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Rocky-intertidal cheilostome bryozoans from the vicinity of the Sesoko Biological Station, west-central Okinawa, Japan

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ABSTRACT

To complement previous studies on the diversity of cheilostome bryozoans (Bryozoa: Gymnolaemata: Cheilostomata) in the rocky-intertidal habitat in the North Pacific, we sampled rocky substrata at three sites on the subtropical East China Sea coast of Okinawa, Japan (26°N). We examined 651 colonies or colony fragments by light microscopy or scanning electron microscopy (SEM). The range in single-site richness was 16–36 species, with 52 species detected overall. We provide descriptions and illustrations for all species, including 11 (21.2%) new species (*Thalamoporella karesansui*, *Crassimarginatella eremitica*, *Hippothoa petrophila*, *Stephanotheca fenestricella*, *Calyptotheca sesokoensis*, *Fenestrulina parviporus*, *Arthropoma harmelini*, *Rhynchozoon maculosum*, *Rhynchozoon lunifrons*, *Rhynchozoon ryukyuense*, and *Rhynchozoon scimitar*) and 34 (65.4%) new records for Japan. Species were patchy in local distribution, with 53.8% detected at only one among the three sites, and often rare, with 34.6% represented by only one or two specimens. Most species (94.2%) were encrusting, forming two-dimensional, sheet-like colonies or (in two cases) branching uniserial networks; three species formed small, recumbent colonies. Ascophoran-grade species (82.7%) outnumbered anascan-grade species (17.3%). Biogeographically the fauna we examined is characteristic of the Central Indo-Pacific (CIP) realm of Spalding et al.: among 40 previously described species with distributions known outside the study area, 36 (90.0%) occur in the CIP realm, and 11 (27.5%) are restricted to it. In contrast, only seven species (17.5%) have been reported from the Temperate Northern Pacific realm, including two putatively cosmopolitan species. The high proportion (86.5%) of new records for Japan (including the new species) suggests that the marine bryozoan fauna in far-southern Japan remains largely unexplored. Given that many species were rare or uncommon in the study area and/or patchily distributed among the three sites, further sampling at additional intertidal sites in the Sesoko area will likely detect higher total local richness than the 52 species we found.

http://www.zoobank/urn:lsid:zoobank.org:pub:9FD78C14-60AA-44A9-A9A2-3258E5770D31

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Introduction

This report is the fifth in a series of intensive local studies on the diversity and taxonomy of intertidal bryozoans we have conducted at several localities in the North Pacific over the past 30 years, including Kodiak (Dick and Ross 1988) and Ketchikan (Dick et al. 2005), Alaska; Hawaii Island (Dick et al. 2006); and Akkeshi, Hokkaido, Japan (Grischenko et al. 2007). These studies appear to indicate that cheilostome bryozoans in the rocky inter-tidal zone fail to show a latitudinal diversity gradient, in which species richness in comparable habitat increases from high to low latitudes. Instead, single-site diversity peaks at around 30 cheilostome species at latitudes ranging from ~58°N (Kodiak) to ~20° N (Hawaii), and the greatest total local diversity was detected at Kodiak, the farthest northern locality examined. Grischenko et al. (2007) discussed in detail the apparent diversity pattern and factors (e.g. total area of suitable intertidal and shelf habitat available; habitat diversity) that might affect local diversity.

Confounding interpretation of these studies is the fact that not all of them involved comparable sampling effort, which was high at Kodiak and Akkeshi, but low at Ketchikan and Hawaii. Furthermore, only one of the previously studied sites (Hawaii) was located in a subtropical region characterised by the occurrence of hermatypic corals, where high bryozoan diversity might be expected. For an additional study site at relatively low latitude, we chose the vicinity of the Sesoko Station (part of the Tropical Biosphere Research Centre, University of the Ryukyus) located on Sesoko Island at 26°N latitude, west-central Okinawa, Japan. Although research has been underway at the Sesoko Station since 1971, the bryozoan fauna has been scarcely studied. Mawatari (1987, 1991) published two lists of cheilostomes collected subtidally from artificial substrata in the Sesoko area, totalling 42 species but without descriptions or illustrations; the second list includes six species thought at the time to be new species.

The goals of our study were to estimate the maximum single-site and total local diversity of intertidal cheilostome bryozoans in the Sesoko area; to determine their taxonomic composition and relative abundances; and to examine their biogeography. We provide descriptions and illustrations of all species encountered. We restrict this account to cheilostomes because, except for Hawaii, our previous studies did not treat cyclostomes and thus did not produce comparative data for that group.

Study area and methods

Study area

Okinawa Island (Figure 1) lies at the north-eastern end of the Ryukyu Archipelago, which extends from Yonaguni Island near Taiwan east-north-eastward to Okinawa; this archi-pelago comprises Japan's Okinawa Prefecture. The Ryukyus in turn comprise the south-western part of the Nansei Archipelago, extending 1125 km in an arc from Yonaguni Island to Tanega Island, just south of Kyushu, the most southern of the main Japanese islands. Paralleling the Nansei Archipelago 100 km or more to the west is the Okinawa Trough, a back-arc basin that reaches a depth of 2270 m at its deepest point near Taiwan (Lee et al. 1980). The Okinawa Trough channels the bulk of the warm Kuroshio Current in a north-easterly direction along the archipelago, facilitating the occurrence of
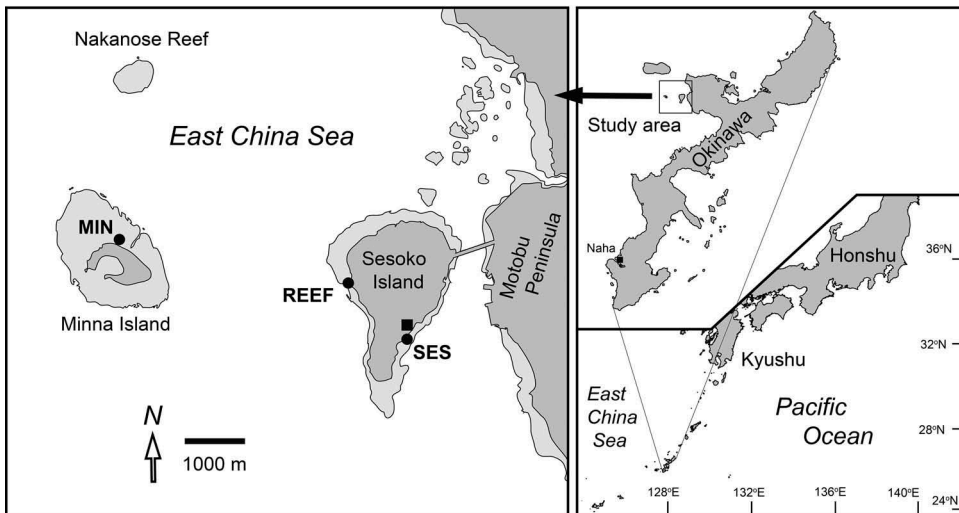
Figure 1. Partial map of Japan (lower right) showing the location of Okinawa (upper right), with the study area enlarged (left); black circles indicates sampling sites (SES, old breakwater near Sesoko Station; REEF, reef-fringe site; MIN, breakwater on Minna Island); black square indicates the Sesoko Station, Tropical Biosphere Research Centre, University of the Ryukyus; dark grey shading indicates land; light grey shading indicates areas of coral reef flat.

subtropical coral reefs at relatively high latitude (26–27°N) on Okinawa (Hohenegger 1994; Liu 2013).

This study was conducted on Sesoko and Minna islands (Figure 1) off the Motobu Peninsula, which juts into the East China Sea on the west side of Okinawa. The environment of this area has been well described (Hohenegger 1994; Hohenegger et al. 1999; Hohenegger and Yordanova 2001; Yordanova and Hohenegger 2002). Mean monthly sea-surface temperature around Sesoko Island ranges from 20°C in February to 28°C in July and August (Loya et al. 2001). Salinity shows little variation, with an annual range of 35.2–35.5‰ at the pier of the Sesoko Biological Station (Tada et al. 2003). Sesoko is separated from the Motobu Peninsula by a channel 10 m deep, with a bridge connecting the island to the mainland. Branches of the Kuroshio Current flow northward in this channel and between Sesoko and Minna islands. A series of patch reefs runs north-east from the north end of Sesoko Island to the Motobu Peninsula, delineating an inner lagoon area 800 m wide and up to 20 m deep. The small Manna and Ookobori Rivers on the Motobu Peninsula flow into this area, providing a low volume of freshwater input. There are fringing coral reefs of varying width along the shore of the peninsula and surrounding Sesoko and Minna islands. The fringing reef on the north end of Sesoko Island is about 200 m wide, becoming 350 m wide on the west side; that around Minna Island reaches 1000 m wide on the north-west side. The channel between Sesoko and Minna islands is 90–110 m deep, with the bottom topology west of the islands steep, falling sharply to around 90 m and 180 m, respectively. The mean monthly tide range in the area is 2.2 m, with the level of extreme low spring tides in the range of −0.2 to 0.2 m relative to mean lower low water (MLLW). On average, 12 tropical storms (winds of 63–119 kph) or typhoons (winds greater than 119 kph) affect Okinawa annually, with the

highest probability of occurrence between 20 June and 17 September (Kimura 1969). As these storms generate strong wind-driven waves that strike exposed intertidal areas with considerable force, they are likely an important factor in the ecology of rocky intertidal bryozoans in our study area.

We collected bryozoans intertidally at two sites on Sesoko Island and one on Minna Island from 12 to 15 March 2005. Brief descriptions of the sites are as follows.

Sesoko site (SES)

Sesoko Island (26.634°N, 127.864°E); 12 and 13 March 2005. This site was an old, ruined, stone and concrete pier (Figure 2(a)) ca. 35 m long, located 200 m south-south-west of the present pier of the Sesoko Biological Station (Figure 1), comprising a long pile of large and small coral boulders and some large chucks of concrete, extending perpendicularly from the beach onto the reef flat, with the boulder rubble lying on coral benchrock and sand. Rocks in the one-quarter of the pier farthest from shore (arrowheads, Figure 2(a)) were examined for bryozoans from about 0.3 m below to 1 m above the water level at low tide. The sparse macroalgal cover on the upper surfaces of rocks (Figure 2(b)) consisted primarily of low tufts of an ulvacean green alga. Bryozoans occurred on the undersides of boulders (Figure 2(c)) or attached to pieces of rock rubble under boulders. In this cryptic habitat was also an abundant fauna of encrusting sponges; gastropod and bivalve molluscs; echinoid, holothuroid, and ophiuroid echinoderms; serpulid polychaetes; and crabs.

Reef site (REEF)

Sesoko Island (26.645°N, 127.856°E); 15 March 2005. This site was located on the west side of Sesoko Island (Figure 1), seaward of the most southern extent of the long, sandy beach extending along the north-western corner of the island, within a small inlet in the fringing reef (Figure 2(d)) in which lay numerous loose, flat coral rocks. The reef flat was covered with a thin mat of ulvacean green algae. Crevices in the coral basement at the edge of the reef crest, and the undersides of loose coral rocks (Figure 2(e)) to a depth of about 0.3 m below the water level at low tide, were examined for bryozoans. An abundant associated fauna in the collecting area included small, living acroporan corals; polyplacophoran and gastropod molluscs, including large *Aplysia* individuals; echinoid, holothuroid, and ophiuroid echinoderms; and tunicates.

Minna site (MIN)

Minna Island (26.651°N, 127.815°E); 14 March 2005. This site was at the end of a stone breakwater roughly 4 m high on the north side of Minna Island (Figure 1), with sampling conducted on the north-west-facing side. The breakwater (Figure 2(f)) consisted of massive boulders of grey, metamorphosed limestone, with smaller boulders and rocks of the same material between them. The rocky rubble in crevices (Figure 2(g)) and the undersides of portable rocks (Figure 2(h)) were examined for bryozoans, from about 0.5 m above to 0.15 m below the water level at low tide. Macroalgal cover at this site was sparse, consisting mostly of crustose coralline algae. A moderately abundant associated fauna included a few small, living acroporan corals; sessile bivalve molluscs; serpulid and spirorbid polychaetes; echinoid, asteroid, and holothuroid echinoderms; and tunicates.
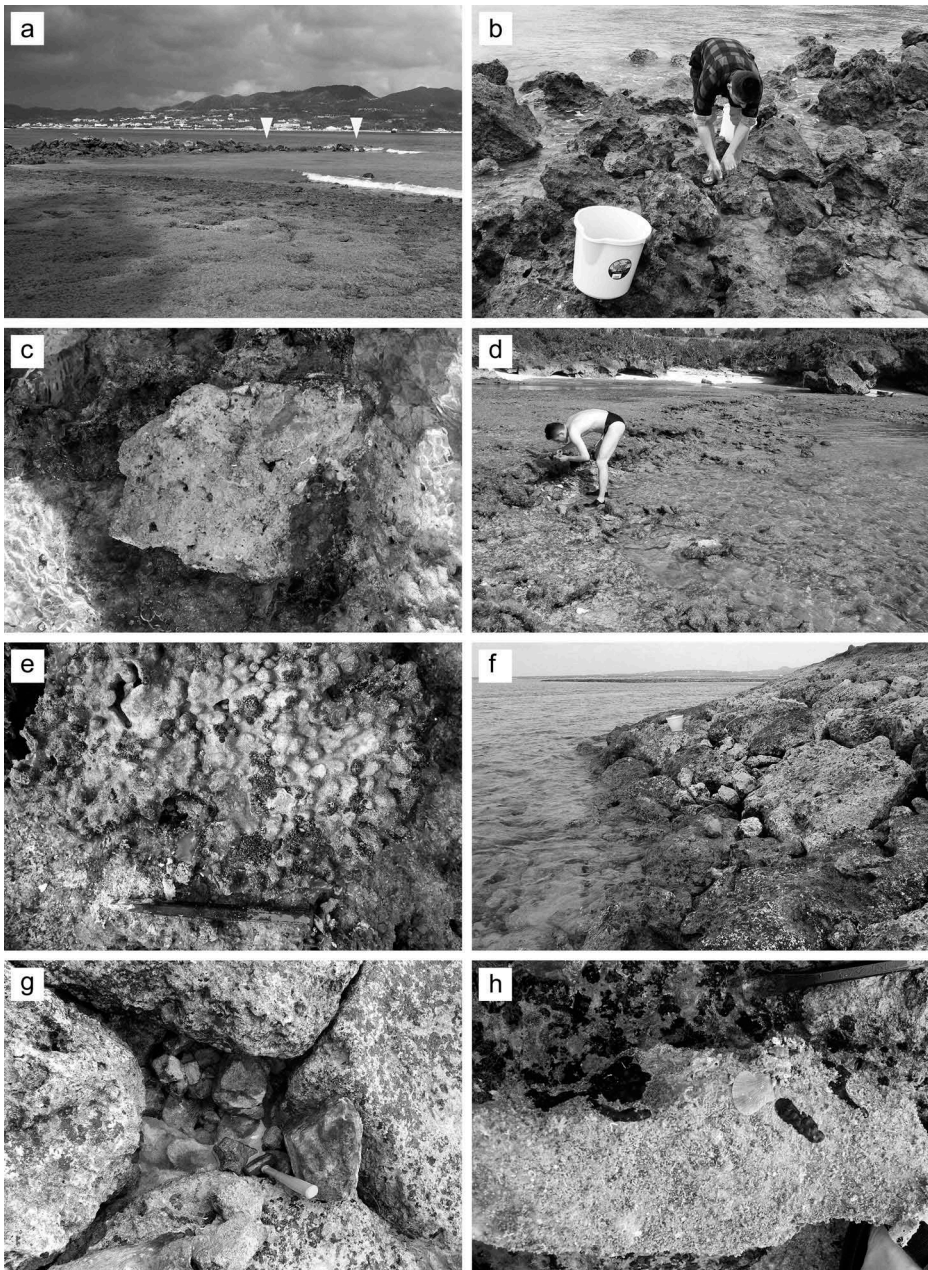
Figure 2. Collecting sites in this study (for locations, refer to Figure 1). (a–c) Collecting site SES at end of ruined stone pier projecting from shore near Sesoko Biological Station, Sesoko Island, Okinawa: (a) view of pier, with arrowheads indicating area in which bryozoans were collected at low tide; (b) overturning coralline boulders to examine undersides for bryozoans; (c) example of overturned coralline boulder bearing encrusting bryozoans. (d, e) Collecting site REEF on Sesoko Island; entire reef is covered with ulvacean green algae: (d) examining coralline rocks at water's edge; (e) example of overturned coralline boulder bearing encrusting bryozoans, with scale given by 20 cm chisel at bottom centre. (f–h) Collecting site MIN at breakwater on Minna Island, composed of non-coralline rocks: (f) overview of collecting area, with scale indicated by bucket left of centre near top; (g) crevice filled with small rocks typically richly encrusted by bryozoans, with 30 cm long hammer indicating scale; (h) example of overturned rock bearing a high diversity of encrusting bryozoans as well as many serpulid and spirorbid polychaetes and other invertebrates; chisel intruding at upper right indicates scale.

Methods

We conducted collecting during a cycle of extreme low tides. Samples were taken from along roughly 10 m of shore at each site, beginning up to 1 h before low tide and continuing up to 1 h after low tide. We examined the undersides of boulders, stones underneath boulders, crevices in reef flat and exposed rock faces for bryozoans. Using a hammer and chisel in the field, we chipped fragments from rocks too large to transport, and carried some rocks of portable size back to the laboratory at Sesoko Station. In the laboratory, we cleaned field samples with bryozoan colonies attached by spraying them with seawater and then dried them in the sun. We used a Dremel tool (Model 395, Type 5; Racine, WI, USA) with a circular diamond-surfaced cutting bit, along with a hammer and chisel, to remove small pieces of rock with bryozoans attached. Having insufficient time and limited microscope facilities, we made little effort to identify specimens at this stage, but instead sought to recognise and collect as many different species as possible by eye and with a hand lens, using colony size, texture and colour, as well as zooid size, as differentiating characters. After specimens (including fragments and small rocks with multiple colonies attached) had dried, we wrapped them in newspaper and transported them to our laboratory at Hokkaido University.

To roughly quantify relative abundance, we counted the whole colonies and colony fragments of each cheilostome species in our collections. In some cases, large colonies were almost certainly fragmented during removal from larger rocks and were thus counted more than once as fragments. However, both colony density (number of colonies) and colony cover (area) are related to the degree of prominence of encrusting bryozoans in an ecosystem, and our combined counts of colonies and fragments reflected a combination of both of these quantifiers.

For scanning electron microscopy (SEM), we cleaned one or more representative specimens of every species encountered in a sodium hypochlorite solution (except for some weakly calcified taxa like *Aetea* and *Beania*), rinsed them in tap water, dried them in air, and attached them to aluminium SEM stubs with water-soluble glue. We coated dried specimens, bleached or unbleached, with Au in a Hitachi-E1045 ion sputter coater and examined them with a Hitachi S-3000N scanning electron microscope at 15 kV accelerating voltage, storing images electronically as bitmap files. We adjusted the size and clarity of image files and assembled them into figures for publication using Adobe Photoshop CS6 Version 13.0 software.

We measured zooidal characters directly from SEM images using ImageJ Version 1.42q software (National Institutes of Health, USA; http://rsb.info.nih.gov/ij). Measurements in the text are in millimetres, presented as the range, followed by the mean and standard deviation in parentheses. We indicate sample sizes as the number of zooids or structures measured, followed by the number of colonies from which the measurements were taken; a sample size of (15, 1) for a zooid-length measurement, for example, means we measured the length of 15 zooids in a single colony.

We examined species distributions in the context of the bioregionalisation of coastal and shelf waters by Spalding et al. (2007), who subdivided the Indo-Pacific (IP) region into three realms. The Western IP realm extends westward from Sumatra to eastern Africa and includes the Indian Ocean and Red Sea. The Central IP realm extends from

southern Sumatra eastward to the Tonga Islands, and from northern Australia (including the Great Barrier Reef) northward to Taiwan and the Ogasawara Islands. The Eastern IP realm extends from Samoa and the Marshall Islands eastward to the Hawaiian Archipelago and Easter Island.

The classification presented herein is that of Gordon (2014). Under *Material examined* for each species, we list only specimens to which museum catalogue numbers have been assigned. Table 1 lists by species the total number of specimens identified. The holotypes and most other specimens from this study are deposited in The National Museum of Nature and Science (catalogue numbers prefixed with NSMT-Te), Tsukuba, Japan; some paratype and other specimens are deposited in the Natural History Museum, London, UK (catalogue numbers prefixed with NHMUK). Detailed collection information (locality, date) is not presented in Material examined, but can be accessed through our specimen numbers following the museum catalogue numbers in parentheses (prefixed by SES, REEF or MIN, referring to the three sampling sites described above).

Terminology and abbreviations of characters measured

For convenience, we use the term 'orifice' for the reduced frontal opening through which the lophophore emerges from the cryptocystal frontal covering in the anascans *Thalamoporella* and *Smittipora*, though other authors have used 'aperture' or even 'opesia' for this opening. Also for convenience, we use the term 'suture line' to refer to the line of calcification between adjacent zooids that in ascophorans is formed by opposing vertical walls and is flanked by a column of areolae on each side; this is not quite correct, as technically the suture line is the undetectable incision between the vertical walls, rather than the walls themselves.

In the terminology of Ostrovsky (2008, 2013) related to cheilostome brooding structures, the term 'ovicell' refers to the entire brooding apparatus, including the ooecium, the brooding cavity and the vesicle closing the ooecium, whereas 'ooecium' refers to the skeletally reinforced hood typically protecting the brooding cavity. Herein we use 'ovicell' in describing the position of the brooding cavity relative to the colony surface (see Ostrovsky 2008, p. 199, fig. 3), and 'ooecium' in describing the typically double-walled skeletal structure around the brooding cavity. For practical purposes, non-specialists using our paper for identifications can consider 'ovicell' and 'ooecium' as roughly synonymous. Difficulties with this loose usage arise in certain situations, however, such as when the ooecium is vestigial (highly reduced) but the actual brooding cavity (part of the ovicell) remains capacious, although immersed in the maternal cystid (e.g. *Crassimarginatella eremitica* sp. nov. and *Smittipora cordiformis* Harmer, 1926 herein; see also Ostrovsky et al. 2007).

Under *Measurements*, uncommonly measured characters or those restricted to certain taxa are written in full. Otherwise, the following abbreviations are combined in various ways to form the abbreviations for characters measured: **Av**, avicularium; **Az**, autozooid; **D**, depth; **Dm**, diameter; **H**, height; **L**, length; **Mat**, maternal; **Op**, opesia; **Or**, orifice; **Ov**, ovicell, ovicelled; **Ros**, rostrum; **Sec**, secondary; **Sin**, sinus; **W**, width; **Z**, zooid.

Table 1. Relative abundance, local occurrence and status in Japan for rocky-intertidal cheilostome bryozoan species detected in west-central Okinawa, Japan.

Species	Figure	Number of fragments				No. sites	Status Japan
		SES	REEF	MIN	Total		
Aetea sp. A	3	–	–	1	1	1	?
Thalamoporella stapifera	3, 4	–	38	9	47	2	x
Thalamoporella karesansui	4	31	2	–	33	2	n
Crassimarginatella eremitica	5	–	1	–	1	1	n
Crassimarginatella extenuata	6	1	–	–	1	1	x
Cranosina coronata	6	9	4	1	14	3	p
Beania cookae	7	–	–	1	1	1	x
Beania hexamicorum	7	–	–	6	6	1	x
Smittipora cordiformis	8	–	–	2	2	1	x
Cribralaria curvirostris	8	–	–	20	20	1	p
Puellina harmeri	9	–	–	6	6	1	x
Vasignyella otophora	10	–	–	2	2	1	x
Hippothoa petrophila	10	–	–	7	7	1	n
Chorizopora brongniartii	11	–	–	2	2	1	?
Poricella spathulata	11	–	1	1	2	2	x
Exechonella sp. A	11	1	–	–	1	1	?
Celleporaria calva	12	1	–	7	8	2	x
Celleporaria desperabilis	13	1	–	–	1	1	x
Celleporaria pilaefera	14	7	3	–	10	2	x
Celleporaria triangula	14	39	–	–	39	1	x
Parasmittina serrula	15	5	–	3	8	2	x
Parasmittina soulesi	16	3	1	–	4	2	x
Parasmittina alanbanneri	17	–	2	3	5	2	x
Pleurocodonellina microperforata	18	16	–	12	28	2	x
Smittina nitidissima	19	–	–	1	1	1	x
Smittoidea pacifica	19	5	–	–	5	1	x
Calyptotheca reniformis	20	5	2	–	7	2	x
Calyptotheca sesokoensis	20	1	–	–	1	1	n
Stephanotheca fenestricella	21	1	–	–	1	1	n
Stylopoma duboisii	22	2	–	1	3	2	?
Stylopoma vilaensis	23	–	–	7	7	1	x
Junerossia copiosa	23	9	38	20	67	3	x
Hippopodina adunca	24	8	–	26	34	2	x
Hippopodina iririkensis	24	7	10	–	17	2	x
Thornelya fuscina	25	1	–	–	1	1	x
Thornelya perarmata	25	2	–	–	2	1	x
Gigantopora pupa	25	1	–	–	1	1	x
Echinovadoma anceps	26	2	–	–	2	1	x
Robertsonidra argentea	27	53	19	1	73	3	x
Robertsonidra porifera	27	1	–	2	3	2	x
Fenestrulina parviporus	28	4	–	–	4	1	n
Arthropoma harmelini	30	30	8	–	38	2	n
Bryopesanser latesco	31	2	–	10	12	2	x
Crepidacantha longiseta	32	2	–	4	6	2	x
Crepidacantha poissonii	32	–	–	1	1	1	?
Torquatella duolamellata	33	3	–	–	3	1	x
Metacleidochasma planulata	33	4	–	2	6	2	x
Rhynchozoon ferocula	34	5	2	–	7	2	x
Rhynchozoon maculosum	35, 36	32	14	20	66	3	n
Rhynchozoon lunifrons	37, 38	11	–	–	11	1	n
Rhynchozoon ryukyuense	39	11	7	–	18	2	n
Rhynchozoon scimitar	36, 40	5	–	–	5	1	n
Total colonies and fragments		321	152	178	651		
Total cheilostome species		36	16	28	(52)		

Species described as new are in bold font. The 'Figure' column indicates the figure(s) herein illustrating each species. 'Number of fragments' indicates the counts of whole colonies and colony fragments for each species, by sampling site (SES, south-eastern Sesoko Island; REEF, north-western Sesoko Island; MIN, Minna Island). 'No. sites' indicates the frequency of occurrence of species among the three sites. Abbreviations for 'Status Japan': x, new record for Japan; n, new species; p, previously reported from Japan; ?, not identified to species, or conspecificity with previous records in Japan unclear.

Results

Local occurrence and abundance

We examined 651 colonies or colony fragments, of which roughly half came from the SES site and one-quarter each from the REEF and MIN sites. We detected 52 cheilostome species (Table 1). The SES site had the highest local species richness (36 species), followed by MIN (28 species) and REEF (16 species), with the high diversity at SES to some extent reflecting the two-fold greater sampling effort there. The occurrence of species appeared to be patchy, with 28 species (53.8%) detected at only a single site, and only four species (7.7%) detected at all three sites (Table 2). Among the 28 species detected at only one site, 12 species (42.9%) were rare, represented by only a single colony.

As a consequence of species' patchiness, the three sites varied in species composition. Among the species detected at only one site, 15 (28.8% of total species) were at SES, 12 (23.1%) at MIN and one (1.9%) at REEF (Table 1). REEF, which was located physically between SES and MIN, was also intermediate in composition; 15 of the 16 species detected there were also found at SES (eight species), MIN (three species) or both (four species). Nine species were found at SES and MIN, but not at REEF.

In terms of relative abundance, 18 (34.6%) of all species were represented by only one or two specimens (Table 2). At the other end of the spectrum, the dominant cheilostomes (high in total abundance and occurring at all three sites) were *Junerossia copiosa* Dick et al., 2006, *Robertsonidra argentea* (Hincks, 1881), and *Rhynchozoon maculosum* sp. nov. (Table 1). *Cranosina coronata* (Hincks, 1881) also occurred at all three sites, but was lower in total abundance.

Most species (45, or 86.6%) we detected were either new to science (11 species, 21.2%) or new records for Japan (34 species, 65.4%) (Tables 1 and 2). We identified only two species previously reported from Japan (*Cranosina coronata* and *Cribralaria curvirostris* Silén, 1941), the former from Pliocene and Pleistocene deposits in the Nansei Archipelago (Kataoka 1961; Hayami 1971), and the latter from the Ogasawara Islands far

Table 2. Summary of relative abundance, local occurrence and status in Japan for rocky-intertidal cheilostome bryozoans detected on Okinawa.

	Number of species	Percentage
Prevalence among sites		
1 site	28	53.8
2 sites	20	38.5
3 sites	4	7.7
Number of colonies or fragments		
1	12	23.1
2	6	11.5
3–10	19	36.5
11–30	7	13.5
31–50	5	9.6
> 50	3	5.8
Status for Japan		
New species	11	21.1
New record for Japan	34	65.4
Previously reported in Japan	2	3.8
Identity unclear	3	5.8
Not identified to species	2	3.8

to the south-east of the Japanese main islands (Silén 1941). The identity of an additional three species – *Chorizopora brongniartii* (Audouin, 1826), *Stylopoma duboisii* (Audouin, 1826), and *Crepidacantha poissonii* (Audouin, 1826) – with previous nominal records from Japan was unclear (see the Remarks sections for these species). We did not identify *Aetea* sp. A and *Exechonella* sp. A to the species level.

Growth form and zooidal grade

Among the 52 cheilostome species we detected, most (49 species, 94.2%) were encrusting and two-dimensional, forming sheets or (in two cases, *Aetea* sp. A and *Hippothoa petrophila* sp. nov.) branching uniserial networks. Colonies of most of the sheet-like species were unilaminar. While we observed selected species in *Celleporaria* and *Rhynchozoon* to form additional layers through occasional frontal budding or colony self-overgrowth, these colonies were also functionally two-dimensional rather than three-dimensional (conical or erect). *Aetea* sp. A differed from other encrusting species in having an encrusting stolonal network that gave rise to erect zooids. Three species [*Beania cookae* Tilbrook et al., 2001; *Beania hexamicorum*, Tilbrook et al., 2001; *Vasignyella otophora* (Kirkpatrick, 1890)] formed small, recumbent, essentially unilaminar colonies in which the zooids were raised from the substratum but attached to it by radicle fibres arising from the basal side. For nearly half (25, 48.1%) of the 52 species detected, the largest colony observed was less (and sometimes much less) than 1 cm in maximum dimension.

A high proportion (43 species, 82.7%) of the cheilostomes we detected had ascophoran-grade zooids, with a hard, protective frontal shield (including the cribrimorphs *Cribralaria curvirostris* and *Puellina harmeri* Ristedt, 1985). Nine species (17.3%) were of anascan grade, with a non-calcified frontal wall, although three of these [*Thalamoporella karesansui* sp. nov.; *Thalamoporella stapifera* (Levinsen, 1909); *Smittipora cordiformis* Harmer, 1926] have an extensive cryptocyst beneath the non-calcified frontal wall, which may afford protection similar to that achieved by ascophoran-grade zooids.

Cheilostomes were by far the major component of the marine bryozoan fauna in the study area. We found no ctenostome species (Class Gynolaemata, Order Ctenostomata) and only five cyclostome species (Class Stenolaemata, Order Cyclostomata), which were low in abundance and contributed much less than cheilostomes in terms of substrate coverage.

Biogeography

Table 3 indicates previously known distributions for 40 of the species we detected on Okinawa, excluding two species identified only to genus and 10 species known at present only from our study area. Most of these 40 species (36, or 90.0%) had been reported from the Central IP realm of Spalding et al. (2007) (see Methods). Fewer than half as many species had been reported from each of the Western IP realm (17 species, 42.5%) and the Eastern IP realm (16 species, 40.0%). Of the 16 Okinawa species ranging into the Eastern IP realm (including two classed as 'cosmopolitan'), all but one (*Vasignyella otophora*) had been reported previously from Hawaii, and two (*Crassimarginetella extenuata* Dick et al., 2006; *Parasmittina alanbanneri* Soule and

Table 3. Reported occurrences of 40 Okinawa cheilostome bryozoan species having previously known distributions among the coastal marine realms defined by Spalding et al. (2007).

Species	Near-shore biogeographical realm					
	TNP	TA	WIP	CIP	EIP	(HI)
Thalamoporella stapifera	–	–	x	x	–	–
Crassimarginatella extenuata	–	–	–	–	x	x
Cranosina coronata	–	–	x	x	–	–
Beania cookae	–	–	–	x	–	–
Beania hexamicorum	–	–	–	x	–	–
Smittipora cordiformis	–	–	x	x	–	–
Cribralaria curvirostris	–	–	–	x	–	–
Puellina harmeri	–	–	x	x	x	x
Vasignyella otophora	–	–	x	x	x	–
Chorizopora brongniartii	c	c	c	c	c	c
Poricella spathulata	–	–	x	x	x	x
Celleporaria calva	–	–	–	x	–	–
Celleporaria desperabilis	–	–	–	x	–	–
Celleporaria pilaefera	–	–	x	x	–	–
Celleporaria triangula	x	–	–	–	–	–
Parasmittina serrula	c	c	–	c	c	c
Parasmittina soulesi	–	–	–	x	–	–
Parasmittina alanbanneri	–	–	–	–	x	x
Pleurocodonellina microperforata	x	–	–	x	–	–
Smittina nitidissima	–	–	c	–	–	–
Smittoidea pacifica	–	–	–	x	x	x
Calyptotheca reniformis	–	–	–	x	–	–
Stylopoma duboisii	x	–	–	x	–	–
Stylopoma vilaensis	–	–	–	x	–	–
Junerossia copiosa	–	–	–	x	x	x
Hippopodina adunca	x	–	x	x	–	–
Hippopodina iririkensis	–	–	x	x	x	x
Thornelya fuscina	–	–	x	x	–	–
Thornelya perarmata	–	–	–	x	–	–
Gigantopora pupa	–	x	–	x	–	–
Echinovadoma anceps	–	–	–	x	–	–
Robertsonidra argentea	x	–	x	x	–	–
Robertsonidra porifera	–	x	–	x	–	–
Fenestrulina parviporus	–	–	–	x	x	x
Bryopesanser latesco	–	–	x	x	x	x
Crepidacantha longiseta	–	–	c	c	c	c
Crepidacantha poissonii	–	–	x	x	x	x
Torquatella duolamellata	–	–	–	x	–	–
Metacleidochasma planulata	–	–	–	x	x	x
Rhynchozoon ferocula	–	–	x	x	x	x
Total species	7	4	17	36	16	15
Percent	17.5	10.0	42.5	90.0	40.0	37.5

TNP, Temperate North Pacific; TA, Temperate Australasia; WIP, Western Indo-Pacific; CIP, Central Indo-Pacific; EIP, Eastern Indo-Pacific; (HI), Hawaii, a province and an ecoregion within the EIP realm. Other abbreviations: x, previous record in realm; c, previous record in realm, but putatively cosmopolitan, occuring in other realms than those included here; –, no previous record.

Soule, 1973) had been known only from Hawaii. Aside from two putatively cosmopolitan species (*Chorizopora brongniartii* and *Crepidacantha longiseta* Canu and Bassler, 1928), only seven species (17.5%) have broad Indo-Pacific distributions, occurring in all three IP realms (Table 4). *Smittina nitidissima* (Hincks, 1880), possibly an anthropogenically distributed species, was known from the Western but not the Central IP realm.

Table 4 summarises the allocation of Okinawa species among the IP and other realms. Previous records of 29 species (72.5%) are restricted to the Indo-Pacific. Among these, 11 species (27.5%) had been reported only from the Central IP realm, which also shares four

Table 4. Occurrence of 40 Okinawa cheilostome bryozoan species having previously known distributions among the coastal marine realms defined by Spalding et al. (2007).

Realm(s)	Number of species	Percentage
Eastern Indo-Pacific (IP) only	2	5.0
Central IP only	11	27.5
Central and Eastern IP only	4	10.0
Western and Central IP only	5	12.5
Western, Central, and Eastern IP only	7	17.5
Total for IP realms	[29]	[72.5]
Temperate North Pacific	5	12.5
Temperate Australasia	2	5.0
Putatively cosmopolitan	4	10.0

Each species is listed in only one category; square brackets indicate sums of preceding values. All but one of the species listed in the temperate realms and the four species listed as 'putatively cosmopolitan' also occur in one or more of the IP realms. The information here is summarised from Table 3.

species (10%) with the Eastern IP realm and five (12.5%) with the Western IP realm. Aside from two of the putatively cosmopolitan species (*Chorizopora brongniartii* and *Parasmittina serrula* Soule and Soule, 1973), few of the species in the Okinawa fauna have previous records from the Temperate North Pacific realm (five species, 12.5%) or the Temperate Australasia realm (two species, 5.0%), and all but one of these (*Celleporaria triangula* Seo, 1994) also occurred in one or more of the IP realms.

Taxonomy

Class **GYMNOLAEMATA** Allman, 1856
Order **CHEILOSTOMATA** Busk, 1852a
Suborder **INOVICELLINA** Jullien, 1888
Superfamily **AETEOIDEA** Smitt, 1868
Family **AETEIDAE** Smitt, 1868
Genus ***Aetea*** Lamouroux, 1812
Aetea sp. A
(Figure 3(a))

? '*Aetea* ?*australis* Jullien': Gordon 1984, p. 39, pl. 8A–D.

Material examined
NSMT-Te 1503 (MIN-1), dried, on SEM stub.

Measurements
Running stolon diameter, 0.018–0.030 (0.024 ± 0.005) (n = 6, 1). Stolon dilatation length 0.26; width, 0.10 (average values, n = 2). Length of erect part of zooid (including circular stalk and expanded 'hood'), 0.43–0.78 (0.619 ± 0.140); stalk length, 0.25–0.54 (0.376 ± 0.103); hood length, 0.19–0.28 (0.241 ± 0.036); ratio, length of hood to total length of erect part of zooid, 0.33–0.44 (0.396 ± 0.042) (all n = 7, 1). Stalk diameter, 0.055–0.072 (0.065 ± 0.005); maximum width of hood, 0.064–0.104 (0.090 ± 0.014); ratio, maximum width of hood to stalk diameter, 1.00–1.58 (1.398 ± 0.184) (all n = 8, 1).
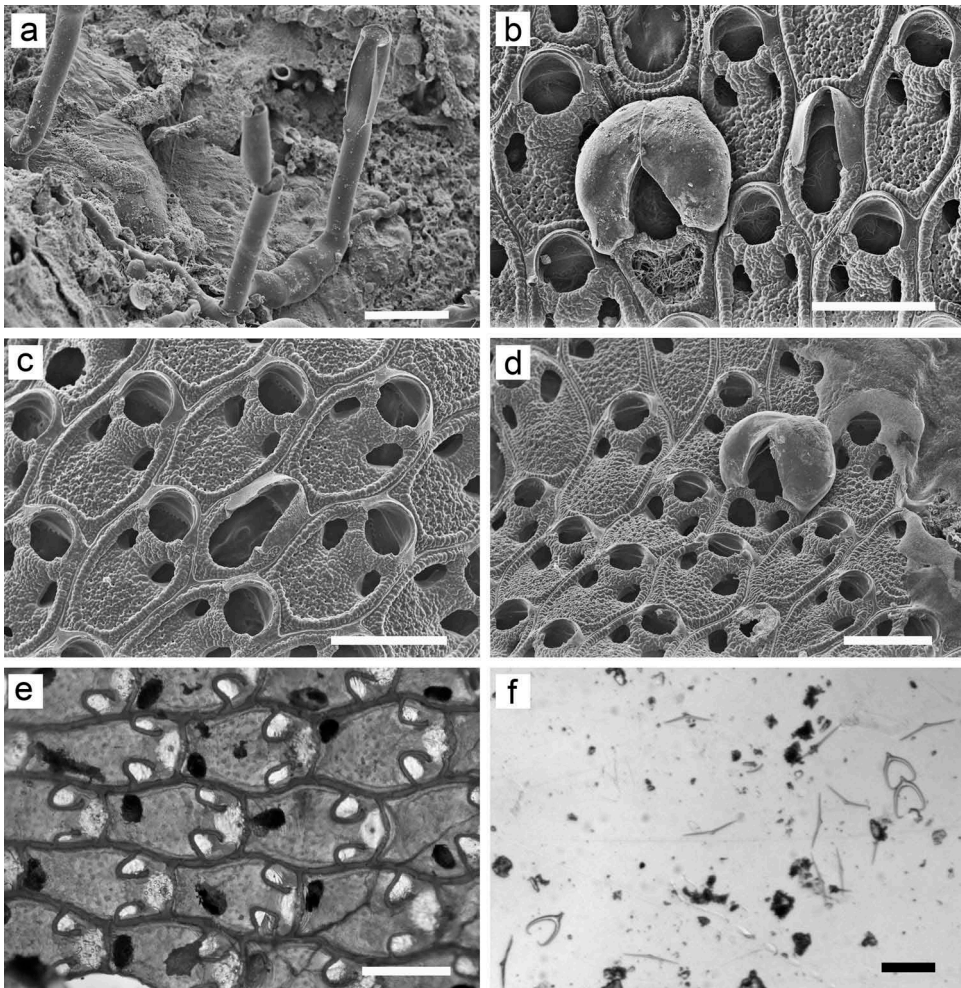
Figure 3. (a) *Aetea* sp. A: NSMT-Te 1053, zooids and interconnecting stolons. (b–f) *Thalamoporella stapifera* (Levinsen): (b) NSMT-Te 1056, autozooids, vicarious avicularium and ovicelled zooid; (c) NSMT-Te 1054, vicarious avicularium, with surrounding autozooids showing no torsion; (d) NSMT-Te 1055, autozooids and ovicelled zooid; note small lateral-oral tubercles on zooid proximal to ovicelled zooid; (e) Reef-2zs, basal surface of colony, showing basal insertions; (f) spicules, including small stirrup-shaped callipers and small to medium, slightly angled compasses. a–d, scanning electron microscopic images; e, f, photomicrographs. Scale bars: a = 250 μm; b–e = 500 μm; f = 100 μm.

Description

Colony small, recumbent, with zooids in branching uniserial series. Recumbent part of zooids consists of long, thin proximal stolon and wider, oblong distal dilatation. Dilatation width roughly 3 times that of stolon. Basic branching pattern cruciform; dilatation can be terminal, or give rise to stolon of daughter zooid from distal end, and/or from lateral margin on one or both sides. Erect part of zooid arises from distal end of dilatation and consists of tubular stalk and expanded hood open on one side (where frontal membrane covers opesia) and distally (where aperture is closed by

operculum). Stalk relatively thick; diameter more than half width of dilatation. Hood relatively long, comprising roughly 30–40% of length of erect part of zooid. Hood widest in mid-region; transversely or slightly obliquely truncate distally. Opesia tapering proximally, forming V-shaped notch where hood meets stalk. Operculum terminal, fitting transverse curvature of distal end of hood. Stolon, dilatation, stalk and hood appear smooth, with no overt, regular annulation.

Remarks

The taxonomy of *Aetea* is poorly resolved. Species in this genus have a simple, rather stereotypical morphology, and some of the characters perceived to be taxonomically informative unfortunately appear to vary ecophenotypically, as Gordon (1984, p. 39) noted for parts of a single colony of *Aetea* cf. *ligulata* growing in different microhabitats. At least part of the material from the Kermadec Ridge, New Zealand, that Gordon (1984) reported as *Aetea* ?*australis* Jullien, 1888, is similar to our specimen in the following characters: the branching pattern appears to be cruciform; the dilatation is markedly wider than the stolon; the erect tubular stalk is thick, roughly half or more as wide as the dilatation; the hood is transversely or slightly obliquely truncate, and comprises nearly half the total length of the erect portion in some zooids; and there are no regular annuli on any part of the zooid.

Occurrence

We found one colony, at the MIN site.

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Suborder **THALAMOPORELLINA** Ostrovsky, 2013
Superfamily **THALAMOPORELLOIDEA** Levinsen, 1902
Family **THALAMOPORELLIDAE** Levinsen, 1909
Genus ***Thalamoporella*** Hincks, 1887
Thalamoporella stapifera (Levinsen, 1909)
(Figures 3(b–f) and 4(f))

</div>

Thalamoporella granulata var. A (*stapifera*) Levinsen, 1909, p. 188, pl. 6, fig. 5(a–e).
Thalamoporella stapifera: Harmer 1926, p. 297, pl. 19, figs 17 and 20–25. Winston and Heimberg 1986, p. 8, figs 13–16.
Not *Thalamoporella stapifera*: Ryland and Hayward 1992, p. 241, fig. 10(d, e).
Not *Thalamoporella stapifera*: Soule and Soule 1970, p. 10, fig. 4(c–g). Soule et al. 1992, p. 13, 31, figs 21 and 47; [= *Thalamoporella molokaiensis* Soule et al., 1999].

Material examined

NSMT-Te 1054 (MIN-Thal1), bleached, on SEM stub; NSMT-Te 1055 (MIN-Thal2), bleached, on SEM stub; NSMT-Te 1056 (MIN-15), bleached, on SEM stub; NSMT-Te 1057, four dried specimens, MIN site; NSMT-Te 1058, 22 dried specimens, REEF site; NSMT-Te 1059, four bleached fragments, REEF site; NHMUK 2016.5.13.1-6, six dried specimens, REEF site.

Measurements

AzL, 0.68–0.96 (0.807 ± 0.076); AzW, 0.36–0.58 (0.458 ± 0.050) (n = 43,3). OrL, 0.20–0.27 (0.235 ± 0.017); OrW, 0.19–0.25 (0.226 ± 0.014) (n = 43, 3). OvL, 0.50–0.60
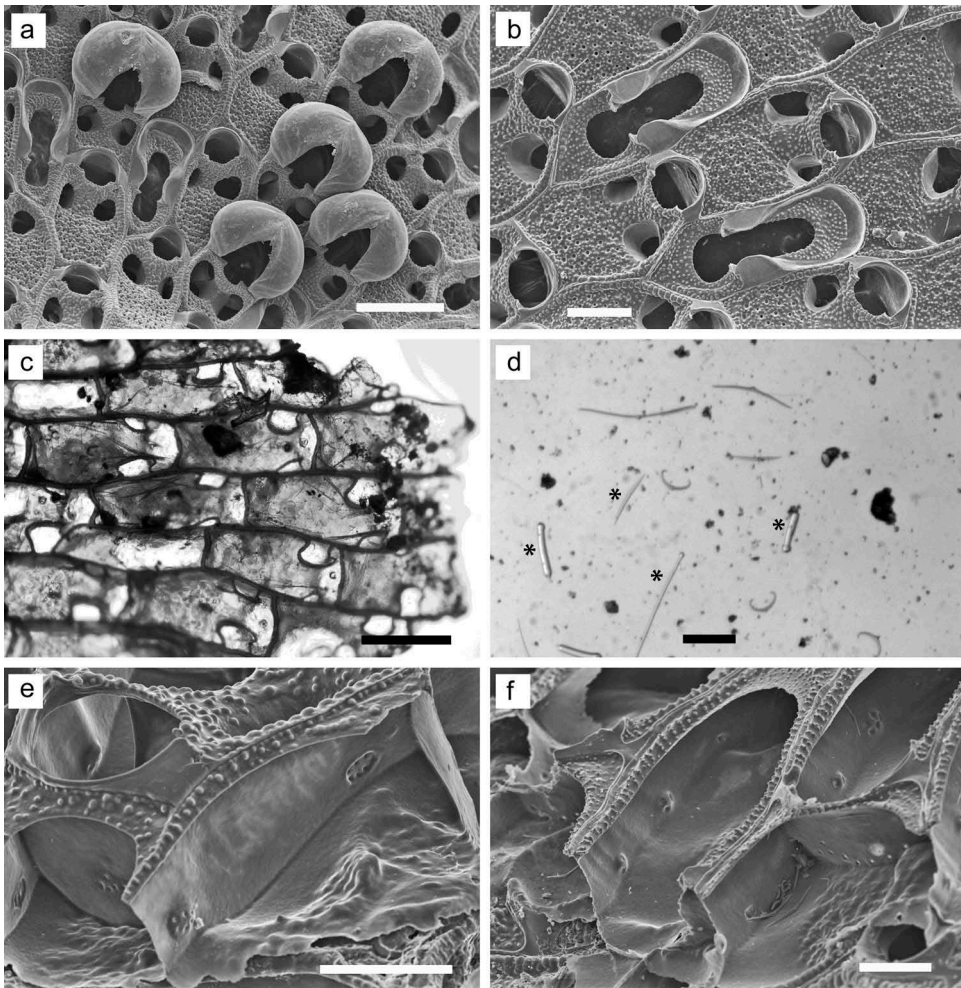
Figure 4. (a–e) *Thalamoporella karesansui* sp. nov.: (a) NSMT-Te 1060 (holotype), autozooids, vicarious avicularium and ovicelled zooids; (b) NHMUK 2016.5.13.7 (paratype), vicarious avicularia and surrounding autozooids; (c) SES-specimen A, basal surface of dried colony, showing basal insertions; (d) NHMUK 2016.5.13.7 (paratype), spicules removed by bleaching, including small C-shaped callipers and medium-sized, slightly angled compasses; asterisks mark sponge spicules; (e) NHMUK 2016.5.13.7 (paratype), interzooidal connections; (f) *Thalamoporella stapifera* (Levinsen), NSMT-Te 1055, interzooidal connections. a, b, e, f, scanning electron microscopic images of bleached material; c, d, photomicrographs. Scale bars: a, c = 500 μm; b = 250 μm; d = 100 μm; e, f = 150 μm.

