
Dp	10	10	10	10	10
Mean (SD)	0.011 (0.003)	0.010 (0.002)	0.013 (0.003)	0.017 (0.005)	0.019 (0.005)
Range	0.005–0.014	0.006–0.014	0.007–0.017	0.010–0.26	0.010–0.028
Lo	5	-	10	10	10
Mean (SD)	0.204 (0.017)	-	0.151 (0.014)	0.126 (0.053)	0.145 (0.011)
Range	0.189–0.234	-	0.126–0.167	0.117–0.132	0.131–0.171
lo	5	-	10	10	10
Mean (SD)	0.156 (0.024)	-	0.152 (0.009)	0.141 (0.049)	0.144 (0.014)
Range	0.122–0.181	-	0.134–0.157	0.133–0.147	0.131–0.171
Lavs	-	-	10	10	10
Mean (SD)	-	-	0.064 (0.090)	0.050 (0.008)	0.071 (0.008)
Range	-	-	0.044–0.157	0.046–0.071	0.057–0.86
lavs	-	-	10	10	10
Mean (SD)	-	-	0.037 (0.010)	0.034 (0.004)	0.040 (0.003)
Range	-	-	0.034–0.064	0.030–0.043	0.033–0.043
Lavi	-	-	5	1	2
Mean (SD)	-	-	0.311 (0.109)	0.558	0.452 (0.189)
Range	-	-	0.188–0.485	-	0.318–0.587
lavi	-	-	5	1	2
Mean (SD)	-	-	0.134 (0.027)	0.197	0.184 (0.043)
Range	-	-	0.086–0.158	-	0.153–0.215
Lavf	-	8	10	10	10
Mean (SD)	-	0.061 (0.006)	0.044 (0.006)	0.044 (0.056)	0.042 (0.043)

.....continued on the next page

TABLE 3. (Continued)

	C. turrita		*C. australis*	*C. buski*	
	Panama[1]	Florida[2]	Australia[3]	Australia[4]	Australia[5]
Range	-	0.052–0.070	0.035–0.51	0.029–0.046	0.043–0.055
lavf	-	8	10	10	10
Mean (SD)	-	0.058 (0.007)	0.038 (0.009)	0.034 (0.058)	0.042 (0.049)
Range	-	0.043–0.072	0.024–0.058	0.027–0.041	0.039–0.052
Lov	-	5	9	3	-
Mean (SD)	-	0.343 (0.057)	0.344 (0.012)	0.324 (0.093)	-
Range	-	0.283–0.434	0.366–0.412	0.321–0.338	-
lov	-	5	9	3	-
Mean (SD)	-	0.495 (0.056)	0.323 (0.012)	0.311 (0.053)	-
Range	-	0.415–0.533	0.273–0.448	0.279–0.383	-
Dovp	-	25	25	25	-
Mean (SD)	-	0.017 (0.004)	0.078 (0.040)	0.015 (0.032)	-
Range	-	0.010–0.027	0.040–0.178	0.010–0.021	-

[1] USNM 68708, Pleistocene, Mount Hope, Panama. [2] MCZ # 92, Florida. [3] USNM 8894, Cape York, Australia. [4] NHMUK 1887.12.9.593, Australia. [5] USNM 9231, Cape York, Australia.

Etymology. Latin *australis*, southern, alluding to the type locality being in Australia.

Description. Colony erect, bilaminar, branching. Zooids hexagonal, longer than wide, delimited by slightly raised lateral walls. Frontal shield heavily calcified, uniformly punctured by 18–34 pseudopores, minutely tubercular. Primary orifice small relative to zooid size, somewhat hoof-shaped, wider than long, sunken, with arcuate anter and broad shallow poster separated by 2 proximolateral down-curved condyles. Secondary orifice non-tubercular. Suboral, elliptical, laterally directed avicularium with 2 sizes, 1 smaller and the other double sized. Frontal avicularia small, elliptical, 2–3 per zooid, placed at zooidal margins, sometimes near ooecial margins. Interzooidal avicularia of 2 sizes, 1 as long as zooids, large, rostrum spatulate, longer than wide, proximal edge rounded, median constriction and distal edge concave, palate occupying half rostral length, with triangular foramen; avicularia smaller than zooids sometimes present, short, rostrum spatulate, wider than long, proximal edge rounded, distal constriction and distal edge concave; palate occupying half rostral length, with oval foramen. Ooecium subglobose, inclined toward zooid surface, minutely tubercular; ectooecium with longitudinal band of 7–18 irregular pseudopores.

Remarks. Busk (1884) described *C. occlusa* (as *Escharoides occlusa*) from the Philippines and Australia, but examination of these specimens revealed three distinct species, *C. occlusa*, *C. australis* n. sp. and *C. buski* n. sp., mainly distinguished by the frontal surface of the zooids, number of ectooecial pseudopores, shape of foramen of the interzooidal avicularia and metrics of zooids, frontal pseudopores and suboral avicularia.

Cigclisula australis n. sp. is characterized by the minutely tubercular frontal shield, two sizes of interzooidal spatulate avicularia (the larger with a triangular foramen, the smaller with an oval foramen, minutely tubercular ooecium and ectooecium with a longitudinal band of 7–18 irregular pseudopores.

Besides *C. occlusa*, *C. australis* n. sp. and *C. buski* n. sp., three other species of *Cigclisula* have erect bilaminar colonies—*C. cautium*, *C. fissurata* and *C. fruticosa*. *Cigclisula cautium* is distinguished from *C. australis* n. sp. by the distribution and size of zooidal pseudopores (mainly marginal and larger, 0.021–0.048 mm diameter, vs uniformly spaced and smaller, 0.007–0.017 mm diameter, in *Cigclisula australis* n. sp.), texture of the frontal shield (smooth in *C. cautium*, minutely tubercular in *C. australis* n. sp.), shape of primary orifice (longer than wide in *C. cautium*, subcircular in *C. australis* n. sp.), and shape of interzooidal avicularia (rostrum foot-shaped in *C. cautium*, spatulate in *C. australis* n. sp.). *Cigclisula fissurata* differs in the distribution of frontal pseudopores (uniform in *C. australis* n. sp., marginal in *C. fissurata*), frontal and interzooidal avicularia (present in *C. australis* n. sp., absent in *C. fissurata*) and number of ectooecial pseudopores (7–18 in *C. australis* n. sp., 2–5 in *C.*

fissurata). *Cigclisula fruticosa* is distinguished by the irregularly punctured frontal shield (pseudopores of *C. australis* n. sp. are uniformly distributed), short U-shaped median sinus (absent in *C. australis* n. sp.), secondary orifice with low blunt processes (non-tubercular in *C. australis* n. sp.) and ectooecium with about six pseudopores (7–18 in *C. australis* n. sp.).

Distribution. Pacific: Australia (Queensland).

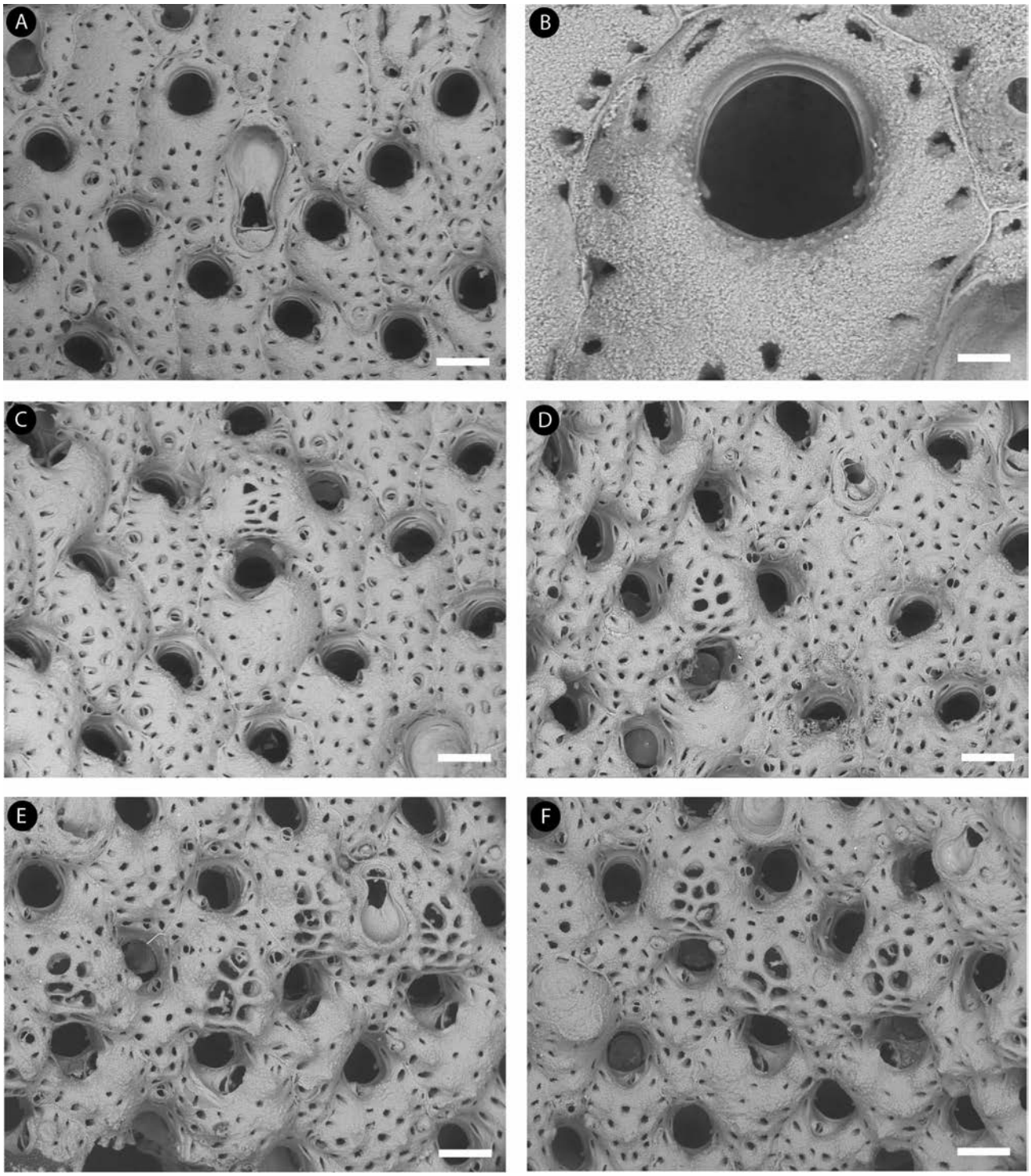

FIGURE 12. *Cigclisula australis* n. sp. **A–F,** USNM 8894, holotype, Australia. **A,** group of zooids and spatulate interzooidal avicularia. **B,** primary orifice. **C,** ovicelled zooid. **D, E, F,** ovicelled zooids with suboral avicularia and an associated spatulate interzooidal avicularium. Scale bars: A, C, D, E, F = 200 μm; B = 50 μm.

***Cigclisula buski* n. sp.**
(Figs 13–14, Table 3)

Escharoides occlusa Busk, 1884: 150 (in part), pl. 21, fig. 8 (?in part). [Cape York, Australia]
Lepralia occlusa: Kirkpatrick 1890: 604, 612 (?in part). [Torres Straits]
Lepralia occlusa: Waters 1909: 152 (in part), pl. 13, fig. 15; pl. 14, figs 1–9, 13 (?in part). [Cape York, Australia]
Cigclisula occlusa: Hastings 1932: p. 43 (in part), text-fig. 13 (?in part). [Australia]
? *Myriozoum occlusum*: Marcus 1921: 20, pl. 1, fig. 8; pl. 2, figs 1–2. [Australia]

Material examined. *Holotype:* NHMUK 1887.12.9.593, '*Escharoides occlusa'*, G. Busk coll., Challenger Expedition, Stn 186, coral mud, off Cape York, Australia, 10°30' S, 142°18' W, ex. Dundee coll. *Paratypes:* NHMUK 1963.2.12.197; NHMUK 1899.7.1.2139; NHMUK 1899.7.1.4487; NHMUK 1887.12.9.591; NHMUK 1994.1.8.282; NHMUK 1994.1.8.283; USNM 9231 [exchange from NHMUK], same data as holotype.

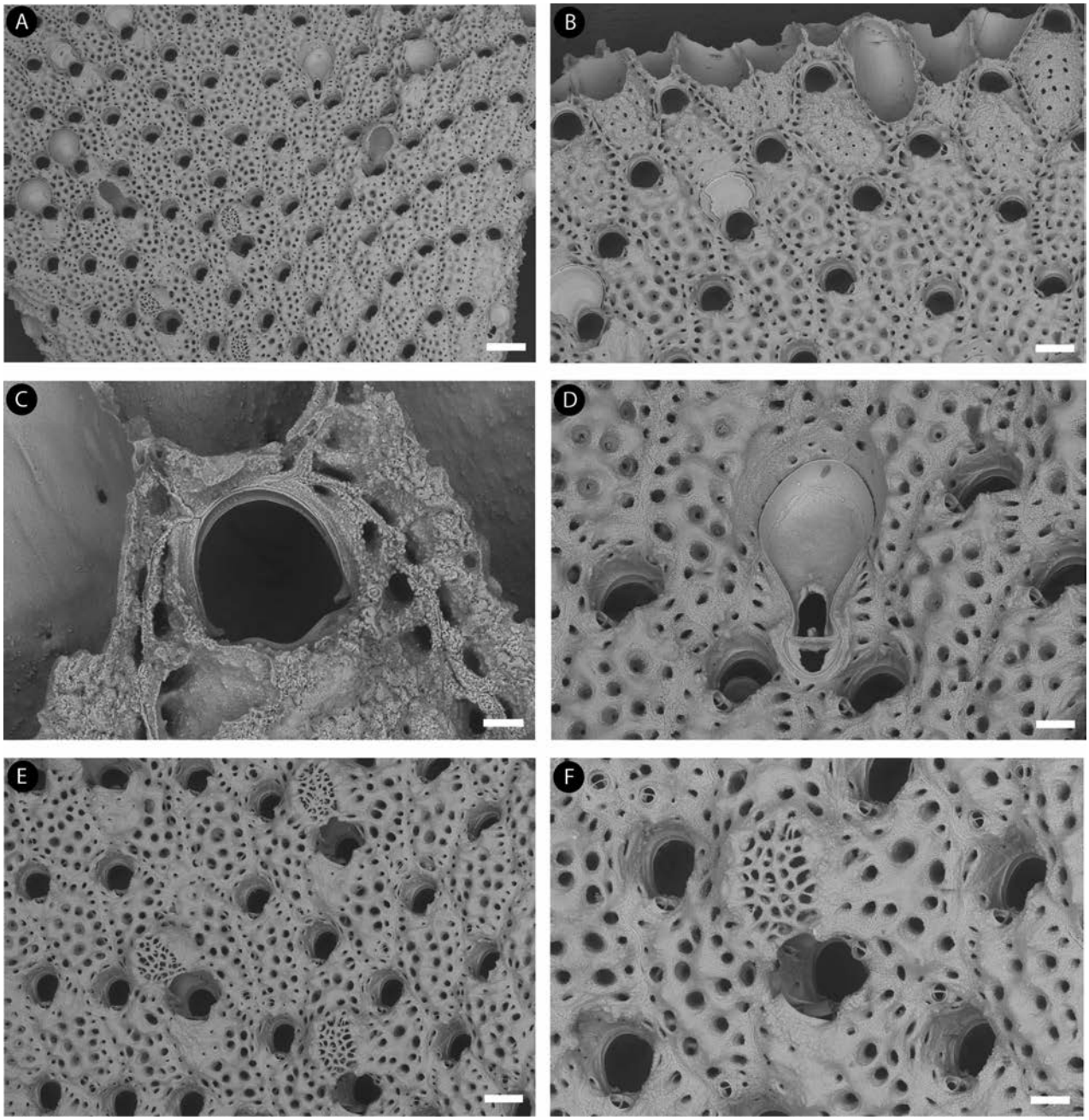

FIGURE 13. *Cigclisula buski* n. sp. **A–F,** NHMUK 1887.12.9.593, holotype, Australia. **A,** erect bilaminar colony. **B,** zooids at growing edge of branch. **C,** primary orifice. **D,** interzooidal spatulate avicularium. **E,** ovicelled zooids. **F,** close-up of ovicelled zooid. Scale bars: A = 400 μm; B, E = 200 μm; C = 400 μm; D, F = 100 μm.

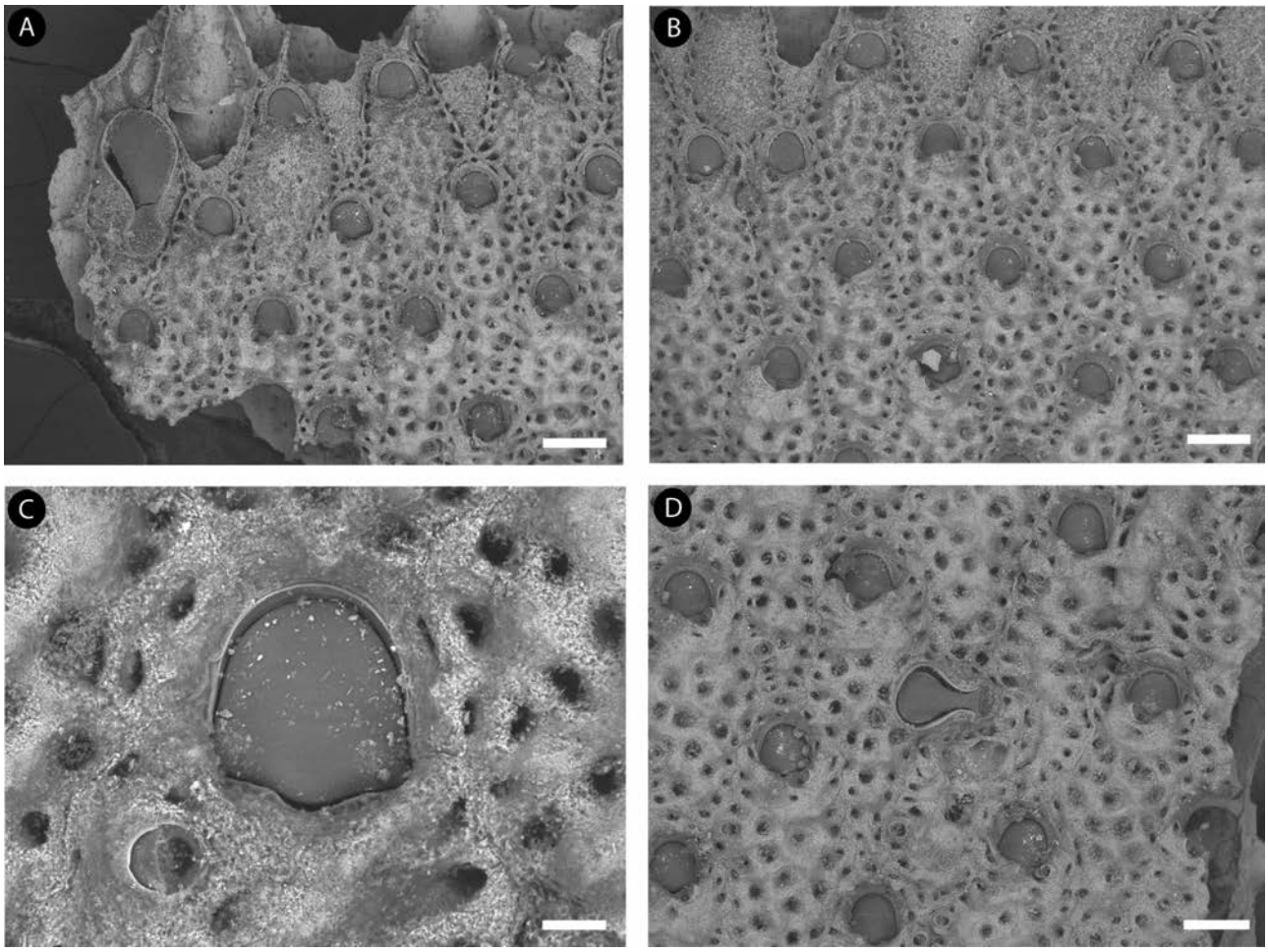

FIGURE 14. *Cigclisula buski* n. sp. **A–D,** USNM 9231, paratype, Australia. **A,** zooids at growing edge of branch, including a spatulate interzooidal avicularium. **B,** group of zooids. **C,** primary orifice and suboral avicularium. **D,** group of zooids, interzooidal spatulate avicularia and elliptical frontal avicularia. Scale bars: A, B = 500 μm; C = 100 μm; D, E, F = 200 μm.

Type locality. Cape York, Australia.

Diagnosis. Erect, frontal shield with small protuberances; usually 1–2 frontal avicularia; interzooidal avicularia of 2 sizes, with oval foramen; ooecium rugose with 38–50 irregular pseudopores.

Etymology. Honorific for George Busk (1807–1886), the notable bryozoologist who studied the original material.

