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Targeted collections reveal new species and records of Bryozoa and the discovery of Pterobranchia in Singapore

Sudhanshi S. **Jain**[1], Dennis P. **Gordon**[2], Danwei **Huang**[1,3,4*], Piotr **Kuklinski**[5] & Lee Hsiang **Liow**[6]

Abstract. There have been 121 bryozoan species recorded from marine and freshwater ecosystems in Singapore. Here, 12 additional species, three of them new to science, are recorded for the first time in Singapore based on a targeted bryozoan collection campaign in 2019, bringing the bryozoan species tally to 133 species. The new records comprise one species each from the orders Cyclostomata and Ctenostomata and 10 species of Cheilostomata. Systematic notes are provided for the nine species representing new geographic records. One of them, a cyclostome of uncertain species identity, is left in open nomenclature. Full descriptions are provided for the new taxa, which comprise *Reptadeonella riatanae*, new species, *Arthropoma subarensis*, new species, and *Microporella sargassophilia*, new species. A full description and illustrations are also provided for topotypic material of a little-known cribrimorph cheilostome, *Cribrilaria vicariata* (Waters, 1923), for which Singapore is the type locality. Selected other species are illustrated by scanning electron microscopy for the first time. The majority of the species were found along the southern islands of mainland Singapore, mostly encrusting on coral rubble. The new records and species supplement the last comprehensive checklist produced in 2016, with prospects for further biodiversity discoveries and ecological analyses of the bryozoological fauna of Singapore. Targeted collecting of Bryozoa also yielded the first record of the hemichordate class Pterobranchia (*Rhabdopleura* sp.) in Singapore.

Key words. biodiversity, Cyclostomata, Ctenostomata, Cheilostomata, Hemichordata

INTRODUCTION

Bryozoa is an ecologically and geologically important phylum of colonial creatures that mostly form a mineralised exoskeleton, with many species essential in providing structural complexity and stability in certain marine ecosystems (Wood et al., 2012; Lombardi et al., 2014). Bryozoans fill crevices by growing underneath sheltered microhabitats, contribute to reef carbonate production and sediment formation, and form habitats for numerous other marine organisms (Gili & Coma, 1998; Wood et al., 2012; Cumming et al., 2018; Bock & Gordon, 2019). They not only have important roles in the benthos, but several species also show promise as sources of anticancer drugs and potential action against viral, brain, and parasitic diseases (e.g., Figuerola & Avila, 2019; Ciavatta et al., 2020). Globally, there are about 6,400 living species of these sessile suspension feeders described so far (World Register of Marine Species, 2021), with considerably greater diversity in the fossil record (Taylor & Waeschenbach, 2015).

The coastal environment of Singapore is home to a plethora of marine species, including bryozoans, found within coral reefs, seagrass meadows, mangrove forests, and many other ecosystems (Tan et al., 2016a; Chou et al., 2019; Lim et al., 2020). Despite being a major shipping hub that has sustained chronic reclamation and urbanisation impacts on its marine habitats, more than 3,000 marine species are known from the shallow waters of Singapore (Ng & Tan, 2000; Tan et al., 2016a, b; Wells et al., 2019; Lim et al., 2020). Bryozoans have been recorded with increasing frequency owing to extensive collecting and taxonomic work performed in recent years. For example, Goh (2010), focusing on biofouling bryozoans, identified seven species from 51 specimens collected. A comprehensive checklist of Bryozoa and Entoprocta in Singapore compiled by Tilbrook & Gordon (2016) presented 118 species of Bryozoa (three Cyclostomata, seven Ctenostomata, 108 Cheilostomata). Three species were inadvertently omitted from that checklist—i.e., *Arbocuspis angulata* (Levinsen, 1909) (reported by Key et al., 2000), *Parellisina albida* (Hincks, 1880a) (Osburn, 1949) and *Exechonella loslosensis*

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[1]Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore 117558, Singapore; Email: huangdanwei@nus.edu.sg (*corresponding author)

[2]National Institute of Water and Atmospheric Research, Private Bag 14901 Kilbirnie, Wellington, New Zealand

[3]Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, Singapore

[4]Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Singapore

[5]Institute of Oceanology, Polish Academy of Sciences, ul. Powstancow Warszawy 55, Sopot 81-712, Poland

[6]Natural History Museum & Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

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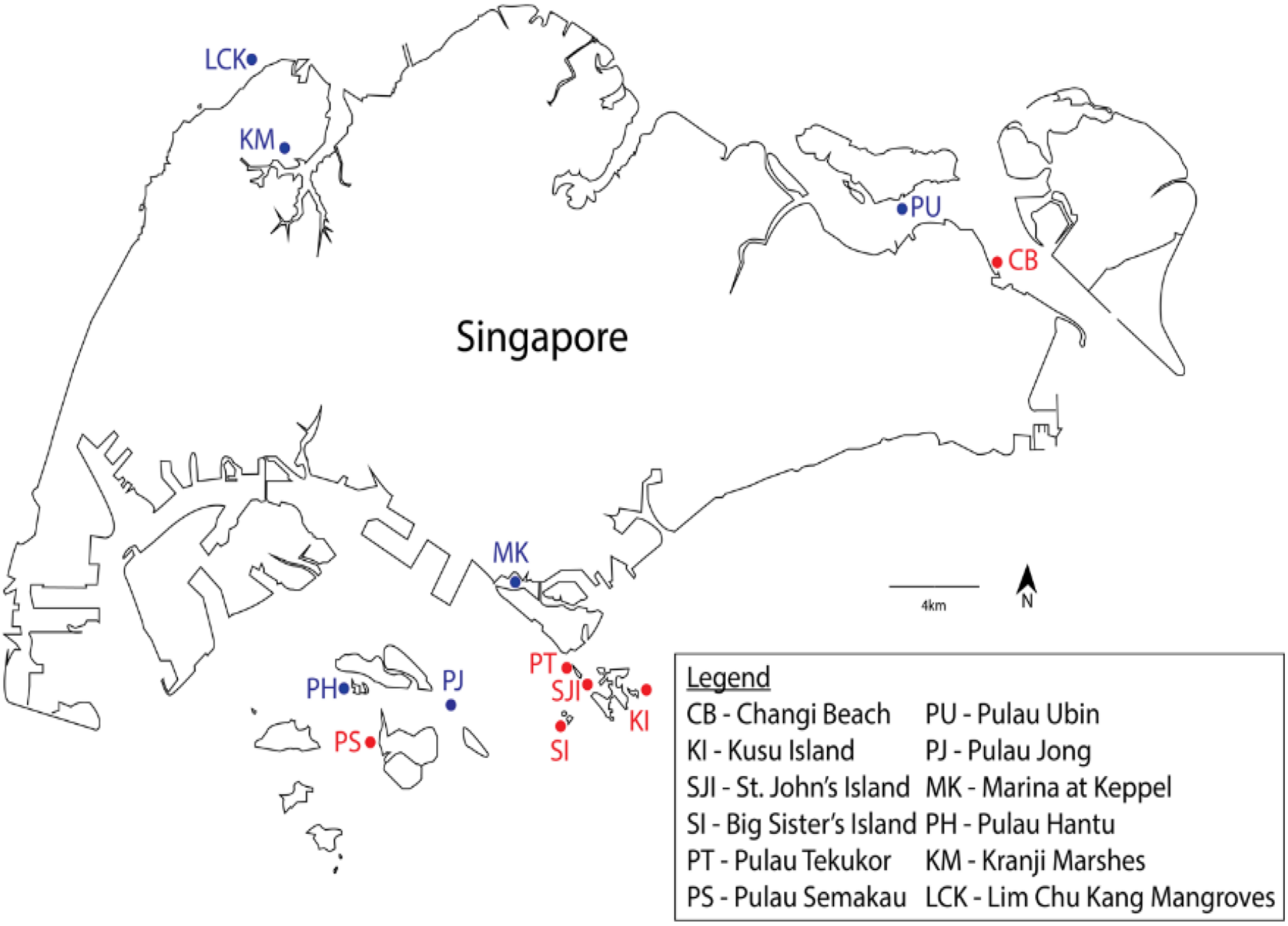

Fig. 1. Map of Singapore showing sites targeted for bryozoan collecting in this study. Sites in red are where new bryozoan records were collected; bryozoans were collected from all sites in previous studies.

Tilbrook, 2006—so 121 species should have been the tally at that time. The total compilation was a result of multiple collections and sampling campaigns carried out in the last decade, including the Comprehensive Marine Biodiversity Survey (CMBS; 2010–2015) which sampled extensively in various coastal ecosystems throughout both the Singapore and Johor Straits (Tan et al., 2015, 2016b), and the Bryozoan and Hydroid Workshop in 2013 which specifically compiled bryozoan checklists from collection data and museum material (Tilbrook & Gordon, 2015; Gordon, 2016).

Following these recent inventories and studies, we here present 12 additional new marine species records from Singapore based on targeted collecting of bryozoans in 2019 for a global molecular-sequencing project (Orr et al., 2022). One new ctenostome bryozoan species has already been described from this collecting (Decker et al., 2021) and here we present additional genus records and describe three new species. All are illustrated by scanning electron microscopy except for a well-known ctenostome species that lacks a skeleton. One species is left in open nomenclature. A full description and illustrations are also provided for topotypic material of a little-known cribrimorph cheilostome, *Cribrilaria vicariata* (Waters, 1923). It had been historically synonymised and was accordingly long overlooked. Selected other species are illustrated by scanning electron microscopy for the first time. We also present the first record of Pterobranchia (phylum Hemichordata), found together with bryozoans on coral rubble.