(0.549 ± 0.034); OvW, 0.59–0.70 (0.644 ± 0.029) (n = 8, 3). AvL, 0.56–0.61 (0.585 ± 0.017); AvW, 0.34–0.38 (0.358 ± 0.014) (n = 6, 3). Stirrup-shaped calliper: H, 0.048–0.061 (0.055 ± 0.003); W, 0.041–0.050 (0.044 ± 0.002); H/W ratio, 1.13–1.38 (1.251 ± 0.074) (n = 17, 1). C-shaped calliper: H, 0.031; W, 0.036; H/W 0.086 (n = 1, 1). Compass length, 0.053–0.165 (0.085 ± 0.022) (n = 40, 1). Largest colony observed 20 × 13 mm.

Description

Colony forming a unilaminar, encrusting sheet, becoming locally multilaminar due to self-overgrowth; light yellowish to greyish tan in colour; often irregular in outline. Zooids (Figure 3(b–d)) distinct. Cryptocyst flat, densely granulated, uniformly perforated with small pseudopores proximal to level of opesiules; completely surrounded by raised, beaded rim. Opesiules oval, elongate, subcircular or irregular in outline; symmetrical in size, or one larger than other. Opesiular insertions (Figure 3(e)) irregular open hooks, though distal end sometimes extends laterally to meet lateral wall, giving closed hook. Orifice (Figure 3(b, c)) subcircular, approximately as long as broad; semicircular distal to articulations; broad, deep sinus proximal to articulations, proximal margin concave or straight. Small, paired knobs present or absent lateral to orifice, this character variable even within colonies. Avicularia (Figure 3(b, c)) shorter than autozooids; ratio of mean AvL to mean ZL, 0.72; middle flanges lacking; articulations small, bracket-like. Mandibular part of rostrum raised, with smooth gymnocystal surface; mandible tapering to rounded, sub-acute tip. No torsion evident among avicularium, sister zooid or other adjacent zooids. Large ooecium of bivalved hyperstomial ovicell (Figure 3(b, d)) somewhat broader than long, with median suture and acute, lanceolate opening. Spicules (Figure 3(f)) comprise small stirrup-shaped callipers and small to medium, slightly angled compasses; one small, C-shaped calliper observed. Zooids interconnect (Figure 4(f)) via broad line of single pores near base of transverse wall and two small, raised pauciporous septula in each lateral wall.

Remarks

Our material is consistent in virtually all characters with the redescription of *T. stapifera* by Soule et al. (1999). We found inter-colony variation in the occurrence of the stirrup-shaped callipers; among three colonies examined, callipers were abundant in one, rare in another and not detected in the third. There was also considerable variation in zooid and orifice size, so much so that it appeared two distinct species were involved; however, in some specimens, a part of the colony having small zooids could be traced to another part of the same colony having large zooids. This size variation may be related to seasonal variation in water temperature.

Occurrence

This species was abundant at REEF and common at MIN (Table 1). It is distributed from the north-eastern Indian Ocean to the western Pacific. Originally described from the Andaman or Nicobar islands (Levinsen 1909), *T. stapifera* has been reported from Timor (Harmer 1926); Lombok, Indonesia (Winston and Heimberg 1986); and the South China Sea (Androsova 1963). Okinawa (~26°N) is the farthest northern record.

Thalamoporella karesansui sp. nov.
(Figure 4(a–e))

Etymology

The specific name is a noun in apposition (Japanese *karesansui*: Zen rock garden), referring to the raked-sand appearance of the granulated floor of the avicularian rostrum.

Material examined

Holotype: NSMT-Te 1060 (SES-43), bleached, on SEM stub. Paratypes: NSMT-Te 1061, dried specimen, SES site; NSMT-Te 1062, seven dried specimens, SES site; NHMUK 2016.5.13.7, SES-Thal1, bleached, on SEM stub; NHMUK 2016.5.13.8–11, four dried specimens, SES site.

Measurements

AzL, 0.63–0.80 (0.702 ± 0.051); AzW, 0.38–0.46 (0.423 ± 0.025) (n = 20, 1). OrL, 0.16–0.21 (0.188 ± 0.012); OrW, 0.18–0.22 (0.200 ± 0.012) (n = 20, 1). OvL, 0.47; OvW, 0.60 (average values, n = 2). AvL, 0.74–0.86 (0.795 ± 0.040); AvW, 0.25–0.34 (0.278 ± 0.025) (n = 15, 1). Calliper H, 0.024–0.030 (0.026 ± 0.003); calliper W, 0.046–0.054 (0.049 ± 0.003); calliper H/W ratio, 0.44–0.65 (0.547 ± 0.081) (n = 7, 1). Compass lengths in several discrete size ranges: 0.069–0.094 (n = 5); 0.144–0.163 (n = 4); 0.193–0.209 (n = 3); 0.364 (n = 1).

Description

Colony forming a unilaminar, encrusting sheet; irregular in outline, up to several centimetres in extent; tightly adhering to substratum; dried specimens pale yellowish-tan. Zooids distinct (Figure 4(a, b)). Cryptocyst finely granulated; area proximal to opesiules flat and perforated with 20–40 small, circular, evenly spaced, often occluded pseudopores. Mural rim narrow, beaded, raised around entire margin of cryptocyst proximal to orifice. Opesiules large; oval or irregular; one often larger than other; zone between opesiules somewhat sunken. Basal insertions (Figure 4(c)) usually paired, but asymmetrical, of different shape and size between the two sides, consisting of two hooks, or one hook and one bar; usually closed distally by looping back to reconnect with lateral wall. Orifice (Figure 4(a, b)) usually broader than long, with broad sinus between bracket-like hinge articulations; proximal margin of sinus straight or slightly convex; orifice broadly D-shaped distal to articulations. Avicularia (Figure 4(a, b)) fairly common, longer than autozooids (ratio of average AvL to average ZL, 1.14; ratio of AvL to length of sibling zooid, 0.95–1.26, average 1.12); cryptocyst broad, flat, entirely granulated. Rostral opening narrow, elongate, occupying more than half the total length of avicularium. Mandibular articulations conspicuous, sharp, bracket-like, at proximal edge of broad, smooth, nearly semicircular, medially directed flange on each side. Mandibular part of rostrum spatulate distal to flanges; sides parallel or tapering proximomedially towards flanges; rounded-truncate distally; floor below mandible wide, flat, evenly granulated. Mandible (not shown) narrow in region between central flanges, spatulate distally; margin thin, smooth, lacking denticles. Avicularium-associated torsion mild and variable; many avicularium-sibling pairs show no torsion, but some appear to show slight torsion of avicularium, sibling zooid, or both; adjacent zooids not torqued. Spicules (Figure 4(d)) include small C-shaped callipers rather uniform in size, and several sizes of slightly angled compasses (see *Measurements*). Ovicell (Figure 4(a)) hyperstomial; ooecium bivalved, broader than long, smooth, with median suture; distal arch of opening rounded or acute. Zooids interconnect (Figure 4(e)) via group of uniporous septula in central third of distal wall and one elliptical multiporous septulum in each distolateral wall.

Remarks

This species is allied with *Thalamoporella tubifera* Levinsen, 1909, on the basis of having large zooid size (average ZL, 0.70 mm); the orifice with a rather deep, widely arcuate margin proximal to the opercular articulations; torsion weak or lacking in avicularia, sibling and adjacent zooids; spatulate avicularia not greatly shorter or longer than autozooids; and spicules in the form of small, C-shaped callipers and compasses of varying length. After describing variation in nominal *T. tubifera* throughout its range, Soule et al. (1992, p. 61) noted, 'There are some subtle differences within the *tubifera* complex which could lead to separation of this species into distinct populations, if not separate taxa, as for example the French Polynesia specimens', and again (p. 64), 'It seems probable that this widespread and very common species may in fact consist of several closely related taxa'. Unfortunately, proceeding as though variation across the distributional range of nominal *T. tubifera* were intraspecific rather than at least in part interspecific, Soule et al. (1992) presented some distinct measurements for the holotype, but otherwise gave ranges of measurements and average values across all populations, which makes comparisons among the populations they treated impossible.

The type locality of *T. tubifera* Levinsen is Papua New Guinea. Levinsen (1909) indicated the range of zooid length as 0.53–0.73 mm, somewhat smaller than in our material; in the type material, the avicularian rostrum is vase- or lyre-shaped, with very little granulation on the rostral floor beneath the mandible (Levinsen 1909, pl. 4a, fig. 2 (a); see also Soule et al. 1992, fig. 86). Soule et al. (1992, p. 61) noted that zooids and avicularia in the holotype are the smallest among all populations: 'On the basis of size alone, the type of *T. tubifera* lies entirely outside the range of any of the specimens' (from numerous populations across the distributional range of the nominal species). The AvL/ZL ratio in the holotype of *T. tubifera* is 1.00, while the range across all nominal *T. tubifera* populations is 0.85–1.18, with an overall average of 1.01 (Soule et al. 1992). The ratio in *T. karesansui* (1.12–1.14) is larger than in the holotype of *T. tubifera*, and close to the high end of the range across all nominal *T. tubifera* populations. According to Soule et al. (1992), species or populations in the *T. tubifera* complex usually have basal insertions in the form of two widely open hooks. In *T. karesansui*, some zooids have open hooks (or a hook and a bar), but most zooids have each insertion closed distally by a lateral extension that loops back to meet the lateral wall.

If the Okinawa specimens and the type material for *T. tubifera* from Papua New Guinea were the only material available from the *T. tubifera* complex, there would be no hesitation in describing the Okinawa population as a different species from *T. tubifera*, and this is the approach we have taken. The status of other populations will have to be evaluated on a case-by-case basis.

Several other Indo-West Pacific species (Soule et al. 1992) have large, spatulate avicularia like *T. karesansui*, but differ in colony form, zooid size, avicularium size and shape, degree of torquing, form of the basal insertions or other characters; here we will mention two additional encrusting species as an example of the sorts of differences involved. *Thalamoporella granulata* Levinsen, 1909 sensu lato has the avicularia considerably longer than zooids (AvL/ZL, 1.19–1.34) (Soule et al. 1992); both the avicularium and sibling zooid are strongly torqued; opesiule insertions are paired open hooks, or one hook and a bar; and strongly bent (120°) compasses are present. *Thalamoporalla*

granulata (sensu lato) is distributed from Lombok, Indonesia eastward to Tonga and ranges in latitude from the equator to about 20°S, with some questionable records from the Philippines and Taiwan (Soule et al. 1992). *Thalamoporella sibogae* Soule et al., 1992, has smaller zooids (average ZL, 0.54 mm) and proportionally longer avicularia (the AvL/ZL ratio reaches 1.25); the avicularium is straight, but both the sibling and adjacent non-sibling zooids are torqued; and the avicularian mandible has unique chitinous teeth on the margin. *Thalamoporella sibogae* has been reported as far north as the Korean Peninsula (~33°N) (Seo 2005).

Occurrence

This species, presently known only from Okinawa, was abundant at SES and uncommon at REEF (Table 1). *Thalamoporella tubifera* (sensu lato) has a broad Indo-West Pacific distribution, ranging from the Maldive Islands in the Indian Ocean eastward to French Polynesia, and as far north as Taiwan (22°N; Gluhak et al. 2007).

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Suborder **NEOCHEILOSTOMINA** d'Hondt, 1985
Superfamily **CALLOPOROIDEA** Norman, 1903a
Family **CALLOPORIDAE** Norman, 1903a
Genus *Crassimarginatella* Canu, 1900
Crassimarginatella eremitica sp. nov.
(Figure 5)

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Etymology

The specific name is an adjective (Latin *eremiticus*: reclusive, solitary), referring to our finding only a single small colony.

Material examined

Holotype: NSMT-Te 1063 (REEF-9), bleached, on SEM stub.

Measurements

AzL, 0.48–0.55 (0.516 ± 0.023); AzW, 0.38–0.43 (0.404 ± 0.016), OpL, 0.38–0.44 (0.409 ± 0.018); OpW, 0.26–0.34 (0.304 ± 0.019) (n = 15, 1). One colony, 5.3 × 3.0 mm.

Description

Colony (Figure 5(a)) forming a unilaminar, encrusting sheet; dried specimen light orange. Zooids (Figure 5(b, c)) delineated by deep groove; gymnocyst moderately wide proximally and/or laterally. Opesia elliptical to irregularly oval, surrounded by narrow, raised mural rim. Cryptocyst (Figure 5(d)) narrow, nearly vertical, smooth around inner margin, serrated around mural rim, except in vicinity of orifice. Non-reproductive zooids in zone of astogenetic change bear two pairs of short, blunt, erect orificial spines, and four to eight short, tapering, acute, slightly or markedly curved opesial spines. Most zooids in zone of astogenetic repetition have single pair of thick, distolateral orificial spines and two to four opesial spines. All spines non-articulated, hollow, arising from gymnocyst. Vestigial ooecium (Figure 5(d, e)) is formed by next-distal autozooid as a visor-like structure around distal end of zooid; pointed, with pseudopore at tip. Vestigial ooecium
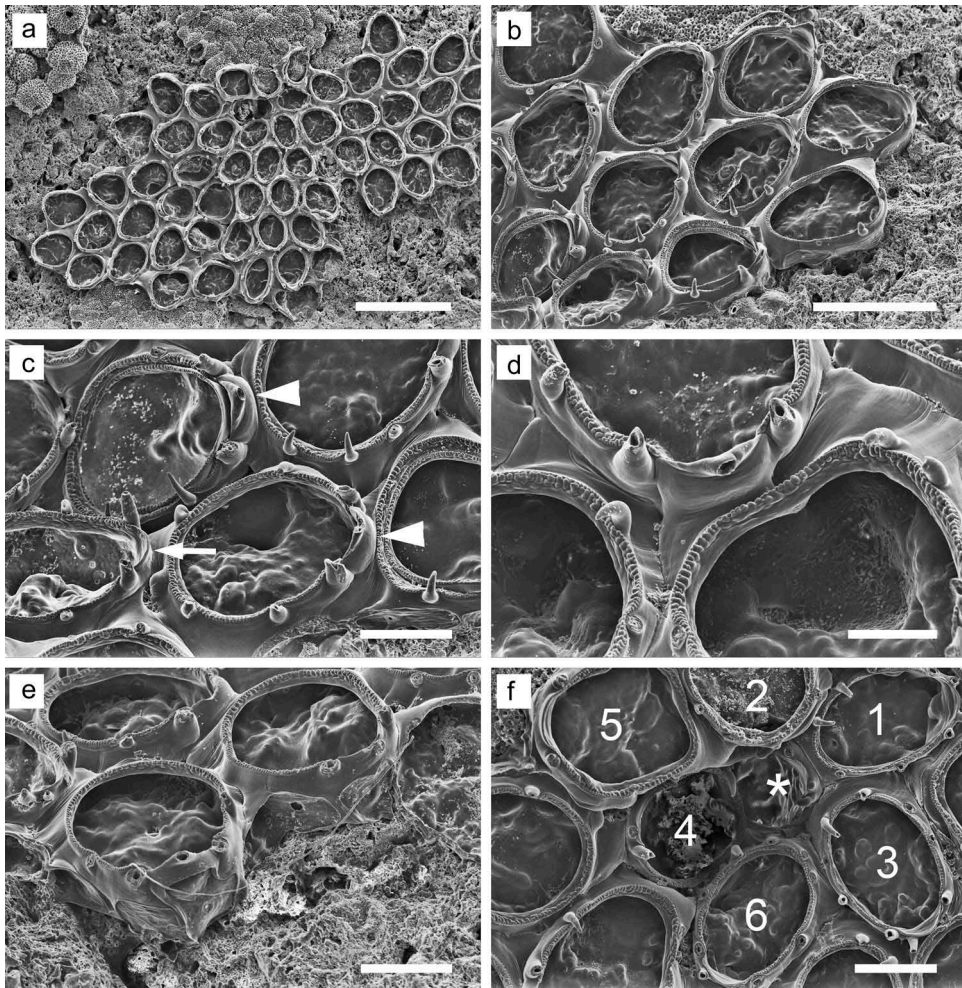
Figure 5. *Crassimarginatella eremitica* sp. nov., NSMT-Te 1063 (holotype): (a) frontal view of colony; (b) enlargement showing autozooids; (c) autozooids with vestigial ooecium (arrowheads) and lacking ooecium (arrow); (d) frontodistal view of zooid showing vestigial ooecium; (e) marginal autozooids, showing zones of interzooidal contact, each bearing a uniporous septulum, and a forming vestigial ooecium; (f) ancestrula (asterisk) and periancestrular zooids (1, distal; 2, 3, distolateral; 4, proximal; 5, 6 proximolateral). All panels are scanning electron microscopic images of the specimen after bleaching. Scale bars: a = 1.0 mm; b = 500 μm; c, e, f = 200 μm; d = 100 μm.

is indicative of embryonic incubation in a brood sac immersed in distal part of maternal zooid. Colony precocious; most zooids more than two generations away from ancestrula bear ooecium. Zooids interconnect by uniporous septula, one in transverse wall and one or two in each distolateral wall, leading to large, more-or-less tubular interzooidal chambers. Basal walls calcified. Ancestrula (Figure 5(f)) partly obscured in our specimen due to substratum irregularity; tatiform, 0.25 mm wide, with two pairs short, straight orificial spines at distal end and at least one curved spine more proximally; surrounded by six periancestrular zooids.

Remarks

The generic assignment of this species is unclear. Gordon (1984) subdivided *Crassimarginatella* Canu, 1900 into three subgenera: *Corbulella*, for species having vicarious avicularia with opesial spines and a serrated rostral rim, and a prominent ovicell with a single broad fenestra; *Crassimarginatella*, for species in which the vicarious avicularia lack spines and serration, and the ovicell is either prominent and unifenestrate, or small and cap-like; and *Valdemunitella*, for species having a bifenestrate ovicell. Tilbrook et al. (2001) raised all three subgenera to the rank of genus.

This species clearly bears vestigial ooecia, making it difficult to place in *Corbulella*. *Crassimarginatella* is a better fit because the generic diagnosis permits small, cap-like ooecia (Gordon 1984), and the genus now contains some species having prominent, well-developed ooecia and others with vestigial ooecia (Ostrovsky et al. 2009). Our specimen lacks vicarious avicularia, and it is unknown whether they occur in this species. *Crassimarginatella eremitica* shares with *Cr. extenuata* (next description) a moderately wide, somewhat irregular gymnocyst; relatively few spines scattered irregularly around the opesia; and zooids loosely connected by tube-like interzooidal chambers. With its short, fang-like opesial spines and vestigial ooecium with a median pseudopore, *C. eremitica* differs from any previously described species in either *Corbulella* or *Crassimarginatella*.

Occurrence

We found a single small colony at the REEF site, the only known locality.

Crassimarginatella extenuata (Dick, Tilbrook, and Mawatari, 2006)
(Figure 6(a–d))

Corbulella extenuata Dick, Tilbrook, and Mawatari, 2006, p. 2207, Figure 4(a–d).

Material examined

NSMT-Te 1064 (SES-41), bleached, on SEM stub.

Measurements

AzL, 0.53–0.65 (0.586 ± 0.047); AzW, 0.35–0.49 (0.387 ± 0.048) (n = 7,1). OpL, 0.32–0.39 (0.346 ± 0.028); OpW, 0.24–0.29 (0.263 ± 0.024) (n = 7, 1).

Description

One small, periancestrular colony observed, containing 25 zooids, with only about seven zooids in zone of astogenetic repetition (Figure 6(a)); forming a unilaminar, encrusting sheet; light yellowish-tan. Zooids distinct, delineated by a groove. Gymnocyst smooth, sloping, well exposed proximally, tapering laterally. Opesia oval, widest in middle or proximal third, occupying two-thirds to three-quarters of frontal area; distal margin straight (Figure 6(d)). Cryptocyst well developed, coarsely granulated, steeply sloping; widest proximally, tapering laterally, narrowest distally, but complete around straight distal margin of opesia. Zooids distally with small, low, smoothly rounded gymnocystal cap in midline. Six to nine coarse, hollow spines (modal number, 8; n = 7) around opesial
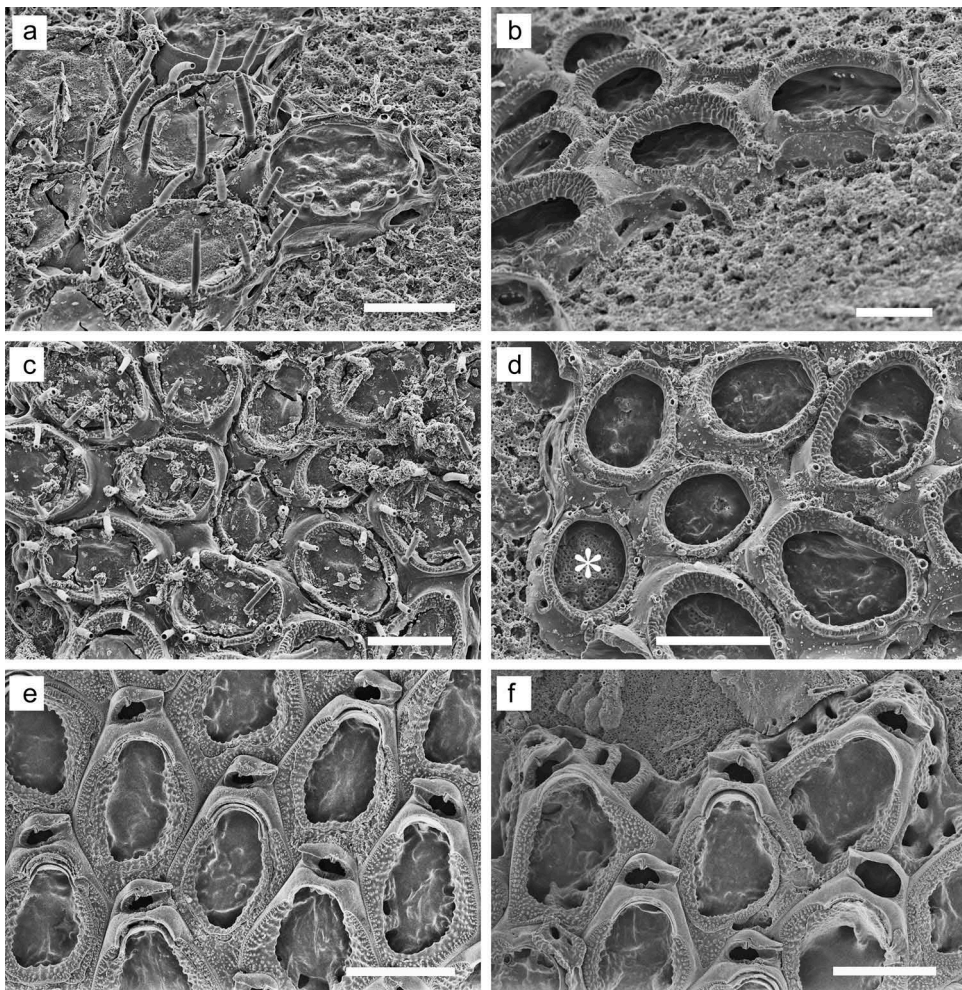
Figure 6. (a–d) *Corbulella extenuata* Dick, Tilbrook, and Mawatari, NSMT-Te 1064: (a) autozooids; (b) oblique view of colony margin showing interzooidal connections and presumed vestigial ooecium at early stage of formation (far top right); (c) ancestrula and periancestrular zooids; (d) same ancestrula (asterisk) as in panel (c) after bleaching, with daughter zooids lost from left side. (e, f) *Cranosina coronata* (Hincks), NSMT-Te 1065: (e) autozooids (the central three showing regenerative, intramurally budded cystids); (f) autozooids at colony margin (central zooid with intramurally budded cystid). Panels are scanning electron microscopic images of dried (a, c) or bleached (b, d–f) specimens. Scale bars: a = 250 μm; b–d = 300 μm; e, f = 400 μm.

margin (Figure 6(a, b)), including usually two pairs of orificial spines; spines erect or slightly tilted inward, reaching nearly as long as opesial width. Ancestrula (Figure 6(c, d)) of same form as subsequent zooids, but smaller, with three orificial and five opesial spines; connecting with six periancestrular zooids, of which proximal three are larger than distal three. Zooids interconnect (Figure 6(b)) via broad pore chamber with around five pores in transverse wall, and two pore chambers in each distolateral wall, each with two to four pores.

Remarks

The generic assignment of this species, originally described from Hawaii (Dick et al. 2006) as *Corbulella extenuata*, is problematic (see also remarks for *Cr. eremitica* above). A presumed vicarious avicularium in the holotype specimen appears to lacks spines and to lack serration on the rostral rim, indicative of *Crassimarginatella* rather than *Corbulella* (Gordon 1984). The nature of the ovicell is unclear. In our small specimen from Okinawa, the cap-like structure at the distal end of the zooid, which Dick et al. (2006) interpreted as a vestigial ooecium, is present in the ancestrula and periancestrular zooids. The cap in the ancestrula bears a median spine base, whereas in other zooids it bears neither a spine nor a pseudopore, suggesting it is simply a swelling in the distal zooidal wall. It may be that this species produces prominent ovicells, which are simply absent in the two specimens of this species found to date.

Occurrence

We found a single small colony at the SES site. Only two small colonies of this species have been reported, one at Hawaii and one at Okinawa; the currently known distribution is the subtropical, central to western North Pacific.

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Genus ***Cranosina*** Canu and Bassler, 1933
Cranosina coronata (Hincks, 1881)
(Figure 6(e, f))

</div>

Membranipora coronata Hincks, 1881, p. 147, pl. 10, fig. 1.
Setosellina coronata: Harmer 1926, p. 265, pl. XVI, figs 2–4.
For other synonyms and records, see Harmer (1926) and Tilbrook (2006).

Material examined

NSMT-Te 1065 (MIN-3), bleached, on SEM stub; NSMT-Te 1066, five dried specimens, SES site; NSMT-Te 1067, three dried specimens, REEF site.

Measurements

AzL, 0.53–0.72 (0.614 ± 0.050); AzW, 0.39–0.50 (0.430 ± 0.035). OpL, 0.36–0.53 (0.419 ± 0.044); OpW, 0.20–0.28 (0.232 ± 0.025). AvRosL, 0.16–0.25 (0.198 ± 0.023). (All n = 15, 1). Largest colony observed 10 mm across.

Description

Colony forming an irregular, unilaminar, encrusting sheet; off-white in colour. Zooids distinct, hexagonal, separated by thin incision. Opesia large, widest in middle or proximal third. Cryptocyst broad, sloping with coarse granulation organised in irregular rows perpendicular to opesial margin, not extending around orifice; cryptocystal texture completely covers tapering proximal end of zooids. Distal end of zooid raised as a smooth gymnocystal cowl around orifice. Interzooidal avicularium distal to each zooid; rostrum tilted in proximal direction and pointing laterally or distolaterally; wide, prominent hinge denticles, but no complete hinge bar; mandible (not shown) long, filiform, sometimes exceeding width of zooid. Spines and ovicells lacking. Ancestrula not observed.

Remarks

Species in this genus lack ooecia and brood embryos in an internal sac (Harmer 1926; Ostrovsky et al. 2009; Ostrovsky 2013). Interestingly, apparently as a means of regeneration following the internal destruction of a zooid by predation, many zooids in our specimens have an intramurally budded cystid, with a secondary sloping cryptocyst laid down inside and overlapping the first (with the two cystids delineated by a suture line between the cryptocysts and a gap between the respective smooth distal margins).

Tilbrook (2006, p. 25, pl. 2E) noted that the interzooidal avicularium in this species has the mandible directed proximolaterally, and illustrates this condition in a specimen from the Solomon Islands. In our specimen, the long axis of the rostrum points laterally or, more often, slightly distolaterally, an orientation also figured by Harmer (1926, pl. XVI, fig. 3), Ryland and Hayward (1992, fig. 2(e)) and Liu et al. (2001, pl. 18, fig. 5).

Occurrence

This species occurred at all three sites, but was most abundant at SES (Table 1). *Cranosina coronata* is quite common in the Into-West Pacific (Tilbrook 2006). In Japan, it has been previously reported from the Pleistocene Ryukyu Limestone, northern Nansei islands (Kataoka 1961) and the Pliocene Shinzato tuff, Shimajiri Formation, Okinawa (Hayami 1971; Sakagami et al. 1980).

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Superfamily **BUGULOIDEA** Gray, 1848
Family **BEANIIDAE** Canu and Bassler, 1927
Genus ***Beania*** Johnston, 1840
Beania cookae Tilbrook, Hayward, and Gordon, 2001
(Figure 7(a, b))

</div>

Beania cookae Tilbrook, Hayward, and Gordon, 2001, p. 48, fig. 5(e, g).
Beania klugei: Hayward and Ryland 1995, p. 542, fig. 6(a).

Material examined

NSMT-Te 1068 (MIN-28), dried, on SEM stub.

Measurements

AzL, 0.80–1.20 (0.939 ± 0.087) (n = 6, 1). AzW, 0.20–0.21 (0.205 ± 0.005) (n = 4, 1). AvL, 0.114–0.119 (0.117 ± 0.003), AvD, 0.064–0.069 (0.067 ± 0.003) (n = 3, 1). Average AvL/AvD ratio, 1.7 (n = 3, 1).

Description

One colony observed; tiny (~15 zooids), recumbent, loosely attached parallel to substratum by basal radicles, frontal side of zooids facing up; colony off-white, tinged slightly with orange. Zooids (Figure 7(a)) bud single daughter zooid basodistally, and one from proximolateral wall on each side. Zooids elongate, with squared distal corners; tapering in proximal one-quarter to narrow cylinder at point of origin. Frontal wall entirely membranous; other walls weakly calcified. Each distolateral corner bears small, non-articulated spinous process; no articulated spines observed, but one zooid shows minute spine scar on lateral margin between avicularium attachment and distal process.
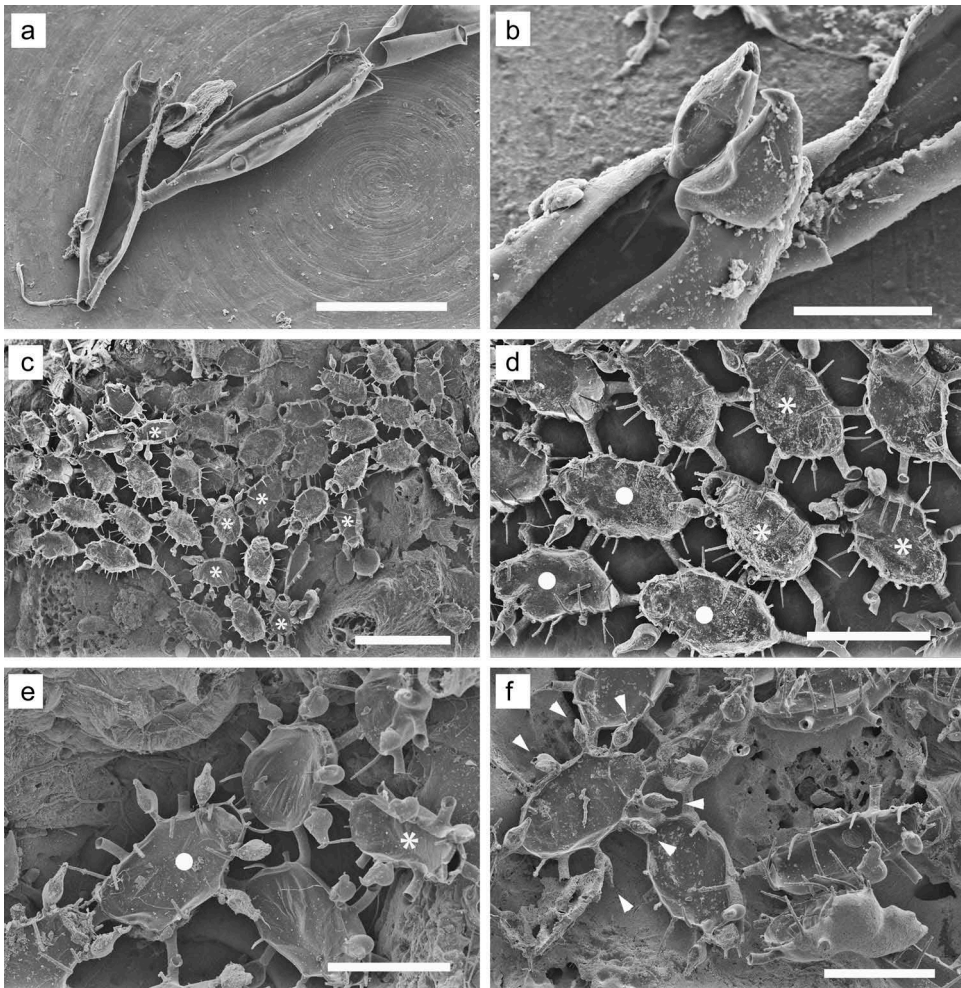
Figure 7. (a, b) *Beania cookae* Tilbrook, NSMT-Te 1068, dried specimens: (a) part of colony branch showing two complete autozooids; (b) enlargement of distal end of autozooid showing paired avicularia. (c–f) *Beania hexamicorum* Tilbrook, Hayward, and Gordon, dried specimens: (c) NHMUK 2016.5.13.12, frontal view showing recumbent colony loosely attached to substratum, with asterisks indicating autozooids that have more than one avicularium on a single side; (d) enlargement of left part of colony in previous panel, with autozooids having only single or paired avicularia proximo-lateral to orifice (asterisks, autozooids with pair of stout suboral spines meeting in midline; circles, autozooids with large operculum and lacking suboral spines); (e) NSMT-Te 1069, autozooids with two pairs of avicularia; asterisk and circle as in panel d; (f) NSMT-Te 1069, autozooid with three pairs of avicularia (arrowheads). All panels are scanning electron microscopic images. Scale bars: a, d = 500 μm; b = 100 μm; c = 1.0 mm; e, f = 400 μm.

Avicularia (Figure 7(b)) paired, one attached by short peduncle on each lateral margin at level of base of operculum; chamber somewhat bulbous; rostrum hooked at end; mandible long-triangular, occupying about half the length of membranous rostral area. Avicularium length to depth ratio about 1.7. No ovicells or ancestrula in our specimen.

Remarks

Tilbrook et al. (2001) discussed the differences between *Bugula cookae* and the similar species *B. klugei* Cook, 1968. We identified our specimen as the former based on the domed shape of the avicularia. Mean zooid length is smaller (0.94 mm) than in the holotype (1.23 mm) from Vanuatu (Tilbrook et al. 2001), although this difference may be due to our small colony consisting partly of zooids in the zone of astogenetic change.

Occurrence

We found a single small colony at the MIN site. This species appears to be restricted to the subtropical and tropical western Pacific, previously reported from Vanuatu and (as *B. klugei*) and from the Great Barrier Reef (Hayward and Ryland 1995).

Beania hexamicorum Tilbrook, Hayward, and Gordon, 2001
(Figure 7(c–f))

Beania hexamicorum Tilbrook, Hayward, and Gordon, 2001, p. 50, fig. 4(c, d).
?*Beania sp*.: Hayward 1988, p. 288, fig. 4(b).

Material examined

NSMT-Te 1069 (MIN-34), dried, on SEM stub; NSMT-Te 1070, two colony fragments, dried, MIN site; NHMUK 2016.5.13.12 (MIN-18), dried, on SEM stub; NHMUK 2016.5.13.13–14, two colony fragments, dried, MIN site.

Measurements

OpL, 0.49–0.58 (0.534 ± 0.026); OpW, 0.22–0.37 (0.292 ± 0.029) (n = 20, 1). AvL, 0.13–0.22 (0.158 ± 0.023) (n = 21, 1).

Description

Colony (Figure 7(c)) forming a small, unilaminar sheet, raised from surface of substratum and loosely attached to it by occasional thin rhizoids arising from basal side of zooids; tan in colour. Zooids (Figure 7(d)) oval, thin walled, lightly calcified, each linked to surrounding zooids by up to six evenly spaced tubular connections; distance between adjacent opesiae equal to or somewhat less than half the opesial width. Three or (less often) four short, erect spines distal to orifice; another small spine on each side lateral to orifice, erect or angled inward; three to nine longer, straight or slightly curved spines arising from opesial rim proximal to avicularium on each side, angled over opesia; additionally up to five straight, horizontally oriented basal spines on each side arising just below opesial rim, directed into spaces between adjacent zooids (Figure 7(d)). Basal spines variably present; some or most zooids in some colonies lack them (Figure 7(f)). Zooids dimorphic; one type (asterisks, Figure 7(d, e)) has pair of relatively thick, straight or curved spines proximolateral to orifice, angled over proximal margin of orifice and meeting in midline, forming distinct suborificial strut, with orifice small and well defined; other type (circles, Figure 7(d, e)) lacks these distinct spines and has larger, broader orifice defined by opercular margin. Avicularia (Figure 7(d–f)) single or paired proximo-lateral to orifice, arising from opesial rim, with short peduncle, bulbous chamber and narrow, laterally compressed rostrum with hooked tip. Many zooids have second pair of

avicularia proximal to orificial pair, in the region 1/3–1/2 the length of zooid from distal end; one zooid (Figure 7(f)) has two additional pairs in this region.

Remarks

Our material resembles *Beania hexamicorum* from Vanuatu (Tilbrook et al. 2001) in the following characters. Average zooid size is similar (Okinawa, 0.53 × 0.29 mm; Vanuatu, 0.57 × 0.31 mm); the avicularia are identical in shape and similar in average length (Okinawa, 0.16 mm; Vanuatu, 0.14 mm); zooids are rather closely spaced, connecting with neighbours by up to six evenly spaced tubes; there are similar complements of distal and lateral marginal spines; and zooids can produce more than one pair of avicularia (Okinawa, up to three pairs were observed; Vanuatu, up to five pairs). The main difference in the two populations is that zooids in our material can produce straight accessory spines from the basal side that project into the interzooidal spaces (Figure 7(d)); however, this character is variable, as not all zooids produced these basal spines (Figure 7(e)). While Tilbrook et al. (2001) did not mention zooidal dimorphism in *B. hexamicorum*, this would be an easy character to overlook; it is not possible to check from their illustration, as they figured only two zooids. Tilbrook et al. (2001) listed, as a synonym of *B. hexamicorum*, 'Beania sp.' reported from Mauritius by Hayward (1988), who considered his material too fragmentary either to reliably identify to species or to describe as new. While the avicularium shape is similar, Hayward (1988) did not mention more than a single pair of avicularia.

Occurrence

We found six colonies, all at the MIN site. Tilbrook et al. (2001) reported this species to be common on the undersides of pieces of coral rubble at Erakor Island, Efate, Vanuatu. Without verification of Hayward's (1988) record from Mauritius, we consider this species to have a western-Pacific distribution, with Vanuatu the only previously known locality.

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Superfamily **MICROPOROIDEA** Gray, 1848
Family **ONYCHOCELLIDAE** Jullien, 1882
Genus ***Smittipora*** Jullien, 1882
Smittipora cordiformis Harmer, 1926
(Figure 8(a, b))

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Smittipora cordiformis Harmer, 1926 (part), p. 260, pl. 16, figs 14–18.
Smittipora cordiformis: Hayward and Ryland 1995, p. 543, fig. 6(c). Tilbrook et al. 2001, p. 52, fig. 6(g). Tilbrook 2006, p. 74, pl. 12A.

Material examined

NSMT-Te 1071 (MIN-6), bleached, on SEM stub; NSMT-Te 1072, dried specimen, MIN site.

Measurements

AzL, 0.65–0.86 (0.791 ± 0.053); AzW, 0.34–0.53 (0.456 ± 0.049); OpL (to base of proximal lip), 0.17–0.20 (0.187 ± 0.007); OpW, 0.14–0.16 (0.151 ± 0.007) (n = 15, 1). AvL, 0.52–0.75 (0.623 ± 0.063); AvW, 0.24–0.34 (0.293 ± 0.026) (n = 15, 1). MatZL, 0.55–0.76
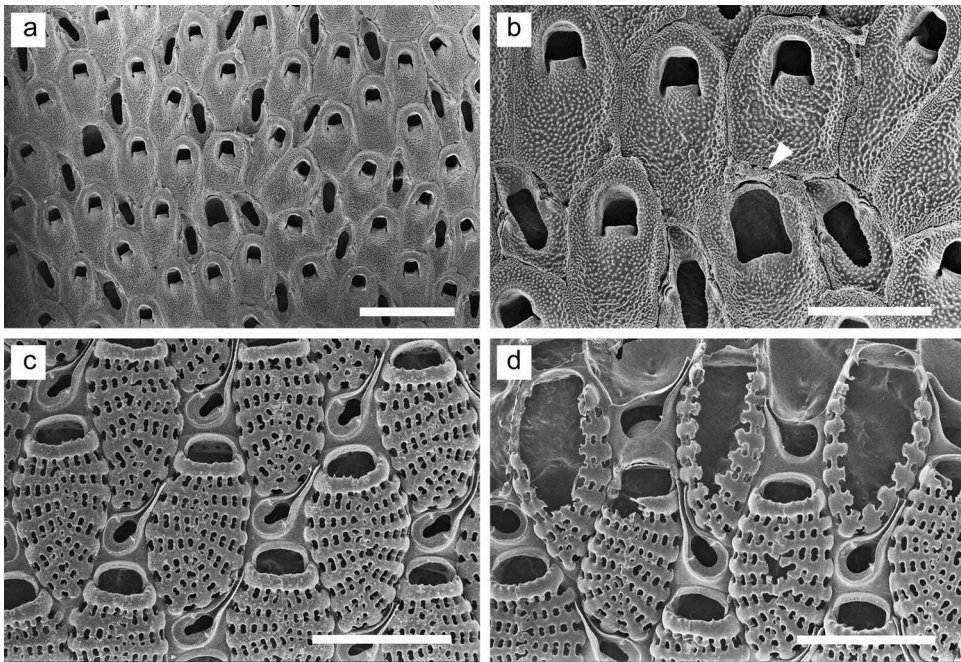
Figure 8. (a, b) *Smittipora cordiformis* Harmer, NSMT-Te 1071: (a) frontal view of colony; (b) enlargement showing autozooids, maternal zooid with vestigial ooecium (arrowhead) and inter-zooidal avicularia. (c, d) *Cribralaria curvirostris* Silén, NSMT-Te 1073: (c) autozooids and vicarious avicularia; (d) autozooids at colony margin, including one bearing an ovicell. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b–d = 500 μm.

(0.694 ± 0.097); MatZW, 0.45–0.55 (0.492 ± 0.055); MatZOpL, 0.27–0.34 (0.306 ± 0.027); MatZOpW, 0.20–0.25 (0.221 ± 0.022) (n = 4, 1). Largest colony fragment 24 mm across.

Description

Colony (Figure 8(a)) forming a unilaminar, encrusting sheet; dried colony light reddish brown, with 'salt-and-pepper' appearance due to pigmented ectocyst over cryptocyst surrounded by white raised zooidal margins; operculum dark brown, appearing black; rachis and bifurcate base of avicularian mandible also dark brown. Zooids (Figure 8(a, b)) distinct, closely appressed, with suture line between them. Cryptocyst sunken, uniformly granulated, sides sloping from margin to lowest area in centre, proximal to opesia. Opesia of non-maternal zooids subterminal, elongate-D-shaped, sides nearly parallel; proximal margin with broad lappet flanked by narrow sinus on each side. Sunken inside distal curvature of opesia is a broad, straight or slightly convex shelf, occasionally forming a distinct, conical median projection. Opesia of internally brooding maternal zooids (Figure 8(b)) terminal, much larger than that of non-maternal zooids; elongate-D-shaped, with nearly parallel sides, or campanulate, widest proximally; proximal margin straight or slightly convex, sometimes with conspicuous lappet flanked by sinuses. Along distal curvature of maternal opesia is a smooth, curved, visor-like vestigial ooecium delineated laterally by a suture on each side (Figure 8(b), arrowhead). Avicularia inter-zooidal; shorter and narrower than autozooids, with elongate opening widest distally.

Mandibular pivot is a comma-shaped slit on each side; opesial part of rostral opening surrounded by granulated cryptocystal shelf. Avicularia (Figure 8(a, b)) asymmetrical distally, one margin nearly straight and the other strongly curved. Avicularian mandible (not shown) with bifurcate base and long rachis about as long as avicularian cystid; proximal half of rachis has colourless, transparent, hemi-ovoid wing on each side. Spines lacking. Ancestrula not observed.

Remarks

This species is characterised by dimorphism between brooding and non-brooding zooids, and by having an asymmetrical avicularian rostrum. Autozooids in our specimens are larger (average L × W, 0.79 × 0.46 mm) than in populations in the Solomon Islands (L × W, 0.65 × 0.40 mm; Tilbrook 2006) and Great Barrier Reef (~0.55 × 0.40 mm; Hayward and Ryland 1995), and the avicularia are conspicuously smaller than the flanking autozooids. Harmer (1926, p. 261) noted in the original description that the opesia usually has 'a conspicuous median tubercle present within its distal border' and clearly shows this structure in his illustrations. We observed only one zooid in our specimens to have this median tubercle; most zooids have, in place of the tubercle, a straight or broadly convex thickening that appears as a low shelf, and some zooids lack any trace of a projection.

Occurrence

We found only two colonies, both at the MIN site. *Smittipora cordiformis* is broadly distributed in the Indo-West Pacific. Harmer (1926) originally described it from depths of 0–32 m in the Celibes, Indonesia, and reported other specimens from Burma (Myanmar), Singapore or the Philippines, and the Adimarante Islands in the Indian Ocean. It has subsequently been reported from the Great Barrier Reef (Hayward and Ryland 1995), Vanuatu (Tilbrook et al. 2001) and the Solomon Islands (Tilbrook 2006).

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Superfamily **CRIBRILINOIDEA** Hincks, 1879
Family **CRIBRILINIDAE** Hincks, 1879
Genus ***Cribralaria*** Silén, 1941
Cribralaria curvirostris Silén, 1941
(Figure 8(c, d))

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Cribralaria curvirostris Silén, 1941, p. 122, figs 182 and 183.

Material examined

NSMT-Te 1073 (MIN-7), bleached, on SEM stub; NSMT-Te 1074 (MIN-7-1), bleached on SEM stub; NSMT-Te 1075, six dried specimens, MIN site; NHMUK 2016.5.13.15-17, three dried specimens, MIN site.

Measurements

AzL, 0.53–0.67 (0.603 ± 0.039); AzW, 0.32–0.42 (0.361 ± 0.029) (n = 20, 1). OrL, 0.07–0.09 (0.081 ± 0.008); OrW, 0.16–0.20 (0.178 ± 0.012) (n = 20, 1). Exposed OvL, 0.11; OvL

including distal, endoozoidal part not evident in unbleached specimens, 0.16; OvW, 0.21 (n = 1). Largest colony observed 20 × 13 mm.

Description

Colony forming a unilaminar, encrusting sheet; glistening white in colour. Zooids (Figure 8(c)) oval, distinct. Costal shield high, convex, with 15–19 (usually 16–18; modal number, 17) well-defined costae, including suboral pair; adjacent costae separated by three to six (usually five) conspicuous, kidney-shaped intercostal foramina. Paired costae forming proximal margin of orifice are thicker than others, and each has three to five minute denticles along distal edge. Orifice much broader than long, with smooth, raised distal rim. Avicularia (Figure 8(c, d)) large, interzooidal, the chambers approximately square in outline; located between distal end of one zooid and proximal end of the next; sometimes lacking from extensive portions of colonies. Rostrum long; narrow and acute distally; directed distolaterally; slightly curved around proximal end of succeeding autozooid; opesia oval or pear shaped; cross-bar incomplete, with pivot consisting of pair of condyles. Ovicell (Figure 8(d)) endozooidal; ooecium formed by, and sunken in, cystid of distal avicularium; ooecium visible externally only as slightly convex crescentic area distal to orifice; entire ooecium evident only in bleached specimens. Zooids interconnect via uniporous septula, at least two in transverse wall and three to five in each distolateral wall. Ancestrula not observed.

Remarks

Silén's (1941) illustrations of this species show a suture running along the midline of each costa, equidistant between two flanking columns of intercostal foramina. This does not make intuitive sense, as one would expect a suture instead between each pair of adjacent costae, indicating lateral fusion of the costae. However, the condition shown by Silén is evident in various cribrimorphs as the frontal shield develops during zooidal ontogeny, with a column of pores and half of each adjacent costa developing as a unit and later fusing with adjacent units. Ontogenetically mature zooids of *C. curvirostris* show the suture running through the midline of a column of pores, as expected.

Occurrence

This species occurred only at the MIN site, where it was abundant (Table 1). The only previous report of *C. curvirostris* is from 120 m depth east of Chichijima (~27.083°N, 142.183°E) in the Ogasawara (Bonin) island group (Silén 1941), roughly 900 km due east of our study area.

