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Diversity and taxonomy of rocky-intertidal Bryozoa on the Island of Hawaii, USA

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Abstract

This study examines the diversity of bryozoans found at four rocky intertidal sites (Kiholo Bay, Whittington Beach Park, Kealakekua Bay, and Kapa'a Beach Park) on the Island of Hawaii, USA. Bryozoans were patchily distributed, with few or no bryozoans, or low species diversity, at three protected or semi-protected sites, and unexpectedly high diversity at one exposed site. Species richnesses at the four sites were zero, one, five, and 32 species, respectively. Species diversity at the richest site was within the range of single-site diversities previously reported from optimal sites in temperate latitudes. We provide descriptions and SEM illustrations for 32 species recorded, which include a new genus (*Funerossia*) in the Family Stomachetosellidae and 10 new species (*Alderina flaventa*, *Corbulella extenuata*, *Puellina septemcryptica*, *Funerossia copiosa*, *Calyptotheca kapaaensis*, *Bryopesanser serratus*, *Cribellopora souleorum*, *Metacleidochasma verrucosa*, *Disporella compta*, and *Favosipora adunca*). The species encountered included 23 (72%) ascophorans, four (13%) anascans, two (6%) cribrimorphs, three (9%) cyclostomes, but no ctenostomes. All species were encrusting and essentially two-dimensional in growth form. Most species occurred on a substratum of lava rock, though not exclusively so. Of 23 species distributed outside the Hawaiian Islands, five (22%) have putatively cosmopolitan distributions and 18 (78%) Indo-West Pacific distributions; 19 (83%) are new records for the Hawaiian Islands. We briefly discuss freshwater influence and predation as possible factors in the patchy distribution of the intertidal bryozoans, and stress tolerance and larval-settlement specificity as factors in the composition of the intertidal assemblage.

Keywords: Biodiversity, biogeography, ecology, endemism, Indo-West Pacific, intertidal Bryozoa, new species, species richness, taxonomy

Introduction

Bryozoans comprise a phylum of modular, sessile, primarily marine animals that occur in all the world's seas, from polar regions to the tropics and from the shore to abyssal depths. More than 5700 species of recent marine bryozoans have been described (Gordon 1999),

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with the greatest species diversity generally obtaining on tropical shelves in the 0–100 m depth interval (e.g. Gordon 1999). Perhaps because of the greater subtidal species diversity of bryozoans, the significant contribution of bryozoans to shore communities began to be appreciated only in the latter half of the 20th century. Early studies focused on the ecological factors determining the distributions of species common on shores, particularly those encrusting algae (reviewed by Ryland 1967, 1970, 1974a, 1976; and Ryland and Stebbing 1971). At the same time, interest in the ecology of intertidal bryozoans spurred investigations on their taxonomy and, indirectly, their diversity (Ryland 1962, 1974b).

Gordon (1972) was the first to succinctly summarize the important synecological role of intertidal bryozoans, which are a major competitor for space in cryptic habitats. Only more recently, however, have bryozoans begun to be documented as one of the most species-rich components of lower-intertidal communities. Studies in both northern and southern temperate localities have detected local intertidal species richnesses of more than 70 species in rocky habitats (Gordon 1980; Dick and Ross 1988; Dick et al. 2005).

Studies of intertidal bryozoan diversity in subtropical and tropical regions have provided conflicting results. Some studies have indicated high diversities of low-intertidal, coral reef-associated bryozoans. For example, Ryland and Hayward (1992) and Hayward and Ryland (1995) reported 124 species of bryozoans collected mostly intertidally from Heron Island, Great Barrier Reef (23°S); however, some of their samples were subtidal, and the contribution of these to the exceptionally high species richness is unclear. In a series of rocky-intertidal transects in the Bay of Bengal, Rao and Ganapati (1985) found a much lower diversity, only 22 bryozoan species. Soule et al. (1988, p96) concluded after extensive general fieldwork in the Hawaiian Islands, “Whereas bryozoans are common in rocky tidepools in the temperate zone, the authors have observed that in the tropics the warm, intensely lighted tidepools in dark volcanic rocks and coral rubble shores do not generally support a bryozoan fauna. The limited intertidal zone, with a range of less than 1 m, combined with intense light and insolation, offers less suitable habitat for colonization by intertidal fauna than that of the 2 m to 5 m intertidal habitats of temperate shores.”

However, even at temperate latitudes, bryozoans tend to be patchily distributed along rocky shores, with the highest species diversity occurring in semi-protected, cryptic rock-pile habitats (defined by Dick and Ross 1988; see also Dick et al. 2005). cursory examination of such a site at Perico Island, Gulf of Panama (8°N; M. H. Dick, unpublished data), indicated roughly 25 species, a single-site richness as high as that typically found at temperate latitudes.

Are bryozoans generally depauperate intertidally in tropical regions, or have previous workers simply not looked for them in appropriate habitats? In this study, we addressed these questions by examining on the Island of Hawaii (19–20°N) several low-intertidal, protected or semi-protected shore sites with a layered rock-pile structure similar to sites where high bryozoan diversity has been observed at temperate latitudes.

Study area and methods

Four rocky-intertidal sites (Figure 1) on the southeastern and western coasts of the Island of Hawaii were investigated between 25 February and 4 March 2005. Permission to collect in non-prohibited areas was granted by the State of Hawaii Department of Land and Natural Resources (permit number PRO-2005-36). Boulders and smaller rocks close to the water’s edge at low tide were overturned and examined, beginning up to an hour before low tide and continuing for up to 1.5 hours after low tide. The study sites were as follows.

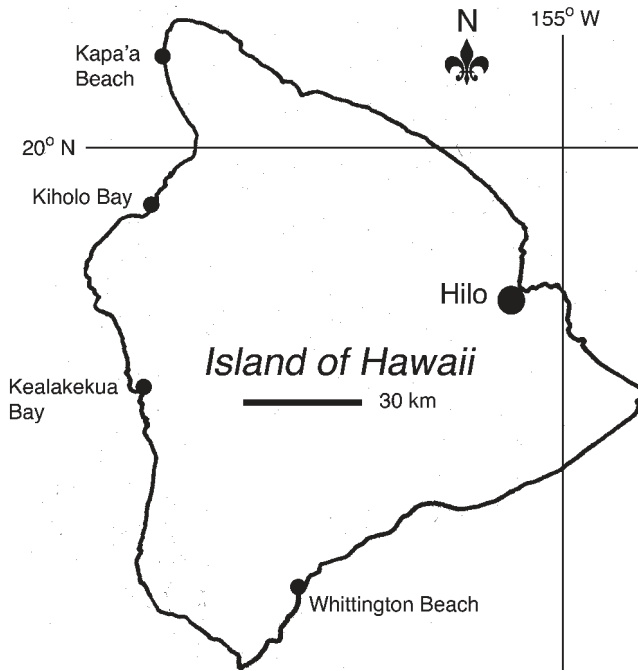


Figure 1. Outline map of the Island of Hawaii, showing the location of the main town, Hilo, and the four localities examined for bryozoans (smaller circles).

Kealakekua Bay (25 February 2005) (Figure 2A)

Low tide 0.03 m referenced to mean lower low water; duration of field observations 1.5 h. This site, located 0.2 km south of the Captain Cook Monument, is a shallow inlet in the sheltered bight that comprises the NW corner of Kealakekua Bay; due to its location, it is completely sheltered from any strong wave action. The bottom and sides of the inlet are lined with a loose, shallow layer of worn boulders and cobbles of lava and coral rock; underneath the boulders is a moderate amount of coral sand and silt, due to the sheltered nature of the inlet. The inlet is completely drained of water at low tide. Some of the boulders harboured dense aggregations of mussels (*Isognomon perna*) on their undersides; however, many boulders were nearly bare underneath, with only a few small, flat, encrusting sponges. Other organisms on the undersides of boulders or in the rubble beneath them included several species of sea urchins, a black brittle star, several species of holothurians, several species of gastropods, and small crabs. Since this site lies in a Marine Life Conservation District, collecting was prohibited; bryozoan colonies were identified by hand lens on both coral boulders and lava. This was possible only because bryozoan diversity was low, with the fauna consisting predominantly of two easily recognized species.

Whittington Beach Park (27 February 2005) (Figure 2B)

Low tide -0.03 m referenced to mean lower low water; duration of field observations 2.5 h. This site consists of a narrow lagoon paralleling the shore, protected on the seaward side by a solid lava barrier breached by a main and several smaller channels. The protected, landward shore of the lagoon comprises true rock-pile habitat, a deep, multi-layered covering of lava boulders small enough to be turned over, with smaller lava cobbles and

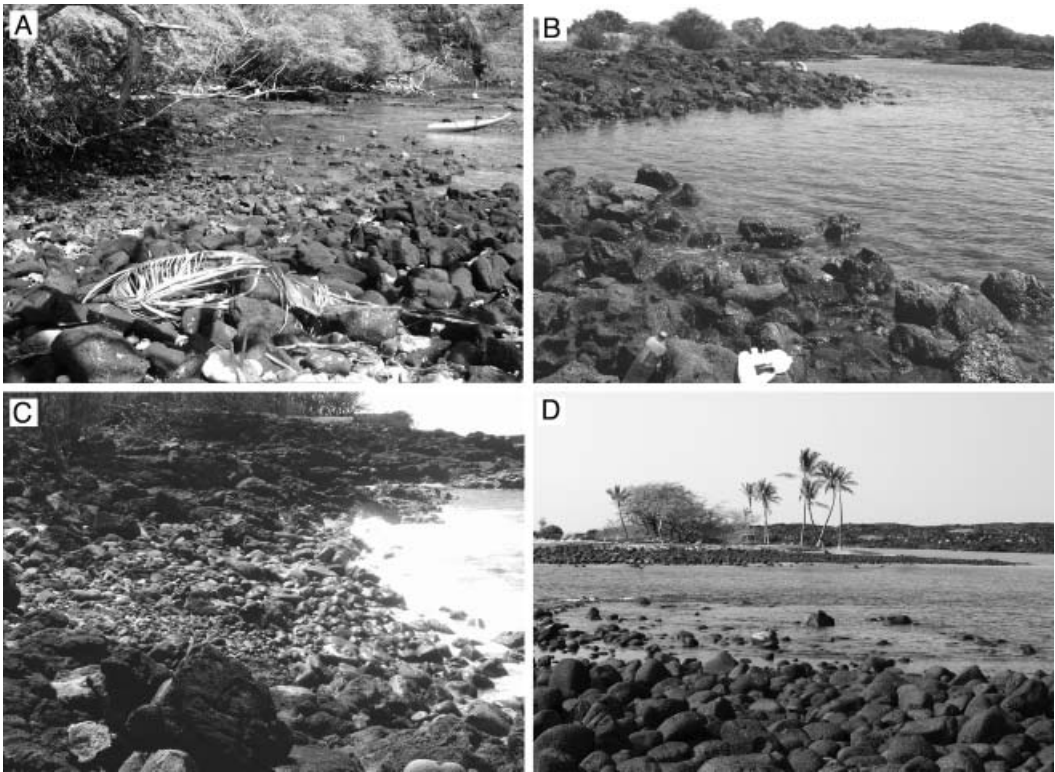


Figure 2. Photographs of rock-pile habitats examined at study sites on the Island of Hawaii; all taken within an hour of low tide (-0.03 to $+0.15$ m referenced to mean lower low water). (A) Kealakekua Bay; study site is shallow inlet beginning at centre and extending to just below left centre; plastic kayak at upper right indicates scale. (B) Whittington Beach Park; sheltered lagoon inside benchrock barrier, part of which can be seen in distance at far upper right; scale indicated by water bottle at lower left. (C) Kapa'a Beach Park; an exposed site with rounded-boulder beaches (centre) and solid benchrock (in distance, upper right); sampling site was a tidepool in the benchrock just beyond the upper right of the photograph. (D) Kiholo Bay; entrance to large lagoon separated from the sea by a long barrier spit, on which palm and other trees are growing; end of spit is seen just above right centre, with lagoon evident beyond that in the distance; the shallow area with boulders protruding from water, left to right just below centre, was examined for bryozoans; photograph taken about an hour before low tide.

pebbles among and beneath them. Due to strong tidal currents in the lagoon, there was little silt underneath rocks. Landward of the lagoon is a sheltered, silty tidal-pond complex connected to the lagoon by a narrow channel. The undersides of many boulders at the water's edge at low tide harboured dense aggregations of mussels (*Isognomon perna*); flat, encrusting sponges were also a major space-occupier underneath boulders at this site. Other organisms observed included nemerteans, abundant spirorbid and serpulid polychaetes, cowries and several other types of shelled gastropods, nudibranchs, chitons, holothurians, and a few sea urchins.

Kapa'a Beach Park (1 March 2005) (Figure 2C)

Low tide 0.15 m referenced to mean lower low water; duration of field observations 1 h. This locality is relatively exposed and subject to heavier wave action than the other sites examined. The shore consists of rough beaches of large, lava boulders rounded by rolling,

as well as areas of solid lava shore with scattered tidepools of various sizes worn in the rock. The undersides of rocks were examined both on the boulder beaches and in tidepools. Most rocks lacked bryozoans; however in several tidepools up to 0.45 m deep, located above the water's edge at low tide, jagged, stably wedged rocks were found that contained high densities of bryozoan colonies on the undersides (top layer) or all sides (lower layers). Associated organisms in the tidepools where bryozoans were collected included black brittle stars, flat barnacles, and several species of sea urchins. The upper surfaces of bryozoan-encrusted rocks exposed to light were heavily encrusted with flexible macroalgae and encrusting coralline algae. Where they occurred, bryozoans were the main surface-covering organism, competing for space with a low density of encrusting sponges, moderately abundant spirorbid tubeworms, and sometimes coralline algae. The shingle urchin (*Colobocentrotus atratus*) and limpets were common on rock surfaces around the tidepools where bryozoans occurred, indicating a moderately high-energy shore. Several portable lava boulders as well as smaller cobbles and pebbles were collected.

Kiholo Bay (4 March 2005) (Figure 2D)

Low tide 0.00 m referenced to mean lower low water; duration of field observations 1.25 h. This site consists of a bay hooking northward into a long inlet inside a barrier spit, with a small island in the mouth of the bay between the tip of the spit and mainland shore. The shores of both the spit and the island consist of true rock-pile habitat, a multi-layered covering of lava boulders small enough to be turned over, with smaller lava cobbles and pebbles among and beneath them. Inland of the mouth of the bay are extensive freshwater ponds fed by a river. Freshwater springs seep into the bay, providing a layer of cold freshwater on the surface approximately 0.3 m deep, distinguished from the warmer seawater beneath by a thermocline–halocline boundary. The undersides of boulders were examined around the shores of the small island at the mouth of the bay, especially among layered lava boulders and cobbles on the shallow reef-flat extending north from the island. Aggregations of the mussel *Isognomon perna* were common on the undersides of boulders, as were flat encrustations of several sponge species. Other organisms on the undersides of boulders or in the rubble beneath them included errant polychaete worms, abundant spirorbid tubeworms, nudibranchs, holothurians, sea urchins, and several species of gastropods. Kiholo Bay is a Fishery Management Area where collecting is prohibited; however, this made no difference, as no bryozoans were found there.

Fragments containing bryozoan colonies were removed from the boulders collected at Kapa'a Beach Park by means of a Dremel tool (Dremel Co., Racine, WI, USA) with a diamond-cutting bit and by hammer and chisel; not all colonies could be removed. Specimens thus obtained, as well as whole smaller stones, were air-dried and wrapped in tissue paper for transport. Since single boulders of portable size have been used as the sampling unit in some other studies (e.g. Dick and Ross 1988), specimens from one heavily encrusted boulder were kept separate from the rest, in order to obtain an idea of the species richness that might occur on it. As our study was limited in scope, designed only to rapidly survey whether diverse bryozoan assemblages occurred intertidally on the Island of Hawaii, we made no effort to quantify the surface areas of rocks examined, with the exception of the boulder just mentioned.

In the laboratory, colonies on stones and rock fragments were examined by stereoscopic microscope. Measurements were made at 80× magnification with an ocular micrometer and are presented in the text, in millimetres, as a range followed in parentheses by the mean

and standard deviation. Unless otherwise noted, the sample size for each measurement was $n=10$, generally from one colony. Abbreviations used for measurements are as follows: ZL, zooid length; ZW, zooid width; OpL, opesia length; OpW, opesia width; OrL, orifice length; OrW, orifice width; AzOrL, AzOrW, autozooidal orifice length and width (in species with dimorphic orifices); SecOrL, SecOrW, length and width of secondary orifice; OvZOrL, OvZOrW, length and width of orifice of ovicellate zooids (in species with dimorphic orifices); OvL, ovicell length; OvW, ovicell width.

Selected specimens to be examined by SEM were immersed in a sodium hypochlorite solution until the soft tissue was removed, rinsed in water, and air-dried. Specimens thus prepared were mounted with double-sided adhesive tape on aluminium SEM stubs, coated with Pd-Pt in a Hitachi E-1030 sputter coater, and observed with a Hitachi S-2380N scanning electron microscope at 15 kV accelerating voltage. All images were stored electronically as TIFF files at a resolution of 500 pixels cm^{-1} , using ImageCatcher software.

Some colonies became fragmented in the removal of specimens from large rocks. For counts of individuals per species, both whole colonies and colony fragments were treated as individual units. The totals are thus overestimates of the true number of colonies per species. Nonetheless, the numbers presented in Table I are, depending on the species, proportional to the true number of colonies or to the average size of colonies, or both, and thus give a rough indication of the relative contributions of the species to the bryozoan assemblages at the collecting sites.

Since many previous studies in the tropics have dealt primarily with coral reef-associated bryozoans (e.g. Winston 1986; Winston and Heimberg 1986; Hayward 1988; Gordon 1989b; Ryland and Hayward 1992; Hayward and Ryland 1995; Tilbrook 2006), we made an effort to note whether bryozoans were attached directly to the rock substratum, as opposed to calcareous substrata on the rocks.

The classification utilized here for cheilostomes follows the Interim Classification of Families and Genera of Cheilostomata (Working Classification for Treatise, August, 2006) compiled by D. P. Gordon (unpublished). To conserve space, authors of genera and higher taxa are not included in the References section. The synonymies are limited, including only the reference for the original description and one or two additional references. Holotype and some paratype specimens have been deposited in The Natural History Museum, London (NHM); additional paratype specimens have been deposited in the Yale Peabody Museum, Yale University, New Haven, CT, USA (YPM).

Results

Species diversity

In all, this study detected 32 bryozoan species, though diversity was extremely patchy among the sampling sites (Table I). At Kiholo Bay, no bryozoans were observed. At Whittington Beach, several dead colonies of *Hippopodina iririkiensis* were found. At Kealakekua Bay, five species were observed, of which three remained unidentified, with *H. iririkiensis* the predominant species. At Kapa'a Beach Park, 19 species occurred within areas of suitable microhabitat totalling approximately 940 cm^2 on a single large but portable boulder; examination of three smaller portable boulders and several pebbles added another 13 species, for a total of 32 species at the site. The three species highest-ranking in abundance at Kapa'a were *Junerossia copiosa*, *Parasmittina serrula*, and *Chorizopora brogniartii*; *H. iririkiensis*, the most abundant species at the bryozoan-depauperate sites, ranked fifth.

Table I. Bryozoan species identified in this study, their substrata, and their approximate relative abundance at two intertidal sites.

Species	Substratum ^a	Kealakekua Bay	Kapa'a Shore		
			Large rock	Other rocks	Total
<i>Alderina flaventa</i> n. sp.	C(R)	–	1	9	10
<i>Parellisina albida</i>	R	–	7	12	19
<i>Corbulella extenuata</i> n. sp.	R	–	–	2	2
<i>Antropora minor</i>	C	–	–	1	1
<i>Beania discodermae</i>	R	–	–	2	2
<i>Micropora rimulata</i>	R	–	–	6	6
<i>Puellina harmeri</i>	R(C)	–	7	1	8
<i>Puellina septemcryptica</i> n. sp.	C(R)	–	3	–	3
<i>Hippothoa flagellum</i>	R	–	p	–	p
<i>Chorizopora brogniartii</i>	R	–	15	20	35
<i>Poricella spathulata</i>	R(C)	20	8	2	10
<i>Drepanophora corrugata</i>	R	–	–	1	1
<i>Escharoides longirostris</i>	R	–	1	2	3
<i>Parasmittina serrula</i>	R	–	17	21	38
<i>Watersipora</i> “subovoidea”	C(R)	–	7	8	15
<i>Fumerossia copiosa</i> n. sp.	R	–	57	13	70
<i>Hippopodina iririkiensis</i>	C(R)	47	4	14	18
<i>Cosciniopsis lonchaea</i>	R	–	–	4	4
<i>Calyptotheca kapaaensis</i> n. sp.	R	–	–	2	2
<i>Cheiloporina haddoni</i>	R	–	–	1	1
<i>Bryopesanser serratus</i> n. sp.	R	–	1	2	3
<i>Fenestulina caseola</i>	R (AC)	–	–	5	5
<i>Cribellopora souleorum</i> n. sp.	R (AC)	–	3	2	5
<i>Nimba saxatilis</i>	R	–	2	–	2
<i>Crepidacantha carsioseta</i>	R	–	–	6	6
<i>Crepidacantha longiseta</i>	R	–	1	3	4
<i>Metacleidochasma verrucosa</i> n. sp.	R	–	–	1	1
<i>Rhynchozoon ferocula</i>	R	–	2	2	4
<i>Rhynchozoon splendens</i>	C	–	–	1	1
<i>Disporella pristis</i>	?	–	–	1	1
<i>Disporella compta</i> n. sp.	R	–	2	–	2
<i>Favosipora adunca</i> n. sp.	R	–	6	1	7
Total species		5 ^b	19	28	32

Numbers indicate colonies or colony fragments collected or, at Kealakekua, number of colonies observed without collection; p in place of a number indicates the species was present but not quantified. Since no bryozoans were found at Kiholo Bay, and only three dead colony fragments of *Hippopodina iririkiensis* at Whittington Beach, these localities are not included in the table.

^aR, observed only on rock but might also encrust calcareous substrata; C, observed only on calcareous substrata; R(C), almost exclusively on rock, but occasionally on calcareous substrata; R(AC), colonies observed on rock, but ancestrulae observed settled on calcareous substrata; C(R), primarily on calcareous substrata, but occasionally extending on to rock or entirely on rock.

^bTotal includes three species, each observed as a single colony, that were not collected and could not be identified.

Growth form and substratum

Ascophoran cheilostomes were by far the largest component of the Hawaiian intertidal bryozoan fauna. The 32 species found included 23 (72%) ascophorans, four (13%) anascans, two (6%) cribrimorphs, three (9%) cyclostomes, but no ctenostomes. All species were encrusting in growth form; no erect forms, either flexible or rigid, were found. Most of the ascophoran colonies were unilaminar, though frontal budding was observed in some

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species. *Rhynchozoon splendens* and *Drepanophora corrugata* built up a secondary layer in parts of the colony, and colonies of *Funerossia copiosa* occasionally showed a few frontally budded zooids. However, the colonies of these species were essentially two-dimensional, rather than nodular.