MATERIAL AND METHODS

All specimens were hand-collected from the intertidal zone or by SCUBA in deeper waters in May 2019. Intertidal collections were conducted at Changi Beach (near Carpark 7; 1.3740°N, 104.0070°E), Kranji Marshes (1.4204°N, 103.7203°E), Lim Chu Kang Mangroves (1.4460°N, 103.7082°E), Marina at Keppel Bay (1.2642°N, 103.8129°E), Pulau [= Island] Hantu Besar (lagoon; 1.2272°N, 103.7486°E), Pulau Semakau (1.2080°N, 103.7550°E), and Pulau Ubin (jetty; 1.4026°N, 103.9725°E). SCUBA dives were performed at the reefs off Big Sister's Island (or Pulau Subar Laut; 1.2125°N, 103.8362°E), Kusu Island (1.2257°N, 103.8599°E), Pulau Jong (1.2140°N, 103.7875°E), Pulau Tekukor (1.2299°N, 103.8376°E), Pulau Hantu (1.2273°N, 103.7469°E), and St. John's Island (1.2192°N, 103.8456°E), to collect bryozoans between 1 and 17 m depth (Fig. 1).

Encrusting colonies were collected along with the substrata (e.g., rocks, plastic pipes, glass bottles). Samples were immediately stored in seawater for transport and then

Table 1. Details of collection sites and dates.

Site	GPS coordinates	Depth (m)	Date	No. of specimens	No. of new species records
Big Sister's Island	1.2125° N, 103.8362° E	15–17	3 May 2019	68	5
Pulau Tekukor	1.2299° N, 103.8376° E	1–17	6 May 2019	32	2
Kusu Island	1.2257° N, 103.8599° E	15–17	3 May 2019	30	2
Changi Beach	1.3740° N, 104.0070° E	0	9 May 2019	44	1
Pulau Semakau	1.2080° N, 103.7550° E	0	7 May 2019	34	1
St. John's Island	1.2192° N, 103.8456° E	4–7	6 May 2019	8	1
Pulau Ubin	1.4026° N, 103.9725° E	0	10 May 2019	32	0
Marina at Keppel Bay	1.2642° N, 103.8129° E	0	9 May 2019	13	0
Pulau Jong	1.2140° N, 103.7875° E	13–15	4 May 2019	11	0
Pulau Hantu (lagoon)	1.2272° N, 103.7486° E	0	4 May 2019	11	0
Lim Chu Kang Mangroves	1.4460° N, 103.7082° E	0	8 May 2019	3	0

scraped off the substratum upon microscopic examination. For most specimens, part of the colony (1–2 cm^2) was stored in molecular grade 100% ethanol for DNA sequencing in another project (Orr et al., 2022) and/or sequestered for chemical analyses. The rest of such divided samples were air-dried for subsequent scanning electron microscopy (SEM) prior to long-term preservation. Colonies that were too small were directly air-dried. Colony fragments were analysed by SEM before and after treatment with household bleach to highlight skeletal characters such as autozooids (feeding zooids), avicularia (zooid polymorphs), ovicells (reproductive structures) and others.

Specimens prepared for scanning electron microscopy (SEM) were metal-coated in gold-palladium or left uncoated, and photographed using a Hitachi TM4040PLUS Tabletop SEM (Natural History Museum, Oslo) and a Leica MC190 HD Microscope Camera mounted on a Leica M205C Stereo Microscope (Reef Ecology Laboratory, Singapore). Measurements of morphological characters were made of scanned images using Fiji (ImageJ) software (Schindelin et al., 2012). Metrics for newly described species are given in µm as the range, followed by the mean and number of measurements. The key characters have the following abbreviations: ZL, zooid length; ZW, zooid width; OL, orifice length; OW, orifice width; AvL, avicularium length; AvW, avicularium width; AvML, avicularium mandible length; VavL, vicarious avicularium length; VavW, vicarious avicularium width; OvL, ovicell length; OvW, ovicell width.

RESULTS

A total of 285 bryozoan specimens were collected from 11 sites across Singapore (Fig. 1). No bryozoans were found at Kranji Marshes. Overall, 127 taxa were recorded (114 Cheilostomata, 8 Ctenostomata, and 5 Cyclostomata). The highest number of species (50) was found at Big Sister's Island, followed by Changi Beach (24), Pulau Semakau (22), and Pulau Tekukor (20). Locality data are given in Table 1. Of these taxa, 115 were recorded in a comprehensive checklist by Tilbrook & Gordon (2016). The remaining 12 taxa comprise three new species and nine new geographic records for Singapore. Eleven of them are named, with one species left in open nomenclature owing to uncertain species identity. A pterobranch hemichordate, *Rhabdopleura* sp., was found at one locality (Pulau Tekukor), on a piece of coral also encrusted by Bryozoa. It is worth noting that part of the reason for the moderately high number of species at Changi Beach was because of the availability of artificial substrata like broken porcelain, bottle glass and plastic. Rocks at the southeastern end of the beach also yielded bryozoans in damp, shaded crevices.

CHECKLIST OF NEW RECORDS AND SPECIES

Phylum Bryozoa Ehrenberg, 1831

Class Stenolaemata Borg, 1926

Order Cyclostomata Busk, 1852

Suborder Tubuliporina Milne Edwards, 1838
  Superfamily Tubuliporoidea Johnston, 1837
    Family Tubuliporidae Johnston, 1837
      Exidmonea sp., Kusu Island (Fig. 2A, B)

Class Gymnolaemata Allman, 1856

Order Ctenostomata Busk, 1852

Suborder Stoloniferina Ehlers, 1876
  Superfamily Walkerioidea Hincks, 1880
    Family Mimosellidae Hincks, 1877
      Bantariella verticillata (Heller, 1867), St. John's Island

Order Cheilostomata Busk, 1852

Suborder Flustrina Smitt, 1868
  Superfamily Calloporoidea Norman, 1903
    Family Heliodomidae Vigneaux, 1949
      Setosellina constricta Harmer, 1926, Big Sister's Island (Fig. 2E)
  Superfamily Buguloidea Gray, 1848
    Family Candidae d'Orbigny, 1851
      Canda pecten Thornely, 1907, Big Sister's Island (Fig. 2F)
    Family Bugulidae Gray, 1848
      Caulibugula mortenseni (Marcus, 1925), Kusu Island (Fig. 3A–C)
  Superfamily Adeonoidea Busk, 1884
    Family Adeonidae Busk, 1884
      Reptadeonella riatanae, new species, Pulau Tekukor (Fig. 4A–C)
      Reptadeonella cellulanus Tilbrook, Hayward & Gordon, 2001, Big Sister's Island (Fig. 4D)
  Superfamily Smittinoidea Levinsen, 1909
    Family Smittinidae Levinsen, 1909
      Pleurocodonellina microperforata Tilbrook, 2006, Pulau Semakau (Fig. 5A)
  Superfamily Schizoporelloidea Jullien, 1882
    Family Lacernidae Jullien, 1888
      Arthropoma subarensis, new species, Big Sister's Island (Fig. 5B–D)
    Family Microporellidae Hincks, 1879
      Microporella sargassophilia, new species, Pulau Tekukor (Fig. 6A–E)
    Family Hippopodinidae Levinsen, 1909
      Thornelya fuscina Tilbrook, Hayward & Gordon, 2001, Big Sister's Island (Fig. 7A)
  Superfamily Celleporoidea Johnston, 1838
    Family Hippoporidridae Vigneaux, 1949
      Scorpiodinipora costulata (Canu & Bassler, 1929), Changi Beach (Fig. 7B)

Phylum Hemichordata Bateson, 1885

Class Pterobranchia Lankester, 1877

Subclass Graptolithina Bronn, 1849

Order Rhabdopleurida Fowler, 1892

    Family Rhabdopleuridae Harmer, 1905
      Rhabdopleura sp., Pulau Tekukor (Fig. 7C–F)

SYSTEMATIC NOTES ON NEW RECORDS

Exidmonea sp.

(Fig. 2A, B)

Only a single colony fragment c. 5 mm long, with several bifurcations, was found in the collection. It lacks basal kenozooids, and so is attributed to the cyclostome genus *Exidmonea* David, Mongereau & Pouyet, 1972 instead of *Idmidronea* Canu & Bassler, 1920. Mean branch width is 353 µm proximally, narrowing to 248 µm in distal parts of the colony fragment. Peristomes are arranged in fascicles of two, curving to right and left along the apex of the branches. The frontal-most peristomes have a mean peristome length of 235 µm, whereas the lower peristomes are very short (< 55 µm long). Mean apertural diameter (or length if asymmetrical) of uppermost peristomes is 89 µm whereas that of lower peristomes is 124 µm. At the proximal-most axil of the colony fragment is a swollen densely pseudoporous V-shaped gonozooid. There is no apparent ooeciostome but there is a round ooeciopore. This diminutive species may be new to science. It somewhat resembles material that Harmer (1915) described and illustrated (possibly from the Celebes Sea, but Harmer's station attribution doesn't accord with Siboga Expedition data). He ascribed it to "*Tubulipora atlantica* var. *flexuosa*" but this Atlantic species [= *Exidmonea flexuosa* (Smitt, 1873), illustrated by Winston, 2005] has longer peristomes in fascicles of three and a compact inflated sac-like gonozooid. Harmer (1915) included *Idmonea tenella* Ortmann, 1890 from Japan in the synonymy of *E. flexuosa* and the two species appear very close. Unfortunately, Ortmann (1890) provided only small line drawings and the species has not been illustrated since (and may no longer exist—see Mawatari, 1997), so comparison is difficult. Canu & Bassler (1929) described two new diminutive species from the Philippines—*Idmonea filiformis* and *Idmonea parvula*—that may belong to *Exidmonea* and which appear similar to our specimen from Singapore. *Idmonea filiformis* had fascicles of only two peristomes, and a cited peristome diameter of 80 µm, but branch width was larger (500 µm) than in our specimen (353 µm); *I. parvula* had a cited peristome diameter