<div align="center">

Genus *Puellina* Jullien, 1886
***Puellina harmeri* Ristedt, 1985**
(Figure 9)

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Puellina harmeri Ristedt, 1985, p. 26, figs 1, 6(a–e), 7(a–k), 8(a–j) and 9(a–d).
Puellina harmeri: Dick et al. 2006, p. 2212, fig. 6(a).
Cribrilaria harmeri: Hayward 1988, p. 290, pl. 3c.
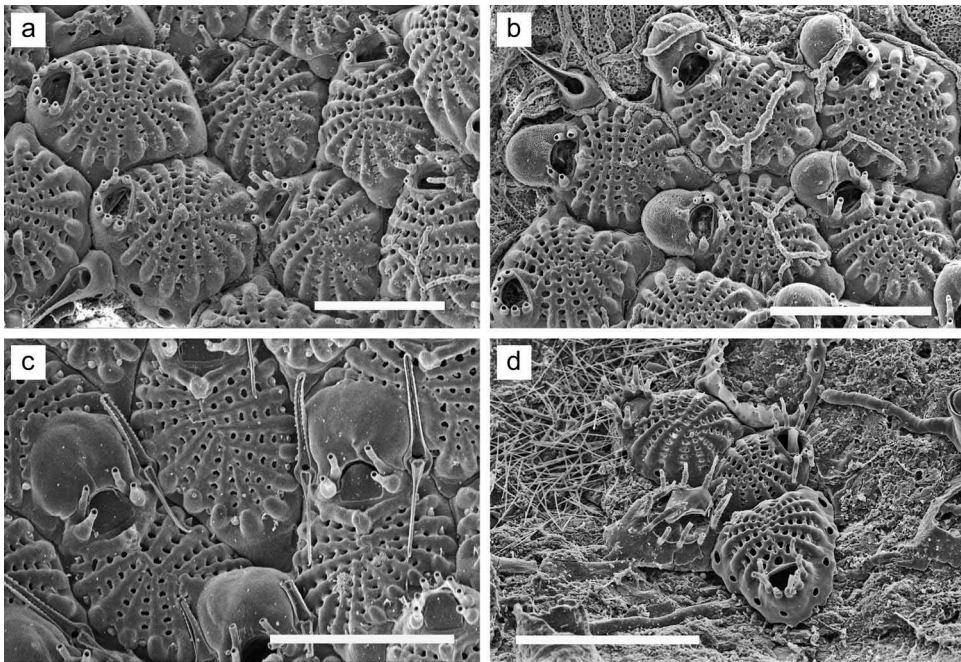?*Puellina vulgaris* Ryland and Hayward, 1992, p. 244, fig. 12(b, c).

Figure 9. *Puellina harmeri* Ristedt, 1985, scanning electron microscopic images of bleached (a, b, NSMT-Te 1077), unbleached (c, NSMT-Te 1076) and lightly bleached (d, NSMT-Te 1078) specimens: (a) autozooids; (b) ovicelled autozooids, with marginal avicularium; (c) ovicelled autozooids with long, single or paired lateral oral avicularia; (d) ancestrula and three periancestrular autozooids. Scale bars: a = 200 μm; b–d = 300 μm.

Material examined

NSMT-Te 1076 (MIN-9), dried (unbleached), on SEM stub; NSMT-Te 1077, specimen MIN-9/1, bleached, on SEM stub; NSMT-Te 1078 (MIN-30), ancestrula, bleached, on SEM stub.

Measurements

AzL, 0.25–0.36 (0.314 ± 0.030); AzW, 0.18–0.29 (0.226 ± 0.027) (n = 20, 1). Non-ovicelled zooids: OrL, 0.04–0.06 (0.050 ± 0.009); OrW, 0.06–0.08 (0.062 ± 0.007) (n = 7, 1). OvL, 0.09–0.13 (0.110 ± 0.012); OvW, 0.11–0.12 (0.116 ± 0.006) (n = 12, 1). AvRosL: adventitious avicularia, 0.15–0.21 (0.182 ± 0.018) (n = 12, 1); marginal vicarious avicularia, 0.13, 0.14 (n = 2, 1). Largest colony observed 8 mm across.

Description

Colony forming an irregular, unilaminar, encrusting sheet. Frontal shield (Figure 9(a)) slightly convex, with 14–16 costae (mode, 15), including suboral pair; raised boss at bend of costal spines variably present within and among zooids. Adjacent costae separated by three to seven (usually five or six) intercostal foramina, including the papilla foramen; papilla foramen about as large as largest of other intercostal foramina. Suboral pair of costae often with tips raised, forming a pointed boss. Suboral lumen single; small, about

same size as largest of intercostal pores. Orifice D-shaped, varying within same colony from broader than long to longer than broad. Non-ovicelled zooids with seven closely spaced oral spines; ovicelled zooids with two spines on each side of orifice. Avicularia of two types: interzooidal (Figure 9(b)), budded at growing edge, with broad base contacting substratum, later surrounded by autozooids; and adventitious (Figure 9(c)), sparsely present in some parts of colony, abundant in other parts, budded from and recumbent on marginal gymnocyst, single or paired lateral to orifice, pointing distally. Rostrum of both types variable in length, sometimes longer than ovicell; narrow, sides nearly parallel, edges variable in sculpturing, smooth or serrate even within same colony. Ovicell prominent (Figure 9(b, c)), closed by operculum. Ooecium smooth, globose, often with slight median ridge or boss proximally. Ancestrula (Figure 9(d)) tatiform, with 12 spines evenly distributed around opesial margin; ancestrula buds a triplet of daughter zooids, distally and distolaterally; daughter zooids similar to but smaller than subsequent zooids, with seven oral spines.

Remarks

Our specimen matches well the original description of this species from the Philippines (Ristedt 1985), although Ristedt reported slightly more (15–17) costae per zooid. The origin of the ooecium is variable in this species; the ooecial fold can be formed either by the distal zooid (Figure 9(c)), by a distal kenozooid visible from above, or by a distal kenozooid with no frontal part visible from above (Figure 9(b)) (Ostrovsky 1998, 2013), with all three variants sometimes occurring in the same colony.

It is not clear how *P. harmeri* differs from *Puellina vulgaris* Ryland and Hayward, 1992, originally described from the Great Barrier Reef, Australia. Judging from the original description, the latter species differs from the former only in having slightly smaller zooids and a shorter avicularian rostrum. Rostrum length is not a reliable character, however, as it varies within colonies, both in material reported as *P. harmeri* (e.g. Dick et al. 2006, p. 2212, fig. 6(a, c, e, g)) and that reported as *P. vulgaris* (e.g. Tilbrook 2006, p. 95, pl. 15E). Ryland and Hayward (1992) did not describe the ancestrula for *P. vulgaris*. The original description for *P. harmeri* indicates a tatiform ancestrula with 12 spines (Ristedt 1985), as was observed in both the Hawaii (Dick et al. 2006) and Okinawa populations. Specimens from the Solomon Islands identified as *P. vulgaris* have a tatiform ancestrula with 14 spines (Tilbrook 2006), although the avicularia, zooid measurements and range in number of costae are quite similar to those in our specimens. Tilbrook et al. (2001) also reported *P. vulgaris* as quite common at Vanuatu, but did not observe the ancestrula in that population. Without a better idea of the range of variation in nominal *P. harmeri* and *P. vulgaris*, it is premature to declare them synonymous, but the possibility cannot be ruled out.

Occurrence

Puellina harmeri was uncommon in the study area; we found six colonies, all at the MIN site. This is a widely distributed, shallow-water, tropical to subtropical, Indo-West Pacific species, previously reported from the Philippines (Ristedt 1985), Mauritius (Hayward

1988) and Hawaii (Dick et al. 2006). This range encompasses that of the similar and possibly synonymous species *P. vulgaris*, reported from the Great Barrier Reef (Ryland and Hayward 1992), Vanuatu (Tilbrook et al. 2001) and the Solomon Islands (Tilbrook 2006).

<div align="center">

Superfamily **CATENICELLOIDEA** Busk, 1852b
Family **CATENICELLIDAE** Busk, 1852b
Genus *Vasignyella* Gordon, 1989
Vasignyella otophora (Kirkpatrick, 1890)
(Figure 10(a))

</div>

Catenaria otophora Kirkpatrick, 1890, p. 17, Plate 5, fig. l(a–c).
Savignyella otophora: Harmer 1957, p. 763, pl. 51, figs 19–21.
Vasignyella otophora: Gordon 1989, p. 453, figs 13–15. Ryland and Hayward 1992, p. 247, fig. 14(a). Tilbrook et al. 2001, p. 60.

Material examined

NSMT-Te 1079 (MIN-4), dried, on SEM stub; NSMT-Te 1080, dried fragments, MIN site.

Measurements

AzL, 0.94–1.13 (1.016 ± 0.060); AzW, 0.23–0.27 (0.249 ± 0.016) (n = 8). OrL, 0.124; OrW, 0.101 (average values, n = 2, 1).

Description

Colony consisting of zooids in branching uniserial series; recumbent, loosely attached to substratum by rhizoids budded from proximal basal side of dilated portion of zooids. Branching pattern irregular, with zooids giving rise to two (up to three?) daughter zooids from basal side near distal end of dilatation, or anywhere along lateral margin. Zooids clavate, with narrow cauda comprising one-quarter to two-fifths of total zooid length gradually expanding to form dilated portion; zooids often appear curved due to bend in frontal direction at point where cauda meets dilatation. Frontal wall gymnocystal, smooth, with one or two longitudinal series of frontal pseudopores on each side (one along frontolateral margin, and another more medially); pseudopores conspicuous, circular, infundibular. Five or six large, circular, uniporous septula along each lateral margin. Orifice small, oval, longer than broad; terminal. Proximal margin of orifice formed by two flattened, truncated costal spines with suture line between them. Oral spines lacking. Avicularia small, paired, lateral to orifice; rostrum raised, facing laterally; mandible triangular. Ovicells not observed.

Occurrence

We found two small colonies, both at the MIN site. Originally described from Tizard Bank (Spratly Islands), South China Sea (Kirkpatrick 1890), *Vasignyella otophora* has a broad Indo-West Pacific distribution, ranging from the Sudanese Red Sea (Dumont 1981) eastward to Samoa (Gordon 1989). Our specimen at Okinawa represents the farthest northern record of this distinctive species.
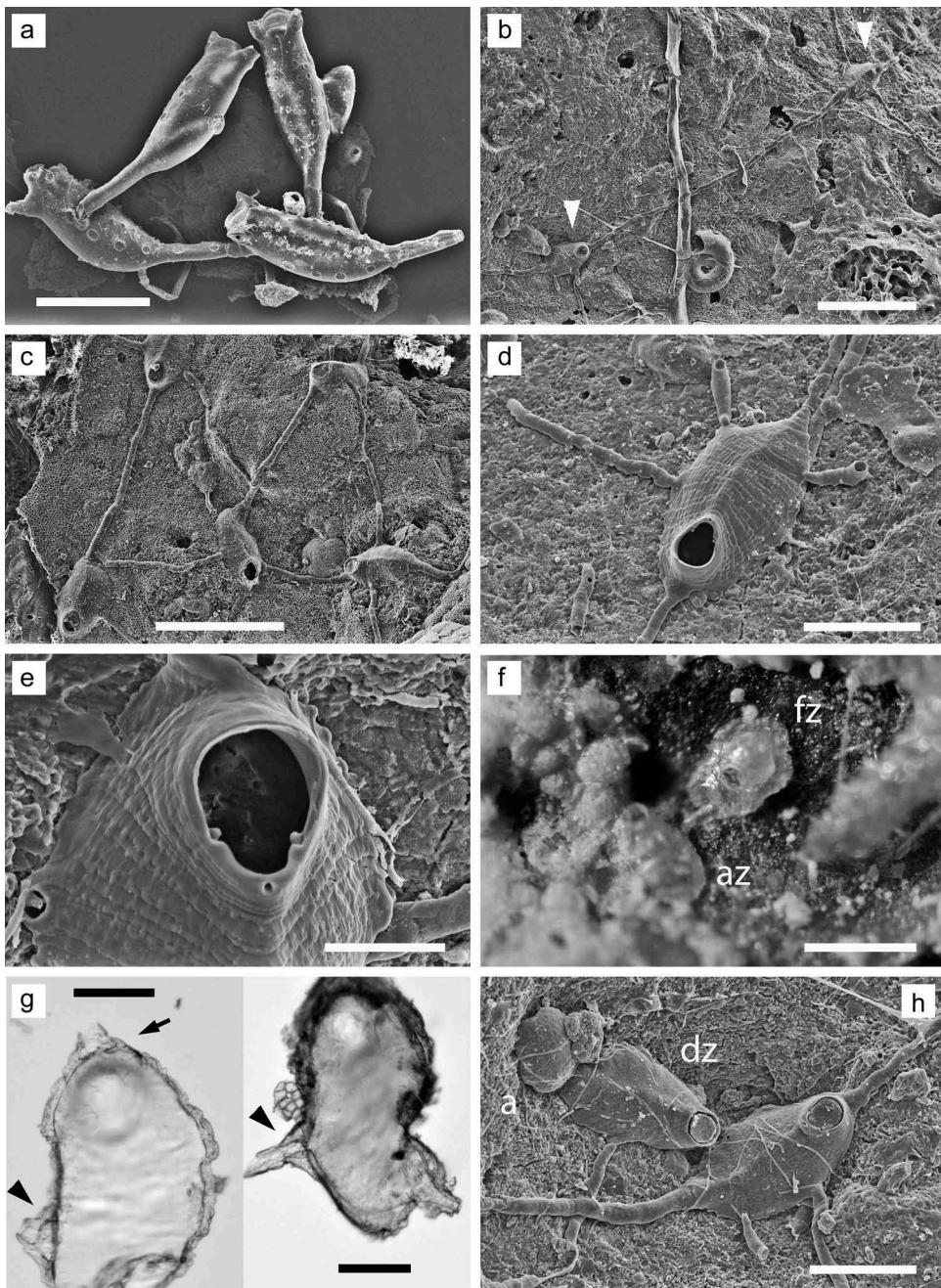
Figure 10. (a) *Vasignyella otophora* (Kirkpatrick), NSMT-Te 1079: four autozooids from branched, erect colony. (b–h) *Hippothoa petrophila* sp. nov.: (b) NSMT-Te 1082 (paratype), part of uniserial colony, with two zooidal dilatations, or 'zooids' (arrowheads), linked by long caudal portion, or 'stolon'; (c) NHMUK 2016.5.13.18 (paratype), part of anastomosed uniserial colony; (d) NSMT-Te 1083 (paratype), autozooid with paired proximolateral zooeciules; (e) NSMT-Te 1082 (paratype), autozooidal orifice; (f) photomicrograph of dried specimen showing autozooid (az) that has budded an ovicelled female zooid (fz) from the lateral margin; (g) photomicrographs of the basal side of zooids, showing lateral (arrowheads) and distal (arrow) interzooidal connections; (h) NSMT-Te 1082, presumed ancestrula (a) that has given rise to a single daughter zooid (dz), with a non-connected zooid at lower right. Panels (f) and (g) are photomicrographs; all other panels are scanning electron microscopic images; the specimens in panels (c) to (e) were lightly bleached. Scale bars: a–c = 500 μm; d, h = 150 μm; e = 50 μm; f = 25 μm; g = 10 μm.

Superfamily **HIPPOTHOOIDEA** Busk, 1859
Family **HIPPOTHOIDAE** Busk, 1859
Genus *Hippothoa* Lamouroux, 1821
Hippothoa petrophila sp. nov.
(Figure 10(b–h))

? *Hippothoa flagellum*: Dick et al. 2006, p. 2216, fig. 7(a, b).

Material examined

Holotype: NSMT-Te 1081 (MIN-8/1; *Pleurocodonellina microperforata* also present). Paratypes: NSMT-Te 1082 (MIN-30; *Poricella spathulata* and ancestrula of *Puellina harmeri* also present), lightly bleached, on SEM stub; NSMT-Te 1083 (MIN-31), lightly bleached, on SEM stub; NHMUK 2016.5.13.18 (MIN-14), on SEM stub.

Etymology

The specific name is a Latinised adjective from the Greek *petra* (rock) and *philos* (loving), referring to the apparent preference of this species in colonising bare rock substrata rather than calcareous substrata.

Measurements

Az dilatation L, 0.26–0.38 (0.298 ± 0.031); W, 0.14–0.20 (0.171 ± 0.018) (n = 19). Cauda L, 0.18–1.50 (0.693 ± 0.433) (n = 13); cauda W (at centre between dilatations), 0.023–0.031 (0.026 ± 0.003) (n = 15). AzOrL, 0.055–0.069 (0.063 ± 0.005); AzOrW, 0.043–0.057 (0.052 ± 0.004) (n = 18). Ovicelled zooid exclusive of ovicell: L, 0.15; W, 0.14 (n = 1). OvL exclusive of marginal lamina, 0.15; OvW, 0.13 (n = 1). Zooeciule L, 0.060–0.085 (0.075 ± 0.07) (n = 5).

Description

Colony unilaminar, encrusting, composed of zooids in branching uniserial series; zooidal dilatations (hereafter, 'zooids') connected by narrow, stolon-like caudae (hereafter, 'caudae') to form branching (Figure 10(b)) and sometimes anastomosing (Figure 10(c)) network spreading over broad areas of substratum relative to zooid size; cauda often long, up to 6 times length of zooid. Zooids (Figure 10(b–d, h)) hyaline, elongate-oval in outline. Frontal wall transversely convex, with transverse striae; cancelli evident between striae on unworn zooids, giving a lattice pattern; striae proximal to orifice angled proximally in chevron pattern (Figure 10(d, e)). Rounded median keel extends from proximal margin of orifice at least to middle of zooid and often to proximal end. Zooids produce up to three daughter zooids, one distally and one from each lateral margin; lateral daughter zooid may be produced only on one side. Some zooids produce zooeciule from proximolateral margin on one or both sides; zooeciules (Figure 10(d, h)) short, cylindrical, roughly same diameter as caudae, length about one-half zooid width; opening circular and usually turned frontally. Zooeciules generally uncommon, but zooids lacking zooeciules may show a zooecium scar – a small, circular external opening – proximolaterally on one or both sides. Orifice (Figure 10(d, e)) raised; oriented parallel to frontal plane; longer than broad; with deep, U-shaped sinus (Figure 10(e)) flanked by small brackets; small, knob-like condyles in angles of sinus brackets; small, circular

pseudopore in orificial rim just proximal to sinus. Ovicelled zooid (Figure 10(f)) budded distolaterally from autozooid on one side only (n = 5); zooid exclusive of ovicell less than half as long as autozooid, connected by a short cauda; orifice D-shaped, with broad, shallow sinus. Ovicell closed by operculum; surrounded by calcified marginal lamina. Smooth ectooecium appears to bear small central pseudopore and sometimes has a median carina. Lateral pore chambers (Figure 10(g)) leading to autozooidal caudae are large, conical. We were unable to observe form of pores or pore chambers leading to zooeciules. Distal communication pore single, median. Presumed ancestrula (Figure 10 (h)) kenozooidal (hemispherical, without orifice), giving rise to single daughter zooid similar to but smaller than subsequent zooids.

Remarks

Gordon (1984) provided descriptions for and summarised differences among Pacific species of uniserial *Hippothoa* having zooids with a long cauda, including *H. flagellum* Manzoni, 1870; *H. calciophila* Gordon, 1984; *H. distans* MacGillivray, 1869; *H. divaricata* Lamouroux, 1821 ssp. *pacifica* Gordon, 1984; and *H. peristomata* Gordon, 1984. Other studies (Ryland and Gordon 1977; Gordon and Hastings 1979; Hastings 1979; Moyano 1986) have also provided information on this group, and here we mention only a few key characters distinguishing *H. petrophila* from these other uniserial, caudate species.

    Hippothoa petrophila is defined by the following suite of characters: small dilatations (~0.3 mm long); long caudae, up to 6 times dilatation length; frontal wall with keel and transverse striations; cruciate branching pattern, although not all zooids produce a daughter cauda on both sides; a large, conical pore chamber and smaller pore or pore chamber in each lateral wall, with the former giving rise to a daughter cauda and the latter to a zooeciule (some zooids have a large pore chamber only on one side; zooeciules and presumably the connections that give rise to them may be present on one side only, or lacking); a single distal communication pore, as occurs in *H. calciophila* and *H. flagellum* (Gordon 1984, p. 109, fig. 10(a, d)); ovicelled zooids smaller than autozooids and connected to the latter by a short cauda; ovicell with a thickened marginal lamina; and a kenozooidal ancestrula, without orifice, giving rise to a single daughter zooid. *Hippothoa petrophila* also appears to preferentially inhabit bare rock substrata; in our samples, it occurred only on small patches of rock not encrusted with coralline algae or heavily encrusted with other calcareous organisms.

    Uniserial, caudate congeners differ from *Hippothoa petrophila* in the following key characters (other characters may differ as well). *Hippothoa flagellum* has smooth zooids lacking a keel, and only one pore chamber in each lateral wall (zooeciules replace daughter caudae, rather than supplement them). *Hippothoa distans* has smooth zooids, ovicelled zooids larger than autozooids, a perforate central area on the ovicell, and a tatiform rather than a kenozooidal ancestrula. *Hippothoa calciophila* has longer dilatations (0.37–0.40 mm), generally shorter caudae and ovicelled zooids as large as autozooids. *Hippothoa divaricata* has ovicelled zooids about as large as autozooids, and has two distal communication pores (Gordon 1984, p. 109, fig. 10(c)). *Hippothoa peristomata* has somewhat larger dilatations, a shallow orificial sinus flanked proximally by a pair of low tubercles, and only one pore chamber in each lateral wall, and apparently lacks zooeciules; while ovicelled zooids are smaller than autozooids as in *H. petrophila*, the ovicell lacks the thick surrounding marginal lamina seen in the latter.

Specimens from Hawaii Island identified as *H. flagellum* (Dick et al. 2006) may actually be *H. petrophila*. In the Hawaiian population, colonies are attached to rock substrata, as they were on Minna Island in our study area, and show the following additional similarities to Okinawan material: the dilatations have transverse striations and a median keel; the orifice is similar in position and shape, with a deep, U-shaped proximal sinus; caudae can be up to several times as long as dilatations; ovicelled zooids are smaller than autozooids and budded distolaterally; the ovicell has a thick marginal lamina; and zooeciules are present. The nature of the interzooidal connections and distribution of zooeciules need to be reexamined in Hawaiian specimens to check their identity.

Occurrence

This species was common at the MIN site, the only known locality. Its actual abundance was difficult to document, because colonies are composed of small, widely spaced zooids.

Family **CHORIZOPORIDAE** Vigneaux, 1949
Genus ***Chorizopora*** Hincks, 1879
Chorizopora brongniartii (Audouin, 1826) sensu lato
(Figure 11(a, b))

Indo-Pacific records:
Chorizopora brongniarti: Canu and Bassler 1930, p. 14. Sakakura 1935, p. 18.
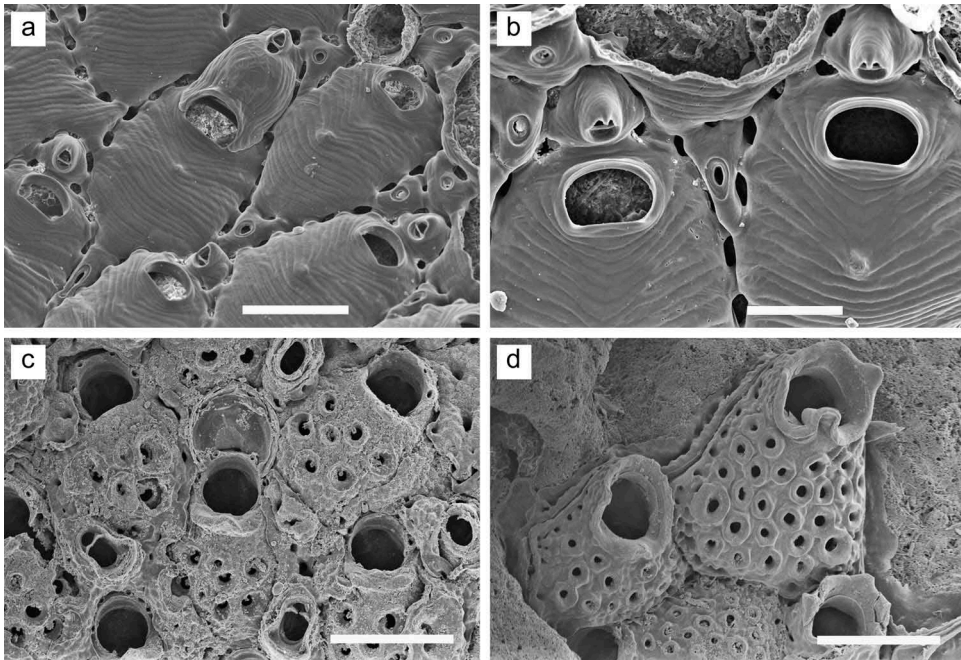
Figure 11. (a, b) *Chorizopora brongniartii* (Audouin) sensu lato, NSMT-Te 1084: (a) ovicelled and non-ovicelled autozooids, interzooidal avicularia and kenozooids; (b) autozooidal orifices. (c) *Poricella spathulata* (Canu and Bassler), NSMT-Te 1085: autozooids, interzooidal avicularia and developing ooecium. (d) *Exechonella* sp. A, NSMT-Te 1086: autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 200 μm; b = 100 μm; c = 300 μm; d = 400 μm.

Chorizopora brongniartii: Gordon 1984, p. 113, pl. 44C. Hayward 1988, p. 326. Scholz and Cusi 1991, p. 412, pl. 3, fig. 4. Ryland and Hayward 1992, p. 249, fig. 13(c). Liu et al. 2001, p. 540, pl. 36, figs 5 and 6; Tilbrook et al. 2001, p. 64, fig. 8(c). Kaselowsky 2004, p. 62. Tilbrook 2006, p. 102, pl. 17B–D. Dick et al. 2006, p. 2217, fig. 7(c, d).

Material examined

NSMT-Te 1084 (MIN-32), bleached, on SEM stub.

Measurements

AzL, 0.34–0.44 (0.388 ± 0.029); AzW, 0.24–0.31 (0.268 ± 0.019) (n = 15, 1). OrL, 0.055–0.067 (0.061 ± 0.004); OrW, 0.083–0.099 (0.092 ± 0.005) (n = 15, 1). Average OvZOrL, 0.063; OvZOrW, 0.103 (n = 3, 1). AvL, 0.073–0.089 (0.081 ± 0.005); AvW, 0.083–0.108 (0.096 ± 0.007) (n = 15, 1). OvL, 0.208–0.209 (0.208 ± 0.001); OvW, 0.162–0.172 (0.168 ± 0.005) (n = 3, 1). Largest colony observed 3 mm across.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 11(a)) vitreous, translucent; distinct, separated by shallow groove and interzooidal foramina between tubular connections; variable in outline. Frontal wall gymnocystal, moderately convex, with smooth texture and shallow transverse ribbing; ribbing chevron-shaped distal to small mammillate umbo. Umbo approximately in centre of zooid, separated from proximal orificial margin by distance greater than orifice length. Orifice (Figure 11(b)) raised; broader than long; widest in middle, recurving to meet straight proximal margin; condyles lacking. Orifice weakly dimorphic; that of ovicelled zooids slightly but discernably broader than that of non-ovicelled zooids. Small, roughly triangular kenozooid (Figure 11(a, b)) proximal to most zooids; central, marginated frontal opening of variable shape. Small interzooidal avicularium (Figure 11(b)) distal to each zooid; rostrum oval, angled at about 45° to frontal plane, with small distal hook; crossbar complete; opesial area proximal to crossbar semicircular; mandible rounded-triangular. Ovicell (Figure 11(a)) hyperstomial, conspicuous; opening with thickened rim; closed by operculum. Ooecium longer than broad, and associated with distal avicularium; ectooecium with longitudinal ribbing following ovicell contour; pseudopores lacking. Spines lacking. Ancestrula not observed.

Remarks

Various authors (e.g. Gordon 1984; Hayward and Ryland 1999; Tilbrook et al. 2001; Hayward and McKinney 2002) have considered *Chorizopora brongniartii* to have a worldwide distribution in temperate to tropical waters. Due to the improbability of populations maintaining genetic continuity over vast areas (such as between the Atlantic and Pacific), however, this nominal species undoubtedly represents a species complex (Dick et al. 2006; Tilbrook 2006), with small but consistent differences among geographically separate populations representing interspecific variation. Various Pacific populations identified as *C. brongniartii* show such distinguishing characters. In specimens from Hawaii Island (Dick et al. 2006), the avicularium typically associated with the ovicell is lacking or highly reduced; zooids lack a frontal tubercle; and the ancestrula differs (Dick et al. 2006) from that reported (Hayward and Ryland 1999) for British *C. brongniartii*. In specimens from the

Kermadec Ridge, New Zealand, the kenozooid proximal to zooids is often converted to an avicularium, and the frontal umbo is close to the orifice and comprises a sharp, spinous process. In a specimen from the Solomon Islands (Tilbrook 2006), non-ovicelled zooids have the orifice nearly as long as broad, and zooids are completely surrounded by kenozooids, some of which are replaced by small interzooidal avicularia. While our specimens from Okinawa are probably not conspecific with *C. brongniartii* (Audouin), their identity will best be resolved in the context of a global generic revision.

Occurrence

We detected two small colonies, both at the MIN site. Nominal *Chorizopora brongniartii* was previously reported in Japan from the Pleistocene Jizodo Formation, Boso Peninsula, Chiba Prefecture (Sakakura 1935).

<div align="center">

Superfamily **Arachnopusioidea** Jullien, 1888
Family **Arachnopusiidae** Jullien, 1888
Genus ***Poricella*** Canu, 1904
Poricella spathulata (Canu and Bassler, 1929)
(Figure 11(c))

</div>

Hiantopora spathulata Canu and Bassler 1929, p. 116, pl. 11, fig. 12.
Tremogasterina spathulata: Cook 1977, p. 136, text-figs 1(b) and 8(a), pl. 5A. Ryland and Hayward 1992, p. 249, fig. 13(e).
Poricella spathulata: Tilbrook et al. 2001, p. 65, fig. 10(b). Tilbrook 2006, p. 113, fig. 16(b). Dick et al. 2006, p. 2218, fig. 7(e, f). Gluhak et al. 2007, p. 413, figure 18(a–d).
For additional synonyms and records, see Cook (1977) and Tilbrook (2006).

Material examined

NSMT-Te 1085 (REEF-3), bleached, on SEM stub.

Measurements

AzL, 0.39–0.52 (0.453 ± 0.039); AzW, 0.22–0.35 (0.293 ± 0.033) (n = 15, 1). OrL, 0.11–0.14 (0.122 ± 0.010); OrW, 0.11–0.16 (0.133 ± 0.011) (n = 13, 1). OvL, 0.18; OvW, 0.24 (n = 1).

Description

Colony forming a unilaminar, encrusting sheet; our specimen 3 mm in diameter. Zooids distinct when young; boundaries indistinct with age. Frontal wall convex, texture coarsely granulated, perforated by five to eight large, lunate foramina, each surrounded by smooth infundibular area; three to five slit-like areolae along each lateral margin. Average orifice width slightly greater than length; semicircular anter separated from equally broad poster by small, low, proximomedially directed condyles. Distal margin with two pairs spines. Scattered between zooids are conspicuous avicularia arising from marginal pores; rostrum on raised chamber parallel or angled to frontal plane, usually flared and spatulate distally; hinge bar complete or incomplete; rostrum variable in direction. No large vicarious avicularia observed. One incompletely formed ovicell present in our specimen. Ancestrula not observed.

Remarks

With its infundibular, lunate frontal pores and spatulate avicularia, this is so distinctive a form that previous authors reporting it have often not included detailed descriptions. Illustrations representing different geographical populations (e.g. Cook 1977; Ryland and Hayward 1992; Tilbrook et al. 2001; Dick et al. 2006; Tilbrook 2006) indicate differences among populations, such as in spine number, orientation of the adventitious avicularia, degree of distal flare of the mandible, presence or absence of large vicarious avicularia, and number of frontal foramina.

Poricella spathulata is common in certain tropical and semitropical habitats, especially inner reef flats (Tilbrook et al. 2001). It was the most common bryozoan species at Vanuatu (Tilbrook et al. 2001), and likewise at Heron Island, Great Barrier Reef, where it occurred in over half the samples examined (Ryland and Hayward 1992). Dick et al. (2006) found it to be abundant at Kealakekua Bay, Hawaii Island, on the undersides of coral-rubble fragments on an intertidal cobble beach subject to high temperatures at low tide.

Occurrence

We found only a single dead colony at the REEF site. This species is broadly distributed in the Indo-Pacific region. Cook (1977) summarised records from the Red Sea, Indian Ocean, South China Sea, Philippines and north-east Australia; it has also been reported from Vanuatu (Tilbrook et al. 2001), the Solomon Islands (Tilbrook 2006), Hawaii (Dick et al. 2006) and Taiwan (Gluhak et al. 2007).

Family **EXECHONELLIDAE** Harmer, 1957
Genus ***Exechonella*** Duvergier, 1924
Exechonella sp. A
(Figure 11(d))

Material examined

NSMT-Te 1086 (SES-10), bleached, on SEM stub.

Remarks

The budding pattern in our single young colony does not clearly indicate which zooid is the ancestrula, if it remains. With the large, marginated foramina, well-developed peristome, and subcircular orifice with weak condyles, this species clearly belongs in *Exechonella*, although diagnostic characters such as ovicells and avicularia are absent. The zooids are moderately large: the larger complete zooid in Figure 11(d) measures 0.76 by 0.66 mm, and zooids in mature colonies would be larger. One orifice measured 0.202 mm long by 0.204 mm wide. The suboral flange and blunt projections on the peristomial rim are unusual, as no other species reported from the Indo-Pacific region has them.

Occurrence

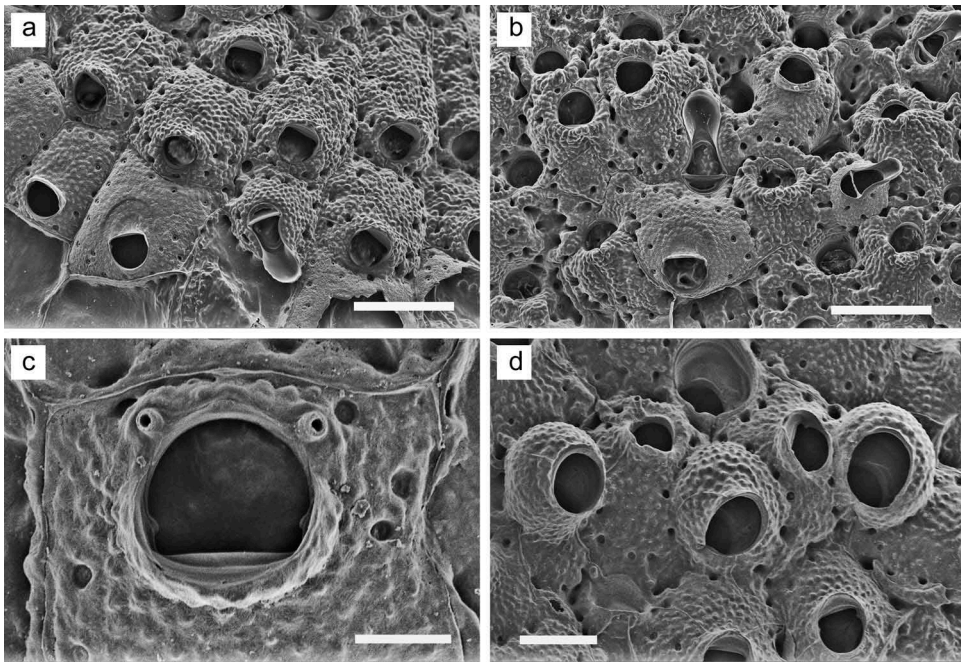We found only a single young colony at the SES site.

Figure 12. *Celleporaria calva* Tilbrook: (a) NSMT-Te 1087, zooids near colony margin; note the lack of oral spines; (b) NSMT-Te 1087, autozooids and two types of vicarious avicularia; (c) NSMT-Te 1088, autozooid near colony margin, showing primary orifice and pair of oral spines; (d) NSMT-Te 1088, ovicells. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, b = 500 μm; c = 100 μm; d = 250 μm.

Superfamily **LEPRALIELLOIDEA** Vigneaux, 1949
Family **LEPRALIELLIDAE** Vigneaux, 1949
Genus ***Celleporaria*** Lamouroux, 1821
Celleporaria calva Tilbrook, 2006
(Figure 12)

Celleporaria calva Tilbrook, 2006, p. 140, pl. 25D–F.

Material examined
NSMT-Te 1087 (SES-23), bleached, on SEM stub; NSMT-Te 1088 (MIN-25), bleached, on SEM stub; NSMT-Te 1089, three dried specimens, MIN site; NHMUK 2016.5.13.19-21, three dried specimens, MIN site.

Measurements
Colony without oral spines. AzL, 0.49–0.80 (0.642 ± 0.091); AzW, 0.34–0.55 (0.433 ± 0.066) (n = 16, 1). OrL, 0.13–0.18 (0.149 ± 0.013); OrW, 0.16–0.19 (0.175 ± 0.010) (n = 13, 1). Spatulate vicarious avicularium: AvRosL, 0.48; AvRosW at crossbar, 0.14 (n = 1).

Colony with oral spines. AzL, 0.50–0.77 (0.643 ± 0.083); AzW, 0.39–0.58 (0.474 ± 0.056) (n = 11, 1). OrL, 0.14–0.15 (0.143 ± 0.005); OrW, 0.17–0.19 (0.178 ± 0.006) (n = 8, 1). OvL, 0.30–0.34 (0.312 ± 0.027); OvW, 0.34–0.36 (0.351 ± 0.011) (n = 3, 1). Rostrum of spatulate vicarious avicularium, three size categories: Small – L, 0.18–0.24 (0.204 ± 0.031); W at crossbar, 0.07–0.08 (0.077 ± 0.008) (n = 3, 1). Medium – L, 0.32–0.39 (0.351 ± 0.035); W at crossbar, 0.14–0.19 (0.157 ± 0.025) (n = 3, 1). Large – L, 0.513; W at crossbar, 0.225 (n = 1). Largest colony observed 30 mm across.

Description

Colony encrusting, flat, sheet-like; unilaminar at margin, but frontal budding occurs in interior (Figure 12(b)); colour off-white. Marginal zooids (Figure 12(a)) distinct, delineated by groove; with age (Figure 12(b, d)), boundaries less distinct. Frontal wall convex, uniformly coarsely granulated; with 10 to 12 areolae around periphery, at margin or offset some distance from margin; sometimes with a few pseudopores scattered in central area. Primary orifice hoof-shaped, broader than long, with straight proximal margin; condyles small, blunt, rounded, somewhat distal to proximal margin. Raised rim (Figure 12(c)) around proximal margin of orifice, sometimes forming slight point. Suboral avicularium lacking. In one of two colonies examined by SEM, most zooids show a pair of short, ephemeral, tubular distal oral spines or spine bases (Figure 12(c)); other colony entirely lacks spines. No adventitious avicularia observed. Scattered interzooidal avicularia (Figure 12(a, b)) occur, of several sizes, with the largest more than twice as long and broad as the smallest. Chamber of newly budded large avicularium about half the size of an autozooid, with marginal pores and granulated surface; with age, avicularian cystid becomes immersed. Crossbar complete; rostrum wide at crossbar, narrowest just distal to crossbar, and flared, spatulate, often somewhat scoop-shaped distally, with edge around distal curvature weakly serrate. Rostrum of smallest interzooidal avicularia scarcely spatulate. Ovicell (Figure 12(d)) hyperstomial, with large, circular to oval opening. Ooecium thick-walled, globose, slightly broader than long, largely obscuring primary orifice; covered by secondary calcification with same texture as frontal wall, arising from two or three neighbouring zooids and showing sutures on the ooecial surface. Ancestrula not observed.

Remarks

Most species in *Celleporaria* have a suboral avicularium associated with the peristome or orificial margin; *C. calva* is unusual in lacking suboral or any other adventitious avicularia. Other diagnostic characters include the hoof-shaped primary orifice; lack of a well-developed peristome; spatulate interzooidal avicularia of several sizes; and the unusual globose ovicell with a large opening. The original description (Tilbrook 2006) also indicates that this species lacks oral spines; however, while this was true of the colony from the SES site, most marginal zooids in a colony from the MIN site had a pair of short, ephemeral oral spines or spine bases.

Occurrence

We found one specimen at SES and seven at MIN. *Celleporaria calva* was previously known only from the Solomon Islands (Tilbrook 2006).
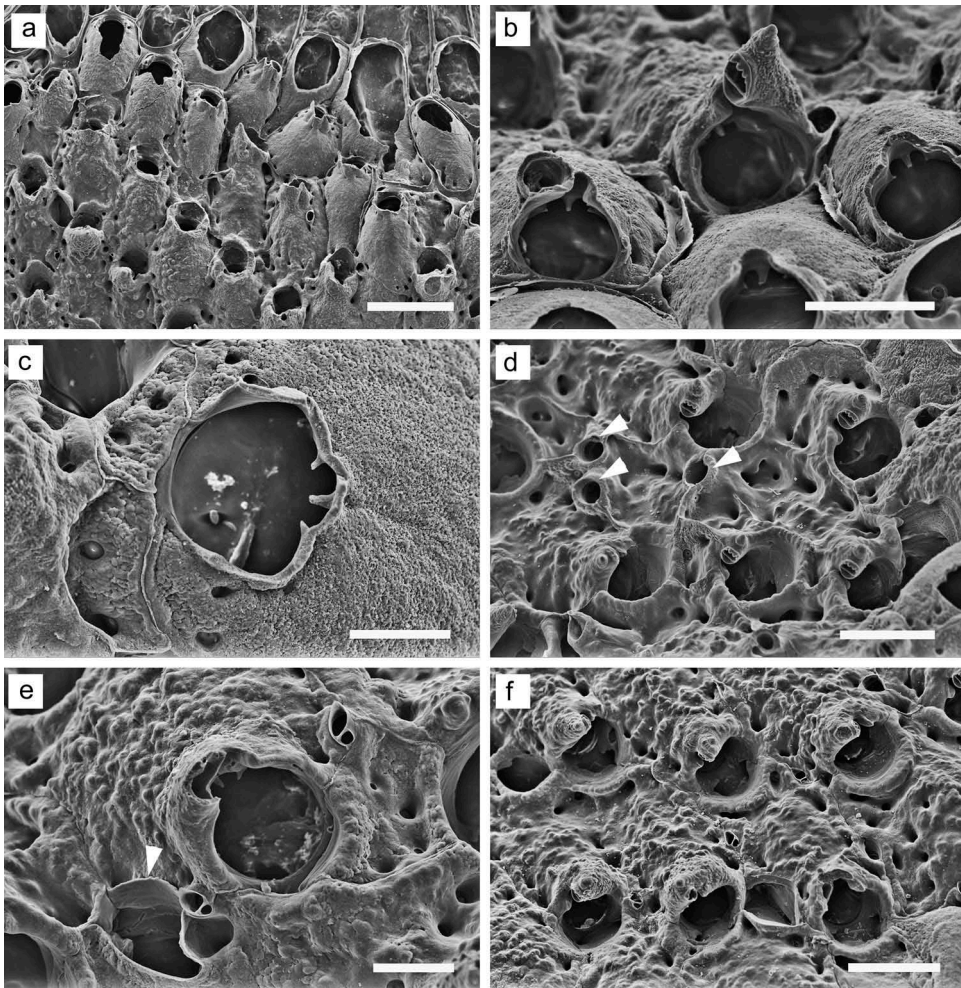
Figure 13. *Celleporaria desperabilis* Ryland and Hayward, NSMT-Te 1090: (a) young autozooids near colony margin; (b) young autozooids near colony margin, in frontodistal view; (c) primary orifice near colony margin; (d) autozooids, showing suboral avicularium adjacent to sinus; circular interzooidal openings indicated by arrowheads; (e) autozooid with pair of tiny avicularia lateral to orifice, and irregular interzooidal opening (arrowhead); (f) ovicells that appear to be aborted or incompletely developed, bounded by thickened rim distal to orifice. All panels are scanning electron microscopic images of the specimen after bleaching. Scale bars: a = 500 μm; b = 200 μm; c, e = 100 μm; d, f = 250 μm.

Celleporaria desperabilis Ryland and Hayward, 1992
(Figure 13)

Celleporaria desperabilis Ryland and Hayward, 1992, p. 251, fig. 15(e, f).

Material examined

NSMT-Te 1090 (SES-20), bleached, on SEM stub; NSMT-Te 1091, part of same colony as NSMT-Te 1090, dried.

Measurements

AzL, 0.48–0.80 (0.613 ± 0.084); AzW, 0.27–0.43 (0.336 ± 0.045) (n = 15, 1). OrL, 0.12–0.16 (0.136 ± 0.013); OrW, 0.14–0.17 (0.153 ± 0.010) (n = 7, 1). OvL, 0.16–0.21 (0.184 ± 0.017); OvW, 0.22–0.27 (0.243 ± 0.023) (n = 6, 1). One colony, 40 × 20 mm.

Description

Colony encrusting, sheet-like; unilaminar at margin but becoming multilaminar in interior due to frontal budding; in living colony, intermittent patches of violet-black ectocyst adhering to surface, worn away to white in most areas. Zooids near margin (Figure 13(a)) recumbent; variable in size and shape; delineated by groove and incision; boundaries soon becoming indistinct (Figure 13(d)). Frontally budded zooids in colony interior wider than those at margin, oval to circular in outline, haphazardly oriented. Frontal wall convex, irregularly coarsely granulated to tuberculate, with four to six small, round, irregularly spaced areolae along each lateral margin; with increasing calcification, areolae become enlarged and variable in size and shape. Between zooids are scattered enlarged openings (Figure 13(d, e)), circular or irregular in outline and bounded by a distinct rim, indicating marginal chambers of unknown function; openings occluded by ectocyst in living colony. Primary orifice (Figure 13(c)) broader than long; proximal margin concave, with rounded median sinus bearing narrow, tapering denticle in midline, flanked by smaller, distomedially directed denticle on each side; sinus and denticles usually symmetrical, but sometimes median denticle curved laterally; condyles lacking. With age, primary orifice becomes sunken in peristome (Figure 13(d)). Oral spines lacking. Early in ontogeny zooids develop suboral avicularian chamber proximal to orifice (Figure 13(b)), offset to one side or other; chamber bears a blunt umbonate process that can become a moderately tall, conical process with age; rostrum raised at high angle to frontal plane, usually facing laterally; mandibular portion semicircular, with blunt denticles at end; opesial portion smaller, semicircular; crossbar thin, complete. Suboral avicularian chamber flanks a distinct secondary peristomial sinus (Figure 13(e)). Zooids uncommonly bear a tiny, often asymmetrical, adventitious avicularium (Figure 13 (e)) lateral or proximolateral to orifice on one or occasionally both sides; mandible short-lanceolate or semicircular; crossbar thin, complete. No other frontal or vicarious avicularia observed. Ovicells (Figure 13(f)) in our specimen appear to be aborted or incompletely developed, their positions indicated by a thick, vertical, faintly crenulate semicircular rim extending distal to the orifice, completely open on top. Ancestrula not observed.

Remarks

Compared to our specimen, material from the Great Barrier Reef treated in the original description has somewhat larger suboral avicularia, and the orificial denticles are stouter and more widely spaced, with the median denticle variable (quadrate or anvil-shaped, often notched or bifid, or divided into two separate, slender denticles). However, the features of the peristome, lack of spines, paucity or lack of interzooidal avicularia, and occurrence and shape of the tiny adventitious avicularia all support this identification. The original description (Ryland and Hayward 1992) mentions large marginal pores but does not specifically mention the large, rimmed openings between zooids as seen in our material.
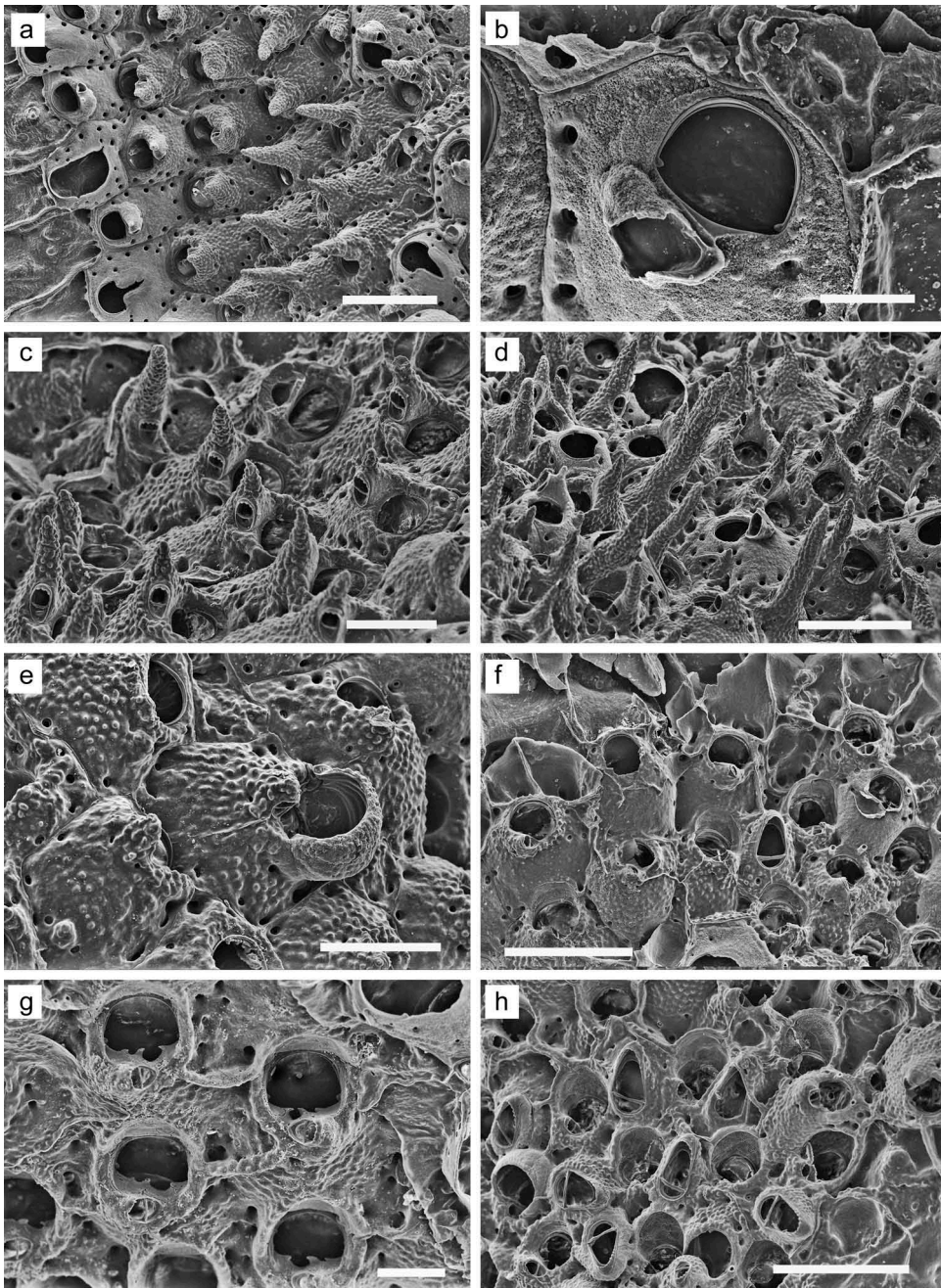
Figure 14. (a–e) *Celleporaria pilaefera* (Canu and Bassler), (a–d) NSMT-Te 1092, (e) SES-22: (a) autozooids near colony margin; (b) primary orifice; (c) suboral avicularia and typical suboral umbonate processes; (d) very long suboral umbonate processes; (e) ovicelled and non-ovicelled autozooids. (f–h) *Celleporaria triangula* Seo, NSMT-Te 1097: (f) autozooids and vicarious avicularium near colony margin; (g) primary orifices; (h) colony interior, with autozooids, vicarious avicularia and developing ooecia. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, d–f, h = 500 μm; b = 100 μm; c = 250 μm; g = 150 μm.