At least some of the colonies of most species were found attached directly to the lava substratum (Table I), though many of these species were also found on calcareous substrata upon the rock surface. However, some species were found mostly or exclusively on calcareous substrata. *Alderina flaventa* and *Watersipora* “*subovoidea*” were usually found overgrowing a layer of crustose coralline algae, though colonies sometimes extended past the boundary of this substratum on to the rock itself. The single colonies found for *Antropora minor* and *Rhynchozoon splendens* were each encrusting the calcareous tubes of polychaete worms. *Puellina harmeri* was usually found on serpulid worm tubes or on dead colonies of *Funerossia copiosa*, though it also occurred on rock. At Kealakekua Bay, *Hippopodina iririkiensis* was much more abundant on coral rubble than on rocks, though colonies were observed on both substrata. At the same locality, *Poricella spathulata* almost exclusively occurred in small cavities in lava boulders, though one colony encrusted a serpulid tube attached to the lava. *Fenestrulina caseola* and *Cribellopora souleorum* were both found primarily encrusting on rock, though in each case, two ancestrulae were found, and the ancestrulae had settled on encrusting coralline algae.

Taxonomy

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATIDA Busk, 1852
Suborder NEOCHEILOSTOMINA d’Hondt, 1985
Infraorder FLUSTRINA Smitt, 1868
Superfamily CALLOPOROIDEA Norman, 1903
Family CALLOPORIDAE Norman, 1903
Genus *Alderina* Norman, 1903
Alderina flaventa new species
 (Figure 3A–C)

? *Alderina smitti* Osburn 1950, p 59 (in part?).

Type material

Holotype: NHM 2006.7.21.1, specimen HI-50, bleached, coated for SEM; Kapa’a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratypes: same locality and collecting information as for holotype. Paratype 1, NHM 2006.7.21.2, specimen HI-42, bleached, coated for SEM. Paratype 2, NHM 2006.7.21.3, unbleached specimen. Paratype 3, NHM 2006.7.21.4, unbleached specimen; with *Parellisina albida* and *Hippopodina iririkiensis*. Paratype 4, YPM-38550, unbleached specimen; with *Funerossia copiosa*. Paratype 5, YPM-38551, unbleached specimen.

Etymology

The species name derives from the Latin *flavens* (yellow or gold coloured), referring to the conspicuous frontal pigmentation.

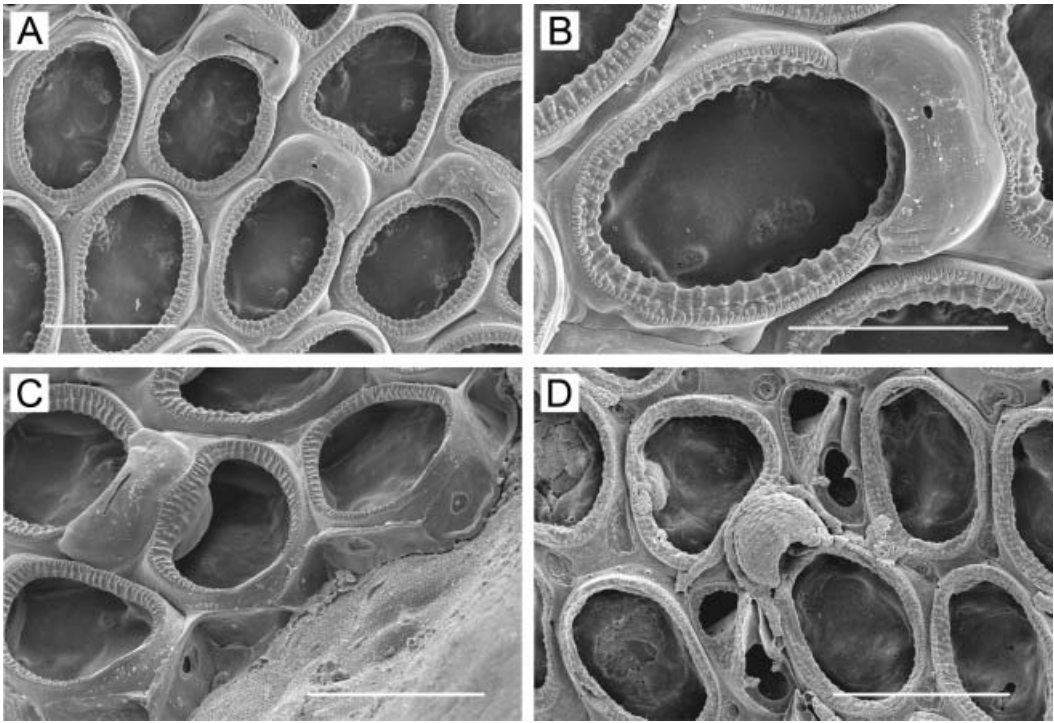


Figure 3. (A–C) *Alderina flaventa* n. sp., holotype (NHM 2006.7.21.1): (A) group of autozooids and ovicellate zooids; (B) ovicellate zooid; (C) colony margin showing uniporous septula. (D) *Parellisina albida* (Hincks): autozooids, ovicellate zooid, and interzooidal avicularia. All specimens bleached. Scale bars: 500 μ m (A, C, D); 400 μ m (B).

Measurements

ZL, 0.63–0.75 (0.656 ± 0.038). ZW, 0.39–0.48 (0.438 ± 0.032). OpL, 0.30–0.54 (0.451 ± 0.060). OpW, 0.26–0.33 (0.295 ± 0.021). OvL, 0.20–0.23 (0.208 ± 0.011). OvW, 0.38–0.45 (0.395 ± 0.033) (ovicells $n=5$).

Description

Colony unilaminar, encrusting, sheet-like, tan in colour; living zooids with white walls and with patchily distributed, golden-yellow granular pigmentation visible under transparent frontal membrane; margin of operculum with a reddish brown bordering sclerite. Zooids (Figure 3A, B) moderately large; oval or barrel-shaped in outline; distinct, separated by a shallow groove; basal wall completely calcified. Gymnocyst narrow, smooth, sloping basally, typically surrounding the zooid. Mural rim raised, sharp, finely crenulate on top. Cryptocyst narrow, sloping, tapering distally; coarsely crenulate, with beaded ribs perpendicular to circumference. Opesia (Figure 3A, B) broadly oval, elliptical, or bluntly triangular, the outline scalloped due to the cryptocystal ribbing. Spines and avicularia lacking. Ovicell (Figure 3A–C) raised, smooth, broader than long, closed by operculum; often with a narrow transverse slit or small irregular pore on top due to incomplete closure of ectocyst; tabula lacking. Zooids interconnect (Figure 3C) by a single uniporous septulum in the distal wall and one or two in each distolateral wall.

Remarks

Osburn (1950) reported two species of *Alderina* from the Pacific coast of North America, *A. brevispina* (O'Donoghue and O'Donoghue, 1926) and *A. smitti* Osburn, 1950. The former has larger zooids than our material, sometimes a minute spine or nodule lateral to the orifice, and a prominent transverse ridge across the ovicell. *Alderina smitti*, originally described from Florida as *Membranipora irregularis* Smitt, 1873 (a name preoccupied by *Membranipora irregularis* d'Orbigny), has been considered to be broadly distributed in the subtropical to tropical western Atlantic and eastern Pacific (Osburn 1950). However, it is unlikely that all the reports of this nominal species represent a single species, since descriptions indicated in Osburn's (1950) synonymy show considerable variation. Hastings (1930), for example, indicated a coarsely granulated ovicell in material from the tropical eastern Pacific. Both the original (Smitt 1873) and Osburn's (1950) subsequent descriptions show the opesia broadest proximally, and Osburn indicates smaller zooids than ours for material from the eastern Pacific. There are few records of the genus from the Indo-West Pacific; a report of *A. imbellis* (Hincks, 1860), a northern Atlantic species, from the Philippines (Canu and Bassler 1929) is almost certainly erroneous. Gordon (1986) described *Alderina pacifera* (as *Antropora pacifera*) from New Zealand (see Tilbrook 1998).

Distribution

This is the first record of an *Alderina* from the Hawaiian Islands. The species is known only from Kapa'a on the Island of Hawaii.

Genus *Parellisina* Osburn, 1940
***Parellisina albida* (Hincks, 1880)**
 (Figure 3D)

Membranipora albida Hincks 1880, p 81, Plate 10, Figure 5.

Parellisina albida: Hayward and Ryland 1995, p 538.

Parellisina curvirostris: Ryland and Hayward 1992, p 229, Figure 2d; ?Soule et al. 1988, p 147.

Measurements

ZL, 0.50–0.70 (0.590 ± 0.076). ZW, 0.33–0.43 (0.366 ± 0.032). OpL, 0.35–0.46 (0.397 ± 0.033). OpW, 0.21–0.28 (0.245 ± 0.018). OvL, 0.20–0.26 (0.232 ± 0.027). OvW, 0.20–0.28 (0.245 ± 0.028) (ovicell $n=7$).

Description

Colony unilaminar, encrusting, coarse, tan in colour. Zooids moderately large, separated by a deep groove. Gymnocyte negligible laterally, sometimes a little wider proximally, with one or a pair of minute uniporous openings evident frontally in angles of proximal gymnocyte, surrounded by a wide, finely granulated zone (these marginated unipores perhaps represent incipient kenozooids). Cryptocyte narrow, sloping, more or less constant in width proximally and laterally, with coarse granulation. Opesia occupying almost whole of frontal area, oval or somewhat irregular. Subtriangular or quadrate spaces between zooids occupied by large interzooidal avicularia, each associated with a distal kenozooid; rostrum raised, laterally curved and slightly twisted, one rostral edge higher than the other;

mandible broad at base, extended into sharp latero-basal lobes that taper rapidly to a narrow, long-triangular, almost setose mandible with a hooked tip; opesia of kenozooid irregular in shape, subtriangular, oval, or irregular, and variable in size even within a colony, generally equal to or larger than avicularian opesia. Spines lacking. Ovicell raised, globose, narrower than zooid, imperforate, the surface roughened with low, rounded tubercles, the proximal margin concave.

Remarks

Both this species and *P. falcata* (MacGillivray, 1869), reported from Australia, have a laterally curved avicularian mandible with sharp lateral extensions at the base; *P. falcata* differs in having zooids with a wide proximal cryptocyst (Osburn 1949). Although *P. curvirostris* (Hincks, 1862), originally described from Britain, has been considered circumglobal in warm-temperate and subtropical waters, many Pacific records of this species need to be re-examined. Our material differs from British *P. curvirostris* in having a granulated cryptocyst on the kenozooid, marginated pores on the proximal zooidal gymnocyst, and much larger zooids. Tilbrook (2006) recently recorded two species of *Parellisima* from the Solomon Islands, *P. suluensis* (Osburn 1949) and a new species, *P. mboliensis*.

Distribution

Originally described from an unspecified locality in the Indo-Malayan area (Hincks 1880), *P. albida* has subsequently been reported from the Great Barrier Reef, Australia (Ryland and Hayward 1992; Hayward and Ryland 1995). Our material might be conspecific with nominal *P. curvirostris* previously reported from Hawaii (Soule et al. 1988).

Genus *Corbulella* Gordon, 1984
***Corbulella extenuata* new species**
 (Figure 4A–D)

Type material

Holotype: NHM 2006.7.21.5, specimen HI-61, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide.

Etymology

The species name derives from the Latin *extenuata* (weak, slight), referring to the reduced ovicell.

Measurements

ZL, 0.48–0.60 (0.558 ± 0.0425). ZW, 0.38–0.45 (0.405 ± 0.028). OpL, 0.30–0.38 (0.335 ± 0.023). OpW, 0.23–0.25 (0.241 ± 0.010).

Description

Colony unilaminar, encrusting, sheet-like, tan in colour. Zooids distinct, well separated by deep grooves; in bleached specimens, small lacunae evident between broad zones of interzooidal connection. Several zooids show complete regeneration of a new zooid within

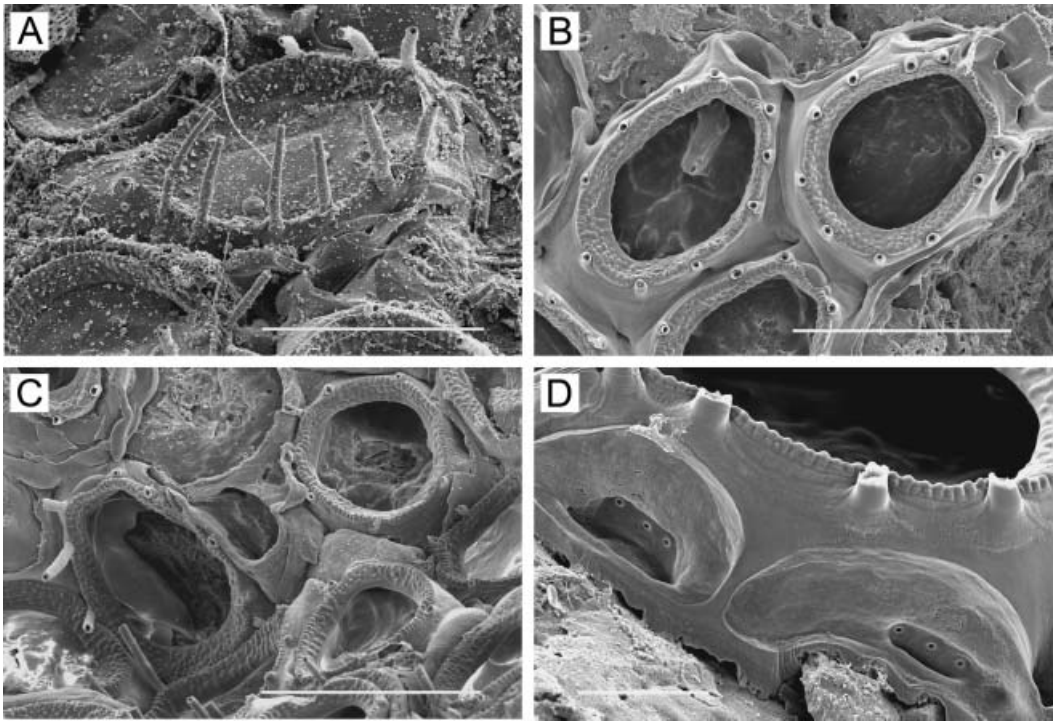


Figure 4. *Corbulella extenuata* n. sp., holotype (NHM 2006.7.21.5): (A) autozoooid, unbleached; (B) marginal zoooids, bleached; note cap-like reduced ovicells; (C) autozoooids and interzoooidal avicularium (centre), bleached; (D) lateral wall of marginal autozoooid showing septula, bleached. (B–D) are from same colony as (A), after bleaching. Scale bars: 500 μm (A, C, D); 400 μm (B).

the opesia of another, and in one case, two successive such regenerations. Gymnocyst (Figure 4A, B) smooth, sloping, visible around the zoid, extensive proximally, narrower laterally. Mural rim sharp, crenulate; cryptocyst a well-developed, sloping, coarsely granulated band inside mural rim, narrower distally than proximally. Around mural rim, 7–14 well-developed tubular spines (Figure 4A), the distal two pairs in the vicinity of the orifice thicker than the rest, with the distal pair erect and the second pair tilted toward midline; the other, more proximal spines thinner, often tilted over opesia, but not meeting in midline. Opesia (Figure 4B) oval, widest near middle or proximally. Ovicell vestigial, comprising a small cap (Figure 4B); both the mural rim and opesial margin are transversely straight at the distal end of the zoid, with the crenulated mural rim traversing the proximofrontal surface of the cap. What appears to be an interzoooidal avicularium (Figure 4C) is present, comprising about one-quarter the area of an autozoooid, without pivotal constrictions or hinge bar, without spines, the rostrum tapering and twisted distally. Zoooids interconnect by triporous septulae (Figure 4D).

Remarks

Only a single, small colony of quality useful for SEM observation was found. This species resembles *Corbulella corbula* (Hincks, 1880), which was reported from the Hawaiian Islands as *Pyrulella corbula* (Soule et al. 1988). However, that species has a narrower cryptocyst not continuing around the distal rim of the opesia; longer spines often meeting in the midline,

with a pair lateral to the orifice sometimes greatly elongated; a conspicuously developed ovicell; and vicarious avicularia around the same size as autozooids. In having a reduced, cap-like ovicell, *Corbulella extenuata* is similar to *Crassimarginatella spatulifera* Harmer, 1926 (*Corbulella* and *Crassimarginatella* were formerly considered subgenera within *Crassimarginatella*; see Gordon 1984; Tilbrook 2001). However, the latter species lacks spines and has vicarious avicularia larger than the autozooids. *Crassimarginatella corniculata* Tilbrook, 2001 has the ovicell even further reduced, evident only as a slightly raised distal margin on endozooidally brooding zooids.

Distribution

Kapa'a Beach on the Island of Hawaii is the only known locality.

Family ANTROPORIDAE Vigneaux, 1949

Genus *Antropora* Norman, 1903

Antropora minor (Hincks, 1880)

(Figure 5A, B)

“?Membranipora trifolium S. Wood, var. *minor*” Hincks 1880, p 87, Plate 11, Figure 6.

Antropora minor: Tilbrook 1998, p 34, Figure 2A–F; 2006, p 30, Figure 4B; Tilbrook et al. 2001, p 41, Figure 3A.

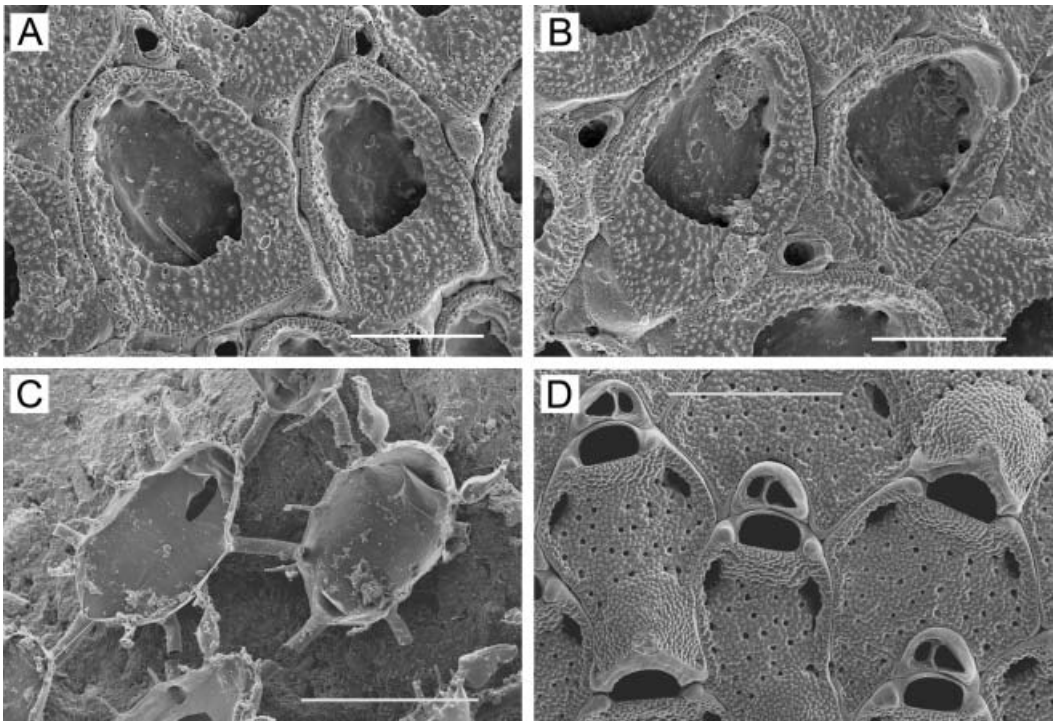


Figure 5. (A, B) *Antropora minor* (Hincks): (A) autozooids, bleached; (B) autozooids, bleached; zooid at right is a brooding zooid, with a raised, smooth distal margin that may represent a vestigial ovicell. (C) *Beania discodermiae* (Ortmann): autozooids, unbleached. (D) *Micropora rimulata* Canu and Bassler: autozooids and ovicellate zooids, bleached. Scale bars: 200 μ m (A, B); 500 μ m (C, D).

Measurements

ZL, 0.35–0.48 (0.422 ± 0.044). ZW, 0.23–0.35 (0.273 ± 0.039). OpL, 0.21–0.28 (0.240 ± 0.023). OpW, 0.14–0.16 (0.149 ± 0.009).

Description

Colony unilaminar, encrusting. Gymnocyst scarcely evident; cryptocyst (Figure 5A, B) very wide and shallowly sloping proximally, narrowing and steep distally, with coarse, rather irregularly arranged tubercles; opesia large, irregularly oval or subtriangular. Interzooidal avicularia small, on a raised cystid; some zooids have a kenozooidal papilla at proximal end, replacing or together with an avicularium. Ovicells lacking, but the raised, smooth distal zooidal margin in fertile zooids (Figure 5B) may represent a vestigial ovicell. Spines lacking. Autozooid-sized vicarious avicularia can occur, but are absent in our specimen.

Remarks

Only one small, dead colony fragment was found, at Kapa'a.

Distribution

Circumtropical (Tilbrook, 1998); not previously reported from the Hawaiian Islands.

Superfamily BUGULOIDEA Gray, 1848
Family BEANIIDAE Canu and Bassler, 1927
Genus *Beania* Johnston, 1840
Beania discodermiae (Ortmann, 1890)
(Figure 5C)

Diachoseris discodermiae Ortmann 1890, p 26, Plate 1, Figure 23.

Beania discodermiae: Gordon 1984, p 45, Plate 11D, E.

Measurements

OpL, 0.50–0.58 (0.554 ± 0.030). OpW, 0.28–0.31 (0.294 ± 0.012). AvL, 0.13–0.18 (0.153 ± 0.017).

Description

Zooids well separated, each connecting with others by six narrow tubular extensions, the distance between opesiae greater than half the opesial width. Five short, thin spines around distalmost curvature and four slightly longer spines more proximally along each lateral margin; spines erect or angled outward, not obscuring opesia. Pedunculate avicularia single or paired lateral to orifice, with a bulbous chamber and narrow, laterally compressed rostrum; avicularium length greater than twice avicularium width.

Distribution

Japan, Malaysia, New Zealand (Gordon 1984). This is the first record from the Hawaiian Islands.

Superfamily MICROPOROIDEA Gray, 1848
Family MICROPORIDAE Gray, 1848
Genus *Micropora* Gray, 1848
Micropora rimulata Canu and Bassler, 1929
 (Figure 5D)

Micropora rimulata Canu and Bassler 1929, p 137, Plate 14, Figure 4.

? *Micropora coriacea*: Canu and Bassler 1927, p 7, Plate 1, Figure 6.

Measurements

ZL, 0.53–0.75 (0.663 ± 0.069), not including distal avicularium. ZW, 0.40–0.54 (0.479 ± 0.043). AzOrL, 0.08–0.10 (0.090 ± 0.008). AzOrW, 0.14–0.18 (0.156 ± 0.014). OvZOrL, 0.10–0.11 (0.105 ± 0.006). OvZOrW, 0.16–0.19 (0.169 ± 0.010). OvL, 0.25–0.33 (0.290 ± 0.025). OvW, 0.25–0.30 (0.280 ± 0.017).