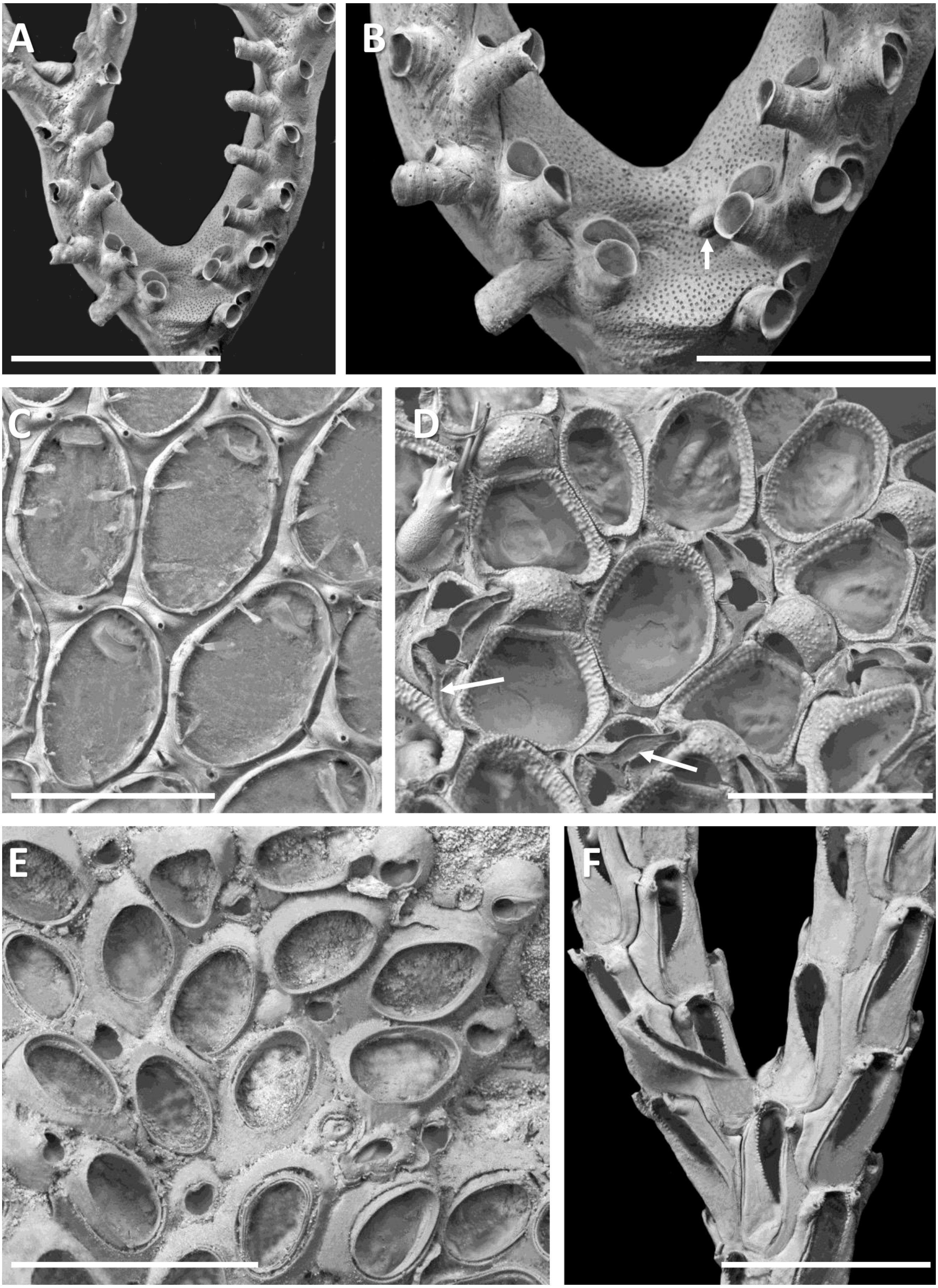

Fig. 2. A, B, *Exidmonea* sp., respectively showing dichotomous branching and a gonozooid; the ooeciopore is indicated by an arrow; C, *Arbopercula angulata* Levinsen, 1909; D, *Parellisina albida* (Hincks, 1880a), arrows indicate two of the open avicularian mandibles; E, *Setosellina constricta* Harmer, 1926; F, *Canda pecten* Thornely, 1907, note the curved avicularium at the bottom of the left-hand branch. Scale bars = 1 mm (A); 0.5 mm (B–F).

of 90 µm (matching ours) and a smaller branch width (400 µm) but 2–3 peristomes per fascicle. More material from Singapore and study of the specimens of Canu & Bassler (1929) are needed for adequate taxonomic characterisation and comparison.

Bantariella verticillata **(Heller, 1867)**

This widespread ctenostomatous species of warmer waters is moderately common in the western Pacific, where it has been recorded from Korea (Seo, 2011) and Japan (Silén, 1942) to Indonesia (Harmer, 1915) and eastern Australia (Cook et al., 2018). It occurs on a variety of substrata, including algae, as clusters or rosettes of erect zooids arising from short kenozooids near a stolon node.

Setosellina constricta **(Harmer, 1926)**

(Fig. 2E)

This species was discovered on coral rubble as spot-like colonies 2–3 mm in diameter. Autozooids are 210–379 µm long (mean 299 µm) with oval opesiae, and each is typically associated with a small interzooidal avicularium at their distal end, the mandible of which is setiform. There are no ooecia. This species has been discovered in the Middle Miocene of Java, where tiny colonies 1–2 mm in diameter once lived interstitially on sand grains (Di Martino et al., 2019).

Canda pecten **Thornely, 1907**

(Fig. 2F)

Colonies are erect, planar, biserial, and dichotomously branching. On the frontal side of branches autozooids face obliquely away from the branch axis, while on the abfrontal side is a disconnected series of triangular vibracula, each with a setiform mandible that curves round the frontal side. Short transverse rootlets from vibracular chambers connect adjacent branches at intervals. Autozooidal opesiae taper proximally and characteristic frontal avicularia curve obliquely across branches near a bifurcation (Fig. 2F). There is no scutal spine. The species is principally Indo-West Pacific in its distribution (Harmer, 1926; Tilbrook, 2006).

Caulibugula mortenseni **(Marcus, 1925)**

(Fig. 3A–C)

Brownish-orange species forming clusters of long stalks up to 30 cm long, each of which ends in an array of radiating branches (Marcus, 1925) that, underwater, give the appearance of a starburst (Fig. 3A). Branches are narrowly biserial and some zooids bear an elongate birds-head avicularium at their proximal end (Fig. 3C). The type locality is Sunda Strait, Indonesia.

Reptadeonella cellulanus **Tilbrook, Hayward & Gordon, 2001**

(Fig. 4D)

Our material is generally in accord with this species, which seems to be somewhat variable in the size and orientation of the suboral avicularium and height of the peristome. Autozooids measure 561–818 µm long (mean 629 µm) and 264–477 µm wide (mean 362 µm), close to that of colonies from Efate, Vanuatu (type locality), with a mean zooid length of 650 µm and width of 340 µm (Tilbrook et al., 2001), whereas zooids from the Solomon Islands were cited as being 500–600 µm long and 300–400 µm wide (Tilbrook, 2006). Tilbrook (2006) noted that the ancestrula of this species is not single as originally reported but comprises a triad of zooids. Harmer (1957) illustrated putative *Reptadeonella joloensis* (Bassler, 1936) from Singapore, but, as L. Vieira (pers. comm., 2022) pointed out, Harmer's illustration may represent what is now *R. cellulanus*, which means that *R. joloensis* may not be a part of the Singapore bryofauna (as listed by Tilbrook & Gordon, 2016). Scanning electron microscopy of the material in the Cambridge Museum examined by Harmer (from the southern Philippines) would clarify the issue.

Pleurocodonellina microperforata **Tilbrook, 2006**

(Fig. 5A)

Our material accords with Tilbrook's description of this species from the Solomon Islands in virtually all respects, except that the latero-oral avicularia in the type material tend to have slightly more acute rostral tips. Autozooids in a measured specimen from Singapore are 475–552 µm long (mean 522 µm) and 218–331 µm wide (mean 250 µm), compared to the cited means of ~500 µm long and 300 µm wide (Tilbrook, 2006).

Thornelya fuscina **Tilbrook, Hayward & Gordon, 2001**

(Fig. 7A)

Our material is not perfectly preserved, with many orifices and avicularia damaged, but enough characters are available to determine the species. Key features include the orifice (which is not parallel-sided as in *Thornelya ceylonica* (Thornely, 1905) and has a narrower sinus), and the small avicularia, which are fewer than in *T. ceylonica* and can sometimes be arranged in a set of three, comprising a pair flanking an orifice and another, distal to the orifice, on the succeeding zooid. This arrangement is the origin of the name *fuscina* (three-pronged fork). There are three oral spines. The occasional large avicularia illustrated by Tilbrook (2006) in *T. fuscina* were not seen in our material. Autozooids measure 407–586 µm long (mean 501 µm) and 294–443 µm wide (mean 358 µm), compared to that of colonies from Efate, Vanuatu (type locality), with a mean zooid length of 560 µm and width of 460 µm (Tilbrook et al., 2001); zooids from the Solomon Islands were cited as averaging 570 µm long and 480 µm wide (Tilbrook, 2006). Zooids in the Singapore material overlap with published ranges for length but are non-overlapping for width. The only other validated *Thornelya* species from the tropical western Pacific is *T. perarmata* Harmer, 1957; it differs from *T. fuscina* in having narrow parallel-sided orifices, six oral spines, and numerous small adventitious avicularia distributed around the margins of the zooid as well as near the orifice. *Hippomenella mila* Scholz, 1991 from the Philippines may belong to *Thornelya* (see Tilbrook, 2006: 342; Bock, 2022), but it has orifices that are as wide as long and 5–8 oral spines.