Occurrence

We found a single colony at the SES site. This species was previously known only from the type locality, Heron Island, Great Barrier Reef.

Celleporaria pilaefera (Canu and Bassler, 1929)
(Figure 14(a–e))

Holoporella pilaefera Canu and Bassler 1929, p. 422, pl. 60, figs 2–6.

Celleporaria pilaefera: Hayward 1988, p. 343, pl. 16e, f. Tilbrook et al. 2001, p. 70, fig. 13 (a–c). Tilbrook 2006, p. 135, pl. 24A, B.

Not *Celleporaria pilaefera*: Scholz 1991, p. 300, pl. 10, fig. 4.

Material examined

NSMT-Te 1092 (SES-21), bleached, on SEM stub; NSMT-Te 1093 (REEF-5), bleached, on SEM stub; NSMT-Te 1094, dried colony, SES site; NSMT-Te 1095, dried colony, SES site; NSMT-Te 1096, two dried fragments, REEF site; NHMUK 2016.5.13.22 (SES-22), bleached, on SEM stub; NHMUK 2016.5.13.23-25, three dried fragments, SES site.

Measurements

AzL, 0.37–0.59 (0.461 ± 0.057); AzW, 0.23–0.39 (0.322 ± 0.035) (n = 45, 3). OrL, 0.09–0.15 (0.121 ± 0.012); OrW, 0.12–0.19 (0.152 ± 0.012) (n = 45, 3). OvL × OvW, 0.26 × 0.32, 0.19 × 0.29 (n = 2). Largest colony observed 12 mm across.

Description

Colony forming an encrusting sheet, initially unilaminar but becoming multilaminar and disc-like due to frontal budding; whitish to light tan; operculum light brownish-yellow. Zooids at colony margin (Figure 14(a)) irregularly hexagonal, barrel-shaped or nearly quadrate; delineated by incision and shallow groove. Frontal wall convex, uniformly finely granulated, with eight to 13 small, round areolae around margin; areolae sometimes offset from margin. Primary orifice (Figure 14(b)) D-shaped, with shallowly concave proximal margin; slightly broader than long. Condyles small, rounded; close to corners of orifice, pointing proximomedially. Oral spines lacking. Early in ontogeny, uniporous septum in frontal wall gives rise to suboral avicularian chamber proximal to orifice, offset to one side or other; chamber bears conical umbonate process (Figure 14(a, c)); rostrum raised at high angle to frontal plane, facing laterally; mandibular portion semicircular, with blunt denticles at end; opesial portion smaller, semicircular; crossbar thin, complete. With age, frontal area proximal to orifice becomes raised and thickened; process atop avicularian chamber granulated like rest of frontal wall and ranging in size from a scarcely evident umbo, to a very tall (up to 0.65 mm), cylindrical process (Figure 14(d)). Ovicell (Figure 14(e)) hyperstomial, with wide opening; ooecium cup-like, often asymmetrically placed with respect to midline of maternal zooid; covered with secondary calcification, granulated like frontal wall. Aside from a single suboral avicularium per zooid, no other frontal or vicarious avicularia observed. Ancestrula not observed.

Remarks

Our material appears to be conspecific with specimens recently described and illustrated as *C. pilaefera* from Mauritius (Hayward 1988), Vanuatu (Tilbrook et al. 2001) and the

Solomons (Tilbrook 2006). Zooid size and all other characters are similar, with one glaring exception. In all other populations reported, colonies have large, spatulate vicarious avicularia, which are entirely lacking in our specimens. In some other populations, however, the vicarious avicularia have been noted as sparse (Tilbrook et al. 2001) or rare (Tilbrook 2006). It is noteworthy that in only one of 10 colonies did zooids develop tall, cylindrical suboral projections; zooids in the others either lacked a projection on the suboral avicularium or had only a small conical process.

Canu and Bassler (1929) originally described *C. pilaefera* from the Philippines. There has been no redescription of the type material, and some question remains (Tilbrook et al. 2001) as to whether the material in the more recent studies mentioned above has been correctly attributed to *C. pilaefera*. The identity of Philippine material that Scholz (1991) identified as *C. pilaefera* is also questionable, as autozooids bear five conspicuous oral spines.

Occurrence
Celleporaria pilaefera was moderately common, with 10 colonies detected at the SES and REEF sites. This species is broadly distributed in the Indo-West Pacific, with the known range extending from Mauritius eastward to Vanuatu and the Solomon Islands, and as far northward as Okinawa.

Celleporaria triangula Seo, 1994
(Figure 14(f–h))

Celleporaria triangula Seo, 1994, p. 189, pls. 1, 2.
Celleporaria triangula: Seo 2005, p. 397, pls. 120B, 121.

Measurements
AzL, 0.44–0.47 (0.455 ± 0.017); AzW, 0.32–0.36 (0.338 ± 0.018) (n = 3, 1). OrL (including sinus), 0.12–0.16 (0.134 ± 0.014); OrW, 0.14–0.18 (0.158 ± 0.012) (n = 13, 1). OvL, 0.21–0.24 (0.225 ± 0.016); OvW, 0.25–0.26 (0.256 ± 0.002) (n = 3, 1). Largest colony observed 9 mm across.

Material examined
NSMT-Te 1097-a (SES-13), bleached, on SEM stub (with *Parasmittina soulesi*); NSMT-Te 1098, 15 dried specimens, SES site; NHMUK 2016.5.13.26-38, 13 dried specimens, SES site.

Description
Colony encrusting, multilaminar, forming a low mound. Zooids at colony margin (Figure 14(f)) irregularly hexagonal; zooidal boundaries indistinct in colony interior. Frontal wall coarsely granulated, with three or four small, circular areolae along each lateral margin. Newly budded zooids at margin or interior of colony margin occasionally show one or two spine scars or small, cylindrical spine bases distal to the orifice; most zooids show no trace of spines. Primary orifice (Figure 14(g)) broader than long, roughly D-shaped; with small, blunt, condyles near corners. Proximal orificial margin slightly concave, with three small, falciform or denticulate processes delineating asymmetrical proximal sinuses (one larger, one smaller). Peristome a thick, low rim proximal and lateral to orifice; primary orifice not deeply sunken and usually visible. Small suboral

avicularium on raised, sometimes slightly umbonate chamber proximal to orifice, contributing to proximal peristome; rostrum oval, acute to frontal plane, bluntly denticulate around distal margin; crossbar complete; mandible D-shaped, directed frontolaterally. Large interzooidal avicularia are scattered abundantly among autozooids; chamber raised, granulated like frontal wall except at rostral end; rostrum raised distally, bluntly serrate around distal margin; crossbar complete; mandible blunt-triangular. Ovicells (Figure 14(h)) incompletely developed in our material; the most complete is cowl-shaped, not yet covered with granulated secondary layer.

Remarks

In her remarks accompanying the original description of *C. triangula*, Seo (1994) listed a number of *Celleporaria* species that have denticles on the proximal orificial margin. Taxonomists giving weight to the presence of these denticles have likely misidentified specimens of a variety of species as *C. tridenticulata* (Busk, 1881), *C. vagans* (Busk, 1881) or *C. aperta* (Hincks, 1882a), which have been perceived as widely distributed; see Tilbrook (2006) for a discussion of the problem. Tilbrook (2006, pl. 28A, B) illustrated a syntype specimen for *C. tridenticulata* that has orificial denticles quite different from those in *C. triangula*, and has lanceolate interzooidal avicularia. Tilbrook (2006, pl. 28C, D) also illustrated a paratype specimen of *C. vagans*; the denticles again differ from in *C. triangula*, and the interzooidal avicularia are spatulate, with a palmate mandible. Harmer (1957) considered *C. aperta* to have a very broad Indo-Pacific distribution, but both Hincks's (1882a) original description and redescriptions by Winston and Heimberg (1986) and Ryland and Hayward (1992) show the orifice with a small, rounded median sinus lacking a median denticle. The variation that Harmer (1957, p. 674, text-fig. 56) illustrated in the orificial denticles of *C. aperta* includes some of that seen in *C. triangula*, and indeed some of the specimens he included in the former may actually be the latter. *Celleporaria triangula* differs from congeners in the following combination of characters: one or two ephemeral oral spines; orificial denticles delineating major and minor sinuses, with the denticles themselves quite variable; interzooidal avicularia having a blunt-triangular (rather than spatulate, lanceolate or acute) mandible; and a bluntly denticulate distal margin of the rostrum in both the suboral and interzooidal avicularia.

Occurrence

Celleporaria triangula was restricted to the SES site, where it was abundant (Table 1). This species was previously known only from the vicinity of Cheju Island in the East China Sea, and from the Strait of Korea off the coast of South Korea (Seo 1994).

<div align="center">

Superfamily **SMITTINOIDEA** Levinsen, 1909
Family **SMITTINIDAE** Levinsen, 1909
Genus ***Parasmittina*** Osburn, 1952
Parasmittina serrula Soule and Soule, 1973
(Figure 15)

</div>

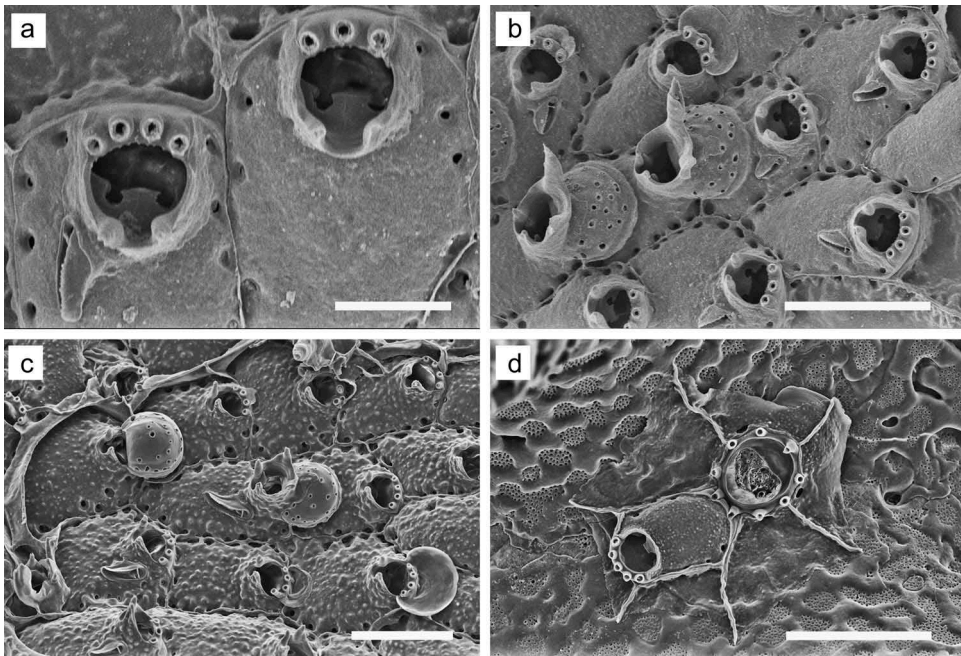*Parasmittina serrula* Soule and Soule, 1973, p. 396, fig. 3(d–f).

Figure 15. *Parasmittina serrula* Soule and Soule, (a, b) NSMT-Te 1099, (c, d) NSMT-Te 1100: (a) orifices, showing lyrula and condyles; (b), ovicelled autozooids, with small suboral avicularia; (c) ovicelled autozooids, with larger suboral avicularia; (d) ancestrula and first daughter zooid. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 100 μm; b–d = 300 μm.

Parasmitttina serrula: Gordon 1984, p. 96, pl. 35B, C. Winston 1984, p. 23, fig. 45. Ryland and Hayward 1992, p. 272, figs 23(e, f) and 24(a). Dick et al. 2006, p. 2221, fig. 9(a–d). ? *Parasmittina serrula*: Scholz 1991, p. 325, pl. 29, figs 1, 2 and 4. Tilbrook et al. 2001, p. 76, fig. 14(a, b). Tilbrook 2006, p. 154, pls. 29C, 31A–C.

Material examined
NSMT-Te 1099 (MIN-22), bleached, on SEM stub; NSMT-Te 1100 (MIN-13), bleached, on SEM stub (with *Crepidacantha poissonii*); NSMT-Te 1101, dried specimen, SES site (with *Calyptotheca reniformis*).

Measurements
AzL, 0.28–0.47 (0.374 ± 0.053); AzW, 0.19–0.29 (0.239 ± 0.028) (n = 20, 1). SecOrL (including sinus), 0.08–0.10 (0.090 ± 0.007); SecOrW, 0.08–0.10 (0.089 ± 0.006) (n = 20, 1). OvL, 0.16–0.18 (0.167 ± 0.006); OvW, 0.18–0.22 (0.198 ± 0.011) (n = 13, 1). Longest AvRosL per zooid, 0.08–0.12 (0.096 ± 0.013) (n = 20, 1). Largest colony observed 7 × 4 mm.

Description
Colony forming an irregular, unilaminar, encrusting sheet; white in colour. Zooids (Figure 15(a–c)) distinct, outlined by opposing columns of small areolae with a line of calcification between them; six or seven areolae along each lateral margin. Frontal wall

convex; smooth or sparsely granulated. Primary orifice deeply immersed, broader than long, lyrula (Figure 15(a)) ranging from tapering and truncate, to moderately broad and alate; condyles blunt, weakly denticulate at end, directed proximomedially. Peristome a raised collar, often tall, with a conspicuous, U-shaped secondary sinus (Figure 15(a)); zooids often have a sharp, umbonate or conical, sometimes wing-like projection on peristomial rim on each side of groove. Zooids have three or four ephemeral distal oral spines, in about equal proportions. In zooids destined to produce an ovicell, distal margin of secondary orifice serrate (Figure 15(a)). Ovicells typically widespread in colony, present in third or fourth zooid generation from ancestrula. Ovicell (Figure 15(b, c)) hyperstomial; smooth, with conspicuous pseudopores except in proximocentral region, periphery covered with secondary calcification. Peristome extends across proximal edge of ooecium, giving rise to low or tall, conical or horn-like process on each side (Figure 15 (b)). Zooids lack a frontal avicularium (41%) or have a single one (59%) (n = 46) on either side proximal to orifice; rostrum strongly tilted to one side, upper rostral edge serrate; crossbar thin or lacking; mandible elongate, tapering, blunt, pointing proximally or angled slightly medially or laterally. Enlarged avicularia (not shown) occurred but were rare in our material; those observed were single, on either side of orifice, pointing proximally, nearly as long as zooid; rostrum sub-spatulate, widening distally, with coarsely toothed rim. Ancestrula (Figure 15(d)) tatiform, with moderately wide proximal cryptocyst and nine marginal spines; first daughter zooid has five orificial spines.

Remarks

The original description and illustrations of *Parasmittina serrula* from Maui, Hawaiian archipelago (Soule and Soule 1973), indicate small zooids (average ZL, 0.37 mm; ZW, 0.28 mm); a granulated frontal wall; usually four oral spines; a denticulate distal orificial margin; a narrow to medium-width, tapering, non-alate lyrula rather widely separated from the condyles; often tall projections on the peristome lateral to the sinus groove; small, usually paired frontal avicularia lateral or proximolateral to the orifice, with the rostrum pointing proximally, turned onto one side, and having the upper edge finely serrate; occasional giant avicularia replacing the smaller type, with coarsely serrate rostral margins; and a tatiform ancestrula with a wide proximal cryptocyst and eight marginal spines.

Most populations described subsequent to the original description have similarly small zooids, but vary in the range and mode of oral spine number, lyrula shape, the frequency of single versus paired lateral-oral avicularia, and the number of spines on the ancestrula. In fact, some of this variation may not be intraspecific, and some previous records of *P. serrula* may actually represent different species. For example, in nominal *P. serrula* from the Solomon Islands (Tilbrook 2006), the lyrula is narrow, tapering, non-alate and relatively distant from the condyles (as expected in *P. serrula*), but other characters differ from those in Hawaiian material: zooid size is much larger (ca. 0.65 × 0.40); the lateral-oral avicularia are longer, of somewhat different shape, scarcely elevated and not tilted as much laterally; the peristome is mildly asymmetrical and much thinner, without horn-like projections proximally and/or distally on the peristomial rim; and zooids show an additional, non-tilted type of small frontal avicularia. Material from Vanuatu (Tilbrook et al. 2001) described as *P. serrula* likewise may not be that species. Judging from the SEM images, zooids are around the same size as in Hawaiian material, but the peristome

is thin and mildly asymmetrical, and the lyrula is low, moderately broad and conspicuously alate. Finally, the identity of Philippine material (Scholz 1991) with *P. serrula* is questionable. Scholz did not provide measurements; the ancestrula has nine spines, as at Okinawa, and enlarged avicularia with a serrate margin occur, as is typical of *P. serrula*. However, zooids appear to lack tilted, single or paired lateral-oral avicularia but instead have non-tilted adventitious avicularia with a smooth rostral edge, situated in the midline proximal to the orifice; the shapes of the peristome and proximal sinus are unusual for *P. serrula*; and there appear to be two or three oral spines. The lyrula is not evident in Scholz's figures.

Our material differs from the original and most subsequent descriptions in that zooids either lack a lateral-oral avicularium or have only a single one, in about equal proportions. Additionally, enlarged avicularia were rare; we observed them in only a few zooids in colony NSMT-Te 1101. Finally, the pronounced, paired, horn-like projections on the distal peristomial rim have not been reported in other populations, though previous workers may have missed them in the frontal-view SEM images typically used for illustrations (e.g. see Dick et al. 2006, fig. 9(a)). As a further complication, among several specimens at Okinawa, colonies showed either of two distinct morphologies. In one (Figure 15(a, b)), the zooids have a smooth frontal wall and the lyrula is moderately broad and weakly alate. In the other (Figure 15(c)), the frontal wall is granulated (as is typical of *P. serrula*) and the lyrula is narrower, tapering and either non-alate or weakly alate. Since other characters are similar in the two forms (small zooid size; three or four oral spines; lateral-oral avicularia single or lacking; paired, horn-like projections can occur both proximally and distally on the peristomial rim), we attribute the observed differences to intraspecific, inter-colony variation. However, the differences also mirror the situation in an Alaskan *Rhynchozoon* population (Dick and Mawatari 2005) in which two morphological types with minor differences represented genetically divergent lineages and probably different species.

Occurrence

We found a total of eight colonies, at the SES and MIN sites (Table 1). Nominal *Parasmittina serrula* is broadly distributed in the subtropical to tropical, central to western Pacific. It has previously been reported from Hawaii, the Solomon Islands, Vanuatu, the Philippines, Kermadek Ridge (New Zealand) and the Great Barrier Reef (see the synonyms for references). There is also a curious disjunct record from Carrie Bow Cay (Belize) in the Caribbean (Winston 1984). The Caribbean material appears indistinguishable from Hawaiian material and may reflect anthropogenic dispersal on ships' hulls from the Pacific through the Panama Canal.

Parasmittina soulesi Scholz and Cusi, 1991
(Figure 16)

Parasmittina soulesi Scholz and Cusi, 1991, p. 416, pl. 5, figs 1–4.
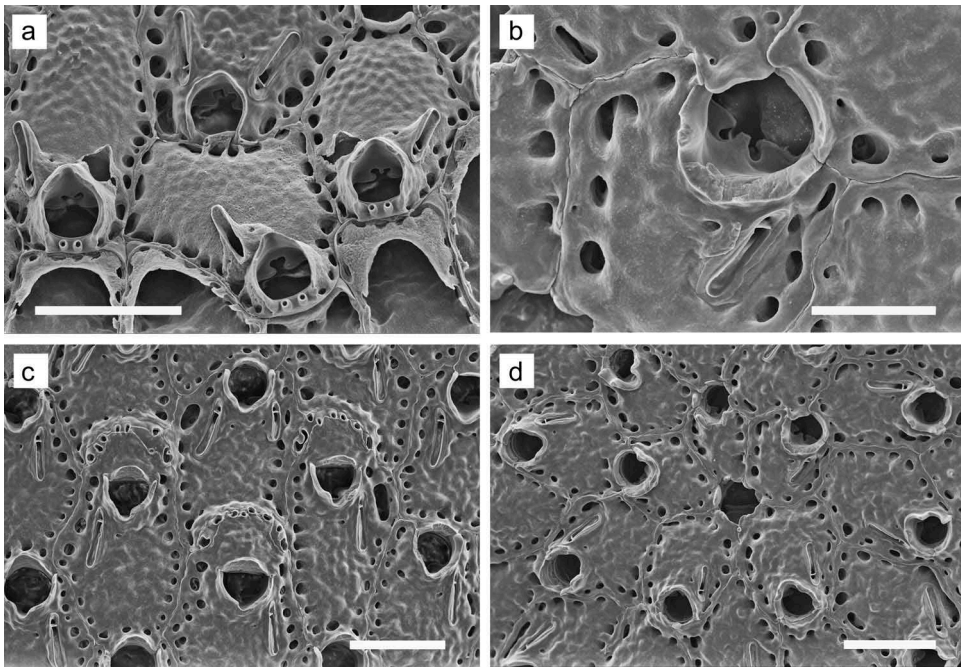?*Pleurocodonellina soulesi*: Tilbrook 2006, p. 172, pl. 37A, B.

Figure 16. *Parasmittina soulesi* Scholz and Cusi, NSMT-Te 1097: (a) marginal autozooids, showing alyrulate orifice (bottom centre) and orifice with weakly developed lyrula (right); (b) orifice with well-developed lyrula; (c) ovicelled autozooids; (d) periancestrular zooids (one distal, two distolateral, and two proximolateral; ancestrula obscured, but very broad lyrula evident. All panels are scanning electron microscopic images of bleached specimen. Scale bars: a = 300 μm; b = 100 μm; c, d = 250 μm.

Material examined

NSMT-Te 1097 (SES-13), bleached, on SEM stub (with *Celleporaria triangula*); NSMT-Te 1102, bleached, dried specimen, SES site; NHMUK 2016.5.13.39, bleached, dried specimen, SES site.

Measurements

AzL, 0.42–0.66 (0.517 ± 0.056); AzW, 0.28–0.40 (0.311 ± 0.033) (n = 20, 1). OrL, 0.10; OrW, 0.12 (n = 1). SecOrL (including sinus), 0.11–0.15 (0.127 ± 0.007); SecOrW, 0.10–0.12 (0.107 ± 0.006) (n = 20, 1). OvL, 0.13–0.16 (0.15 ± 0.015); OvW, 0.18–0.25 (0.22 ± 0.033) (n = 4, 1). Largest colony observed 9 mm across.

Description

Colony circular or irregular, forming a unilaminar, encrusting sheet; light tan to very light chestnut in colour when dried. Zooids distinct, outlined by suture and marginal pores. Frontal wall slightly convex, weakly dimpled in young, marginal zooids (Figure 16(a)), nearly flat and more strongly dimpled with age; around 10 small, circular to oval areolae along each lateral margin. Primary orifice (Figure 16(a, b)) immersed, difficult to observe; proximal margin more or less straight, formed by large, blunt, medially directed condyles; each condyle with band of minute denticles extending from tip to nearly halfway to lateral margin. Lyrula quite variable, ranging from minute denticle in sinus between

condyles (Figure 16(a)), to narrow, tapering, non-alate projection bisecting sinus, reaching level of tips of condyles (Figure 16(b)). Peristome low to moderately tall, slightly asymmetrical, with secondary sinus variably developed; often bearing one or two low flanges or pointed projections on each side. Marginal zooids with two spines (Figure 16 (a)) distal to orifice. Frontal avicularia (Figure 16(a–c)) single (77%) or paired (23%) (n = 82, 1) proximolateral to orifice, sometimes lacking. Rostrum elevated from frontal surface in young zooids (Figure 16(a)), but less so in secondarily calcified older zooids (Figure 16(c)); tilted slightly laterally to one side; narrow, elongate, rounded distally. Rostral margins smooth. Medial to each avicularium is small pseudopore; young, marginal zooids have tiny pseudopore in each side of the avicularian chamber. No giant avicularia observed. Ovicell (Figure 16(c)) subimmersed. Ooecium broader than long; covered with and surrounded by secondary calcification originating from maternal and distal zooids, same texture as frontal wall; with around eight conspicuous pseudopores in a crescent around the top periphery; proximal margin raised as crescentic lip forming distal part of peristome. Zooids interconnect by uniporous septula, up to six in each distolateral wall and up to six in the distal wall. One ancestrular complex observed (Figure 16(d)); ancestrula (mostly obscured by surrounding zooids) appears to have a very broad lyrula; surrounded by triplet of small zooids distally and distolaterally, and pair of larger zooids proximolaterally.

Remarks

While Scholz and Cusi (1991, p. 417) noted in the original description of *P. soulesi* from the Philippines that 'a lyrula is lacking', the low median projection responsible for the bifoliate sinus in their specimen can be interpreted as a reduced lyrula. This character is variable in our specimens: zooids can lack the central projection altogether (giving a deep, basally broad sinus) or have a low median denticle (giving a bifoliate sinus) (Figure 16(a)), or bear a long, tapering, terminally truncate tooth, essentially a lyrula (Figure 16(b)). Our specimens further differ from the Philippine specimen in having fewer, larger pseudopores around the distal margin of the ooecium (around eight, compared to 14–20), and in lacking the conspicuous rows of heavy denticles on the condyles. Specimens that Tilbrook (2006) reported as *Pleurocodonellina soulesi* from the Solomon Islands differ from Philippine and Okinawan material in having two or three distal spines; much larger areolae; raised zooidal margins; hypertrophied spatulate avicularia; and small denticles at the tips of the condyles.

Soule and Soule (1973) erected the genus *Pleurocodonellina* for *Parasmittina*-like species lacking a lyrula, designating *Pleurocodonellina lahainae* Soule and Soule, 1973 as the type species. The original generic description included a round primary aperture with a wide, curving sinus between lateral condyles; no median denticle (i.e. no lyrula); a single (rarely paired), acute, non-median frontal avicularium; and a subimmersed ovicell with a crescent of small pseudopores. Soule and Soule (1973) discussed some additional species that might go into *Pleurocodonellina*, the best known of which was *Smittina signata* Waters, 1889, which has a narrow, U-shaped orificial sinus and a broad crescent of 60–70 small pseudopores in the ectooecium. We note that while the original description did not mention oral spines, and Soule et al. (1995) reiterated that *Pleurocodonellina* lacks oral spines, marginal zooids in the original illustrations (Soule and Soule 1973) of *P. lahainae*, the type species, each have a single distal spine scar. Ryland and Hayward

(1992, p. 273) addressed this issue by amending the generic diagnosis for *Pleurocodonellina* to include distal oral spines.

The only character separating *Pleurocodonellina* from *Parasmittina* appears to be lack of a lyrula in the former and presence in the latter. The two genera overlap considerably in the number and distribution of ooecial pseudopores, another character putatively distinguishing between them. Thus, while Tilbrook (2006) transferred *Parasmittina soulesi* to *Pleurocodonellina*, we have retained it in *Parasmittina* by virtue of its small but variable lyrula. In some zooids in our specimens, the lyrula is about the size of that typically present in some other species in *Parasmittina*, such as *P. trunculata* Tilbrook, 2006.

Soule et al. (1995, p. 219) argued that lack of a lyrula should prohibit placement of *Pleurocodonellina* in Smittinidae: 'Placing alyrulate species in Smittinidae is … an oxymoron, although they may belong to the same superfamily'. *Parasmittina soulesi* is intermediate between *Pleurocodonellina* and *Parasmittina*, with some zooids in our specimens having a simple orificial sinus (as in *Pleurocodonellina*) and others having a well-developed lyrula (as in *Parasmittina*). One interpretation of this variation is that *P. soulesi* is a *Parasmittina* species undergoing evolutionary loss of the lyrula – and this leads to further speculation that *Pleurocodonellina* may prove to be an alyrulate lineage embedded within *Parasmittina*.

Occurrence

We found a total of four colonies, at the SES and REEF sites. This species was previously known only from the Philippines and the Solomon Islands.

Parasmittina alanbanneri Soule and Soule, 1973
(Figure 17)

Parasmittina alanbanneri Soule and Soule, 1973, p. 385, fig. 3(a–c).

Material examined

NSMT-Te 1103 (MIN-12), bleached, on SEM stub (with *Bryopesanser latesco*); NSMT-Te 1104 (MIN-17), bleached, on SEM stub; NSMT-Te 1105 (REEF-7), bleached, on SEM stub; NSMT-Te 1106, dried specimen, MIN site; NSMT-Te 1107, dried specimen, REEF site.

Measurements

AzL, 0.33–0.46 (0.397 ± 0.038); AzW, 0.21–0.35 (0.279 ± 0.038) (n = 15, 2). SecOrL (including sinus), 0.09–0.12 (0.102 ± 0.008); SecOrW, 0.09–0.11 (0.099 ± 0.005) (n = 15, 2). OvL, 0.17–0.20 (0.183 ± 0.010); OvW, 0.17–0.22 (0.191 ± 0.014) (n = 11, 2). Longest AvRosL per zooid, 0.06–0.11 (0.081 ± 0.014) (n = 16, 2). Largest colony observed 9 mm across.

Description

Colony forming an irregular, unilaminar, encrusting sheet; light tan in colour. Zooids (Figure 17(a, c, d)) distinct, boundaries indicated by opposing columns of areolae and suture line. Frontal wall convex, tuberculate, rugose; five to seven small areolae along
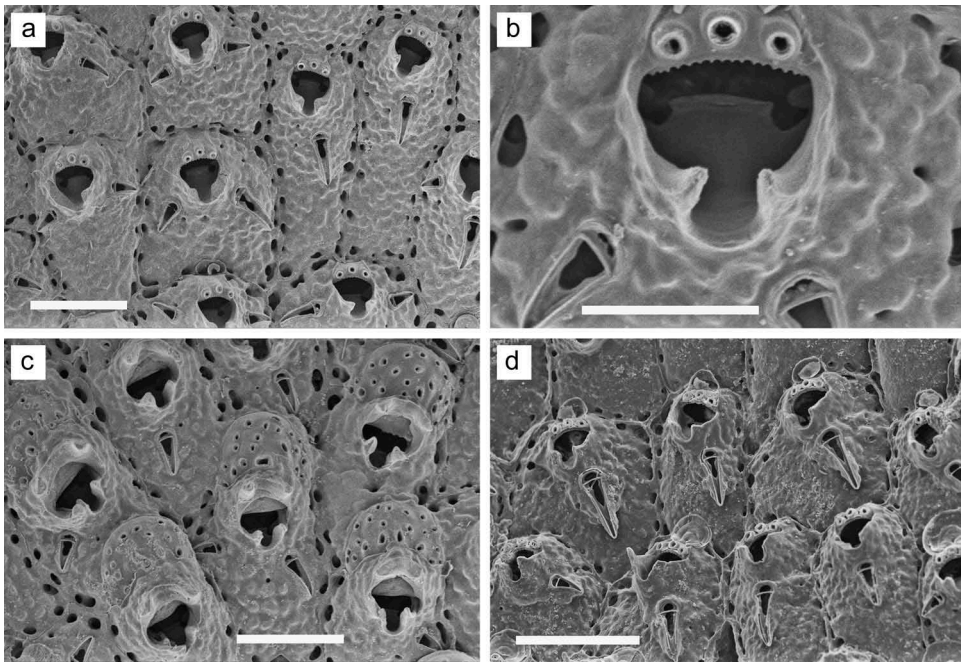
Figure 17. *Parasmittina alanbanneri* Soule and Soule, (a–c) NSMT-Te 1104, (d) NSMT-Te 1105: (a) autozooids; (b) orifice, showing broad lyrula and strong condyles; (c) ovicelled and non-ovicelled autozooids; (d) autozooids, with larger, single avicularia. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 250 µm; b = 100 µm; c = 200 µm; d = 300 µm.

each lateral margin. Primary orifice with very broad, low, alate lyrula (Figure 17(b)). Condyles blunt, with minute denticles at tip; angled proximomedially, nearly meeting lyrula and forming a small, oval notch on each side. Main part of secondary orifice subtrapezoidal in shape, lateral margins tapering towards secondary peristomial sinus; sinus deep, U-shaped, conspicuous; peristomial rim often with a projection on each side lateral to sinus; distal margin of secondary orifice gently curved, with 13 to 16 minute, sharp, evenly spaced denticles. Three oral spines (Figure 17(a, b, d)) close to distal margin of secondary orifice. Zooids have one (39%), two (61%) or three (2%) frontal avicularia (n = 38, 1). If paired, the avicularia are proximolateral or lateral to orifice, directed proximolaterally or laterally, occasionally slightly distolaterally, but often differing from one another in the angle from the midline; if single, avicularium is proximolateral to orifice and directed proximolaterally, or close to midline, pointing proximally or slightly proximolaterally. Rostrum slightly raised from frontal plane, not tilted laterally; rostral plane slightly decurved; rostral edges smooth; crossbar typically complete; mandible long-triangular, acute. In one colony, some zooids have a hypertrophied avicularium proximolateral to orifice (Figure 17(d)), up to twice the length of the smaller avicularia. A small pseudopore is occasionally present to one side or other of an avicularium. Ovicell (Figure 17(c)) hyperstomial; peristome extends across proximal quarter to third of ooecium, forming a raised, thick semicircular band, often with a heavy tubercle on each side. Ectooecium smooth, with about 20 conspicuous

pseudopores over entire area distal to peristome. Proximal edge of ooecium visible within peristome, usually serrate. Ancestrula not observed.

Remarks

Our specimens show the following characters indicated in the original description of *P. alanbanneri* from Hawaii (Soule and Soule 1973): small zooid size (average zooid size 0.40 × 0.28 mm, compared to 0.41 × 0.31 mm in Hawaiian material); rugose frontal wall; small marginal pores; a low, very broad, alate lyrula; small, single or paired frontal avicularia close to the orifice, with an acute, long-triangular mandible; the avicularian rostrum scarcely elevated from the frontal surface, not tilted and with smooth edges; and scattered pseudopores over the entire surface of the ooecium. Differences are as follows. In Hawaiian *P. alanbanneri*, the avicularia are typically situated lateral to the orifice, with the rostrum directed laterally or nearly so. In our specimens, while some paired avicularia are situated and oriented in this manner, most are proximolateral to the orifice and directed proximolaterally; when they are single, avicularia are often positioned near the midline proximal to the orifice and point proximally or nearly so. Zooids in Hawaiian *P. alanbanneri* have three to six spines, whereas those in our specimens have invariably three; however, many of the zooids in SEM images in Soule and Soule (1973) have three spines, which may be the modal number in Hawaii. Finally, there was no indication that the distal orificial margin is denticulate in Hawaiian *P. alanbanneri*, although this character might easily have been overlooked in the low-quality SEM images accompanying the original description.

Occurrence

We found a total of five colonies, at the REEF and MIN sites. *Parasmittina alanbanneri* was previously known only from the Hawaiian archipelago (Oahu, Molokai, and Hawaii islands) (Soule and Soule 1973).

Genus ***Pleurocodonellina*** Soule and Soule, 1973
Pleurocodonellina microperforata Tilbrook, 2006
(Figure 18)

Pleurocodonellina microperforata Tilbrook, 2006, p. 173, pl. 37C, D.
Pleurocodonellina signata: Tilbrook et al. 2001, p. 78. Liu et al. 2001, p. 632, pl. 59, figs 1–3.

Material examined

NSMT-Te 1108 (MIN-8), bleached, on SEM stub; NSMT-Te 1109 (MIN-40), bleached, on SEM stub; NSMT-Te 1110 (MIN-41), bleached, on SEM stub; NSMT-Te 1111 (MIN-42), bleached, on SEM stub; NSMT-Te 1112 (SES-12), bleached, on SEM stub; NSMT-Te 1113 (SES-55), bleached, on SEM stub; NSMT-Te 1114 (SES-56), bleached, on SEM stub; NSMT-Te 1115 (SES-57), bleached, on SEM stub; NSMT-Te 1116 (SES-58), bleached, on SEM stub; NSMT-Te 1117, two dried specimens, SES site; NSMT-Te 1118, six dried specimens, MIN site; NHMUK 2016.5.13.40-42, three dried specimens, SES site.
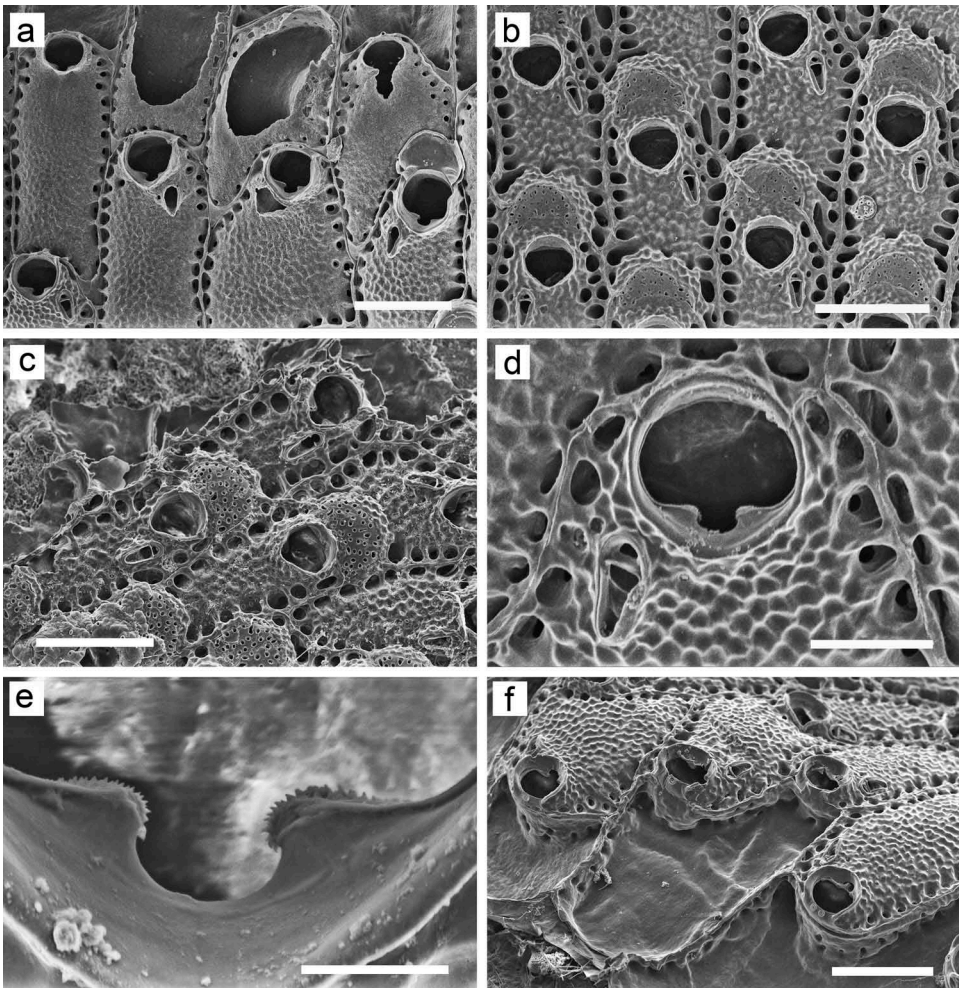
Figure 18. *Pleurocodonellina microperforata* Tilbrook: (a) NSMT-Te 1108, marginal autozooids showing one or two distal oral spine scars; (b) NSMT-Te 1108, ovicelled autozooids; (c) NSMT-Te 1112, ovicelled autozooids, with blunt suboral avicularia and larger pseudopores in ooecia; (d) NSMT-Te 1108, primary orifice, with sides of oral sinus nearly perpendicular; (e) NSMT-Te 1110, enlargement of orifice showing condylar denticulation; (f) NSMT-Te 1114, marginal autozooids, showing distribution of uniporous septula in vertical walls. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a–c, f = 300 μm; d = 100 μm; e = 30 μm.

Measurements

AzL, 0.47–0.76 (0.585 ± 0.081); AzW, 0.25–0.39 (0.325 ± 0.043) (n = 15, 1). OrL (including sinus), 0.11–0.15 (0.128 ± 0.010); OrW, 0.11–0.15 (0.125 ± 0.009) (n = 15, 1). OvL, 0.18–0.20 (0.186 ± 0.008); OvW, 0.19–0.22 (0.206 ± 0.009) (n = 15, 1). AvRosL, 0.07–0.09 (0.083 ± 0.006) (n = 15, 1). Largest colony observed 15 mm across.

Description

Colony irregular or roughly circular, forming a unilaminar, encrusting sheet; dried specimens light tan or tinged with light reddish brown; embryos orange. Zooids (Figure 18(a–c))

delineated by flanking areolae and suture line. Frontal wall dimpled, with 8–15 conspicuous areolae along each lateral margin, fewer along proximal margin. Primary orifice (Figure 18(d)) has anter broader than long; sinus broadly U-shaped, with nearly straight sides, or slightly drop shaped; flanked by bracket-like condyles, each having a long zone of minute denticles (Figure 18(e)). Marginal zooids with 0–2 tiny distal oral spines (evident as spine scars in Figure 18(a)), soon covered. Peristomial rim sharp, low, continuous around orifice in both ovicelled and non-ovicelled zooids. Single avicularium proximolateral to orifice, directed proximally or less commonly proximolaterally or proximomedially; pivot bar complete; mandible short- or long-triangular, acute (Figure 18(b)) or rounded (Figure 18(c)) at end. Ovicell prominent, but with increased secondary calcification can become subimmersed or even endozooidal, flush with colony surface. Ooecium is bounded proximally by raised peristomial lip; dimpled secondary calcification leaves crescentic smooth central area with many tiny, irregular pseudopores in ectooecium. Zooids interconnect by numerous uniporous septula in the distolateral and distal walls (Figure 18(f)). Ancestrula (not shown) like autozooids, but smaller, surrounded by a distal, paired distolateral and paired proximolateral daughter zooids.

Remarks

A similar species, *Pleurocodonellina signata* (Waters, 1889), was once regarded as nearly circumtropical on shallow reefs. Tilbrook (2006) distinguished two new morphospecies similar to *P. signata* in the Solomon Islands, describing them as *P. microperforata* and *P. macroperforata*. We identified our material as *M. microperforata* on the basis of the often nearly square orificial sinus (not markedly drop shaped); the small suboral avicularium proximolateral to the orifice, usually with a triangular mandible; and small pseudopores in the ooecium. In *Pleurocodonellina microporforata* from the Solomon Islands (Tilbrook 2006), zooids can have single or paired avicularia (we observed only single avicularia), and the avicularia are usually directed proximolaterally (in our specimens, they are quite often directed proximally). Both *P. signata* and *P. macroperforata* differ from *P. microporforata* in tending to have longer avicularia and a drop-shaped rather than a parallel-sided orificial sinus, and *P. macroporforata* has larger pseudopores in the ooecium. In *P. signata*, the proximolateral-oral avicularia are enlarged in some zooids, reaching up to two-thirds the zooid length; in *P. macroperforatea*, the proximolateral-oral avicularia are single, invariably directed proximomedially, and sometimes replaced by a large, spatulate avicularium reaching up to two-thirds the zooid length.

One specimen from the SES site (Figure 18(c)) is atypical; compared to other specimens, the avicularia are more rounded distally, the pseudopores in the ooecium appear larger and the oral sinus tends to be drop-shaped. While this specimen could represent another species, it is not clear that this is the case: the avicularia are similar in size range and position to those in other colonies, and the condylar denticulation is the same. Furthermore, there is intracolony variation in other colonies in the shape of the oral sinus (sometimes it is drop shaped) and shape of the mandible (sometimes rounded).

Occurrence

This species was common at the SES and MIN sites (Table 1). *Pleurocodonellina microperforata* is broadly distributed in the subtropical to tropical western Pacific, previously

known from the Solomon Islands, Vanuatu, and the East and South China Seas (Tilbrook 2006).

Genus *Smittina* Norman, 1903b
Smittina nitidissima (Hincks, 1880)
(Figure 19(a, b))

Porella nitidissima Hincks, 1880, p. 78, pl. 10, fig. 2.
Smittina nitidissima: Harmelin et al. 2009, p. 180, fig. 8(a–f) (see this reference for additional synonyms).

Material examined

NSMT-Te 1119 (MIN-2), bleached, on SEM stub.

Measurements

AzL, 0.42–0.63 (0.55 ± 0.059); AzW, 0.26–0.41 (0.32 ± 0.044) (n = 15, 1). SecOrL, 0.11–0.15 (0.12 ± 0.011); SecOrW, 0.11–0.14 (0.12 ± 0.009) (n = 15, 1). OvL, 0.18–0.22 (0.20 ± 0.015); OvW, 0.22–0.28 (0.25 ± 0.014) (n = 15, 1). Single colony, 6 mm in diameter.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 19(a)) delineated by groove and suture line. Frontal wall convex, weakly rugose, covered with small
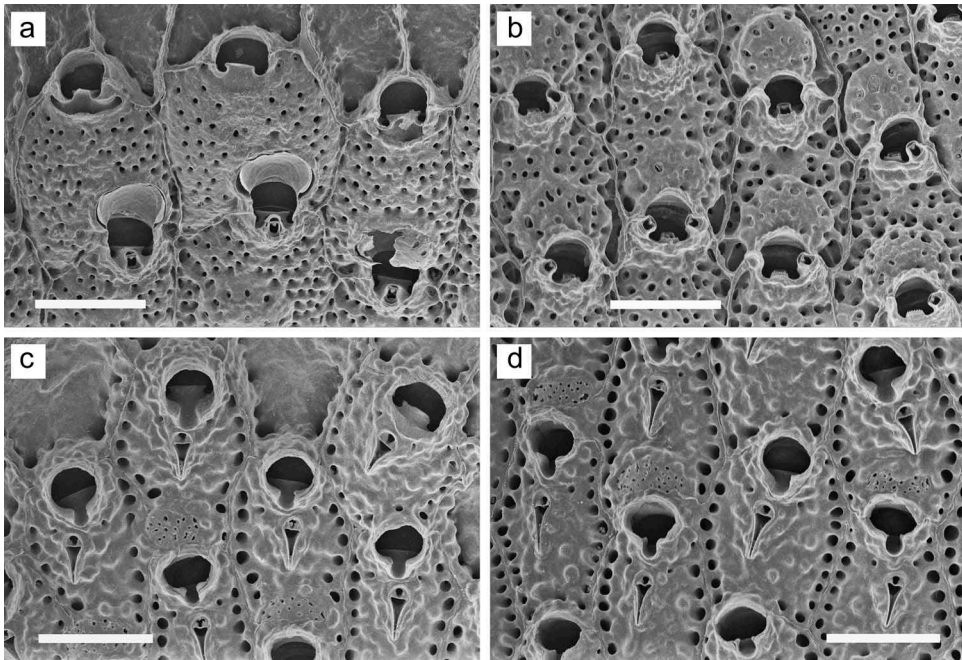
Figure 19. (a, b) *Smittina nitidissima* (Hincks), NSMT-Te 1119: (a) autozooids at colony margin; (b) ovicelled autozooids, with 0–2 lateral oral avicularia. (c, d) *Smittoidea pacifica* Soule and Soule, NSMT-Te 1120: (c) zooids at colony margin; (d) ovicelled and non-ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars = 300 μm.

pseudopores; with a few small areolae along lateral and proximal margins. In older zooids, pseudopores can form a trabecular network in the thickened secondary calcification. Primary orifice immersed; D-shaped, with very broad, alate lyrula; condyles blunt, weakly developed, proximolateral to lyrular alae. Ovicelled zooids have a median suboral avicularium inside peristome; rostrum perpendicular or angled to frontal surface; spatulate, with serrate edge distally. Most zooids have one or two additional avicularia on peristomial rim lateral to orifice, similar in size and shape to median avicularium, rostrum angled to frontal plane and directed proximolaterally. Ovicell (Figure 19(b)) hyperstomial in young zooids, becoming subimmersed or sometimes endozooidal with age, when secondary calcification covers ooecium (except for pseudopores); ooecium is uniformly covered with around 12 circular to irregular pseudopores; secondary calcification forms thin, raised lip along proximal ooecial margin. Ancestrula not observed.