Description

Colony unilaminar, encrusting, sheet-like, white in colour, with glistening ectocyst. Zooids variable in shape; irregularly rounded-hexagonal, barrel-shaped, or tapering pyriform in outline; sometimes as broad as long; distinct, delineated by a thin incision and a thickened, raised, granulated margin most pronounced where it borders the opesiules. Frontal wall flat to slightly convex, finely granulated, evenly perforated with fine pores, with a large, elongate opesiule, often tapering proximally, on each side proximolateral to orifice. Orifice elevated from frontal surface by a raised, granulated proximal border confluent with raised zooidal margins lateral to opesiules; flanked by a smooth knob on each side. Orifice dimorphic; almost quadrate with rounded distolateral corners in non-ovicellate zooids; broader than long, semicircular, and larger in ovicellate zooids. Ovicell distinct, about as broad as long, partly sunken in frontal wall of distal zooid, imperforate, finely granulated with same texture as frontal wall, the proximal margin with a smooth, raised, chevron-shaped lip usually with a tubercle at the apex; closed by operculum. An avicularium lies distal to orifice of non-ovicellate zooids; chamber raised, smooth, almost semicircular in outline, the rostrum occupying most of the top; hinge bar complete; mandible acute, longer than broad, in the shape of a right triangle, distal edge slightly longer than the proximal, pointing laterally or slightly proximolaterally. Spines lacking.

Remarks

We identify our material as *M. rimulata* on the basis of similar zooidal measurements; the imperforate ovicell narrower than zooid width; the chevron-shaped ridge, with an apical median boss, forming the proximal margin of the ovicell (in the original description by Canu and Basler 1929, the boss is slightly separate from the ridge as a central tubercle on the ovicell); the dimorphism in orifice size between ovicellate and non-ovicellate zooids (not as pronounced in our material as in the original description); and particularly the shape and orientation of the avicularian mandible. Canu and Bassler (1927) reported nominal *M. coriacea* (Johnston, 1847), a European species (see Harmer 1926 for a discussion of this species' nomenclatural problems), from 335–483 m depth off Oahu; the specimen they illustrated is similar in many respects to our material and may be conspecific.

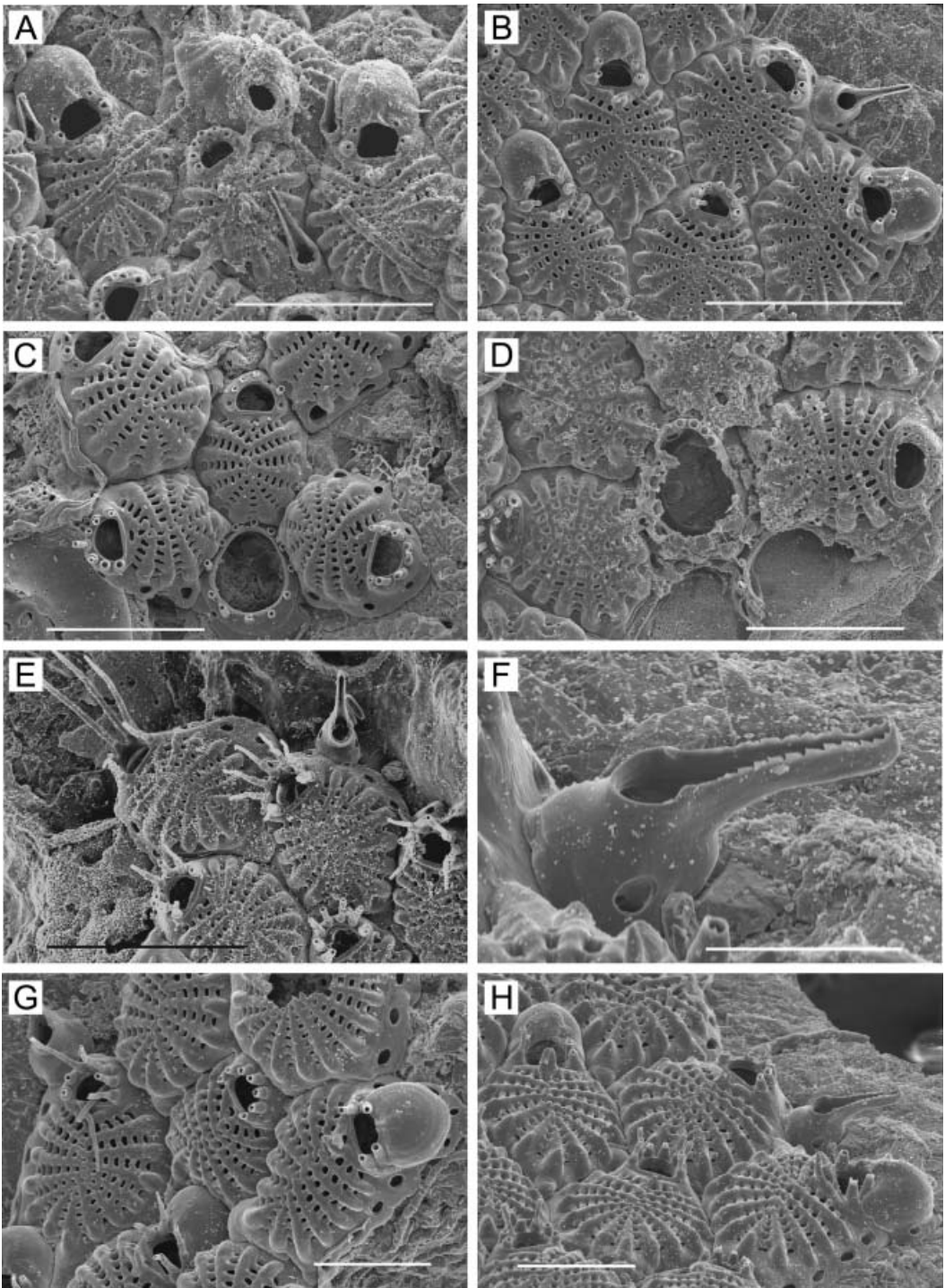


Figure 6. (A, C, E, G) *Puellina harmeri* Ristedt: (A) autozooid, ovicellate zooids, and avicularia; (C) ancestrula and periancestrular zooids; (E) marginal zooids, showing long distal spines and marginal avicularium; (G) oblique view of autozooids and ovicellate zooids. (B, D, F, H) *Puellina septemcryptica* n. sp.: (B) paratype (NHM 2006.7.21.7),

Soule et al. (1988) reported two *Micropora* species of uncertain identity from the Hawaiian Islands.

Distribution

The only other report of *M. rimulata* is from the Philippines (Canu and Bassler 1929).

Infraorder ASCOPHORA Levinsen, 1909
“Grade” ACANTHOSTEGA Levinsen, 1902
Superfamily CRIBRILINOIDEA Hincks, 1879
Family CRIBRILINIDAE Hincks, 1879
Genus *Puellina* Jullien, 1886
Puellina harmeri Ristedt, 1985
 (Figure 6A, C, E, G)

Puellina harmeri Ristedt 1985, p 26, Figures 1, 6a–e, 7a–k, 8a–j, 9a–d.

Cribrilaria harmeri: Hayward 1988, p 290, Plate 3c.

Measurements

ZL, 0.30–0.43 (0.334 ± 0.037). ZW, 0.23–0.28 (0.255 ± 0.017). OrL, 0.04–0.07 (0.052 ± 0.008). OrW, 0.06–0.08 (0.068 ± 0.006). OvL, 0.14–0.18 (0.159 ± 0.015). OvW, 0.14–0.17 (0.156 ± 0.010).

Description

Colony unilaminar, encrusting, forming small whitish patches; zooids separated by a sharp groove. Frontal shield in astogenetically mature zooids (Figure 6A, E, G) composed of 15–18 (mode=16) fused costae that rise at an angle to the margin, then turn gently to form the slightly convex surface of the shield; a boss is poorly developed or lacking at the angle of the turn; four to six (mode=five) intercostal pores between adjacent costae. Subapertural lumen generally single, conspicuous, close to proximal margin of orifice, bounded proximally by short pair of costae that sometimes form a small umbo in midline; sometimes a second, smaller suboral lumen is present just proximal to the first. Primary orifice (Figure 6C) semicircular, proximal margin straight, with seven stout, closely spaced oral spines. Small, irregularly shaped kenozooids occur rarely among feeding zooids, with a smooth gymnocystal rim, fewer than 10 costae, and no orifice. Ovicellate zooids with five oral spines; ovicell (Figure 6A) globose, smooth, with a slight, proximodistally elongate ridge or umbo near proximal margin; ovicell incorporates one pair of spines and abuts another at proximolateral corners, with fifth spine hidden by ovicell and probably lost. Interzooidal avicularia (Figure 6A, E) uncommon, usually arising from distolateral corner of a zooid, the chamber bulbous, the rostrum long and tapering, with serrate edges; some zooids have on one or both sides of ovicell a smaller adventitious avicularium (Figure 6A) pointing distally, connecting to a pore in proximolateral wall of ovicell; ovicell of type C, a distal component of a maternal zooid (Bishop and Househam 1987). Ancestrula

autozooids, ovicellate zooids, and a marginal avicularium; (D) holotype (NHM 2006.7.21.6), ancestrula and periancestrular zooids; (F) paratype, enlargement of marginal avicularium seen in (B); (H) paratype, oblique view of most of the same zooids as seen in (B). All specimens bleached. Scale bars: 400 μ m (A, B, E); 200 μ m (C, D, G, H); 100 μ m (F). Note that pairs (A, B), (C, D), and (G, H) are to same scale.

(Figure 6C) tatiform, with 12 spines; initially gives rise to a distal and a pair of distolateral daughter zooids.

Remarks

Our material may have smaller zooids and ovicells than indicated in Ristedt's (1985) original description, although this is unclear, since Ristedt included only maximum zooidal measurements. Orifice measurements are very similar, as are virtually all morphological features, including the 12-spined tatiform ancestrula, periancestrular zooids with around 10 costae, and a type C (Bishop and Househam 1987) ovicell.

Three nominal species of tropical *Puellina* with seven oral spines have previously been described: *P. africana* Hayward and Cook, 1983; *P. harmeri* Ristedt, 1985; and *P. vulgaris* Ryland and Hayward, 1992. *Puellina africana* is distinct in having fewer costae than the latter two species, and a triangular suboral area with up to five large pores. However, it is not entirely clear from the description of *P. vulgaris* what distinguishes it from *P. harmeri*. Ryland and Hayward (1992) mentioned as diagnostic characters for *P. vulgaris* seven oral spines, a conspicuous subapertural lacuna, and a rather small avicularium. The first two characters apply as well to *P. harmeri*, and avicularium size in *P. vulgaris* appears to fall within the range of intercolony variation in *P. harmeri*. Zooid size is an ambiguous character, as Ristedt (1985) mentioned only maximum zooidal dimensions, whereas Ryland and Hayward (1992) gave an average. Tilbrook (2006) described the ancestrula of *P. vulgaris* as tatiform, but with 14 spines rather than the 12 spines originally reported for *P. harmeri* and present in our material. Although these two species may eventually prove to be synonymous, further study is needed to determine whether this is the case.

Distribution

Ristedt (1985) originally described *P. harmeri* from the Philippines, but also reported it from the Red Sea and Seychelle Islands, noting that it was the most common and widely distributed among the five Indo-Pacific *Puellina* (*Cribrilaria*) he studied; Hayward (1988) reported it from Mauritius. This is the first record for the Hawaiian Islands.

***Puellina septemcryptica* new species**

(Figure 6B, D, F, H)

Type material

Holotype: NHM 2006.7.21.6, specimen HI-5 (part), two ancestrular colonies encrusting *Junerosia copiosa*, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratype: NHM 2006.7.21.7, same locality and collecting information as for holotype; specimen HI-11 (part); one minute fragment.

Etymology

The species name derives from the Latin *septem* (seven) and the latinized Greek *kruptos* (hidden).

Measurements

ZL, 0.25–0.33 (0.281 ± 0.0229). ZW, 0.16–0.24 (0.196 ± 0.023). OrL, 0.04–0.05 (0.042 ± 0.005). OrW, 0.04–0.06 (0.052 ± 0.007). OvL, 0.10–0.14 (0.118 ± 0.013). OvW, 0.11–0.14 (0.128 ± 0.009).

Description

Colony unilaminar, encrusting, forming small whitish patches; zooids separated by a sharp groove. Frontal shield (Figure 6B, H) composed of 14–18 (mode=14) fused costae that rise at an angle to the margin, then turn sharply to form the nearly flat surface of the shield; a boss is present at the angle of the turn; four to six (mode=five) intercostal pores between adjacent costae. Subapertural lumen single, close to proximal margin of orifice, bounded proximally by short pair of costae that sometimes form a small umbo in midline; umbo sometimes quite raised, sharp (Figure 6H). Primary orifice (Figure 6B) semicircular, broader than long in non-ovicellate zooids, proximal margin straight, with seven stout, closely spaced oral spines. Interzooidal kenozooids were not observed. Ovicell (Figure 6B, H) globose, smooth, with a slight, proximodistally elongate ridge or umbo near proximal margin; ovicell incorporates one pair of spines and abuts another at proximolateral corners. Interzooidal avicularia (Figure 6B, F, H) uncommon, usually arising from distolateral corner of a zooid, the chamber bulbous, the rostrum long and tapering, with serrate edges (Figure 6F); avicularia associated with ovicell not observed. Ovicell of type C, a distal component of the maternal zooid (Bishop and Househam 1987). Ancestrula (Figure 6D) a zooid similar to but smaller than subsequent zooids, with the frontal costae incompletely developed in our specimen; initially buds a distolateral pair of daughter zooids, and eventually is surrounded by additional lateral and proximolateral pairs of daughter zooids.

Remarks

We found two *Puellina* species on the Island of Hawaii; in addition to having clearly different ancestrulae, one of them has conspicuously larger zooids than the other. We have identified the species with larger zooids as *P. harmeri* on the basis of occasionally having one or two avicularia associated with an ovicell, and having a tatiform ancestrula with 12 spines. The smaller species on the Island of Hawaii has a non-tatiform ancestrula, which thus distinguishes it from *P. harmeri* and *P. vulgaris*, and primarily on this basis, we describe it as a new species, *P. septemcryptica*.

Puellina septemcryptica differs from *P. harmeri* on the Island of Hawaii in having smaller zooids, ovicells, and orifices (compare Figure 6B with 6A, which are to the same scale), a non-tatiform ancestrula (compare Figure 6D with 6C), and periancestrular zooids having 13–14 costae rather than the 11–12 in *P. harmeri*; the ancestrular budding pattern is also different. The frontal shield of *P. septemcryptica* is flatter, with a comparatively strong boss at the marginal curvature of each costa. The frontal shield of *P. harmeri* is more convex; a boss is less consistently present, and is less pronounced when it is present (compare Figure 6H with 6G). Finally, avicularia are less common in *P. septemcryptica* than in *P. harmeri*, and the avicularia sometimes closely associated with the ovicell that occur in the latter were not observed in *P. septemcryptica*.

Distribution

Puellina septemcryptica is known only from Kapa'a Shore, Island of Hawaii.

“Grade” HIPPOTHOOMORPHA Gordon, 1989
Superfamily HIPPOTHOOIDEA Busk, 1859
Family HIPPOTHOIDAE Busk, 1859
Genus *Hippothoa* Lamouroux, 1821
Hippothoa flagellum Manzoni, 1870
(Figure 7A, B)

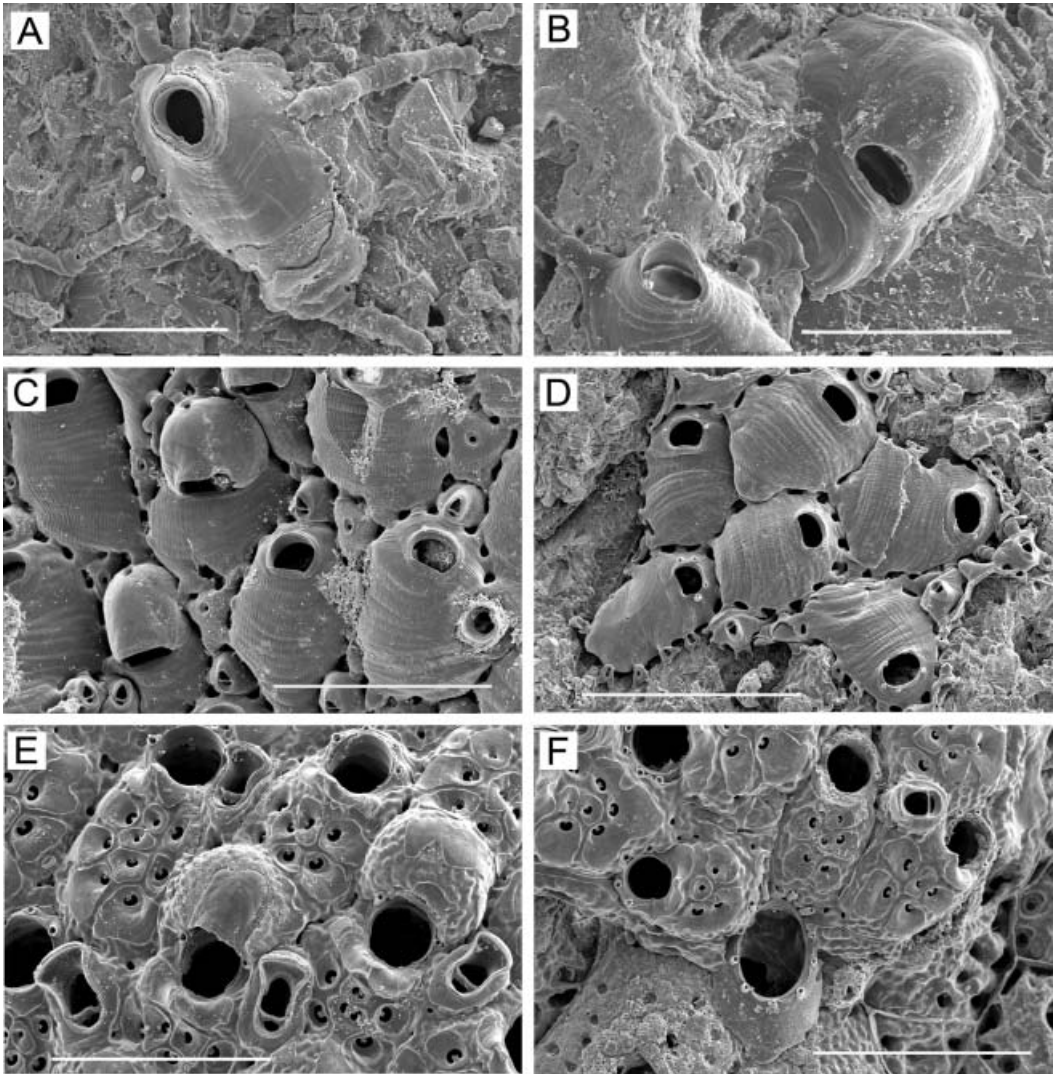


Figure 7. (A, B) *Hippothoa flagellum* Manzoni: (A) autozooid; (B) autozooid (part) and ovicellate zooid. (C, D) *Chorizopora brogniartii* (Audouin) *sensu lato*: (C) autozooids, ovicellate zooids, interzooidal kenozooids, and avicularia; (D) ancestrula (lower left) and early astogeny. (E, F) *Poricella spathulata* (Canu and Bassler): (E) autozooids, ovicellate zooids, and interzooidal avicularia; (F) ancestrula (bottom centre) and periancestral zooids. All specimens bleached. Scale bars: 200 μ m (A, B); 500 μ m (C–F).

Hippothoa flagellum Manzoni 1870, p 328.

Hippothoa flagellum: Hayward and Ryland 1999, p 88, Figures 17C, D, 18; Tilbrook et al. 2001, p 62, Figure 9C, D.

Measurements

ZL (exclusive of cauda), 0.21–0.29 (0.242 ± 0.028). ZW, 0.12–0.19 (0.148 ± 0.022). OrL, 0.05–0.06 (0.054 ± 0.006). OrW, 0.04–0.06 (0.043 ± 0.006). OvL, 0.14–0.17 (0.151). OvW, 0.14–0.16 (0.150) (ovicell $n=2$).

Description

Colony unilaminar, encrusting, white, consisting of fine network of tiny zooids interconnected by long caudae; zooids bud in cruciform fashion, connecting to as many as four other zooids. Frontal wall hyaline, convex, transversely striated; cauda one to several times as long as dilated portion of zooid. Polymorphs include autozooids, female zooids, and zooeciules. Primary orifice of autozooid (Figure 7A) longer than broad, the poster proximal to minute condyles deep and U-shaped. Female zooids budded laterally from autozooids; female secondary orifice (Figure 7B) including ovicell margin is roughly D-shaped, with small condyles in the corners and the proximal margin shallowly concave. Ovicell (Figure 7B) imperforate except for a minute pore near proximal margin.

Distribution

Hippothoa flagellum Manzoni has been regarded as a cosmopolitan species, occurring in shallow shelf habitats from subpolar regions to the tropics. However, detailed study will likely resolve it into a worldwide complex of morphologically similar, geographically limited species, an enterprise that is beyond the scope of this study. This is the first record of the nominal species from the Hawaiian Islands.

Family CHORIZOPORIDAE Vigneaux, 1949

Genus *Chorizopora* Hincks, 1880

Chorizopora brogniartii (Audouin, 1826) sensu lato (Figure 7C, D)

Flustra brogniartii Audouin 1826, p 240.

Chorizopora brogniartii: Gordon 1984, p 113, Plate 44C; Tilbrook et al. 2001, p 64, Figure 8C; Tilbrook 2006, p 102, Figure 17B–D.

Measurements

ZL, 0.30–0.45 (0.398 ± 0.043). ZW, 0.25–0.30 (0.264 ± 0.017). OrL, 0.06–0.07 (0.063 ± 0.0016). OrW, 0.09–0.11 (0.099 ± 0.009). OvL, 0.15–0.18 (0.169 ± 0.011). OvW, 0.18–0.23 (0.196 ± 0.017) (ovicell $n=6$).

Description

Colony unilaminar, encrusting; zooids interconnect by tubular pore chambers. Frontal wall gymnocystal, thin-walled, hyaline, non-spinous, finely transversely ridged, with finer

perpendicularly orientated striae. Orifice (Figure 7C) more than semicircular, broader than long, with proximal margin straight or slightly convex; orifice of ovicellate zooids larger than that of non-ovicellate zooids. Avicularia interzooidal, often immediately distal to a zooid; interzooidal kenozooids present. Ovicell (Figure 7C) raised, hemispherical, smooth, imperforate, not associated with an avicularium. Ancestrula (Figure 7D) similar to but smaller than subsequent autozooids, with four orificial spines and a tiny mid-frontal pore.