Scorpiodinipora costulata (Canu & Bassler, 1929)
(Fig. 7B)

This species may represent a complex of cryptic species or an example of a human-mediated tropicopolitan coloniser. The Singapore material accords in all respects with the description given by Harmelin et al. (2012), who analysed known records of this species (under various names) from different oceans and selected a type from Romblon, Philippines. Autozooids in the unilamellar encrusting colonies of this species are relatively simple in that they lack oral spines, avicularia, and ovicells. The imperforate frontal shield has radial ridges, and the orifice is elongate-oval with a slight submedial constriction where the condyles are placed. Autozooids in our material measure 302–429 μm long (mean 363 μm) and 171–292 μm wide (mean 227 μm). Harmelin et al. (2012) provided measurements for material from Lebanon, the Red Sea, Oman, Ghana, and Brazil (but not Romblon). Zooid length in the Singapore material is closest to that from Brazil (360 μm) and zooid width to that from Ghana (221 μm).

TOPOTYPIC MATERIAL OF A LITTLE-KNOWN CRIBRIMORPH

Singapore is the type locality (no further site information is given in the historical literature) for a cribrimorph species first named and described as *Puellina innominata* var. *vicariata* by Waters (1923). It was synonymised by Harmer (1926) and subsequently overlooked in the literature. Our collecting yielded additional specimens of this scarcely known, but taxonomically valid, species. Accordingly, we redescribe it here based on the new material. The type specimen is in the Manchester Museum, U.K., and not readily amenable to scanning electron microscopy. The description below is based on a colony that was encrusting rock in the low intertidal at Pulau Semakau. Part of the same material was retained for molecular sequencing.

Superfamily Cribrilinoidea Hincks, 1879

Family Cribrilinidae Hincks, 1879

Genus *Cribrilaria* Canu & Bassler, 1929

Cribrilaria vicariata (Waters, 1923), new combination
(Fig. 3D, E)

Puellina innominata var. *vicariata* Waters, 1923: 559, pl. 17, fig. 3.
Colletosia radiata: Harmer, 1926: 475 (part). Non *Eschara radiata* Moll, 1803.
Cribrilaria aff. *radiata*: Ristedt, 1985: 20, fig. 3e–h. Non *Eschara radiata* Moll, 1803.
Puellina vicariata: Tilbrook & Gordon, 2016: 597.

Material examined. BLEED 1540 (University of Oslo), Pulau Semakau, Singapore, 0 m, 7 May 2019.

Description. Colony extensive, forming uni–bilayered sheets up to 4–5 cm in diameter. Zooids subhexagonal [350–482 μm long (mean 403 μm), 217–385 μm wide (mean 292 μm), n = 14]. Costal shield almost flattened, with no recognisable gymnocyst, comprising 18–24 pinnate costae very variable in length and width, the most proximal ones typically shortest, while even some lateral costae very narrow; no pelmatidia; first row of costae fused medially below the proximal edge of the orifice, forming conspicuous narrow groove with an almost rounded proximal pore; outermost intercostal pores large and rounded; almost 6 intercostal lacunae with 1–2 minute denticles projecting into each lacuna. Orifice high-arched [44–68 μm long (mean 51 μm), 65–102 μm wide (mean 74 μm), n = 14] and bordered by 4–5 (mostly four) narrow spines. Avicularia interzooidal and variable in length [231–642 μm long (mean 350 μm), 103–173 μm wide (mean 143 μm), n = 4], but notable for their proportionately long, very narrowly curving or rarely straight rostrum that can be weakly denticulate; distal tip rounded, palatal foramen elongate, no mandibular pivots; the proximal cryptocyst smooth. Avicularian cystid asymmetrically wider on one side than the other. Ovicells prominent, resting on concavity of distal costal field [172–239 μm long (mean 200 μm), 152–188 μm wide (mean 175 μm), n = 4]. Ooecium more or less smooth with a slight median keel and imperforate, maternal orifice often larger than non-ovicellate zooids, flanked on each side by a pair of spines. Kenozooids interzooidal, with cribrate frontals and no orifice, commonly occurring in clusters in the colony.

Remarks. This distinctive species has not been described since 1923. It differs from the European species *Cribrilaria innominata* (Couch, 1844) in several important respects. The latter has only 9–14 costae (most commonly 11–12), 1–5 intercostal lacunae (none denticulate) and four oral spines in ovicellate zooids; avicularia are proportionally shorter and straight. *Cribrilaria vicariata* is one of the more robust species of *Cribrilaria*, forming relatively thick, extensive crusts a few centimetres in diameter. The distinctive kenozooids illustrated by Waters (1923) were observed by us but not illustrated by SEM at the time of collecting (or subsequently).

Tilbrook & Gordon (2016) recorded a second species in Singapore (as *Puellina* sp.) but did not determine the species. It is possible that it may correspond to "*Cribrilina radiata*" of Jullien (1881: 205; though not this European species), who reported finding several small colonies on stems of the gorgonian *Melithaea australis* (as *Anicella*). He noted that they were especially remarkable for the straightness of the avicularia, which rules out *C. vicariata*. *Cribrilaria egretta* Ryland & Hayward, 1992 (as *Puellina*) from Heron Island, Great Barrier Reef, is very close to *C. vicariata* and may be conspecific. It appears to differ in having oral-spine bases that are wider and close together. We here follow Rosso et al. (2018) in treating the three subgenera of *Puellina* as full genera.

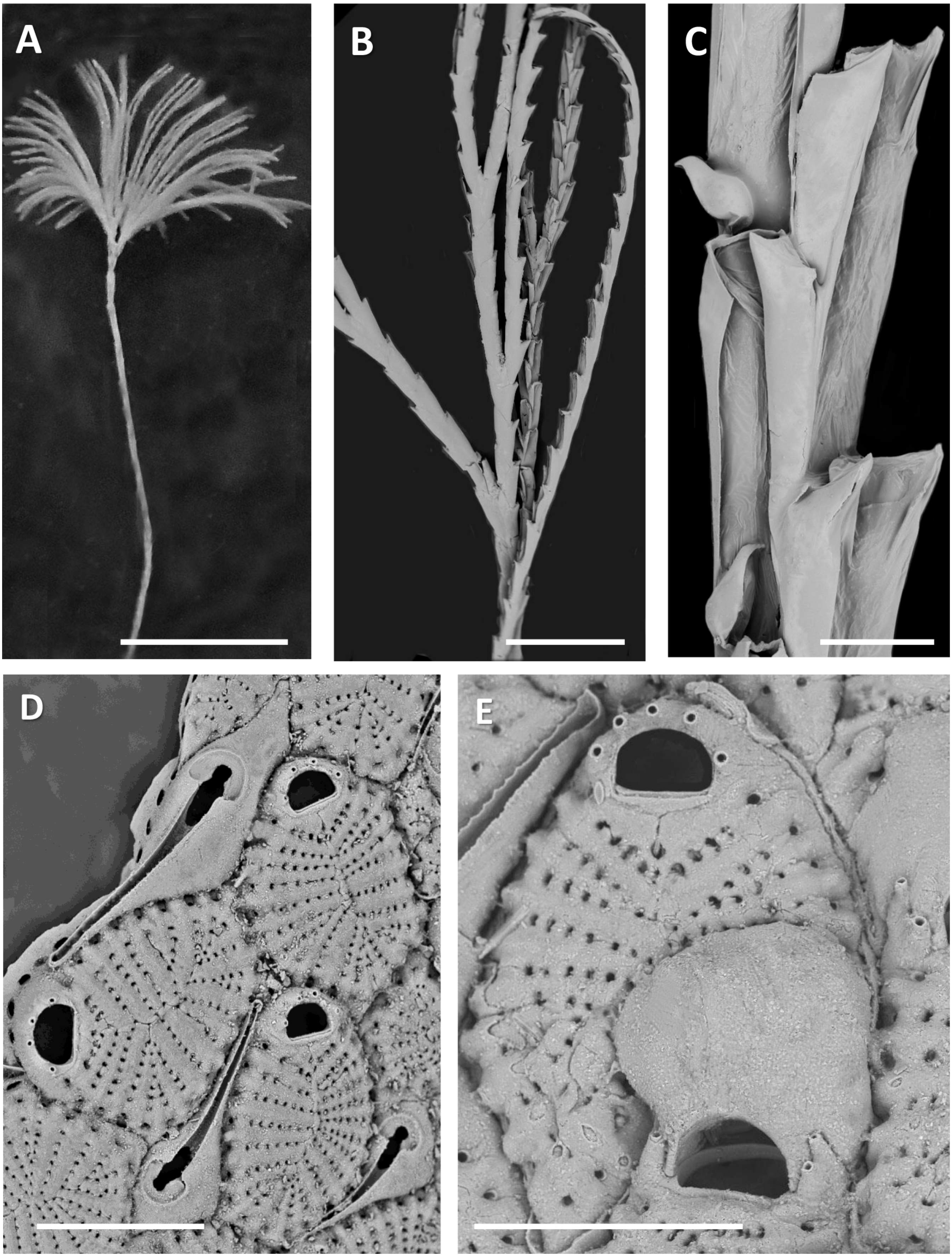

Fig. 3. A–C, *Caulibugula mortenseni* (Marcus, 1925); A, a single stem from a very large multistemmed colony; B, frontal and abfrontal sides of branches; C, autozooids and two birds-head avicularia; D, E, *Cribrilaria vicariata* (Waters, 1923); D, autozooids with four oral spine-bases and avicularia; E, a zooid with five oral spine-bases and an ovicell. Scale bars = 2 mm (A); 0.1 mm (B, C); 0.3 mm (D); 0.2 mm (E).