Remarks
Harmelin et al. (2009) provided a good description of this species based on Lebanese material and reviewed various previous records worldwide. Zooids in our specimen have a broader lyrula than in the Lebanese material, but other characters match well.

Occurrence
We found a single colony at the MIN site. This species was originally described from Madeira (Hincks 1880). Harmelin et al. (2009) considered there to be valid records from Brazil, the Mediterranean, West Africa and the Red Sea, and suggested that the small colony size and typically abundant ovicells might facilitate dispersal on ships. These authors also noted, however, the alternative possibility that scattered, geographically disjunct populations might constitute a species complex distributed globally in warm waters.

<div align="center">

Genus **Smittoidea** Osburn, 1952
Smittoidea pacifica Soule and Soule, 1973
(Figure 19(c, d))

</div>

Smittoidea pacifica Soule and Soule, 1973, p. 380, fig. 1(e–h).
Smittoidea pacifica: Ryland and Hayward 1992, p. 268, fig. 24(e, f). Tilbrook et al. 2001, p. 78, fig. 18(e). Tilbrook 2006, p. 177, fig. 38(a, b).
Not *Smittoidea pacifica*: Rho and Kim 1981, p. 65, pl. 5, figs 4 and 5. Seo 2005, p. 416, pl 142(b) and 143.

Material examined
NSMT-Te 1120 (SES-4), bleached, on SEM stub; NSMT-Te 1121, dried specimen, SES site; NSMT-TE 1122 (SES-53), bleached, on SEM stub.

Measurements
AzL, 0.48–0.67 (0.549 ± 0.057); AzW, 0.28–0.45 (0.344 ± 0.046) (n = 15, 1). SecOrL (including sinus), 0.14–0.19 (0.152 ± 0.013); SecOrW, 0.12–0.15 (0.130 ± 0.008) (n = 15, 1). AvRosL, 0.09–0.16 (0.136 ± 0.024); AvRosW, 0.04–0.06 (0.052 ± 0.006) (n = 15, 1). OvL,

0.13–0.17 (0.152 ± 0.012); OvW, 0.20–0.25 (0.225 ± 0.020) (n = 8, 1). Largest colony observed 10 mm across.

Description

Colony irregularly circular, forming an encrusting, unilaminar sheet; off-white, with glistening ectocyst. Zooids (Figure 19(c)) delineated by line of calcification flanked by columns of areolae. Frontal wall convex, tuberculate; each lateral margin with up to 12 small, circular areolar openings. Primary orifice deeply immersed, broader than long, with broad, moderately high, alate lyrula occupying most of proximal margin. Condyles small, rounded on each side at level of top of lyrula; close to alae, delineating a roughly circular sinus on each side. Peristome raised, complete; secondary orifice with deep proximal pseudosinus. Pair of tiny pseudopores proximolateral to peristomial sinus, probably associated with avicularian chamber. Single median avicularium proximal to orifice; rostrum slightly raised from frontal surface, directed proximally; mandible long-triangular, acute; crossbar complete. Ovicell (Figure 19(c, d)) endozooidal. Ooecium broader than long; transverse central area of ectooecium free of secondary calcification and covered with minute pseudopores. Peristome extends continuously across proximal part of ooecium. Oral spines lacking. Ancestrula not observed.

Remarks

Our material matches well the original description of this species from Oahu, Hawaiian archipelago (Soule and Soule 1973), and except for having slightly larger zooid size, is virtually indistinguishable from material from the Great Barrier Reef (Ryland and Hayward 1992). Material from the Solomon Islands (Tilbrook et al. 2001) is similar in most characters, except that zooids have much larger areolar openings relative to zooid size. Korean material reported as *S. pacifica* (Rho and Kim 1981; Seo 2005) appears to be another species; compared to *S. pacifica*, zooids have a much larger median avicularium with a wider, non-acute mandible; the areolae are proportionally much larger; and the pseudopores in the ooecium are much larger.

Occurrence

We found five colonies at the SES site. Soule and Soule (1973) noted that at least some of the material they examined from the Galapagos Islands appeared identical to Hawaiian material, but observed six oral spines on a zooid in one specimen, indicating a species other than *Smittoidea pacifica*. Ryland and Hayward (1992) expressed doubt whether *S. pacifica* occurs at all in the Galapagos or, by extension, in the eastern Pacific. We consider *S. pacifica* to be distributed in the subtropical to tropical, central to western Pacific, with records from Hawaii, Vanuatu, the Solomon Islands and Okinawa.

Family **LANCEOPORIDAE** Harmer, 1957
Genus ***Calyptotheca*** Harmer, 1957
Calyptotheca reniformis Tilbrook, 2006
(Figure 20(a))

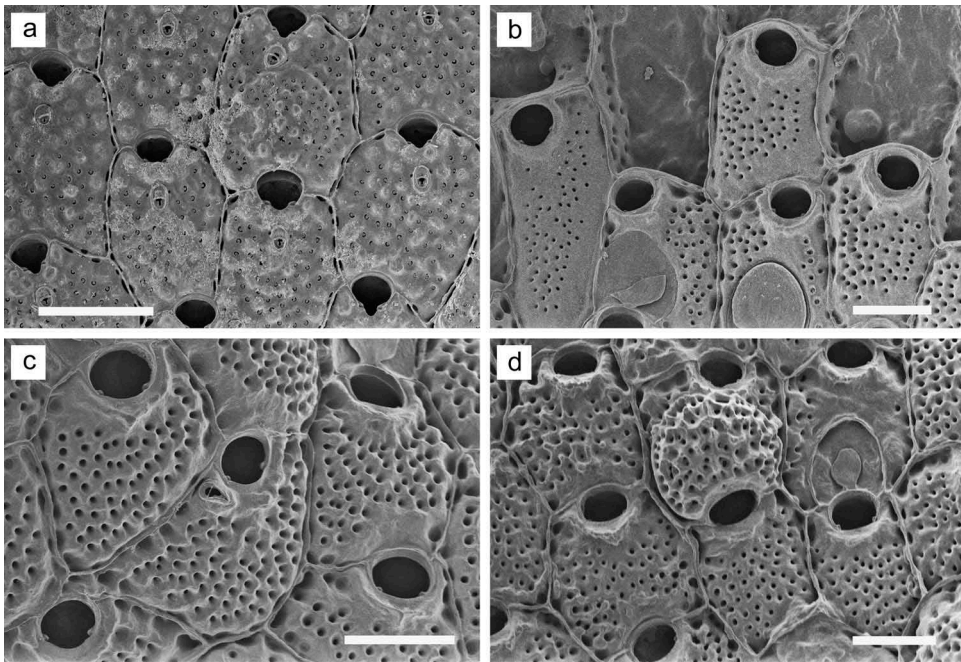*Calyptotheca reniformis* Tilbrook, 2006, p. 228, pl. 50A–C.

Figure 20. (a) *Calyptotheca reniformis* Tilbrook, 2006, NSMT-Te 1125, ovicelled and several non-ovicelled autozooids. (b–d) *Calyptotheca sesokoensis* sp. nov., NSMT-Te 1128 (holotype): (b) autozooids at colony margin; (c) autozooids, one with rare lateral-oral avicularium; (d) ovicelled and non-ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars = 300 µm.

Material examined

NSMT-Te 1125 (SES-5), bleached, on SEM stub; NSMT-Te 1126, two dried specimens, SES site; NSMT-Te 1127 (REEF-2), bleached, on SEM stub; NSMT-Te 1101, dried specimen, SES site (with *Parasmittina serrula*); NHMUK 2016.5.13.72, dried specimen, SES site (with *Torquatella duolamellata*).

Measurements

AzL, 0.39–0.58 (0.473 ± 0.042); AzW, 0.27–0.39 (0.330 ± 0.029) (n = 20, 1). AzOrL, 0.089–0.110 (0.099 ± 0.007); AzOrW, 0.083–0.114 (0.106 ± 0.009) (n = 12, 1). OvZOrL (secondary), 0.096–0.114 (0.103 ± 0.006); OvZOrW, 0.12–0.13 (0.123 ± 0.005) (n = 7, 1). OvL, 0.24–0.35 (0.303 ± 0.037); OvW, 0.26–0.35 (0.309 ± 0.033) (n = 7, 1). Largest colony observed 11 × 5 mm.

Description

Colony forming a unilaminar, encrusting sheet; off-white, slightly tinged with orange. Zooids (Figure 20(a)) distinct, separated by raised suture line. Frontal wall flat to weakly convex, completely covered with low tubercles, among which are tiny pseudopores having narrow, reniform opening; five to nine slit-like areolar openings along each lateral margin. Orifice of non-ovicelled zooids pear-shaped, with U-shaped sinus separated from anter by conspicuous condyles; condyles denticulate at end. Secondary

orifice of ovicelled zooids wider than primary orifice of non-ovicelled zooids, with shallower, broader sinus. Single small adventitious avicularium in midline proximal to orifice; rostrum oval, raised, mandible directed proximally, crossbar complete; rostrum separate from orifice by about one rostral length. Ovicell (Figure 20(a)) large; subimmersed or endozooidal; ooecium covered with tubercles and tiny reniform pseudopores. Spines lacking. Ancestrula not observed.

Remarks

This species is easily recognisable by its distinctive reniform pores. Our material well matches Tilbrook's (2006) original description and illustrations; differences from the holotype specimen include a more conspicuously tuberculate, rugose frontal wall and ooecium; a somewhat deeper oral sinus on ovicelled zooids; and ovicells that are not as deeply embedded.

Occurrence

We found seven colonies, at the SES and REEF sites. This species was previously known only from the Solomon Islands (Tilbrook 2006).

Calyptotheca sesokoensis sp. nov.
(Figure 20(b–d))

Etymology

The specific name is a Latinised adjective referring to the type locality, Sesoko Island, Okinawa.

Material examined

Holotype: NSMT-Te 1128 (SES-1), bleached, on SEM stub.

Measurements

AzL, 0.51–0.68 (0.585 ± 0.049); AzW, 0.31–0.55 (0.403 ± 0.062) (n = 20, 1). AzOrL, 0.13–0.15 (0.136 ± 0.008); AzOrW, 0.15–0.16 (0.156 ± 0.005) (n = 5, 1). OvZOrL, 0.13–0.15 (0.143 ± 0.008); OvZOrW, 0.17–0.18 (0.178 ± 0.004) (n = 6, 1). OvL, 0.33–0.42 (0.366 ± 0.037); OvW, 0.40–0.47 (0.419 ± 0.033) (n = 4, 1). One colony fragment, 12 × 6 mm.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 20(b–d)) distinct, delineated by raised suture line flanked by areolae; variable in shape, irregularly hexagonal, rectangular, barrel shaped or spindle shaped, sometimes wider than long. Frontal wall moderately convex, mildly rugose, uniformly covered with circular infundibular pseudopores; with five to seven slit-like areolae along each lateral margin, areolae sometimes enlarged. Orifice (Figure 20(c)) transversely oval; condyles prominent, blunt; sinus broad, concave, its curvature more or less continuous with that of anter. Orifice usually located in midline, but sometimes offset to distolateral corner on either side (Figure 20(b)). Orifice weakly dimorphic, slightly larger in

ovicelled than in non-ovicelled zooids. Zone proximal and lateral to orifice thickened and raised as low, crescentic ridge, smooth on inner curvature. Proximal end of zooid often with wide zone of smooth, imperforate gymnocyst that, together with corresponding zone around orifice of preceding zooid, forms flared, smooth, cormidial peristomial region (Figure 20(c)). Only one avicularium observed in entire colony (Figure 20(c)); small (rostrum 0.09 mm long), proximolateral to orifice; crossbar thin, complete; mandible long-triangular, acute, pointing proximomedially. Ovicell (Figure 20(d)) large, hyperstomial. Ooecium covered with rugose secondary calcification, with pseudopores distributed over entire surface. Zooids interconnect by up to five uniporous septula in transverse wall and five or more in each distolateral wall. Spines lacking. Ancestrula not observed.

Remarks

Calyptotheca sesokoensis sp. nov. is similar to *C. rupicola* Hayward and Ryland, 1995, described from the Great Barrier Reef, Australia. The latter species likewise has avicularia present only rarely; when present, they are similar in position and orientation to those in *C. sesokoensis*, but have a rostrum about twice as long. *Calyptotheca rupicola* also differs in having a broader orifice relative to orifice length; pseudopores over the entire frontal wall, which is more coarsely rugose, with rounded tubercles between pseudopores; and a curved band of stout tubercles proximal to the orifice. Zooids in *C. rupicola* lack the smooth proximal gymnocystal area that contributes to the cormidial circum-oral region seen in *C. sesokoensis*. Another similar species is *Calyptotheca tenuata* Harmer, 1957, zooids of which have an unpaired avicularium proximolateral to the orifice. In *C. tenuata*, the avicularia are larger and more frequent than in *C. sesokoensis*; the orifice is broader and likewise lacks the smooth, cormidial circum-oral region seen in *C. sesokoensis*. The cormidial circum-oral region in *C. sesokoensis* resembles that in material from China that Liu et al. (2001, pl. 62, figs 5 and 6); identified as *C. parcimunita* Harmer, 1957, a species originally described from Indonesia. The Chinese material differs from our specimen in having tiny avicularia, single or paired lateral or distolateral to the orifice, with an acute, long-triangular mandible directed medially.

Occurrence

We found a single colony at the SES site, the only known locality.

Genus **Stephanotheca** Reverter-Gil, Souto, and Fernández-Pulpeiro, 2012
Stephanotheca fenestricella sp. nov.
(Figure 21)

Etymology

The specific name is a noun in apposition formed from the Latin *fenestra* (window) and *cella* (chamber), referring to the well-delineated pseudoporous area atop the ovicell.

Material examined

Holotype: NSMT-Te 1123, one dried colony, in three parts, SES site; NSMT-Te 1124 (SES-52), part of same colony as NSMT-Te 1123, bleached, on SEM stub.
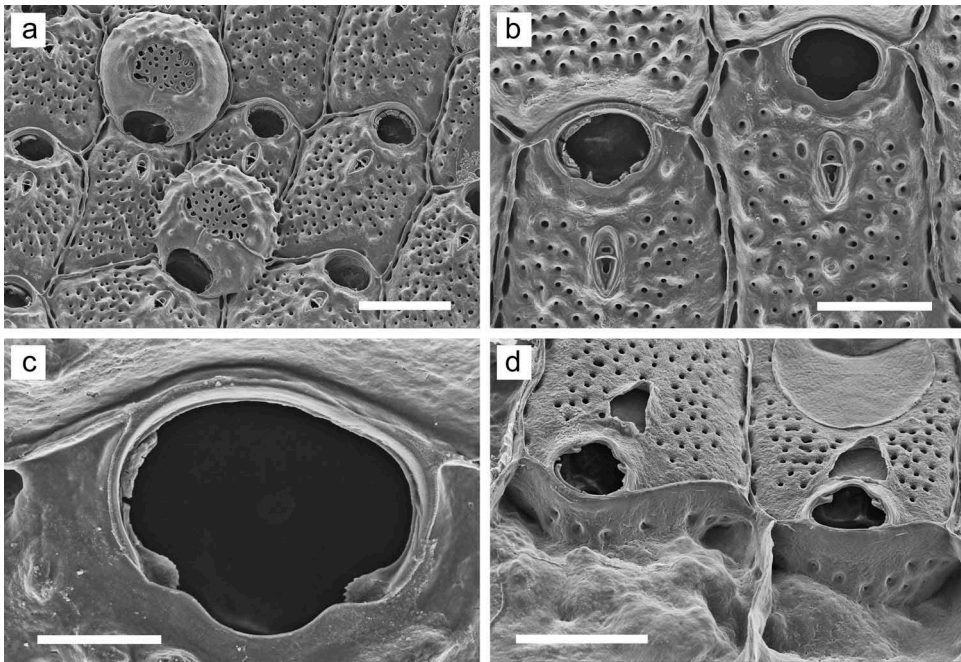
Figure 21. *Stephanotheca fenestricella* sp. nov., NSMT-Te 1124 (holotype): (a) ovicelled and non-ovicelled autozooids; (b) orifices and suboral avicularia; (c) enlargement of orifice; note weakly denticulate condyles; (d) colony margin, showing uniporous septula in transverse walls. All panels are scanning electron microscopic images of the specimen after bleaching. Scale bars: a = 250 μm; b = 150 μm; c = 50 μm; d = 200 μm.

Measurements

AzL, 0.42–0.64 (0.508 ± 0.072); AzW, 0.27–0.45 (0.368 ± 0.055) (n = 15, 1). AzOrL, 0.083–0.115 (0.098 ± 0.006); AzOrW, 0.112–0.125 (0.118 ± 0.005) (n = 15, 1). OvZOrL, 0.088–0.119 (0.104 ± 0.008); OvZOrW, 0.123–0.144 (0.135 ± 0.007) (n = 11, 1). OvL, 0.30–0.34 (0.322 ± 0.017); OvW, 0.30–0.40 (0.362 ± 0.033) (n = 9, 1). One colony, 20 mm in maximum dimension.

Description

Colony forming a unilaminar, encrusting sheet; dried specimen light tan in colour. Zooids (Figure 21(a)) distinct, delineated by shallow grove and suture line flanked by opposing columns of areolae; shape quite variable, ranging from much longer than broad to nearly as broad as long. Frontal wall weakly convex, densely covered with small, infundibular pseudopores except in narrow zone around periphery; surface somewhat rugose, with scattered small tubercles. Six to 11 slit-like areolae along each lateral margin. Orifice terminal; with low, narrow rim distally and laterally, and smooth imperforate zone laterally and proximally; often with 'necklace' of four to six tubercles along margin of smooth zone. Primary orifice (Figure 21(b, c)) broader than long; dimorphic, markedly broader in ovicelled zooids than in those lacking capacity to form ovicell; with broadly concave proximal sinus between prominent, rounded condyles. Condyles

smooth or weakly denticulate at tip. Avicularium (Figure 21(a, b)) single, in midline proximal to orifice. Rostrum elongate, separated from orifice by less than one rostral length; distal end slightly raised, pointing proximally; with complete, curved crossbar almost in middle; mandible acute, about twice as long as broad. Ovicell (Figure 21(a)) hyperstomial, conspicuous, slightly broader than long, closed by operculum. Ooecium covered with thick secondary calcification bearing scattered tubercles, except in flat, transversely oval area in centre that is covered with numerous circular or irregular pseudopores; pseudoporous area often ringed by tubercles; surficial sutures indicate contributions to secondary calcification from up to four neighbouring zooids. Zooids interconnect by row of uniporous septula (Figure 21(d)) in each of transverse and distolateral walls. Ancestrula not observed.

Remarks

Reverter-Gil et al. (2012) established *Stephanotheca* to accommodate a distinct group of species formerly placed in *Schizomavella* Canu and Bassler or other genera, and recognised several additional previously undescribed species that belong in this group. Generic characters for *Stephanotheca* include a frontal wall with pseudopores; broad orificial sinus flanked by distinct condyles; dimorphic orifices between maternal and non-maternal zooids; no oral spines; a usually median suboral avicularium; and a prominent ovicell closed by the operculum, with a well-defined central area having pseudopores. *Stephanotheca fenestricella* differs from the approximately 12 species currently placed in *Stephanotheca* (Bock 2016) in having a narrow, acute median suboral avicularium with a distinctly long-triangular mandible. The other species have an oval suboral avicularium; a larger, triangular frontal avicularium displaced to the proximal end of the zooid; or a large, triangular suboral avicularium occupying most of the length of the zooid (Reverter-Gil et al. 2012; Cumming 2015).

At present, the distribution of *Stephanotheca* appears to be disjunct, with six species known from the Mediterranean, two from the eastern Atlantic and four from Australia, with no records between Australia and Europe (Reverter-Gil et al. 2012; Cumming 2015). Our study area on Okinawa is likewise somewhat disjunct from northern Australia, lying in the East China Sea roughly 5000 km to the north-north-west. However, there are indications that additional *Stephanotheca* species occur in the tropical to temperate western Pacific. Canu and Bassler (1929) designated two varieties of *Schizomavella ambita* (Waters 1889), originally described from Australia, in the western Pacific: var. *granulosa* from 192 m depth in the Philippines and var. *granulata* from an unspecified depth at 'Cape Tsiuka, Sea of Japan' (actually within Tsugaru Strait, northern Japan, according to the accompanying coordinates). Reverter-Gil et al. (2012) transferred *Schizomavella ambita* Waters to *Stephanotheca*, and one or both of these varieties could represent a species in *Stephanotheca*. While the descriptions and illustrations in Canu and Bassler (1929) are poor, neither variety appears to have avicularia of the same shape as *Stephanotheca fenestricella*.

Occurrence

We found a single colony at the SES site, the only known locality.

Superfamily **SCHIZOPORELLOIDEA** Jullien, 1883
Family **SCHIZOPORELLIDAE** Jullien, 1883
Genus *Stylopoma* Levinsen, 1909
Stylopoma duboisii (Audouin, 1826)
(Figure 22)

Flustra? *duboisii* Audouin, 1826, p. 239.
Stylopoma duboisii: Tilbrook 2001, p. 8, fig. 2(c–f).
?*Stylopoma duboisii*: Hirose 2010, p. 129, pl. 221A, B.
See Tilbrook (2001) for synonyms following his revision of the genus.

Material examined

NSMT-Te 1129 (MIN-21), bleached, on SEM stub; NSMT-Te 1130, two dried specimens, SES site.

Measurements

AzL, 0.43–0.61 (0.506 ± 0.043); AzW, 0.23–0.39 (0.317 ± 0.041) (n = 20, 1). OrL (without sinus), 0.06–0.08 (0.074 ± 0.005); OrW, 0.10–0.12 (0.108 ± 0.004); OrSinL, 0.02–0.04 (0.028 ± 0.005) (n = 20, 1). OvDm, 0.46–0.54 (0.511 ± 0.026) (n = 7, 1). AvRosL, 0.04–0.06 (0.051 ± 0.005) (n = 8, 1). Largest fragment observed 10 mm across.
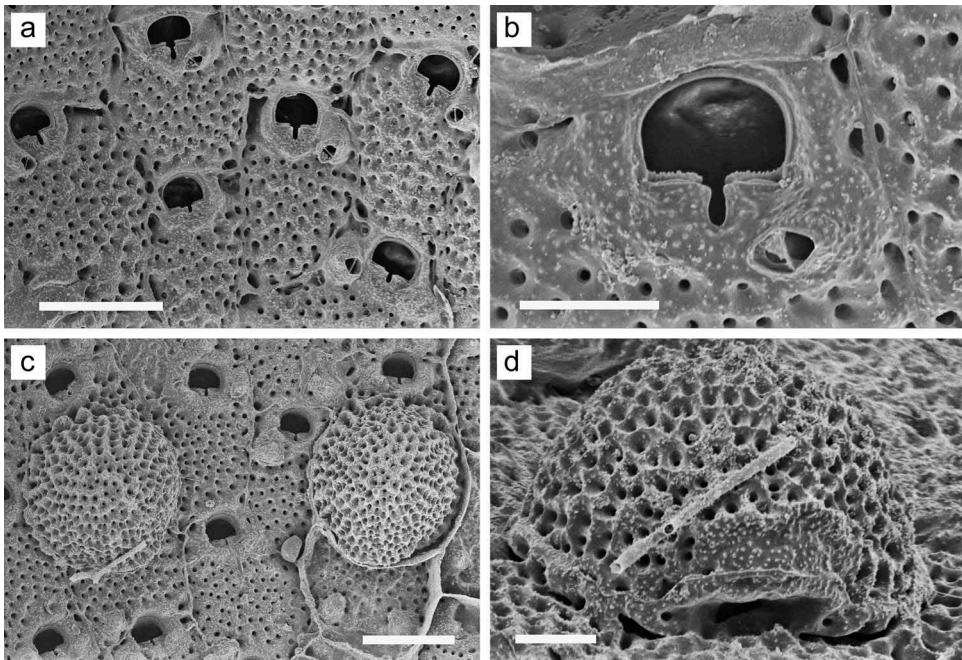
Figure 22. *Stylopoma duboisii* (Audouin), NSMT-Te 1129: (a) autozooids; (b) orifice; (c) autozooids and ovicells; (d) oblique view of ovicell, showing aperture. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, c = 300 μm; b, d = 100 μm.

Description

Colony forming a unilaminar, encrusting sheet; occasional frontally budded zooids occur on colony surface. Zooidal (Figure 22(a)) boundaries delineated by marginal areolae and suture line. Frontal wall weakly convex, minutely granulated, covered with numerous small, infundibular pseudopores, except in peristomial region; five to seven slit-like areolae along each lateral margin. Primary orifice (Figure 22(b)) D-shaped, with deep, U-shaped proximal sinus having parallel sides; sinus occasionally wider proximally, somewhat drop-shaped. Condyles occupy entire flat proximal orificial margin on each side, reaching opening of sinus or nearly so, serrate on top, with rounded tip. Orifice completely surrounded by thickened, slightly elevated, granulated peristomial rim, sometimes with blunt umbo on one or both sides proximolateral to orifice. Small, single avicularium (Figure 22(a, b)) on raised chamber on either side proximolateral to orifice; rostrum inclined to frontal surface, crossbar complete; mandible a small, equilateral triangle, directed distolaterally; many zooids lack an avicularium. No large vicarious avicularia observed. Ovicell (Figure 22(c)) hyperstomial, conspicuous; with transverse opening (Figure 22(d)) at base; distal margin of opening thickened, with semicircular area above lacking pseudopores; labellum appears to be straight, entire; aperture D-shaped. Ooecium entirely covered with infundibular pseudopores; texture granulated like frontal wall. No spines. Ancestrula not observed.

Remarks

Stylopoma duboisii is very similar to *S. velatum* Tilbrook et al., 2001. According to Tilbrook (2001), the latter has a more semicircular orifice that is distinctly broader than long, but this difference is negligible; the average width/length ratios of the orifice exclusive of the sinus calculated for the two species from Tilbrook's (2001) measurements are 1.4 and 1.5, respectively, and orifice shape varies considerably even within our specimens. Average zooid size is essentially indistinguishable among *S. duboisii* (L, 0.50; W, 0.35), *S. velatum* (L, 0.52; W, 0.36) (Tilbrook 2001), and our specimen (L, 0.51; W, 0.32). Tilbrook (2001, fig. 11(d, e)); shows the adventitious avicularium in *S. velatum* to have a small chamber and to lie close to the orifice; in *S. duboisii* and our specimen, the chamber is larger relative to rostrum size; the rostrum is more elevated and tends to lie outside the peristomial rim. A key difference between the two species is a D-shaped aperture and entire, straight labellum (see Tilbrook 2001 for the meanings of 'labellum' and 'aperture') in the ooecial opening in *S. duboisii* versus an oval aperture and split labellum in *S. velatum*. Although Tilbrook's (2001) illustration of the ooecial opening for the latter species is not clear, our specimen clearly has a D-shaped aperture, and the labellum appears to be entire.

Occurrence

We found two colonies at SES and one at MIN. Tilbrook (2001) lists the range of *S. duboisii* sensu stricto (i.e. after his revision of the genus) as extending from the Red Sea to Malaysia, New Guinea and the Philippines; and the range of *S. velatum* as the western Pacific, including the South China Sea, Great Barrier Reef, Vanuatu and Tahiti. The occurrence of *S. duboisii* at Okinawa constitutes a northward range extension in the western Pacific. Hirose (2010) reported a single specimen of *S. duboisii* from Sagami Bay, Pacific coast of central

Honshu, Japan; while his identification seems compatible with *S. duboisii*, his illustration consists of two light micrographs, and this record needs confirmation by SEM.

Stylopoma vilaensis Tilbrook, 2001
(Figure 23(a–c))

Stylopoma vilaensis Tilbrook, 2001, p. 29, fig. 12(a–c).

Material examined
NSMT-Te 1131 (MIN-5), bleached, on SEM stub; NSMT-Te 1132, lot of two dried specimens, MIN site; NHMUK 2016.5.13.43–46, lot of four dried specimens, MIN site.
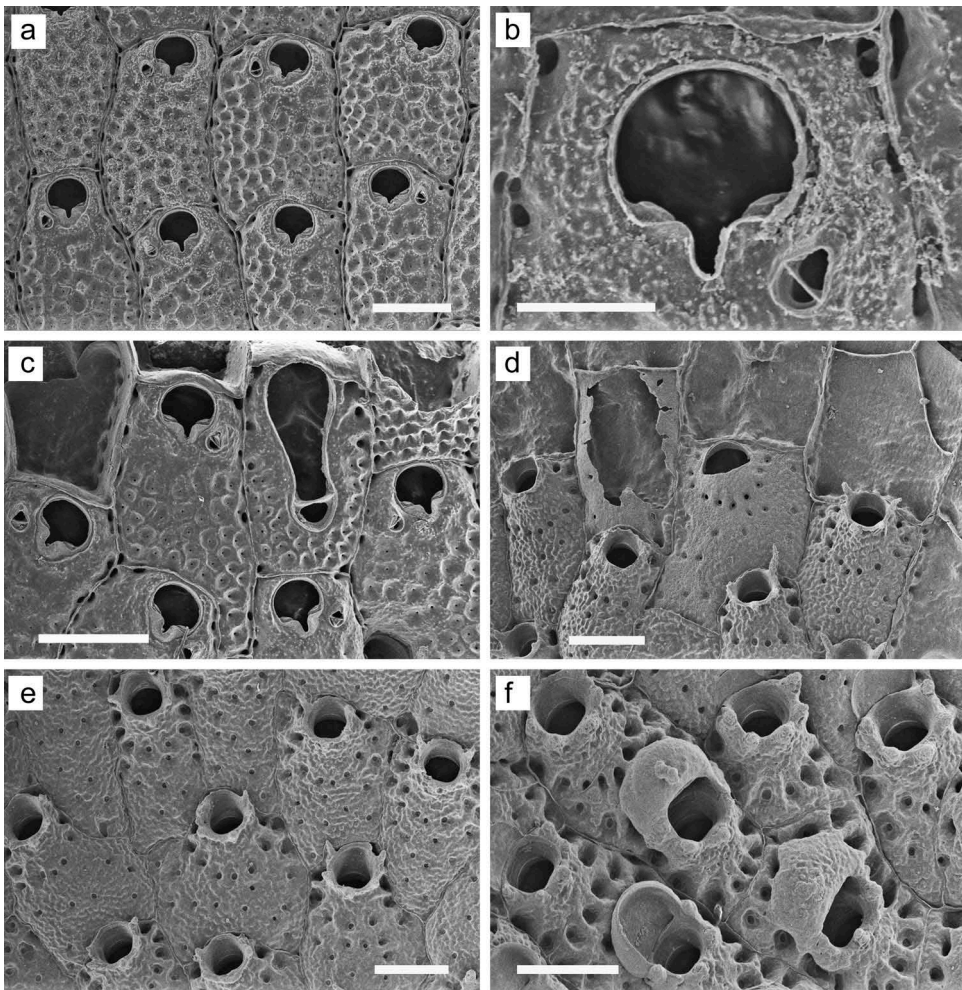

Figure 23. (a–c) *Stylopoma vilaensis* Tilbrook, NSMT-Te 1131: (a) autozooids; (b) orifice; (c) autozooids and vicarious avicularium at colony margin. (d–f) *Junerossia copiosa* Dick, Tilbrook, and Mawatari, NSMT-Te 1133: (d) young autozooids at colony margin; (e) older autozooids in colony interior; (f) heavily calcified ovicelled and non-ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, c–f = 300 μm; b = 100 μm.

Measurements

AzL, 0.51–0.69 (0.617 ± 0.049); AzW, 0.30–0.53 (0.395 ± 0.062). OrL (including sinus), 0.14–0.16 (0.150 ± 0.008); OrW, 0.14–0.16 (0.145 ± 0.006). Adventitious AvRostL, 0.05–0.08 (0.062 ± 0.007) (all preceding, n = 15, 1). Vicarious AvRostL, 0.458 (n = 1). Largest colony fragment 25 × 15 mm.

Description

Colony forming a unilaminar, encrusting sheet; colour white, with light brown opercula. Zooids (Figure 23(a)) distinct, delineated by suture line flanked by areolae. Frontal wall weakly convex, minutely granulated, uniformly covered with minute pseudopores except in zone proximal to orifice; each pore at base of infundibular depression. Eight to 10 slit-like areolae along each lateral margin, fewer along proximal and distal margins. Primary orifice (Figure 23(b)) terminal or nearly so; anter broader than long; median proximal sinus long, V-shaped; orifice completely surrounded by thick, slightly raised, granulated peristomial rim. Condyles sloping, smooth, without sculptured cap. Adventitious avicularium proximolateral to orifice on one side or other, lacking in some zooids; rostrum inclined to frontal plane, pointing distolaterally, with complete crossbar; mandible an equilateral triangle. Vicarious avicularia (Figure 23(c)) uncommon; same size as autozooids, with large, broadly spatulate rostrum; crossbar complete, mandible directed distally. No spines. Ovicell and ancestrula not observed.

Remarks

This species is characterised by the long, V-shaped suboral sinus; smooth, tapering condyles; minute frontal pores in infundibular depressions; small adventitious suboral avicularia; and vicarious avicularia with a large, broadly spatulate mandible. In the original description, Tilbrook (2001) notes that the suboral avicularia may be single or paired, although we observed no paired ones.

Occurrence

We found seven colonies or fragments at the MIN site. This species has been previously reported from 1–2 m depth at Vanuatu, and 0–54 m depth at East Timor (Tilbrook 2001).

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Family **STOMACHETOSELLIDAE** Canu and Bassler, 1917
Genus ***Junerossia*** Dick, Tilbrook, and Mawatari, 2006
Junerossia copiosa Dick, Tilbrook, and Mawatari, 2006
(Figure 23(d–f))

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Junerossia copiosa Dick, Tilbrook, and Mawatari, 2006, p. 2227, fig. 10(a–h).
'Genus and species, not determined': Tilbrook 2006, p. 147, fig. 21(d–f).

Material examined

NSMT-Te 1133 (MIN-5), two specimens, bleached, on SEM stub; NSMT-Te 1134, three dried specimens, SES site; NSMT-Te 1135, four dried specimens, MIN site; NSMT-Te 1136, 23 dried specimens, REEF site; NHMUK 2016.5.13.47-51, five dried specimens, REEF site.

Measurements

AzL, 0.57–0.85 (0.661 ± 0.063); AzW, 0.32–0.59 (0.437 ± 0.069) (n = 31, 1). SecOrL, 0.13–0.19 (0.162 ± 0.017); SecOrW, 0.14–0.17 (0.155 ± 0.012) (n = 25, 1). OvL, 0.21–0.22 (0.214 ± 0.006); OvW, 0.31–0.34 (0.320 ± 0.012) (n = 6, 1). Largest colony observed 20 × 13 mm.

Description

Colony forming an encrusting sheet; mostly unilaminar, but frontal budding produces secondary layer in local areas; white, covered with glistening ectocyst. Zooids (Figure 23 (d–f)) irregular in size and shape; delineated by groove. Frontal shield well calcified, finely granulated, covered with widely spaced pseudopores except in orificial region; with increased calcification, pseudopores become infundibular and frontal surface quite rugose (Figure 23(f)). Areolae inconspicuous. Primary orifice (Figure 23(d)) much broader than long, semicircular, visible only in young zooids at colony margin, soon obscured by thick, raised, tapering peristome, with characteristic 'necklace' of pores at base; peristomial lip with up to six or seven digitiform processes; secondary orifice approximately circular. Spines lacking. Ovicell (Figure 23(f)) hyperstomial, completely covered with secondary calcification of same granulated texture as frontal shield, often with rugose area or small umbo on top; pseudopores lacking. Embryos inside ovicells light yellow in our dried specimens.

Remarks

The material from Okinawa is indistinguishable from specimens from the type locality (Kapa'a Beach, Hawaii Island); for a full description, see Dick et al. (2006).

Occurrence

Junerossia copiosa was prominent in the study area, common at the SES site and abundant at the REEF and MIN sites (Table 1). Likely broadly distributed in warm Pacific waters, this species was previously known from Hawaii Island (Dick et al. 2006) and Guadalcanal, Solomon Islands (Tilbrook 2006).

<div align="center">

Family **HIPPOPODINIDAE** Levinsen, 1909
Genus ***Hippopodina*** Levinsen, 1909
Hippopodina adunca Tilbrook, 2006
(Figure 24(a, b))

</div>

Hippopodina adunca Tilbrook, 2006, p. 248, pl. 54C, D.
Hippopodina feegeensis: Philipps 1900, p. 446, pl. 63, fig. 7. Ristedt and Hillmer 1985, p. 137, pl. 2, fig. 12. Winston and Heimberg 1986, p. 16, figs 28–30. Hayward 1988, p. 319. Ryland and Hayward 1992 (in part), p. 256, fig. 17(a). Seo 1992, p. 150, pl. 1, figs 6 and 7. Tilbrook 1999 (in part), p. 451. Tilbrook et al. 2001, p. 88, fig. 18(a). Seo 2005, p. 431, pl. 159.

Material examined

NSMT-Te 1137 (MIN-24), bleached, on SEM stub; NSMT-Te 1138, seven dried specimens, MIN site; NSMT-Te 1139, two dried specimens, SES site; NSMT-Te 1140, large dried specimen, MIN site; NSMT-Te 1168 (MIN-35), bleached, on SEM stub (with
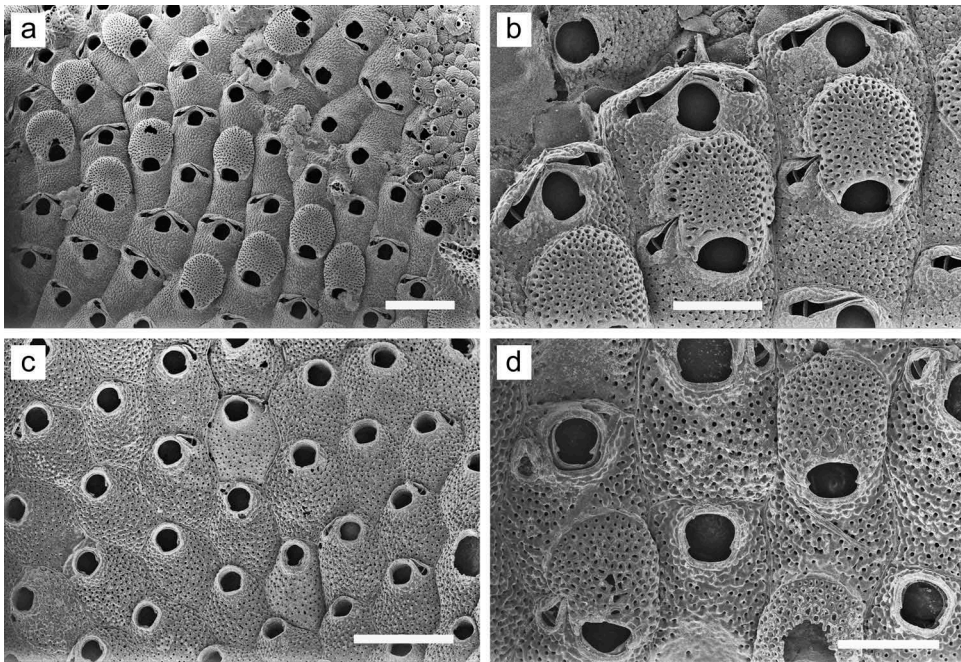
Figure 24. (a, b) *Hippopodina adunca* Tilbrook, NSMT-Te 1137: (a), view of colony; note small relative size of zooids in overgrowing *Puellina harmeri* colony at upper right; (b) ovicelled and non-ovicelled autozooids; note unusual presence of avicularium on ovicelled zooids. (c, d) *Hippopodina iririkiensis* Tilbrook, NSMT-Te 1141: (c) view of colony; (d) ovicelled and non-ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, c = 1.0 mm; b, d = 500 µm.

Crepidacantha longiseta); NHMUK 2016.5.13.52-55, four dried specimens, MIN site; NHMUK 2016.5.13.56-58, three dried specimens, SES site.

Measurements

AzL, 0.80–1.09 (0.910 ± 0.080); AzW, 0.60–0.87 (0.708 ± 0.083) (n = 16, 1). AzOrL, 0.21–0.25 (0.230 ± 0.011); AzOrW, 0.19–0.24 (0.225 ± 0.012) (n = 16, 1). OvL, 0.64–0.78 (0.742 ± 0.047); OvW, 0.56–0.70 (0.658 ± 0.047) (n = 7, 1). SecOrOvZ: L, 0.19–0.23 (0.211 ± 0.014); W, 0.24–0.28 (0.261 ± 0.015) (n = 7, 1). Largest fragment 35 × 25 mm, but larger colonies occurred.

Description

Colony (Figure 24(a)) forming an extensive, mostly unilaminar, encrusting sheet; self-over-growth or frontal budding can produce secondary layer in parts of colony; living colonies light reddish brown. Zooids large; rectangular or irregularly hexagonal, sometimes wider than long; distinct, separated by a groove. Frontal wall convex, finely granulated, covered with numerous tiny, closely spaced pseudopores. Orifice keyhole shaped; short, wide poster separated from anter by prominent condyles; proximal margin slightly concave. Avicularia adventitious, single or paired, distolateral to orifice across distal margin, angled slightly distomedially; mandible setiform, hooked at tip, directed distomedially and reach-ing midline or close to it, slightly curved in distal direction; hinge bar complete. Ovicell

(Figure 24(b)) hyperstomial, globose, longer than broad, closed by operculum; ooecium occupying half or more of frontal shield of next-distal zooid, entirely covered with small, closely spaced pseudopores. Secondary orifice of ovicelled zooids D-shaped, shorter and wider than primary orifice of non-ovicelled zooids. Some ovicelled zooids retain a small avicularium on one side, in the usual position, with tip of rostrum extending slightly inside ooecial margin. Spines lacking. One ancestrular complex observed, forming a triad.

Remarks

Hippopodina adunca is superficially similar to and can be confused with *Hippopodina feegeensis* Busk, 1884. Tilbrook (2006) clarified the differences between the two and listed several previous records attributable to the former that had been mistakenly assigned to the latter. One among several diagnostic differences is that the ancestrular complex in *H. adunca* is a triad, as in *H. iririkiensis* (next description), whereas that in *H. feegeensis* is a tetrad. Among the specimens we identified as *H. adunca*, one clearly shows a triad ancestrular complex. A previous record of *H. feegeensis* from Japan (Mawatari 1974) has proven not to be *H. adunca*, but rather *H. tahitiensis* Leca and d'Hondt, 1993 (Tilbrook 2006).

Occurrence

Hippopodina adunca was common at the SES site, where it co-occurred with *H. iririkiensis*, and abundant at the MIN site, where it did not (Table 1). This species is broadly distributed in shallow waters of the Indo-West Pacific from Mauritius westward to Fiji (Tilbrook 2006) and northward to Korea (Seo 1992, 2005).

Hippopodina iririkiensis Tilbrook, 1999
(Figure 24(c, d))

Hippopodina iririkiensis Tilbrook, 1999, p. 454, fig. 2(a, c, e).
Hippopodina iririkiensis: Tilbrook et al. 2001, p. 90, fig. 18(b). Tilbrook, 2006, p. 245. Dick et al. 2006, p. 2229, fig. 11(a).

Material examined

NSMT-Te 1141 (REEF-1), bleached, on SEM stub; NSMT-Te 1142, dried colony with ancestrular complex, REEF site; NSMT-Te 1143, seven dried specimens, REEF site; NSMT-Te 1144, five dried specimens, SES site.

Measurements

AzL, 0.82–1.03 (0.925 ± 0.071); AzW, 0.57–0.83 (0.711 ± 0.069) (n = 15, 1). OrL, 0.19–0.26 (0.229 ± 0.018); OrW, 0.19–0.24 (0.218 ± 0.014) (n = 15, 1). OvL, 0.57–0.70 (0.637 ± 0.044); OvW, 0.46–0.60 (0.534 ± 0.044) (n = 7, 1). Largest fragment observed, 30 × 13 mm.

Description

Colony forming a unilaminar, encrusting sheet, sometimes covering extensive areas; light tan in colour. Zooids (Figure 24(c)) large, distinct, delineated by a groove. Frontal wall convex, finely granulated, covered with numerous tiny, closely spaced pseudopores. Orifice keyhole shaped; short, wide poster separated from anter by

conspicuous condyles; proximal margin concave. Orifice surrounded by low, raised rim. Primary orifice weakly dimorphic; generally wider in ovicelled (evident in zooids with developing ooecia) than in non-ovicelled zooids. Avicularia adventitious, lateral to the orifice; crossbar complete; mandible long-triangular; directed distomedially or sometimes distally; tip of rostrum not reaching zooidal midline. Avicularium lacking in most zooids, single in a few zooids; paired in only one among hundreds of zooids in several colonies. Ovicell (Figure 24(d)) hyperstomial, globose, longer than broad, closed by operculum; ooecium completely covered with small, closely spaced, infundibular pseudopores. Ancestrular complex (one observed) consists of triad of primary zooids.

Remarks

Avicularium frequency appears to vary among populations. Tilbrook (1999, p. 454) noted for specimens from Vanuatu, 'adventitious avicularia often paired, sometimes single or lacking'. Dick et al. (2006) found the converse on Hawaii Island, where avicularia were usually single but sometimes paired. Among our specimens from Okinawa, most zooids lack an avicularium; when present, it is usually single.

Occurrence

Hippopodina iririkiensis was common at both the SES site, where it co-occurred with *H. adunca*, and the REEF site, where it did not (Table 1). This species is widely distributed in the subtropical to tropical Indo-Pacific, with records from Mauritius, Indonesia, Australia, Indonesia, the Philippines and Vanuatu (Tilbrook 1999; Tilbrook et al. 2001); the Solomon Islands (Tilbrook 2006); and Hawaii (Dick et al. 2006). It also appears to occur in the Mediterranean (Tilbrook 1999), where it may have been introduced from the Red Sea through the Suez Canal.

<div align="center">

Genus ***Thornelya*** Harmer, 1957
Thornelya fuscina Tilbrook, Hayward, and Gordon, 2001
(Figure 25(a))

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Thornelya fuscina Tilbrook, Hayward, and Gordon, 2001, p. 90, fig.17(e, f).
Thornelya fuscina: Tilbrook 2006, p. 249, pl. 54E, F.

Material examined

NSMT-Te 1145 (SES-11), bleached, on SEM stub.

Measurements

AzL, 0.42–0.64 (0.534 ± 0.077); AzW, 0.28–0.48 (0.388 ± 0.060) (n = 12, 1). OrL, 0.15–0.17 (0.162 ± 0.004); OrW, 0.13–0.14 (0.129 ± 0.004) (n = 12, 1).

Description

Colony forming a unilaminar, encrusting sheet; our specimen small, comprising about 40 zooids. Zooids distinct; frontal wall convex, tumid; weakly rugose, covered by numerous circular, sometimes infundibular pseudopores, except in raised zone around orifice; around eight usually slit-like but sometimes round areolae along each lateral margin.
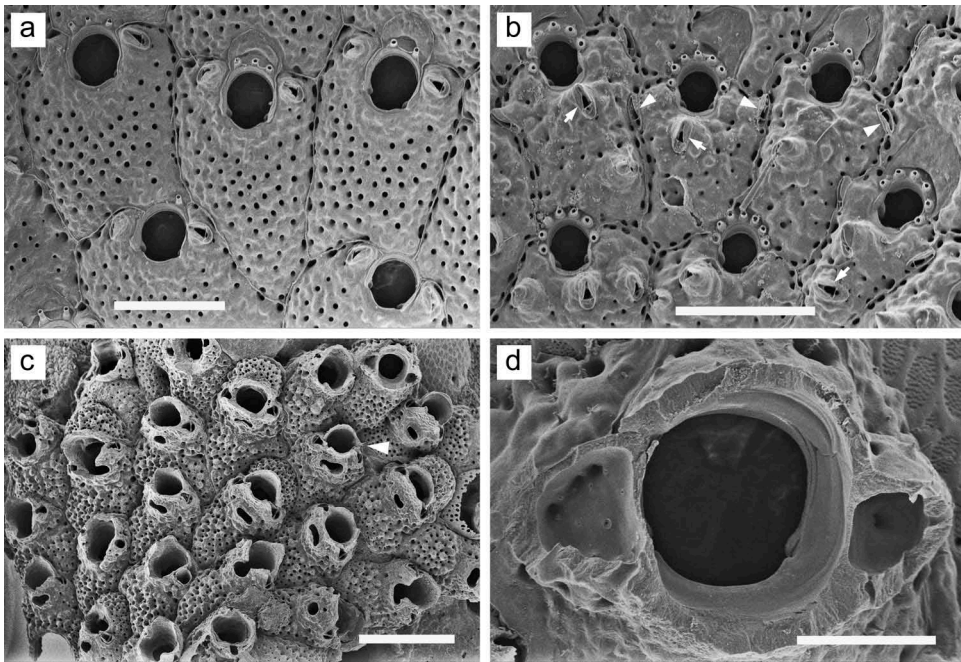
Figure 25. (a) *Thornelya fuscina* Tilbrook, Hayward, and Gordon, NSMT-Te 1145: autozooids. (b) *Thornelya perarmata* Harmer, NSMT-Te 1146: autozooids; arrows and arrowheads indicate two types of adventitious avicularia (see the text). (c, d) *Gigantopora pupa* (Jullien), NSMT-Te 1147: (c) colony view, showing ovicelled and non-ovicelled autozooids (arrowhead, minute oral spine); (d) orifice. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a, b = 300 μm; c = 1.0 mm; d = 200 μm.