Description. Colony erect, bilaminar, branching. Zooids hexagonal, longer than wide, delimited by slightly raised lateral walls. Frontal shield thickly calcified, with small protuberances, uniformly punctured by 10–46 pseudopores. Primary orifice small relative to frontal shield, somewhat hoof-shaped, as long as wide, sunken, with high-arched anter; condyles in proximolateral corners delimit a very weakly defined poster with shallow median sinus. Secondary orifice raised, non-tubercular, subcircular. Suboral avicularium elliptical, laterally placed and distally directed, of 2 sizes, 1 small (0.046–0.071 mm long), the other double-sized, commonly associated with ovicelled zooids and zooids in center of branches. Frontal avicularia small, common, elliptical, 1–2 per zooid, placed at zooidal margins. Interzooidal avicularia of 2 sizes, 1 small the other double-sized; both longer than wide, with broadly spatulate mandible; rostrum with rounded proximal edge, median constriction distinct and distal edge concave; calcified palate occupying more than half rostral length, with oval foramen. Ooecium subglobose, slightly prominent; with small protuberances; ectooecium with longitudinal band of 38–50 irregular pseudopores.

Remarks. Along with *C. australis* n. sp., this species comprised part of the material described as *Escharoides occlusa* by Busk (1884). Re-examination of the type material led us to reassign them to three different species (see Remarks under *C. occlusa* and *C. australis* n. sp.).

Cigclisula buski n. sp. is characterized by the frontal shield and ooecium with small protuberances, two sizes of interzooidal spatulate avicularia, both with an oval foramen, and an ectooecium with a longitudinal band of 28–50 irregular pseudopores.

Cigclisula buski n. sp. resembles *C. cautium*, *C. fruticosa* and *C. fissurata* in having erect bilaminar colonies, but differs in possessing suboral avicularia of two sizes, a frontal shield with 23–46 pseudopores and ectooecium with 38–50 pseudopores. The species also differs from *C. fissurata* in the distribution of frontal pseudopores (uniform in *C. buski* n. sp., marginal in *C. fissurata*) and frontal and interzooidal avicularia (absent in *C. fissurata*). *Cigclisula fruticosa* differs in the distribution of frontal pseudopores (uniform in *C. buski* n. sp., irregular in *C. fruticosa*), shape of primary orifice (subelliptical in *C. buski* n. sp., an elongate D shape with a short U-shaped median sinus in *C. fruticosa*) and secondary orifice (non-tubercular in *C. buski* n. sp. and with blunt processes in *C. fruticosa*).

Distribution. Pacific: Australia (Queensland and Torres Straits).

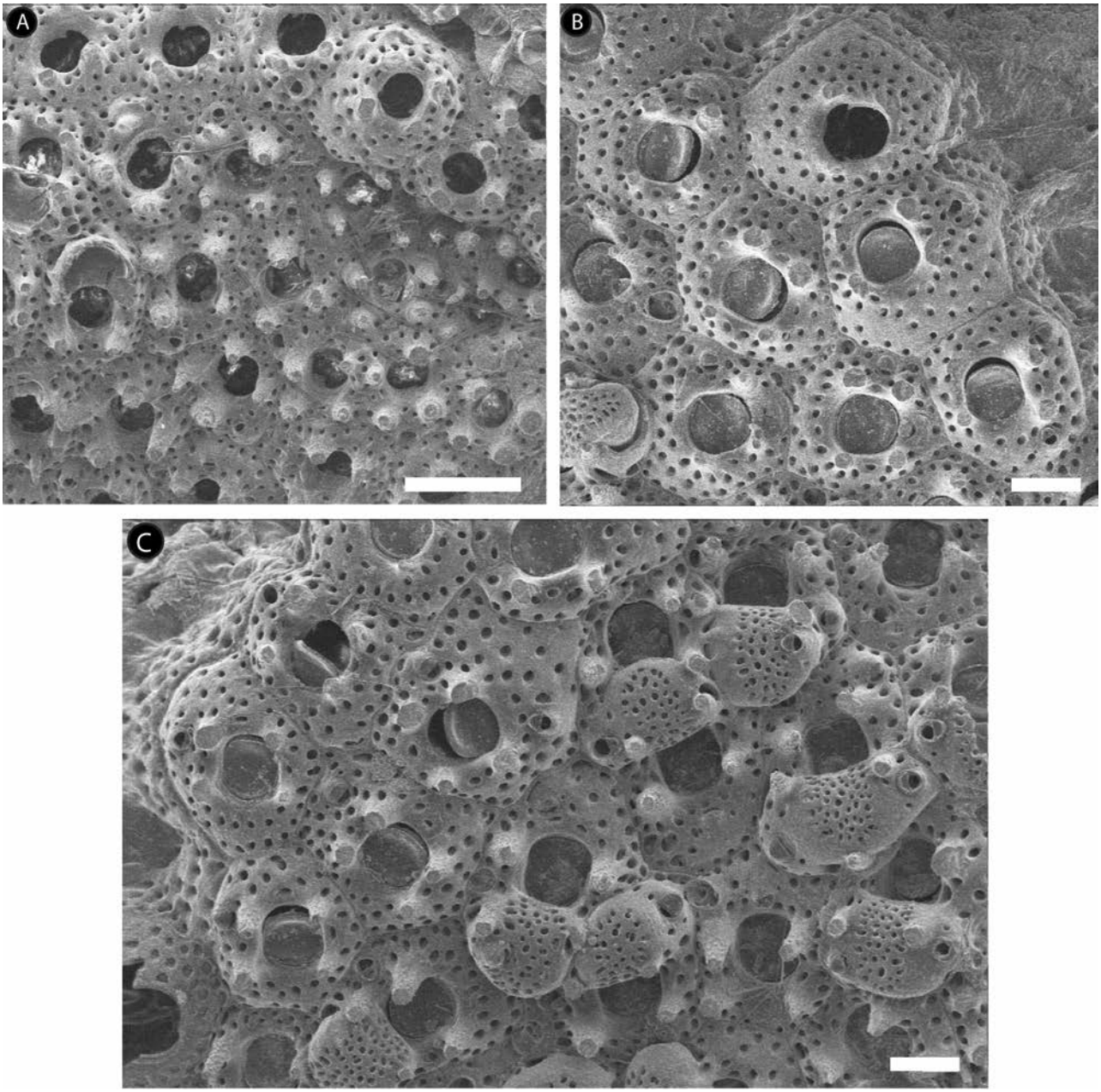

FIGURE 15. *Cigclisula fistulosa* n. sp. **A,** USNM 603768, paratype, Panama; **B, C,** USNM 603767, holotype, Panama. **A,** zooids at colony center. **B,** group of zooids and primary orifice. **C,** ovicelled zooids and elliptical frontal avicularia. Scale bars: A = 500 μm; B, C = 100 μm.

***Cigclisula fistulosa* n. sp.**

(Fig. 15, Table 4)

Material examined. *Holotype:* USNM 603767, CHE593B, Atlantic coast of Panama. *Paratype:* USNM 603768, CHE622, Atlantic coast of Panama.

Diagnosis. Encrusting, frontal shield uniformly punctured by 30–60 pseudopores; secondary orifice surrounded by 4 to 5 solid tubercles; frontal avicularia large, 0.057–0.082 mm long, 0.048–0.070 mm wide; ooecium with 1–3 tubercles and 1–2 avicularia, ectooecium with longitudinal band of 32–55 irregular pseudopores.

Etymology. From latin *fistulosus,* porous, alluding to the uniformly punctured frontal shield.

Description. Colony encrusting, uni- to multilaminar. Zooids hexagonal, becoming polygonal with increasing calcification, as long as wide, delimited by distinct grooves. Frontal shield thickly calcified, uniformly punctured by 30–60 pseudopores, smooth. Primary orifice large relative to area of frontal shield, almost centered, subcampanuliform, longer than wide, sunken, with arcuate anter and slightly broader poster separated by 2 down-curved condyles at about one third orifice length. Secondary orifice surrounded by 4–5 (often 4) solid tubercles. Suboral avicularium absent. Frontal avicularia large (0.057–0.082 mm long, 0.048–0.070 mm wide), elliptical, single (rarely 2), placed at proximal margin of zooid. Ooecium somewhat elevated, wider than long, inclined to zooid surface, often bearing 1–3 tubercles and 1–2 avicularia; ectooecium with longitudinal band of 32–55 irregular pseudopores.

Remarks. *Cigclisula fistulosa* n. sp. was previously attributed to *Cigclisula turrita* (as *Trematooecia*). The two species are distinguished, however, by the frontal shield (irregularly punctured in *C. turrita* and uniformly punctured in *C. fistulosa* n. sp.), autozooid size (larger in *C. turrita*: 0.454–0.816 mm long, 0.506–0.858 mm wide; cf. *C. fistulosa* n. sp.: 0.296–0.699 mm long, 0.343–0.607 mm wide), interzooidal avicularia (present only in *C. turrita*), and the number of ectooecial pseudopores (25–38 in *C. turrita*, 32–55 in *C. fistulosa* n. sp.).

Cigclisula fistulosa n. sp. resembles *C. psammophila* and *C. perforata* n. sp. in having encrusting colonies, solid tubercles around the secondary orifice and no interzooidal avicularia, but differs in having 30–60 pseudopores in the frontal shield, ooecia with 1–3 tubercles and 1–2 avicularia, and ectooecium with 32–55 pseudopores. Also, *C. fistulosa* n. sp. has a small primary orifice and ovicells and larger frontal avicularia than in *C. perforata* n. sp. (Table 2).

Distribution. Atlantic: Panama.

TABLE 4. Morphometric data for *Cigclisula* species studied (in mm).

	C. fistulosa	***C. osburni***	***C. perforata***	***C. winstonae***
	Panama[1]	Mexico[2]	Panama[3]	Belize[4]
Lz	10	10	6	10
Mean (SD)	0.489 (0.130)	0.572 (0.047)	0.576 (0.052)	0.493 (0.048)
Range	0.296–0.699	0.490–0.633	0.525–0.647	0.410–0.568
lz	10	10	6	10
Mean (SD)	0.478 (0.075)	0.518 (0.043)	0.549 (0.079)	0.495 (0.086)
Range	0.343–0.607	0.427–0.686	0.490–0.633	0.316–0.585
Dp	10	10	10	10
Mean (SD)	0.018 (0.009)	0.019 (0.002)	0.012 (0.003)	0.015 (0.004)
Range	0.007–0.034	0.016–0.023	0.008–0.019	0.008–0.022
Lo	10	10	6	10
Mean (SD)	0.188 (0.012)	0.187 (0.009)	0.224 (0.011)	0.188 (0.011)
Range	0.174–0.215	0.173–0.207	0.212–0.240	0.168–0.206
lo	10	10	6	10
Mean (SD)	0.165 (0.010)	0.167 (0.009)	0.170 (0.006)	0.169 (0.011)
Range	0.149–0.180	0.153–0.188	0.160–0.178	0.156–0.191
Lavs	-	-	-	-

.....continued on the next page

TABLE 4. (Continued)

	C. fistulosa Panama[1]	*C. osburni* Mexico[2]	*C. perforata* Panama[3]	*C. winstonae* Belize[4]
Mean (SD)	-	-	-	-
Range	-	-	-	-
lavs	-	-	-	-
Mean (SD)	-	-	-	-
Range	-	-	-	-
Lavi	-	-	-	6
Mean (SD)	-	-	-	0.150 (0.027)
Range	-	-	-	0.121–0.187
lavi	-	-	-	6
Mean (SD)	-	-	-	0.097 (0.015)
Range	-	-	-	0.082–0.123
Lavf	10	5	3	10
Mean (SD)	0.070 (0.009)	0.050 (0.004)	0.054 (0.005)	0.046 (0.007)
Range	0.057–0.082	0.046–0.057	0.048–0.059	0.036–0.060
lavf	10	5	3	10
Mean (SD)	0.059 (0.008)	0.037 (0.007)	0.045 (0.002)	0.039 (0.006)
Range	0.048–0.070	0.028–0.045	0.044–0.048	0.032–0.050
Lov	8	1	3	7
Mean (SD)	0.261 (0.016)	0.349	0.330 (0.006)	0.491 (0.033)
Range	0.233–0.285	-	0.324–0.336	0.431–0.529
lov	8	1	3	-
Mean (SD)	0.309 (0.041)	0.373	0.337 (0.014)	-
Range	0.246–0.383	-	0.323–0.352	-
Dovp	25	5	25	25
Mean (SD)	0.011 (0.003)	0.021 (0.009)	0.008 (0.002)	0.033 (0.010)
Range	0.006–0.021	0.010–0.031	0.005–0.012	0.020–0.056

[1] USNM 603767, Atlantic coast of Panama. [2] USNM 603769, Lower California, Mexico. [3] USNM 603764, Atlantic coast of Panama. [4] USNM 376607, Carrie Bay, Belize.

Cigclisula osburni n. sp.

(Fig. 16, Table 4)

Trematooecia hexagonalis: Osburn 1952: 503 (part), pl. 60, fig. 7. [Gulf of California and Mexico]
Not *Holoporella hexagonalis* Canu & Bassler, 1930a: 38, pl. 7, fig. 1. [Galápagos Islands]
Trematooecia hexagonalis: Soule 1961: 59. [California]
Trematooecia hexagonalis: Soule & Soule 1964: 40. [Isla Conchas, California]

Material examined. *Holotype:* USNM 603769, '*Trematooecia hexagonalis'*, Hancock Stn 229, San Jose del Cabo, Baja California, Mexico, 149 m. *Additional specimens:* USNM 603770, '*Trematooecia hexagonalis'*, Pacific coast of Panama.

Diagnosis. Encrusting, zooids with 1–2 rows of large marginal pores; ooecium tubercular and ectooecium with longitudinal band of 27–39 irregular pseudopores.

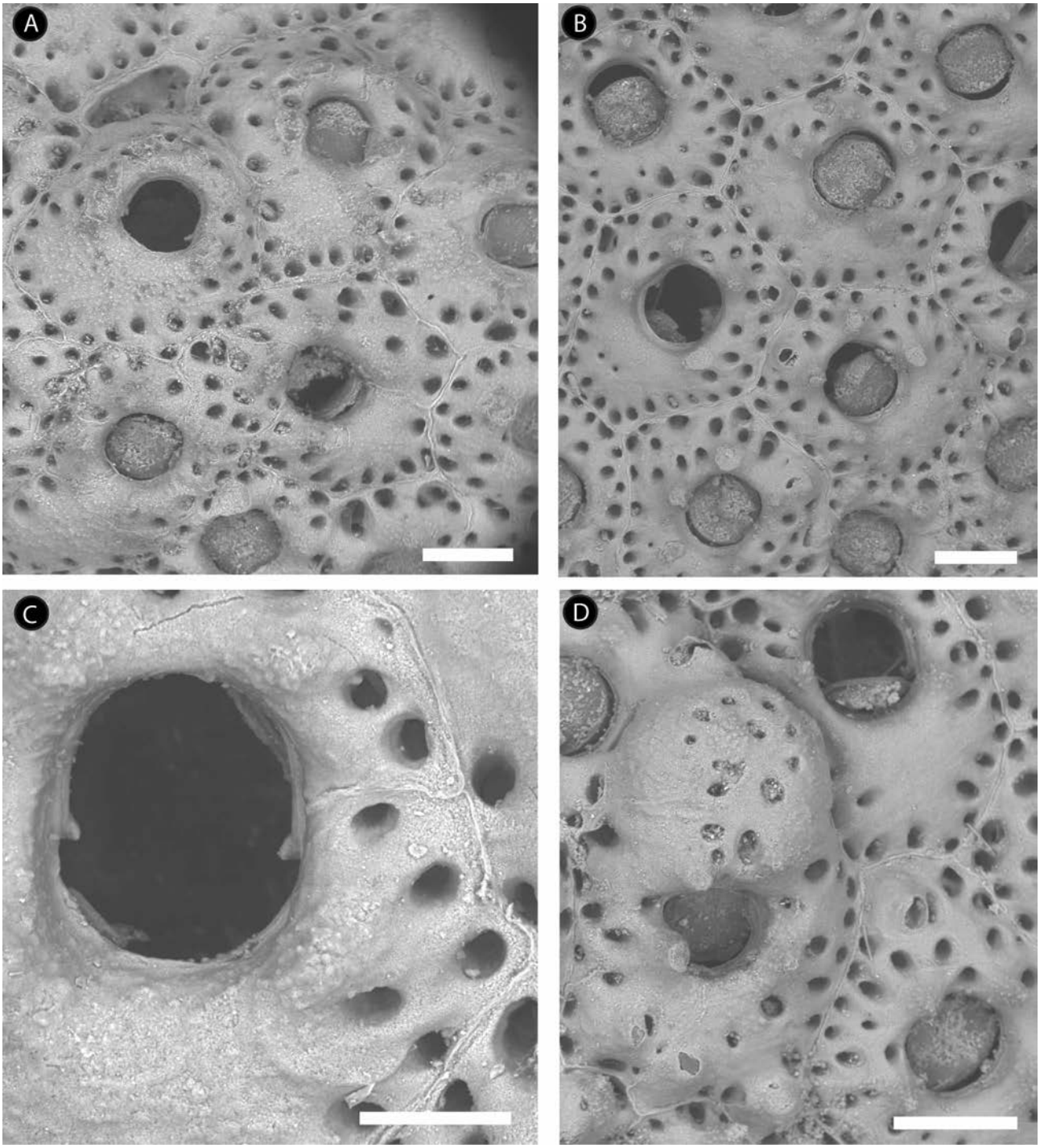

FIGURE 16. *Cigclisula osburni* n. sp. **A, C,** USNM 603769, holotype, Mexico. **A, B,** groups of zooids. **C,** primary orifice. **D,** ovicelled zooid. Scale bars: A, B = 200 µm; C = 100 µm; D = 200 µm.

Etymology. Named in recognition of the major contribution of Raymond Carroll Osburn (1872–1955) to bryozoan taxonomy.

Description. Colony encrusting, uni- to multilaminar. Zooids hexagonal to polygonal, as long as wide, delimited by slightly raised lateral walls. Frontal shield thickly calcified, with 1–2 rows of 20–40 marginal pseudopores and areolar pores, smooth. Primary orifice large relative to area of frontal shield, centered, subelliptical, longer than wide, sunken, with arcuate anter and deep semicircular poster separated by 2 down-curved condyles set nearly mid-length. Secondary orifice surrounded by 4–5 (usually 4) solid tapered tubercles. Suboral avicularium absent. Frontal avicularia small, elliptical, single, placed at zooidal margins. Ooecium subglobose, inclined to zooid surface, often tubercular; ectooecium with longitudinal band of 27–39 irregular pseudopores.

Remarks. *Cigclisula osburni* n. sp. was previously attributed to *Trematooecia hexagonalis* (see remarks under *C. porosa*), which it resembles in having encrusting colonies, a secondary orifice with solid tubercles and no interzooidal avicularia. Differences include zooid size (larger in *C. osburni* n. sp. than in *T. hexagonalis*), the number of frontal pseudopores (20–40 in *C. osburni* n. sp., 36–51 in *T. hexagonalis*) and the ectooecium (porous in *C. osburni* n. sp., with a U-shaped membranous area in *T. hexagonalis*).

Cigclisula osburni n. sp. resembles *C. psammophila*, *Cigclisula perforata* n. sp. and *Cigclisula fistulosa* n. sp. in having encrusting colonies, a secondary orifice with solid tubercles and no interzooidal avicularia, but differs in having 1–2 rows of 21–41 marginal pores and an ectooecium with a longitudinal band of 27–39 irregular pseudopores. The primary orifice of *C. osburni* n. sp. is shorter than in *C. perforata* n. sp. and its zooids and frontal pseudopores larger than in *C. fistulosa* n. sp. (Table 3).

Distribution. Eastern Pacific: California and Mexico.