Remarks

There are some differences between our material and that described from other localities. For example, Hayward and Ryland (1999) indicate an oval ancestrula with four frontal spines for British material, whereas an ancestrula we observed (Figure 7D) is elongate and lacks frontal spines. Furthermore, an avicularium is generally associated with the ovicell in specimens from Britain, Vanuatu (Tilbrook et al. 2001), and New Zealand (Gordon 1984), but not in our material. Nominal *C. brogniartii* from New Zealand has a sharp suboral “papilla” (Gordon 1984). In Britain, *C. brogniartii* is sublittoral, whereas specimens similar to this species occur intertidally in Panama (M. H. Dick, unpublished data) and Hawaii. Hayward and Ryland (1999) furthermore mentioned that considerable variation exists in zooid size among geographically separate populations. These sorts of variation suggest that nominal *C. brogniartii* includes a number of distinct species worldwide; however, it is beyond the scope of this paper to resolve this issue.

Distribution

Putatively circumglobal, in tropical and temperate shelf habitats (Tilbrook et al. 2001). This is the first record from the Hawaiian Islands.

“Grade” UMBONULOMORPHA Gordon, 1989
Superfamily ARACHNOPUSIOIDEA Jullien, 1888
Family ARACHNOPUSIIDAE Jullien, 1888
Genus *Poricella* Canu, 1904
Poricella spathulata (Canu and Bassler, 1929)
 (Figure 7E, F)

Hiantopora spathulata Canu and Bassler 1929, p 116, Plate 11, Figures 13, 14.

Tremogasterina spathulata: Ryland and Hayward 1992, p 249, Figure 13e.

Poricella spathulata: Tilbrook et al. 2001, p 65, Figure 10B; Tilbrook 2006, p 113, Figure 16B.

Measurements

ZL, 0.45–0.65 (0.538 ± 0.055). ZW, 0.26–0.48 (0.350 ± 0.062). OrL, 0.13–0.15 (0.140 ± 0.006). OrW, 0.12–0.14 (0.129 ± 0.007). OvL, 0.16–0.24 (0.208 ± 0.031). OvW, 0.23–0.30 (0.260 ± 0.033) (ovicell $n=5$).

Description

Colony unilaminar, encrusting, white, small. Frontal wall convex, with minute marginal pores and with 7–10 large, crescentic pores (Figure 7E) in centre, each surrounded by a

broad rim, giving the frontal a tessellated appearance. Orifice longer than broad, proximal margin straight, poster about one-third of orifice length and delineated by small lateral condyles; proximal to orifice is a thick crescentic ridge, rising to an umbo or sharp point. Scattered between zooids are large avicularia (Figure 7E), budded distolaterally from zooids, with a truncate-spatulate rostrum and mandible of the same shape. Large, vicarious avicularia have been reported in this species (Cook 1977; Tilbrook et al. 2001) but we did not observe them in the specimens from Hawaii. Ovicell (Figure 7E) raised, globose, imperforate, the surface rugose but with irregular smooth areas. Marginal zooids with four distal spines. Ancestrula (Figure 7F) tatform, with 11 spines.

Remarks

This was one of the two dominant bryozoan species at Kealakekua Bay. The other, *Hippopodina irikiensis*, grew predominantly on coral rubble, whereas *P. spatulata* was found exclusively in the surface cavities of porous lava boulders.

Distribution

Widely distributed in Indo-West Pacific, from Red Sea to Philippines; Great Barrier Reef, Australia; Mauritius; Vanuatu (for references, see synonymies). This is the first record for the Hawaiian Islands.

Superfamily LEPRALIELLOIDEA Vigneaux, 1949

Family LEPRALIELLIDAE Vigneaux, 1949

Genus *Drepanophora* Harmer, 1957

Drepanophora corrugata (Thornely, 1905)

(Figure 8A, B)

Rhyncopora corrugata Thornely 1905, p 118, Figure 5.

Drepanophora corrugata: Harmer 1957, p 1080, Plate 70, Figures 29–31; Hayward 1988, p 338, Plate 14c, d.

Measurements

ZL, 0.48–0.65 (0.538 ± 0.066). ZW, 0.28–0.46 (0.369 ± 0.055). OrL, 0.09–0.14 (0.112 ± 0.013). OrW, 0.13–0.16 (0.151 ± 0.008).

Description

Two small colonies adjacent to one another, lacking ovicells, the larger 3.5 mm in diameter, were found on lava rock. Colony encrusting, multiserial, unilaminar at first but becoming multilaminar by frontal budding. Zooids in primary layer irregularly hexagonal, oval, or barrel-shaped, separated by a deep groove; in secondary layer, zooids haphazardly orientated and zooidal boundaries indistinct. Frontal wall (Figure 8A) well calcified, markedly convex, inflated; imperforate except for two to four round areolar pores well spaced along each lateral margin; rugose with uniform, low, rounded tubercles. Primary orifice transversely elliptical, the proximal margin typically with a pair of long, prominent, acute lateral condylar processes, with a similarly long and acute denticle between them (Figure 8B), often offset to a greater or lesser extent to one side or the other; there is considerable variation in the arrangement of these three orificial processes. In older zooids, primary orifice lies deep in peristome, difficult

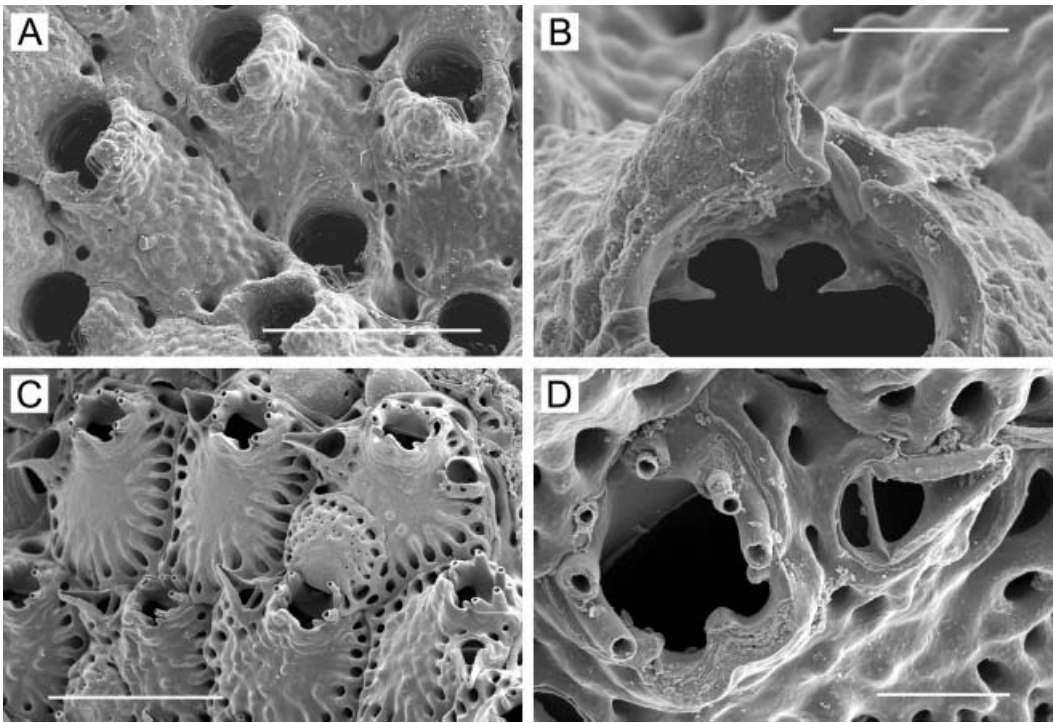


Figure 8. (A, B) *Drepanophora corrugata* (Thornely): (A) autozooids; (B) enlargement of orifice from distal view showing lyra and condyles. (C, D) *Escharoides longirostris* (Dumont): (C) autozooids and one ovicellate zooid; (D) enlargement of orifice and lateral oral avicularium. All specimens bleached. Scale bars: 500 μm (A, C); 100 μm (B, D).

to observe. Peristome a thick, raised rim, highest proximally; discontinuous, with a deep, more or less circular sinus flanked by the avicularian rostrum near the midline and a sharp, coarse, conical peristomial process lower down arising from the margin of the peristome. Suboral avicularian chamber umbonate; avicularian rostrum offset slightly from midline, oval in outline, angled acutely from the frontal plane, facing laterally, cross bar complete; mandible semicircular, directed obliquely upward from plane of colony surface. Secondary orifice, including the peristomial sinus, longer than broad, irregularly pyriform due to the sinus. Spines lacking. Ovicell not observed in our material, but Harmer (1957) illustrated it has hyperstomial, globose, with a pair of large foramina.

Distribution

Originally described from Ceylon (Thornely 1905); also reported from Indonesia (Harmer 1957) and Mauritius (Hayward 1988). This is the first record for the Hawaiian Islands.

Family ROMANCHEINIDAE Jullien, 1888

Genus *Escharoides* Edwards, 1836

Escharoides longirostris Dumont, 1981

(Figure 8C, D)

Escharoides longirostris Dumont 1981, p 630, Figure 1A.

Escharoides longirostris: Hayward 1988, p 293; Hayward and Ryland 1995, p 548, Figure 8A; Tilbrook et al. 2001, p 70.

Measurements

ZL, 0.38–0.54 (0.479 ± 0.050). ZW, 0.40–0.48 (0.448 ± 0.030). OrL, 0.12–0.14, (0.131 ± 0.007). OrW, 0.11–0.15 (0.130 ± 0.011). OvL, 0.21–0.26 (0.245 ± 0.015). OvW, 0.24–0.34 (0.289 ± 0.030).

Description

Colony small, the largest observed 4.5 mm × 3.0 mm; unilaminar, encrusting, sheet-like. Zooids irregularly hexagonal or barrel-shaped, distinct, delineated by a fine incision. Frontal wall moderately convex, imperforate centrally, with numerous circular areolar pores closely spaced along margins, sometimes with an additional row at lateral corners of zooid; texture smooth in young zooids, with buttresses of secondary calcification (Figure 8C) growing centripetally between areolae; with age, frontal uniformly tuberculate or with scattered nodules. Primary orifice (Figure 8D) reminiscent of a fleur-de-lis in shape, with a large, coarse median denticle and swollen lateral projections; the proximal margin is raised and thickened to form a low peristome, and the denticle and lateral projections extend along the length of the inner surface. Three pairs of spines (Figure 8D) flank the orifice laterally and distally. Lateral to proximal margin of orifice is a large adventitious avicularium on one or both sides (Figure 8C, D), sometimes lacking; the laterally directed rostrum up to 0.25 mm long but generally shorter, laterally compressed, often hooked at the end, with the rostral margin finely serrate; mandible long-triangular, acute. Avicularian chamber with a row of areolae at the base. Ovicell (Figure 8C) hemispherical, somewhat flattened, slightly broader than long, ringed by conspicuous circular pores around margin, with scattered minute pores inside that, the perforate area rugose with age; smooth and imperforate centrally and proximally; proximolateral corners of ovicell abut the middle pair of spines.

Distribution

Originally described from the Sudanese Red Sea (Dumont 1981), this species has also been reported from Mauritius (Hayward 1988) and Vanuatu (Tilbrook et al. 2001). This is the first record of the genus and the species from the Hawaiian Islands.

“Grade” LEPRALIOMORPHA Gordon, 1989
Superfamily SMITTINOIDEA Levinsen, 1909
Family SMITTINIDAE Levinsen, 1909
Genus *Parasmittina* Osburn, 1952
Parasmittina serrula Soule and Soule, 1973
 (Figure 9A–D)

Parasmittina serrula Soule and Soule 1973, p 386, Figure 3D–F.

Parasmittina serrula: Ryland and Hayward 1992, p 272, Figures 23e, f, 24a; Tilbrook et al. 2001, p 76, Figure 14E, F; Tilbrook 2006, p 154, Figures 28C, 31A–C.

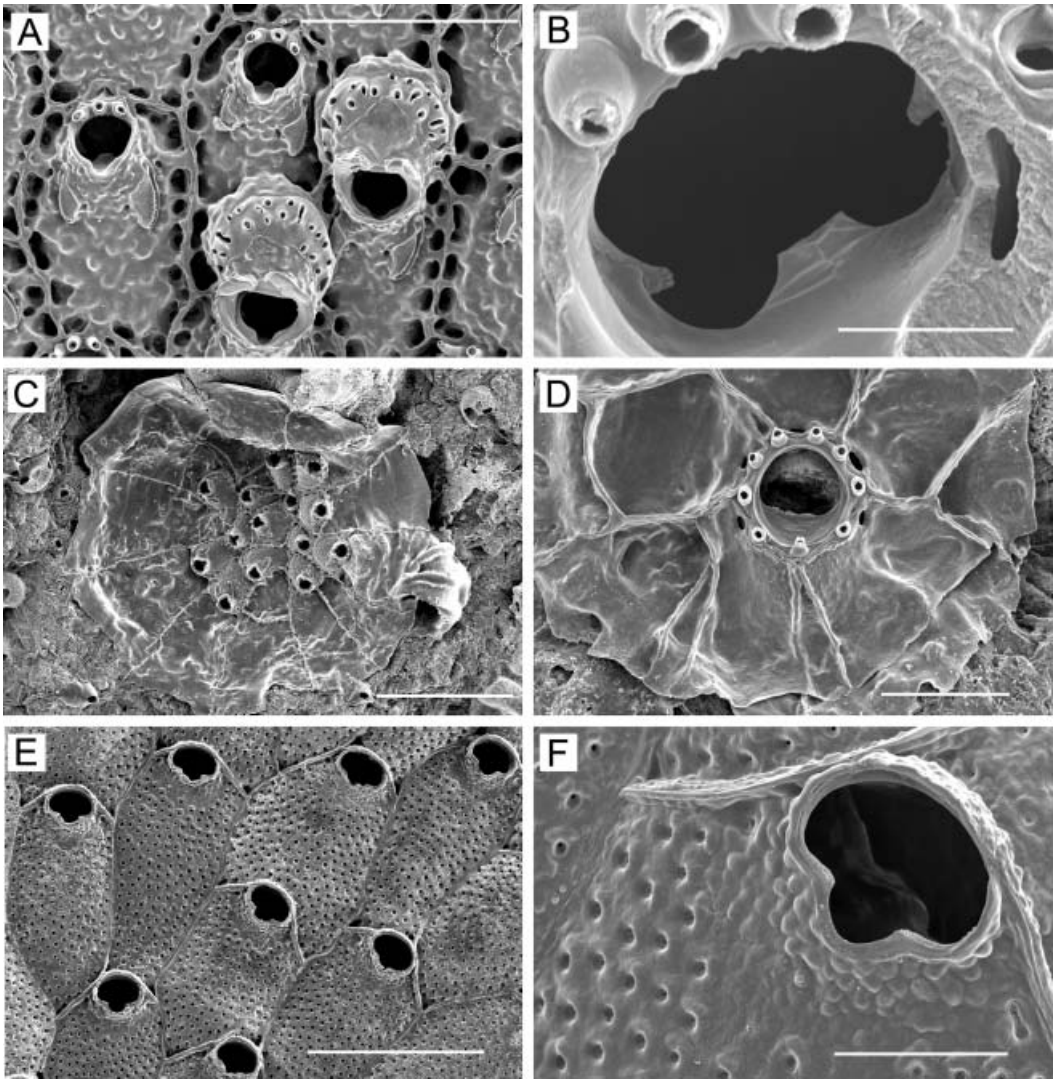


Figure 9. (A–D) *Parasmittina serrula* Soule and Soule: (A) autozooids and ovicellate zooids; (B) enlargement of orifice; (C) young colony showing wide marginal lamina; (D) ancestrula and surrounding marginal lamina. (E, F) *Watersipora subovoidea sensu* Harmer: (E) autozooids; (F) enlargement of orifice. All specimens bleached. Scale bars: 400 μm (A); 50 μm (B); 1 mm (C, E); 200 μm (D, F).

Measurements

ZL, 0.28–0.53 (0.378 ± 0.077). ZW, 0.24–0.36 (0.278 ± 0.035). SecOrL, 0.09–0.12 (0.098 ± 0.009). SecOrW, 0.09–0.11 (0.105 ± 0.010). OvL, 0.15–0.21 (0.185 ± 0.017). OvW, 0.20–0.25 (0.235 ± 0.018).

Description

Colony unilaminar, encrusting, tan-white in colour, surrounded by a wide marginal lamina (Figure 9C). Frontal wall (Figure 9A) convex, tuberculate, surrounded by conspicuous

marginal pores. Primary orifice (Figure 9B) sunken deep in peristome, broader than long, serrate along distal margin, with a truncate lyrula and conspicuous, proximomedially directed condyles that are denticulate at tip. Peristome a thick, raised collar, often with a groove along inside proximal surface that shows as a sinus in the secondary orifice (Figure 9A). An avicularium (Figure 9A) lies proximolateral to orifice on one or both sides, sometimes lacking; the smooth-sided chamber is laid over on one side and is both decurved and slightly laterally curved; rostrum long and narrow, typically pointing proximally, serrated on one edge; the avicularia vary considerably in size and orientation, and occasionally one at the base of the peristome is hypertrophied as a giant avicularium with one rostral edge highly and the other moderately serrated, though this type is uncommon in our material. Ovicell (Figure 9A) raised, globose; either with two rows of large, irregular pores peripherally and imperforate in centre, or with pores scattered over whole surface, this variation occurring within a single colony; proximal lip of ovicell raised, confluent with peristome. Marginal and non-ovicellate zooids typically with three (two to four) stout distal spines (Figure 9B). Ancestrula (Figure 9D) modified-tatiform, opesial area small, D-shaped, surrounded by nine spines; ancestrula becomes surrounded by broad marginal lamina interrupted by vertical walls, before periancestrular zooids differentiate.

Distribution

Broadly distributed. Reported from the Hawaiian Islands and Vanuatu; the Great Barrier Reef, Australia; the Philippines; and New Zealand (for references, see synonymies). Also reported from the Caribbean (Winston 1984), although this disjunct population warrants investigation as an anthropogenic introduction or as a cryptic sister species to the Pacific form.

Family WATERSIPORIDAE Vigneaux, 1949

Genus *Watersipora* Neviani, 1895

Watersipora subovoidea sensu Harmer, 1957

(Figure 9E, F)

Dakaria subovoidea: Harmer 1957, p 1022, Plate 69, Figure 12 (in part).

? *Watersipora edmondsoni* Soule and Soule 1968, p 215, Plate 2, Figure 6; Soule and Soule 1975, p 307, Plate 1, Figure 7, Plate 4, Figure 6.

Watersipora edmondsoni: Winston and Heimberg 1986, p 17, Figures 38–40.

Watersipora subovoidea sensu Harmer: Tilbrook et al. 2001, p 75, Figure 18F.

Measurements

ZL, 1.03–1.60 (1.179 ± 0.175). ZW, 0.55–0.75 (0.620 ± 0.060). OrL, 0.15–0.18 (0.163 ± 0.009). OrW, 0.20–0.25 (0.223 ± 0.012).

Description

Unilaminar, encrusting; colour iridescent black when alive, iridescent black or dark grey tinged with reddish brown when dried; operculum shiny, opaque black. Zooids (Figure 9E) large, delineated by a raised line of calcification; variable in shape, irregularly hexagonal to long-oval or spindle-shaped, sometimes quite elongate. Frontal wall (Figure 9E) slightly

convex, covered uniformly with small pores, the distance between pores roughly two to three pore diameters; imperforate in a rugose lunate zone (Figure 9F) of varying width proximal to orifice; each frontal pore surrounded by a slightly raised margin that is broader on distal side, giving frontal wall a scaled appearance. There may be one or two larger areolar pores on each side lateral to margin, though some zooids lack them; proximolateral angles of zooids often sunken, appearing as enlarged areolae. Orifice (Figure 9F) terminal, slightly raised from level of frontal wall, the orificial margin a raised, rounded rim; orifice clearly broader than long, the large anter semicircular, with a deep, distinctly U-shaped proximal sinus occupying about the middle third of the proximal margin; condyles flattened on broad condylar shelves flanking sinus. Spines and ovicells lacking.

Remarks

Characters common to colonies from Hawaii (this study), Bali (Winston and Heimberg 1986), and Vanuatu (Tilbrook et al. 2001) include an orifice clearly broader than long, with a U-shaped sinus sharply defined by prominent, shelf-like condyles; a raised orificial collar; an imperforate area proximal to the orifice that is often ornamented with smooth tuberculation, especially on the collar; asymmetrically margined pores that impart a slightly scaled appearance to the frontal wall; and an iridescent, black colour in living and dried colonies. Our specimens thus appear to be conspecific with material from these Indo-West Pacific sites. However, the identity of this species is unclear. It differs from the reddish to light tan colonies and the pattern of the operculum originally described for *W. edmondsoni* from the Hawaiian Islands (Soule and Soule 1968), and with which Winston and Heimberg (1986) identified specimens from Bali. Harmer (1957) noted a black or grey cuticle and operculum, numerous pores, and an orifice similar in shape to that in our material for what he considered to be *Watersiopora subovoidea*; however, the extensive synonymies he listed for this nominal species indicate a virtually circumtropical distribution with much variation. The genus *Watersiopora* badly needs worldwide taxonomic revision (see Ryland 1974c for a discussion of some of the problems), ideally based on both morphological and molecular data.

Distribution

Bali, Hawaiian Islands, Vanuatu.

Superfamily SCHIZOPORELLOIDEA Jullien, 1883

Family STOMACHETOSELLIDAE Canu and Bassler, 1917

Genus *Junerossia* new genus

Type species

Junerossia copiosa n. sp., this study.

Etymology

The genus is named in honour of Professor June R. P. Ross for her significant contributions to the knowledge of fossil and Recent Bryozoa.

Diagnosis

Frontal wall cryptocystidean, sparsely perforated over the entirety except in a zone proximal to orifice that represents an umbonuloid component of the shield, the margin of this zone delineated externally by a semicircle of pores and internally by a ring scar. The frontal pores are tiny pseudopores identical in form to the uniporous septula in the vertical walls; frontal pores marginated by thickening of frontal wall. Orifice subterminal, the proximal and distal margins broadly arcuate; condyles not evident from external view, but present internally near junction of ring scar and distal semicircle of orifice. Peristome a thick, moderately tall rim around orifice, often with several nodules on top. Ovicell opens into peristome, not closed by zooidal operculum; imperforate; covered with interior-walled calcification like frontal wall. Frontal budding occurs. Basal wall heavily calcified. Zooids interconnect by uniporous septula. Ancestrula similar in form to later zooids but imperforate except for two or three frontal pores on each side proximolateral to orifice; gives rise to five daughter zooids.