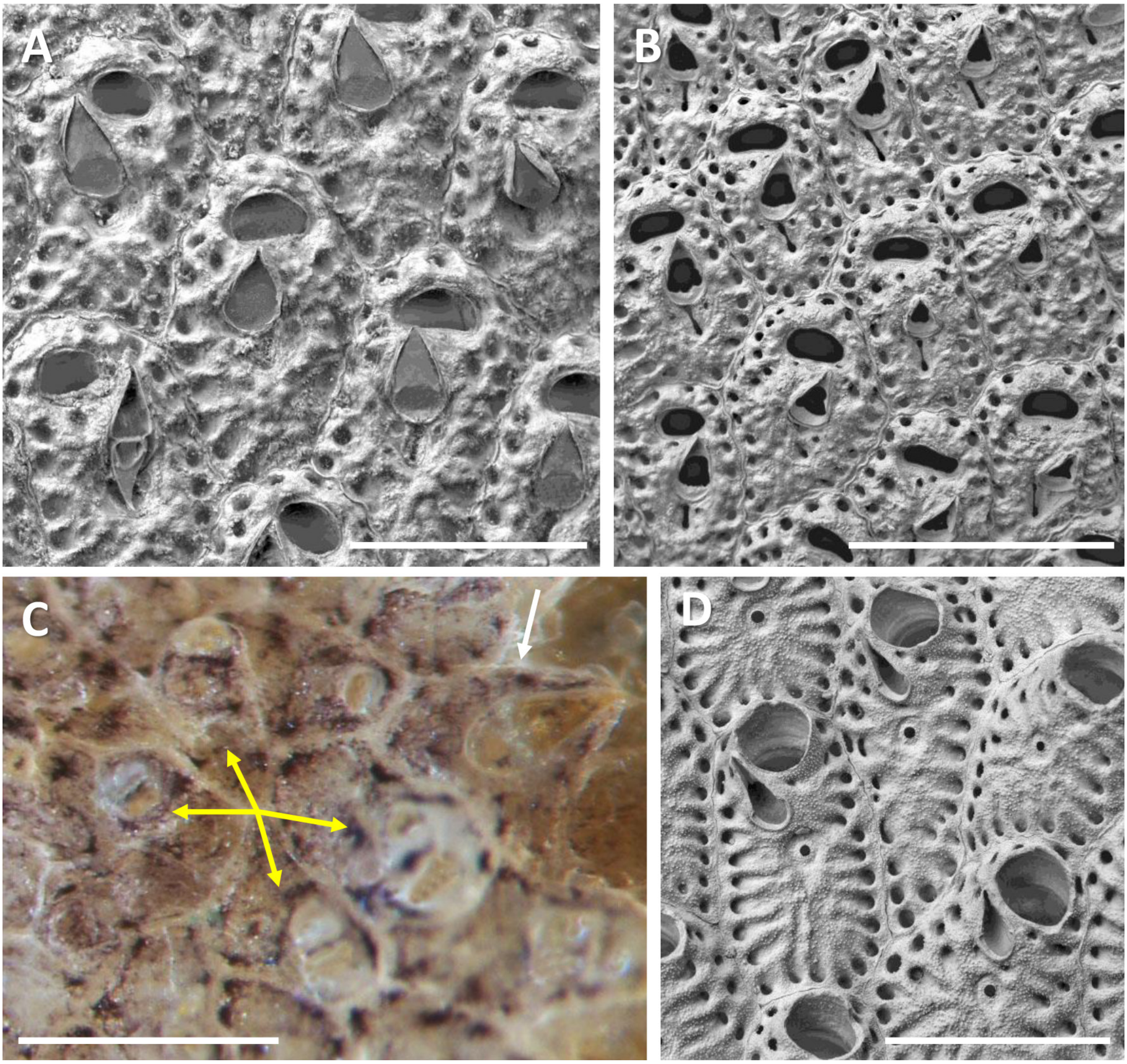

Fig. 4. A–C, *Reptadeonella riatanae*, new species; A, unbleached autozooids, and avicularia with mandibles in place; B, bleached autozooids with long slit-like spiramina; C, light micrograph showing an ancestrular tetrad (radiating yellow arrows) and a vicarious avicularium (white arrow); D, *Reptadeonella cellulanus* Tilbrook, Hayward & Gordon, 2001. Scale bars = 0.5 mm (B, D); 0.3 mm (A, C).

DESCRIPTIONS OF NEW SPECIES

Reptadeonella riatanae, new species
(Fig. 4A–C)

Material examined. Holotype: ZRC.BRY.0923 (Zoological Reference Collection, Lee Kong Chian Natural History Museum; collected as SG2019 No. 126; sequenced as BLEED No. 1523), Pulau Tekukor (1.2299°N, 103.8376°E), Singapore, 15–17 m, coll. S.S. Jain & P. Kuklinski, 6 May 2019.

Etymology. Honorific for Ria Tan, tireless promoter of knowledge of Singapore's biodiversity, notably through the WildSingapore website (http://www.wildsingapore.com).

Diagnosis. Colony encrusting, unilaminar, small. Zooidal frontal shield nodular-tubercular. Orifice transversely oval to bean-shaped. Spiramen longitudinally slit-like, immediately proximal to avicularium. Suboral adventitious avicularium single, variable in size, not symmetrically placed; rostrum acute. Large vicarious avicularia rare, at colony margin, of similar shape to adventitious avicularia. Obvious gonozooids not evident, but some autozooids have larger orifices. Ancestrular complex a tetrad.

Description. Colony encrusting, unilaminar, multiserial, up to 5–7 mm diameter, found on sponge. Colour in life purplish. Zooids arranged regularly in quincunx or surrounded by seven zooids at the bifurcation of zooid rows, separated by furrows with a thin boundary line. Zooids variably subhexagonal, widest in middle or parallel-sided [ZL 345–563 (429), n = 15; ZW 235–297 (256), n = 15]. Frontal shield umbonuloid, with nodular-tubercular surface and 19–23 conspicuous marginal areolar-septular pores. Orifice wider than long, oval to bean-shaped, with straight to slight convex proximal margin [OrL 40–59 (52), n = 15; OrW 76–104 (91), n = 15]. A single conspicuous avicularium on each autozooid, borne adventitiously between the orifice and spiramen, variable in size [AvL 95–149 (123), n = 15; AvW 52–84 (71), n = 15]; the rostrum triangular, somewhat longer than wide, with tiny distal palate and large subquadrate foramen, the proximal margin of the mandible arcuate; avicularian cryptocyst subcrescentic smooth; mandible concealing spiramen when open. Spiramen elongate (up to 70 µm long) and exceptionally narrow, especially midlength, orientated longitudinally or obliquely so proximal to the avicularium. Vicarious avicularia occur at or near the colony margin, the rostrum and opesia having the same proportions as the adventitious avicularia [VavL 240–300 (263), n = 4; VavW 157–203 (176), n = 4]. Gonozooids not evident, but some of the larger zooids with wider orifices may function as such. Ancestrular complex a tetrad of zooids, their proximal ends converging.

Remarks. The Bryozoa Home Page (Bock, 2022) lists 35 described species of *Reptadeonella*, 28 of which are living and the remainder exclusively fossil. All are restricted to particular regions, with 11 species now known from the tropical to subtropical western Pacific and eastern Indian Oceans. Prior to 2001, only three species were known from the region (Harmer, 1957). Tilbrook et al. (2001) added three more species (two of them new) from Vanuatu, Tilbrook (2006) described four more from the Solomon Islands, and Yang et al. (2018) described a new species from subtropically influenced Jeju Island, South Korea. None of these has a slit-like spiramen and, in those for which early astogeny is known, the ancestrular complex is a triad not a tetrad. Examination of descriptions and illustrations of all remaining living species of *Reptadeonella* shows that they all have a circular or transversely crescentic or oval spiramen (e.g., Almeida et al., 2015; Haugen et al., 2020; Winston & Jackson, 2021). The two Miocene species from Kalimantan also have a circular spiramen (Di Martino & Taylor, 2015).

Distribution. The species is so far known only from Singapore.

Arthropoma subarensis, new species

(Fig. 5B–D)

Material examined. Holotype: ZRC.BRY.0908 (Zoological Reference Collection, Lee Kong Chian Natural History Museum; collected as SG2019 No. 51; sequenced as BLEED No. 1466B), Big Sister's Island (1.2125°N, 103.8362°E), Singapore, 15–17 m, coll. S.S. Jain, D. Huang & P. Kuklinski, 3 May 2019.

Etymology. Named for the Malay name of the island, Pulau Subar Laut, where this species was discovered. The island is part of the Sisters' Islands Marine Park (Jaafar et al., 2018).

Diagnosis. Colony encrusting unilaminar, small. Zooidal frontal shield with numerous simple pseudopores either side of an imperforate median strip; three rows of pseudopores continue around orifice. Orificial sinus longitudinally oval, the distal part constricted by condyle tips. Four short stumpy unjointed oral spines present. Endooecial surface evenly and minutely reticulated with a cluster of tiny pores at the bottom of each dimple. Ovicell opening non-cleithral.

Description. Colony encrusting, unilaminar, multiserial, up to 4–6 mm diameter. Colour in life translucent pale orange. Zooids arranged regularly in quincunx, separated by a thin boundary line. Zooids variably subhexagonal, some parallel-sided [ZL 500–743 (606), n = 11; ZW 303–599 (483), n = 11]. Frontal shield lepralioid, smooth overall, with 4–6 series of simple funnel-shaped pseudopores on each side of a longitudinally imperforate central area; three rows of pseudopores continue distally around the orifice. Orifice comprising a near-semicircular anter, a little wider than long, and a longitudinally oval sinus [OL 147–188 (164), n = 11; OrW 125–177 (150), n = 11]. Shoulders of orifice straight, bearing very long and narrow smooth-edged condyles, the tips of which partially constrict the sinus opening. Orificial anter bordered by four oral spines, these short, tapering, non-articulated and hollow with a small apical pore. No avicularia. Ovicell conspicuous, hyperstomial; ooecium with almost wholly membranous ectooecium, excepted by a proximal ectooecial calcified border, thin, smooth; calcified endooecium with surface reticulated into a network of polygonal ridges defining dimples, with a cluster of microscopic perforations at the bottom of each dimple. Orifice non-cleithral, flanked on each side by a single spine [OvL 226–272 (251), n = 7; OvW 223–327 (283), n = 7]. Ancestrula not seen.