***Cigclisula perforata* n. sp.**

(Fig. 17, Table 4)

Trematooecia hexagonalis: Cheetham *et al.* 1999: 177. [Atlantic coast of Panama]
Not *Holoporella hexagonalis* Canu & Bassler, 1930a: 38, pl. 7, fig. 1. [Galápagos Islands]

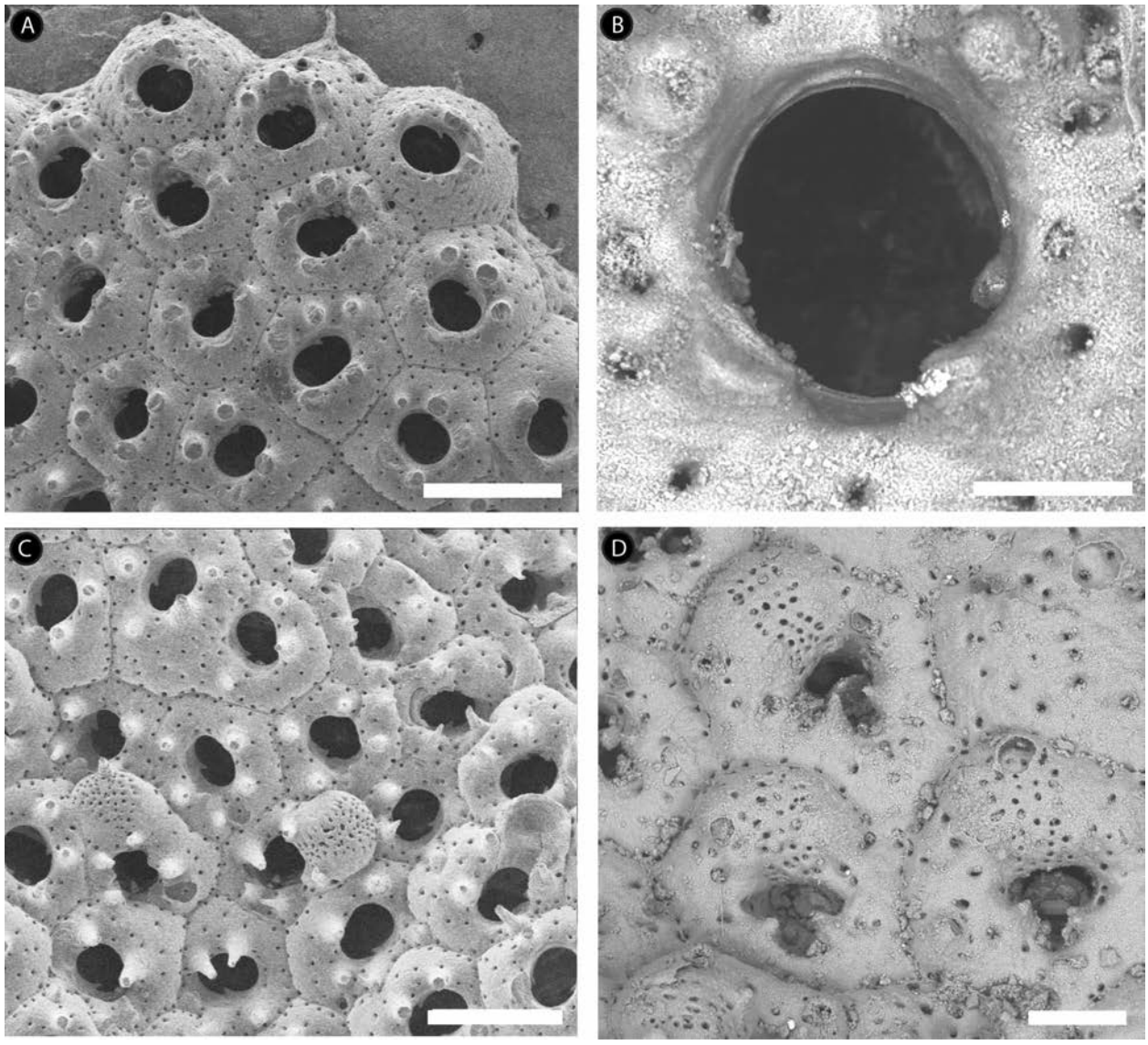

FIGURE 17. *Cigclisula perforata* n. sp. **A, C,** USNM 603764, holotype, Panama; **B, D,** USNM 603765, paratype, Panama. **A,** zooids at growing edge of colony. **B,** primary orifice. **C,** group of zooids, some ovicelled. **D,** ovicelled zooids and tiny elliptical frontal avicularia. Scale bars: A = 500 μm; B = 100 μm; C = 500 μm; D = 200 μm.

Material examined. *Holotype:* USNM 603764, '*Trematooecia hexagonalis'*, Recent, Atlantic coast of Panama. *Paratypes:* USNM 603765, '*Trematooecia hexagonalis'*, Recent, Atlantic coast of Panama; USNM 603766, '*Trematooecia turrita'*, Plio–Pleistocene, Bocas del Toro Group, Isla Colon, Panama.

Diagnosis. Encrusting, zooids with small pseudopores c. 0.006–0.018 mm diameter; primary orifice subcircular, only a little longer than wide, with triangular incurved condyles; ectooecium with longitudinal band of 27–80 irregular pseudopores.

Etymology. Latin *perforatus,* perforated, alluding to the numerous ovicellar pseudopores.

Description. Colony encrusting, uni- to multilaminar. Zooids hexagonal, becoming polygonal with growth, longer than wide, limited by distinct grooves. Frontal shield heavily calcified, irregularly punctured by 30–47 small (0.006–0.018 mm diameter) pseudopores, smooth. Primary orifice large relative to frontal shield, centered, subcircular, only a little longer than wide, sunken, with arcuate anter and deeply concave poster with shallow median sinus, 2 incurved condyles set about one third orifice length. Secondary orifice surrounded by 4–5 (usually 4) solid tubercles. Suboral avicularium absent. Frontal avicularia small, elliptical, single (rarely 2), at proximal margin of zooid. Ooecium moderately prominent, inclined to zooid surface, sometimes bearing tubercles; ectooecium with longitudinal band of 27–80 irregular pseudopores.

Remarks. This species was previously attributed to *Trematooecia hexagonalis* Cheetham *et al.* (1999). Like *Cigclisula perforata* n. sp., *T. hexagonalis* has encrusting colonies with hexagonal to polygonal zooids, but they are readily distinguished by the details of the ooecium (ectooecium with slit-like membranous window in *T. hexagonalis*, irregular pseudopores in *C. perforata* n. sp.). Additional species of *Cigclisula* with encrusting colonies and tubercles around the secondary orifice are *C. porosa*, *C. psammophila*, *C. turrita* and *C. winstonae* n. sp. *Cigclisula perforata* n. sp. is distinguished from *C. porosa* by the distribution and diameter of frontal pseudopores (regularly spaced and large, 0.015–0.032 mm diameter in *C. porosa*; mainly marginal and small, about 0.008–0.0019 mm diameter in *C. perforata* n. sp.) and presence of tubercles around the secondary orifice (absent in *C. porosa* and present in *C. perforata* n. sp.). *Cigclisula psammophila* differs in its small zooids, immersed ovicells and in the absence of avicularia. *Cigclisula turrita* differs from *C. perforata* n. sp. in having interzooidal avicularia and ooecia with 25–38 ectooecial pseudopores. In *C. winstonae* n. sp. the ooecium is readily distinguished from those of *C. perforata* n. sp. in having 3–9 large ectooecial pseudopores.

Distribution. Plio/Pleistocene (Isla Colon, Caribbean) to Recent (Atlantic: Panama).

Cigclisula winstonae n. sp.

(Fig. 18, Table 4)

Trematooecia turrita: Winston 1984: 32, figs 67–68. [Belize]
Not *Lepralia turrita* Smitt, 1873: 66, pl. 6, figs 226–228. [Florida]
Trematooecia turrita: Winston & Woollacott 2009: 285, fig. 33. [Barbados]

Material examined. *Holotype:* USNM 376607, '*Trematooecia turrita'*, J.E. Winston det., 1984, Carrie Bow Cay, Belize.

Diagnosis. Encrusting *Cigclisula* with zooids limited by distinct wavy grooves; 2 or more frontal avicularia per zooid; ooecium immersed, ectooecium with longitudinal band of 3–9 irregular large (0.020–0.056 mm diameter) pseudopores.

Etymology. Named after Judith Ellen Winston, for her contribution to bryozoology.

Description. Colony encrusting, uni- to multilaminar forming small mounds. Zooids irregularly polygonal, as long as wide, limited by distinct wavy grooves. Frontal shield thickly calcified, irregularly punctured by 23–46 pores. Primary orifice large relative to frontal shield, centered, oval, longer than wide, sunken, with arcuate anter and slightly narrower concave poster, separated by 2 down-curved condyles. Secondary orifice frequently surrounded by 4–5 (usually 4) long solid tubercles. Suboral avicularium absent. Frontal avicularia small, elliptical, usually 2–3 per zooid, on frontal shield between tubercles near orifice; serrated distal rostral margins. Interzooidal avicularia smaller than zooids, short, rostrum spatulate, wider than long, proximal edge rounded and distal edge concave; calcified palate occupying less than half rostral length, with rounded foramen. Ooecium fully immersed; ectooecium with longitudinal band of about 3–9 irregular large (0.020–0.056 mm diameter) pseudopores.

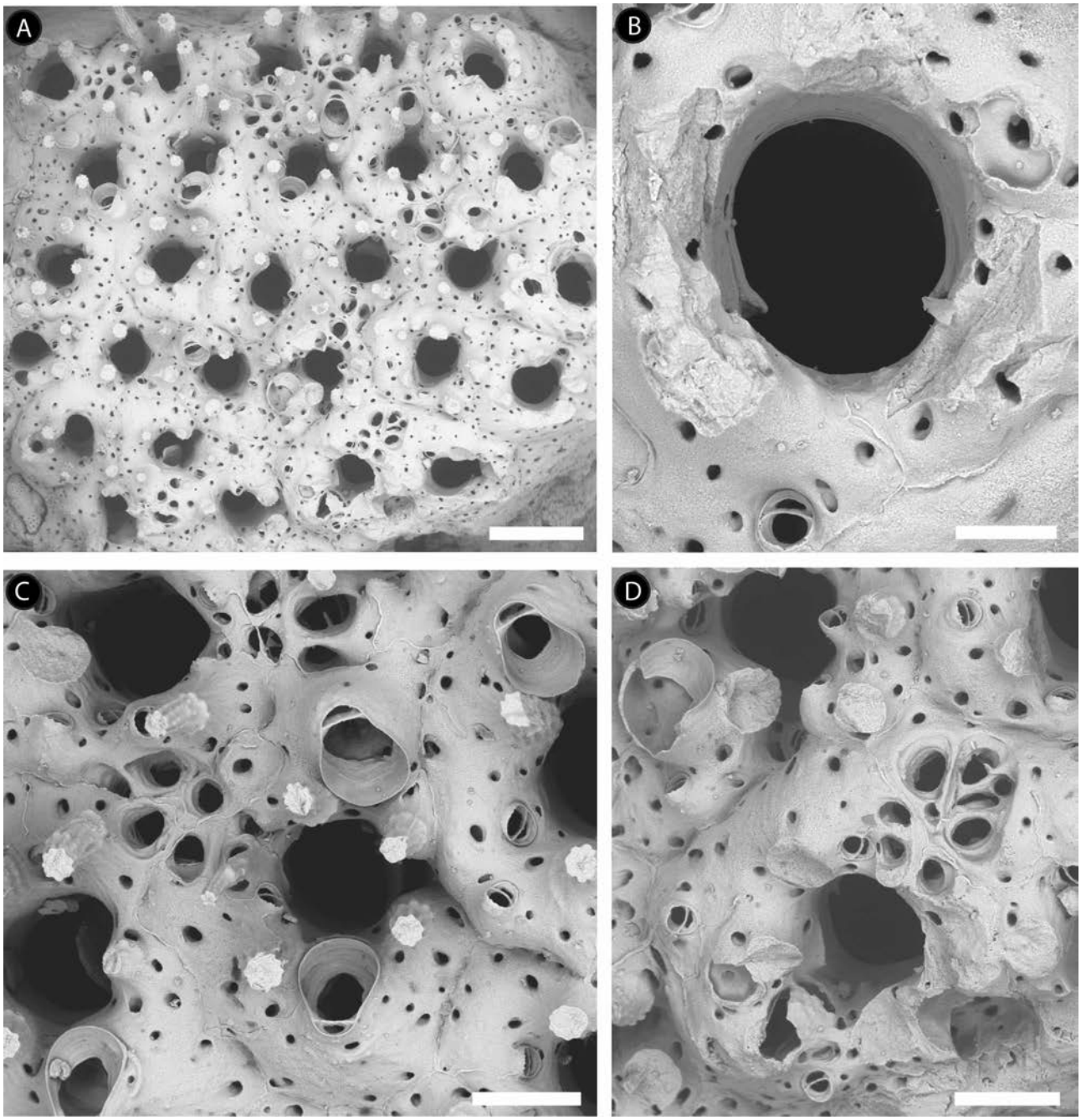

FIGURE 18. *Cigclisula winstonae* n. sp. **A–D,** USNM 376607, holotype, Belize. **A,** encrusting colony. **B,** primary orifice and elliptical frontal avicularia. **C,** group of ovicelled zooids and short, spatulate interzooidal avicularia. **D,** ovicelled zooid. Scale bars: A = 500 μm; B =100 μm; C, D = 200 μm.

Remarks. Although identified as *Trematooecia turrita* (Winston 1984; Winston & Wollacott 2009), the morphology of the ooecium is strikingly different between *C. turrita* and *C. winstonae* n. sp. Whereas *C. turrita* has a prominent ovicell and ectooecium with a longitudinal band of 25–38 pseudopores, *C. winstonae* n. sp. has an immersed ovicell and ectooecium with a longitudinal band of 3–9 large pseudopores. The species also differ in the shape of the interzooidal avicularia—linguiform in *C. turrita*, spatulate in *C. winstonae* n. sp.

Cigclisula winstonae n. sp. and *C. psammophila* are the only species of *Cigclisula* with fully immersed ooecia. Both species are distinguished by zooid size and colony size (smaller and unilamellar in *C. psammophila*), frontal shield (irregularly punctured in *C. winstonae* n. sp., marginally punctured in *C. psammophila*) and frontal and interzooidal avicularia (present in *C. winstonae* n. sp., absent in *C. psammophila*).

Distribution. Caribbean: Belize and Barbados.

Genus *Trematooecia* Osburn, 1940

Type species. *Trematooecia aviculifera* (Canu & Bassler, 1923), now fixed under ICZN Article 70.3, misidentified as *Trematooecia turrita* (Smitt, 1873) in the original designation by Osburn (1940).

Diagnosis (revised). Colony encrusting, uni- to multilaminar or erect and bilaminar. Autozooids heavily calcified. Frontal wall with frontal pseudopores and marginal areolar pores. Primary orifice transversely D-shaped or hoof-shaped. Secondary orifice formed by raised, rounded tubercles often obscuring the primary orifice. Suboral avicularium often present, seated within peristome near primary orifice. Interzooidal and adventitious avicularia with complete crossbar. Ovicell acleithral, with coarse surface calcification, ectooecium with a single membranous frontal area.

Remarks. *Trematooecia* was erected by Osburn (1940) to accommodate *L. turrita* Smitt, 1873, designated type species, and *Trematooecia protecta* Osburn, 1940. Re-examination of the specimens studied by Osburn (1940) from Puerto Rico (Guanica Harbor, 9–32 m), Tortugas Island (20–27 m) and Curaçao (all USNM Acc. No. 208837), allow us to reassign these colonies as *T. aviculifera*, as suggested by Banta & Carson (1977) and Winston (2005). The main difference between *T. aviculifera* and *C. turrita* is the ectooecium, with a circular uncalcified area in *T. aviculifera* and a longitudinal band of irregular pseudopores in *C. turrita*. Other differences pertain to the condyles (absent in *T. aviculifera*, present in *C. turrita*) and frontal avicularia (absent in *T. aviculifera*, dimorphic in *C. turrita*), but these characters seem to be variable within both *Trematooecia* and *Cigclisula*.

Owing to the misidentification of *T. aviculifera* as *C. turrita*, some other species were subsequently incorrectly attributed to *Trematooecia*, hence the genus has included species with two different types of ectooecium: (i) with an uncalcified central area, characteristic of *Trematooecia*, and (ii) with a median band of pseudopores, typical of *Cigclisula*. Thus, some species previously assigned to *Cigclisula* are here reassigned to *Trematooecia*, viz. *Trematooecia arborescens* (Canu & Bassler, 1928) n. comb., *Trematooecia gemmea* (Winston & Woollacott, 2009) n. comb., *Trematooecia hexagonalis* (Canu & Bassler, 1930) and *Trematooecia verticalis* (Maplestone, 1910) n. comb.

Trematooecia aviculifera (Canu & Bassler, 1923)

(Figs 19–24, Table 5)

Holoporella turrita: Osburn 1914: 217. [Tortugas Island, Florida]
Not *Lepralia turrita* Smitt 1873: 66, pl. 6, figs 226–228. [Florida; =*Cigclisula turrita*, see above]
Holoporella aviculifera Canu & Bassler, 1923: pl. 46, fig. 2. [Pleistocene, Mount Hope, Panama Canal]
Holoporella turrita: Osburn 1927: 131. [Curaçao Island, Caribe]
Holoporella turrita: Canu & Bassler 1928a: 145, text-fig. 33C–D. [Gulf of Mexico]
Trematooecia turrita: Osburn 1940: 458, pl. 8, fig. 72. [Guanica Harbor, Puerto Rico; Tortugas Island, Florida; Curaçao Island, Caribe]
? *Trematooecia aviculifera*: Powell 1971: 773. [Margarita and. Galesta Island, Panama Canal]
Cigclisula aviculifera: Banta & Carson 1977: 402, fig. 4F. [Costa Rica, Caribe]
Trematooecia aviculifera: Winston 1984: 31, figs 65–66. [Florida, Caribe]
Trematooecia aviculifera: Winston 2005: 107, figs 298–303. [Florida, Caribe]

Material examined. *Holotype:* USNM 68709, *Holoporella aviculifera*, F. Canu & R. Bassler det., Pleistocene, Panama Canal. *Additional specimens:* USNM 603771, *Trematooecia turrita*, Jan Thielbaai, Curaçao, approx. 21 m; USNM 603772, *Trematooecia turrita*, R. Osburn det., 1908, Tortugas, Florida, 27 m; USNM 603773, Acc. No. 208837, *Trematooecia turrita*, R. Osburn det., 1915, off Guanica Harbor, Puerto Rico, 55 m; USNM 603774, *Trematooecia turrita*, R. Osburn det., 1920, Curaçao Bay; USNM 376606, *Trematooecia aviculifera*, Carrie Bow Cay, Belize; USNM 603775, *Trematooecia aviculifera*, Belize, Carrie Bow Cay, CBC 14.5.75–1, 14–38 m, B. Spracklin Coll; USNM 603776, *Trematooecia aviculifera*, Curaçao; USNM 603777, *Trematooecia aviculifera*, Belize, Fisherman's Cay; USNM 603778, *Trematooecia aviculifera*, Saint Georges's Cay, Belize; USNM 603782, CHE 618, *Trematooecia aviculifera*, Panama; USNM 603284, T.a. 17, *Trematooecia aviculifera*, J. Sanner det., Panama; USNM 603285, T.a. 8, *Trematooecia aviculifera*, J. Sanner det., Panama; USNM 603286, T.a. 3 and 4, *Trematooecia aviculifera*, J. Sanner det., Panama.

Description. Colony encrusting, uni- to multilaminar, the latter forming forming large mounds. Skeleton red. Zooids of initial layer subrectangular, those from frontally budded layers irregularly polygonal, longer than wide, limited by slightly raised lateral walls. Frontal shield heavily calcified, marginally punctured by 7–14 pseudopores. Primary orifice small relative to frontal shield, transversely D-shaped, wider than long, sunken, with arcuate anter and straight or weakly convex poster. No condyles. Secondary orifice surrounded by 4–6 (usually 4) whitish solid

tubercles. Suboral elliptical avicularium laterally orientated. Interzooidal avicularium large, wider than long, rostrum obovate; calcified palate occupies more than half rostral length; foramen rounded. Ooecium subglobose, initially seen as horizontal on zooid surface before becoming partly immersed in secondary calcification, wider than long; ectooecium with frontal semicircular membranous area.

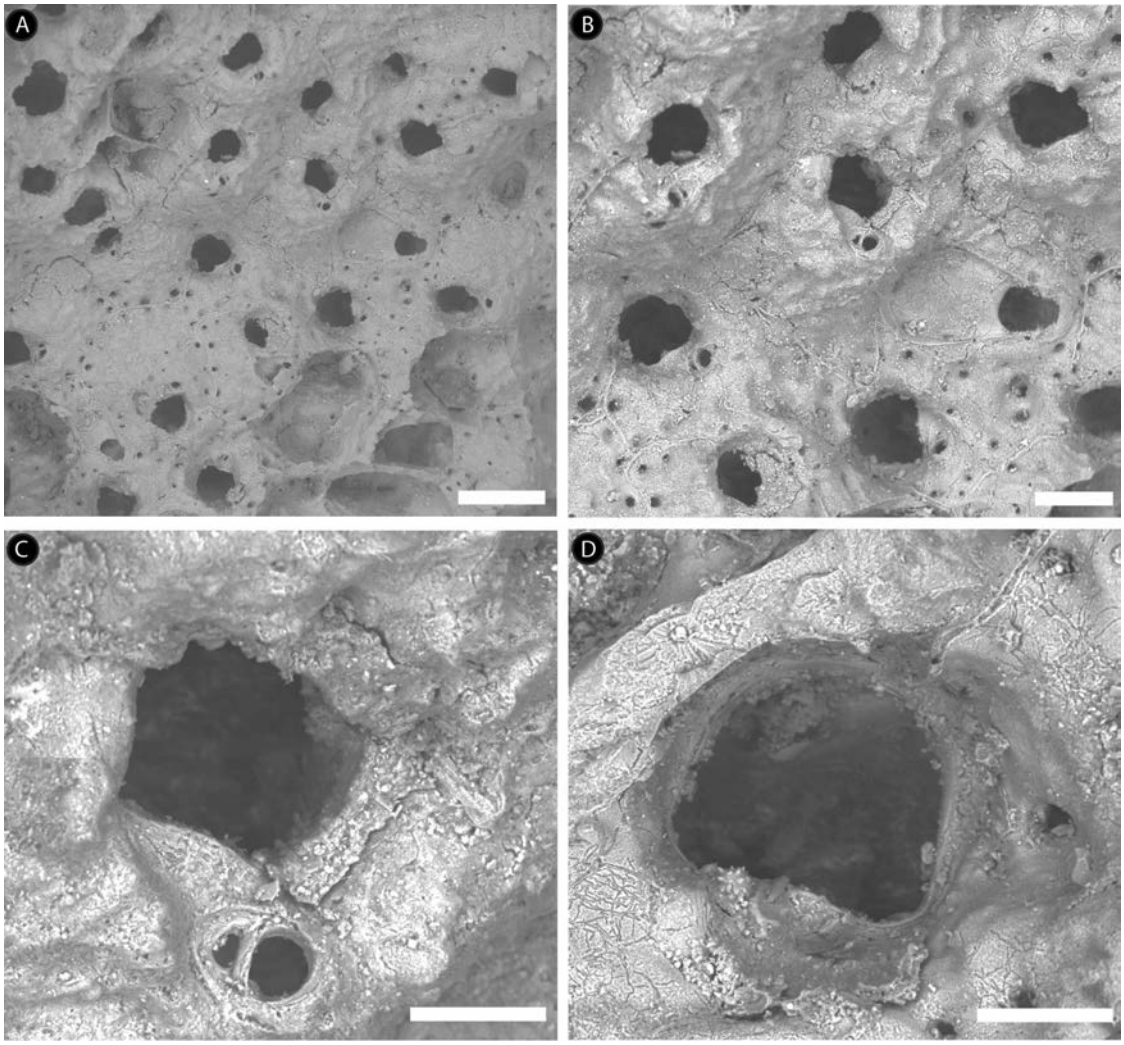

FIGURE 19. *Trematooecia aviculifera* (Canu & Bassler, 1923). **A–D,** USNM 68709, holotype, Panama Canal. **A,** encrusting colony. **B,** group of zooids and interzooidal avicularium. **C,** primary orifice and suboral avicularium. **D,** primary orifice. Scale bars: A = 500 µm; B = 200 µm; C, D = 100 µm.