Remarks

The familial placement of this genus is difficult. Gordon (2000) discussed a number of species across several “lepraliomorph” (Gordon 1989a) families, including families of Schizoporelloidea, that have a frontal shield with extensively or moderately developed umbonuloid components; thus the composition of the frontal shield in *Junerossia* does not in itself seem diagnostic. Three families include combinations of some of the characters seen in *Junerossia*, but placement is not entirely satisfactory in any of them, and depends upon which characters are given weight at the familial level. One family is the Cyclicoporidae, represented by the genus *Cyclicopora* Hincks, 1884, which is quite similar to *Junerossia* in the following characters: a perforate frontal shield with a crescentic imperforate area proximal to the orifice suggestive of an umbonuloid component; a subcircular orifice lacking condyles; spines and avicularia lacking; and a globose ovicell covered with finely tubercular interior-walled calcification. However, the ovicell is perforate in *Cyclicopora*, and Canu and Bassler (1920, Figure 125) indicated a spinocystally or kenozooidally derived frontal wall quite different internally from that of *Junerossia*, and an orifice lacking even internal condyles.

Members of the monogeneric family Pacificincolidae, recently erected by Liu and Liu (1999), are similar to *Junerossia* in the following characters: an often unilaminar, encrusting growth form; evenly perforated cryptocystidean frontal wall; hyperstomial, imperforate ovicells covered with tuberculate calcification; avicularia usually absent; and no oral spines. However, in contrast to *Junerossia*, pacificincolids have an orifice usually referred to as “bell-shaped”, with distinct condyles evident at most stages of zooidal ontogeny; a small suboral heterozooid of unknown function (Nielsen 1981); large, multiporous interconnecting septula; ovicells closed by the zooidal operculum; and an ancestrula that characteristically buds a triplet of daughter zooids.

Another family is the Stomachetosellidae. Species of *Stomachetosella* lack oral spines and avicularia, and nodular or tubercular sculpturing on the rim of the peristome is evident in some species (e.g. *S. tuberculata* Androsova, 1958). Also within *Stomachetosella* are species with a transversely elliptical orifice lacking at least overt condyles (e.g. *S. abyssicola* Osburn, 1952). Furthermore, there are species with an imperforate ovicell covered with coarsely granulate interior-walled calcification (e.g. *S. normani* Hayward, 1994); the single pore (e.g. *S. sinuosa* Busk, 1860) or elongate foramen (e.g. *S. tuberculata*

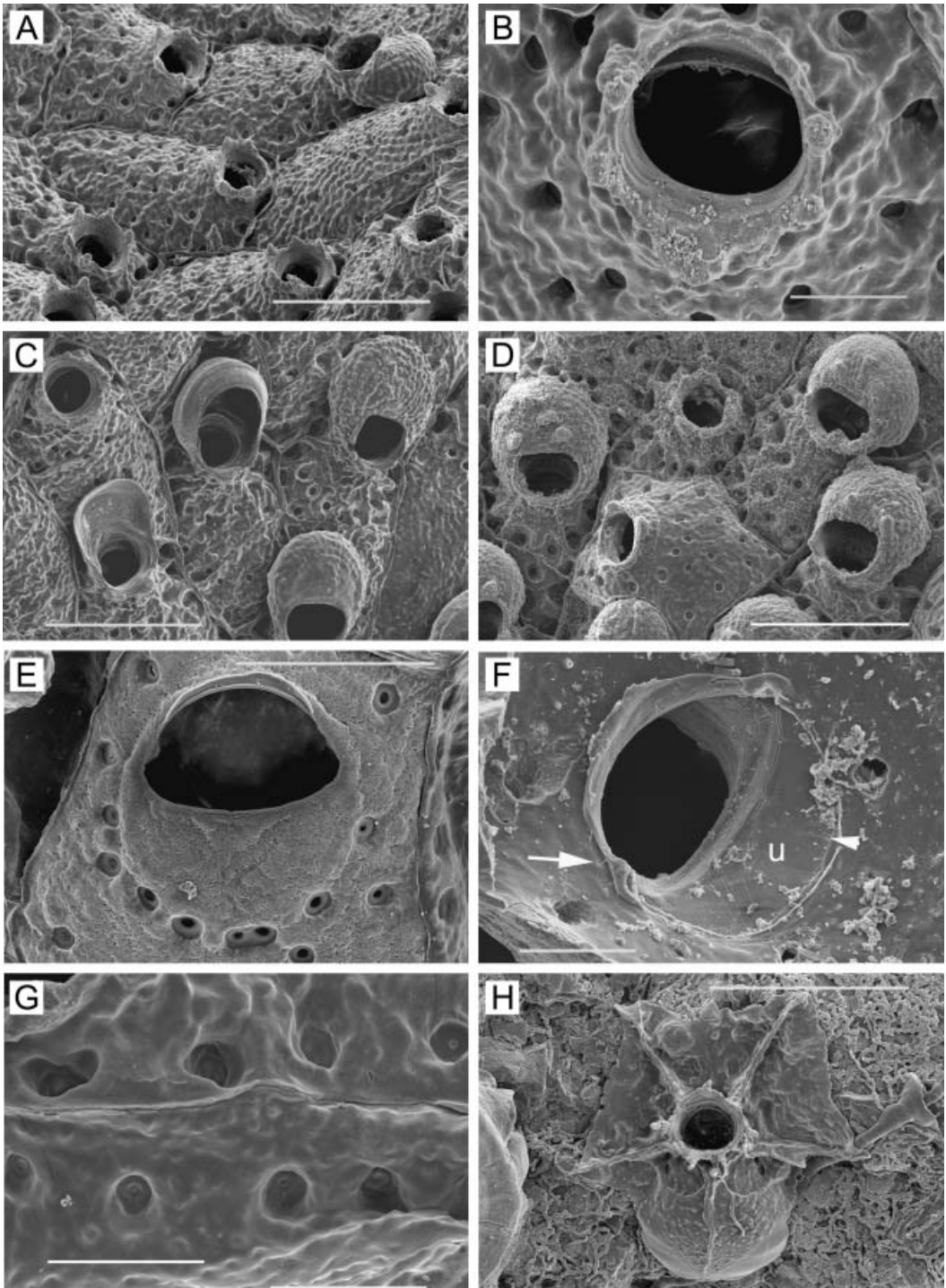


Figure 10. *Junerossia copiosa* n. gen., n. sp., intertidal specimens from Sesoko Island, Okinawa, Japan (C, E) and Kapa'a Shore, Island of Hawaii (A–B, D, F–H): (A) holotype (NHM 2006.7.21.8), autozooids and ovicellate zooid; (B) holotype, enlargement of orifice; (C) stages in ovicell formation; (D) paratype 2 (NHM 2006.7.21.10),

Androsova, 1958) in the ovicell of some species seems to reflect incomplete closure of a fundamentally imperforate ovicell. In addition, species of *Stomachetosella* can have either pore chambers or septula (Kluge 1975). However, unlike *Junerossia*, species of *Stomachetosella* also typically have a cormidial secondary orifice, and ovicells are partly or entirely immersed.

At present, the sum of characters of *Junerossia* seems to favour placement in the Stomachetosellidae. However, with its globose hyperstomial ovicell, raised peristome, frontal shield with a significant umbonuloid component marginated by frontal pores, and uniporous septula, it is distinct from other stomachetosellid genera and, indeed, from other cheilostome genera. It will be interesting to determine whether the frontal walls of other stomachetosellids have mixed lepralioid–umbonuloid frontal shields.

***Junerossia copiosa* new species**
(Figure 10A–H)

“Genus and species, not determined”: Tilbrook 2006, p 147, Figure 21D–F.

Type material

Holotype: NHM 2006.7.21.8, specimen HI-56, bleached, coated for SEM; Kapa’a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratypes: same locality and collecting information as for holotype. Paratype 1, NHM 2006.7.21.9, two unbleached fragments, one with embryos. Paratype 2, NHM 2006.7.21.10, specimen HI-2, bleached, coated for SEM. Paratype 3, NHM 2006.7.21.11, specimen HI-79, bleached, coated for SEM. Paratype 4, NHM 2006.7.21.12, specimen HI-17 (ancestrula), bleached, coated for SEM. Paratype 5, NHM 2006.7.21.13, specimen bleached. Paratype 6, NHM 2006.7.21.14, specimen bleached. Paratype 7, YPM-38552, specimen bleached. Paratype 8, YPM-38553, specimen bleached. Paratype 9, YPM-38554, ancestrular complex, specimen unbleached. Paratype 10, YPM-38555, 23 fragments, bleached and unbleached.

Etymology

The species name derives from the Latin *copiosus* (plentiful, abundant).

Measurements

ZL, 0.50–0.85 (0.640 ± 0.109). ZW, 0.35–0.58 (0.450 ± 0.066). OrL, 0.09–0.10 (0.096 ± 0.006). OrW, 0.12–0.14 (0.129 ± 0.007). OvL, 0.16–0.20 (0.177 ± 0.013). OvW, 0.25–0.29 (0.256 ± 0.012).

autozooid and ovicellate zooids in primary layer, and frontally budded autozooid; (E) enlargement of exterior view of umbonuloid component of shield of a marginal zooid, with condyles visible; (F) interior view of frontal shield near orifice, showing umbonuloid component (u) separated from lepralioid component by ring scar (arrowhead); note condyles at intersection of ring scar and distal margin of primary orifice (one marked by arrow); (G) holotype, uniporous septula in lateral wall (lower) and frontal wall (upper); (H) paratype 4 (NHM 2006.7.21.12), ancestrula. All specimens bleached. Scale bars: 500 μ m (A, C, D, H); 200 μ m (E); 100 μ m (B, F, G).

Description

Colony encrusting, sheet-like, forming irregularly shaped patches, the largest observed 2.1 cm × 1.4 cm; unilaminar at first, but producing frontally budded zooids singly or in groups, which impart an irregular, thickened appearance to the colony; off-white in colour, with a glistening transparent ectocyst; often with a broad, calcified marginal lamina representing incipient zooids. Zooids arranged in distinct radial series; boundaries distinct, sometimes marked by a raised line of calcification; irregularly hexagonal, quadrate, or barrel-shaped. Frontal wall (Figure 10A, C, D) slightly to moderately convex, perforated by small, well-spaced circular pores; tuberculate between pores; areolar pores scarcely evident as occasional slit-like openings parallel and adjacent to margin; with increased calcification, the frontal wall becomes thick and rugose, and the surface openings to frontal pores become larger and infundibular. A semicircular imperforate area proximal to the orifice constitutes an umbonuloid component of the frontal shield; this is especially evident externally in marginal zooids (Figure 10E) and on the interior of the frontal shield (Figure 10F), where the umbonuloid component is delineated by a ring scar. Frontal pores are identical in size and form to the uniporous septula that constitute interzooidal connections in the lateral and distal walls (Figure 10G). Visible orifice (Figure 10B) broader than long, irregularly elliptical, with both the proximal and distal borders smooth curves; newly formed orifice in marginal zooids (Figure 10E) with semicircular anter separated from broader, shallower poster by blunt-conical condyles, which are not externally apparent at later stages. Primary orifice obscured by thick, low, cylindrical peristome (Figure 10A, D) of same texture as frontal wall, the rim sometimes flared and often ornamented with up to seven nodular processes. Often a transversely crescentic row (Figure 10A, C, E) of more closely spaced frontal pores rings the base of the peristome, along the proximal margin of umbonuloid shield component. Ovicell (Figure 10C, D) is globose, hyperstomial; broader than long, imperforate, the surface tuberculate like frontal wall, sometimes with scattered nodules, proximal margin straight or slightly convex, confluent with lateral walls of peristome. Embryo orange, visible through ovicell wall. Spines and avicularia lacking. Ancestrula (Figure 10H) is pyriform in shape, imperforate except for two or three pores proximolateral to orifice, but with peristome and primary orifice similar to those of older zooids; peristomial rim with several irregular spinous processes; ancestrula first produces a broad marginal lamina that eventually gives rise to five periancestrular zooids (one distal, two distolateral, two proximolateral).

Remarks

The shape of the primary orifice is somewhat ambiguous in this species. What appears to be the true primary orifice is evident only in marginal zooids; it is hat-shaped, with a broad poster separated from a semicircular anter by conspicuous condyles (Figure 10E). The poster becomes filled in with growth of the peristome (Figure 10F). In ontogenetically mature zooids, the opening visible in external view (Figure 10B) could equally be considered a new primary orifice, or a secondary orifice. Condyles are evident only early in zooidal ontogeny (Figure 10E) and internally (Figure 10F). This suggests that some other ascophorans reported as lacking condyles would bear re-examination.

Distribution

A single colony fragment designated as “genus and species undetermined” due to lack of adequate material was illustrated by Tilbrook (2006) from Guadalcanal, Solomon Islands. This species is fairly common intertidally on coral rubble in the vicinity of Sesoko Island,

Okinawa, Japan (M. H. Dick and A. V. Grischenko, unpublished data). It thus appears to be widely distributed in the subtropical to tropical, central to western Pacific.

Family HIPPOPODINIDAE Levinsen, 1909

Genus *Hippopodina* Levinsen, 1909

Hippopodina irikiensis Tilbrook, 1999

(Figure 11A)

Hippopodina irikiensis Tilbrook 1999, p 454, Figure 2a, c, e.

Hippopodina irikiensis: Tilbrook et al. 2001, p 90, Figure 18B; Tilbrook 2006, p 245.

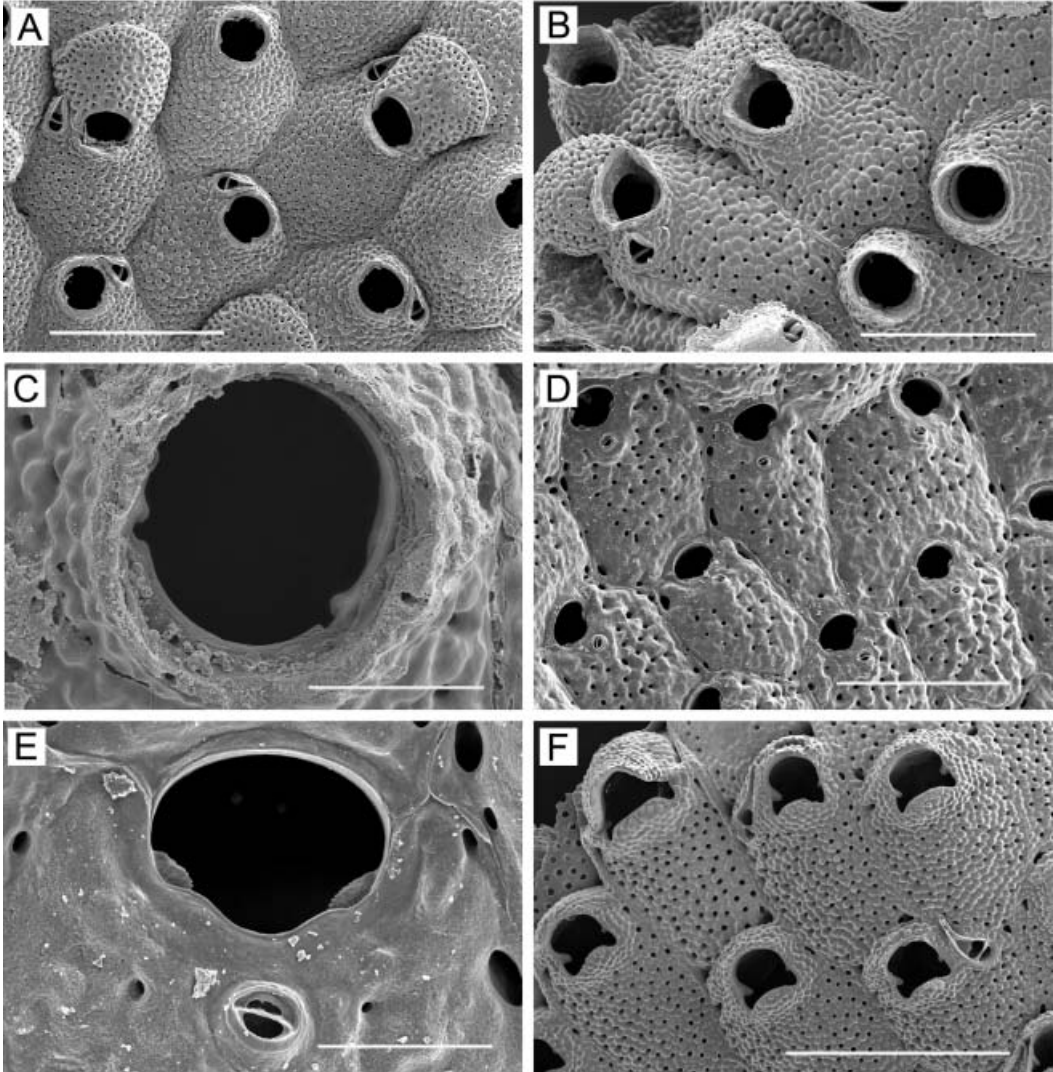


Figure 11. (A) *Hippopodina irikiensis* Tilbrook: autozooids and ovicellate zooids. (B, C) *Cosciniopsis lonchaea* (Busk): (B) autozooids and ovicellate zooids; (C) enlargement showing shapes of primary and secondary orifices. (D, E) *Calyptotheca kapaensis* n. sp., holotype (NHM 2006.7.21.15): (D) autozooids; (E) enlargement of primary orifice and suboral avicularium. (F) *Cheiloporina haddoni* Harmer: autozooids and one ovicellate zooid (upper left). All specimens bleached. Scale bars: 1 mm (A, B, F); 200 μ m (C); 500 μ m (D); 100 μ m (E).

Measurements

ZL, 0.85–1.03 (0.940 ± 0.062). ZW, 0.68–0.88 (0.735 ± 0.063). OrL, 0.19–0.21 (0.207 ± 0.007). OrW, 0.20–0.24 (0.216 ± 0.0112). OvL, 0.53–0.65 (0.573 ± 0.051). OvW, 0.50–0.60 (0.553 ± 0.042).

Description

Colony unilaminar, encrusting, glistening, white with a tinge of lavender; zooids large; frontal wall moderately inflated, granulated, completely covered with minute pores. Orifice has been described as “keyhole-shaped” or “bell-shaped”, with a shallow poster separated from a longer anter by obtuse-triangular condyles; proximal orificial margin concave; oral spines lacking. Avicularia situated distolateral to orifice, usually single, sometimes paired; ovicell about as broad as long, partly embedded in frontal wall of distal zooid, raised, globose, with the same texture and perforation as the frontal wall.

Remarks

Several of the triad ancestrular complexes characteristic of *H. iririkiensis* were observed among the Hawaiian specimens. This species is distinguished from a similar congener, *H. feegeensis*, in having a concave rather than a straight proximal orificial margin. *Hippopodina iririkiensis* was the most widely distributed species found in the study; it occurred at all three sites where bryozoans were found, was the only bryozoan species found at Whittington Beach, and was the spatially and numerically dominant species at Kealakekua Bay.

Distribution

Tropical Indo-West Pacific: Vanuatu, North Queensland, Fiji, Philippines, Mauritius, Red Sea; Mediterranean (for references, see synonymies). This is the first record for the Hawaiian Islands.

Family GIGANTOPORIDAE Bassler, 1935

Genus *Cosciniopsis* Canu and Bassler, 1927

Cosciniopsis lonchaea (Busk, 1884)

(Figure 11B, C)

Lepralia lonchaea Busk 1884, p 146, Text figure 43.

Cosciniopsis lonchaea: Ryland and Hayward 1992, p 258, Figure 17b; Tilbrook et al. 2001, p 87, Figure 17C, D; Tilbrook 2006, p 239, Figure 52D.

Measurements

ZL, 1.13–1.43 (1.243 ± 0.083). ZW, 0.65–0.93 (0.803 ± 0.087). OrL, 0.25–0.33 (0.270 ± 0.025). OrW, 0.23–0.26 (0.248 ± 0.010). OvL, 0.43–0.50 (0.463 ± 0.032). OvW, 0.55–0.63 (0.600 ± 0.035) (ovicell $n=4$).

Description

Colony unilaminar, encrusting; ectocyst a rich chocolate to sienna colour; zooids large. Frontal wall smoothly tuberculate, covered with minute pores except for area proximal to

peristome. Peristome well developed, same texture as frontal wall. Zooids often with a distomedially directed frontal avicularium appressed to peristome on one side, mandible equilateral, acute. Primary orifice (Figure 11C) nearly circular, with small, rounded condyles separated by a notch from concave proximal orificial margin. Oral spines lacking. Ovicell (Figure 11B) globose, hyperstomial, broader than long, same texture as frontal wall, uniformly perforated by minute pores; secondary orifice of ovicellate zooids round-triangular in outline.

Remarks

Zooid size is larger than reported for other populations, but otherwise the morphology of Hawaiian specimens is indistinguishable from that of specimens from other populations (e.g. Ryland and Hayward 1992; Tilbrook et al. 2001).

Distribution

Widely distributed in Indo-West Pacific, from Red Sea to Tahiti and Hawaii (Tilbrook et al. 2001).

Family LANCEOPORIDAE Harmer, 1957

Genus *Calyptotheca* Harmer, 1957

***Calyptotheca kapaaensis* new species**

(Figure 11D, E)

Type material

Holotype: NHM 2006.7.21.15, specimen HI-37, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratype: NHM 2006.7.21.16, same locality and collecting information as for holotype; unbleached specimen.

Etymology

The species name is derived from the type locality, Kapa'a.

Measurements

ZL, 0.45–0.83 (0.580 ± 0.122). ZW, 0.26–0.48 (0.383 ± 0.058). OrL, 0.08–0.10 (0.086 ± 0.008). OrW, 0.11–0.14 (0.125 ± 0.009).

Description

Colony unilaminar, encrusting, tan-white in colour. Zooids moderately inflated, separated by a groove and often a raised suture line. Frontal wall (Figure 11D) well calcified, rugose, covered with small, circular pores that are densest in central area, fewer or lacking close to the lateral and proximal margins, where there can be a few larger marginal pores. Orifice (Figure 11E) markedly broader than long, anter broadly semicircular, separated from poster by a rounded shelf on each side; in the inside curvature of each shelf is a prominent semicircular condyle that is serrated on the edge; poster is a broad sinus extending between

the condyles. Medial suboral avicularium (Figure 11D, E) tiny, separated from orifice by less than twice the width of the avicularium; rostrum nearly circular, tilted at an acute angle, with a tiny, semicircular mandible directed proximally; no other frontal avicularia observed. Oral spines lacking. No ovicells present in our specimens.

Remarks

Our specimens resemble several other *Calypptotheca* species with a small, median suboral avicularium and large, serrated condyles, including *C. inclusa* (Thornely, 1906), *C. incompta* (Hayward, 1988), and *C. reniformis* Tilbrook, 2006 (Winston and Heimberg 1986; Hayward 1988; Tilbrook 2006). However, the orifice of *C. inclusa* is about as broad as long, with a narrower sinus, and the suboral avicularium is proportionately larger than in *C. kapaaensis*. In *C. incompta*, the suboral avicularium is small and oval, and the orifice is markedly broader than long, as in *C. kapaaensis*. However, the pores of *C. incompta* are slit-like rather than circular; zooids can have an additional, larger frontal avicularium near the proximal margin, which was not seen in our specimens; and the sinus is narrower and tapering. In *C. reniformis*, the frontal pores are reniform and the orifice is pear-shaped. Measurements of both *C. inclusa* and *C. incompta* given in the literature indicate smaller zooids than for our specimens. We place this species into *Calypptotheca* based on the diagnosis of that genus by Tilbrook (2006); the shelf-like platform on the edge of the distal orificial rim is scarcely developed, but is evident in SEM images.