Remarks. Living *Arthropoma* used to be regarded as essentially monospecific, with the name *Arthropoma cecilii* (Audouin, 1826) accorded to specimens from many parts of the world geographically very distant from that species' Atlanto-Mediterranean range (see synonymies in Osburn, 1952; Harmer, 1957; Gordon, 1984). Subsequently, eight additional recent species have been named, five of them in the past decade, including two from the western Pacific. Six of these species are listed by Bock (2022) on the Bryozoa Home Page and two others are indicated in Harmer's synonymy, i.e., *Arthropoma gandyi* (Haswell, 1880) and *Arthropoma mediolaevis* (Ortmann, 1890). *Arthropoma subarensis*, new species, differs from *A. cecilii* in the combination of oral spines, a broad imperforate area of frontal shield, 2–3 rows of pseudopores distal to the orifice and a reticulate ooecial surface (see Chimenz Gusso et al., 2014). The only other species with oral spines is *Arthropoma occidua* Winston & Jackson, 2021 from Jamaica, with 2–3 spines, but these are entirely distal and the ooecial surface is only faintly textured.

The identity of *Arthropoma cecilii* (the type species of the genus) is itself problematic. The original material was probably collected from the Red Sea, and Atlanto-Mediterranean and Red Sea specimens attributed to this

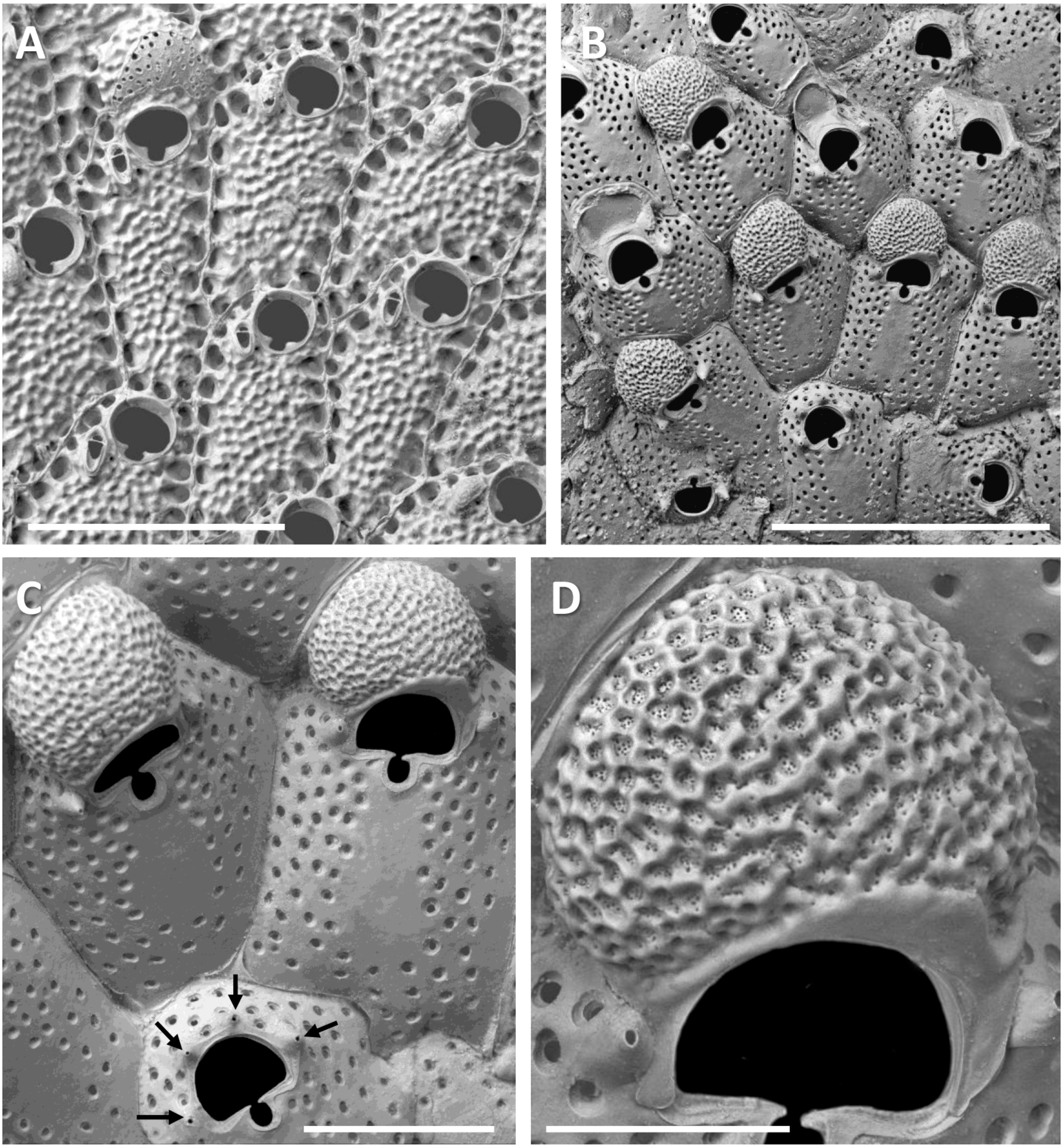

Fig. 5. A, *Pleurocodonellina microperforata* Tilbrook, 2006, with one ovicellate zooid and a small avicularium adjacent to each orifice; B–D, *Arthropoma subarensis*, new species, at three magnifications; note the four arrowed spine bases in C, with paired spine bases in ovicellate zooids; D shows the reticulate dimpled patterning of the ovicell endooecium, with minute perforations at the bottom of each dimple. Scale bars = 0.5 mm (A, B); 0.2 mm (C); 0. 1 mm (D).

species differ. For example, that described from Britain by Hayward & Ryland (1999) has a minutely pitted and granular-tessellated endooecial surface, whereas that illustrated from the Red Sea (Ostrovsky et al., undated) is likewise pitted but not granular, but that illustrated by Chimenz Gusso et al. (2014) is not pitted but has a highly rugose surface. The material illustrated by these authors probably constitutes three different species. The comprehensive molecular phylogeny presented by Orr et al. (2022) pairs nominal *A. cecilii* with *A. subarensis*, new species, and we have no hesitation including the latter in *Arthropoma* despite its moderately distinctive ooecium.

Arthropoma gandyi from the Great Barrier Reef was never illustrated, but Harmer (1957: 1002) examined a specimen from the Haswell collection in the Manchester Museum and included it in the synonymy of *A. cecilii*. Haswell (1880) had described zooids as centrally imperforate, with a deep orificial sinus constricted at its entrance and the ovicells as having a subgranular surface. These characters differ from the material from Heron Island erroneously attributed to *A. cecilii* by Ryland & Hayward (1992), which means there are two species of the genus in Queensland waters. *Arthropoma mediolaevis* from Japan was illustrated by Ortmann (1890) as having a centrally imperforate area, but with many more pseudopores proximal to this area than in *A. subarensis*, new species.

Distribution. The species is so far known only from Singapore.

Microporella sargassophilia, new species
(Fig. 6A–E)

Material examined. Holotype: ZRC.BRY.0924 (Zoological Reference Collection, Lee Kong Chian Natural History Museum; collected as SG2019 No. 128; sequenced as BLEED No. 1525), Pulau Tekukor (1.2299°N, 103.8376°E), Singapore, 1 m, coll. S.S. Jain & P. Kuklinski, 6 May 2019.

Etymology. Named for the macroalgal host, *Sargassum ilicifolium* (see Yip et al., 2018), on which the species was found.

Diagnosis. Colony encrusting on *Sargassum* laminae, unilaminar, tiny. Zooidal frontal shield nodular and sparsely pseudoporous, pores simple; thin gymnocystal margin around each zooid. Orifice with 3–5 (mostly three) jointed oral spines; proximal rim smooth, inner distal margin minutely denticulated. Ascopore non-reticulate, crescentic, denticulate, set within small raised gymnocystal area. Avicularia single, sparse, not found on every zooid, set some distance from ascopore. Ovicell surface like that of frontal shield but with few or no pseudopores apically; proximofrontal margin of ooecium with smooth raised band of calcification; some zooids with broad bridge of calcification embracing orifice distal to ascopore, the tip of an oral spine sometimes showing on each side inside its rim. Ancestrula tatiform with 11 spines.