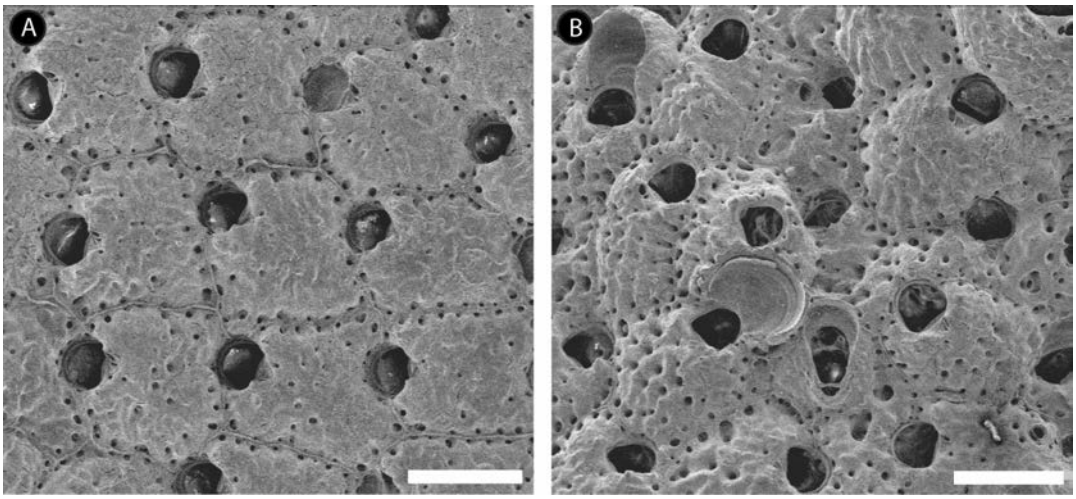

FIGURE 20. *Trematooecia aviculifera* (Canu & Bassler, 1923). A–D, USNM 603782, CHE 618, Panama. **A,** zooids at growing edge of colony. **B,** group of zooids with broken ovicells and interzooidal avicularium. Scale bars: A, B = 500 µm.

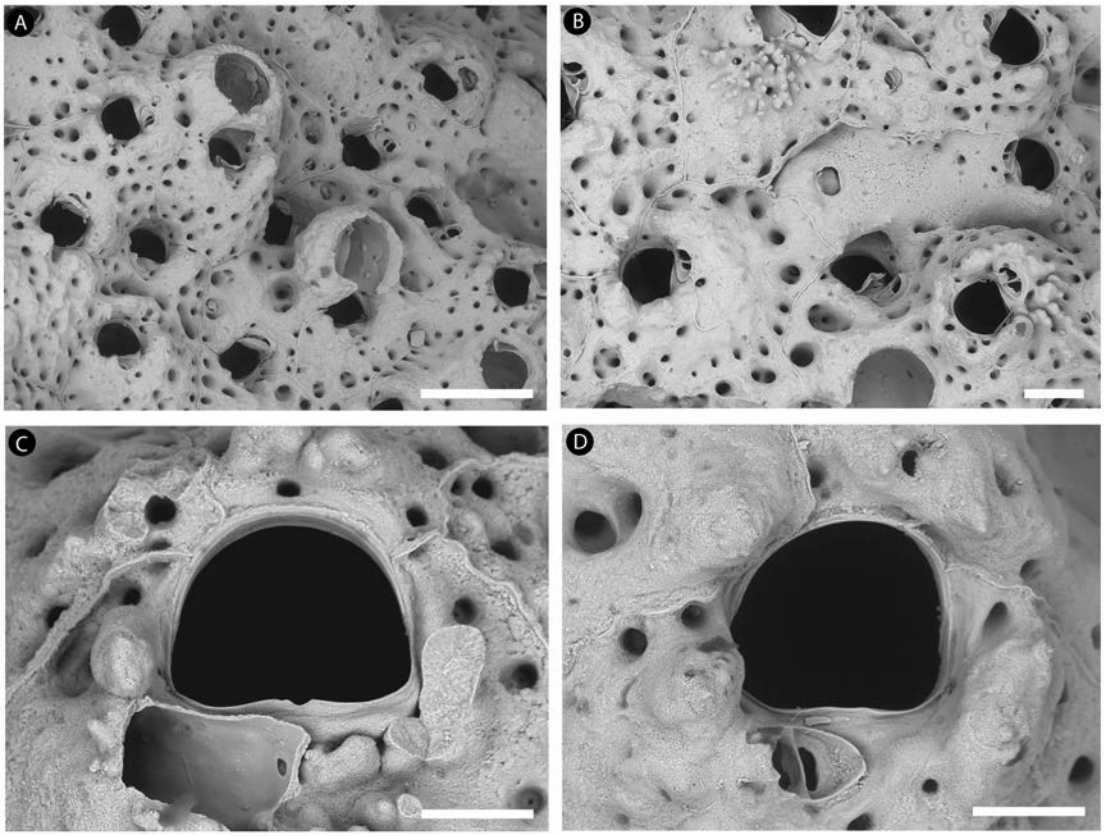

FIGURE 21. *Trematooecia aviculifera* (Canu & Bassler, 1923). **A–D,** USNM 376606, Panama. **A, B,** group of zooids and ovicelled zooids. **C,** primary orifice. **D,** primary orifice and suboral avicularium. Scale bars: A = 500 μm; B = 200 μm; C, D = 100 μm.

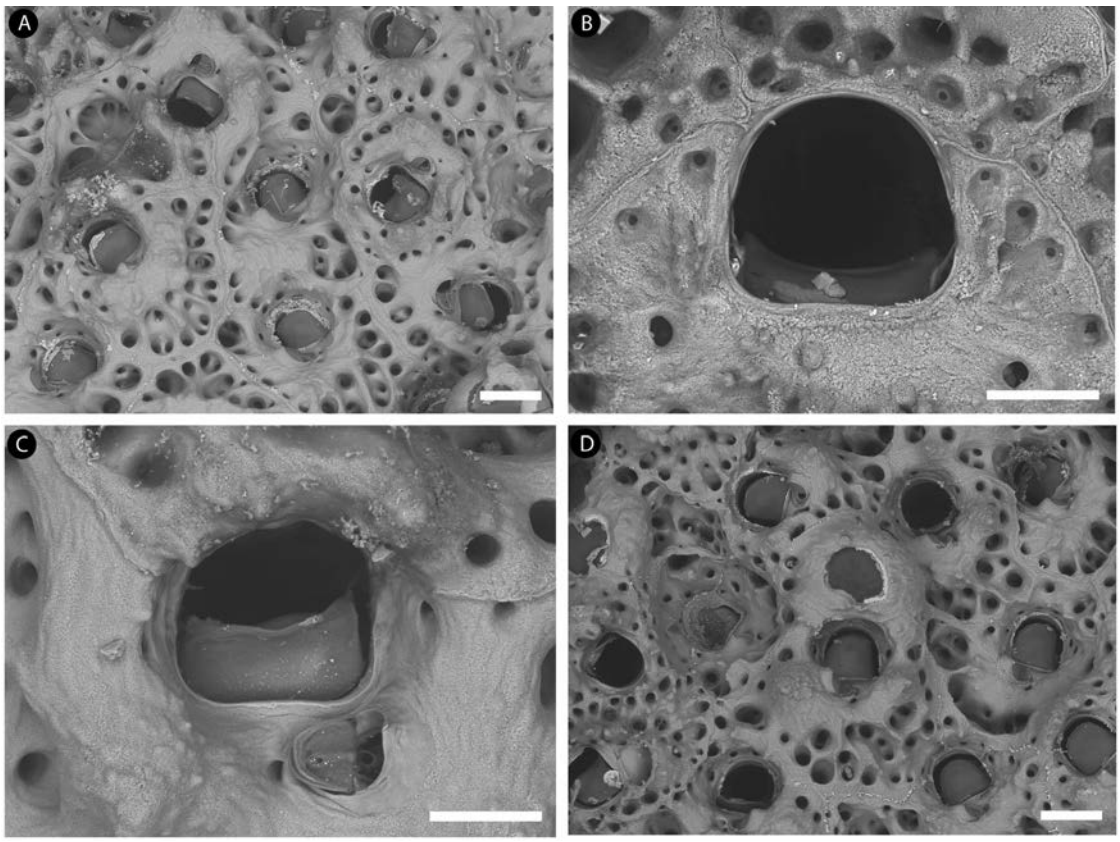

FIGURE 22. *Trematooecia aviculifera* (Canu & Bassler, 1923). **A–D,** USNM 603774, Curaçao. **A,** group of zooids. **B,** primary orifice. **C,** primary orifice and suboral avicularium. **D,** ovicelled zooid. Scale bars: A = 200 μm; B, C = 100 μm; D = 200 μm.

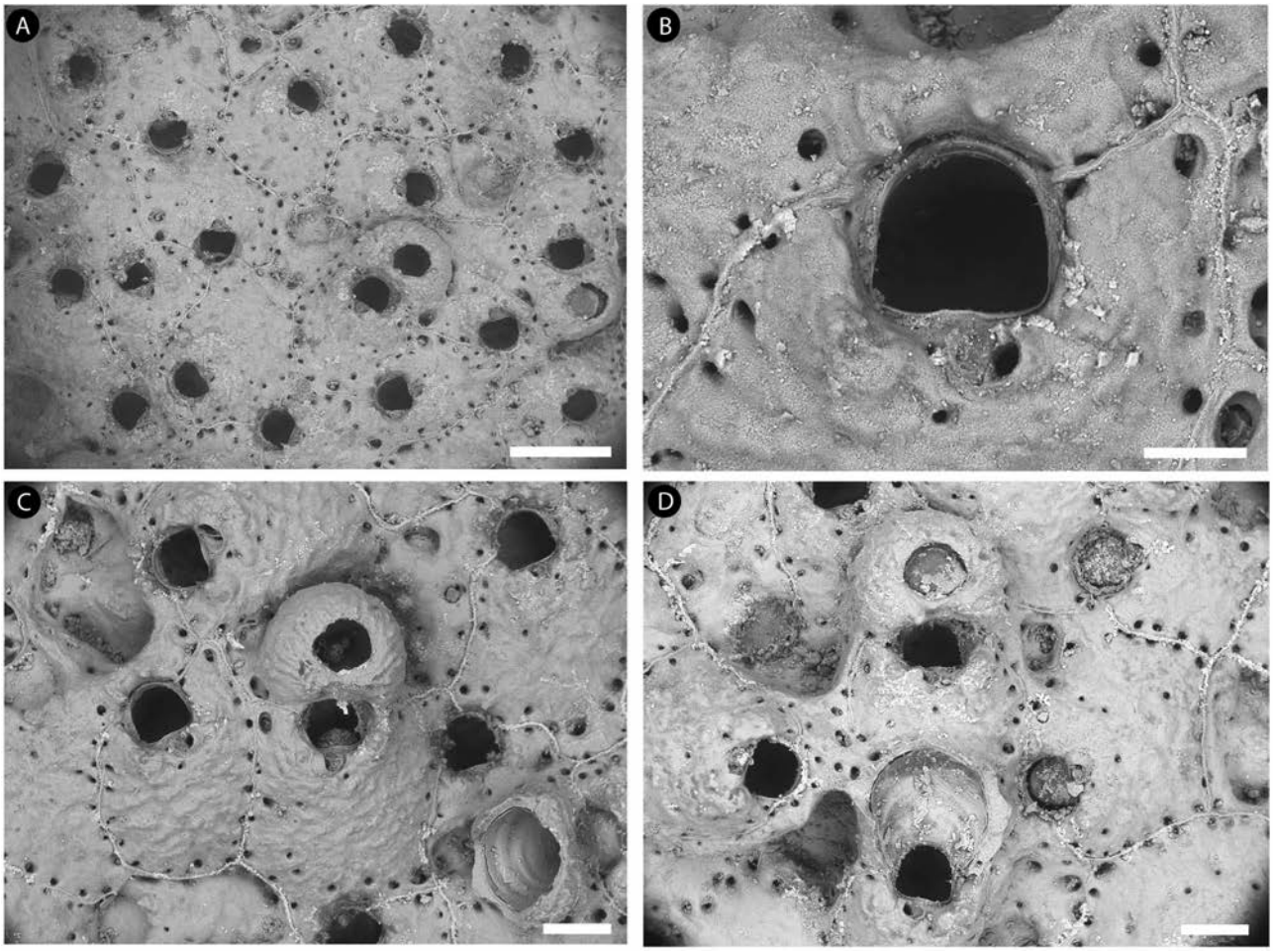

FIGURE 23. *Trematooecia aviculifera* (Canu & Bassler, 1923). **A–D**, USNM 603778, Honduras. **A,** group of zooids. **B,** primary orifice and suboral avicularium. **C, D,** ovicelled zooid. Scale bars: A = 500 µm; B = 100 µm; C, D = 200 µm.

FIGURE 24. *Trematooecia aviculifera* (Canu & Bassler, 1923). **A**, USNM 603284, Panama; **B,** USNM 603285, Panama; **C,** USNM 603286, Panama. **A–C,** unilamellar and multilamellar colonies retaining red pigmentation. Scale bars = 1 cm.

Remarks. According to Winston (2005), Smitt (1873) did not differentiate *T. aviculifera* from *Celleporaria albirostris*. Osburn (1940) also misidentified *T. aviculifera* as *Trematooecia turrita* (Smitt, 1873) (= *Cigclisula turrita*; Fig. 11), and erected the genus *Trematooecia* for this species. Both *T. aviculifera* and *C. turrita* species have heavily calcified, encrusting colonies, often with a tubercular secondary orifice. They are distinguished, however, by the morphology of ooecia and avicularia (see above, under Remarks on *Trematooecia*).

Canu & Bassler (1923) described *T. aviculifera* based on a fossil specimen (USNM 68709; Fig. 19) from Panama Canal. They described small frontal avicularia, but none has been found in examined material. *Trematooecia aviculifera* is characterized by the transversely D-shaped orifice, suboral elliptical avicularium laterally directed and obovate interzooidal avicularium.

TABLE 5. Morphometric data for *Trematooecia* species studied (in mm).

	T. aviculifera				
	Panama Canal[1]	Panama[2]	Belize[3]	Curaçao[4]	Honduras[5]
Lz	9	14	7	8	15
Mean (SD)	0.691 (0.091)	0.688 (0.093)	0.534 (0.080)	0.570 (0.071)	0.609 (0.083)
Range	0.418–0.549	0.574–0.820	0.401–0.620	0.445–0.668	0.429–0.790
lz	9	14	7	8	15
Mean (SD)	0.470 (0.070)	0.562 (0.158)	0.591 (0.071)	0.506 (0.104)	0.559 (0.095)
Range	0.350–0.557	0.320–0.794	0.527–0.771	0.393–0.691	0.381–0.773
Dp	10	14	10	10	10
Mean (SD)	0.024 (0.005)	0.029 (0.006)	0.040 (0.0015)	0.037 (0.011)	0.022 (0.004)
Range	0.016–0.031	0.018-0.043	0.015–0.058	0.023–0.059	0.015–0.029
Lo	9	14	7	8	15
Mean (SD)	0.158 (0.022)	0.173 (0.011)	0.163 (0.018)	0.170 (0.018)	0.148 (0.011)
Range	0.112–0.183	0.148–0.194	0.133–0.187	0.135–0.195	0.128–0.168
lo	9	14	7	8	15
Mean (SD)	0.176 (0.011)	0.188 (0.019)	0.188 (0.012)	0.180 (0.008)	0.170 (0.011)
Range	0.189–0.156	0.164-0.227	0.164–0.204	0.172–0.199	0.153–0.197
Lavs	9	8	7	8	15
Mean (SD)	0.083 (0.012)	0.093 (0.008)	0.129 (0.016)	0.116 (0.013)	0.099 (0.010)
Range	0.058–0.099	0.080–0.109	0.108–0.156	0.085–0.126	0.080–0.120
lavs	9	8	7	8	15
Mean (SD)	0.056 (0.006)	0.052 (0.012)	0.071 (0.013)	0.063 (0.014)	0.064 (0.007)
Range	0.044-0.062	0.030–0.070	0.055–0.866	0.032–0.081	0.051–0.075
Lavi	2	1	-	-	-
Mean (SD)	0.386 (0.120)	0.429	-	-	-
Range	0.301–0.471	-	-	-	-
lavi	2	1	-	-	-
Mean (SD)	0.169 (0.041)	0.210	-	-	-
Range	0.139–0.198	-	-	-	-
Lavf	-	-	-	-	-
Mean (SD)	-	-	-	-	-
Range	-	-	-	-	-
lavf	-	-	-	-	-
Mean (SD)	-	-	-	-	-
Range	-	-	-	-	-
Lov	2	2	2	2	2
Mean (SD)	0.353 (0.053)	0.334 (0.058)	0.376 (0.014)	0.328 (0.042)	0.326 (0.013)
Range	0.315–0.391	0.293–0.376	0.365–0.389	0.298–0.358	0.316–0.345
lov	2	2	2	2	2
Mean (SD)	0.439 (0.006)	0.382 (0.049)	0.470 (0.030)	0.444 (0.123)	0.454 (0.017)

.....continued on the next page

TABLE 5. (Continued)

	T. aviculifera				
	Panama Canal[1]	Panama[2]	Belize[3]	Curaçao[4]	Honduras[5]
Range	0.434–0.443	0.347–0.417	0.448–0.492	0.356–0.531	0.434–0.471
Lovf	2	-	2	2	2
Mean (SD)	0.177 (0.058)	-	0.262 (0.027)	0.165 (0.009)	0.164 (0.006)
Range	0.136–0.218	-	0.242–0.281	0.158–0.172	0.158–0.172
lovf	2	-	2	2	2
Mean (SD)	0.240 (0.035)	-	0.235 (0.011)	0.193 (0.029)	0.176 (0.06)
Range	0.215–0.265	-	0.245–0.261	0.172–0.214	0.158–0.172

[1] USNM 68709, Pleistocene, Panama Canal. [2] USNM 603782, Panama. [3] USNM 376606, Belize. [4] USNM 603776, Curaçao. [5] USNM 603778, Belize

Trematooecia aviculifera resembles *Trematooecia osburni* Marcus, 1955, *Trematooecia protecta* Osburn, 1940 and *Trematooecia ridleyi* (Kirkpatrick, 1890) in having encrusting colonies, a marginally punctured frontal shield, globose ooecium and ectooecium with a frontal circular membranous area. *Trematooecia aviculifera* differs from *T. osburni* in the presence of tubercles around the secondary orifice and in having a suboral avicularium. *Trematooecia aviculifera* differs from *T. protecta* in the absence of condyles and frontal avicularia and in the position of the ooecium (inclined in *T. protecta*, horizontal in *T. aviculifera*). Autozooids, suboral avicularia and ooecia are also shorter in *T. protecta* than in *T. aviculifera* (Table 3). *Trematooecia aviculifera* differs from *T. ridleyi* in the size of the zooids and ooecium (all smaller in *T. ridleyi*) and in the absence of frontal avicularia (conspicuous in *T. ridleyi*).

Trematooecia aviculifera has been reported by some authors (Canu & Bassler 1928a; Osburn 1914, 1927, 1940; Banta & Carson 1971; Winston 1984, 2005) from the Gulf of Mexico, Florida, Puerto Rico, and Costa Rica. This species is probably one of the most abundant bryozoans on Caribbean coral reefs (Winston 1984, 1986, 2005). Colonies grow from a single lamina to form large mounds that remain red even when dead (Fig. 24). Because of the colony color and presence of tubercles, the species is also called "bleeding teeth bryozoan" (Charpin 2014). Owing to some physical property of the calcification, the species has a fluorescent green coloration at depths below 7m (Winston 1984), one of the reasons why *T. aviculifera* is easily noticed by divers.

Distribution. Pleistocene (Panama) to Recent (Atlantic: Florida to Venezuela).

Trematooecia arborescens (Canu & Bassler, 1928) n. comb.