Distribution

Kapa'a Shore, Island of Hawaii, is the only known locality.

Family CHEILOPORINIDAE Bassler, 1936

Genus *Cheiloporina* Canu and Bassler, 1923

Cheiloporina haddoni Harmer, 1902

(Figure 11F)

Lepralia haddoni Harmer 1902, p 299, Figures 38, 39.

Smittia perforata Okada 1923, p 228, Figure 26.

Measurements

ZL, 0.75–0.99 (0.846 ± 0.064). ZW, 0.43–0.65 (0.533 ± 0.075). OrL, 0.18–0.23 (0.197 ± 0.016). OrW, 0.21–0.25 (0.230 ± 0.012). OvL, 0.325. OvW, 0.475 (ovicell $n=1$).

Description

Colony unilaminar, encrusting, sheet-like; tan in colour; ectocyst and operculum light yellow. Zooids hexagonal to barrel-shaped, longer than broad. Frontal wall slightly convex, granulated, covered with tiny pores uniformly distributed over entire surface, often with larger areolar openings at proximolateral corners of zooid and lateral to orifice. Orifice raised on imperforate, granulated peristome; with strong condyles; poster slightly broader than anter; proximal orificial margin convex, flattened on top in zooids with an ovicell. Orifice dimorphic, much broader proximolaterally in zooids with an ovicell than in those without. Some zooids have an avicularium on one side of orifice, the rostrum

long-triangular, acute, curved laterally. Ovicell comprises a flattened, sac-like enlargement of distal end of zooid, the surface granulated. Spines lacking.

Remarks

Our material is similar to Harmer's (1902) original description in overall zooidal measurements, in having the orifice dimorphic between zooids with and without an ovicell, and in having a long-triangular avicularium on one side of the orifice in some zooids. Our specimens differ in having the orifice broader than long in zooids not bearing an ovicell; in having smaller, more numerous pores, and in having the avicularian rostrum typically curved laterally, rather than straight.

Distribution

Previously known from Torres Straits (Harmer 1902); the Straits of Korea (Okada 1923); Aru I., Indonesia (Harmer 1957); and the Hawaiian Islands, locality unspecified (Soule et al. 1988).

Family ESCHARINIDAE Tilbrook, 2006

Genus *Bryopesanser* Tilbrook, 2006

Bryopesanser serratus new species

(Figure 12A–C)

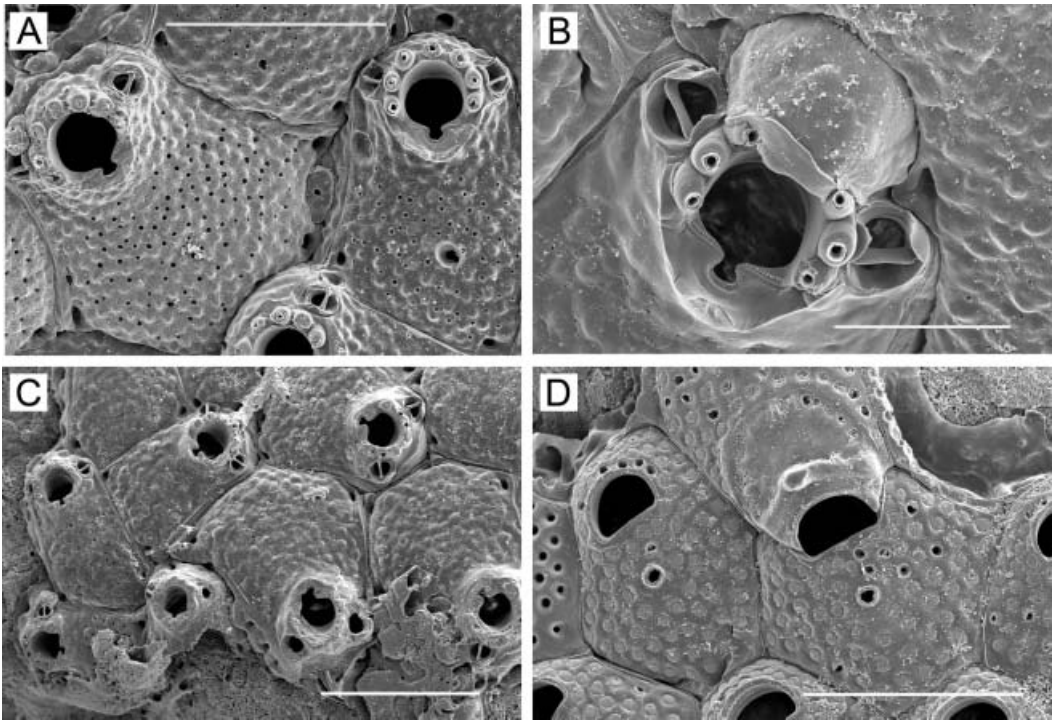


Figure 12. (A–C) *Bryopesanser serratus* n. sp.: (A) paratype 1 (NHM 2006.7.21.18), autozooids; note predation hole in right-hand zooid; (B) holotype (NHM 2006.7.21.17), enlargement of distal end of an ovicellate zooid; (C) paratype 2 (YPM-38556), ancestrula (lower left-of-centre, broken) and periancestrular zooids, showing a spiral budding pattern. (D) *Fenestulina caseola* Hayward: autozooid and ovicellate zooid. All specimens bleached. Scale bars: 400 μ m (A); 200 μ m (B); 500 μ m (C, D).

Type material

Holotype: NHM 2006.7.21.17, specimen HI-66, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratypes: same locality and collecting information as for holotype. Paratype 1, NHM 2006.7.21.18, specimen HI-3 (part), with *Puellina* sp., bleached, coated for SEM. Paratype 2, YPM-38556, specimen HI-70, bleached, coated for SEM.

Etymology

The species name is from the Latin *serratus* (serrated), referring to the mandible of the avicularium.

Measurements

ZL, 0.50–0.75 (0.640 ± 0.084). ZW, 0.30–0.60 (0.430 ± 0.079). OrL (exclusive of sinus), 0.11–0.12 (0.112 ± 0.005). OrW, 0.12–0.14 (0.131 ± 0.009) (orifice $n=5$). OvL, 0.15–0.18 (0.162 ± 0.011). OvW, 0.18–0.20 (0.183 ± 0.008).

Description

Colony unilaminar, encrusting, sheet-like, small and irregular, the largest observed about 5 mm × 3 mm, with ovicells; light tan to cream in colour. Zooids irregularly hexagonal, widest at proximal third, narrowing distally, separated by a thin incision. Frontal wall (Figure 12A) moderately convex, uniformly granulated, covered with minute pores; pores may become constricted or occluded with increased calcification; there is a small, circular areolar pore at each of the angles of the lateral margin. Primary orifice (Figure 12A, B) exclusive of sinus broader than long; condylar shelves decorated with a row of fine denticles; condyles smooth, sloping; narrow sinus expanded proximal to opening. Peristome (Figure 12B) slightly raised, comprising a sharp, curved rim proximal to the orifice and a thickened rim laterally and distally that bears the swollen, closely set bases of seven oral spines; peristome not obscuring primary orifice. There is a large avicularium (Figure 12A–C) on one or both sides of the orifice; the area of the rostrum is equivalent to about half that of the orifice; rostrum with complete hinge bar and large, oval opesial opening; rostrum tilted distomedially, the mandibular end highly concave to accommodate mandible; mandible conspicuous, stout, setiform, serrate, extending beyond rostrum for a distance equal to or somewhat greater than zooidal width. Ovicell raised, hemispherical, broader than long, the proximolateral corners incorporating the distalmost two paired spines; with a smooth-textured but somewhat rugose surface; the proximal margin raised, thickened, sometimes developed into a smooth flange. The distal part of an ancestrula is shown in Figure 12C; ancestrula smaller than, but of the same form as, subsequent zooids, including the oral avicularia, though spines are lacking; ancestrula gives rise to a daughter zooid laterally, and then to zooids of increasing size in a spiral budding pattern.

Remarks

Two similar-appearing species (*B. latesco* and *B. capitaneus*) described by Tilbrook (2006) from the Solomon Islands differ from *B. serratus* in having the long avicularian mandibles in the shape of a fan or duck's foot, rather than stout, tapering, and serrated. Unfortunately,

after observing the atypical mandibles, we inadvertently bleached all three specimens we collected of *B. serratus*, and thus cannot provide an illustration of this key character. In addition to the shape of the avicularian mandible, the following characters in combination separate *B. serratus* from the two species from the Solomons and from an Atlantic species, *B. pesansensis*, treated by Tilbrook (2006): zooids moderate in size; peristome flared, without proximal mucro; proximal margins of orifice flanking the sinus sloping rather than straight; frontal pores simple; both ovicell and avicularia large in proportion to orifice size, compared to the other species.

The diagnosis of the genus *Bryopesanser* (Tilbrook 2006) includes fan-shaped mandibles. The serrated mandibles in *B. serratus* suggest that this generic character should be amended, because other characters indicate that the Hawaiian species belongs in this genus.

In his 2006 monograph, Tilbrook mentioned that he had been able to distinguish 11 morphologically distinct and geographically limited species of *Bryopesanser* among material from around the world that had been attributed to *B. pesansensis*; he included descriptions and illustrations of only three of these. All of these species are highly similar in gross morphology, but differ in fine details and the relative sizes of the orifice, avicularia, frontal pores, and ovicell.

Distribution

Kapa'a Beach, Hawaii Island is the only known locality. Nominal *B. pesansensis* has previously been recorded from the Hawaiian Islands (Canu and Bassler 1927; Soule et al. 1988).

Family MICROPORELLIDAE Hincks, 1879

Genus *Fenestulina* Jullien, 1888

Fenestulina caseola (Hayward, 1988)

(Figure 12D)

Fenestulina caseola Hayward 1988, p 325, Plate 10d.

Fenestulina caseola: Ryland and Hayward 1992, p 280, Figure 26d; Tilbrook 2006, p 217, Figures 46F, 47F.

Measurements

ZL, 0.48–0.60 (0.543 ± 0.040). ZW, 0.35–0.45 (0.406 ± 0.034). OrL, 0.08–0.09 (0.083 ± 0.005). OrW, 0.13–0.15 (0.138 ± 0.004). OvL, 0.024. OvW, 0.031 (ovicell $n=1$).

Description

Colony unilaminar, encrusting, white; frontal wall smooth, only moderately inflated, completely covered with large pores, each occluded by a finely cribriform plate with tri-radial suture lines. Orifice D-shaped, broader than long, proximal margin straight, oral spines lacking. Ascopore ringed by a narrow rim; opening irregular, elliptical, or lunate in outline, the margin irregularly denticulate; separated from orifice by about length of orifice. Ovicell smooth, sunken in frontal wall of distal zooid, flattened, with chevron-shaped transverse ridge with small umbo at apex, and with semicircle of pores just inside the periphery.

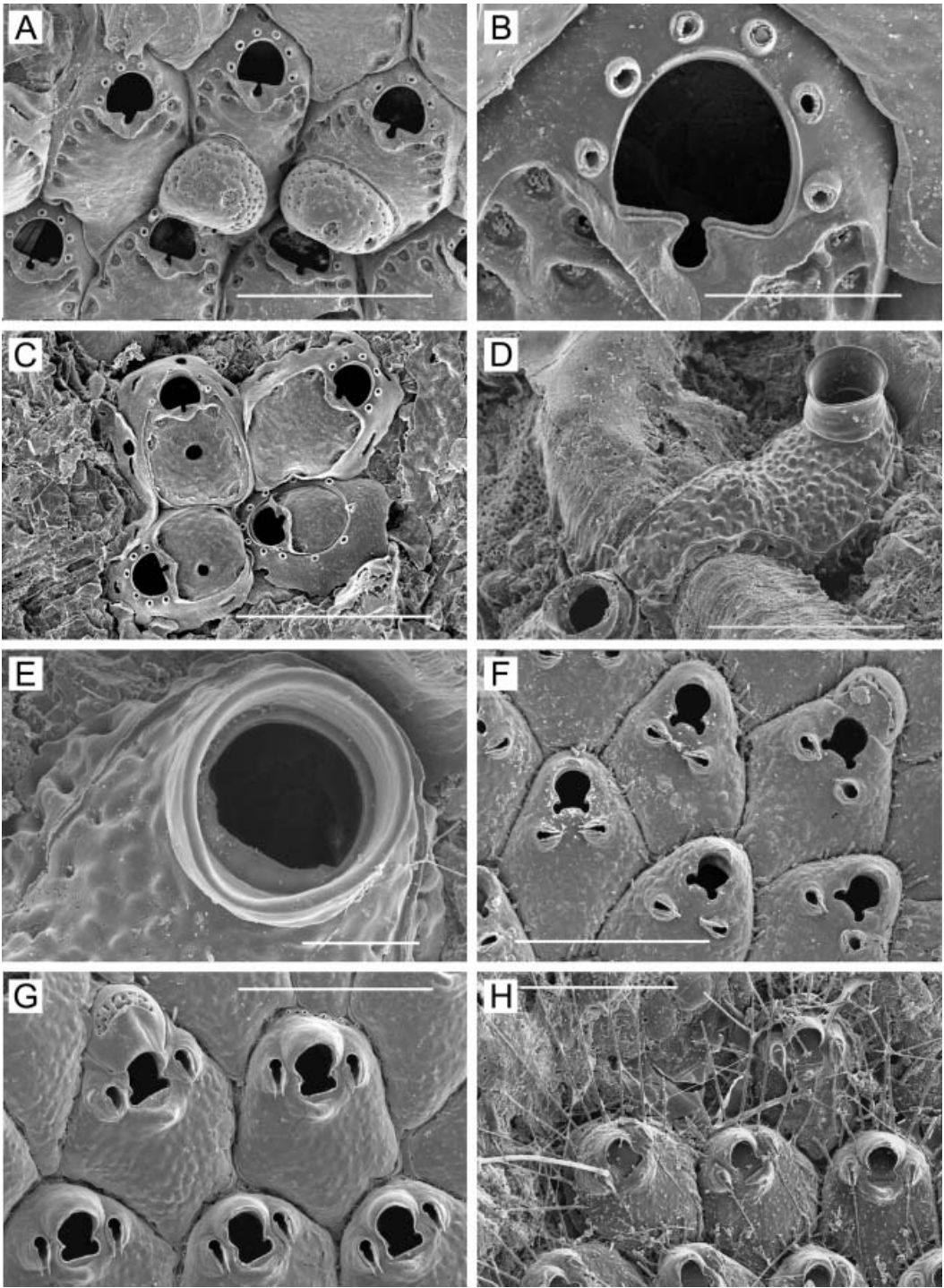


Figure 13. (A–C) *Cribellopora souleorum* n. sp., paratype 1 (NHM 2006.7.21.20): (A) autozooids and ovicellate zooids; note predation hole in ovicell at right and scars on both ovicells; (B) enlargement of orifice; (C) ancestrula (lower right) and three periancestrular zooids; note predation holes in frontal walls of two zooids. (D, E) *Nimba*

Distribution

Mascarene Islands, Indian Ocean; Great Barrier Reef (for references, see synonymies). This is the first record for the Hawaiian Islands.

Family LACERNIDAE Jullien, 1888

Genus *Cribellopora* Gautier, 1957

Cribellopora souleorum new species

(Figure 13A–C)

Type material

Holotype: NHM 2006.7.21.19, unbleached specimen; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratypes: same locality and collecting information as for holotype. Paratype 1, NHM 2006.7.21.20, specimen HI-3 (part), bleached, coated for SEM. Paratype 2, YPM-38557, specimen HI-8, bleached, coated for SEM; with *Parasmittina serrula*. Paratype 3, YPM-38558, unbleached specimen.

Etymology

The species is named in honour of John D. and Dorothy F. Soule, who studied Hawaiian bryozoans for decades.

Measurements

ZL, 0.35–0.50 (0.410 ± 0.041). ZW, 0.25–0.36 (0.300 ± 0.031). OrL, 0.06–0.07 (0.066 ± 0.004). OrW, 0.08–0.09 (0.085 ± 0.006). OvL, 0.14–0.20 (0.167 ± 0.021). OvW, 0.19–0.20 (0.198 ± 0.004) (ovicell $n=6$).

Description

Colony small, the largest observed 4 mm × 3 mm, unilaminar, encrusting, sheet-like, white in colour. Zooids irregularly hexagonal to barrel-shaped, distinct, separated by a sharp incision, the lateral walls sloping slightly so that a small amount of lateral gymnocyst is visible, forming a sharp boundary with frontal wall. Frontal wall (Figure 13A) slightly to moderately convex, smooth, imperforate except for a single row of large, stellate pores along each lateral margin. Primary orifice (Figure 13B) semicircular, typically broader than long, with a small, distinct, teardrop-shaped median sinus with a restricted opening; proximal margin straight except for sinus; condyles a long, smooth cap on condylar shelves flanking sinus. Smooth gymnocystal calcification surrounds orifice, forming a flat, slightly raised flange proximal to orifice. Three pairs of short, straight spines flank the orifice laterally and distally. Peristome lacking. Ovicell (Figure 13A) raised, globose, conspicuous,

saxatilis Hayward and Ryland: (D) autozoid; (E) enlargement showing primary and secondary orifices. (F) *Crepidacantha carsioeta* Winston and Heimberg: autozooids and one ovicellate zooid. (G, H) *Crepidacantha longiseta* Canu and Bassler: (G) autozooids and one ovicellate zooid; (H) unbleached specimen showing long avicularian mandibles and dense marginal setose spines. All specimens except (H) bleached. Scale bars: 400 μm (A, C); 100 μm (B, E); 500 μm (D, F–H).

slightly broader than long, resting on frontal wall of succeeding zooid, smooth textured, with numerous minute pores difficult to observe with light microscopy; pores sometimes covered by smooth calcification in central and proximal region; orificial margin of ovicell with a narrow flange, sometimes upturned. Ancestrula (Figure 13C) of mixed type; tatiform with opesia opening surrounded by 11 spines, but with frontal wall and orifice of mature form inside opesia; one pair of stellate pores proximolateral to orifice. Budding pattern spiral; ancestrula produces one distal zooid, with the following two periancestrular zooids formed in angle between preceding daughter zooid and ancestrula, on one side only. Avicularia lacking.

Remarks

The following combination of characters distinguishes *Cribellopora souleorum* from previously described species: single row of stellate pores along lateral margins; constricted opening to sinus; six oral spines; long, smooth condyles; ovicell covered with minute pores.

Distribution

Kapa'a Beach on the northwest coast of Hawaii Island is the only known locality.

Genus *Nimba* Jullien in Jullien and Calvet, 1903
Nimba saxatilis Hayward and Ryland, 1995
(Figure 13D, E)

Nimba saxatilis Hayward and Ryland 1995, p 558, Figure 11D, E.

Nimba saxatilis: Tilbrook et al. 2001, p 83, Figure 8D.

Measurements

ZL, 0.55–0.80 (0.648 ± 0.077). ZW, 0.28–0.39 (0.330 ± 0.049) (zooid $n=7$). OrL, 0.09–0.10 (0.099 ± 0.003). OrW, 0.12–0.14 (0.126 ± 0.007) (orifice $n=5$).

Description

Colony encrusting, with autozooids arranged in irregularly branching uniserial series. Zooids distinctly longer than broad, rounded distally. Lateral walls low, perforate, separated from frontal wall by suture line. Frontal wall (Figure 13D) slightly convex, finely tuberculate, with tiny marginal pores in distal half and tiny pores over entire surface near proximal end. Primary orifice (Figure 13E) semicircular, with a broad, shallow sinus with straight proximal margin, separated from anter by a shelf on each side bearing a small condyle. Peristome (Figure 13D) tall, smooth, cylindrical, flared slightly at top, sometimes eroded away; secondary orifice oval or circular. Oral spines and avicularia lacking.

Distribution

Great Barrier Reef, Australia; Vanuatu (see synonymies for references). This is the first record for the Hawaiian Islands.

Superfamily MAMILLOPOROIDEA Canu and Bassler, 1927
Family CREPIDACANTHIDAE Levinsen, 1909
Genus *Crepidacantha* Levinsen, 1909
Crepidacantha carsioseta Winston and Heimberg, 1986
(Figure 13F)

Crepidacantha carsioseta Winston and Heimberg 1986, p 27, Figures 64–66.
Crepidacantha carsioseta: Ryland and Hayward 1992, p 277, Figure 25d; Tilbrook et al. 2001, p 92, Figure 16A.

Measurements

ZL, 0.45–0.60 (0.506 ± 0.040). ZW, 0.26–0.41 (0.323 ± 0.041). OrL, 0.09–0.10 (0.097 ± 0.005). OrW, 0.07–0.10 (0.083 ± 0.010). OvL, 0.13–0.16 (0.134 ± 0.013). OvW, 0.15–0.19 (0.170 ± 0.014).

Description

Colony unilaminar, encrusting, light tan to off-white in colour. Frontal wall finely tuberculate, imperforate except for small, scarcely evident marginal pores. Primary orifice constricted laterally by obliquely triangular condylar processes; proximal margin convex. Oral spines lacking. A pair of frontal avicularia lies proximal to orifice, both pointing medially, often slightly offset from one another, with long-setose mandibles; marginal zooids with numerous long, spinous processes around zooidal margin. Ovicell raised, globose, smooth, with crescent of pores in a single row.

Distribution

Bali, Indonesia; Great Barrier Reef, Australia; Vanuatu (see synonymies for references). This is the first record for the Hawaiian Islands.

Crepidacantha longiseta Canu and Bassler, 1928
(Figure 13G, H)

Crepidacantha longiseta Canu and Bassler 1928, p 135, Plate 21, Figures 3, 4.
Crepidacantha longiseta: Gordon 1984, p 113, Plate 44C; Tilbrook et al. 2001, p 92, Figure 16B.

Measurements

ZL, 0.40–0.53 (0.461 ± 0.048). ZW, 0.33–0.43 (0.368 ± 0.030). OrL, 0.09–0.11 (0.102 ± 0.007). OrW, 0.08–0.09 (0.084 ± 0.005). OvL, 0.15–0.20 (0.178 ± 0.022). OvW, 0.18–0.23 (0.203 ± 0.019) (ovicell $n=5$).

Description

Colony unilaminar, encrusting, light tan to off-white in colour. Frontal wall finely tuberculate, imperforate, with small, scarcely evident marginal pores. Primary orifice (Figure 13G) constricted laterally by obliquely triangular condylar processes; proximal

margin straight. Oral spines lacking. Peristome proximal to orifice slightly developed as a thick, crescent-shaped ridge with a slight umbo in midline. A pair of avicularia lies lateral to orifice, both pointing proximally with long-setose mandibles; zooids with numerous long, spinous processes (Figure 13H) around zooidal margin. Ovicell (Figure 13G) raised, globose, smooth, slightly ridged in midline, with a double row of small pores in a crescent near distal end.