Primary orifice not immersed; longer than broad; condyles conspicuous, rounded, directed proximomedially; poster broadly concave. Marginal zooids have two (39%), three (54%) or four (7%) small, ephemeral tubular distal spines (n = 28). Avicularia adventitious; small, paired, in distolateral corners of zooid, lateral to orifice; chamber raised, bearing small pseudopore at proximal end. Rostrum raised distally; mandible long-triangular, acute, directed distomedially or sometimes medially; crossbar complete. No complete ovicells observed. Ancestrula not observed.

Remarks

This species has small, usually paired lateral-oral avicularia and relatively few oral spines. According to other descriptions, the ovicell is hyperstomial; the ooecium is globose, slightly broader than long, similar in texture to the frontal wall, with small pseudopores over the entire surface, and closed by the maternal operculum. Type material from Vanuatu (Tilbrook et al. 2001) differs from our specimen in having three or four rather than two to four oral spines, and some zooids have a third, median avicularium associated with the orifice, which we did not observe. Some zooids in specimens from the Solomon Islands have one of the lateral-oral avicularia markedly larger than the other (Tilbrook 2006), which we also did not observe. For a discussion of differences among species in *Thornelya*, see *Remarks* for *T. perarmata* below.

Occurrence

We found a single colony at the SES site. *Thornelya fuscina* is widely distributed in the subtropical to tropical Indo-West Pacific, previously reported from Sri Lanka, New Guinea (32 m), Tuvalu (146 m) and Vanuatu (Tilbrook et al. 2001), and from the Solomon Islands (Tilbrook 2006).

Thornelya perarmata Harmer, 1957
(Figure 25(b))

Thornelya perarmata Harmer, 1957, p. 1105, pl. 73, figs 6–8.
Thornelya perarmata: Ryland and Hayward 1992, p. 258, fig. 17(c, d).

Material examined

NSMT-Te 1146 (SES-3), bleached, on SEM stub; NHMUK 2016.5.13.59, dried specimen, SES site (with ?*Exechonella* sp., *Celleporaria triangula*, *Cranosina coronata*).

Measurements

AzL, 0.38–0.51 (0.442 ± 0.047); AzW, 0.27–0.34 (0.308 ± 0.025) (n = 10, 1). OrL, 0.12–0.13 (0.121 ± 0.006); OrW, 0.09–0.10 (0.096 ± 0.003) (n = 10, 1). Larger of two colonies 4 mm across.

Description

Colony forming a unilaminar, encrusting sheet. Zooids irregular in size and shape, sometimes broader than long; distinct, delineated by groove and suture line flanked by areolae. Frontal wall markedly convex, coarsely tuberculate, rugose, sparsely covered with scattered pseudopores; young, marginal zooids lack pseudopores in extensive central region proximal to orifice. Up to 13 small areolae along each lateral margin. Orifice not deeply immersed; longer than broad; broadest in centre of anter; keyhole shaped; poster broadly concave, separated from anter by conspicuous rounded condyles. Distal margin with six (63%), seven (35%) or eight (2%) stout, straight tubular spines; large, conspicuous spine scars evident even in older zooids near colony centre. Peristome lacking. Zooids bear up to four adventitious avicularia, of two types. One type (arrows, Figure 25(b)) has raised, circular or oval chamber, with rostrum highly angled from frontal plane; crossbar complete; mandible triangular, about twice as long as broad, acute; chamber usually with one or two small pseudopores proximal to rostrum. This type can occur anywhere on frontal wall, with mandible pointing in any direction. The other type (arrowheads, Figure 25(b)) arises from an areolar pore, usually in distolateral corner of zooid, on one or both sides; chamber negligible; rostrum slightly raised from frontal surface distally, tilted laterally towards one side, rostral axis parallel to zooidal margin; cross bar complete; mandible acute, triangular, length at least 3 times width; pointing distally or proximally. No complete ovicells observed. Ancestrula not observed.

Remarks

According to other descriptions, the ovicell is hyperstomial, with numerous pseudopores, and with or without an avicularium on the frontal surface. Our specimens are

quite similar to material described from the Great Barrier Reef (Ryland and Hayward 1992), in which zooids have six oral spines and the same two types of avicularia. Three species have been assigned to *Thornelya*: *T. ceylonica* (Thornely 1905); *T. perarmata* Harmer, 1957; and *T. fuscina* Tilbrook et al., 2001. *Thornelya fuscina* has somewhat larger zooids, more pores in the frontal wall, and fewer oral spines (2–4 versus 6–8) than *T. perarmata*, and differs in the form, number and position of avicularia. According to Tilbrook et al. (2001), the zooidal orifice is narrower relative to length in *T. fuscina* than in *T. perarmata*, though this is only marginally evident from our material (OrL/OrW, 1.35 and 1.26, respectively). While *T. ceylonica* also has six to eight oral spines as in *T. perarmata*, its primary orifice is putatively wider relative to length, with a shallower poster, and avicularia are more numerous (Harmer 1957; Tilbrook et al. 2001); to date, *T. ceylonica* has not been examined by SEM. *Hippomenella mila* Scholz, 1991, originally described from the Philippines, may also be assignable to *Thornelya*.

Occurrence

We found two colonies, both at the SES site. Originally described from the Weigeu Islands, western New Guinea (Harmer 1957), this species had subsequently been reported only from the Great Barrier Reef (Ryland and Hayward 1992).

<div align="center">

Family **GIGANTOPORIDAE** Bassler, 1935
Genus ***Gigantopora*** Ridley, 1881
Gigantopora pupa (Jullien, 1903)
(Figure 25(c, d))

</div>

Galeopsis pupa Jullien, in Jullien and Calvet, 1903, p. 95, pl. 12, fig. 1.
Galeopsis pupa: Canu and Bassler 1929, p. 272, text-fig. 110(a–d), pl. 28, figs 1 and 2.
Gigantopora pupa: Harmer 1957, p. 880, pl. 60, figs 3 and 9. Gordon 1984, p. 79, pl. 26F.
   Hayward and Ryland 1995, p. 557, fig. 11(a).

Material examined

NSMT-Te 1147 (SES-2), bleached, on SEM stub.

Measurements

AzL, 0.95–1.15 (1.063 ± 0.061); AzW, 0.57–0.83 (0.672 ± 0.072) (n = 10, 1). OrL, 0.257; OrW, 0.249 (n = 1). OvL, 0.32–0.49 (0.387 ± 0.076); OvW, 0.54–0.62 (0.591 ± 0.034) (n = 4, 1). Fragment observed was part of a larger colony estimated to be about 1 cm in diameter.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 25(c)) large, coarse, distinct. Frontal wall quite convex, covered with coarse, rounded tubercles interspersed with small pseudopores over entire surface proximal to peristome. Areolar openings not evident. Primary orifice (Figure 25(d)) subcircular, about as broad as long, with blunt condyles; curvature of anter nearly continuous with that of poster. Peristome tall; continuous, or with proximal and distal lips separated by a sulcus on each side. Large spiramen on bulbous swelling on proximal side of peristome; spiramen variable in size and shape: circular, oval, crescent shaped, dumbbell shaped or long-elliptical. Avicularia

paired, one on each side of peristome on slightly raised chamber; rostrum highly angled from frontal plane, pointing proximomedially, with tip generally touching proximal peristomial lip; mandible short-triangular, acute; crossbar complete. Ovicell (Figure 25 (c)) hyperstomial; ooecium broader than long, with highly rugose surface and numerous pseudopores, like frontal wall; peristome extends around proximal margin of ooecium. One zooid in our specimen bears a minute hollow spine (Figure 25(c), arrowhead) on peristomial rim, lateral to orifice. Ancestrula not observed.

Remarks

As a synonym of *G. pupa* (Jullien), Harmer (1957) listed *Gigantopora* (as *Galeopsis*) *brevicapitata* Canu and Bassler, 1929 from the Philippines, stating that he was unable to distinguish between them. According to Canu and Bassler (1929), the former differs from the latter in having a shorter ooecium and a more salient spiramen placed lower on the peristome. In any case, Canu and Bassler (1929) also reported *Gigantopora pupa* from the Philippines.

Occurrence

We found a single colony at the SES site. This species occurs in the western Pacific, with previous records from Torres Strait (Harmer 1957) and the Great Barrier Reef (Hayward and Ryland 1995), Australia; New Zealand (Gordon 1984); and the Philippines (Canu and Bassler 1929).

Family **ECHINOVADOMIDAE** Tilbrook, Hayward, and Gordon, 2001
Genus ***Echinovadoma*** Tilbrook, Hayward, and Gordon, 2001
Echinovadoma anceps Tilbrook, Hayward, and Gordon, 2001
(Figure 26)

Echinovadoma anceps Tilbrook, Hayward, and Gordon, 2001, p. 84, fig. 16(c–e).

Material examined

NSMT-Te 1148 (SES-7), bleached, on SEM stub.

Measurements

AzL, 0.36–0.43 (0.396 ± 0.022); AzW, 0.25–0.38 (0.310 ± 0.037) (n = 15, 1). OrL, 0.10–0.13 (0.116 ± 0.009); OrW, 0.11–0.13 (0.119 ± 0.005) (n = 15, 1). OvL, 0.15–0.20 (0.167 ± 0.012); OvW, 0.19–0.24 (0.205 ± 0.011) (n = 15, 1). Larger of two colonies 3.5 mm across.

Description

Colony forming a unilaminar, encrusting sheet (Figure 26(a)). Zooids (Figure 26(a, b)) small, delineated by shallow groove. Frontal wall convex, completely covered with minute pseudopores interspersed with rounded tubercles; areolae around margin slit-like, indistinct. Primary orifice about as broad as long; anter transversely oval, separated from broadly rounded poster by conspicuous sharp condyles. Proximal and lateral margins of orifice developed as broad, flared flange, often with lateral and proximomedian lobes. Oral spines lacking. Ovicell (Figure 26(c)) hyperstomial; ooecium consisting of two spinous lateral lobes, fused in upper distal midline, but
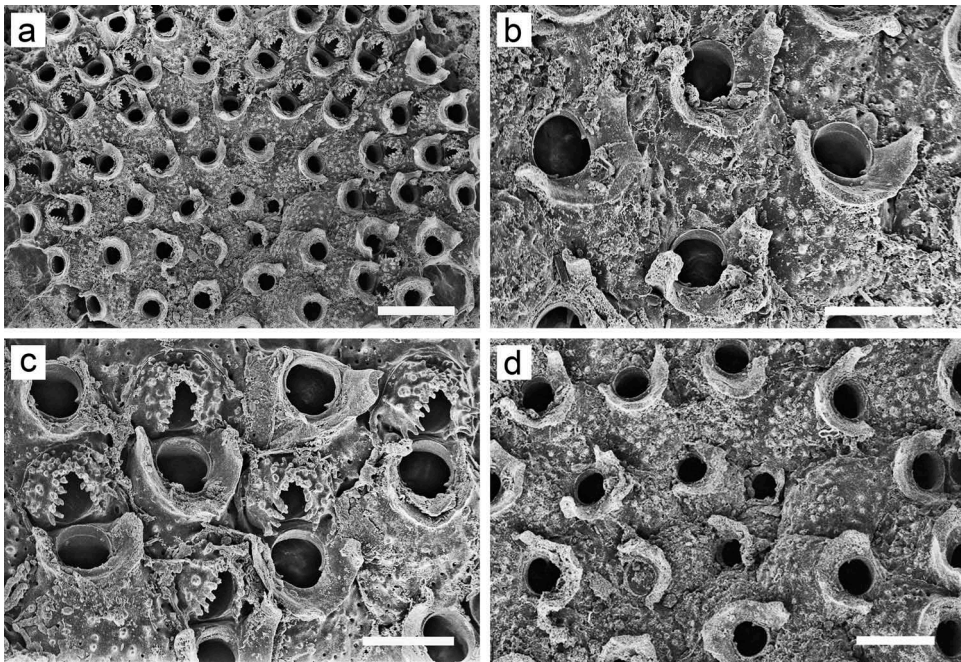
Figure 26. *Echinovadoma anceps* Tilbrook, Hayward, and Gordon, NSMT-Te 1148. (a) view of colony; (b) autozooids; (c) ovicelled autozooids; (d) enlargement of centre of colony in (a), showing ancestrular complex. All panels are scanning electron microscopic images of dried, naturally dead colony. Scale bars: a = 500 μm; b, c = 200 μm; d = 250 μm.

leaving small, oval foramen distally and larger, triangular opening proximally; ooecium covered with tubercles like those on frontal wall; margins of ovicell openings with cylindrical, spine-like denticles. One colony shows a central ancestrular complex (Figure 26(d)), although it is not clear which of two small, central zooids is the ancestrula, nor is the budding pattern clear.

Remarks
This species is the sole representative of a presently monotypic family and genus. Our specimens well match the original description.

Occurrence
We found two small colonies at the SES site. The only other known locality is Poanangisu, Efate, Vanuatu (Tilbrook et al. 2001).

<div align="center">

Family **ROBERTSONIDRIDAE** Rosso, Scinto, and Sinagra, 2010
Genus ***Robertsonidra*** Osburn, 1952
Robertsonidra argentea (Hincks, 1881)
(Figure 27(a–c))

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Schizoporella argentea Hincks, 1881, p. 158, pl. 9, fig. 6(a).

Robertsonidra argentea: Ryland and Hayward 1992, p. 261, fig. 19(b). Liu et al. 2001, p. 644, pl. 60, figs 1–4. Tilbrook 2006, p. 261, pl. 57E, F.

For additional synonyms, see Tilbrook (2006).

Material examined

NSMT-Te 1149 (MIN-16), bleached, on SEM stub; NSMT-Te 1150, dried specimen, MIN site; NSMT-Te 1151, large colony, dried, SES site; NSMT-Te 1152, 32 dried specimens, SES
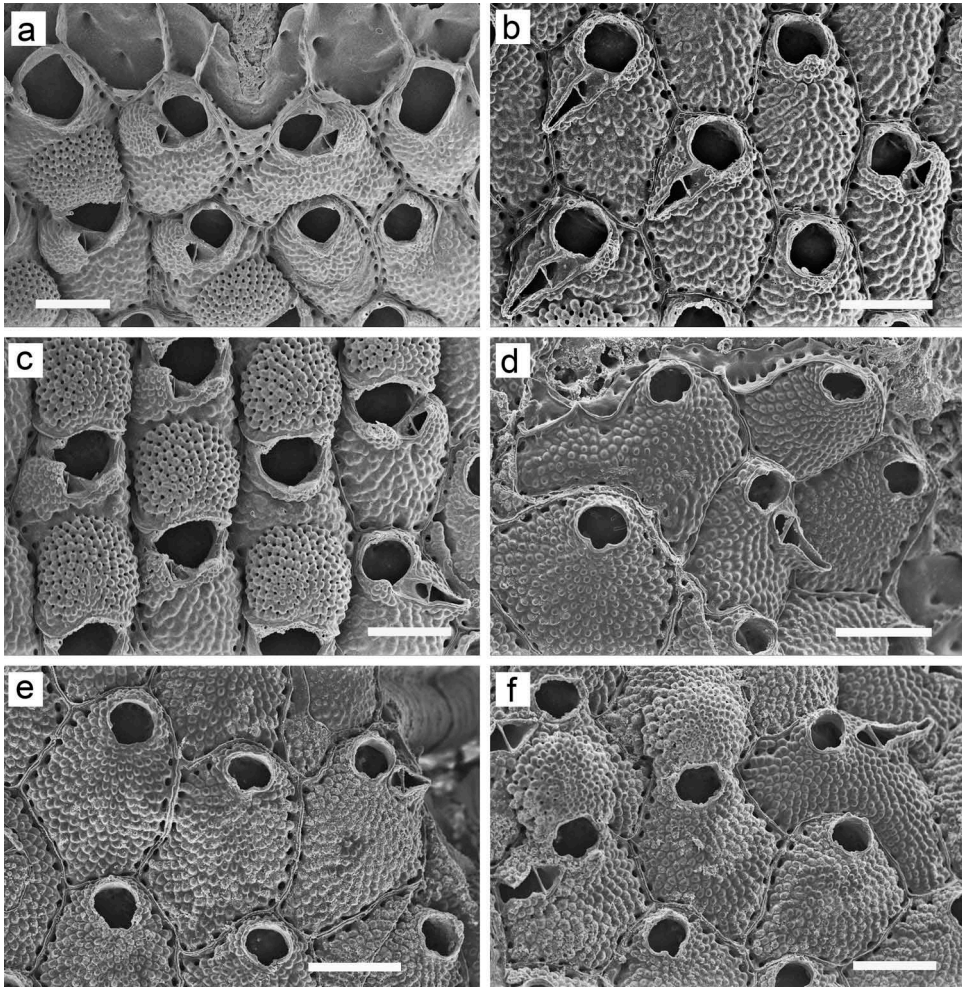

Figure 27. (a–c) *Robertsonidra argentea* (Hincks), NSMT-Te 1149: (a) autozooids near colony margin; (b) autozooids, showing two types of avicularia; (c) ovicelled and non-ovicelled autozooids. (d–f) *Robertsonidra porifera* (Maplestone), NSMT-Te 1155: (d) autozooids near colony margin, one showing more-common large avicularium; (e) autozooids, one showing uncommon smaller avicularium; (f) ovicelled and non-ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars = 300 μm.

site; NSMT-Te 1153, bleached, dried specimen, SES site; NHMUK 2016.5.13.90, five dried specimens, REEF site.

Measurements

AzL, 0.59–0.88 (0.693 ± 0.070); AzW, 0.31–0.48 (0.416 ± 0.059) (n = 15, 1). OrL, 0.15–0.19 (0.170 ± 0.009); OrW, 0.15–0.19 (0.174 ± 0.011) (n = 15, 1). OvL, 0.33–0.42 (0.377 ± 0.026); OvW, 0.32–0.44 (0.377 ± 0.027) (n = 13, 1). Largest colony observed at least 60 mm across.

Description

Colony forming a unilaminar, encrusting sheet, often covering extensive areas of substratum; dried specimens white to greyish in colour. Zooids (Figure 27(a, b)) distinct, delineated by opposing areolae and suture line. Frontal wall quite convex, without pseudopores, uniformly covered with rounded tubercles; seven to 11 areolae along each lateral margin, fewer along transverse margins. Primary orifice (Figure 27(a)) as wide as long, lacking condyles; proximal half broadly V-shaped, slightly asymmetrical. One or two minute distal oral spines. Peristome low, comprising raised flange on one side proximolateral to orifice and avicularian chamber on other. Single avicularium usually present proximolateral to orifice, occurring in two types: smaller type (Figure 27(a, c)) has rostrum raised from frontal plane, pointing distolaterally, with short-triangular mandible; larger type (Figure 27(b)) has rostrum lying parallel to frontal plane, long-triangular mandible pointing proximolaterally. Some zooids lack avicularium. Ovicell (Figure 27(c)) hyperstomial, more densely tuberculate than frontal wall, evenly and densely covered with tiny pseudopores. Ovicelled zooids have pair of tiny, widely spaced spines on orificial rim, at proximolateral corners of ooecium. Zooids interconnect by small uniporous septula. Ancestrula not observed.

Remarks

This species is distinguished by the broadly V-shaped proximal oral sinus, lack of condyles, presence of one or two tiny oral spines, peristomial flange and dimorphic avicularia.

Occurrence

Robertsonidra argentea was abundant at the SES and REEF sites (Table 1), with only a single colony found at the MIN site. This is a broadly distributed Indo-West Pacific species. Hincks (1881, p. 158) originally reported it from 'Africa, on coral'; Hayward and Ryland (1992) surmised that this probably meant East Africa. There are subsequent records from the Red Sea, Indonesia, the Philippines, the Great Barrier Reef, China and the Solomon Islands (Tilbrook 2006).

<p style="text-align:center">Robertsonidra porifera (Maplestone, 1909)
(Figure 27(d–f))</p>

Schizoporella porifera Maplestone, 1909, p. 416, pl. 27, fig. 16.
Robertsonidra porifera: Tilbrook 2006, p. 263, pl. 58A–C.
Robertsonidra novella: Ryland and Hayward 1992, p. 261, fig. 19(a).
Robertsonidra novella: Tilbrook et al. 2001, p. 92, fig. 18(d).

Material examined

NSMT-Te 1155 (MIN-26), bleached, on SEM stub; NSMT-Te 1156, dried specimen, SES site.

Measurements

AzL, 0.50–0.69 (0.602 ± 0.066); AzW, 0.37–0.50 (0.443 ± 0.037) (n = 15, 1). OrL, 0.10–0.13 (0.114 ± 0.009); OrW, 0.13–0.15 (0.138 ± 0.006) (n = 15, 1). OvL, 0.26–0.38 (0.308 ± 0.040); OvW, 0.31–0.40 (0.362 ± 0.029) (n = 9, 1). Largest colony observed 30 × 20 mm.

Description

Colony forming a unilaminar, encrusting sheet; white or faintly yellowish in colour. Zooids (Figure 27(d–f)) distinct, delineated by areolae and suture line. Frontal wall weakly convex, without pseudopores, completely and densely covered with small tubercles, with nine to 12 small areolae along each lateral margin. Orifice (Figure 27(d)) transversely elliptical, with a small, shallow, semicircular proximal sinus; surrounded by low, narrow, smooth rim; peristome lacking. Slight umbo often present proximal to orifice. Most autozooids show evidence of one or (more commonly) two small, ephemeral spines distal to orifice; ovicelled zooids often show a pair of more widely spaced spine bases lateral to orifice. Single frontal avicularium uncommonly present proximolateral to orifice. Avicularia either of two types: in one (Figure 27(e)), mandible acute, short-triangular, directed laterally; in other (Figure 27(d)), mandible long, tapering, rounded at tip, directed proximolaterally. No paired avicularia observed, and most zooids lack avicularium. Ovicell (Figure 27(f)) hyperstomial; ooecium globose, more densely tuberculate than frontal wall, covered with minute pseudopores. Ancestrula not observed.

Remarks

Apparently unaware of Maplestone's (1909) description (as *Schizoporella porifera*) of this species from the Gilbert Islands, Ryland and Hayward (1992) described the same species as *Robertsonidra novella* from the Great Barrier Reef. Tilbrook (2006) rectified this apparent error.

Occurrence

We found one colony at the SES site and two at the MIN site. *Robertsonidra porifera* is broadly distributed in shallow habitats in the subtropical to tropical western Pacific. It has been reported from the Gilbert Islands (Maplestone 1909), the Great Barrier Reef (Ryland and Hayward 1992), Vanuatu (Tilbrook et al. 2001) and the Solomon Islands (Tilbrook 2006); Tilbrook (2006) noted that it also occurs in the South China Sea and Victoria, southern Australia, but did not give specific records.

<div align="center">

Family **MICROPORELLIDAE** Hincks, 1879
Genus ***Fenestrulina*** Jullien, 1888
Fenestrulina parviporus sp. nov.
(Figure 28)

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Fenestrulina caseola: Ryland and Hayward 1992, p. 280, fig. 26(d). Tilbrook 2006, p. 217, figs 46(f) and 47(f). Dick et al. 2006, p. 2235, fig. 12(d).
?*Fenestrulina catasticos*: Scholz 1991, p. 315, pl. 16, fig. 6, pl. 17, fig. 7.
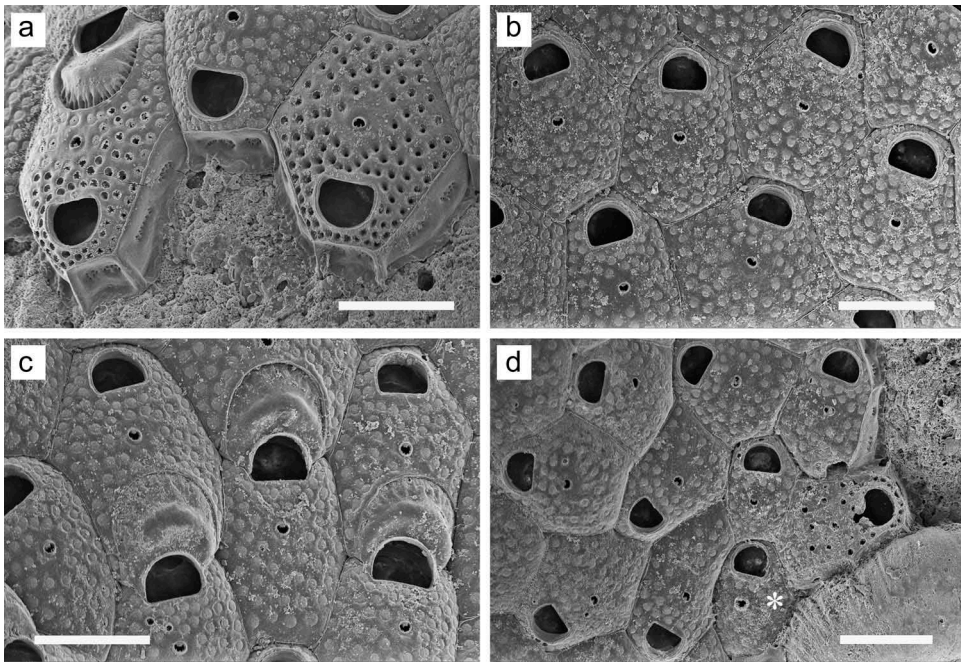Not *Fenestrulina caseola* Hayward, 1988, p. 325, pl. 10d.

Figure 28. *Fenestrulina parviporus* sp. nov., NSMT-Te 1158 (paratype): (a) autozooids at colony margin; (b) autozooids; (c) ovicelled and non-ovicelled autozooids; (d) ancestrula (asterisk) and periancestrular zooids. All panels are scanning electron microscopic images of a bleached specimen. Scale bars = 300 μm.

Etymology

The specific name is a noun in apposition combining the Latin *parvus* (small) and *porus* (pore), referring to the proportionally small ascopore compared to the congener *F. caseola*.

Material examined

Holotype: NSMT-Te 1157, dried specimen, SES site. Paratype: NSMT-Te 1158 (SES-6), bleached, on SEM stub.

Measurements

AzL, 0.48–0.65 (0.571 ± 0.053); AzW, 0.34–0.57 (0.431 ± 0.069) (n = 15, 1). OrL, 0.11–0.12 (0.113 ± 0.004); OrW, 0.14–0.16 (0.147 ± 0.008) (n = 15, 1). OvL, 0.24–0.34 (0.28 ± 0.031); OvW, 0.25–0.29 (0.27 ± 0.012) (n = 13, 1). Ascopore W 0.026–0.036 (0.030 ± 0.003); distance orifice to ascopore, 0.12–0.16 (0.137 ± 0.008); ratio between ascopore-to-orifice distance and ascopore width, 3.78–5.58 (4.582 ± 0.449) (n = 15, 1). Largest colony observed 11 × 4 mm.

Description

Colony forming a unilaminar, encrusting sheet; white in colour. Zooids (Figure 28(a, b)) distinct, irregularly hexagonal, outlined by a fine incision. Frontal wall moderately convex; completely covered with infundibular pseudopores except in area surrounding ascopore; each pseudopore has a cribriform covering. Orifice (Figure 28(a)) D-shaped,

broader than long, proximal margin straight. Ascopore small, transversely elliptical, surrounded by raised rim; inner margin denticulate or smooth, usually with projection from distal side, resulting in lunate opening. Ascopore distance from orifice equal to, or slightly greater than, orifice length. Ovicell (Figure 28(c)) subimmersed. Ooecium with conspicuous, thick, crescent- or chevron-shaped transverse ridge on top, and surrounded by sharp, raised border; periphery inside border depressed, with minute pseudopores separated by ridges. Spines lacking. Zooids interconnect (Figure 28(a)) by two large, circular to oval multiporous septula in transverse wall and two extensive, elongate-oval multiporous septula in each distolateral wall. Ancestrula (Figure 28(d), asterisk) smaller than but otherwise similar to subsequent zooids, budding one daughter zooid distally and another distolaterally, with spiral budding ensuing from the opposite distolateral position.

Remarks

Fenestrulina parviporus sp. nov. is very similar to *Fenestrulina caseola* Hayward, 1988, originally described from Mauritius. Our material differs from the latter as follows. The ascopore is proportionally smaller, and is open rather than covered with anastomosing rays or a cribriform plate; there is an imperforate zone surrounding the ascopore; and the orifice is D-shaped, whereas in *F. caseola* it is broader relative to length, with more sharply rounded lateral margins recurving to the proximal margin. Various Pacific specimens identified as *C. caseola* in previous studies show characters like those in the Okinawa material: the ascopore is small and lunate, surrounded by an imperforate zone, and the orifice is D-shaped. The average ratio between the ascopore-to-orifice distance and ascopore width is similar in Pacific specimens: 4.44 (n = 2), Great Barrier Reef (Ryland and Hayward 1992); 4.06 (n = 2), Hawaii Island (Dick et al. 2006); 4.33 (n = 5), Solomon Islands (Tilbrook 2006); and 4.58 (n = 15), Okinawa (this study). The ratio is 1.58 (n = 2) in *F. caseola* from Mauritius (Hayward 1988), reflecting the greater width of the ascopore.

Another similar species is *F. catasticos* Gordon, 1984, described from the Kermadec Islands near New Zealand. That species has a small, lunate ascopore lying at the bottom of a concavity surrounded by a distinct, raised rim; the ooecium is less sunken and has a coarse central umbo from which thick ribs radiate; the pseudopores distal to the orifice are surrounded by a line of calcification, delineating a distinct 'panel' of pores; and there are three large basal pore-chambers in the distal half of each zooid (Gordon 1984), whereas *F. parviporus* has a total of six multiporous septula in the distal half. Material from the Philippines that Scholz (1991) identified at *F. catasticos* seems more similar to *F. parviporus*, although the ratio between ascopore-to-orifice distance and ascopore width is less (3.25) in the one mature zooid Scholz illustrated. Scholz did not show or describe the ovicell, which would help identify the Philippine species.

Taxonomically informative characters in the better-studied confamilial genus *Microporella* include orifice shape and the size, shape, position and covering (or lack thereof) of the ascopore, and these characters are undoubtedly also informative in *Fenestrulina*. On this basis, we consider material previously described as *F. caseola* to comprise two species: *F. caseola*, presently known only from Mauritius but perhaps more broadly distributed in the Indian Ocean, and *F. parviporus*, broadly distributed in the western and central Pacific.

Occurrence

We found four colonies, all at the SES site. This species is broadly distributed in the western to central, tropical to subtropical Pacific; there are previous records (as *F. caseola*) from the Great Barrier Reef, the Solomon Islands and Hawaii.

Family **LACERNIDAE** Jullien, 1888
Genus ***Arthropoma*** Levinsen, 1909
Arthropoma harmelini sp. nov.
(Figure 29)

Etymology

The specific name is a Latinised noun in the genitive case, after Dr. Jean-Georges Harmelin, in acknowledgement of his substantial contributions to bryozoology and generous assistance in this study.

Material examined

Holotype: NSMT-Te 1159 (SES-28), bleached, on SEM stub. Paratypes: NSMT-Te 1160, five dried specimens, SES site; NSMT-Te 1161, two dried specimens, SES site; NSMT-Te 1162, three dried specimens, REEF site; NHMUK 2016.5.13.60-71, 12 dried specimens, SES site.

For comparison, putative *A. cecilii* from the vicinity of Marseille, France, collected by J. G. Harmelin: NSMT-Te 1163 (MA-1), Rior Island, 70 m, on dendritic sand, 11 June 1971, bleached, on SEM stub; NSMT-Te 1164 (MA-2), Frioul Island, on dendritic sand, 65 m, 21 April 1971, bleached, on SEM stub.

Measurements

Okinawa: AzL, 0.55–0.70 (0.629 ± 0.045); AzW, 0.37–0.54 (0.452 ± 0.048) (n = 15, 1). OrL (exclusive of sinus), 0.10–0.13 (0.109 ± 0.008); OrW, 0.14–0.18 (0.155 ± 0.010) (n = 15, 1). OvL, 0.26–0.37 (0.322 ± 0.031); OvW, 0.32–0.38 (0.346 ± 0.015) (n = 15, 1). Largest colony observed roughly circular, 25 mm across.

For comparison, measurements from a Mediterranean specimen (vicinity of Marseille, France) presumed to be *Arthropoma cecilii* (Figure 30): AzL, 0.66–0.79 (0.715 ± 0.040); AzW, 0.42–0.55 (0.493 ± 0.043) (n = 15, 1). OrL (exclusive of sinus), 0.13–0.16 (0.151 ± 0.008); OrW, 0.17–0.21 (0.191 ± 0.009) (n = 15, 1). OvL, 0.40–0.47 (0.429 ± 0.025); OvW, 0.37–0.41 (0.389 ± 0.016) (n = 8, 1).

Description

Colony forming a unilaminar, encrusting sheet; light yellowish tan. Zooids (Figure 29 (a)) irregularly hexagonal; distinct, delineated by a suture line. Frontal wall mildly convex, completely covered with small pseudopores, although some zooids lack pseudopores (Figure 29(c, d)) in midline proximal to orifice; one to three rows of pseudopores lateral and distal to orifice (Figure 29(a)). Primary orifice (Figure 29(b)) D-shaped, with shallow sinus in midline; sinus usually constricted at opening, circular or transversely oval in outline; row of inconspicuous denticles on proximal orificial margin to each side of sinus. Primary orifice weakly dimorphic in size; generally slightly larger (wider and/or longer) in ovicelled zooids or zooids capable of forming ovicell than in non-ovicelled zooids. Distal margin of orifice raised as a low rim, sharp
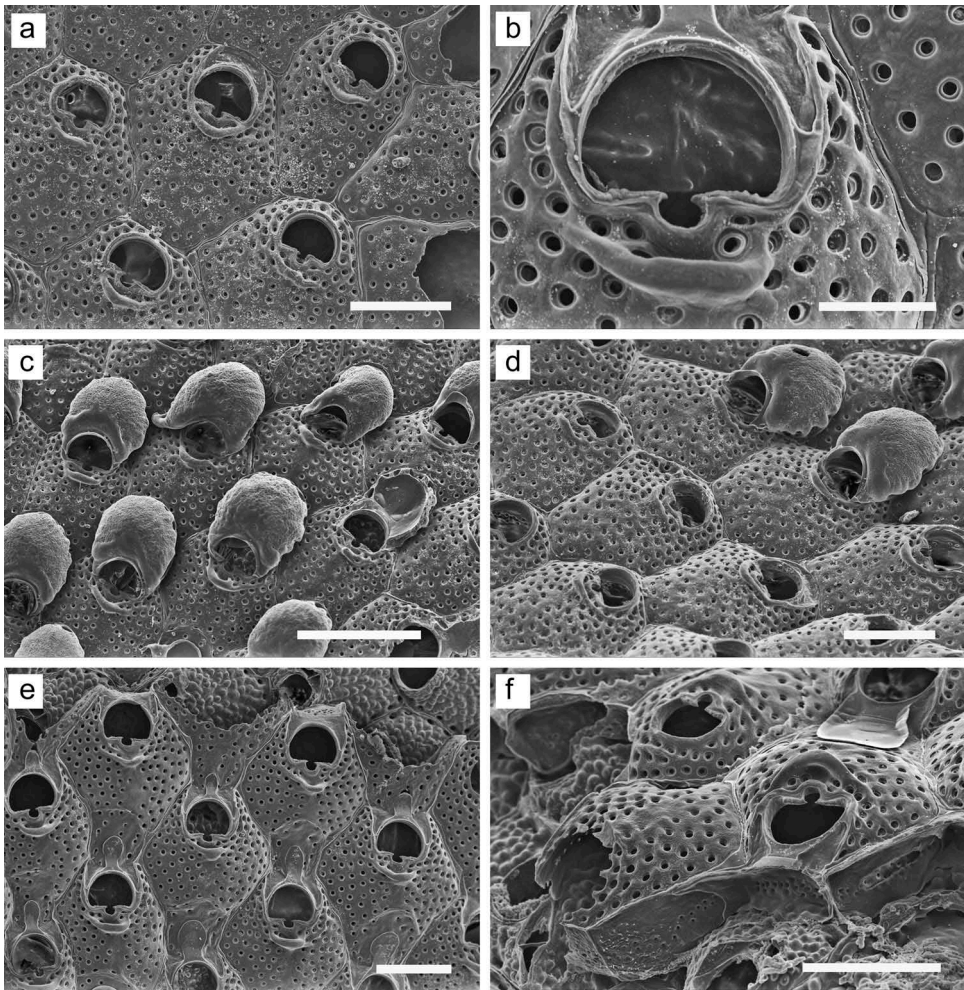
Figure 29. *Arthropoma harmelini* sp. nov., NSMT-Te 1159 (holotype): (a) autozooids, showing crescentic suboral umbo, which in top-centre zooid is continuous with peristomial rim; (b) orifice; (c) ovicelled autozooids, with one ovicell showing a lateral extension; note there is no row of pseudopores between orifice and floor of developing ooecium; (d) ovicelled and non-ovicelled autozooids; (e) autozooids with developing ooecia; note lack of pseudopores between orifice and floor of ooecium; (f) colony margin, showing interzooidal connections. All panels are scanning electron microscopic images of bleached specimen. Scale bars: a, c, e, f = 300 µm; b = 100 µm; d = 500 µm.

or thickened. Just proximal to orifice, most zooids have a low, crescentic or chevron-shaped umbo, usually with some pseudopores in area between umbo and orifice; in some cases, ends of umbo extend distolaterally to meet circum-oral rim, forming an entire peristomial rim (top central zooid in Figure 29(a)). Ovicell (Figure 29(c, d)) hyperstomial. Ooecium without pseudopores, except at periphery; minutely pitted on the surface; with a smooth, broad crescentic or chevron-shaped zone along proximal margin; ooecial periphery wavy at base, with regularly spaced pseudopores. Floor of developing ovicell (Figure 29(e)) meets distal orificial margin, with no intervening pseudopores. Embryo orange in dried specimens. Spines and avicularia lacking.

Zooids interconnect (Figure 29(f)) by long zone of up to 20 pores in each of the transverse and distolateral walls. Ancestrula not observed.

Remarks

Our specimens are identifiable with *Arthropoma cecilii* (Audouin 1826) sensu lato. This nominal species has a putative global distribution from cool-temperate to tropical waters between about 50°N and 40°S, with records from depths ranging from around 25 m (Harmer 1957) to as great as 1235 m (Canu and Bassler 1929). There are records from the Mediterranean, Britain, Brazil, the Galapagos, Costa Rica (Pacific), central California, British Columbia, Japan, the Philippines, the China Sea, the Great Barrier Reef, New Zealand, the Indian Ocean and South Africa (Canu and Bassler 1929; Osburn 1952; Harmer 1957; Gordon 1984). Harmer (1957, p. 1003) noted, '*A. cecilii* is so easily recognized that most of the records are probably correct'. Unfortunately, this perception has resulted in many authors simply reporting this species without description or illustration; there are several such records from Pleistocene and Recent Japan (Okada 1923; Sakakura 1935, 1938; Okada and Mawatari 1936, 1938; Mawatari 1952, 1963).

One explanation for this apparently global distribution is that *A. cecilii* has been widely spread on ship hulls over the past several centuries. An alternative explanation is that nominal *A. cecilii* actually represents a broadly distributed complex of morphologically similar species. In fact, slight morphological differences exist among geographically separate populations, indicative of population isolation and genetic divergence; these differences have to do with the sculpturing on the ooecium, extent of a frontal area proximal to the orifice that lacks pseudopores, depth and shape of the orificial sinus, presence or absence of a median suboral umbo, presence or absence of one or more rows of pseudopores between the orifice and ovicell floor (evident in zooids with incompletely formed ovicells), and zooid size.

Arthropoma cecilii (Audouin 1826) was originally described from Egypt, but the type locality is unknown. Two of Savigny's plates (Audouin 1826) show what appear to be *Arthropoma* specimens. Audouin (1826) designated one of these (Savigny Plate 8) as *Flustra ? cecilii* and the other (Savigny Plate 10) as *Flustra latreillei*. The latter probably came from the Red Sea (J.-G. Harmelin personal communication), as Savigny's Plate 10 shows the bryozoan colony encrusting a branch of an *Acropora* coral. Although d'Hondt (2006) considered both plates to represent *Arthropoma cecilii*, it is possible they represent different species, especially if one specimen came from the Red Sea and the other from the Mediterranean, because there was no connection between the Mediterranean and Red Sea prior to the opening of the Suez Canal in 1869.

British *A. cecilii* described in Hayward and Ryland (1999) has larger zooids (average ZL about 0.75 mm; average ZW about 0.50 mm) than *A. harmelini* (comparable values, 0.63 mm and 0.45 mm, respectively) and further differs from the latter in having a deeper, narrower, U-shaped orificial sinus and a small, mammillate umbo in the midline some distance proximal to the orifice. In Hayward and Ryland (1999, fig. 94(a)), zooids appear to have a narrow zone, extending along about two-thirds of the midline proximal to the orifice, that lacks pseudopores. There is no indication whether a zone of pseudopores separates the floor of the ovicell from the distal orificial margin.

In Mediterranean specimens from near Marseille (Figure 30), which may or may not be conspecific with British *A. cecilii* populations, zooids are about the same size as indicated for British material but larger than in our specimens (see Measurements above). There is a distinct area, proximal to the orifice, that lacks pseudopores (Figure 30(a, d)), extending about two-thirds the distance to the proximal end of the zooid; the proximal orificial sinus is U-shaped (Figure 30(b)) and longer than broad, with a constricted opening; some zooids show a very slight umbo (Figure 30(c)) just proximal to the orificial sinus; and one or two rows of frontal pseudopores are evident between the distal margin of the orifice and the floor of the ovicell (Figure 30(a, c, d)). Some ooecia in the Marseille population show a distorted lateral expansion (Figure 30(a)), a trait also occasionally observed in the Okinawan specimens (Figure 29(c)).

There appear to be several *Arthropoma* species in Japan. Ortmann (1890) described (as *Schizoporella cecilii*) a new variety (now *A. cecilii* var. *mediolaevis*) from 40 fathoms (73 m) depth in Sagami Bay, on the basis of its having on the frontal wall a more extensive median area lacking pseudopores than in the typical form; presumably Ortmann had seen Atlantic or Mediterranean *A. cecilii* and this character struck him as different. Hirose's (2010, pl. 189A, B) SEM images of a Sagami Bay specimen identified as *A. cecilii* show an extensive area lacking pseudopores, and small, paired tubercles lateral to the orifice; zooids are large (average ZL × ZW,
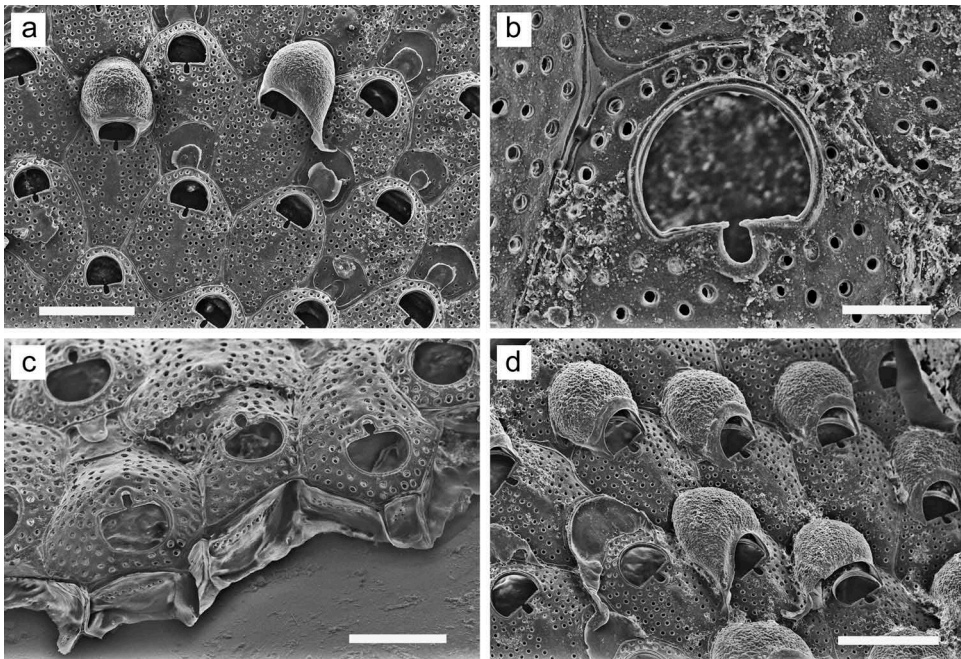

Figure 30. Presumed *Arthropoma cecilii* (Audouin) from the Mediterranean (vicinity of Marseille, France) collected by J.G. Harmelin; NSMT-Te 1163 (a, c), NSMT-Te 1164 (b, d): (a) zooids with forming or fully formed ooecia, one of which has a lateral extension; note row of pseudopores between orifice and floor of ooecium; (b) orifice; (c) colony margin, showing interzooidal connections; (d) ovicelled autozooids; note two rows of pseudopores between orifice and floor of incompletely formed ooecium, and lateral extensions on ovicells at lower right. All panels are scanning electron microscopic images of bleached material. Scale bars: a, d = 500 μm; b = 100 μm; c = 300 μm.

0.73 × 0.56 mm) and appear to lack a frontal umbo. Zooids in two other panels in the same plate (Hirose 2010, pl. 189C, D) have a shorter, rounder suboral sinus, raising the question whether they are from the same colony as the first two panels. Hirose (2010, pl. 190) also illustrates from Sagami Bay another two colonies identified as 'Arthropoma n. sp.' that have much smaller zooids (average ZL × ZW, 0.43 × 0.40 mm). It is not clear that these two colonies are conspecific with one another. The specimen in his pl. 190A, B has relatively few, large, densely packed pseudopores; a distinctly U-shaped sinus; and one row of large pseudopores between the orifice and the floor of the ovicell. The other (his pl. 190 C) has a shallower sinus and a large frontal area that lacks pseudopores. Grischenko and Mawatari (2006, fig. 1(g)); illustrate a subtidal Sagami Bay specimen identified as *A. cecilii* in which zooids have a narrow non-pseudoporous zone occupying only half the frontal length proximal to the orificial sinus, which is oval or teardrop-shaped. This species, with an extensive zone of pores evident between the distal orificial margin and the ovicell floor, is clearly different from that in Hirose's (2010, pl. 189A–B) specimen in which the floor of the ovicell arises directly from the orificial margin, with no intervening pseudopores.

In summary, SEM images in Hirose (2010) and Grischenko and Mawatari (2006) indicate at least three species of *Arthropoma* in Sagami Bay; it is unclear which, if any, represents Ortmann's (1890) *A. cecilii* var. *mediolaevis*. *Arthropoma harmelini* differs from two of these species (Grischenko and Mawatari 2006, fig. 1(g); Hirose 2010, pl. 190A, B) in lacking pseudopores between the orificial margin and floor of the developing ovicell; from the third (Hirose 2010, pl. 189A, B) in sinus shape; and from all three in having a crescentic suboral umbo that sometimes contributes to a continuous peristomial rim. Our specimens might be conspecific with *Arthropoma cecilii* reported by Kataoka (1961) from the Pleistocene of Kikai Island, roughly 300 km north-east of our study site. While Kataoka did not provide a description, a low-magnification photomicrograph appears to show a short, broad sinus and a median frontal zone lacking pseudopores; zooid measurements are similar to those in our material (by chance, the mean zooid length is identical).

Occurrence

Arthropoma harmelini was abundant at the SES site and common at the REEF site (Table 1); these are the only known localities.