(Figs 25–26, Table 6)

Rhynchozoon arborescens Canu & Bassler, 1928b: 32, pl. 7, figs 4–10. [Bahia and Rio de Janeiro, Brazil]
Rhynchozoon arborescens: Souza 1989: 502. [Bahia, Brazil]
Cigclisula arborescens: Vieira *et al*. 2010a: 29, figs 67–72. [Rio de Janeiro and São Paulo, Brazil]

Material examined. *Lectotype:* USNM 8565 (see Vieira *et al.* 2010a), *Rhynchozoon arborescens*, F. Canu & R. Bassler det., Bahia and Rio de Janeiro, Brazil. *Additional specimens:* NHMUK 1899.7.1.5283; NHMUK 1899.7.1.5290, '*Lepralia adamitica'*, G. Busk col., HMS 'Herald', John Adams Bank (Victoria Bank, Espírito Santo, Brazil); UFBA 527, *Trematooecia arborescens*, A.C. Almeida det., Camaçari, Bahia, 14–38 m; UFBA 553, *Trematooecia arborescens*, A.C. Almeida det., Camaçari, Baía de Todos os Santos, Brazil; UFBA 555, *Trematooecia arborescens*, A.C. Almeida det., Camaçari, Bahia, 50 m; MZUSP 0315, *Cigclisula arborescens*, L.M. Vieira det., project REVIZEE South SCORE, RV 'Prof. Wladimir Besnard', station 6662, Rio de Janeiro, 135 m; MZUSP 0316, *Cigclisula arborescens*, L.M. Vieira det., project REVIZEE South SCORE, RV 'Prof. Wladimir Besnard', station 6674, São Paulo, 122 m; MZUSP 0317, *Cigclisula arborescens*, L.M. Vieira det., project REVIZEE South SCORE, RV 'Prof. Wladimir Besnard', station 6678, São Paulo, 99 m.

Description. Colony erect, bilaminar, branching. Skeleton red. Zooids hexagonal to polygonal, generally longer than wide, delimited by slightly raised sinuous margins. Frontal shield heavily calcified, marginally

punctured by 18–24 pores, smooth. Primary orifice large relative to frontal shield, elliptical, longer than wide, sunken, with an arcuate anter and deeply concave poster, separated by 2 proximolateral downcurved condyles. Secondary orifice surrounded by 4–6 low, blunt processes. Suboral, elliptical, laterally directed avicularium of 2 sizes, the smaller with smooth distal rostral margins, the larger with serrated distal rostral margins. Frontal avicularia small, elliptical with serrated distal rostral margins, often 2 per zooid, placed at zooidal margins. Interzooidal avicularia at colony margins, large, longer than wide, rostrum spatulate; calcified palate occupying more than half rostral length; foramen rounded. Ovicelled zooids larger than non-ovicelled zooids. Ooecium immersed, flattened hood; ectooecium granular with frontal semicircular to circular membranous area.

Remarks. Vieira *et al.* (2010a) transferred this species from *Rhynchozoon* Hincks, 1895 to *Cigclisula* based on the frontal shield, peristomial complex and ooecium, but comparison with *C. occlusa*, the type species of the genus, shows clear differences in the ectooecium compared to *Trematooecia*, to which genus *R. arborescens* must be transferred.

Large, erect species of *Trematooecia* have routinely been assigned to *Cigclisula*, including not only the example of *C. arborescens* (Vieira *et al*. 2010a) but also *C. verticalis* (Hageman *et al*. 1998, following Hastings 1932 and Harmer 1957) and *C. gemmea* (Winston & Woollacott 2009). However, both erect and encrusting colonies can be found in *Cigclisula* and *Trematooecia*. We argue that these two genera can be distinguished morphologically only by ooecial structure, hence the absence of fertile colonies may make species assignment difficult.

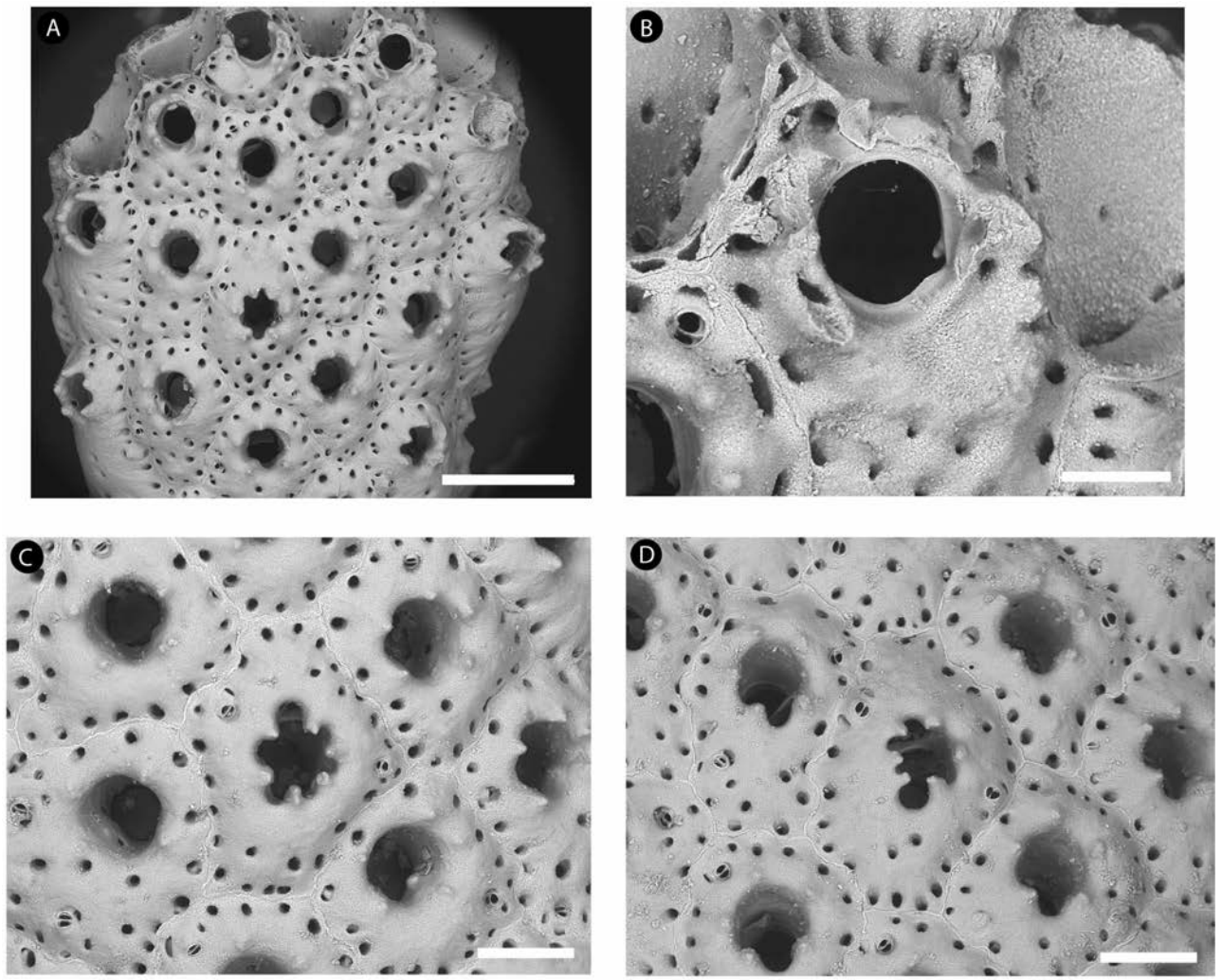

FIGURE 25. *Trematooecia arborescens* (Canu & Bassler, 1928). **A–D,** USNM 8565, lectotype, Brazil. A, zooids at growing edge of branch. **B,** primary orifice. C, D, ovicelled zooids and tiny elliptical frontal avicularia. Scale bars: A = 500 µm; B = 100 µm; C, D = 200 µm.

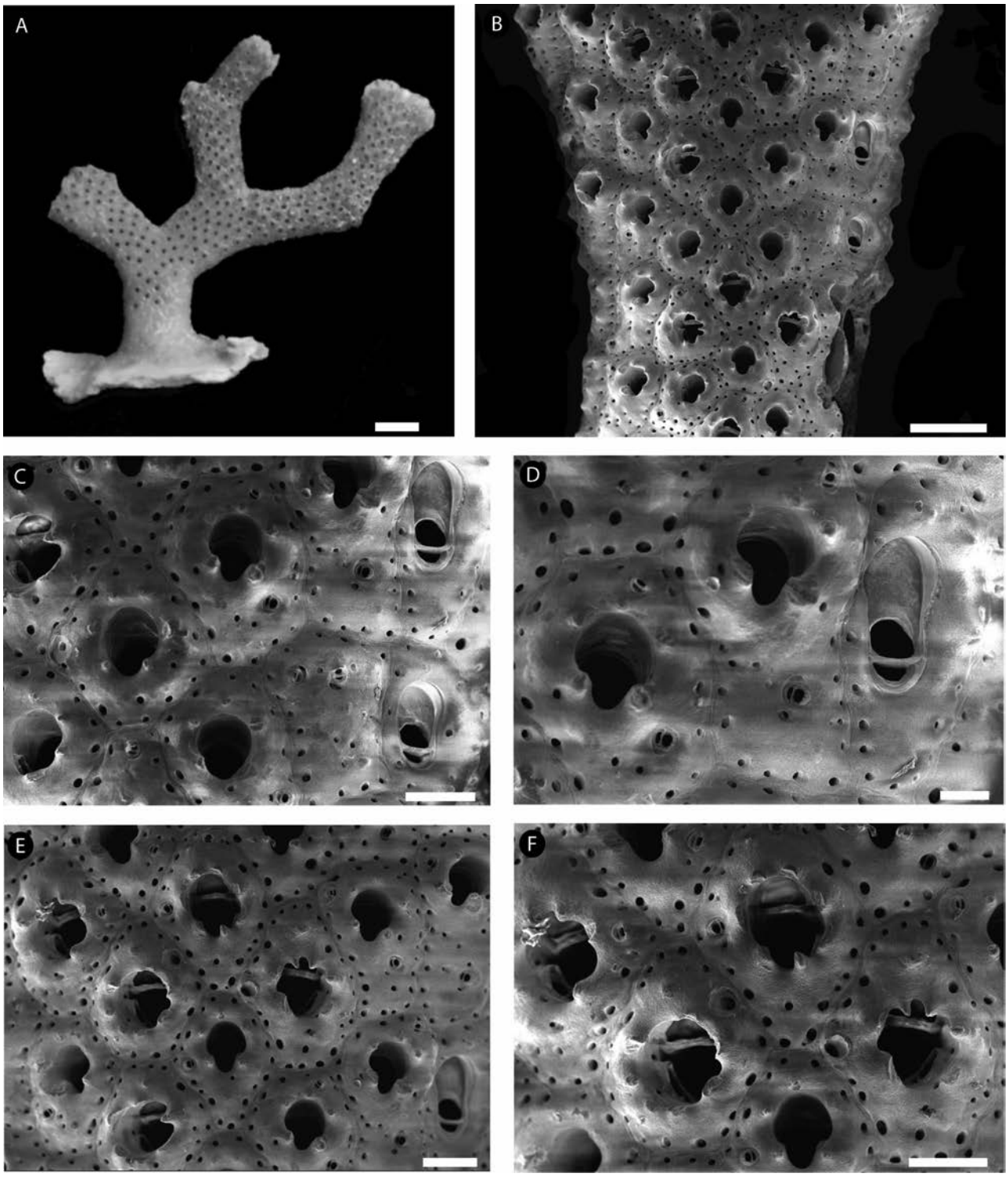

FIGURE 26. *Trematooecia arborescens* (Canu & Bassler, 1928). **A–D,** UFBA 555, Brazil. **A,** entire erect colony. **B,** close-up of branch. **C, D,** zooids with tiny, elliptical frontal avicularia and spatulate interzooidal avicularia. **E,** ovicelled zooids. **F,** close-up of ovicelled zooids. Scale bars: A = 1 mm; B = 500 µm; C, E, F = 200 µm; D = 100 µm.

Uniquely in the genus, *Trematooecia arborescens* has immersed ooecia and short blunt processes around the secondary orifice. This species resembles *T. gemmea* and *T. verticalis* in having erect bilaminar colonies and a marginally punctured frontal shield, but differs in the immersed ooecium and an ectooecium with a frontal circular membranous area. Other differences between *T. arborescens* and *T. gemmea* are the secondary orifice (with solid tubercles in *T. gemmea* and low blunt processes in *T. arborescens*). *Trematooecia verticalis* is distinguished by the absence of tubercles around the secondary orifice and lack of suboral avicularia.

Distribution. Atlantic: Brazil (Bahia to São Paulo).

TABLE 6. Morphometric data for *Trematooecia* species studied (in mm).

	T. arborescens		***T. hexagonalis***	***T. protecta***	
	Brazil[1]	Brazil[2]	Galápagos[3]	Puerto Rico[4]	Puerto Rico[5]
Lz	8	10	10	10	10
Mean (SD)	0.478 (0.044)	0.535 (0.070)	0.613 (0.062)	0.519 (0.073)	0.588 (0.086)
Range	0.396–0.527	0.395–0.625	0.507–0.707	0.371–0.605	0.448–0.707
lz	8	10	10	10	10
Mean (SD)	0.367 (0.056)	0.377 (0.068)	0.538 (0.032)	0.460 (0.046)	0.482 (0.053)
Range	0.288–0.461	0.266–0.473	0.507–0.591	0.357–0.520	0.405–0.570
Dp	10	10	10	10	10
Mean (SD)	0.016 (0.003)	0.021 (0.009)	0.015 (0.002)	0.022 (0.006)	0.020 (0.006)
Range	0.011–0.021	0.008–0.043	0.010–0.018	0.013–0.032	0.008–0.035
Lo	8	-	10	10	10
Mean (SD)	0.137 (0.005)	-	0.216 (0.010)	0.172 (0.022)	0.169 (0.013)
Range	0.130–0.146	-	0.202–0.297	0.117–0.193	0.148–0.197
lo	8	-	10	10	10
Mean (SD)	0.122 (0.006)	-	0.211 (0.018)	0.180 (0.017)	0.186 (0.012)
Range	0.110–0.130	-	0.183–0.234	0.147–0.200	0.168–0.208
Lavs	8	-	-	10	10
Mean (SD)	0.058 (0.019)	-	-	0.072 (0.014)	0.076 (0.004)
Range	0.044–0.050	-	-	0.054–0.088	0.068–0.082
lavs	8	-	-	10	10
Mean (SD)	0.036 (0.019)	-	-	0.037 (0.017)	0.035 (0.016)
Range	0.022–0.050	-	-	0.035–0.050	0.032–0.052
Lavi	-	2	-	-	4
Mean (SD)	-	0.292 (0.050)	-	-	0.393 (0.027)
Range	-	0.256–0.327	-	-	0.371-0.432
lavi	-	2	-	-	4
Mean (SD)	-	0.119 (0.065)	-	-	0.207 (0.019)
Range	-	0.114–0.123	-	-	0.179-0.221
Lavf	8	10	10	10	10
Mean (SD)	0.037 (0.005)	0.043 (0.004)	0.035 (0.005)	0.078 (0.011)	0.057 (0.064)
Range	0.028–0.045	0.037–0.049	0.027–0.042	0.066–0.095	0.048–0.064
lavf	8	10	10	10	10
Mean (SD)	0.033 (0.003)	0.040 (0.007)	0.033 (0.002)	0.074 (0.008)	0.056 (0.018)
Range	0.028–0.039	0.032-0.051	0.028–0.036	0.062–0.087	0.031–0.083
Lov	-	8	2	2	3
Mean (SD)	-	0.283 (0.002)	0.352 (0.007)	0.296 (0.011)	0.268 (0.038)
Range	-	0.240–0.313	0.347–0.357	0.288–0.304	0.223–0.292
lov	-	8	2	2	3
Mean (SD)	-	0.312 (0.003)	0.375 (0.019)	0.346 (0.020)	0.390 (0.037)

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TABLE 6. (Continued)

	T. arborescens		*T. hexagonalis*	*T. protecta*	
	Brazil[1]	Brazil[2]	Galápagos[3]	Puerto Rico[4]	Puerto Rico[5]
Range	-	0.277–0.365	0.361–0.388	0.331–0.360	0.359–0.431
Lovf	-	4	-	2	3
Mean (SD)	-	0.068 (0.006)	-	0.118 (0.006)	0.139 (0.025)
Range	-	0.056–0.070	-	0.114–0.122	0.116–0.166
lovf	-	4	-	2	3
Mean (SD)	-	0.122 (0.002)	-	0.180 (0.009)	0.230 (0.032)
Range	-	0.118–0.125	-	0.173–0.187	0.207–0.267

[1] USNM 8565, Bahia, Brazil. [2] UFBA 555, Bahia, Brazil. [3] USNM 8513, Galápagos Islands. [4] USNM 11831, Guanica Harbor, Puerto Rico. [5] USNM 603780, Guanica Harbor, Puerto Rico

Trematooecia clivulata Tilbrook, 2006

Holoporella turrita: Canu & Bassler 1929: 420, text-fig. 164, pl. 59, figs 1–5. [Philippines]
Cigclisula turrita: Harmer 1957 (in part): 1059, pl. 69, figs 21, 23–24. [Indonesia]
Trematooecia turrita: Ristedt & Hillmer 1985: 137, pl. 2, fig. 7. [Philippines]
Trematooecia clivulata Tilbrook, 2006: 287, pl. 62D–F. [China Sea, Philippines, Vanuatu, Fiji]

Remarks. *Trematooecia clivulata* is characterized by zooids that are almost flat, a secondary orifice bordered by 4–5 solid tubercles, no suboral avicularia, a frontal avicularium associated with each zooid and an ectooecium with a narrow membranous window (Tilbrook 2006). The species was previously misidentified as *C. turrita*, but the two species are distinguished by the shape of the primary orifice (larger in *T. clivulata*) and the surface of the ectooecium (slit-like membranous window in *T. clivulata*, pseudoporous in *C. turrita*).

Distribution. Indo-Pacific: China Sea, Fiji, Philippines, Solomon Islands and Taiwan.

Trematooecia gemmea (Winston & Woollacott, 2009) n. comb.

Cigclisula gemmea Winston & Woollacott, 2009: 281, fig. 32A–F. [Barbados]

Remarks. The ectooecium with a median inverted U-shaped membranous area requires reassignment of this species to *Trematooecia*. It is distinguished from all congeners by large spatulate interzooidal avicularia of varying sizes distributed on the outer edges of colonies (see Winston & Woollacott 2009).

Distribution. Caribbean: Barbados.

Trematooecia hexagonalis (Canu & Bassler, 1930)
(Fig. 27, Table 6)

Holoporella hexagonalis Canu & Bassler, 1930a: 38, pl. 7, fig. 1. [Galápagos Islands]
Trematooecia hexagonalis: Osburn 1952: 503 (part). [only Galápagos; specimens from Gulf of California and Mexico belong to *Cigclisula osburni* n. sp.]
Not *Trematooecia hexagonalis*: Soule 1961: 59. [California; = *Cigclisula osburni* n. sp.]
Not *Trematooecia hexagonalis*: Soule & Soule 1964: 40. [Isla Conchas; = *Cigclisula osburni* n. sp.]

Material examined. *Holotype:* USNM 8513, *Holoporella hexagonalis*, F. Canu & R. Bassler det., Albatross Station D. 2813, Galápagos Islands.

Description. Colony encrusting, uni- to multilaminar. Zooids hexagonal, becoming polygonal with increasing calcification, generally longer than wide, delimited by slightly raised sinuous margins. Frontal shield heavily

calcified, uniformly punctured by 36–51 pseudopores, granular. Primary orifice somewhat hoof-shaped, longer than wide, with arcuate anter delimited from broader concave poster by 2 downcurved condyles at about one-third zooid length. Secondary orifice surrounded by 4 solid tubercles. Frontal avicularia small, elliptical, usually 1, rarely 2, per zooid, placed at proximal zooidal margin. Interzooidal avicularia absent. Ooecium subglobose, as long as wide; ectooecium granular with median slit-like membranous area.

Remarks. When Canu & Bassler (1930a) described this species they stated that the specimen lacked ooecia. Examination of the holotype by SEM, however, showed that two zooids have ooecia, each with a proximally facing slit-like ectooecial frontal membranous window (not visible in Figs 27 E–F owing to specimen orientation) that is typical for *Trematooecia*.