Distribution

Putatively circumtropical; Brazil, Caribbean, Mauritius, Vanuatu, and western Indian Ocean (Tilbrook et al. 2001). This is the first record for the Hawaiian Islands.

Superfamily CELLEPOROIDEA Johnston, 1838
Family PHIDOLOPORIDAE Gabb and Horn, 1862
Genus *Metacleidochasma* Soule, Soule, and Chaney, 1991
Metacleidochasma verrucosa new species
 (Figure 14A–C)

? *Metacleidochasma ovale* Soule et al. 1991, p 480, Plate 1, Figure 7, Plate 4, Figures 1, 2.

Type material

Holotype: NHM 2006.7.21.21, specimen HI-46, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide.

Etymology

The species name derives from the Latin *verrucosus* (warty), referring to the finely tuberculate frontal wall.

Measurements

ZL, 0.29–0.53 (0.370 ± 0.068). ZW, 0.21–0.33 (0.272 ± 0.032). OrL, 0.09–0.11 (0.104 ± 0.008). OrW, 0.08–0.09 (0.084 ± 0.006).

Description

A single small colony was found, 4 mm × 2.5 mm. Colony unilaminar, encrusting, sheet-like, white; zooids irregularly hexagonal, rounded distally. Frontal wall (Figure 14A) flat, finely tuberculate, with a single rimmed pore near each lateral margin near middle of zooid; many zooids have a low umbo on each side lateral to orifice. Orifice (Figure 14B) terminal, keyhole-shaped, the anter an interrupted circle in outline and separated from broad, curved poster by prominent, sharp condyles directed posteromedially. Marginal zooids usually with three distal spines (range two to four). Our specimen lacks avicularia and ovicells, though other species of this genus typically have frontal avicularia and a globose ovicell that is immersed to a greater or lesser extent, with a slit near proximal margin (Soule et al. 1991). Ancestrula (Figure 14C) like subsequent zooids and with a similar orifice, but smaller, without frontal pores, and with five distal spines; surrounded by six periancestrular zooids: one distal, two distolateral, two proximolateral, one proximal.

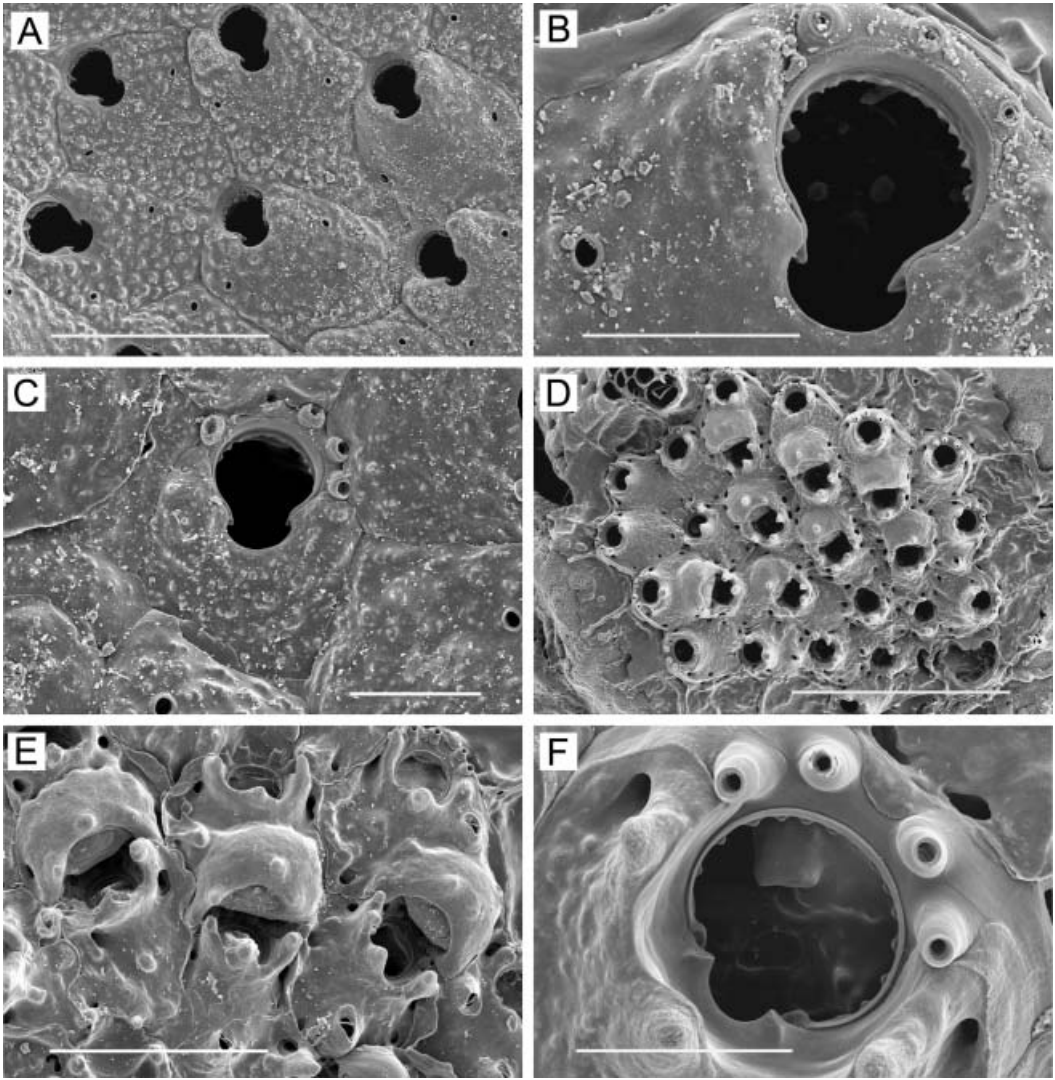


Figure 14. (A–C) *Metacleidochasma verrucosa* n. sp., holotype (NHM 2006.7.21.21): (A) autozooids; (B) enlargement of orifice; (C) ancestrula. (D–F) *Rhynchozoon ferocula* Hayward: (D) view of entire colony; this small colony of 27 zooids has produced eight ovicells; (E) ovicellate zooids; (F) enlargement of primary orifice. All specimens bleached. Scale bars: 400 μm (A, E); 100 μm (B, C, F); 1 mm (D).

Remarks

Soule et al. (1991) originally described a similar species, *M. ovale*, from Lahaina, Maui, Hawaiian Islands, and reported this species to occur broadly in the Indo-West Pacific. Tilbrook et al. (2001) later synonymized *M. ovale* with *M. planulata* (Canu and Bassler, 1929), originally described from the Philippine region. Although Soule et al. (1991) did not describe the ancestrula of *M. ovale*, Tilbrook et al. (2001) illustrated a tatiform ancestrula for *M. planulata*. The ancestrula (Figure 14C) in our single specimen is clearly not tatiform, and our specimen further differs from descriptions of *M. planulata* and *M. ovale* in having a coarsely tuberculate frontal wall, even in periancestrular zooids, and marginal zooids usually with three rather than four distal spines.

Distribution

Kapa'a Beach on the northwest coast of Hawaii Island is the only known locality.

Genus *Rhynchozoon* Hincks, 1895
***Rhynchozoon ferocula* Hayward, 1988**
(Figure 14D–F)

Rhynchozoon ferocula Hayward 1988, p 332, Plate 13a–c.

Rhynchozoon ferocula: Tilbrook et al. 2001, p 100, Figure 22A, B; Tilbrook 2006, p 297, Figure 65E, F.

Measurements

ZL, 0.28–0.36 (0.326 ± 0.032). ZW, 0.18–0.25 (0.220 ± 0.022). OrL, 0.08–0.10 (0.086 ± 0.008). OrW, 0.08–0.10 (0.087 ± 0.007). OvL, 0.12–0.15 (0.135 ± 0.010). OvW, 0.16–0.20 (0.183 ± 0.015).

Description

Colony unilaminar, encrusting, sheet-like, becoming a low mound-like disc with frontal budding in older colonies; white in colour; minute, the largest observed 3 mm × 2 mm; rapidly becoming fertile, with ovicellate zooids beginning as soon as second generation after ancestrula; one colony (Figure 14D) 1.5 mm in diameter has 27 zooids, eight of which have ovicells. Colony surrounded by calcified lamina one or two zooid lengths deep, representing basal walls of newly forming zooids. Marginal zooids hexagonal or barrel shaped. Frontal wall moderately convex, smooth at first, but later lumpy with uniform low tuberculation or a few small nodules, or rugose; imperforate except for two to four areolae along each lateral margin. Primary orifice (Figure 14F) width approximately equal to length (including sinus); beaded with 11–14 denticles; proximal sinus U-shaped, about one-third the width of the orifice, flanked by distinct condylar shelves, each buttressed with a ridge; condyles small, rounded, not reaching sinus. Marginal zooids with two to five (mode=four) short, tapering, tubular oral spines around distal margin. Peristome developed proximally and laterally as a thickened, raised lip, typically with paired, conical or nodular lateral projections and an additional one to three similar projections between them. A suboral avicularium is entirely lacking in our specimens. Some zooids have a small frontal avicularium (Figure 14E) along the lateral or proximal margin, the rostrum raised at an angle to the frontal surface, the acute mandible longer than broad and usually pointing toward the zooidal margin. Ovicell (Figure 14E) hemispherical, conspicuous; covered with heavy calcification continuous with frontal wall of succeeding zooid, or sometimes with contributions from two zooids delineated by a suture line; smooth in texture or faintly rugose or granulose, often with a small mammiform projection on top and occasionally with small nodules lateral to tabula; labellum complete along proximal margin, delineating a transversely elliptical tabula.

Remarks

There are some difference between the Hawaiian specimens and material previously described from other localities. The sinus is more open, with the sides forming nearly a right angle with the condylar shelves, and zooids bear no more than a single frontal

avicularium. We identify our material as *R. ferocula* on the basis of the small, discoid colony with a broad marginal lamina; the relatively small, few areolar pores; usually four oral spines; the peristome consisting of a thickened lip with processes; the lack of a suboral avicularium; and the small, transversely elliptical tabula of the ovicell. The condylar shelves, although not constricting the opening to the sinus, are buttressed with a sharp ridge like that in material from other localities.

Distribution

Originally described from Mauritius (Hayward 1988), this species has also been found at Vanuatu (Tilbrook et al. 2001). This is the first record for the Hawaiian Islands.

Rhynchozoon splendens Hayward, 1988 (Figure 15A–C)

Rhynchozoon splendens Hayward 1988, p 335, Plate 13f, g.

Rhynchozoon splendens: Ryland and Hayward 1992, p 294, Figures 31f, 32a, b; Tilbrook et al. 2001, p 100, Figure 22A, B.

? *Rhynchozoon rostratum*: Winston and Heimberg 1986, p 38, Figures 95–98.

Measurements

ZL, 0.48–0.70 (0.569 ± 0.061). ZW, 0.28–0.48 (0.386 ± 0.065). OrL, 0.09–0.10 (0.098 ± 0.004). OrW, 0.10–0.11 (0.108 ± 0.006). OvL, 0.175. OvW, 0.225 (ovicell $n=1$).

Description

One colony found; encrusting, multilaminar, light tan in colour, covered by shiny ectocyst; growing on a serpulid tube; 9 mm × 15 mm in extent. Zooids distinct only at margin; oval, hexagonal, or irregular in outline; oral spines lacking. Frontal wall (Figure 15A, C) moderately convex in young zooids, rugose, with interareolar buttresses between large areolae. Zooidal boundaries indistinct with age; frontal wall rugose; areolar openings enlarged. Primary orifice (Figure 15B) slightly broader than long, with low, broad, U-shaped sinus demarcated by condylar shelves; condyles rounded, conspicuous; orificial rim with around 19 denticles; becoming deeply immersed in peristome. Secondary orifice (Figure 15C) with up to six processes, usually conical or nodular but sometimes long and acute. Oral avicularium (Figure 15A) large, on a raised chamber, situated immediately proximolateral to orifice; rostrum often angled 60° or more from frontal plane of zooid, hooked at tip; mandible long-triangular, directed laterally or distolaterally; with age, oral avicularium immersed in peristome. Many zooids have a frontal avicularium (Figure 15C) pointing in any direction, the mandible equilateral or nearly so. Many of the frontal avicularia have a diamond-shaped rostrum, meaning that the proximal end of the rostrum is acute, as is the mandibular end. Ovicell (Figure 15A, C) completely immersed, opening low in peristome; endooecium showing as granulated, circular tabula in peristome.

Distribution

Broadly distributed throughout the Indo-West Pacific (Tilbrook et al. 2001). This is the first record for the Hawaiian Islands.

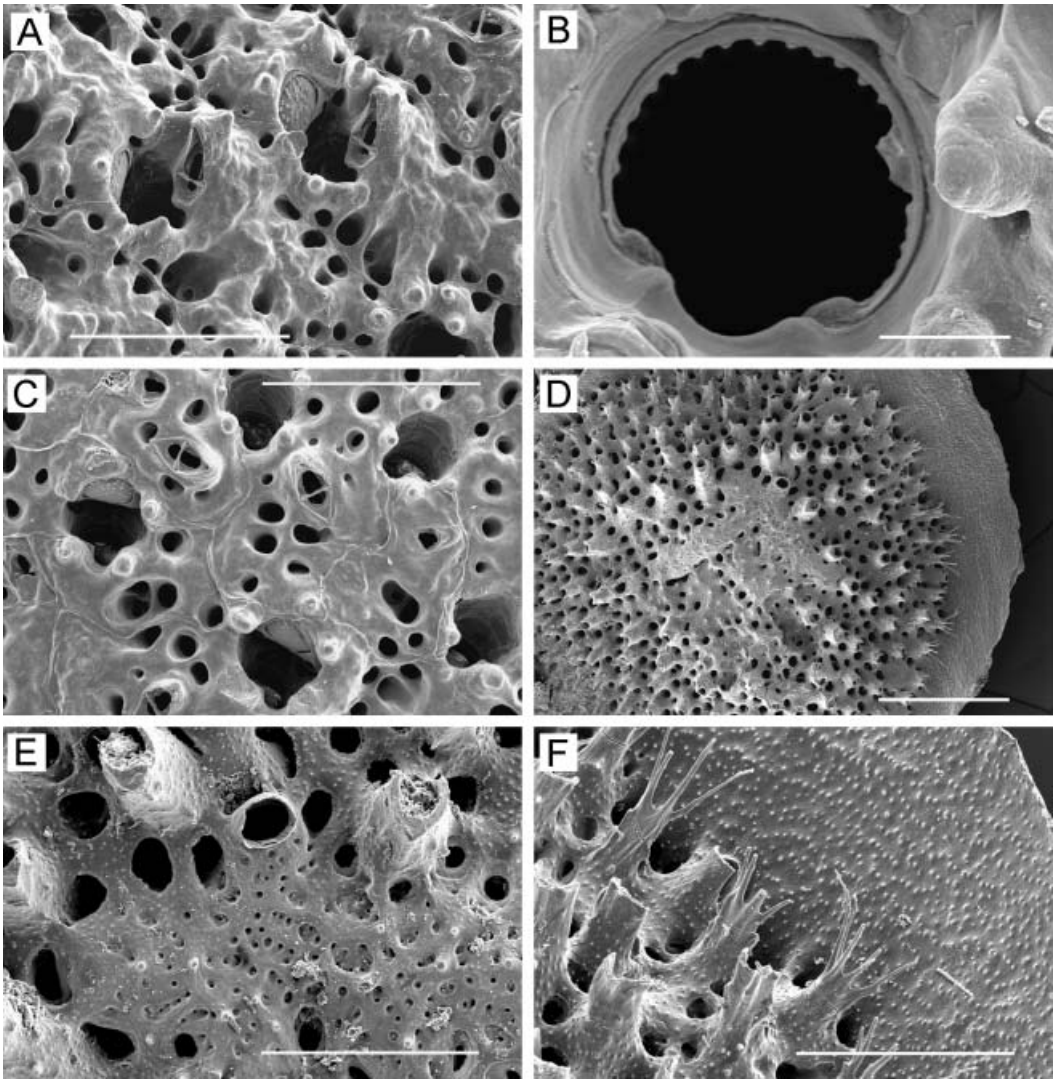


Figure 15. (A–C) *Rhynchozoon splendens* Hayward: (A) ovicellate zooids, showing asymmetrically orientated oral avicularia; (B) enlargement of primary orifice; (C) autozooids and ovicellate zooids; diamond-shaped rostra of frontal avicularia are also evident. (D–F) *Discoporella pristis* MacGillivray: (D) partial view of entire colony, showing irregular brood chamber in centre, with oeciostome; (E) enlargement of part of brood chamber and oeciostome (top centre); (F) colony margin, showing characteristically granulated marginal lamina and peristomes ending in long processes. All specimens bleached. Scale bars: 500 μm (A, C); 50 μm (B); 1 mm (D); 400 μm (E, F).

Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATIDA Busk, 1852
Suborder CERIOPORINA Hagenow, 1851
Family DENSIPORIDAE Borg, 1944
Genus *Discoporella* Gray, 1848
Discoporella pristis (MacGillivray, 1884)
 (Figure 15D–F)

Discoporella pristis MacGillivray 1884, p 126, Figure 3, 3a, b.

Disporella pristis: Gordon and Taylor 2001, p 260, Figures 22–30.

Measurements

Diameter of peristome at colony margin 0.05–0.07 (0.060 ± 0.006); diameter of kenozooidal opening near colony margin 0.04–0.07 (0.056 ± 0.009).

Description

Based on a single circular colony 3.5 mm in diameter. Colony (Figure 15D) mound-shaped, adnate, the lamellar margin slightly raised; whitish in colour. Peristomes distinct, not connate, but organized in approximately radial columns with the zooids offset from one column to the next, so that they are quincuncially arranged. Entire surface of colony finely granulated (Figure 15E, F), including the marginal lamella, which shows no radial striae. Peristomes with elevated extension on macular side that is semicircular in transverse section and in marginal zooids is often prolonged at end into as many as six long, sharp processes (Figure 15F). Interior walls of kenozooids with sparse, small, sharp denticles. Centre of colony occupied by a brood chamber (Figure 15D) that is about one-third of colony diameter in extent, consisting of two elongate, irregular lobes; surface of chamber irregularly porous, in the process of becoming thickened with reticulate calcification. One oeciostome present (Figure 15E), located at abmacular edge of brood chamber, the opening oval, raised on a low peristome; internal surface of oeciostome covered with minute spines.

Remarks

Our specimen agrees well with the description by Gordon and Taylor (2001) of small, neanic colonies of this species. According to these authors, colonies can become quite large, up to 6 cm in extent, and with more than a hundred maculae.

Distribution

Broadly distributed in the Indo-West Pacific from Japan through Indonesia, New Zealand, the Great Barrier Reef, southern Australia, eastern and southern Africa (referenced in synonymies by Gordon and Taylor 2001). This is the first record for the Hawaiian Islands.

***Disporella compta* new species** (Figure 16A–D)

Type material

Holotype: NHM 2006.7.21.22, specimen HI-53, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratype 1, NHM 2006.7.21.23, same locality and collecting information as for holotype, specimen HI-71, partly overgrown by *Funerossia copiosa*, bleached, coated for SEM.

Etymology

The species name is from the Latin *comptus* (formed, framed, neat), referring to the well-delineated maculae imparting a tidy appearance to the surface of the colony.

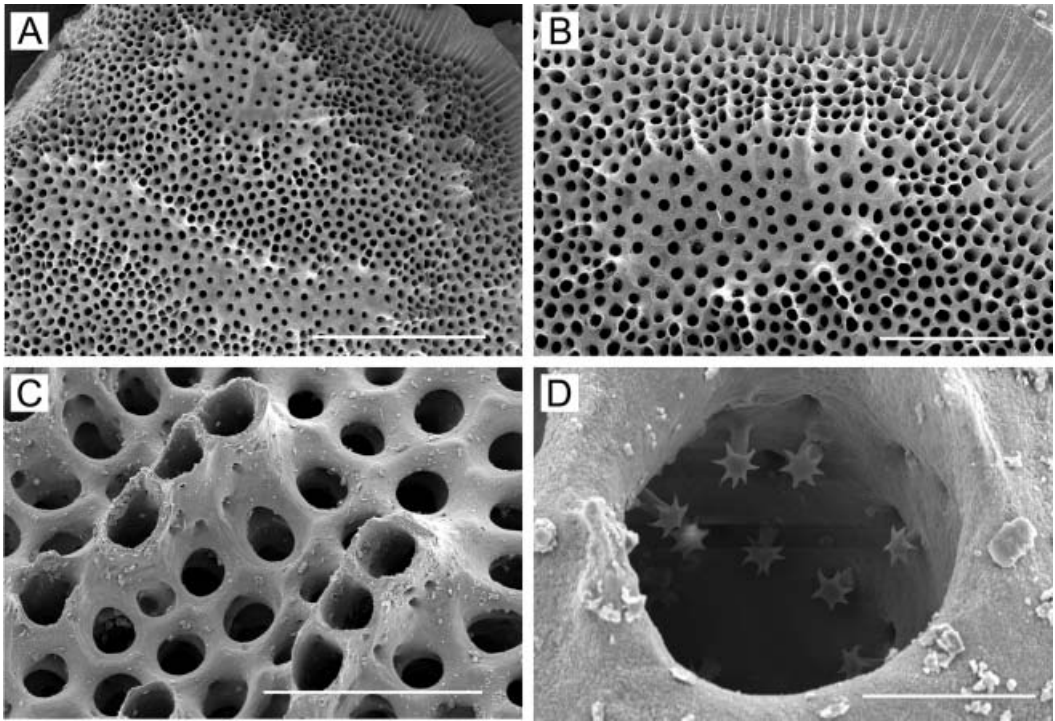


Figure 16. *Disporella compta* n. sp., holotype (NHM 2006.7.21.22): (A) partial view of colony, showing one elongate and two oval maculae among seven maculae present in colony; (B) enlargement of a macula; (C) columns of fused peristomes of three to four autozooids; (D) enlargement of kenozooidal opening showing palm-tree-shaped pinhead spinules. All specimens bleached. Scale bars: 2 mm (A); 1 mm (B); 400 μ m (C); 50 μ m (D).

Measurements

Peristomial openings slightly longer in radial than transverse direction, 0.08–0.10 (0.089 ± 0.009) \times 0.07–0.09 (0.080 ± 0.008), respectively. Kenozooidal openings 0.08–0.11 (0.088 ± 0.015).