Description. Colony encrusting, unilaminar, multiserial, tiny, up to only about 3 mm diameter, found only on the laminae of *Sargassum ilicifolium*. Colony colour whitish-transparent. Zooids subhexagonal, widest about midlength, interzooidal boundaries in furrows with thin, slight edges of gymnocyst visible in places [ZL 286–407 (350), n = 20; ZW 192–446 (275), n = 20]. Frontal shield pustulose, very sparsely pseudoporous (12–18 pores in zone of astogenetic repetition), pores simple. Orifice transversely D-shaped with straight to slightly concave proximal margin; proximal smooth and non-denticulated, but inner face of distal oral arch weakly denticulate [OrL 43–61 (53), n = 20; OrW 64–100 (81), n = 20]. Typically three basally articulated oral spines, 4–5 near colony origin, joints not dark. Ascopore transversely bean-shaped and weakly denticulate, set within the distal half of a slightly raised, smooth, shallow gymnocystal area; area between ascopore and proximal margin of orifice relatively smooth with a few tiny pustules. Avicularia sparse, single, not on every zooid, produced from an areolar-septular pore, not a pore-chamber; with complete crossbar, rostrum triangular overall with concave sides, the distal tip broadly rounded, open, channel-like. Mandible setiform, stiletto-like with expanded triangular base [AvL 52–69 (61), n = 7; AvW 43–54 (48), n = 7; AvML 118–147 (128), n = 7]; open mandible not reaching to opposite margin of zooid. Ovicell conspicuous, globular, ooecial surface pustulose like the frontal shield with a few peripheral pseudopores; strongly personate, but not in all zooids, with a broad bridge of calcification embracing the orifice distal to the ascopore, the tip of an oral spine showing on each side inside its rim in some zooids [OvL 168–216 (190), n = 9; OvW 188–215 (199), n = 9]. Embryos reddish. Interzooidal communications comprising well-developed basal pore-chambers, 1–2 on each lateral wall and 2–3 small such chambers below and around the orifice. Ancestrula tatiform, with elongate-oval opesia bordered by 11 spines; gymnocyst smooth (AnL 262–280 (271), n = 2; AnW 180–228 (204), n = 2). Two daughter zooids produced, each in a distolateral position.

Remarks. We closely examined three fertile colonies at 1.88–2.00 mm maximum length. The largest of the three had 31 zooids (8 frontally broken), of which 11 were ovicellate and three bore an avicularium. A colony of 26 zooids had seven that were ovicellate and four bore an avicularium. The third colony had 25 zooids, of which seven bore ovicells and four had an avicularium. Thus c. 26–28% of the zooids in a sexually reproducing colony are actively producing larvae.

Tilbrook (2006) noted that relatively few *Microporella* species had been described with personate ovicells, mentioning three of them—*Microporella personata* (Busk, 1854) from the Falkland (Malvinas) Islands, *Microporella orientalis* Harmer, 1957 from Indonesia, and *Microporella harmeri* Hayward, 1988 from Mauritius. *Microporella orientalis* differs from *M. sargassophilia*, new species, in developing extensive sheet-like colonies on hard substrata, that there are many more pseudopores in the frontal shield, and that the personate rim is not associated with spines. *Microporella harmeri* has large lateral avicularia, numerous pseudopores, and a denticulate proximal orificial rim (see also Harmelin et al., 2011).

There are several other warm-water personate species. *Microporella epihalimeda* Tilbrook, 2006 from the Solomon Islands forms small colonies on the calcareous green alga *Halimeda* but differs from *M. sargassophilia*, new species, in having pustules between the ascopore and orifice and on the proximal face of the personate process as well as no spines associated with the personate process, characters shared with *Microporella hawaiiensis* Soule, Chaney & Morris, 2003. In *Microporella pontifica* Osburn, 1952 from western Mexico and *Microporella wrigleyi* Soule, Chaney & Morris, 2004 from California, the ascopore is embraced by the personate process. This is not the case in *Microporella lepueana* Soule, Chaney & Morris, 2004 from American Samoa, but this species has a denticulate oral rim and often paired avicularia. Harmelin et al. (2011) described six personate species, three of them new, from the tropical Indian Ocean. Of these, the closest in morphology to *M. sargassophilia* is *Microporella genisii* (Audouin, 1826) from the Red Sea and eastern Mediterranean. It occurs on the marine angiosperm

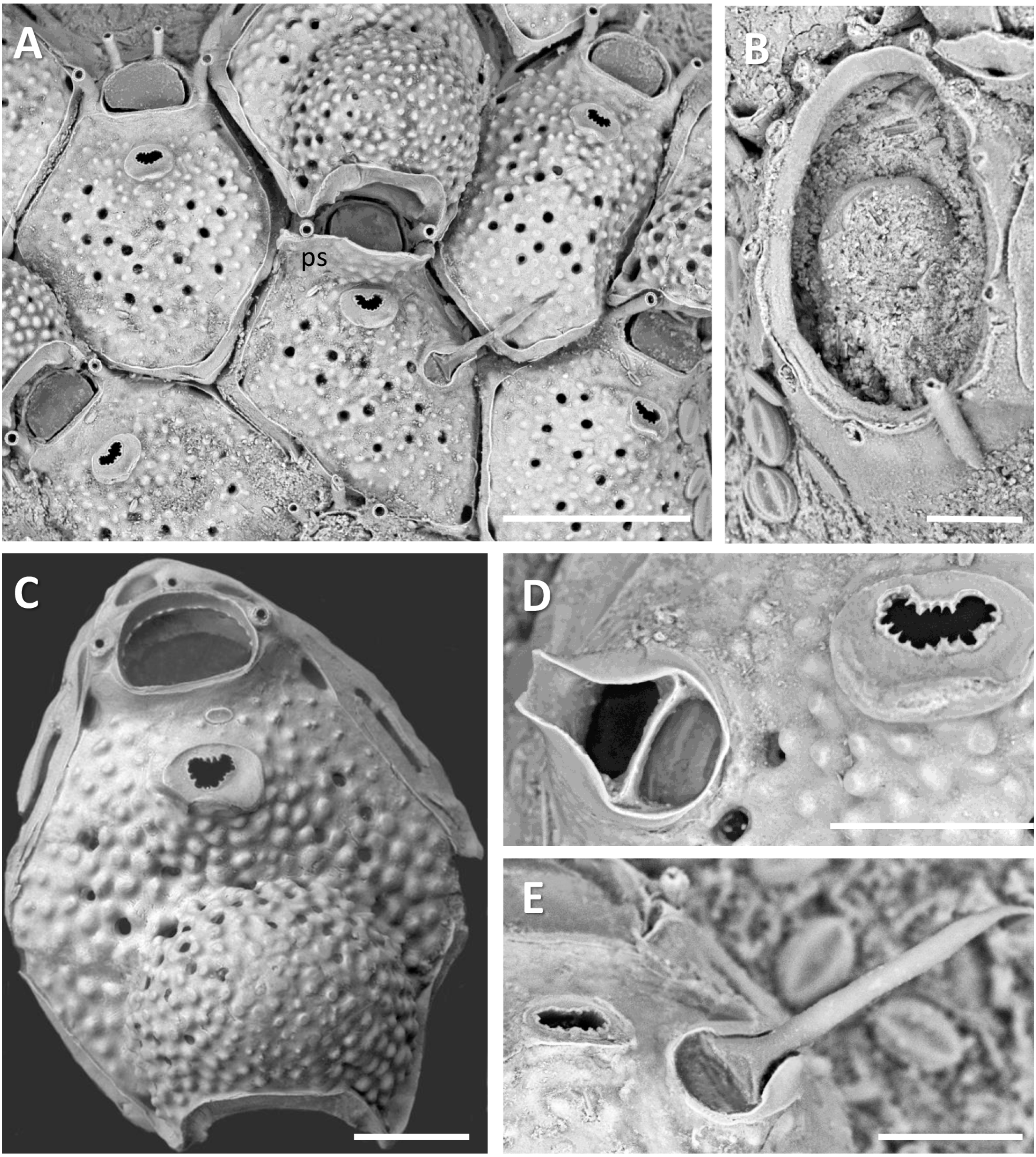

Fig. 6. A–E, *Microporella sargassophilia*, new species; A, part of fertile colony showing three ovicellate orifices and an avicularium with mandible; note the well-developed persona (ps), appearing as an erect ridge between the ascopore and orifice in one zooid; B, tatiform ancestrula; C, isolated zooid (with proximal ovicell) showing distribution of basal pore-chambers; minute denticulation is visible inside the orificial rim; D, avicularian cystid and ascopore; E, avicularium with mandible. Scale bars = 0.2 mm (A); 0.05 mm (B, D, E); 0.1 mm (C).

Cymodocea as well as hard substrata and has a pair of spines inside the corners of the personate peristome. It differs from *M. sargassophilia* in having up to six oral spines in proximal parts of the colony, that the ascopore is closer to the orifice and the area between is pustulose, and that the orifice has slight denticulation of the proximal rim but not the distal rim. The only other warm-water personate species is *Microporella clypeiformis* Liu in Liu, Yin & Ma, 2001 from China. It differs, inter alia, in having only a narrow peristomial bridge.

In the description, it has been noted that the avicularium in *M. sargassophilia*, new species, is budded from an areolar-septular pore, in contrast to those *Microporella* species in which the avicularian cystid extends to the substratum, replacing a basal pore-chamber. Hastings (1963) made