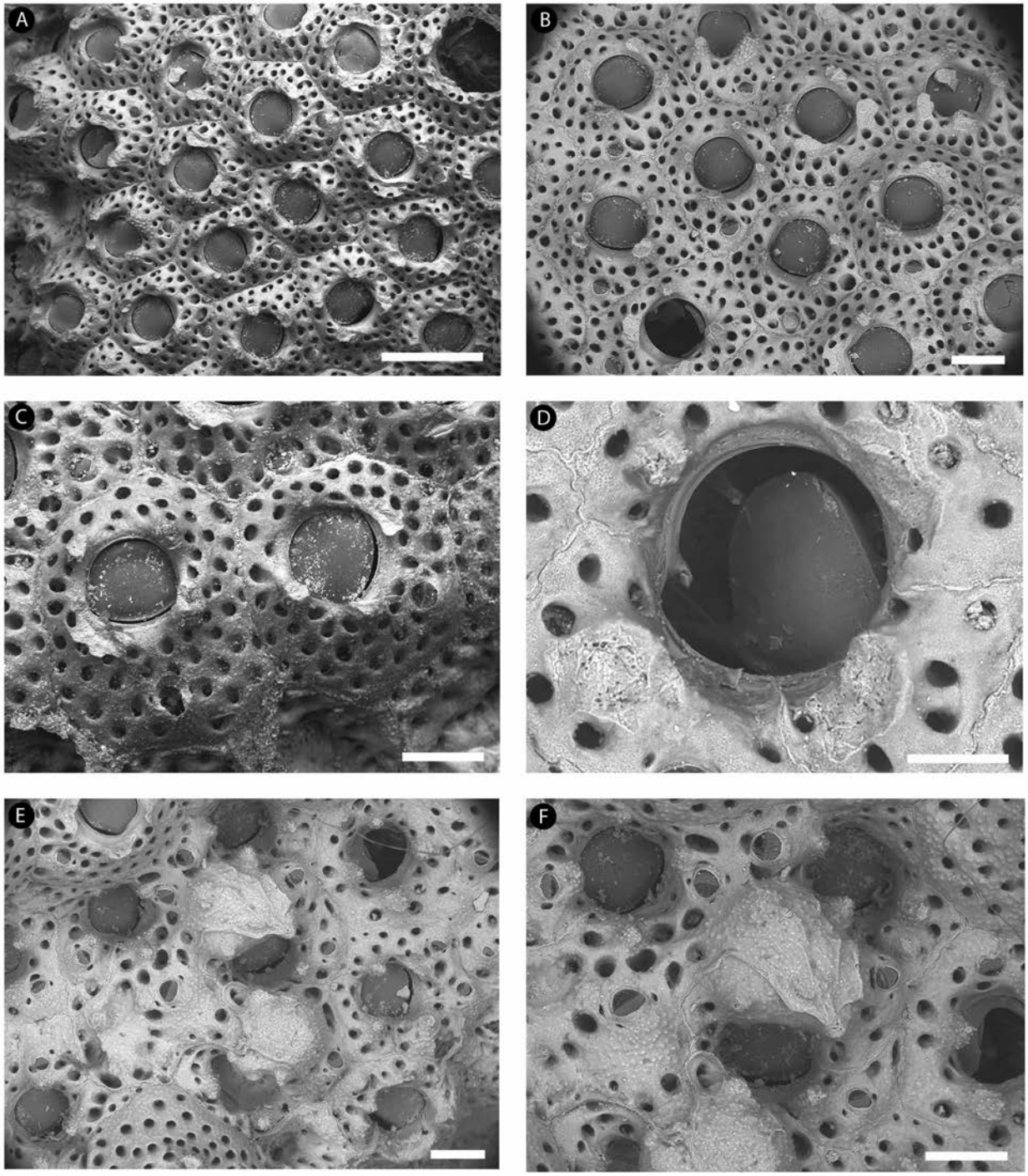

FIGURE 27. *Trematooecia hexagonalis* (Canu & Bassler, 1930). **A–F,** USNM 8513, holotype, Galápagos Islands. **A, B,** groups of zooids. **C,** close-up of zooids and opercula. **D,** primary orifice. **E, F,** ovicelled zooids and small, elliptical frontal avicularia. Scale bars: A = 500 µm; B = 200 µm; C, E, F = 200 µm; D = 100 µm.

Trematooecia hexagonalis is characterized by a frontal shield with 36–51 more-or-less evenly distributed pseudopores, four solid tubercles around the secondary orifice, no suboral or interzooidal avicularia and a granular ectooecium with a median inverted slit-like membranous window. *Trematooecia hexagonalis* resembles *T. clivulata* and *Trematooecia ligulata* Ayari & Taylor, 2008 in having encrusting colonies, tubercles around the secondary orifice and an ectooecium with a frontal slit, but differs in the uniformly punctured frontal shield, elliptical frontal avicularia and lack of interzooidal avicularia.

Owing to the uniformly punctured frontal shield and the presence of tubercles around the secondary orifice, specimens from Atlantic coast of Panama (= *Cigclisula perforata* n. sp.; see above) and the Pacific (= *Cigclisula osburni* n. sp., see above; see also Osburn 1952; Soule 1961; Soule & Soule 1964) are assigned to *T. hexagonalis*. This species is distinguished by the ectooecium with a median inverted U-shape membranous area, while that in *C. perforata* n. sp. and *C. osburni* n. sp. has irregular pseudopores.

Trematooecia hexagonalis is known only from the type locality in the Galápagos Islands. According to Canu and Bassler (1930a), the species encrusts shells.

Distribution. Pacific: Galápagos Islands.

Trematooecia ligulata Ayari & Taylor, 2008

Holoporella turrita: Canu & Bassler 1930b: 74, pl. 10, figs 10–16. [Tunisia]
Holoporella turrita: O'Donoghue & de Watteville 1939: 44. [Alexandria]
Holoporella turrita: Gautier 1957: 559, fig. 4. [Syria]
Trematooecia ligulata Ayari & Taylor, 2008: 262, figs 1A–D, 2A–D. [Mediterranean Sea]

Remarks. *Trematooecia ligulata* was previously misidentified as *Holoporella turrita* in Mediterranean waters, but it is distinguished by its ectooecium with a frontal slit-like membranous area (Ayari *et al.* 2008). Two other species of *Trematooecia* with encrusting colonies and fissured ectooecium are *T. clivulata* and *T. hexagonalis*. *Trematooecia ligulata* differs from *T. clivulata* and *T. hexagonalis*, however, in having a suboral avicularium (Ayari *et al.* 2008).

Distribution. Mediterranean Sea.

Trematooecia osburni Marcus, 1955

Trematooecia osburni Marcus, 1955: 311, figs 91–93. [Espírito Santo, Brazil]
Trematooecia osburni: Vieira *et al.* 2008: 29. [Brazil; checklist]

Remarks. We have examined Canada-Balsam slide mounts deposited at MZUSP that are too poorly preserved for adequate redescription. *Trematooecia osburni* has encrusting colonies, only marginal frontal-shield pores, a transversely D-shaped primary orifice without condyles, a non-tubercular secondary orifice, elliptical frontal avicularia, spatulate interzooidal avicularia and no suboral avicularia (Marcus 1955).

The species resembles *T. aviculifera*, *T. protecta* and *T. ridleyi* in having encrusting colonies, a subglobose ooecium and an ectooecium with a circular frontal membranous area, but differs in lacking peristomial tubercles and a suboral avicularium. *Trematooecia osburni* is known only from the type locality in Brazil. According to Marcus (1955) colonies are white and were found encrusting another bryozoan at 35 m depth.

Distribution. Atlantic: Brazil.

Trematooecia protecta Osburn, 1940
(Figs 28–29, Table 6)

Trematooecia protecta Osburn, 1940: 459, pl. 8, figs 66–71. [Puerto Rico]
Trematooecia protecta: Osburn 1947: 45. [Caribe and Colombia]
Trematooecia protecta: Shier 1964: 645. [Florida]

Material examined. *Holotype:* USNM 11831, *Trematooecia protecta*, R. Osburn det., 1940, P.R. 2381, off Guanica Harbor, Puerto Rico, 18 m. *Additional specimens:* USNM 603779, *Holoporella protecta*, Puerto Rico, 2370, off Guanica Harbor, 9 m., Acc. No. 208837; USNM 603780, Acc. No. 208837, *Trematooecia protecta*, R. Osburn det., 1915, off Guanica Harbor, 33 m.

Description. Colony encrusting, uni- to multilaminar. Zooids of initial layer almost rectangular, those from frontally budded layers irregularly polygonal, generally longer than wide, delimited by a raised line. Frontal shield heavily calcified, marginally punctured by 8–33 pseudopores. Primary orifice small relative to frontal shield, more or less transversely D-shaped, wider than long, sunken, with arcuate anter and wider, weakly concave poster, delimited by 2 barely developed condylar swellings near the proximolateral corners. Secondary orifice surrounded by 4–6 (often 4) solid tubercles. Suboral, elliptical, laterally directed avicularium sometimes between the oral tubercles. Frontal avicularia elliptical, usually 1, rarely 2, per zooid, placed at zooidal proximal margin. Interzooidal avicularia as long as zooids, large, with obovate rostrum, wider than long, proximal edge rounded, distal edge deeply concave; calcified palate occupying more than half rostral length, foramen rounded. Ooecium subglobose, wider than long, inclined to zooid surface; ectooecium heavily calcified, sometimes with grooves and tubercles, with frontal semicircular membranous area.

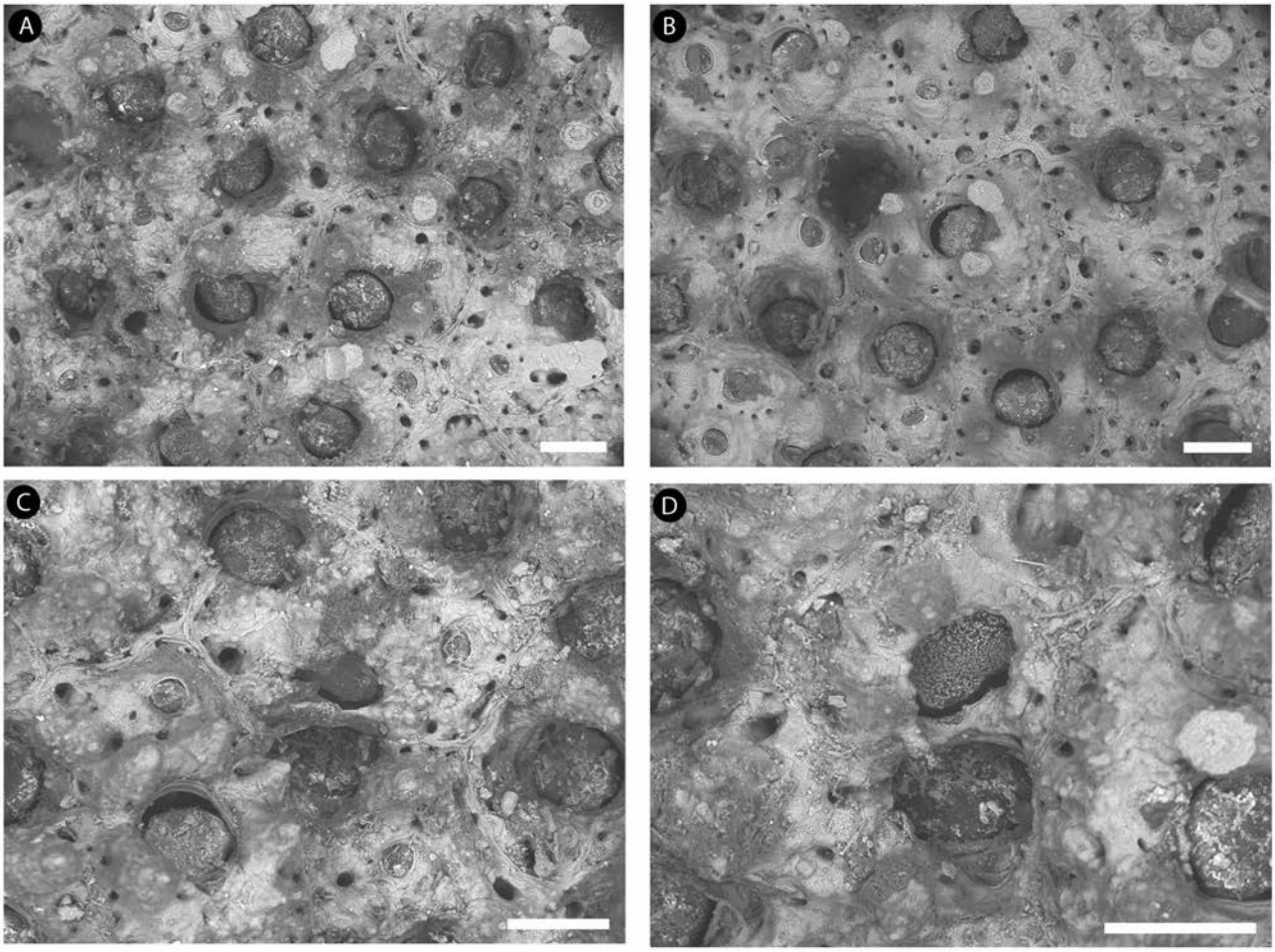

FIGURE 28. *Trematooecia protecta* Osburn, 1940. **A–D,** USNM 11831, holotype, Puerto Rico. **A, B,** groups of zooids with small, elliptical frontal avicularia. **C, D,** ovicelled zooids. Scale bars: A–D = 200 µm.

Remarks. Osburn (1940) did not described the weak lateral condyles mentioned by Shier (1964) and seen by SEM (Fig. 29B). Osburn (1940) and Shier (1964) also described only small elliptical frontal avicularia in *T. protecta*, but examination of specimens from Puerto Rico, however, revealed the presence of large obovate interzooidal avicularia in this species (Fig. 29C).

Trematooecia protecta is characterized by the shape of the primary orifice with its weak condyles, suboral avicularium, interzooidal avicularia with obovate rostrum, elliptical frontal avicularia and ectooecium with frontal

circular membranous area. The species resembles *T. aviculifera*, *T. osburni* and *T. ridleyi* in having encrusting colonies, a subglobose ooecium and an ectooecium with a frontal circular membranous area, but it differs in having at least weakly developed condyles. Other differences pertain to the frontal avicularia and position of the ooecium (inclined in *T. protecta*, horizontal in *T. aviculifera*). *Trematooecia osburni* also differs in lacking suboral avicularium and solid tubercles around the secondary orifice.

Distribution. Atlantic: Florida to Colombia.

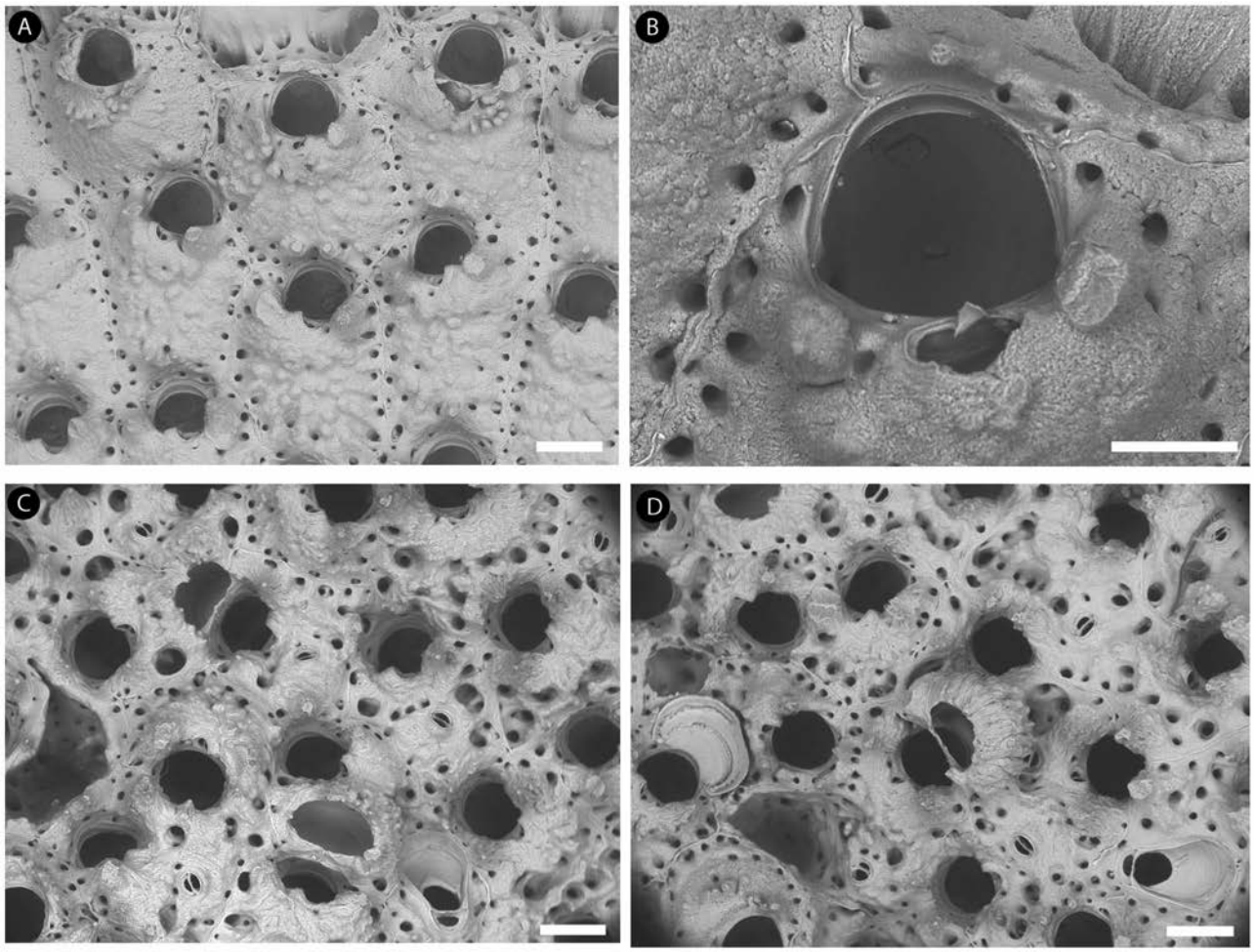

FIGURE 29. *Trematooecia protecta* Osburn, 1940. **A–D,** USNM 603780, Guanica Harbor, Puerto Rico. **A,** zooids at growing edge of colony. **B,** primary orifice. **C, D,** ovicelled zooids and obovate interzooidal avicularia. Scale bars: A = 200 µm, B = 100 µm; C, D = 200 µm.

Trematooecia ridleyi (Kirkpatrick, 1890)

(Figs 30–31, Table 7)

Cellepora ridleyi Kirkpatrick, 1890: 505, fig. 2. [Fernando de Noronha]
Trematooecia ridleyi: Vieira *et al.* 2008: 29 [Brazil; checklist]

Material examined. *Holotype:* NHMUK 1888.4.16.2, *Cellepora ridleyi*, R. Kirkpatrick det., 1888, Fernando de Noronha, Brazil. *Additional specimens:* NHMUK 1899.7.1.3348, *Trematooecia turrita*, G. Busk coll., John Adams Bank (Victoria Bank, Espirito Santo, Brazil); UFBA 465, *Trematooecia ridleyi*, A.C. Almeida det., 2013, Banco Besnard, 19°40' S and 38°08' W. UFBA 623, *Trematooecia ridleyi*, A. C. Almeida det., 2013, Baía de Todos os Santos, 13°10'S and 38°25'W, 15 m.

Description. Colony encrusting, uni- to multilaminar. Zooids polygonal, globose, longer than wide, delimited

by raised margins. Frontal shield heavily calcified, marginally punctured by 10–20 pores and frequently bearing a tubercle-like process. Primary orifice large relative to frontal shield, centered, more or less transversely D-shaped, wider than long, sunken, with arcuate anter and weakly concave poster. No condyles. Peristomial tubercles 3–5 (often 5), solid. Suboral, elliptical, laterally directed avicularium. Frontal avicularia elliptical, rare, often 1 per zooid (rarely 2), placed at proximal zooidal margin. Interzooidal avicularia as long as zooids, longer than wide, with spatulate rostrum, proximal edge rounded and distal edge deeply concave; calcified palate attaining half rostral length; foramen oval. Ooecium subglobose, horizontal to zooid surface, ectooecium heavily calcified, with groove lines and tubercles and a frontal semicircular membranous area.