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Family **ESCHARINIDAE** Tilbrook, 2006
Genus ***Bryopesanser*** Tilbrook, 2006
Bryopesanser latesco Tilbrook, 2006
(Figure 31)

</div>

Bryopesanser latesco Tilbrook, 2006, p. 255, pls. 55D, 56A–C. Tilbrook 2012, p. 46, figs 11–16.
Bryopesanser serratus Dick, Tilbrook, and Mawatari, 2006, p. 2233, fig. 5(d–f).
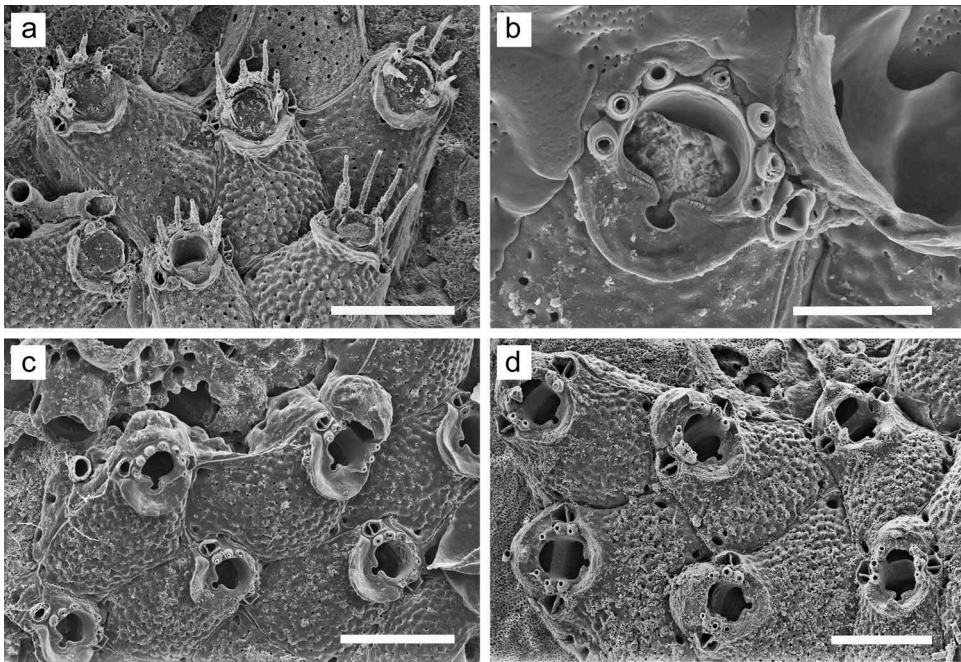For additional synonyms, see Tilbrook (2012).

Figure 31. *Bryopesanser latesco* Tilbrook: (a) NSMT-Te 1167, autozooids; (b) NSMT-Te 1100, orifice; (c) NSMT-Te 1054, ovicelled and non-ovicelled autozooids; (d) NSMT-Te 1103, ovicelled and non-ovicelled autozooids; note sharp projection on proximal peristomial rim in lower-right zooid, and size difference in avicularia between lower right and lower left zooids. Panels are scanning electron microscopic images of dried, unbleached specimen (a) or bleached specimens (b–d). Scale bars: a, c, d = 300 μm; b = 100 μm.

Material examined

NSMT-Te 1054 (MIN-Thal1), bleached, on SEM stub (with *Thalamoporella stapifera*); NSMT-Te 1100 (MIN-13), bleached, on SEM stub (with *Crepidacantha poissonii* and *Parasmittina serrula*); NSMT-Te 1103 (MIN-12), bleached, on SEM stub (with *Parasmittina alanbanneri*); NSMT-Te 1165, dried specimen, MIN site (with *Cribralaria curvirostris*); NSMT-Te 1167 (MIN-19), bleached, on SEM stub (with *Crepidacantha longiseta*).

Measurements

AzL, 0.52–0.64 (0.579 ± 0.041); AzW, 0.30–0.46 (0.376 ± 0.063) (n = 10, 1). OrL, 0.08–0.09 (0.083 ± 0.005); OrW (excluding sinus), 0.09–0.11 (0.105 ± 0.007) (n = 7, 1). OvL, 0.11–0.21 (0.141 ± 0.030); OvW, 0.16–0.24 (0.204 ± 0.024) (n = 15, 1).

Description

Colony forming a unilaminar, encrusting sheet that is typically small; one of those illustrated (Figure 31(d)) measures 3 × 1.5 mm, with 32 zooids, 19 of which have ovicells. Zooids (Figure 31(a)) distinct, delineated by a groove. Frontal wall convex, finely tuberculate, covered with minute pseudopores. Orifice (exclusive of sinus) D-shaped (Figure 31(b)); proximal sinus deep, usually constricted at opening and flaring proximally. Condyles sloping proximomedially; each condyle is serrate on frontal face; proximal margin of orifice to each side of sinus is similarly serrate.

Marginal zooids have seven coarse spines (Figure 31(a)) laterally and distally around orifice; three pairs are evident lateral to orifice in ovicelled zooids. Orifice in non-ovicelled zooids is not deeply immersed. Proximal to orifice is a raised, flared peristomial collar, with the frontodistal surface smooth; outer edge of collar usually sharp, sometimes with median projection. Avicularia small; single or paired lateral to orifice; rostrum truncate, directed distomedially; cross-bar complete. Mandible not observed. Ovicell (Figure 31(c, d)) terminal. Ooecium broader than long, without pseudopores; surface weakly rugose or tuberculate, often with low transverse ridge that sometimes bears a small median umbo. Ancestrula not observed.

Remarks

Bryopesanser is morphologically a rather uniform genus, with 16 Recent species known at present from tropical and subtropical areas. Colonies are typically small; those in *B. latesco* can reach up to roughly 1 cm across, while most other species have smaller maximum size. The most conspicuous character for identification of *B. latesco* is the broadly flared peristomial rim that delineates an extensive smooth area proximal to the orifice (Figure 31(b, c)). Another character is having a 'drop-shaped' oral sinus that is broader than long (Tilbrook 2012); while this is the case in some zooids in our specimens (Figure 31(d)), other zooids have the sinus clearly longer than broad (Figure 31(b)).

Occurrence

We found two colonies at SES and 10 at MIN. This is a widely distributed Indo-Pacific species, documented from the Red Sea, the Gulf of Aden, the Great Barrier Reef, Southeast Asia, the Philippines, Taiwan, Melanesia and Hawaii; there is also a disjunct record from the Caribbean coast of Panama (Tilbrook 2012).

Superfamily **MAMILLOPOROIDEA** Canu and Bassler, 1927
Family **CREPIDACANTHIDAE** Levinsen, 1909
Genus ***Crepidacantha*** Levinsen, 1909
Crepidacantha longiseta Canu and Bassler, 1928 sensu lato
(Figure 32(a, b))

?*Crepidacantha longiseta* Canu and Bassler, 1928, p. 135, pl. 21, figs 3 and 4.
?*Crepidacantha longiseta*: Brown 1954, p. 251, fig. 1(f).
Crepidacantha longiseta: Tilbrook et al. 2001, p. 92, fig. 16(b). Dick et al. 2006, p. 2239, fig. 13(g, h).

Material examined

NSMT-Te 1167 (MIN-19), bleached, on SEM stub (with *Bryopesanser latesco*); NSMT-Te 1168 (MIN-35), bleached, on SEM stub (with *Hippopodina adunca*); NSMT-Te 1169 (SES-37), bleached, on SEM stub; NSMT-Te 1170, MIN site, three dried fragments; NSMT-Te 1171, dried colony, SES site.
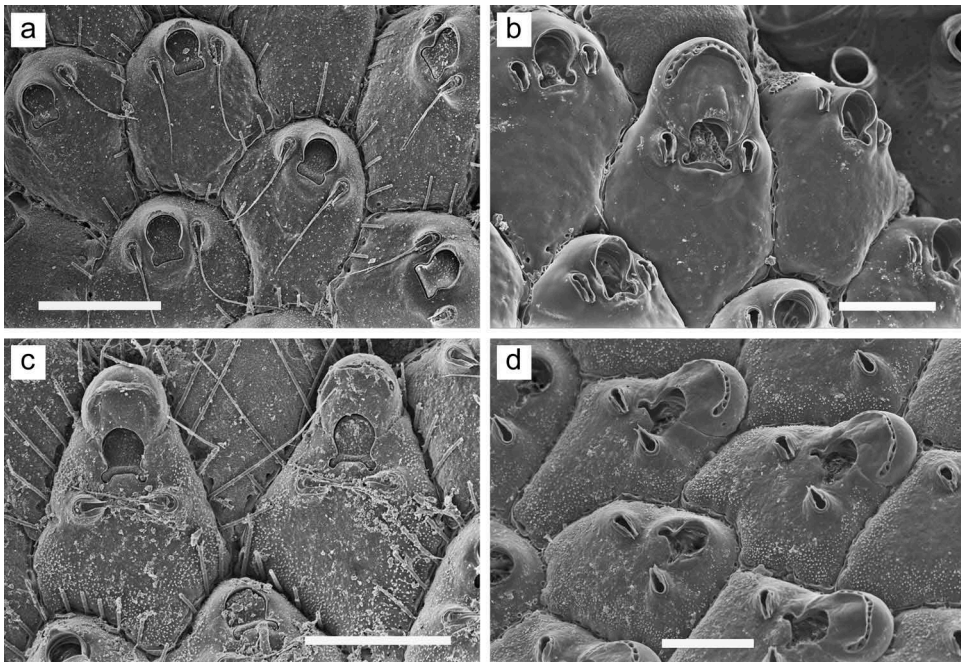
Figure 32. (a, b) *Crepidacantha longiseta* Canu and Bassler: (a) NSMT-Te 1167, autozooids; (b) NSMT-Te 1169, ovicelled and non-ovicelled autozooids. (c, d) *Crepidacantha poissonii* (Audouin), NSMT-Te 1100: (c) ovicelled autozooids; (d) ovicelled and non-ovicelled autozooids. Panels are scanning electron microscopic images of dried, unbleached (a, c) or bleached (b, d) specimens. Scale bars: a, c = 300 μm; b, d = 200 μm.

Measurements

AzL, 0.39–0.54 (0.466 ± 0.049); AzW, 0.32–0.52 (0.374 ± 0.054) (n = 15, 1). OrL, 0.10–0.12 (0.104 ± 0.006); OrW, 0.07–0.09 (0.084 ± 0.006) (n = 15, 1). OvL, 0.199–0.227 (average = 0.210); OvW, 0.209–0.213 (average = 0.211) (n = 3, 2). Largest colony observed 4.7 × 3.6 mm.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 32(a)) distinct, delineated by a sharp incision. Frontal wall convex, tumid, without pseudopores, smooth or minutely granulate in texture. Circular or slit-shaped marginal areolae present but rarely evident with light microscopy and often scarcely with SEM. Orifice subterminal, raised, hoof-shaped, with subcircular anter separated from equally broad poster by conspicuous, low, rounded-triangular condyles; proximal margin straight or slightly convex. Operculum with granular surface. Orifice not immersed; proximal to orifice is a small, low, mammillate or transversely crescentic projection. Zooids have 8–11 (mode = 10) long, thin, straight spines around distal and lateral margins, each spine tilted against frontal wall of adjacent zooid. Frontal avicularia paired, lateral to orifice, directed proximally; rostrum shorter than autozooidal orifice; mandibular part of rostrum elongate, tapering, with end forming trough; mandible (Figure 32(a)) setiform, very long, sometimes reaching proximal border of zooid. Ovicell (Figure 32(b)) terminal, about as

broad as long; closed by operculum. Ooecium with smooth ectooecium; flattened on top, with low median ridge in proximal half evident in cleaned specimens; crescentic foramen of non-calcified ectooecium around frontodistal periphery of ooecium exposing up to 20 pseudopores in a single or double row. Ancestrula, poorly visible in one specimen, appears to be smaller than but of same form as later zooids, with spiral budding pattern, although these details are ambiguous.

Remarks

This species has the proximal margin of the orifice straight or nearly so; around 10 marginal spines; and small, paired frontal avicularia lateral to the orifice that have a long, setose mandible directed proximally. Although the original description mentions a concave poster, the proximal orificial margin appears straight in at least some zooids illustrated by Canu and Bassler (1928, pl. 21, fig. 4). The original description also mentions incomplete calcification of the ectooecium in a frontal area on the ovicell, and a small mucro proximal to the orifice. In his revision of *Crepidacantha*, Brown (1954) illustrated the frontal fenestra on the ooecium in a specimen from Brazil as being transversely oval and positioned atop the ooecium, clearly a different condition than in Pacific material, where the frontal area has been described as horseshoe shaped (Tilbrook et al. 2001) or comprising a crescent near the distal end (Dick et al. 2006). Brown (1954) made no mention of a proximal mucro, and this character seems variable among Pacific populations; it is present in specimens from Hawaii and Okinawa, but appears to be lacking in those from Vanuatu (Tilbrook et al. 2001).

Canu and Bassler (1928) originally described this species from coral and hydroid substrata at depths of 67–201 fathoms (123–368 m) in the western Atlantic (Strait of Florida, off Cuba). Subsequent reports have indicated a much broader range, including Brazil (Brown 1954), Mauritius (Hayward 1988), Vanuatu (Tilbrook et al. 2001) and Hawaii (Dick et al. 2006). It seems unlikely that all these far-flung populations have maintained reproductive continuity, especially between the Pacific and Atlantic, and also unlikely that this species has been spread anthropogenically, as it is typically uncommon in natural habitats, rather than occurring in abundance in harbours. We thus expect that the nominal species will eventually prove to encompass more than one species, with western Pacific material requiring a different name from that originally described from the western Atlantic. For the time being, we use the name *C. longiseta* sensu lato for the specimens from Okinawa.

Occurrence

We found six colonies, at the SES and MIN sites. Although *Crepidacantha longiseta* appears to have a circumglobal distribution in the subtropical and tropical zones (Tilbrook et al. 2001), this is probably not the case, as discussed above.

Crepidacantha poissonii (Audouin, 1826)
(Figure 32(c, d))

Flustra poissonii Audouin, 1826, p. 240, pl. 10, figs 5[1] and 5[2].
Crepidacantha poissonii: Harmer 1957, p. 981 (part). Brown 1954, p. 260, fig. 1(a, b). Liu et al. 2001, p. 674, pl. 71, figs 1–3. Tilbrook 2006, p. 274, pl. 61A–D.

Crepidacantha carsioseta: Tilbrook et al. 2001, p. 92, fig. 16(a); Dick et al. 2006, p. 2239, fig. 13(f).

Not *Crepidacantha carsioseta*: Ryland and Hayward 1992, p. 277, fig. 25(d); [=*C. craticula* Tilbrook, 2006].

Material examined

NSMT-Te 1100 (MIN-13), bleached, on SEM stub (with *Parasmittina serrula*).

Measurements

AzL, 0.43–0.54 (0.483 ± 0.030); AzW, 0.32–0.43 (0.373 ± 0.036) (n = 15, 1). OrL, 0.09–0.12 (0.108 ± 0.007); OrW, 0.08–0.10 (0.090 ± 0.005) (n = 15, 1). OvL, 0.15–0.22 (0.171 ± 0.019); OvW, 0.16–0.20 (0.178 ± 0.011) (n = 13, 1). One colony observed, 8 × 6 mm.

Description

Colony forming a unilaminar, encrusting sheet. Zooids (Figure 32(c)) distinct, delineated by a sharp incision. Frontal wall convex, tumid but flattened on top, without pseudo-pores, minutely granulated; tiny, circular or slit-shaped marginal areolae present but rarely evident with light microscopy and scarcely with SEM. Orifice subterminal, with subcircular anter separated from equally broad poster by conspicuous, low, broadly rounded condyles; poster comprises two distinct lobes separated by a broad, distally flat labium. Operculum with granular surface. Orifice not immersed; proximal mucro lacking. Zooids have 11–15 (mode, 13) long, thin, straight spines around lateral and distal margins, each spine tilted against frontal wall of adjacent zooid. Frontal avicularia paired, proximolateral to orifice, both at same level along transverse line, or slightly offset; directed medially or angled slightly proximally or distally; rostrum on raised chamber, shorter than orifice length; narrow, long-triangular, tapering, with end forming trough; crossbar lacking; mandible (Figure 32(c)) long, setiform but not extending past opposite lateral margin of zooid. Ovicell (Figure 32(d)) terminal, nearly circular in outline, closed by operculum. Ooecium with smooth ectooecium; flattened on top, with broad, indistinct median ridge evident in cleaned specimens; narrow crescentic foramen of non-calcified ectooecium around frontodistal periphery exposing around 10 pseudopores in a single row. Ancestrula not observed.

Remarks

This species is characterised by the markedly trifoliate orifice; the paired avicularia situated proximolateral to the orifice and directed medially; lack of a suboral umbo; and the nearly circular ooecium with a long, narrow crescent of pseudopores towards the distal end; the ovicell is flattened proximal to the fenestra and bears a median ridge. Tilbrook (2006) indicated the presence of a median pointed projection on the distal rim of the orifice, but this is not present in our specimen. Material from Hawaii reported as *C. carsioseta* (Dick et al. 2006) is actually *C. poissonii*; the Hawaiian material has the distinctly trifoliate orifice characteristic of *C. poissonii*, lacks the suboral umbo characteristic of *C. carsioseta*, and shows a projection on the distal orificial rim in the form of a small, blunt transverse mucro. *Crepidacantha carsioseta* appears to have fewer marginal spines than *C. poissonii*. Winston and Heimberg (1986) reported 10 spines for the former, and although Tilbrook (2006) did not mention spine number in designating a neotype

for *C. poissonii* from the Red Sea, our specimen from Okinawa has 11–15 spines, and Hawaiian material has around 12 spines.

Occurrence

We found a single colony at the MIN site. This is an Indo-West Pacific species known from the Red Sea, South China Sea, Vanuatu, the Solomon Islands (Tilbrook 2006) and Hawaii (Dick et al. 2006). While Hirose (2010) reported it from Sagami Bay, Japan, that material might instead represent *Crepidacantha craticula* Tilbrook, 2006, as the convex proximal border (labium) of the orifice seems to be lower and more rounded than in *C. poissonii*.

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Superfamily **CELLEPOROIDEA** Johnston, 1838
Family **TORQUATELLIDAE** Tilbrook, 2006
Genus ***Torquatella*** Tilbrook, Hayward, and Gordon, 2001
Torquatella duolamellata (Scholz, 1991)
(Figure 33(a, b))

</div>

Osthimosia duolamellata Scholz, 1991, p. 302, pl. 11, figs 1–6.
Torquatella duolamellata: Tilbrook et al. 2001, p. 79, fig. 11(a, b). Tilbrook 2006, p. 286, pl. 43A, B.

Material examined

NSMT-Te 1172 (SES-30), bleached, on SEM stub; NSMT-Te 1173, dried specimen, SES site; NHMUK 2016.5.13.72, dried specimen, SES site (with *Calyptotheca reniformis*).

Measurements

AzL, 0.28–0.39 (0.324 ± 0.035); AzW, 0.22–0.32 (0.267 ± 0.025) (n = 15, 1). OrL, 0.096–0.099 (0.098); OrW, 0.95–0.100 (0.098) (n = 2, 1). OvL, 0.11–0.15 (0.140 ± 0.016); OvW, 0.21–0.25 (0.238 ± 0.020) (n = 5, 1). Ancestrula L, 0.271; ancestrula W, 0.166 (n = 1). Ancestrula OrL, 0.066; ancestrula OrW, 0.083 (n = 1). Largest of three colonies 4 × 3 mm.

Description

Colony (Figure 33(a)) forming a unilaminar, encrusting sheet. Zooidal boundaries indistinct (Figure 33(b)); zooids delineated by large marginal openings in layer of secondary calcification. Cylindrical, somewhat flared peristome occupies about half of frontal zooidal area; secondary orifice transversely oval. Primary orifice (Figure 33(b)) as broad as long; anter semicircular, separated from deep, broadly U-shaped poster by pair of small, rounded condyles. Except for ancestrula, zooids lack spines. Small avicularium proximal to orifice, situated deep in peristome, difficult to observe except in some marginal zooids; raised rostral end forms blunt knob; directed frontolaterally. Ovicell (Figure 33(b)) hyperstomial. Ooecium with a transversely oval or elliptical foramen on top, exposing entooecium in cleaned specimens; peristome usually extends around proximofrontal surface. Ancestrula (left centre in Figure 33(a)) produces a triplet of daughter zooids distally and distolaterally.
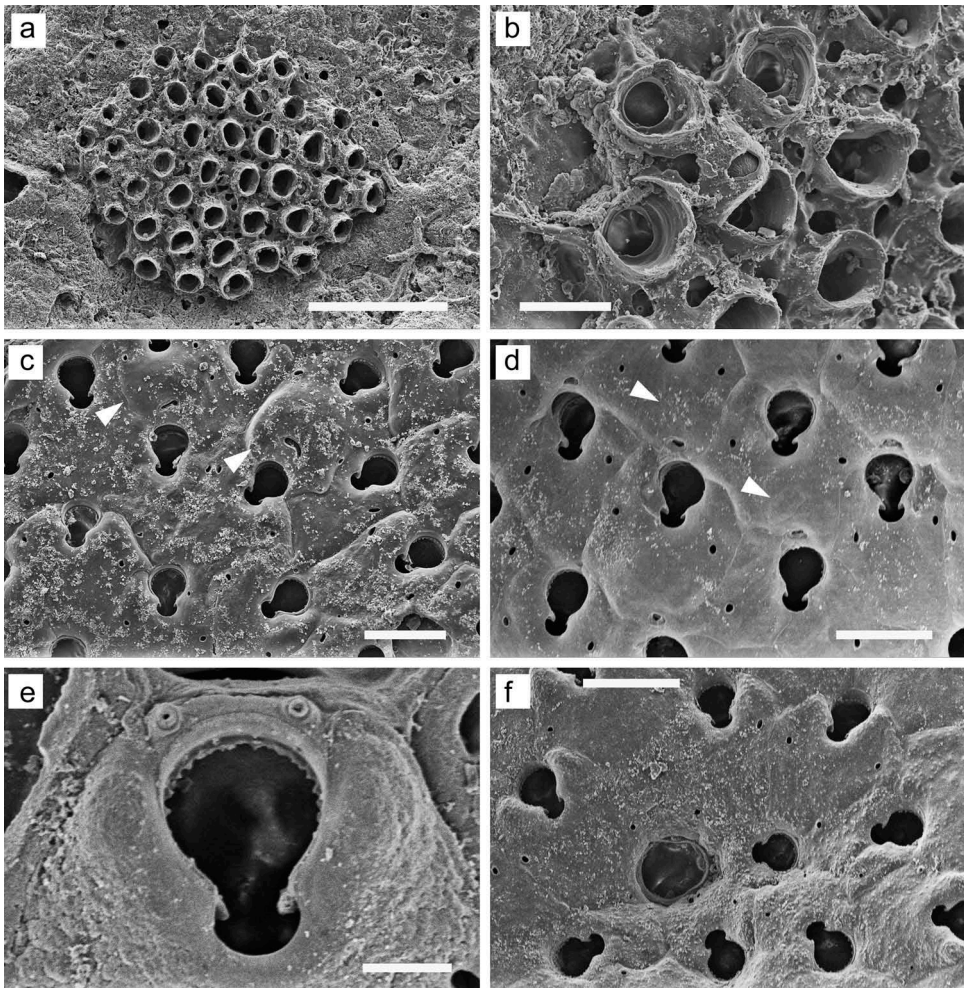
Figure 33. (a, b) *Torquatella duolamellata* (Scholz), NSMT-Te 1172: (a) colony; (b) ovicelled and non-ovicelled autozooids. (c–f) *Metacleidochasma planulata* (Canu and Bassler): (c) NSMT-Te 1175, ovicelled and non-ovicelled autozooids, with arrowheads indicating the positions of two ovicells; (d) NSMT-Te 1176, ovicelled and non-ovicelled autozooids, with arrowheads indicating the positions of two ovicells; (e, f) NSMT-Te 1174, (e) orifice, (f) ancestrula and periancestrular zooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b–d, f = 200 μm; e = 50 μm.

Remarks

Scholz (1991) and Tilbrook et al. (2001) have described and discussed this species in detail. The morphology of the ancestrula is not clear in the specimen we illustrate, but the other accounts report it to be schizoporelloid, with a D-shaped orifice flanked by three pairs of spines. Although frontal budding can occur, our small colony comprised only a single layer. Our specimen is heavily secondarily calcified; previous descriptions of less heavily calcified specimens indicate the primary frontal wall to have small marginal areolae and a few scattered frontal pseudopores.

Occurrence

We found three small colonies at the SES site. This is a subtropical to tropical, western Pacific species. Scholz (1991) found it to be fairly common on the east-central coast of Cebu Island, Philippines, and it has been reported from Vanuatu (Tilbrook et al. 2001) and the Solomon Islands (Tilbrook 2006).

Family **PHIDOLOPORIDAE** Gabb and Horn, 1862
Genus *Metacleidochasma* Soule, Soule, and Chaney, 1991
Metacleidochasma planulata (Canu and Bassler, 1929)
(Figure 33(c–f))

Hippoporina planulata Canu and Bassler, 1929, p. 321, pl. 37, fig. 6.
Metacleidochasma planulata: Tilbrook et al. 2001, p. 97, fig. 21(c–e).
Metacleidochasma ovale Soule, Soule, and Chaney 1991, p. 480, pl. 1, fig. 7, pl. 4, figs 1 and 2.

Material examined

NSMT-Te 1174 (MIN-11), bleached, on SEM stub; NSMT-Te 1175 (SES-24), bleached, on SEM stub; NSMT-Te 1176 (SES-9), bleached, on SEM stub; NSMT-Te 1177, SES site, dried colony.

Measurements

AzL, 0.31–0.40 (0.353 ± 0.023); AzW, 0.25–0.38 (0.295 ± 0.036) (n = 15, 1). OrL, 0.11–0.13 (0.122 ± 0.007); OrW, 0.08–0.09 (0.087 ± 0.004) (n = 15, 1). Largest colony observed 5 mm in diameter.

Description

Colony forming a unilaminar, encrusting sheet; cream coloured. Zooids small, boundaries often indistinct (Figure 33(c, d)). Frontal wall slightly convex, smooth, with only two pseudopores (Figure 33(d)), one inset from margin on each side at approximately widest part of zooid. Orifice (Figure 33(e)) conspicuously keyhole shaped; broader, circular anter separated from narrower, proximally rounded poster by blunt, proximomedially directed condyles; distal margin of orifice beaded below smooth surface rim. Frontal wall lateral to orifice on each side is raised as a thick, low umbo. Marginal zooids bear two or three small, ephemeral spines. Ovicell endozooidal, sometimes evident as a swelling (arrowheads, Figure 33(c, d)) in frontal wall of distal zooid; totally covered by smooth secondary calcification, except for small, curved membranous window near proximal edge. Ancestrula (Figure 33(f)) tatiform, with spines, though these are often obscured by surrounding zooids.

Remarks

Tilbrook et al. (2001) considered *M. ovale*, originally described from Hawaii (Soule et al. 1991), to be a junior synonym of *M. planulata* (Canu and Bassler 1929), originally described from the Philippines. We have accepted this synonymy but note that it needs confirmation, as the characters of the ovicell are not clear in the original description and illustration of Philippine *M. planulata*. Marginal zooids in our specimens have only two or three oral spines, compared to four in Hawaiian material (Soule et al. 1991)

and usually four (range, three to five) in specimens from Vanuatu (Tilbrook et al. 2001). Frontal avicularia occur rarely in Hawaiian populations, but were not reported at Vanuatu or observed in our study.

Occurrence

We found six colonies, at the SES and MIN sites. This species is broadly distributed in the Indo-West Pacific, with previous records from the Philippines (Canu and Bassler 1929); Hawaii (Maui and Kauai islands), Bora Bora, Tonga, Thailand and the Maldives (Soule et al. 1991); and Vanuatu (Tilbrook et al. 2001).

<div align="center">

Genus *Rhynchozoon* Hincks, 1895
Rhynchozoon ferocula Hayward, 1988
(Figure 34)

</div>

Rhynchozoon ferocula Hayward, 1988, p. 332, pl. 13a–c.
Rhynchozoon ferocula: Tilbrook et al. 2001, p. 100, fig. 22(c–e). Tilbrook 2006, p. 297, fig. 65(e, f). Dick et al. 2006, p. 2242, fig. 14(d–f).
Rhynchozoon globosum: Scholz 1991, p. 320, pl. 17, figs 4 and 6.

Material examined

NSMT-Te 1178 (REEF-6), two colonies, bleached, on SEM stub; NSMT-Te 1179 (SES-50), bleached, on SEM stub; NSMT-Te 1180 (SES-17), ancestrula, bleached, on SEM stub; NSMT-Te 1181, three dried specimens, SES site.

Measurements

AzL, 0.27–0.42 (0.355 ± 0.038); AzW, 0.24–0.31 (0.273 ± 0.019) (n = 15, 1). OrL, 0.09–0.11 (0.101 ± 0.007); OrW, 0.08–0.10 (0.089 ± 0.004) (n = 10, 1). OvL, 0.13–0.18 (0.150 ± 0.017); OvW, 0.13–0.20 (0.166 ± 0.020) (n = 11, 1). Largest colony observed 4 × 2 mm.

Description

Colony (Figure 34(a)) small, forming a unilaminar, encrusting sheet; white in colour. Zooids distinct at colony margin (Figure 34(b)), delineated by a fine incision, but boundaries increasingly indistinct towards centre of colony. Zooids typically with one to three (up to six) conspicuous circular areolae (Figure 34(c)) along each lateral margin. Frontal wall convex, smooth, without pseudopores; with two to five coarse, blunt or sharp, umbonate processes around raised, thickened rim proximal to orifice (Figure 34(b)). With age, frontal wall becomes thickened by secondary calcification (Figure 34(e)) and primary orifice becomes immersed in sunken peristome. Primary orifice (Figure 34(d)) slightly longer (including sinus) than broad; anter nearly circular, or broader than long; sinus deep, U-shaped, flanked but not constricted by pair of raised, triangular processes, which are in turn flanked by blunt condyles. Periphery of anter is beaded with 14 to 19 rounded denticles. Marginal zooids have two to four (usually four) low, blunt oral spines (Figure 34(b)); these remain but are obscured within the peristome in older zooids (Figure 34(c–e)). Suboral avicularia lacking. Frontal avicularia uncommon; some zooids have one or two located close to zooidal
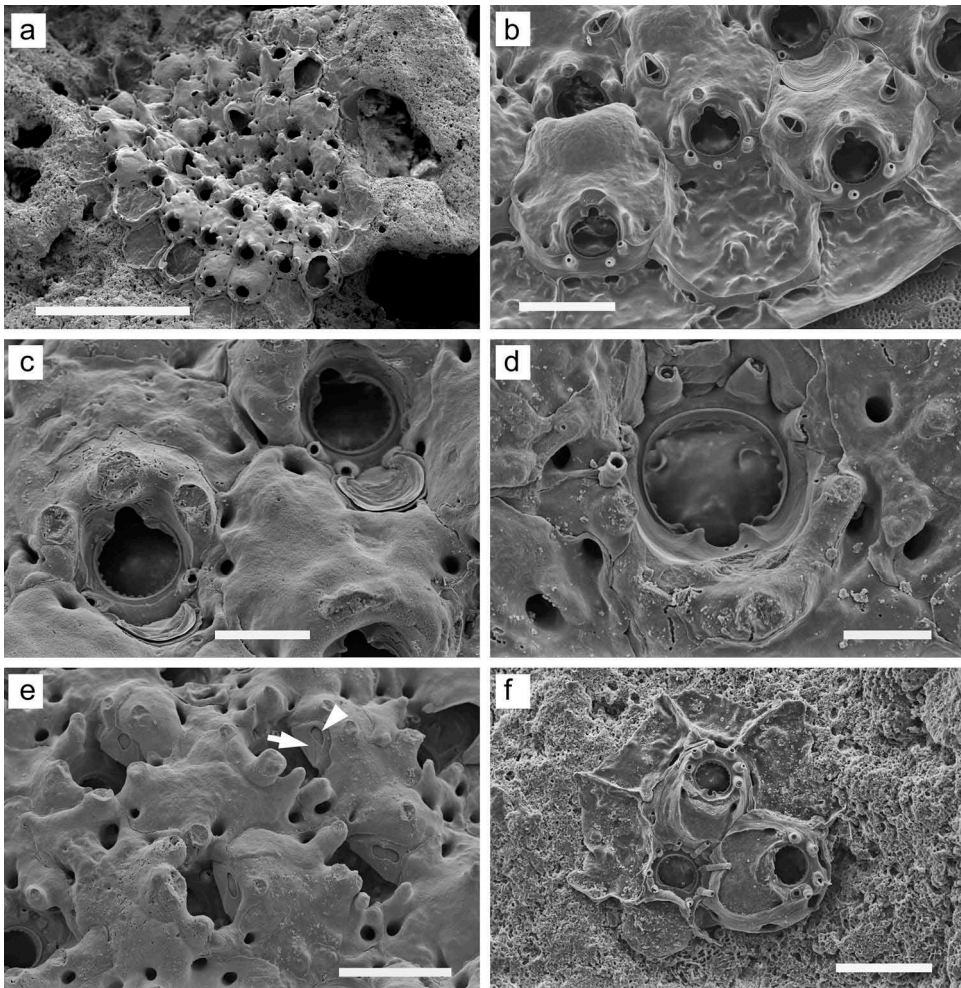
Figure 34. *Rhynchozoon ferocula* Hayward: (a) NSMT-Te 1178, view of smaller colony on SEM stub; (b) NSMT-Te 1179, marginal autozooids; (c–e) NSMT-Te 1178 (larger colony on SEM stub), (c) orifices in (c) mature autozooids, (d) orifice and oral spines, (e) ovicelled autozooids (arrowhead, window in calcified ectooecium; arrow, labellum); (f) NSMT-Te 1180, ancestrula and two daughter zooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b, e, f = 200 µm; c = 100 µm; d = 50 µm.

margin (Figure 34(b)); mandible short-triangular, pointing laterally, proximolaterally or proximally; crossbar complete. Ovicell (Figure 34(e)) initially subimmersed, eventually becoming endozooidal. Ooecium broader than long, covered by layer of secondary calcification originating from adjacent zooids and often bearing one or two coarse umbonate processes on top. Proximal face of ooecium with small, subcircular to transversely elliptical zone of membranous (non-calcified) ectooecium that, in cleaned specimens, becomes a window (Figure 34(e), arrowhead) exposing the entooecium; labellum (band of calcified ectooecium along proximal margin of ovicell (Figure 34(e), arrow) wide, complete. Colony precocious, with fully developed ovicells starting in second daughter-zooid generation from ancestrula. Ancestrula (Figure 34

(f)) oval in outline; initially giving rise to triplet of zooids distally and distolaterally. Ancestrular orifice with straight proximal margin lacking a sinus; surrounded by eight spines.

Remarks

Rhynchozoon ferocula was originally described from Mauritius (Hayward 1988). Our specimens differ from that population in the following characters. The orificial sinus in our material is deeper, broader and more U-shaped, with the opening not constricted by medially curved projections. We observed no zooids to have a lateral-suboral avicularium, whereas this is variably present among zooids in Mauritian *R. ferocula*. The proximal peristomial rim usually bears several prominent projections, whereas Mauritian zooids generally have few. Finally, frontal avicularia are rare in our specimens and have a short-triangular mandible, whereas Mauritian material bears numerous avicularia with a long-triangular mandible, clustered around the zooidal secondary orifices.

There are several Pacific records for *Rhynchozoon ferocula*. Among these, Hawaiian specimens (Dick et al. 2006) are virtually indistinguishable from the Okinawa specimens we describe here. Zooids in *R. ferocula* reported from Vanuatu (Tilbrook et al. 2001) show several characters more like those in Mauritian material, including a shallow orificial sinus flanked by medially curved processes, and avicularia having a long-triangular mandible commonly present; however, suboral avicularia appear to be entirely lacking. Specimens of *R. ferocula* from the Solomon Islands (Tilbrook 2006) likewise share many characters with Mauritian material: zooids often have more than one frontal avicularium each; the mandible is long-triangular; the orificial sinus is drop-shaped, flanked by medially curved projections; and a suboral avicularium is variably present.

Based on the differences mentioned above, the Hawaiian and Okinawan populations might be considered a distinct species from the Mauritian and other Pacific specimens. However, examination of SEM images of nominal *R. ferocula* from Sagafa Bay, Red Sea (Andrew Ostrovsky, unpublished data); argued against this, as one Red Sea specimen shows intracolony variation in the shape of the primary orifice and sinus, with some zooids having a shallow, drop-shaped sinus bordered by medially curved processes, and others a deeper, U-shaped sinus not constricted at the opening, as is characteristic at Hawaii and Okinawa. In addition, the ancestrula is indistinguishable between the Okinawa and Solomon populations, although mature zooids in the latter population are more similar to those in the Mauritian than in the Okinawan population.

Occurrence

We found seven colonies, at the SES and REEF sites. This species is broadly distributed in nearshore habitats in the subtropical to tropical Indo-West Pacific, with previous records from Mauritius, the Red Sea, Vanuatu, the Solomons, the Philippines and Hawaii.

Rhynchozoon maculosum sp. nov.
(Figures 35 and 36(a–d))

Etymology

The specific name is an adjective (Latin *maculosus*: mottled, full of spots), referring to the many areolae speckling the colony, giving it a 'peppered' appearance.

Material examined

Holotype: NSMT-Te 1182, dried specimen, SES site; NSMT-Te 1183 (SES-14), part of same colony as NSMT-Te 1182, bleached, on SEM stub. Paratypes: NSMT-Te 1184 (SES-15),
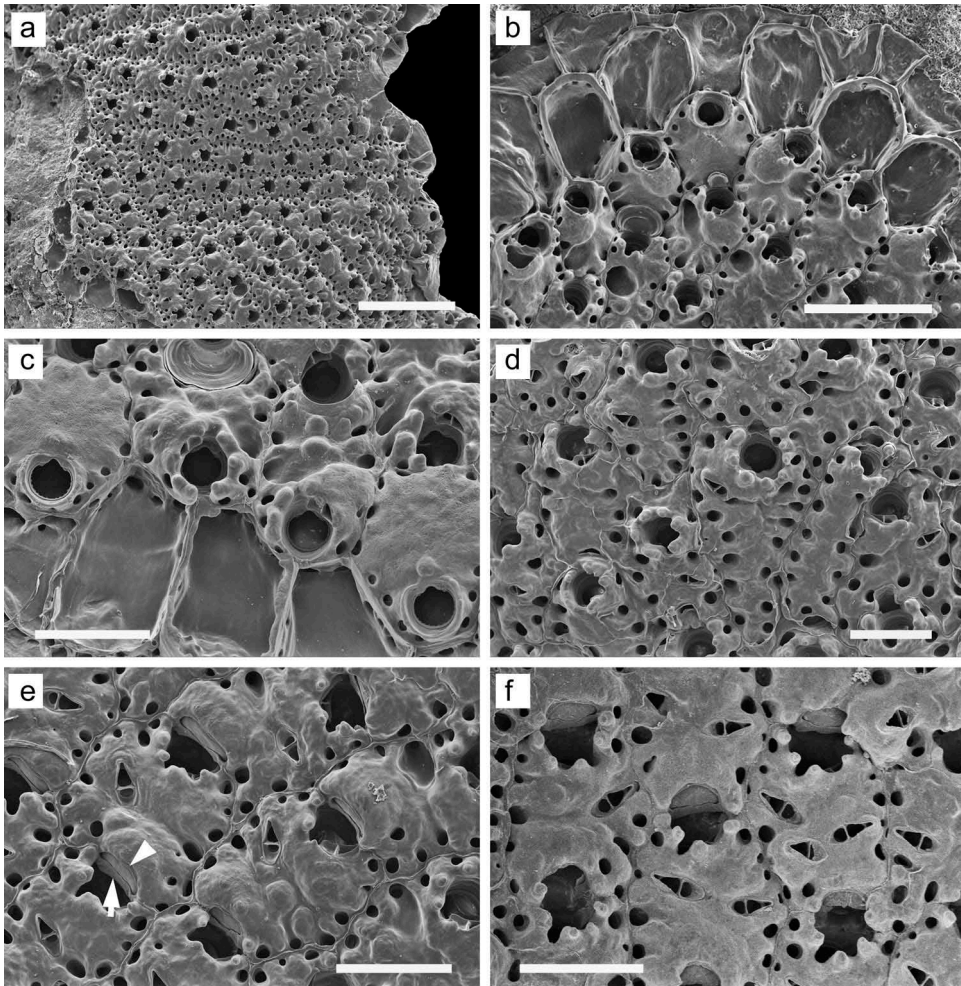

Figure 35. *Rhynchozoon maculosum* sp. nov.: (a) NSMT-Te 1186 (paratype), colony view, showing characteristic 'peppered' appearance due to areolae; (b) NSMT-Te 1184 (paratype), autozooids at colony margin, showing aspect of suboral avicularian chamber; (c) NSMT-Te 1190, autozooids at colony margin, showing orifice shape and position of suboral avicularium; (d) NSMT-Te 1183 (holotype), autozooids; (e) NSMT-Te 1190, ovicelled autozooids (arrowhead, window in calcified ectooecium; arrow, labellum); (f) NHMUK 2016.5.13.73 (paratype), ovicelled autozooids, with abundant frontal avicularia. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b = 500 µm; c–f = 300 µm.
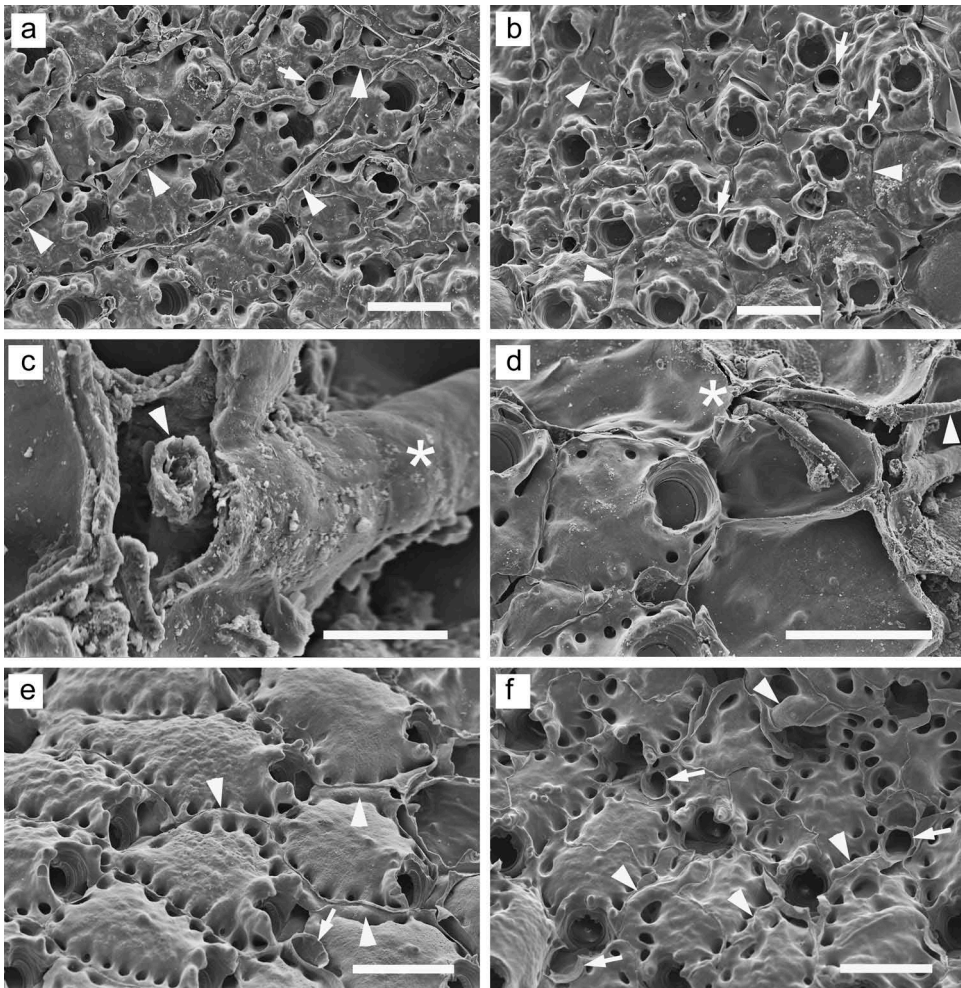
Figure 36. Interzooidal epibiont in two *Rhynchozoon* species. (a–d) *Rhynchozoon maculosum*, NSMT-Te 1187 (paratype): (a, b) calcified tubes (arrowheads) secreted by bryozoan around epibiont, with occasional openings (arrows); (c) enlargement of calcified tube (asterisk), with broken area showing tubular structure of epibiont (arrowhead) in cross section; (d) epibiont emerging from between vertical walls of two newly forming zooids (asterisk); annular structure of emergent epibiont (arrowhead) suggests it may be a hydroid; note that epibiont appears to have suppressed avicularium formation. (e, f) *Rhynchozoon scimitar*, NSMT-Te 1206 (paratype): calcified tubes (arrowheads) secreted by bryozoan around epibiont, with epibiont opening indicated by arrow; note that epibiont appears to have suppressed avicularium formation. Panels are scanning electron microscopic images of bleached (a, b, e, f) or dried but non-bleached (c, d) material. Scale bars: a, b, d–f = 300 μm; c = 50 μm.

bleached, on SEM stub; NSMT-Te 1185 (SES-18), bleached, on SEM stub; NSMT-Te 1186 (SES-19), bleached, on SEM stub; NSMT-Te 1187 (SES-51), bleached, on SEM stub; NSMT-Te 1188 (MIN-20-1), bleached, on SEM stub; NSMT-Te 1189, paratype lot, four dried specimens, SES site; NHMUK 2016.5.13.73 (MIN-20), bleached, on SEM stub; NHMUK 2016.5.13.74-77, four dried specimens, SES site. Other material: NSMT-Te 1190 (SES-47), bleached, on SEM stub with *Rhynchozoon scimitar*; NSMT-Te 1191, 32 dried specimens,

SES site; NSMT-Te 1192, 14 dried specimens, REEF site; NSMT-Te 1193, 12 dried specimens, MIN site; NSMT-Te 1194, dried specimen with externally calcified epibiont, SES site.

Measurements

AzL, 0.46–0.63 (0.543 ± 0.048); AzW, 0.27–0.36 (0.327 ± 0.026) (n = 18, 4). OrL, 0.092–0.128 (0.106 ± 0.009); OrW, 0.097–0.120 (0.106 ± 0.006) (n = 18, 4). OvL, 0.14–0.25 (0.183 ± 0.028); OvW, 0.17–0.26 (0.224 ± 0.021) (n = 15, 2). Largest colony observed 40 × 35 mm.

Description

Colony (Figure 35(a)) forming a unilaminar, encrusting sheet; white or off-white (greyish or faintly tinged with orange or yellow); embryos light orange in dried specimens. Zooids at margin (Figure 35(b, c)) irregularly hexagonal; distinct, delineated by a shallow groove and a suture line flanked by areolae; even with age, zooidal outlines remain more or less discernable. Frontal wall without pseudopores and with four to six circular or oval areolae along each lateral margin. In marginal zooids, frontal wall convex, smooth, somewhat uneven. With increasing secondary calcification, frontal wall rapidly thickens, remaining smooth in surface texture but becoming more rugose, with scattered low, rounded tubercles or nodules; areolar openings increase in size. Primary orifice soon becomes immersed as zooids age, with an asymmetrical pseudosinus forming in rim of secondary orifice, to one side or other of midline. Primary orifice (including sinus) is as long as broad, or occasionally slightly broader than long; anter exclusive of sinus is broader than long. Sinus is moderately deep, rounded-V-shaped, extending between small, rounded condyles. Margin of anter is beaded with 14 or 15 (mode, 15; n = 5, 3) small denticles. Oral spines lacking. With age, rim of secondary orifice usually retains pseudosinus and bears from four to eight small, blunt processes (Figure 35(d–f)) that are irregular, conical or cylindrical in shape. Suboral and frontal avicularia occur. Suboral avicularium develops from hemispherical chamber (Figure 35(b)) occupying one-fifth to one-third the frontal area proximal to the orifice. Avicularian rostrum is offset to one side or other of midline (Figure 35(c)), tilted laterally towards orifice, and directed distolaterally; end hooked; crossbar complete; mandible long-triangular. Base of rostrum is extended as a rounded process (a so-called 'uncinate process') flanking the orificial pseudosinus and jutting into the peristome. With increased secondary calcification, suboral avicularium lies at edge of secondary orifice, or entirely within peristome. Frontal avicularia (Figure 35(e, f)) roughly same size as suboral avicularia; one to four per zooid, or lacking. Rostrum slightly raised from frontal plane distally, not hooked; crossbar complete; mandible acute, about twice as long as wide, directed laterally, distolaterally, proximolaterally or occasionally medially. Rostrum of frontal avicularia is occasionally diamond-shaped, but usually rounded at proximal end. Ovicell initially subimmersed (Figure 35(e)) but later becoming endozooidal (Figure 35(f)). Ooecium broader than long; proximal face with transversely long-elliptical, semicircular or oval zone of membranous (non-calcified) ectooecium that, in cleaned specimens, becomes a window (Figure 35(e), arrowhead) exposing the entooecium; labellum (Figure 35(e), arrow) narrow, usually complete. Ancestrula not observed.

Remarks

This species is similar to *Rhynchozoon rostratum* (Busk 1856), originally described from the eastern Pacific at Mazatlán, Mexico. The two species share the following characters: the suboral and frontal avicularia are similar in size and shape; the suboral avicularia are often immersed within the peristome, have an 'uncinate process' at the base of the rostrum, and have a hooked tip; boundaries between mature zooids are indicated by marginal pores; the secondary orifice bears a deep pseudosinus and is surrounded by conspicuous peristomial processes; and oral spines are lacking (Hastings 1930; Osburn 1952). *Rhynchozoon rostratum* differs from *R. maculosum* in having the exposed entooecial area on the proximal face of the ooecium large, semicircular and opaque white, with the labellum typically lacking or incomplete. In *R. maculosum*, the entooecial zone is markedly transversely long-elliptical or oval, and not conspicuously white, and the labellum is usually complete. *Rhynchozoon rostratum* further differs from *R. maculosum* in having a shallower orificial sinus, a shorter mandible on the suboral avicularium, and fewer processes around the peristome. Finally, Hastings (1930) reported colonies of *R. rostratum* in Panama to have a faintly greenish ectocyst, whereas our dried specimens are faintly yellowish, although this may not be a useful diagnostic character (Soule and Soule 1964). It is noteworthy that an opaque-white zone of exposed entooecium on the ovicell is not in itself diagnostic of *R. rostratum*, as it also occurs in *R. scimitar* sp. nov. described below.