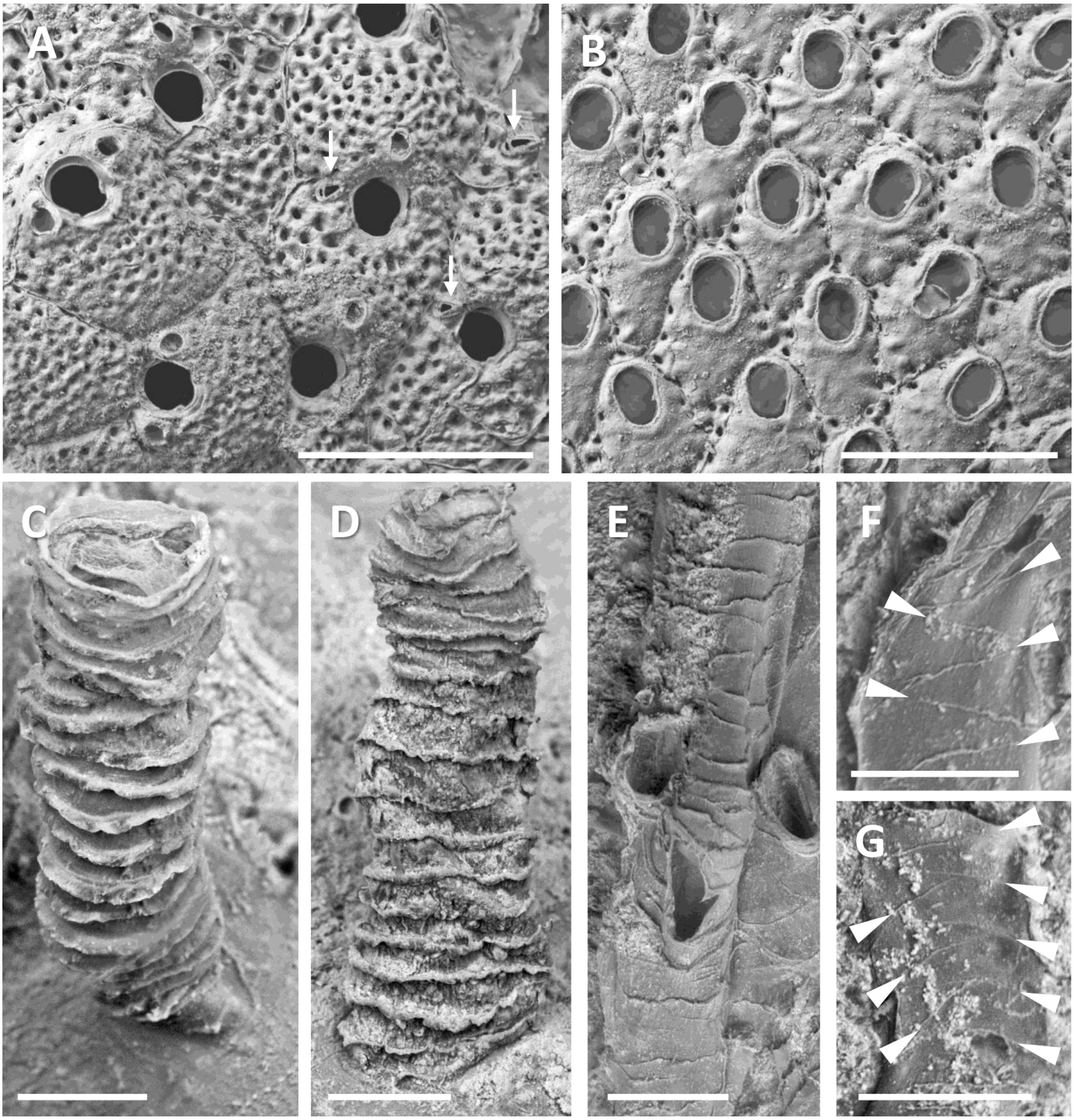

Fig. 7. A, *Thornelya fuscina* Tilbrook, Hayward & Gordon, 2001; white arrows indicate three unbroken latero-oral avicularia; B, *Scorpiodinipora costulata* (Canu & Bassler, 1929); C–G, *Rhabdopleura* sp.; C, D, lateral view of erect tubes with annular fusellar rings; E, part of creeping basal tube in vicinity of three broken bases of erect tubes; here the fusellar sutures are parallel to oblique; F, G, parts of creeping basal tube in which the fusellar sutures (arrowheads) are arranged obliquely. Scale bars = 0.5 mm (A, B); 0.1 mm (C, D); 0.2 mm (E–G).

this distinction, regarding the latter type as effectively interzooidal. Overall, apart from skeletal characters, *M. sargassophilia* is distinctive among personate species for its very small colony size and algal substratum. Colonies are fragile, in that zooids are not strongly interconnected and easily separate when bleached for scanning electron microscopy. Zooid surfaces are generally consistently fouled by diatoms.

Distribution. The species is so far known only from Singapore.

PTEROBRANCHIA IN SINGAPORE

Inasmuch as our targeted collecting of bryozoans yielded the first record of the hemichordate class Pterobranchia for Singapore, we take the opportunity to report *Rhabdopleura* sp. observed at Pulau Tekukor (1.2299°N, 103.8376°E; collected as SG2019 No. 119; sequenced as BLEED No. 1688; coll. S.S. Jain & P. Kuklinski, 6 May 2019). Modern species of Rhabdopleuridae are considered to be living graptolites (Mitchell et al., 2013). The ramifying uniserial colonies, found on coral rubble with bryozoans, are instantly recognisable by their thin creeping tubes in which is a conspicuous black stolon. Erect tubes, each housing the individual zooid that constructs it, arise at intervals from the creeping tubes and are characterised by ringed fusellar ridges (Fig. 7C–E). The tube in *Rhabdopleura* is not a body wall, hence the zooid in this instance (compared to bryozoans) comprises only the soft tentaculated and stalked individual within.

The basal creeping tubes of the colony (tubarium) in the present material are relatively narrow and linear with a slight marginal expansion on either side, or both the tube and expansion can be relatively broad. The central median part of the creeping tube is 144–248 μm wide (mean 200 μm), with variable subparallel to oblique sutures (each marking the boundary between adjacent fusellar strips) that range from 42 to 99 μm apart (mean 66 μm) (Fig. 7F, G). Erect tubes are of variable length, with a diameter of 125–162 μm (mean 144 μm) and bearing conspicuous irregular fusellar rings 27–44 μm (mean 34 μm) apart. The edges of these rings project outwards as 6–13 μm-wide flanges from the tubes.

We are uncertain of the identity of the species, and thus leave it in open nomenclature pending the outcome of molecular sequencing, the results of which can be compared with those published by Beli et al. (2018) and Ramírez-Guerrero et al. (2020).

Hemichordates are already represented in Singapore by two species of class Enteropneusta (acorn worms), found on mud (Ng et al., 2011: 217).

DISCUSSION

Comprehensive surveys of many habitats in Singapore over the last decade have expanded the inventory of bryozoans (Tilbrook & Gordon, 2016). Our targeted collecting in 2019 already yielded one new species, *Pherusella liowae* Decker, Gordon, Spencer Jones & Schwaha, 2021, as well as 12 additional new species and records that are presented in this study. The species detailed herein were collected from a wide range of habitats. Indeed, bryozoans are expected to be found in a variety of habitats, including artificial substrata, owing to their ability to settle on a broad range of surfaces (Watts et al., 1998; Xavier et al., 2021). While 55% of the bryozoans collected by the present authors were found encrusting rocks and coral rubble (not all obligatorily), *Scorpiodinipora costulata* (Fig. 7B) and *Arbopercula angulata* (Levinsen, 1909) (Fig. 2C) were found on a plastic tube trapped within the muddy seagrass meadows of Changi Beach. Other bryozoans found during our targeted collecting encrusted bottle glass, porcelain and ceramic ware, wooden planks, rope and other jetsam, mangrove roots and leaves, and macroalgae along the coasts of mainland Singapore and its southern islands.

Bryozoans are often considered difficult to identify, which is principally because of the scattered literature and a paucity of comprehensive identification guides. They are often also overlooked—as is historically the case in Singapore—because of their frequently small colony sizes and cryptic habit. Targeted searching, especially by bryozoan specialists, inevitably yields many species, of which 127 were found in our survey even though it was not fully comprehensive in geographic coverage. The increase in artificial habitats along the urbanised coastal areas of Singapore, including seawalls and marine trash (Chapman, 2003; Chapman & Bulleri, 2003; Kiessling et al., 2015; Lai et al., 2015; Li et al., 2016; Chou et al., 2019), although destroying much original habitat, may comprise greater substratum diversity that could potentially recruit more bryozoan species. Singapore is now recognised to be the type locality (pre-2000 records give no further precision) for eight bryozoan species: *Parellisina albida* (Hincks, 1880a) (see also Osburn, 1949), *Figularia fissa* (Hincks, 1880b), *Cribrilaria vicariata* (Waters, 1923) (see also Harmer, 1926), *Alcyonidium jauhar* (Tilbrook & Gordon, 2015), *Pherusella liowae* Decker et al., 2021, and the three new species described here. Because little-known *Parellisina albida* has never been illustrated by scanning electron microscopy, we include an image of it in this work (Fig. 2D).

Climate change is driving the decline of tropical marine species (Wiens, 2016), so it would be no surprise that bryozoans will also be impacted (Przeslawski et al., 2008; Swezey et al., 2017; Pagès-Escolà et al., 2018; Lombardi et al., 2020). Increasing seawater temperature and acidity have detrimental effects on the growth and calcification of several bryozoan species around the world that have been studied (Doney et al., 2009; Smith, 2009; Lombardi et al., 2010, 2011; Rodolfo-Metalpa et al., 2010; Durrant et al., 2013; Smith, 2014; Pagès-Escolà et al., 2018). Ocean warming and acidification would therefore likely have negative impacts on bryozoan diversity in Singapore. However, many tropical species remain untested for marine natural products (Tilbrook & Gordon, 2016), while invasive (e.g., *Bugula neritina*, *Watersipora subatra*), cryptogenic (e.g., *Biflustra perambulata*, *Hippoporina indica*), biologically unusual (e.g., *Amphibiobeania epiphylla*), and locally common species (e.g., *Stylopoma viride*), as well as species typical of mangrove roots and associated stranded trash (e.g., *Sundanella sibogae*, *Nolella* cf. *gigantea*) are amenable to ecological and physiological research. More broadly, bryozoans are widespread, found in a variety of habitats in various compositions and morphologies, and thus show great prospect in understanding the effects of global environmental change (Fortunato, 2015). Further sampling at various locations in the tropics is imperative to enhance our understanding of the diversity, distribution, and adaptability of Bryozoa, especially in the southwestern and southern parts of the South China Sea which have been little sampled for this phylum (Gordon, 2016). Elsewhere, as in the Coral Triangle, bryozoans comprise many hundreds of species (Harmer, 1915, 1926, 1934, 1957), but even there they remain significantly undersampled.

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