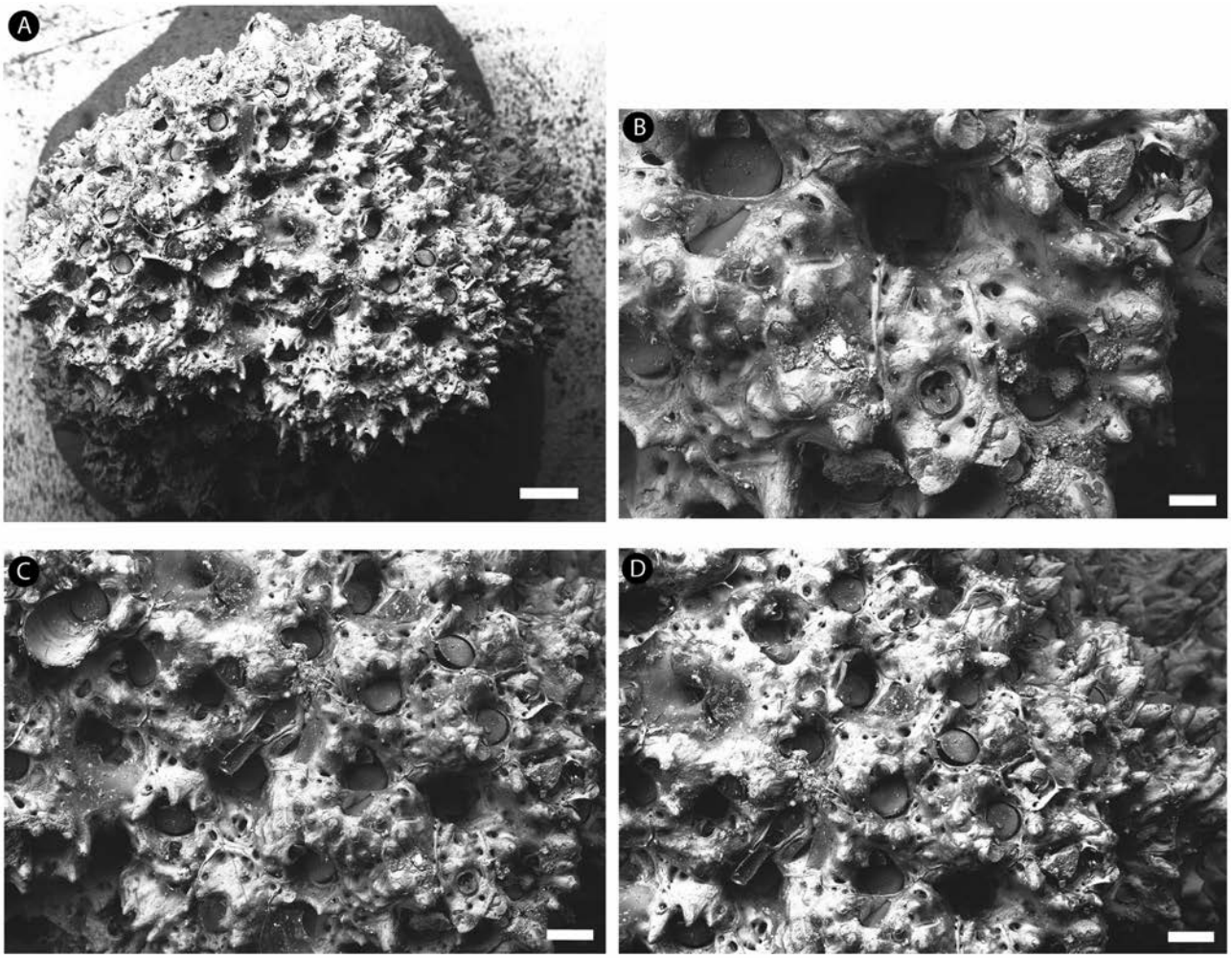

FIGURE 30. *Trematooecia ridleyi* (Kirkpatrick, 1890). **A–D,** NHMUK 1888.4.16.2, holotype, Brazil. **A,** entire encrusting colony. **B,** primary orifice and ovicelled zooid. **C, D,** ovicelled zooids and spatulate interzooidal avicularia. Scale bars: A = 500 µm; B, D = 100 µm; C = 400 µm.

Remarks. *Trematooecia ridleyi* is characterized by encrusting colonies, 10–20 marginal pores in the frontal wall shield, 3–5 solid peristomial tubercles, spatulate interzooidal avicularia and an ectooecium with a frontal circular membranous area.

Three other species of *Trematooecia* also have encrusting colonies and a similar ectooecium: *T. aviculifera*, *T. osburni* and *T. protecta*. Differences pertain to the frontal avicularia (none in *T. aviculifera*) and the number of peristomial tubercles (3–5 in *T. ridleyi*, 4–6 in *T. aviculifera*). *Trematooecia ridleyi* differs from *T. osburni* in having a suboral avicularium and peristomial processes. *Trematooecia protecta* has a forward-angled ooecium and 4–6 peristomial tubercles.

Distribution. Atlantic: Brazil.

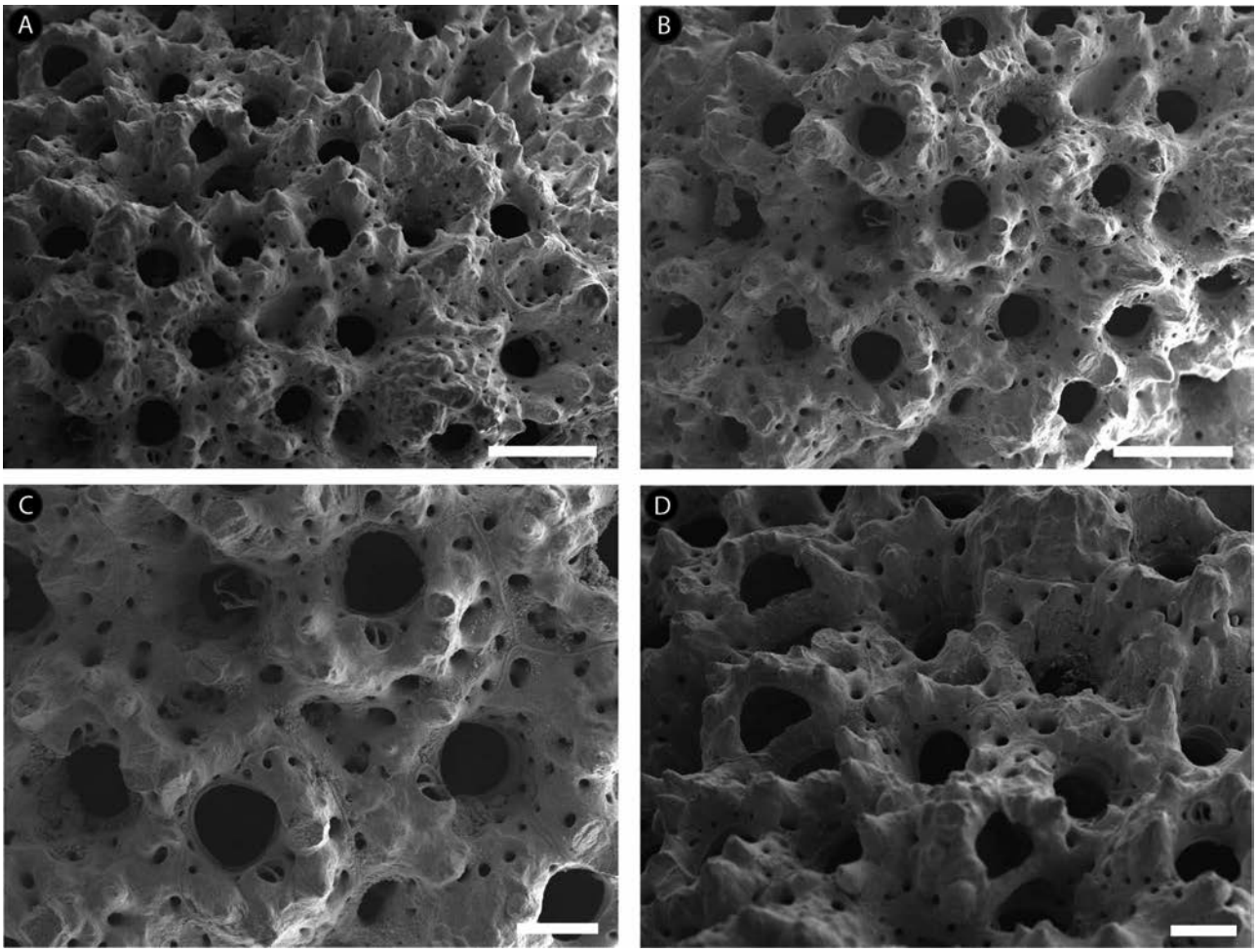

FIGURE 31. *Trematooecia ridleyi* (Kirkpatrick, 1890). **A–D,** UFBA 623, Brazil. **A,** part of encrusting colony. **B,** autozooids, some with a suboral avicularium. **C,** group of zooids showing primary orifices. **D,** ovicelled zooids. Scale bars: A, B = 500 μm; C, D = 200 μm.

TABLE 7. Morphometric data for *Trematooecia* species studied (in mm).

	T. ridleyi		***T. verticalis***	***T. rotunda***
	Brazil[1]	Brazil[2]	Australia[3]	Brazil[4]
Lz	8	10	10	15
Mean (SD)	0.433 (0.048)	0.566 (0.080)	0.783 (0.096)	0.394 (0.038)
Range	0.384–0.490	0.438–0.690	0.647–0.944	0.305–0.468
lz	8	10	10	15
Mean (SD)	0.366 (0.063)	0.530 (0.090)	0.404 (0.053)	0.327 (0.047)
Range	0.251–0.430	0.409–0.648	0.279–0.495	0.284–0.437
Dp	10	10	10	15
Mean (SD)	0.014 (0.004)	0.020 (0.008)	0.028 (0.005)	0.016 (0.003)
Range	0.007–0.022	0.017–0.021	0.023–0.044	0.011–0.024
Lo	7	4	10	15
Mean (SD)	0.162 (0.010)	0.185 (0.019)	0.162 (0.010)	0.138 (0.008)
Range	0.145–0.175	0.174–0.216	0.151–0.180	0.124–0.152

.....continued on the next page

TABLE 7. (Continued)

	T. ridleyi		*T. verticalis*	*T. rotunda*
	Brazil[1]	Brazil[2]	Australia[3]	Brazil[4]
lo	7	4	10	15
Mean (SD)	0.169 (0.009)	0.192 (0.015)	0.159 (0.009)	0.144 (0.013)
Range	0.150–0.184	0.172–0.204	0.144–0.174	0.112–0.159
Lavs	4	10	-	-
Mean (SD)	0.089 (0.009)	0.094 (0.018)	-	-
Range	0.074–0.095	0.072–0.118	-	-
lavs	4	10	-	-
Mean (SD)	0.071 (0.007)	0.064 (0.010)	-	-
Range	0.063–0.078	0.048–0.089	-	-
Lavi	1	-	-	1
Mean (SD)	0.300	-	-	0.205
Range	-	-	-	-
lavi	1	-	-	1
Mean (SD)	0.088	-	-	0.133
Range	-	-	-	-
Lavf	3	-	3	15
Mean (SD)	0.075 (0.023)	-	0.053 (0.009)	0.059 (0.009)
Range	0.050–0.097	-	0.048–0.066	0.043–0.079
lavf	3	-	3	15
Mean (SD)	0.070 (0.011)	-	0.057 (0.004)	0.051 (0.006)
Range	0.058–0.082	-	0.056–0.064	0.043–0.068
Lov	4	2	4	10
Mean (SD)	0.304 (0.068)	0.361 (0.017)	0.403 (0.010)	0.275 (0.045)
Range	0.244–0.398	0.349–0.374	0.393–0.418	0.214–0.341
lov	3	2	4	10
Mean (SD)	0.330 (0.035)	0.473 (0.021)	0.438 (0.017)	0.319 (0.030)
Range	0.291–0.375	0.458–0.489	0.421–0.461	0.271–0.364
Lovf	-	2	4	-
Mean (SD)	-	0.158 (0.005)	0.170 (0.013)	-
Range	-	0.153–0.162	0.156–0.187	-
lovf	-	2	4	-
Mean (SD)	-	0.200 (0.032)	0.091 (0.011)	-
Range	-	0.176–0.223	0.083–0.109	-

[1] NHMUK 1888.4.16.2, Fernando de Noronha, Brazil. [2] UFBA 533, Bahia, Brazil. [3] UFBA 623, Bahia, Brazil. [4] NHMUK 1910.9.19.1, Australia. [4] UFBA 533, Bahia, Brazil.

***Trematooecia verticalis* (Maplestone, 1910) n. comb.**
(Figs 32–33, Table 7)

Cellepora verticalis Maplestone, 1910: 39, pls 7–9, figs 1–2. [South Australia]
Cigclisula verticalis: Hastings 1932: 433, text-fig. 13, K–M. [South Australia]

Material examined. *Syntype*: NHMUK 1910.9.19.1, *Escharoides (Cellepora) verticalis* (Maplestone), National Museum Melbourne, C.M. Maplestone det., Dr Verco, Adelaide, col., Backstairs Passage, South Australia, 14–24 ftm (25.6–43.9 m). *Additional specimen:* NMV [Uncatalogued specimen], *Trematooecia verticalis*, Australia.

Description. Colony erect, multilaminar, flabellate, with some vertical laminae. Zooids hexagonal, longer than wide, delimited by slightly raised margins. Frontal shield heavily calcified, marginally punctured by 16–22 pores, minutely tubercular. Primary orifice small relative to frontal shield, somewhat hoof-shaped, longer than wide, sunken, with arcuate anter and broader moderately concave poster delimited by 2 downcurved condyles at about one-third orifice length. Secondary orifice non-tubercular. Suboral avicularium elliptical, laterally placed, distally directed, of two sizes, one small, the other doubled-sized. Frontal avicularia small, elliptical, rare, single, placed at zooidal margins. Interzooidal avicularium absent. Ooecium subglobose, inclined toward zooid surface, minutely tubercular; ectooecium with slit-like membranous area.

Remarks. Maplestone (1910) described the ooecia as "globose, surface granulated; in the center of the frontal wall, above the aperture, is a large, long, upright, elliptical area (sometimes slightly irregular in shape), with a membranous covering". The ectooecium is thus typical of *Trematooecia* as herein defined.

Trematooecia verticalis is distinguished from other *Trematooecia* by: erect, multilaminar, flabellate colonies, marginally punctured frontal shield, subglobose ooecium and an ectooecium with a slit-like membranous area resembling that in *T. gemmea*; its differs in lacking peristomial tubercles and having a suboral avicularium.

Distribution. Pacific: Australia.

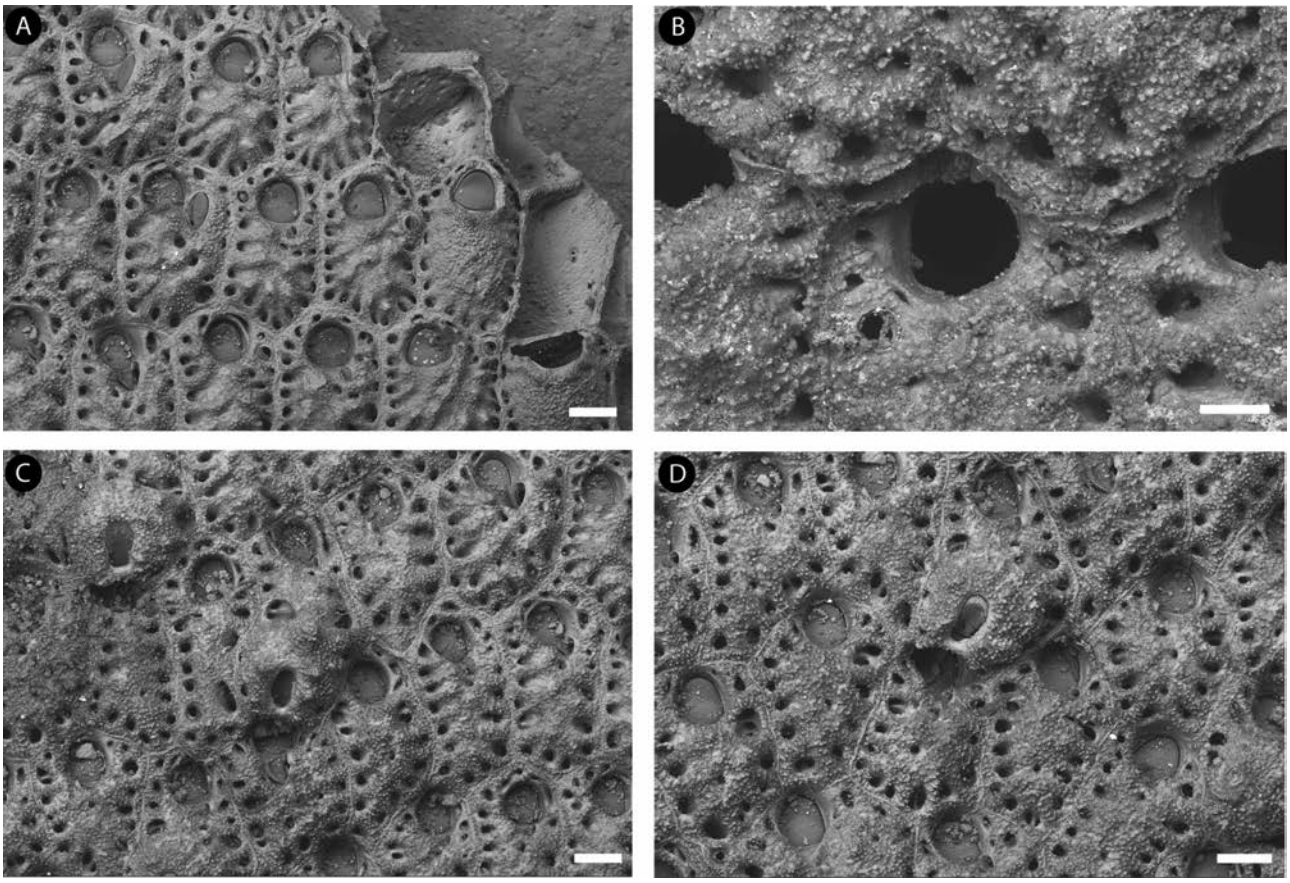

FIGURE 32. *Trematooecia verticalis* (Maplestone, 1910). **A–D,** NHMUK 1910.9.19.1, syntype, Australia. **A,** group of zooids, some with tiny suboral avicularia. **B,** primary orifice and tiny suboral avicularium. **C, D,** ovicelled zooids. Scale bars: A, C, D = 200 µm; B = 100 µm.

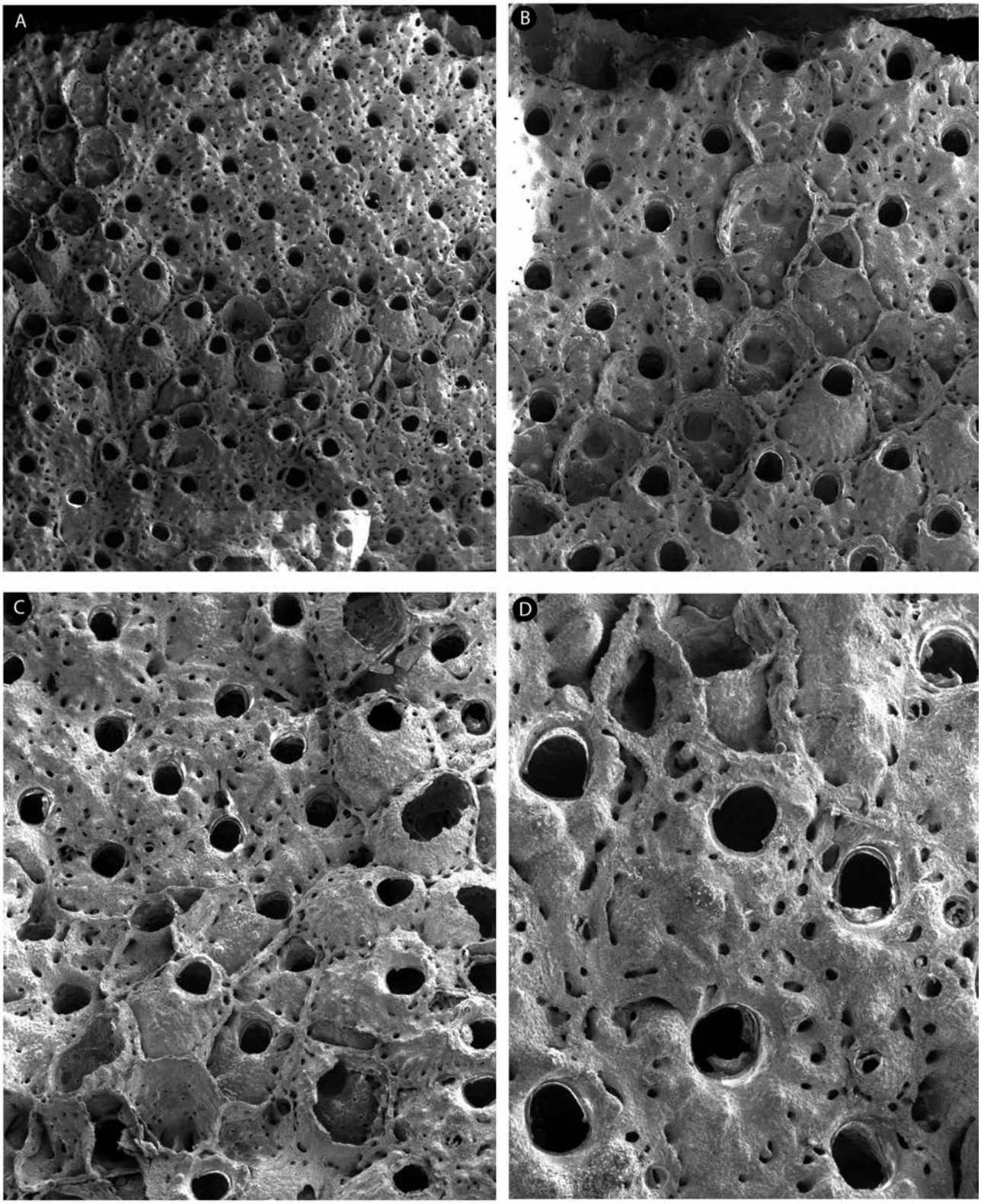

FIGURE 33. *Trematooecia verticalis* (Maplestone, 1910). **A–D,** NMV uncatalogued specimen, Australia. **A, B,** zooids at growing edge of colony. **C,** group of zooids. **D,** primary orifice and tiny frontal avicularia.