Hastings (1930) appears to have been the only author subsequent to the original description to examine Busk's type specimens of *R. rostratum* from Mazatlán, and her description of conspecific material from Panama perhaps warrants more weight than other descriptions, among which there are discrepancies. According to Osburn (1952), *R. rostratum* has a low-boreal to tropical distribution in the eastern Pacific, occurring from Point Conception, California, southward to the Galapagos. He considered *R. rostratum* also to occur in the western Atlantic under the junior synonym *R. verruculatum* (Smitt 1873), although Hastings (1930), Winston (1984), and Winston and Heimberg (1986) have established that these are different species. Some of the records of *R. rostratum* in the eastern Pacific are questionable. Soule and Soule (1964) mentioned marginal zooids with two to four oral spines in material they identified as *R. rostratum* from Scammon's Lagoon, Baja California, Mexico. Soule et al. (1995) reported *R. rostratum* from the Santa Barbara Channel, southern California, USA, to have two oral spines on marginal zooids and a circular or transversely oval entooecial area on the ovicell, with a complete labellum, characters that conflict with Hastings's (1930) redescription of *R. rostratum* from Panamanian material. Specimens from Kodiak, Alaska, reported as *R. rostratum* (Dick and Ross 1988) are instead *R. tumulosum* (Hincks 1882b) (Dick et al. 2005; Dick and Mawatari 2005). We suspect that some of the inconsistencies (e.g. spines present or absent; variation in colony colour and the depth of the oral sinus) among descriptions of nominal *R. rostratum* in the eastern Pacific actually reflect interspecific differences, and that SEM examination of a broad range of material will resolve nominal *R. rostratum* into a number of morphologically distinct species.

Indo-West Pacific records of *R. rostratum* have now been referred to other species. Tilbrook et al. (2001) considered *R. rostratum* reported from Java (Winston and Heimberg 1986) and the Philippines (Scholz 1991) actually to be *R. splendens* Hayward, 1988, and

Gordon (2009) erected a new species, *R. zealandicum*, for New Zealand material previously reported (Gordon 1970) as *R. rostratum*.

Two of the six colonies of *R. maculosum* we examined by SEM had a filamentous, ramifying epibiont in the interzooidal grooves (Figure 36(a–d)). The bryozoan zooids deposited a thin layer of gymnocystal calcification beneath the filaments of the epibiont growing on the colony surface, encased them completely in calcified tubes, or caused the tubes to become completely immersed between zooids by depositing secondary calcification over them (arrowheads, Figure 36(a, b)); in the last case, the tubes emerged to the surface by way of irregularly occurring circular openings (arrows, Figure 36(a, b)). Examination of an unbleached specimen showed that the soft filaments of the epibiont are hollow (arrowhead, Figure 36(c)), and one emergent filament produced an annulated section reminiscent of a hydroid stalk (arrowhead, Figure 36(d)), leading us to speculate that the ramifying epibiotic filaments were hydroid stolons. The epibiont affected the bryozoan colonies in at least two ways: the extensive surficial gymnocystal calcification produced to 'wall off' the epibiont must have incurred an energetic cost, and the epibiont appears to have inhibited the production of avicularia. In one affected colony, zooids produced no avicularia at all; in the other, while some zooids produced avicularia, both the suboral and frontal types were reduced in frequency.

Occurrence

This species was common or abundant at all three sites (Table 1), the only known localities.

Rhynchozoon lunifrons sp. nov.
(Figures 37 and 38)

Etymology

The specific name is a noun in apposition combining the Latin *luna* (moon) and *frons* (forehead, brow), referring to the large zone of exposed entooecium on the ovicell.

Material examined

Holotype: NSMT-Te 1195, colony on worn coral fragment, SES site. Paratypes: NSMT-Te 1196 (SES-44), bleached, on SEM stub; NSMT-Te 1197 (SES-8), bleached, on SEM stub; NSMT-Te 1198 (SES-46), precocious form, bleached, on SEM stub; NSMT-Te 1199, dried colony, SES site; NHMUK 2016.5.13.78-80, three dried fragments, SES site.

Measurements

Common form. AzL, 0.40–0.75 (0.540 ± 0.077); AzW, 0.28–0.44 (0.339 ± 0.044) (n = 30, 2). OrL, 0.112–0.138 (0.125 ± 0.008); OrW, 0.116–0.144 (0.128 ± 0.008) (n = 26, 2). OvL, 0.160–0.213 (0.185 ± 0.018); OvW, 0.197–0.249 (0.216 ± 0.015) (n = 11, 2). Largest colony observed 15 × 13 mm.

Precocious form. AzL, 0.36–0.51 (0.432 ± 0.044); AzW, 0.25–0.37 (0.307 ± 0.034) (n = 15, 1). OrL, 0.101–0.122 (0.110 ± 0.007); OrW, 0.102–0.131 (0.117 ± 0.009) (n = 10, 1). OvL,
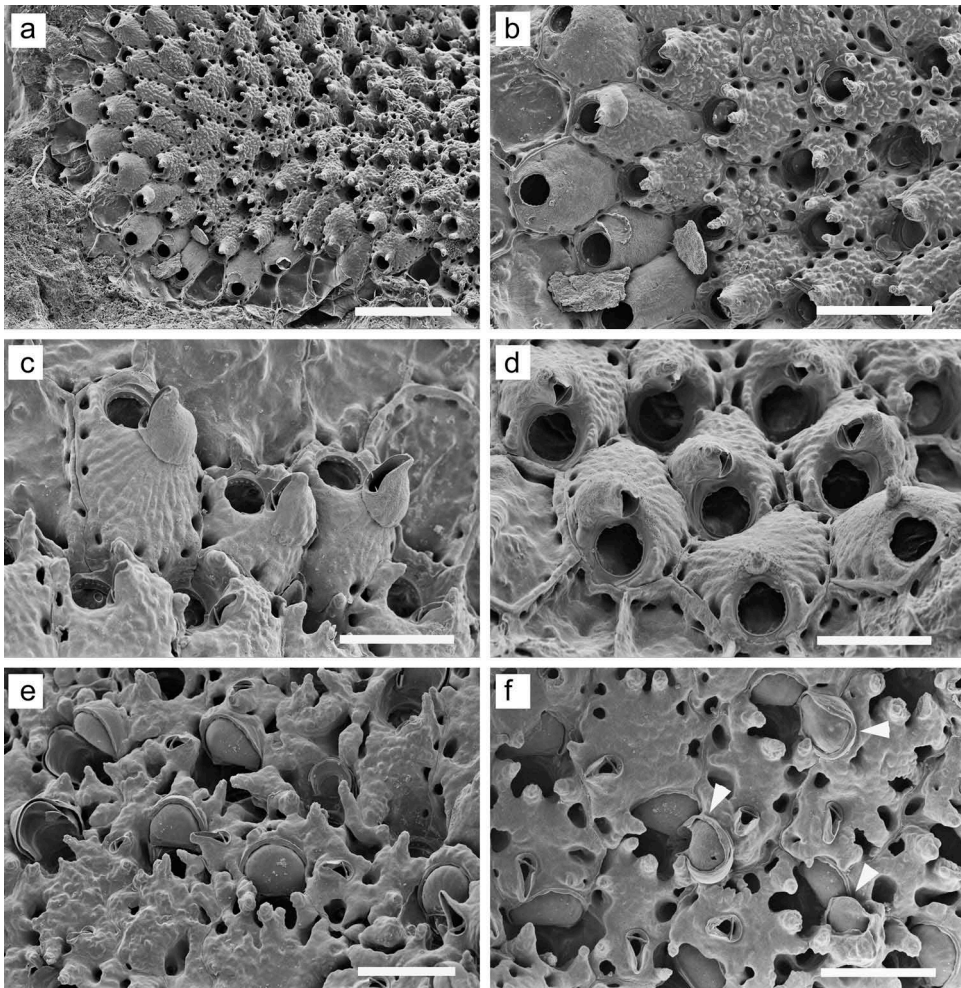
Figure 37. *Rhynchozoon lunifrons* sp. nov.: (a) NSMT-Te 1196 (paratype), colony view; (b) enlargement from preceding panel, showing autozooids typically having three processes associated with orifice; (c–f) NSMT-Te 1197 (paratype), (c) marginal autozooids showing shape and orientation of suboral avicularian chamber, (d) marginal autozooids, showing orifice shape, (e) well-calcified ovicelled autozooids, showing large semicircular area of exposed entooecium on ovicell, (f) endozooidal ovicells, with three zooids showing a second ovicell (arrowheads) lateral to orifice. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b = 500 μm; c–f = 300 μm.

0.151–0.200 (0.174 ± 0.020); OvW, 0.185–0.223 (0.200 ± 0.016) (n = 5, 1). One colony observed, 3.1 × 4.1 mm.

Description
Common form (Figure 37). Colony (Figure 37(a)) forming an encrusting sheet, mostly unilaminar, with occasional small areas of frontally budded zooids comprising a second layer; dried specimens white, with orange embryos. Marginal zooids (Figure 37(b–d)) distinct, delineated by a groove; oval, irregularly hexagonal or barrel-shaped in outline. Frontal wall of marginal zooids highly convex, inflated,

smooth (Figure 37(b)) or rugose (Figure 37(c)), without pseudopores; four to six small, circular areolae along each lateral margin. With increasing calcification (Figure 37(b)), zooidal boundaries become less distinct and areolar openings larger and more irregular, frontal surface develops coarse tubercles, and three to five tapering cylindrical processes develop around proximal peristomial margin. Typically there are three peristomial processes (Figure 37(b)), one in midline and two others paired laterally. Primary orifice (Figure 37(d)) variable within colony; on average about as broad as long; suboral sinus broadly arcuate between rounded, proximomedially sloping condyles, variable in depth. Orifice beaded with 12–15 denticles around periphery distal to condyles (Figure 37(c, d)). Most but not all zooids have a suboral avicularium; chamber evident only in marginal zooids (Figure 37(b–d)), slightly larger than area of developing peristome, arising from one or two marginal areolae; abutting peristomial rim on one side or other of midline. Rostrum raised at high angle to frontal plane, pointing frontolaterally; with age, slightly hooked distally; crossbar complete. Mandible long-triangular, lanceolate, decurved towards end, not hooked. With increasing calcification, suboral avicularian rostrum becomes immersed in peristome and not visible in frontal view (Figure 37(e, f)). Frontal avicularia variably present; some colonies lack them, but in other colonies, heavily calcified zooids frequently bear a single frontal avicularium along proximal or lateral margin (Figure 37(e, f)); rostrum long-triangular, about same size as that of suboral avicularia or somewhat smaller, raised from frontal plane, directed perpendicular to zooidal margin; crossbar complete. Oral spines lacking. Ovicell initially subimmersed (Figure 37(e)) but with age becoming endozooidal (Figure 37(f)). Entire proximal face of ooecium comprises a large zone of membranous (non-calcified) ectooecium that, in cleaned specimens, is seen as exposed entooecium; labellum usually lacking; if present, quite narrow. In colony NSMT-Te 1197, some maternal zooids have initiated the formation of two ooecia (Figure 37(f)), one endozooidal in the usual distal position, the other hyperstomial, lying on colony surface at lateral edge of secondary orifice (Figure 37(f), arrowheads). Vertical walls (Figure 37(d)) low; pore chambers small, at base of wall, each bearing a uniporous septulum; two or three septula in transverse wall, and four or five in each distolateral wall. Ancestrula not observed.

Precocious form (Figure 38). Small, irregularly discoid colony (Figure 38(a)); precocious, with fully developed ovicells starting in second daughter-zooid generation from ancestrula. Morphology as described above, except zooids smaller; young marginal zooids often bear one or two ephemeral distal oral spines (Figure 38(b)); frontal avicularia lacking; suboral avicularia rare, with only one zooid bearing a small, broken chamber (Figure 38(c), arrowhead). Mature, ovicelled zooids (Figure 38(d)) as in the common form above.

Remarks

Young zooids in the one or two generations inside the marginal row in *Rhynchozoon lunifrons* resemble zooids in *R. tristelidion* Tilbrook, 2006, in having a uniformly dimpled frontal surface and three distally directed conical processes arising from the peristomial margin; the size of the chamber of the suboral avicularium and the shape and direction of the rostrum are also similar between the two species. Tilbrook (2006) described *R.*
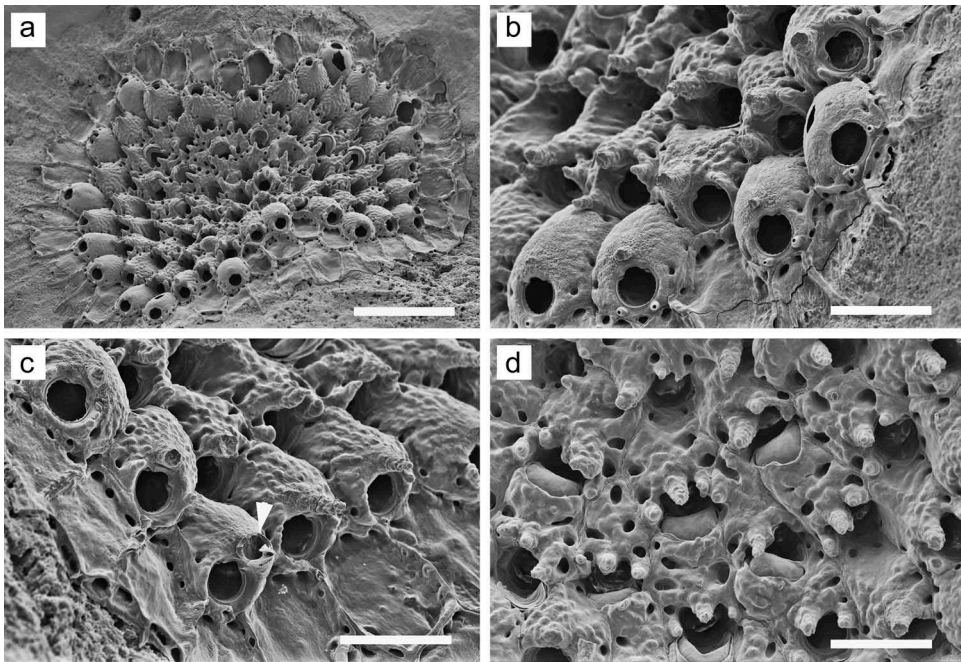
Figure 38. *Rhynchozoon lunifrons* sp. nov., precocious form, NSMT-Te 1198: (a) colony view; (b) marginal autozooids showing orifice shape, and presence of one or two oral spines; (c) autozooids at colony margin, with damaged chamber of suboral avicularium indicated by arrowhead; (d) ovicelled autozooids. Panels are scanning electron microscopic images of a bleached specimen. Scale bars: a = 1.0 mm; b–d = 300 μm.

tristelidion from the Solomon Islands (presently the only known locality for that species) on the basis of four colonies, all of which were young, lacking secondary frontal calcification and key diagnostic characters such as frontal avicularia (if they typically occur) and ovicells. *Rhynchozoon tristelidion* may be similar in growth form to *R. zealandicum* Gordon, 2009, another species with zooids having three peristomial processes. In *R. zealandicum*, colonies produce an extensive, unilaminar basal layer in which zooids lack secondary calcification, ovicells or frontal avicularia; mature zooids showing these characters develop in a zone of frontal budding in the centre of the colony (Gordon 2009, p. 49, fig. 22). In *R. lunifrons*, zooids inside the growing edge rapidly accumulate secondary calcification; the frontal wall becomes more heavily tuberculate, and the peristomial processes become thicker, rougher, and more digitiform than conical. The orifice in our specimens is about as long (including the sinus) as broad (broader than long in *R. tristelidion*), and the orificial sinus varies in depth, from broad and shallow as in *R. tristelidion* to narrower and deeper. While the different pattern of astogenetic change suggests that *R. lunifrons* is a different species from *R. tristelidion*, the possibility remains that the former represents mature colonies of the latter; resolving this question will require examination of mature colonies of *R. tristelidion* from the Solomon Islands.

We found one colony of what we term the 'precocious form' of this species, at the same locality as the common form. Zooid and ovicell morphology are quite similar; the precocious form differs from the common form in having smaller values for all characters measured, and in producing ephemeral oral spines on marginal zooids. Ostrovsky (1998)

has described the development of ovicells in small colonies consisting of a few zooids among cribrimorph species that typically produce larger colonies, and so the precocious form might simply represent an early astogenetic stage of the common form, with marginal zooids in larger colonies ceasing to produce oral spines, and older zooids in the colony interior beginning to produce frontal avicularia. More material is necessary to resolve this question.

Occurrence
We found 11 colonies at the SES site, the only known locality.

Rhynchozoon ryukyuense sp. nov.
(Figure 39)

Etymology
The specific name is a Latinised adjective from the Japanese *Ryûkyû*, the name of the island group that includes Okinawa.

Material examined
Holotype: NSMT-Te 1200, dried colony, SES site. Paratypes: NSMT-Te 1201 (SES-16), bleached, on SEM stub; NSMT-Te 1202 (SES-49), bleached, on SEM stub; NSMT-Te 1203 (REEF-8), bleached, on SEM stub; NSMT-TE 1204, three dried specimens, SES site; NHMUK 2016.5.13.81 (SES-45), bleached, on SEM stub; NHMUK 2016.5.13.82-86, five dried fragments, SES site.

Measurements
AzL, 0.38–0.55 (0.475 ± 0.038); AzW, 0.26–0.42 (0.336 ± 0.039) (n = 30, 2). OrL, 0.093–0.108 (0.101 ± 0.004); OrW, 0.097–0.114 (0.108 ± 0.005) (n = 9, 4). OvL, 0.17–0.22 (0.191 ± 0.016); OvW, 0.21–0.24 (0.220 ± 0.010) (n = 7, 3). Largest colony observed 6.5 × 5.0 mm.

Description
Colony (Figure 39(a)) small, roughly circular, forming a mostly unilaminar, encrusting sheet; greyish off-white. Marginal zooids (Figure 39(b–d)) irregularly hexagonal or barrel-shaped in outline, delineated by a shallow groove and suture line with flanking areolae (Figure 39(d)); zooidal boundaries rapidly becoming indistinct with age, delineated primarily by areolae. Frontal wall moderately convex, lacking pseudopores, initially smooth or minutely pitted, with a few scattered tubercles (Figure 39 (b–d)); young zooids at colony margin with six to 10 small areolae evident along each lateral margin. Frontal wall of heavily calcified zooids (Figure 39(e, f)) mildly rugose, with or without scattered tubercles; peristomial margin with up to six blunt, tapering processes; secondary orifice cormidial, with processes formed on proximal wall of next-distal zooid, from calcification from lateral zooids, and proximal to orifice. Primary orifice (including sinus) slightly broader than long (Figure 39(d)); proximal sinus deep, broad, rounded between blunt condyles; each condyle separated by a groove from edge of sinus. Margin of primary orifice beaded, usually with
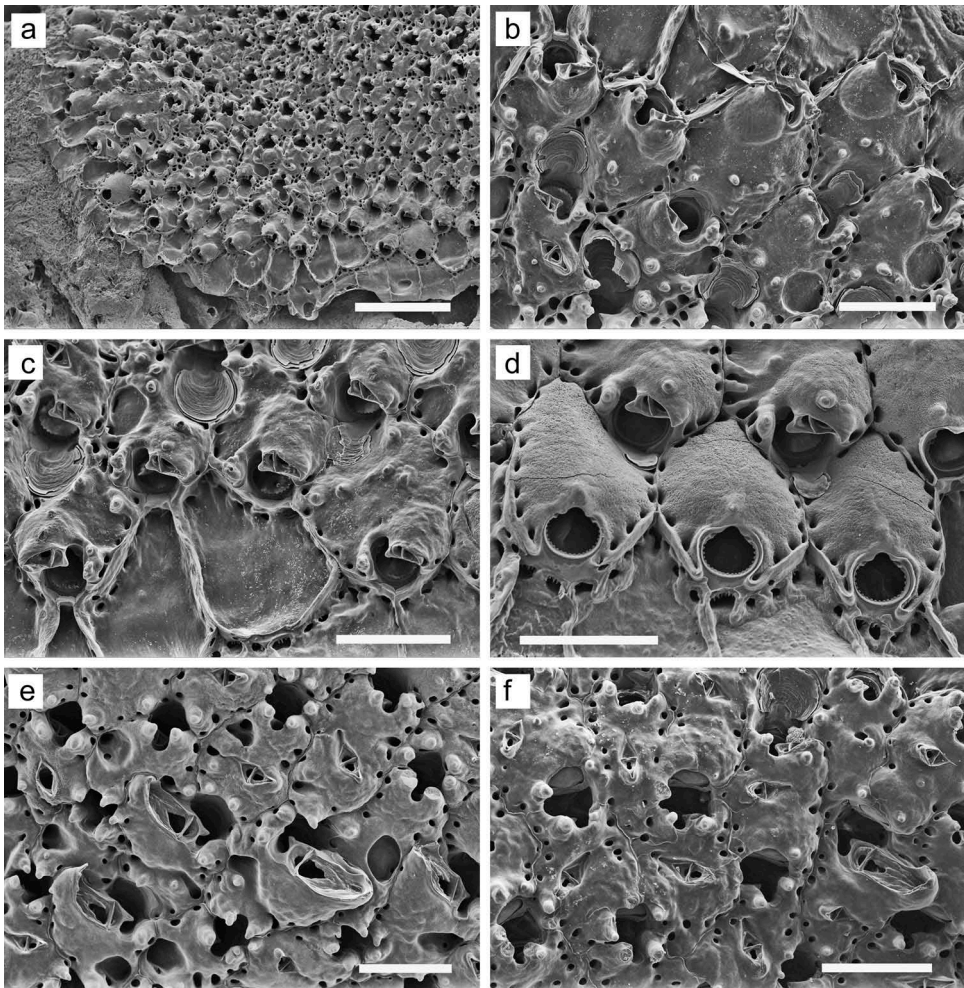
Figure 39. *Rhynchozoon ryukyuense* sp. nov., NSMT-Te 1202 (a–c), NHMUK 2016.5.13.81 (d, e), NSMT-Te 1201 (f), all paratype specimens: (a) colony view; (b) marginal autozooids, showing aspect of suboral avicularian chamber; (c) marginal autozooids, showing shape and orientation of avicularian rostrum; (d) marginal autozooids, showing orifice shape; note denticles associated with basal pore chambers; (e) autozooids, with diamond-shaped frontal avicularia and hypertrophied suboral avicularia; (f) ovicelled autozooids. All panels are scanning electron microscopic images of bleached specimens. Scale bars: a = 1.0 mm; b–f = 300 μm.

18–22 (n = 13, 3) denticles, although some zooids in all colonies have fewer (13–17, n = 3). In mature zooids, primary orifice deeply immersed in peristome. Oral spines lacking. Most zooids have a suboral avicularium (Figure 39(b–d)), with a large, circular or oval chamber evident in marginal zooids on one side of midline or other; chamber often bearing a tubercle. Rostrum large, raised at a moderate angle to frontal surface and strongly tilted laterally towards distal end of zooid; with a conspicuous, rounded process on inner proximal margin. Rostrum hooked distally; crossbar complete; mandible long-triangular. Young zooids have a deep sinus in secondary orifice between proximal end of rostrum and opposing lateral wall, which often bears a

conical process. With age, suboral avicularium becomes deeply immersed in peristome, often not evident in frontal view except for proximal rostral process projecting into peristome. Scattered zooids in some colonies have a hypertrophied suboral avicularium (Figure 39(e, f)), with a greatly enlarged rostrum lying outside the peristome, parallel to frontal plane or raised distally, with a scoop-like distal end; broad distal margin hooked and often coarsely serrate; proximal rostral process conspicuous; crossbar complete. Most zooids in mature colonies have a single frontal avicularium (Figure 39(e, f)); rostrum diamond-shaped, often raised distally, sometimes slightly hooked, crossbar complete; mandible equilateral or somewhat longer than broad, pointing in any direction. Ovicell (Figure 39(f)) endozooidal. Ooecium broader than long, covered by frontal calcification from one or more surrounding zooids, surface irregular, often bearing one or more tubercles. Proximal face of ooecium with transversely oval zone of membranous (non-calcified) ectooecium that, in cleaned specimens, becomes a window exposing the entooecium; labellum narrow, usually complete. Zooids interconnect by uniporous septula, each leading to basal pore chamber (Figure 39(c, d)); usually two or three septula in transverse wall and three or four in each distolateral wall. Most pore chambers bear sharp, stalactite-like denticles projecting from roof of chamber, up to six per chamber (Figure 39(d)). Ancestrula not observed.

Remarks

With diamond-shaped frontal avicularia and a well-developed lateral-suboral avicularium having a prominent proximal process and a hooked rostrum, *Rhynchozoon ryukyuense* greatly resembles *Rhynchozoon splendens* Hayward, 1988, which has been reported from Mauritius (Hayward 1988), Vanuatu (Tilbrook et al. 2001), the Great Barrier Reef (Ryland and Hayward 1992) and Hawaii (Dick et al. 2006), and (as *R. rostratum*) from Indonesia (Winston and Heimberg 1986) and the Philippines (Scholz 1991). Measurements of zooidal characters are not markedly different among these populations and *R. ryukyuense*. The two species differ primarily in the occurrence of hypertrophied suboral avicularia, which have not been reported in any population of *R. splendens*. Although the sharp, stalactite-like denticles on the roof of pore chambers, as seen in *R. ryukyuense*, have not been mentioned in previous reports of *R. splendens*, this character may simply have been overlooked, because Scholz (1991, p. 399, pl. 18, fig. 5); illustrated pore-chamber denticles in Philippine material that Tilbrook et al. (2001) later identified as *R. splendens*. Indeed, pore-chamber denticles may be widespread in *Rhynchozoon*, as *R. scimitar* (see the next species description) also has them. Finally, several previous reports have indicated that zooids in *R. splendens* can bear one or two frontal avicularia, whereas we did not observe more than one per zooid in *R. ryukyuense*. It is noteworthy that among three mature *R. ryukyuense* colonies with ovicells, hypertrophied suboral avicularia were abundant in one, rare (one only) in another and lacking in the third, which we would probably have identified as *R. splendens* had it been the only specimen examined.

Occurrence

We found a total of 18 colonies, at the SES and REEF sites, the only known localities.

Rhynchozoon scimitar sp. nov.
(Figures 36(e–f) and 40)

Etymology

The specific name is a noun in apposition referring to the scimitar-like rostrum of the suboral avicularian.

Material examined

Holotype: NSMT-Te 1205, dried specimen, SES site. Paratypes: NSMT-Te 1190 (SES-47), upper colony (overgrowing *Rhynchozoon maculosum*), bleached, on SEM stub; NSMT-Te 1207 (SES-48B), bleached, on SEM stub; NHMUK 2016.5.13.87 (SES-48A) (part of same colony as SES-48B), unbleached, on SEM stub; NHMUK 2016.5.13.88-89, two dried fragments, SES site.

Measurements

AzL, 0.47–0.62 (0.519 ± 0.044); AzW, 0.29–0.45 (0.365 ± 0.047) (n = 15, 1). OrL, 0.097–0.132 (0.113 ± 0.009); OrW, 0.095–0.110 (0.104 ± 0.005) (n = 15, 2). OvL, 0.19–0.23 (0.213 ± 0.014); OvW, 0.22–0.26 (0.236 ± 0.014) (n = 15, 1). Largest colony observed 22 × 14 mm.

Description

Colony (Figure 40(a)) forming an encrusting sheet; unilaminar, becoming bi- or tri-laminar in older parts of colony due to self-overgrowth or frontal budding; with faint yellowish tinge; exposed entooecial area on ovicell opaque white; embryos in dried specimens opaque light yellow. Zooids at colony margin (Figure 40(b)) irregularly hexagonal, delineated by suture line between opposing columns of areolae; with six to nine small, circular or oval areolae evident along each lateral margin. Frontal wall slightly to moderately convex, without pseudopores, surface somewhat irregular, texture smooth. With moderate calcification (Figure 40(e)) frontal surface becomes flatter, with zooidal boundaries indicated by areolae and suture line. In the oldest, heavily calcified zooids (Figure 40(f)), zooidal boundaries indistinct; frontal wall irregular, with scattered small tubercles. Primary orifice (including sinus) on average longer than broad (Figure 40(b, c)); anter D-shaped; proximal sinus deep, narrow, U-shaped; condyles small, rounded, directed frontodistally. Margin of anter beaded with 19–23 denticles (n = 8, 2). Oral spines lacking. Secondary orifice (Figure 40(e, f)) with distinct, asymmetrical proximal pseudosinus; sometimes a major and minor sinus occur. Around peristomial margin in older zooids are up to six short, blunt, cylindrical or conical processes (Figure 40(f)), arising from secondary calcification from proximal end of next-distal zooid, from one or both lateral zooids, and around proximal margin of orifice. Avicularia lacking in some zooids, but if present, only one avicularium per zooid, either lateral-suboral or frontal. Lateral suboral avicularium (Figure 40(b, d)) with a semicircular chamber immediately proximolateral to orifice on one side or other, arising from one or two areole. Rostrum large, length up to 2 times orifice width, raised distally at about 30° to frontal plane, directed distolater-ally, strongly hooked at end; crossbar complete; mandibular part of rostrum curved, scimitar-like; rostral opening irregular due to coarse denticles around margin of
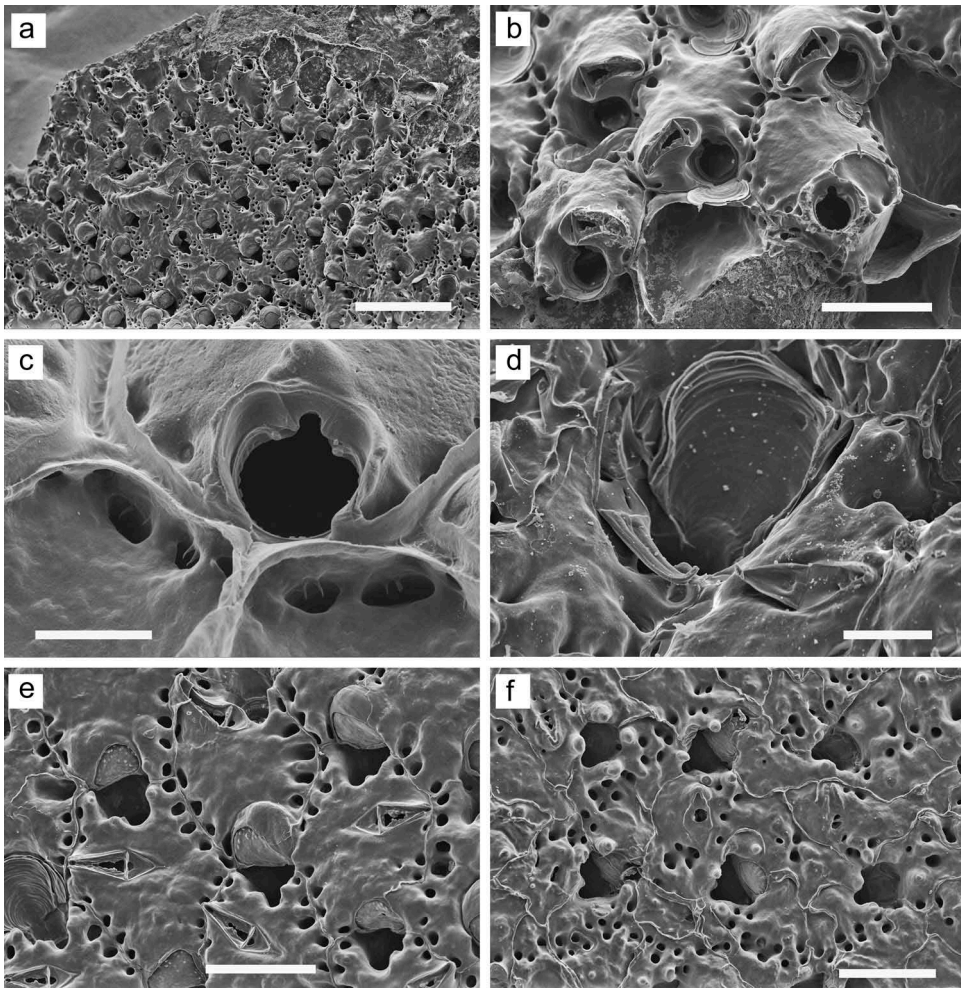
Figure 40. *Rhynchozoon scimitar* sp. nov., NSMT-Te 1207 (paratype) (a, b, d–f), NSMT-Te 1206 (paratype) (c): (a) colony view; (b) marginal autozooids, showing orifice shape and aspect of suboral avicularian chamber; (c) orifice; note denticles associated with basal pore chambers; (d) avicularian mandibles; (e) ovicelled autozooids, with diamond-shaped frontal avicularia and scimitar-like suboral avicularium (top centre); (f) old part of colony, with secondary calcification covering frontal avicularia. Panels are scanning electron microscopic images of bleached specimens, except for (d), which shows the specimen before bleaching. Scale bars: a = 1.0 mm; b, e, f = 300 μm; c, d = 100 μm.

opening; mandible (Figure 40(d)) long-triangular, weakly scimitar-shaped, sharply hooked in opposite direction to rostral hook, tip acute. Suboral avicularium not immersed in peristome, but remains conspicuous at peristomial margin. Frontal avicularia (Figure 40(e)) are situated along lateral zooidal margin on one side or other. Rostrum diamond shaped, parallel to frontal plane or slightly raised distally, directed laterally or distolaterally, about same length and width as rostrum of suboral avicularium but not curved laterally; crossbar complete; mandible slightly to markedly long-triangular, with a slight hook at the end. In heavily calcified zooids, the frontal avicularia can be nearly completely covered by secondary calcification

(Figure 40(f)). Ovicell initially subimmersed (Figure 40(a, e)), later becoming endo-zooidal (Figure 40(f)). Ooecium wider than long; covered with secondary calcification contributed by one to three surrounding zooids and often bearing one or two small tubercles. Proximal face of ooecium with large zone of membranous (non-calcified) ectooecium of variable shape (Figure 40(e, f)), which in cleaned specimens becomes a window of exposed entooecium; exposed entooecium weakly sculptured (pustu-lated or marginally ribbed); labellum narrow, usually (but not always) complete. Zooids interconnect by uniporous septula in distolateral and transverse walls; septula lead to basal pore chambers bearing stalactite-like denticles (Figure 40(c)). Ancestrula not observed.

Remarks

Rhynchozoon scimitar is distinguished by the deep, narrow orificial sinus; zooids having either a moderately large, scimitar-like lateral suboral avicularium that is not submerged in the orifice, or a similarly sized diamond-shaped frontal avicularium, but not both; the distinctly irregular margin of the opening of the avicularian rostrum; the large, weakly sculptured entooecial area on the ovicell that is typically opaque white; and the lack of spines. Few other *Rhynchozoon* species have a similarly deep, narrow orificial sinus. The orifice shape in *R. scimitar* is much like that in *R. solitarium* Tilbrook, 2006, described from the Solomon Islands; orifice size is identical in the latter, and the ovicell has a similarly large, pustulated area of exposed entooecium. *Rhynchozoon solitarium* differs in having hypertrophied suboral avicularia with a spatulate rostrum, and frontal avicularia uncommonly present, with the rostrum broadly rounded proximally rather than diamond shaped. *Rhynchozoon ardeolum* Ryland and Hayward, 1992, described from the Great Barrier Reef, Australia, also has a narrow orificial sinus, but this is shallower than in *R. scimitar; R. ardeolum* also has larger condyles and a hypertrophied lateral-suboral avicularium that is very broad proximally, with a narrow mandible.

One specimen (a fragment measuring 8 × 3 mm) entirely lacked avicularia and ovicells but was identifiable from the orifice shape. By light microscopy we observed between zooids what appeared to be a raised line of calcification, which upon bleaching and SEM examination (Figure 36(e, f)) proved to be a thin layer of gymnocystal calcifica-tion secreted around a filamentous epibiont extending throughout the colony in the interzooidal grooves or between zooids (arrowheads, Figure 36(e, f)), and occasionally emerging to the surface through circular openings (arrows, Figure 36(e, f)). This epibiont may be same that affected *Rhynchozoon maculosum* (see Remarks for that species, and Figure 36(a–d)). As with *R. maculosum*, the epibiont appears to have inhibited avicular-ium production in *R. scimitar*. This apparent inhibition raises the question whether the epibiont somehow protects the bryozoan, thus obviating the need of the latter to produce avicularia; alternatively, the epibiont might inhibit avicularium production to avoid damage to itself.

Occurrence

We found five colonies at the SES site, the only known locality.

Discussion

Species richness

Dick et al. (2005), Dick et al. (2006) and Grischenko et al. (2007) discussed previous studies worldwide that contribute data on the local and regional species richness of intertidal cheilostome bryozoans, and also discussed factors affecting local diversity. Table 5 compares sampling effort and species richness for rocky-intertidal cheilostomes among six localities in the North Pacific. This table is modified from Grischenko et al. (2007, p. 1151, table VI), with the results from Okinawa added. Neither the maximum single-site richness nor the total local richness shows a latitudinal diversity gradient, in which richness is expected to increase with decreasing latitude. However, as formalised by MacArthur and Wilson (1967), the number of species detected will be proportional to the size of the area sampled, and the area sampled (indicated by the number of sampling sites) varies greatly among North Pacific studies of intertidal cheilostomes. This may explain why the highest local diversity was detected at Kodiak, Alaska, the locality highest in latitude, where the sampling effort was massive: all bryozoan colonies were examined on 110 portable rocks heavily encrusted with bryozoans, with six to 24 such rocks examined per sampling site (Dick and Ross 1988). The lowest local diversity was detected on Hawaii Island, the locality lowest in latitude, where sampling effort was also lowest. Conditions suitable for intertidal bryozoans appear to be extremely patchy on Hawaii, and only one optimal site was encountered (Dick et al. 2006). Sampling effort in the Okinawa study is most comparable to that at Ketchikan, Alaska (Dick et al. 2005), where both the maximum single-site richness (28 species) and especially the total local diversity (31 species) were lower. The local diversity (52 species) detected in our study was only slightly lower than that at Kodiak (57 species), despite much lower sampling effort on Okinawa.

The pattern of species' occurrence at Okinawa – that is, the moderately high proportion (34.6%) of rare species (only one or two specimens encountered) and the high proportion of species (53.8%) detected at only a single site – suggests that sampling effort at Okinawa comparable to that at Kodiak (Dick and Ross 1988), Akkeshi (Grischenko et al. 2007) or the Commander Islands (Grischenko 1993, 1994, 2004) would give a much higher estimate of local diversity than the 52 species we detected among three sampling sites. Both the theory and computational tools for extrapolating estimates of total local diversity from sampling data have advanced in recent decades

Table 5. Comparison of the species richness of cheilostome bryozoans in the rocky-intertidal habitat at six localities in the North Pacific, in order of decreasing latitude.

Locality	North latitude	Number of sampling sites	Maximum single-site richness	Total species detected	Study
Kodiak, Alaska	58°	10	33	57	Dick and Ross (1988)
Ketchikan, Alaska	55°	3	28	31	Dick et al. (2005)
Commander Islands	55°	12	37	49	Grischenko (1993, 1994, 2004)
Akkeshi, Japan	43°	9	29	39	Grischenko et al. (2007)
Okinawa, Japan	27°	3	36	52	This study
Island of Hawaii	20°	2	29	29	Dick et al. (2006)

(e.g. Gotelli and Colwell 2001; Colwell et al. 2012; Colwell 2013), and we hope to apply this methodology in a future study to examine diversity patterns in North Pacific intertidal cheilostomes based on the data from existing studies across a range of latitudes.

Biogeography

Some previous studies have examined bryozoan zoogeography in the Indo-Pacific region. Okada and Mawatari (1957) analysed the distributions of genera and species in the total bryozoan fauna and designated three subregions: the Indian Subregion (from the east coast of Africa and Madagascar across the Indian Ocean to the Timor Sea); the Western Pacific Subregion (from the Malay Archipelago to the Coral Sea and northward to the Yellow Sea); and the Central and Eastern Pacific Subregion (Polynesia, eastward to Hawaii and the subtropical to tropical Pacific coast of North America). Each subregion in turn comprised two or more provinces. This classification placed Okinawa in a Chinese Province (East China Sea, Yellow Sea, southern Japan) within the Central and Eastern Pacific region, but Okada and Mawatari (1957) noted that there were so many species in common between the Chinese and Malayan Provinces that it was difficult to draw an exact boundary line between them.

Tilbrook and De Grave (2004) used detrended correspondence analysis (DCA) to examine biogeographical affinities among Indo-West Pacific cheilostome bryozoan faunas, based on species lists from local studies supported by SEM illustrations. These authors detected a split in the bryozoan faunas between the Indian Ocean and Pacific Ocean at three taxonomic levels (family, genus, species), and between the Western Pacific and Hawaii at the family and genus levels. While different taxonomic levels gave different groupings among Western-Pacific faunas, all three levels supported an affinity between faunas in the Solomon Islands and Philippines. At the time of the study, no SEM-supported data were available for southern Japan.

The most recent general biogeographical classification of marine organisms in coastal and shelf waters is that of Spalding et al. (2007), which hierarchically subdivides the world biota into 12 realms, 62 provinces and 232 ecoregions. This classification appears to place Okinawa at the boundary between the Temperate Northern Pacific realm (Warm Temperate Northwest Pacific Province, East China Sea Ecoregion) and the Central Indo-Pacific realm (South Kuroshio Province, South Kuroshio Ecoregion). Our analysis of species distributions (Tables 3 and 4) shows the Okinawan intertidal cheilostome fauna to be overwhelmingly allied with the Central Indo-Pacific (IP) realm. Only 12.5% of the species we identified had been reported from localities within the Temperate North Pacific realm (17.5% if one includes two putatively cosmopolitan species), whereas 72.5% had been reported from the Central IP realm (including species also extending into other realms, and putatively cosmopolitan species), and 27.5% were known only from this realm (Tables 3 and 4). This corroborates Liu (2013), who classified the benthic invertebrate fauna in the East China Sea as belonging to a Japan-China Subtropical Subregion within an Indo-West Pacific Warm Water Biotic Region. Both Liu (2013) and Hohenegger (1994) attributed the high proportion of tropical faunal elements in the East China Sea to northward transport (e.g. by rafting or as larvae) from more southern regions via the warm Kuroshio Current.

Interestingly, while Tilbrook and De Grave (2004) detected a clear separation at the genus level between western Pacific localities and Hawaii, 15 (28.8%) of the 52 species we found on Okinawa had previously been reported from Hawaii, within the Eastern Indo-Pacific realm of Spalding et al. (2007). Dick et al. (2006) reported an even more pronounced connection from the other direction: of 23 intertidal bryozoan species (mostly cheilostomes) with records outside Hawaii, five (22%) were putative cosmopolitans and 18 (78%) also occurred in the broad Indo-West Pacific region. Dick et al. (2006) noted, however, that intertidal bryozoan faunas might not be representative of total faunas in their biogeographical affinities, since species capable of tolerating the stressful intertidal environment might be predisposed to dispersal on ship hulls, floating logs, anthropogenic debris, or rafts of plant material.

Taxonomy

The accuracy of biogeographical analyses at the species level obviously depends both on adequate sampling across regions and on the accuracy of species identifications. In the past few decades, with the now-routine use of SEM for examining bryozoan skeletal morphology, an increasing number of extensive, well-illustrated studies (e.g. Winston and Heimberg 1986; Hayward 1988; Scholz 1991; Ryland and Hayward 1992; Hayward and Ryland 1995; Tilbrook et al. 2001; Dick et al. 2006; Tilbrook 2006) and an increasing number of familial or generic treatments (e.g. Soule and Soule 1973; Ristedt 1985; Tilbrook 1998, 1999, 2001, 2012; Tilbrook and Cook 2004) have led to considerable progress in understanding both the taxonomy and biogeography of Indo-Pacific bryozoans.

This might suggest that little remains to be learned, but nothing could be further from the truth. Studies of Indo-Pacific localities continue to detect high proportions of new cheilostome species – for example 22% on Vanuatu (Tilbrook et al. 2001), 24% on Hawaii Island (adjusted from Dick et al. 2006), 40% in the Solomon Islands (Tilbrook 2006) and 21% on Okinawa (this study). This suggests that a species accumulation curve – the number of known species as a function of some measure of increasing sampling effort – for the Indo-Pacific region would be at present far from reaching an asymptote. In fact, sampling effort has been rather low considering the vast size of the region represented by a handful of localities where intensive collecting has been done in coastal and shelf habitats. Specimens from older expeditions that did cover large areas, though with relatively low sampling effort in any one place (e.g. Harmer 1926, 1957; Canu and Bassler 1929), were often inadequately described, analysed according to old concepts of geographical variation within species (Soule et al. 2002; Dick and Mawatari 2004) and illustrated with low-resolution photomicrographs. Generic treatments reexamining specimens in these older collections with SEM are detecting many new species (e.g. Tilbrook 2001, 2012).

At present, the extent of endemism in Indo-Pacific cheilostome faunas is poorly understood. All species known only from the type locality are apparent local endemics until they are discovered somewhere else. Among 178 cheilostome species that Tilbrook (2006) detected in the Solomon Islands, 52 (29%) were apparently endemic to the Solomons – and more than half of these were detected from only a single colony, meaning they would likely have gone undetected without considerable sampling effort

(as we found on Okinawa, where 23.1% of species were detected from only a single colony). Some proportion of these apparent endemics will eventually be detected elsewhere in subsequent studies. Indeed, until we found them on Okinawa, two species (*Celleporaria calva* and *Calyptotheca reniformis*) were among Tilbrook's (2006) apparent Solomon endemics, and another seven species were apparent endemics in other places – *Crassimarginatella extenuata*, Hawaii Island; *Beania hexamicorum*, Vanuatu (discounting a questionable record from Mauritius); *Cribralaria curvirostris*, Ogasawara Islands; *Celleporaria desperabilis*, Great Barrier Reef; *Celleporaria triangula*, southern Korea; *Parasmittina alanbanneri*, Hawaiian archipelago; and *Echinovadoma anceps*, Vanuatu. It is important to know the proportion of true endemics that can be expected among the apparent endemics in local areas, especially relatively isolated islands and island groups. If islands and island groups throughout the Indo-Pacific prove to harbour many true endemics, then sampling all of these local areas will be necessary to fully understand cheilostome diversity and biogeography in the region. On the other hand, if the proportion of true local endemics proves to be generally low, fewer local areas will need to be intensively sampled.

As a taxonomic tool, SEM is a double-edged sword. While it allows high-resolution examination of bryozoan skeletal morphology, it also shifts to a finer degree of resolution the problem of distinguishing between intra- and interspecific variation among geographically separate populations. In the taxonomic accounts, we mentioned a number of putatively cosmopolitan species or broadly distributed Indo-Pacific species (*Thalamoporella tubifera*, *Chorizopora brongniartii*, *Smittina nitidissima*, *Arthropoma cecilii*, *Parasmittina serrula*, *Crepidacantha longiseta*) that show differences among geographically separate populations, suggesting they might represent multi-species complexes rather than widely distributed species. In an exemplary case, Tilbrook (2006, 2012) resolved the putatively cosmopolitan species *Bryopesanser pesanseris* (Smitt, 1873) into at least 11 species that had been (or would have been) previously identified as *B. pesanseris*. While most of these species have a much more limited geographical distribution than previously accepted for *B. pesanseris*, two (*B. latesco* Tilbrook, 2006; *B. tonsillorum*, Tilbrook, 2012) appear to be broadly distributed from the Indian Ocean to the eastern Pacific. For additional discussion of the general problem of cosmopolitanism in bryozoology, see Soule et al. (2002), Dick and Mawatari (2004) and Harmelin et al. (2011, 2012).

DNA markers provide a means of distinguishing between intra- and interspecific variation, and Dick et al. (2013) found for the cheilostome genus *Cauloramphus* that geographically separate populations that are morphologically similar except for non-overlapping differences in a few characters are usually highly genetically divergent as well – that is, they represent different species. Unfortunately, for practical reasons, bryozoan taxonomy remains largely reliant on skeletal morphology. Even now, bryozoans are often not collected in such a way that specimens are ideal for DNA extraction, especially after long-term storage, as exemplified by our study on Okinawa. Furthermore, type material is often either unsuitable or too limited for DNA extraction. For his Solomon Islands study, for example, Tilbrook (2006) relied on dried specimens collected 20 years before, and many of the new species he described were represented by only a single colony that later became the holotype specimen. Museum curators typically vigorously protect holotypes from any sort of destructive examination, as they

should, although this precludes the use of these specimens in establishing taxonomic identity by means of DNA markers.

The bryozoan fauna in far-southern Japan, and indeed throughout the Nansei Archipelago and eastern East China Sea, is poorly known at present, primarily due to historically low sampling effort and limited activity by bryozoan taxonomists in the region. However, progress is underway. In the past decade research ships have made a number of sampling cruises along the Nansei Archipelago, and a preliminary assessment of the bryozoans in these collections indicates more than 130 species representing 70 genera, with many new records for Japan (Hirose 2017).

Disclosure statement

No potential conflict of interest was reported by the authors.

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