Description

Two colonies found, one complete and the other a fragment. Colony approximately circular, convex, adnate, but with marginal lamina raised from substratum; light violet in colour; marginal lamina traversed by raised, closely spaced radial lines indicating lateral boundaries of incipient zooids; the complete colony measures 7 mm \times 8 mm; the other is broken and partly overgrown by an ascophoran, and measures 6 mm in maximum dimension. Cormidial arrangement of larger colony (Figure 16A) clearly evident, with seven maculae, six of them oval or elongate-oval, and the other narrowly elongate, two-thirds as long as colony diameter; macula of the colony fragment is narrow and elongate. Surfaces of maculae (Figure 16B) sunken, regular; due to constriction of kenozooidal openings, maculae appear less porous than intermacular areas; maculae are well delineated and can be easily counted with the naked eye. Peristomes in uniserial connate radii two to

four peristomes in extent (Figure 16B, C) and orientated perpendicular to macular margin, with occasional single peristomes at periphery of cormidial unit (macular area and surrounding radii); peristomes sometimes vertically orientated near macula but generally angled toward colony margin, tallest at macular end of series, lowest at abmacular end; fused along entire length; ends truncate, somewhat irregular; peristomial openings slightly oval. Kenozooidal openings circular or oval, usually as large as or larger than peristomial openings in areas outside maculae; often constricted by centripetal growth of surface calcification within maculae, but not closed. Two columns of kenozooids between connate columns of peristomes; three to five rows between cormidial (macular) units. Inner walls of kenozooids and zooidal peristomes have numerous palm-tree-shaped pinhead spinules (Figure 16D), the heads with five to seven sharp rays. Brood chambers lacking in our specimens.

Remarks

Disporella compta is similar to *D. californica* (d'Orbigny, 1853) and *D. ovoidea* Osburn, 1953, both of which are fairly widely distributed in the subtropical to tropical Eastern Pacific, sharing with these species the following characters: connate, uniserial radii; pinhead spinules (abundant in *D. californica*, rare in *D. ovoidea*); peristomial tubes only moderately tall, and truncate; colonies small. However, *D. compta* differs from these species in having at most four peristomes in a connate column; *D. californica* has around 10, and *D. ovoidea*, seven. The macular cormidia of *D. californica* appear to be nearly circular (Osburn 1953), larger in proportion to colony size, and hence less numerous than in *D. compta*; furthermore, *D. californica* also commonly undergoes zoarial budding, producing smaller, short-stipitate colonies at the margin, which was not observed in *D. compta*. *Disporella ovoidea* appears typically to have only a single large, central macular area, with radii extending from the macular margin to the colony margin. *Disporella compta* may eventually prove to be a geographic or ecophenotypic variant of one of these species; examination of brood chambers in Hawaiian material will help resolve this issue.

Distribution

Kapa'a beach, Hawaii Island, is the only known locality.

Genus *Favosipora* MacGillivray, 1885

Favosipora adunca new species

(Figure 17A–F)

Type material

Holotype: NHM 2006.7.21.24, specimen HI-58b, bleached, coated for SEM; Kapa'a Beach Park, Island of Hawaii; 1 March 2005; M. H. Dick, collector; intertidal, 0.15 m low tide. Paratypes: same locality and collecting information as for holotype. Paratype 1, NHM 2006.7.21.25, specimen HI-1, bleached, coated for SEM. Paratype 2, NHM 2006.7.21.26, specimen HI-3 (part), bleached, coated for SEM. Paratype 3, NHM 2006.7.21.27, specimen HI-72, bleached, coated for SEM. Paratype 4, YPM-38559, specimen HI-54, bleached, coated for SEM. Paratype 5, YPM-38560, specimen HI-77, bleached, coated for SEM. Paratype 6, YPM-38561, bleached specimen, uncoated.

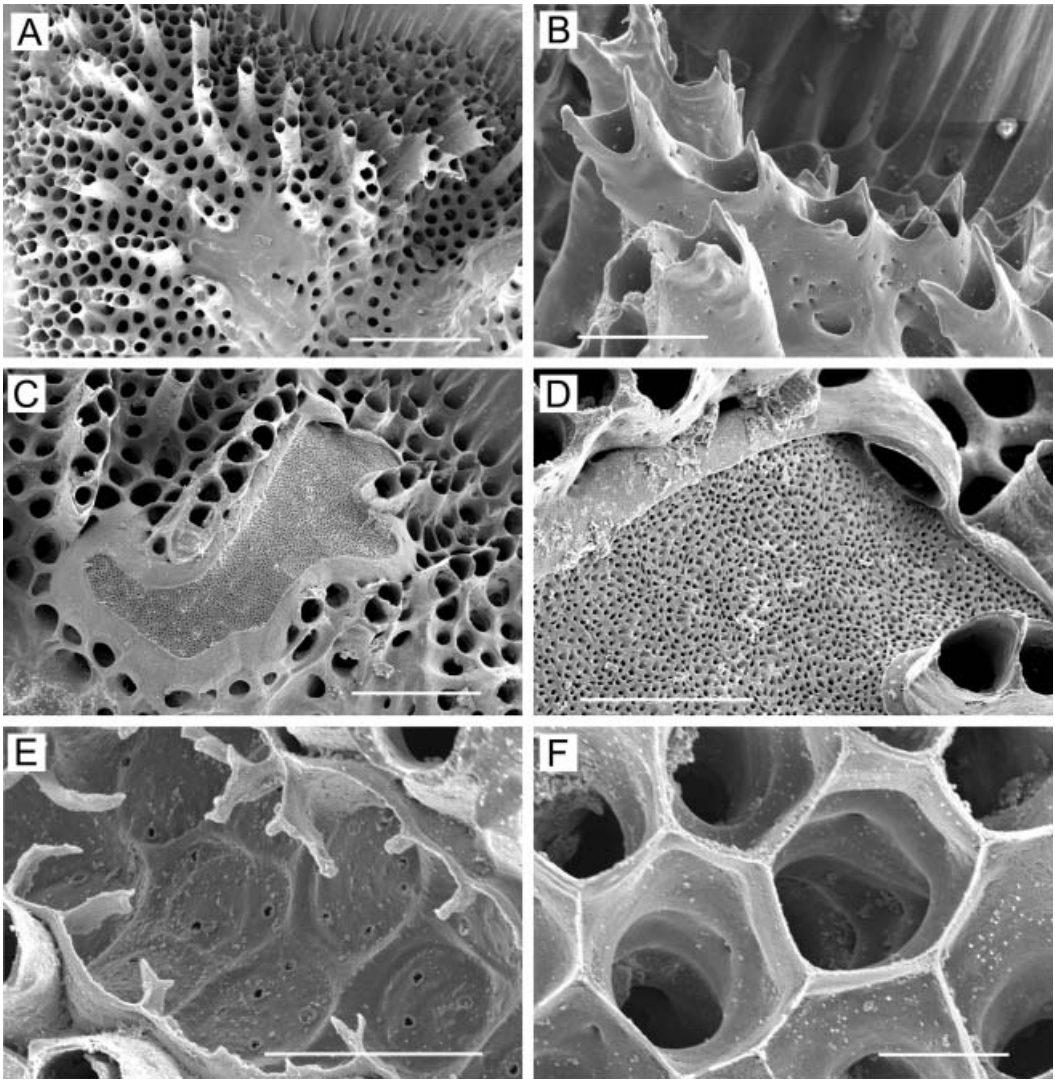


Figure 17. *Favosipora adunca* n. sp.: (A) paratype 1 (NHM 2006.7.21.25), partial view of colony; (B) paratype 1, enlargement of fused peristomes of autozooids; (C) holotype (NHM 2006.7.21.24), brood chamber; (D) holotype, enlargement of brood chamber, showing oeciostome (top, right of centre); (E) paratype 4 (YPM-38559), detail of brood-chamber formation, showing granulated floor and struts of calcification that will contribute to covering; (F) paratype 4, enlargement of kenozooidal openings. All specimens bleached. Scale bars: 1 mm (A); 200 μ m (B, D, E); 500 μ m (C); 100 μ m (F).

Etymology

The species name derives from the Latin *aduncus* (bent in, crooked), referring to the bent oeciostome.

Measurements

Peristome opening near margin slightly elliptical, 0.09–0.13 long (0.108 ± 0.011) \times 0.08–0.11 wide (0.089 ± 0.011); maximum dimension of kenozooidal opening 0.05–0.14

(0.092 ± 0.022) ($n=15$; five measurements from each of three colonies). Brood chamber 1.20–1.38 long \times 0.68–0.80 wide ($n=3$).

Description

Colony small, smallest observed 5 mm \times 3 mm, largest observed 8 mm \times 7 mm; discoid, raised in centre, whitish in colour; roughly circular or arranged along a long axis; with a broad marginal lamina striated with fine ridges orientated perpendicular to margin, indicating incipient zooids; colony adnate over most of centre, but lamina is variably raised from the substratum, sometimes sharply. Central macular area (Figure 17A) of colony tends to be elongate, even in nearly circular colonies; rarely there are two macular centres. Zooidal peristomes (Figure 17A, B) sometimes single or connate in groups of two to four, but usually are in connate radial series of up to 12 zooids, generally uniserial but occasionally partly biserial. Peristomes in a connate row are tall near centre of colony and become progressively shorter toward the margin. Peristomes tapered; bicuspid (Figure 17B), with a blunt-triangular cusp on the admacular and another on the abmacular side; occasionally occluded by a centripetally growing closure plate. Openings of kenozooids can also become constricted or closed by centripetal growth of a horizontal lamina. Calcification of colony surface and interior of peristomes and kenozooids (Figure 17F) smooth, without granulation, mural spines, or pinhead spinules. Brood chamber (Figure 17C–E) elongate, irregular, extending as one or two lobes between two or three adjacent columns of connate peristomes, respectively. The largest colony had three brood chambers, one situated at the edge of the central macular area and the others halfway between the macular area and the margin. Floor of brood chamber (Figure 17E) thinly covering kenozooidal openings, sparsely granulated, with three to six small, circular pores leading to each kenozooid; roof of brood chamber begins to form by centripetally growing struts of calcification. When complete, roof is more-or-less flat, slightly depressed, densely perforated by pseudopores (Figure 17D), sharply delineated from smooth, sloping circumferential wall. Oeciostome (Figure 17D) lies at margin of brood chamber, raised, bent at a right angle so that plane of transversely oval opening is perpendicular to roof.

Remarks

The combined characters of smooth mural surfaces; peristomes bicuspid and typically in long, connate, mostly uniserial series of up to 12; the macular area usually elongate; and the bent oeciostome separate this from other species of *Favosipora*.

Distribution

The genus *Favosipora* is primarily distributed in the Southern Hemisphere; according to Gordon and Taylor (2001), only one other species of this genus, *F. holdsworthii* (Busk, 1875), has been recorded from the Northern Hemisphere. Kapa'a beach, Hawaii Island, is the only known locality.

Discussion

The primary goal of this study was to test the conclusion by Soule et al. (1988) that tropical (and specifically Hawaiian) shores of volcanic rock and coral rubble do not support much

of a bryozoan fauna, due to a small tidal range coupled with the effects of intense heat and sunlight. Is this conclusion supported by our study? The answer is both yes, and no. Bryozoans were very patchily distributed among sites, with some seemingly optimal sites having few or no bryozoans. However, the diversity and abundance of bryozoans at one site were as high as would be expected in optimal sites at higher latitudes.

Four intertidal sites were intensively examined, and only one (Kapa'a Shore) supported an abundant and rich bryozoan assemblage. At the two sites (Kiholo Bay and Whittington Beach) that were most similar to the types of rocky shores that in northern-temperate latitudes support rich bryozoan assemblages (Dick and Ross 1988; Dick et al. 2005), bryozoans were depauperate or lacking: no bryozoans were found at the former site, and only three dead colonies of *Hippopodina iririkiensis* were found at the latter. Both these sites comprised sheltered shores of layered, relatively stable rock-pile habitat with good tidal circulation. Furthermore, the undersides of boulders were abundantly covered with a diverse assemblage of the same kinds of infralittoral-fringe animals as found in the same habitat at higher latitudes: sessile bivalves (in this case, *Isognomon perna*), several species of encrusting sponges, spirorbid and serpulid tubeworms, nudibranchs, nemerteans, errant polychaetes, holothurians, sea urchins, chitons, and gastropods. In short, these Hawaiian lower-intertidal rock-pile communities appeared to be fundamentally similar in structure to those seen at higher latitudes, except for the curious absence of bryozoans.

Why there were few or no bryozoans at Kiholo Bay and Whittington Beach is a mystery. However, in contrast to the two sites where bryozoans were more abundant, both these sites are influenced by freshwater outlets (Polhemus 1966). Numerous freshwater springs and a stream flow into Kiholo Bay, providing an approximately 0.3 m-deep layer of cold freshwater on the surface, separated from the warmer seawater beneath by an obvious thermocline-halocline boundary. At Whittington Beach, a large freshwater pond fed by downslope percolation connects to the shore by a narrow channel. So, low bryozoan diversity at these sites may result from low or variable salinity.

In marine invertebrates, there is a complex relationship between temperature and tolerance of low salinity, which is related to osmoregulation (Verwey 1957). Some species tolerate low salinity best at low temperatures, such as an estuarine amphipod studied by Girisch et al. (1974). However, this relationship depends upon the ambient temperature to which a species is adapted, and other species such as a polychaete studied by Åkesson and Costlow (1978) showed higher tolerance of low salinity at higher temperatures. At Ketchikan, Alaska, Dick et al. (2005) found the bryozoan species diversity at an intertidal site with extensive freshwater influence to be much lower than at more stenohaline, higher-salinity sites, though the abundance of species that did occur was fairly high. At Kodiak, Alaska, most intertidal bryozoans are intermittently exposed to salinities of 17 psu or even lower, but at a maximum water temperature of 12°C (Dick and Ross 1988). It may be that at the higher ambient seawater temperatures of the subtropics and tropics, bryozoan colonies or larvae are much more intolerant of low or variable salinity than at cooler, more temperate latitudes. However, this is not a very satisfactory explanation, for it should apply also to some of the other marine taxa mentioned above (e.g. sponges, nemerteans, flatworms) that contributed to the rich lower-intertidal communities at the Hawaiian study sites.

The observation site at Kealakekua Bay, though apparently not influenced by freshwater, is a highly protected inlet with a dense cover of lava boulders and coral rubble on a slightly sloping bottom. Here, bryozoans are likely exposed to elevated water temperatures due to warming of the shallow water of the inlet, without much cooling by currents. Bryozoan

species diversity was low at this site, but two species (*Poricella spathulata* and *Hippopodina irikiensis*) were fairly abundant, more so than at any other site, suggesting they were particularly tolerant of what must be a highly stressful environment.

The highest species diversity and abundance of bryozoans were found at Kapa'a Shore. This was an exposed site, with the beach consisting of solid benchrock with tidepools, alternating with stretches of rounded boulders or cobbles, indicative of considerable wave action. Bryozoans were found only on angular boulders stably wedged into small tidepools at the water's edge at low tide. We suspect that a diversity of encrusting bryozoans could survive here both because the boulders were stably anchored, and because of the cooling effects of continually splashing waves. In our experience, maximal diversities of bryozoans are not found in such high-energy sites at higher latitudes, although high diversities might also patchily occur there in microhabitats similar to that at Kapa'a.

Another possible factor in the distribution of Hawaiian intertidal bryozoans is predation. We observed what appear to be small drill holes from an unknown predator in the frontal walls or ovicells of several species (*Bryopesanser serratus*, Figure 12A; *Cribellopora souleorum*, Figure 13A, C; *Crepidacantha longiseta*; and *Junerossia copiosa*). Such drill holes have not been observed in the examination of thousands of specimens from Alaska (Dick and Ross 1988; Dick et al. 2005) and northern Japan (A. V. Grischenko, personal communication). A relatively few species, and a relatively few zooids of these species, were affected among the Hawaiian material; however, a predator that can drill through the calcified frontal wall might also be able to penetrate the operculum, so the incidence of predation might have been higher than we detected. In addition, a predator might be a greater factor in the mortality of young, newly settled bryozoan colonies than in that of mature, heavily calcified ones; two of four zooids in an ancestrular complex of *Cribellopora souleorum* had drill holes (Figure 13C). Although we have no evidence whatsoever that predation is a factor limiting bryozoan distribution on the Island of Hawaii, a predator that is abundant in protected sites but not in exposed sites would help explain the observed distribution.

Fairly extensive work on bryozoans has previously been done in the Hawaiian Islands. The major early reports including identifications of Hawaiian material were those of Busk (1881, 1884) and Canu and Bassler (1927). Soule et al. (1988) reviewed previous work, including their own studies, and listed 200 species known from the Hawaiian Islands, including nine ctenostomes, 164 cheilostomes, and 27 cyclostomes. Since then, selected taxonomic studies (Soule, et al. 1991; Soule, et al. 1999, 2003) have reported a few additional species from the archipelago. It is informative, then, that despite this previous work, 19 (59%) of the 32 species we detected represent new Hawaiian records of cosmopolitan or Indo-West Pacific species. This suggests that many additional species remain to be discovered in the Hawaiian Islands.

In a biogeographical analysis of Indo-West Pacific cheilostome bryozoan faunas, Tilbrook and De Grave (2004) reported high levels of endemism at the familial and generic levels for the Hawaiian fauna, consistent with long isolation of this island archipelago. However, they did not analyse the Hawaiian fauna at the species level due to the general paucity of adequate previous SEM documentation of Hawaiian species. Of the 32 species we detected, nine (28%) are new species known only from the Island of Hawaii that might or might not be true endemics. The total proportion of new species (10 out of 32, or 31%), is not exceptionally high, and not in itself indicative of a high degree of endemism at the species level. Recent local studies of intertidal and subtidal bryozoans at northern-temperate latitudes have detected similar levels of new species, 25–35% (Dick and Ross 1988; Soule et al. 1995; Dick et al. 2005), and local studies in tropical western-Pacific

island archipelagos have reported, for example, 22% (Vanuatu; Tilbrook et al. 2001) and 40% (Solomon Islands; Tilbrook 2006) new species.

As Soule and Soule (1988) pointed out, the degree of endemism among Hawaiian bryozoans is unknown, even though high levels of endemism have been reported there for other marine animal groups. These authors noted that, among 28 new species they had reported from the Hawaiian Islands, several had subsequently been found on tropical islands south of the equator. In fact, every newly described species known only from its type locality is an apparent endemic until it is found somewhere else. Our study includes a number of species that were originally described relatively recently from single Indo-West Pacific localities, and which subsequent studies have shown not to be endemic to the local area of discovery (e.g. *Escharoides longirostris*, *Fenestrulina caseola*, *Nimba saxatilis*, *Crepidacantha carsioseta*, *Rhynchozoon ferocula*, *Rhynchozoon splendens*). Only when more of the islands of the central and western Pacific have been adequately studied will it be possible to assess the true level of endemism among Hawaiian bryozoans.

A summary of the biogeographical affinities of the bryozoans reported in our study is presented in Table II. Nine of the 10 new species are omitted, as they are known at present only from the Island of Hawaii. The Hawaiian intertidal fauna is unambiguously allied with the Indo-West Pacific fauna, rather than that of the eastern Pacific. Of the 23 species with known distributions outside the Hawaiian archipelago, five (22%) are considered cosmopolitan, and the rest (78%) also occur in the Indo-West Pacific. Aside from the

Table II. Biogeographic information for the 23 species found in this study that have known distributions extending outside the Hawaiian Islands.

Species	Circumtropical	Indo-West Pacific ^a	New Hawaiian record
<i>Parellisina albida</i>		x	x
<i>Antropora minor</i>	x		x
<i>Beania discodermae</i>		x	x
<i>Micropora rimulata</i>		x	x
<i>Puellina harmeri</i>		x	x
<i>Hippothoa flagellum</i>	x		x
<i>Chorizopora brogniartii</i>	x		x
<i>Poricella spathulata</i>		x	x
<i>Drepanophora corrugata</i>		x	x
<i>Escharoides longirostris</i>		x	x
<i>Parasmittina serrula</i> ^b	x		
<i>Watersipora</i> "subovoidea"		x	
<i>Junerossia copiosa</i> n. sp.		x	x
<i>Hippopodina iririkiensis</i>		x	x
<i>Cosciniopsis lonchaea</i>		x	
<i>Cheiloporina haddoni</i>		x	
<i>Fenestrulina caseola</i>		x	x
<i>Nimba saxatilis</i>		x	x
<i>Crepidacantha carsioseta</i>		x	x
<i>Crepidacantha longiseta</i>	x		x
<i>Rhynchozoon ferocula</i>		x	x
<i>Rhynchozoon splendens</i>		x	x
<i>Disporella pristis</i>		x	x
Percentage	22	78	83

^aIncludes both species restricted to the western Pacific and those with distributions extending into the Indian Ocean.

^bStatus is unclear; since it has been recorded in both the Pacific and Atlantic Oceans, it is here listed as circumtropical.

putatively cosmopolitan species, no species detected by our study is known from the eastern Pacific.

We note, however, that the intertidal bryozoan fauna might not be representative of the Hawaiian fauna as a whole in its biogeographic affinities. The ability of intertidal species to tolerate a relatively stressful environment might mean they were more likely than strictly subtidal species to have been transported relatively recently to the Hawaiian archipelago, for example from the western Pacific attached to the vessels of the prehistoric human colonizers of the Hawaiian Islands (Ziegler 2002), on ships' hulls (Soule and Soule 1968), or on floating logs (Soule and Soule 1973).

In the cold-temperate northeastern Pacific, the assemblage of intertidal bryozoans in rocky habitats is similar in composition over a considerable geographical distance. Dick et al. (2005) found the same genera ranking highest in terms of species richness at two sites 1500 km apart, with the sites having some species in common, as well as geographical replacement of species, within these species-rich genera. It remains to be seen whether a similar pattern obtains in the subtropical to tropical, central to western Pacific.

On Hawaii, larval settlement preferences might to some extent influence the composition of the intertidal bryozoan association. Most of the species detected in our study were observed growing directly on lava rock as the substratum, though in most cases it was unknown whether the ancestrula of a colony had settled directly on the rock, as opposed to rock-associated calcareous substrata such as worm tubes or encrusting coralline algae. In any case, the rock-associated intertidal association on Hawaii might preferentially include species that are generalists in terms of larval settlement requirements. In a study of cheilostome bryozoans in cryptic coral-reef communities in Jamaica, Winston and Jackson (1984) found 29 species encrusting the undersides of corals, but only 15 species on asbestos-cement panels submerged in reef areas; all but one of the species on the panels also occurred on the corals. One explanation could be that nearly half the species in the Jamaica study preferentially settle on coral substrata, and that those that occurred on the panels are generalists in terms of settlement. Winston (1986) pointed out that the three most speciose bryozoan genera in coral-reef environments—*Parasmittina*, *Celleporaria*, and *Rhynchozoon*—all include species characterized as opportunistic, or fouling, occurring on man-made substrata.

Whatever the causes of the pattern of diversity we observed, Soule et al. (1988) were partly correct in asserting that tropical (and specifically Hawaiian) shores of volcanic rock and coral rubble do not generally support a bryozoan fauna. This appears to be true for much of the shoreline around Hawaii Island, both for high-energy, solid-rock shores and highly protected rock-pile shores. However, our study shows that bryozoans can form diverse and dense assemblages in particular microhabitats, and that the single-site species diversity in these habitats can be as high as that observed at temperate latitudes. We suspect that if a number of such sites are examined on the Island of Hawaii, the cumulative intertidal species diversity will also approach, or even exceed, the values of around 70–80 species documented for local areas in northern (Dick and Ross 1988; Dick et al. 2005) and southern (Gordon 1980) temperate regions.

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