***Trematooecia rotunda* n. sp.**
(Fig. 34, Table 7)

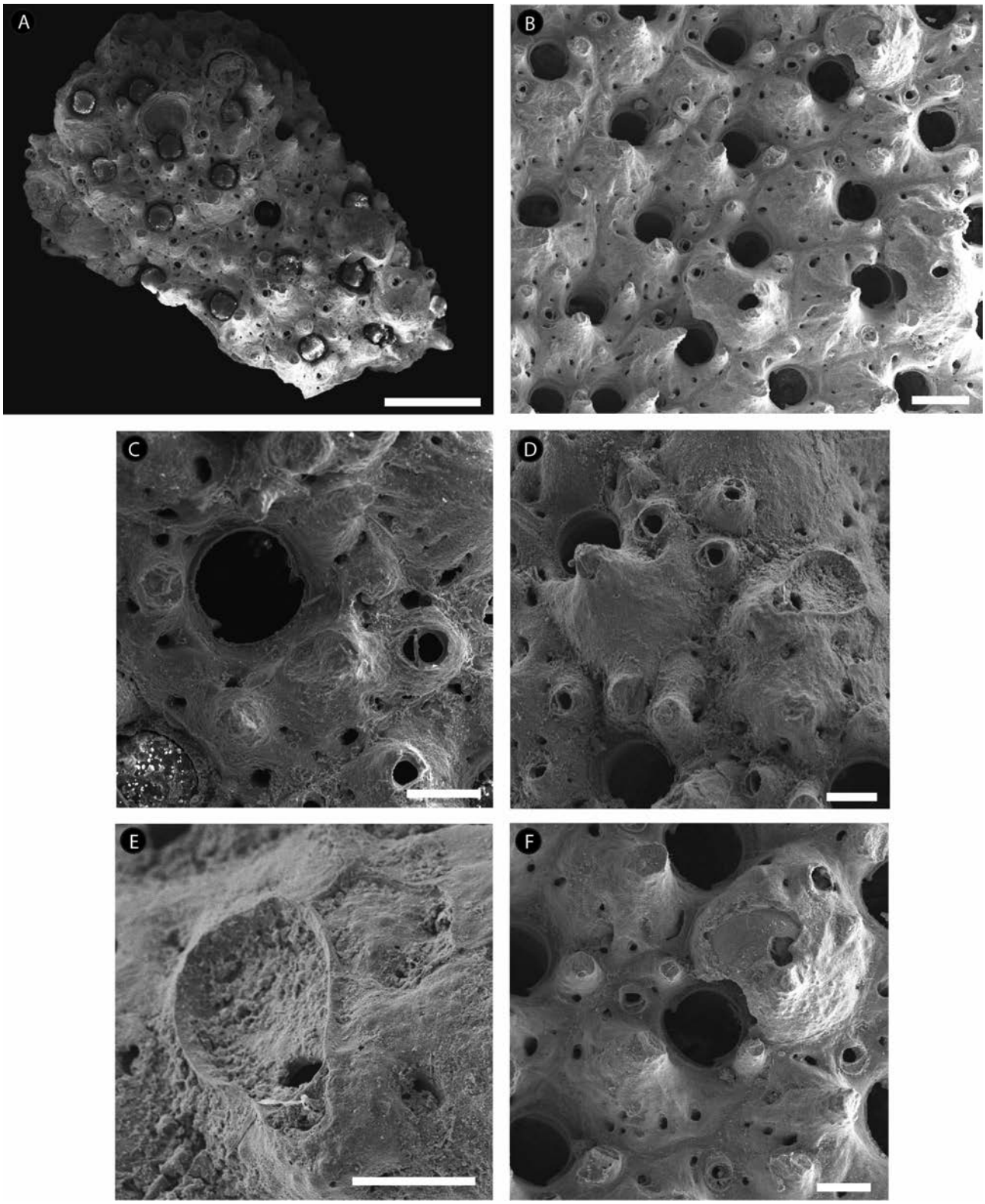

FIGURE 34. *Trematooecia rotunda* n. sp. **A, C**, UFBA 533, holotype, Brazil; **B, D–F,** UFBA 550, paratype, Brazil. A, fragment of encrusting colony. **B,** zooids, some ovicellated. **C,** primary orifice and tubercle with elliptical avicularium. **D,** frontal and interzooidal avicularia. **E,** close-up of interzooidal avicularium. **F,** close-up of ovicelled zooid. Scale bars: A = 500 µm; B = 200 µm; C–F = 100 µm.

Material examined. *Holotype:* UFBA 533, *Trematooecia* sp., A.C. Almeida det., Camaçari, Bahia, Brazil, 1994, 26 m. *Paratype:* UFBA 550, *Trematooecia* sp., A.C. Almeida det., Camaçari, Bahia, Brazil, 2000, 28 m. *Additional*

specimens: UFBA 536, *Trematooecia* sp., A.C. Almeida det., Camaçari, Bahia, Brazil, 2002, 50 m; UFBA 548, *Trematooecia* sp., A.C. Almeida det., Camaçari, Bahia, Brazil, 2002, 23 m.

Diagnosis. Encrusting *Trematooecia* with unilamellar colony and elevated elliptical avicularia on tubercles.

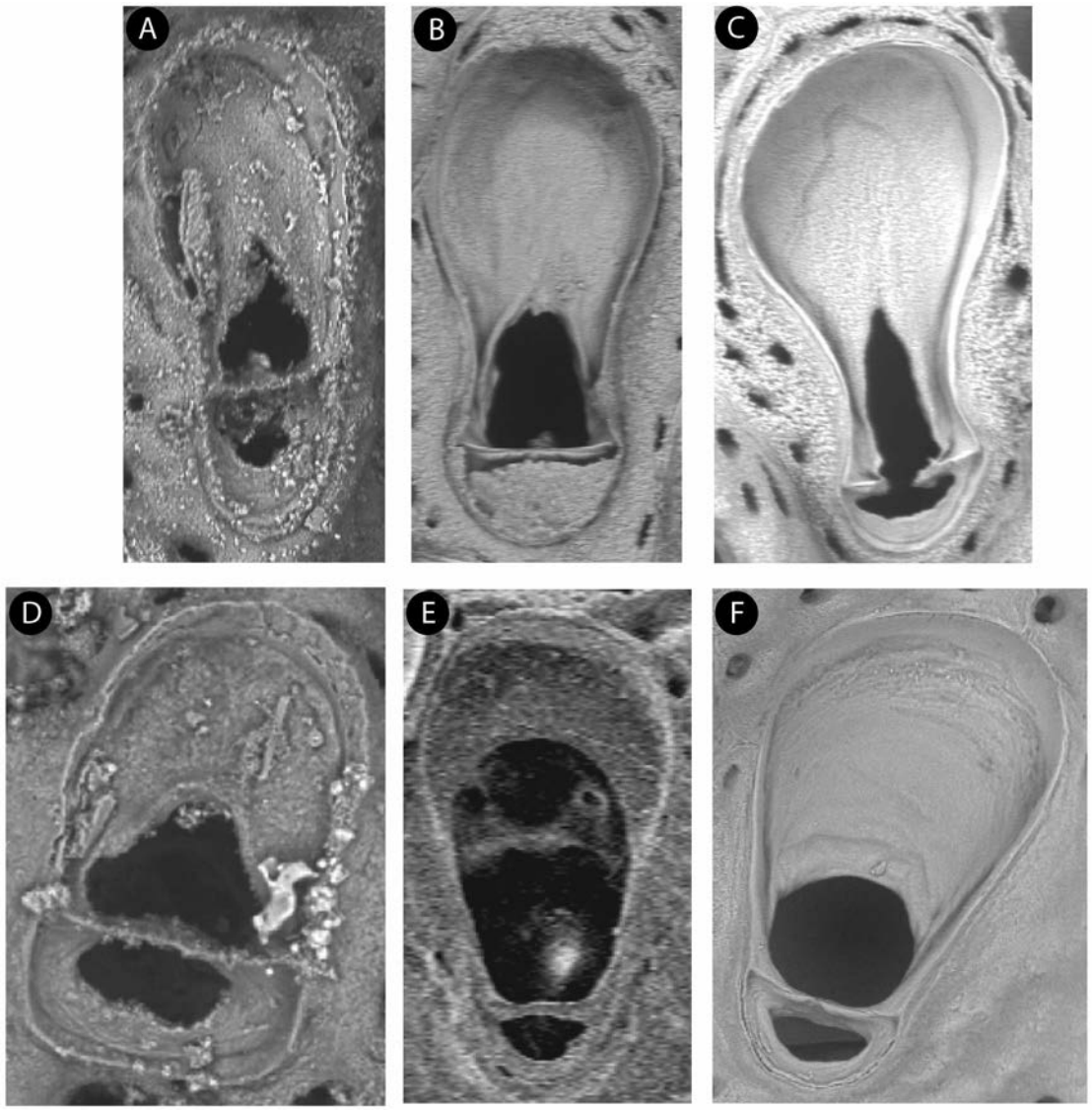

FIGURE 35. Shapes of interzooidal avicularia of Colatooeciidae. **A,** shoe-shaped, rostrum sublinguiform, with weak median constriction (*Colatooecia serrulata*). **B, C,** spatulate, marked median constriction (*Cigclisula australis*, *C. occlusa*). **D,** linguiform, no constriction (*Colatooecia serrulata*). **E, F,** obovate, no constriction (*Trematooecia aviculifera, T. protecta*).

Etymology. Latin *rotunda*, circle, alluding to the rounded autozooids.

Description. Colony encrusting, unilamellar. Zooids hexagonal, becoming rounded-polygonal with increasing calcification, as long as wide, delimited by distinct grooves. Frontal shield heavily calcified, with a few frontal pseudopores and 8–15 marginal areolar pores. Primary orifice large relative to frontal shield, centered, more or less hoof-shaped, wider than long, with arcuate anter and broad concave poster delimited by 2 downcurved condyles at about one-third orifice length. Secondary orifice surrounded by 3–4 (often 4) solid tubercles that frequently bear an elliptical avicularium. Each autozooid with a large suboral tapering umbo. Suboral avicularium absent. Frontal avicularia small (0.043–0.079 mm long, 0.043–0.068 mm wide), elliptical, single (rarely 2), placed at proximal margin of zooid. Interzooidal avicularium large, rostrum obovate; calcified palate occupying more than half rostral length; foramen rounded. Ooecium subglobose, inclined toward zooid surface, often with 1–3 tubercles and a single avicularium; ectooecium with slit-like membranous area.

Remarks. *Trematooecia rotunda* n. sp. is distinguished from all congeners by the combination of unilamellar colony and avicularium-bearing tubercles. Related species with encrusting colonies and a slit-like membranous

area in the ectooecium are *T. clivulata* and *T. hexagonalis*. *Trematooecia rotunda* n. sp. differs from *T. clivulata* in having a hoof-shaped primary orifice (transversely D-shaped in *T. clivulata*) and obovate interzooidal avicularia (spatulate in *T. clivulata*). Differences from *T. hexagonalis* include frontal shield punctuation (uniformly porous in *T. hexagonalis*) and the obovate interzooidal avicularia (absent in *T. hexagonalis*).

Distribution. Atlantic: Brazil.

Discussion

Winston (2005) erected a new monogeneric family, Colatooeciidae, for her new genus *Colatooecia*, which was characterized by a thickly calcified pseudoporous frontal shield with a peristomial spiramen, an ooecium with a median, membrane-covered costate area and avicularia with a complete pivot bar. Vieira *et al.* (2010a) pointed out some morphological similarities with *Cigclisula* and *Trematooecia*, including a similar but non-spiraminate frontal shield and ectooecial perforation(s), and added them to the family.

In fact, *Cigclisula* and *Trematooecia* share several, overlapping morphological characters (see Table 8). The main difference between *Cigclisula* and *Trematooecia* pertains to the ooecium—the ectooecium is multiporous in

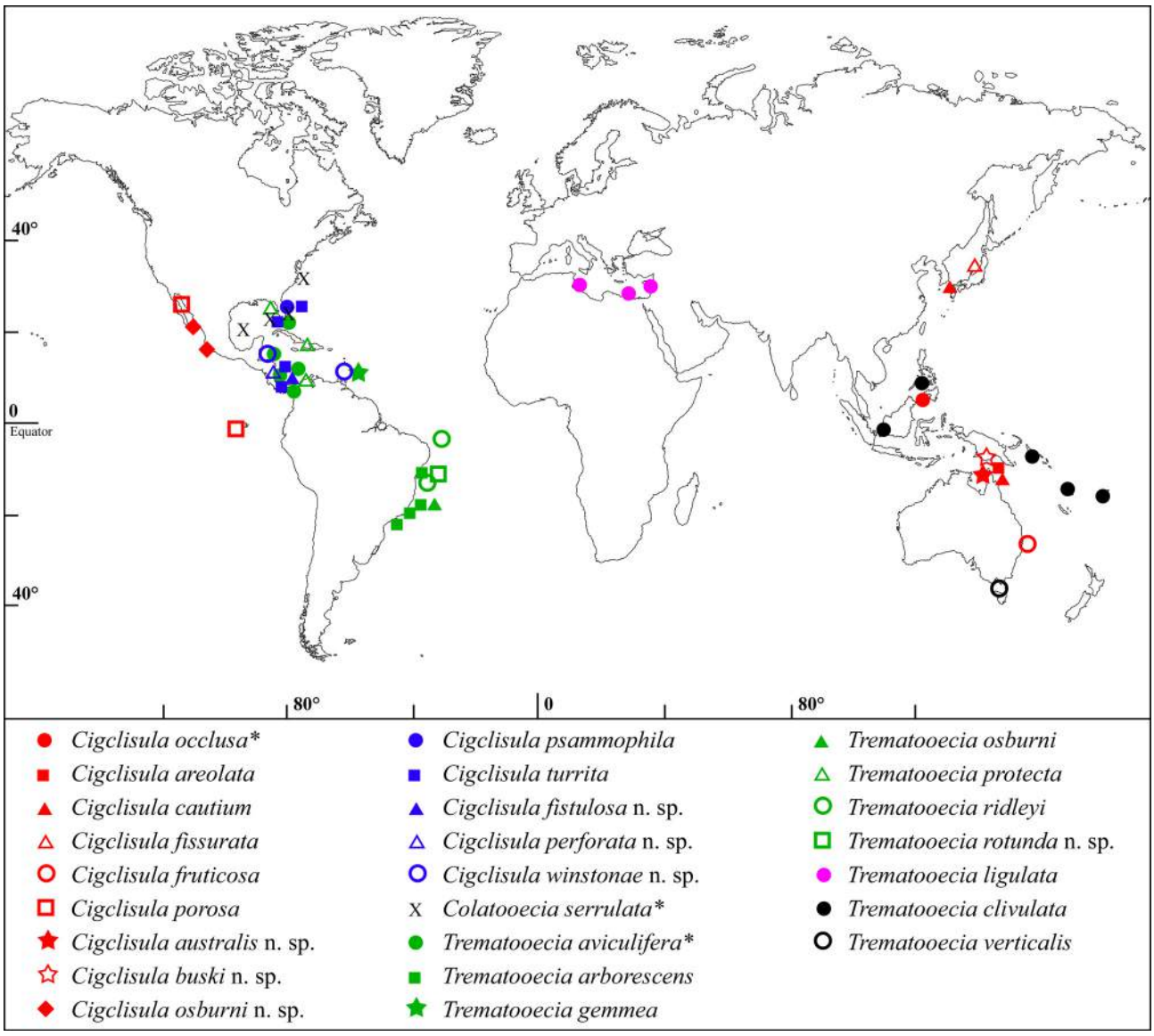

FIGURE 36. Global distribution of Colatooeciidae. The type species of each genus is asterisked. Colours: red, *Cigclisula* species from Pacific; blue, *Cigclisula* species from Atlantic; green, *Trematooecia* species from Atlantic; pink, *Trematooecia* species from Mediterranean; black, *Trematooecia* species from Indo-Pacific and Pacific.

TABLE 8. Morphological characters of species of Colatooeciidae. Number (N), Present (+) and Absent (-), Immersed ovicells (I), Prominent ovicells (P).

Taxa	Colony	Frontal-shield pores		Primary orifice	Condyles	Secondary orifice	Avicularia			Ooecium/Ectooecium
		distribution	N				Interzooidal	Suboral	Frontal	
Colatooecia										
serrulata	erect	uniform	22–36	elliptical/wider than long	-	non-tubercular	foot-shaped	-	rectangular	I / interdigitated costae
Cigclisula										
occlusa	erect	uniform	24–40	hoof-shaped/as long as wide	+	non-tubercular	spatulate	+	elliptical	P / 11–29 pseudopores
areolata	encrusting	marginal	12–24	D–shaped/wider than long	+	non-tubercular	obovate	+	-	P / 6–7 pseudopores
cautium	erect	uniform	14–24	subelliptical/as long as wide	+	non-tubercular	spatulate	+	elliptical	P / 6–7 pseudopores
fissurata	erect	marginal	12–28	subelliptical/as long as wide	?	non-tubercular	-	+	-	P / 2–5 pseudopores
fruticosa	erect	irregular	?	D-shaped/longer than wide, with sinus	+	low, with blunt processes	spatulate	+	elliptical	P / 6–7 pseudopores
porosa	encrusting	uniform	20–50	hoof-shaped/as long as wide	+	non-tubercular	-	-	elliptical	P / 33–48 pseudopores
psammophila	encrusting	marginal	?	D-shaped/longer than wide	+	4–5 solid tubercles	-	-	-	I / about 10 pseudopores
turrita	encrusting	irregular	14–41	elliptical/as long as wide	+	4–5 solid tubercles	tongue-shaped	-	elliptical	P / 25–38 pseudopores
australis n. sp.	erect	uniform	18–34	hoof-shaped/wider than long	+	non-tubercular	spatulate	+	elliptical	P / 7–18 pseudopores
buski n. sp.	erect	uniform	10–46	hoof-shaped/as long as wide	+	non-tubercular	spatulate	+	elliptical	P / 38–50 pseudopores
fistulosa n. sp.	encrusting	uniform	30–60	subcampanuliform/longer than wide	+	4–5 solid tubercles	-	-	elliptical	P / 32–55 pseudopores
osburni n. sp.	encrusting	marginal	20–40	subelliptical/longer than wide	+	4–5 solid tubercles	-	-	elliptical	P / 27–39 pseudopores
perforata n. sp.	encrusting	irregular	30–47	subcircular/longer than wide	+	4–5 solid tubercles	-	-	elliptical	P / 27–80 pseudopores
winstonae n. sp.	encrusting	irregular	23–46	elliptical/longer than wide	+	4–5 solid tubercles	spatulate	-	elliptical	I / 3–9 pseudopores
Trematooecia										
aviculifera	encrusting	marginal	7–14	D-shaped/wider than long	-	4–6 solid tubercles	obovate	+	-	P / circular membrane
arborescens	erect	marginal	18–24	elliptical/longer than wide	+	low, blunt processes	spatulate	+	elliptical	I / circular membrane
clivulata	encrusting	marginal	?	D-shaped/wider than long	+	4–5 solid tubercles	spatulate	-	elliptical	P / slit-like membrane
gemmea	erect	marginal	?	D-shaped/longer than wide	+	4–5 solid tubercles	spatulate	+	elliptical	P / slit-like membrane
hexagonalis	encrusting	uniform	36–51	hoof-shaped/longer than wide	+	4 solid tubercles	-	-	elliptical	P / slit-like membrane
ligulata	encrusting	marginal	?	elliptical/longer than wide	+	3–4 solid tubercles	spatulate	+	elliptical	P / slit-like membrane
osburni	encrusting	marginal	?	D-shaped/wider than long	-	non-tubercular	+ (?)	-	+ (?)	P / circular membrane
protecta	encrusting	marginal	8–33	D-shaped/wider than long	+	4–6 solid tubercles	obovate	+	elliptical	P / circular membrane
ridleyi	encrusting	marginal	10–20	D-shaped/wider than long	-	3–5 solid tubercles	spatulate	+	elliptical	P / circular membrane
verticalis	erect	marginal	16–22	elliptical/longer than wide	+	non-tubercular	-	+	elliptical	P / slit-like membrane
rotunda n. sp.	encrusting	marginal	8–15	elliptical, wider than long	+	3–4 solid tubercles	obovate	-	elliptical	P / slit-like membrane

Cigclisula, uniporous in *Trematooecia*. Subsidiary features of the frontal shield, primary and peristomial orifices and avicularia allow discrimination among the many species in these two genera, as is the case in many other cheilostome genera and families (e.g. Gordon 1993; Ostrovsky 2004; Vieira *et. al.* 2010b; Vieira *et al.* 2014). However, in the absence of ooecia, it would be difficult to assign any new species of *Cigclisula* and *Trematooecia* to either genus using only morphological criteria.

Redescription of the type species of *Cigclisula* and *Trematooecia*, and characterization of the ooecium in relation to these species, has led us to several generic re-assigments, resulting in the following new combinations: *Cigclisula turrita* n. comb., *Cigclisula psammophila* n. comb., *Trematooecia arborescens* n. comb., *Trematooecia gemmea* n. comb., *Trematooecia hexagonalis* n. comb. and *Trematooecia verticalis* n. comb. Seven new species are described: *Trematooecia rotunda* n. sp., *Cigclisula australis* n. sp., *C. buski* n. sp., *C. fistulosa* n. sp., *C. osburni* n. sp., *C. perforata* n. sp. and *C. winstonae* n. sp.

Species of Colatooeciidae are distributed from tropical to subtropical waters in the Atlantic and Indo-Pacific Oceans and one species is reported from the Mediterranean Sea (Fig. 36). Some records of *Cigclisula turrita* from the Indian Ocean and Red Sea still require reexamination and may belong to distinct species. Other species are known only from their type localities and have not been collected again or recognized.

Currently, we recognize one living species of *Colatooecia*, 14 of *Cigclisula* and 11 of *Trematooecia*. The recognition of seven new species of Colatooeciidae, some of them previously included in other named species, gives evidence that the number of known species can increase with the use of SEM imaging, which aids in the recognition of diagnostic characters.

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