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Matthew H. Dick^a, Andrei V. Grischenko^a & Shunsuke F. Mawatari^a

^a COE for Neo-Science of Natural History and Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan

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Intertidal Bryozoa (Cheilostomata) of Ketchikan, Alaska

MATTHEW H. DICK, ANDREI V. GRISCHENKO, & SHUNSUKE F. MAWATARI

COE for Neo-Science of Natural History and Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan

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Abstract

Assemblages of intertidal bryozoans are proving to be more species-rich than generally previously appreciated. This study found 31 species of cheilostome bryozoans at three rocky-intertidal sites at Ketchikan, Alaska, USA. Species richness varied considerably among the three collecting sites: 28 at East Tongass Narrows, 18 at Higgins Point, 10 at Settlers Cove. Each site had species not occurring at the other sites (12, two, and one species, respectively). The number of species per site was within the range of values previously observed in a more extensive study at Kodiak, Alaska, suggesting both similar intertidal species richness at the two localities, and that sampling of other intertidal sites at Ketchikan would detect additional species. Descriptions and scanning electron microscopy (SEM) illustrations are provided for the species found at Ketchikan, and SEM illustrations are included for the holotypes of *Porella acutirostris* Smitt, 1867 and *Schizoporella japonica* Ortmann, 1890; a paralectotype of *Porella columbiana* O'Donoghue and O'Donoghue, 1923; and a specimen of *Cauloramphus pseudospinifer* Androsova, 1958. *Fenestulina delicia* Winston, Hayward, and Craig, 2000 is illustrated and described from subtidal specimens from Sitka, Alaska. Eight species (26% of total species) are described as new (*Cauloramphus multiavicularia* n. sp., *Cauloramphus tortilis* n. sp., *Puellina caesia* n. sp., *Celleporella nodasakae* n. sp., *Porella donoghueorum* n. sp., *Microporella ketchikanensis* n. sp., *Fenestrolides tongassorum* n. sp., and *Rhynchozoon glabrum* n. sp.). *Membranipora serrilamella* Osburn, 1950 and nominal *Membranipora membranacea* (L., 1767) from the north-east Pacific Ocean are considered to be junior synonyms of *Membranipora villosa* Hincks, 1880. *Schizoporella unicornis* var. *japonica* Ortmann, 1890 is elevated to species status as *Schizoporella japonica* Ortmann, 1890; many of the previous records of *Schizoporella unicornis* (Johnston, 1844) from the northern Pacific Ocean are likely attributable to *S. japonica*. Examination of type specimens of *Porella columbiana* O'Donoghue and O'Donoghue, 1923 show that Osburn's (1952) concept of this species was in error; the taxon treated by Osburn and subsequent authors as *P. columbiana* is described herein as *Porella donoghueorum* n. sp. Although *Porella acutirostris* Smitt, 1867 has been previously considered a circumpolar, arctic-boreal species, it is questionable whether this species occurs in the boreal North Pacific. Nominal *P. acutirostris* probably comprises a complex of morphologically similar, closely related species in the northern hemisphere that includes *Porella major* Hincks, 1884 and *Porella columbiana* O'Donoghue and O'Donoghue, 1923. Of the 31 cheilostomes detected intertidally at Ketchikan, only *Schizoporella japonica* and *Fenestulina delicia* are considered as actually or potentially introduced species. The introduction of *S. japonica* (previously reported as *S. unicornis*) to the north-eastern Pacific on Pacific oysters from Japan has been well documented in the literature. *Fenestulina*

Correspondence: Matthew H. Dick, Laboratory of Systematics and Evolution, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan. Email: mhdick@nature.sci.hokudai.ac.jp

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delicia, originally described from Maine in 2000, is reported for the first time from the north-eastern Pacific Ocean.

Keywords: *Biodiversity, Cheilostomata, intertidal Bryozoa, introduced species, new species, species richness, taxonomy*

Introduction

Considering that the intertidal zone is more amenable to direct sampling than subtidal areas, intertidal bryozoan assemblages have been curiously understudied. Although intertidal bryozoans were the focus of many of the pioneering studies on bryozoan ecology (reviewed by Ryland 1967, 1970, 1974, 1976), most of these studies were autecological in scope, investigating the factors influencing particular species' larval settlement, which in turn determined their distribution on the shore. Perhaps the first to recognize the synecological importance of bryozoans in shore ecosystems was Gordon (1972), who wrote in general terms about their place in the food web; the nature of their competitive responses to other bryozoans and to species of other taxa; and their overall importance as competitors for a limited resource, space. Concerning the intertidal community at Goat Island Bay, northern New Zealand, Gordon noted:

Most intertidal bryozoans are incrusting. The space occupied by incrusting species is very great and at Goat Island Bay bryozoans are the predominant component of the sessile fauna under boulders. The main effect of this is to preclude extensive occupation of these surfaces by other sessile animals and reduce numbers of their attendant fauna, such as predators ... Occupation of space is probably the most influential effect of bryozoans on the shore ecosystem.

Intertidal bryozoans are of interest for a number of reasons, in addition to a paraphrasing of Sir Edmund Hillary's dictum, "Because they are there". Collections of intertidal bryozoans contain not only species that are largely restricted to the intertidal and thus can be obtained in no other way, but also a significant sampling of the species that extend into adjacent subtidal areas. Consequently, by collecting intertidally, it is possible to take comparable samples of significant richness at numerous localities over broad geographic ranges, at much less expense than that required by dredging. Such collections are quite useful from the viewpoints of zoogeography and biodiversity.

Lying at the interface between terrestrial and marine biocoenoses, the intertidal zone is particularly susceptible to some agents of human-induced marine environmental degradation, such as oil spills; it is probably as susceptible as subtidal habitats to others, such as chronic pollution. In assessing the extent of environmental degradation or the consequences of environmental changes, assemblages of intertidal organisms again have the advantage over subtidal assemblages that they can be sampled or observed directly, without the requirements of special equipment. Furthermore, the more species-rich these intertidal assemblages are, the greater the resolution they allow, in terms of community-level parameters, in investigations of the effects of environmental change or degradation.

One form of environmental change currently receiving much attention worldwide is related to marine invasions, that is, the introduction and spread of non-native marine species in regions outside their historical range, generally mediated by human activities. Bryozoans are well represented among invasive or fouling sessile animals and have been studied in this context in various parts of the world (e.g. Ryland 1965; Brock 1985; Mawatari and Mawatari 1986; Gordon and Mawatari 1992; Occhipinti Ambrogi and

d'Hondt 1994). Some introduced species have been documented to be extremely abundant intertidally, e.g. nominal *Schizoporella unicornis* in the north-eastern Pacific (Powell 1970; Ross and McCain 1976). However, a factor that impedes both the detection of introduced populations and elucidation of their source is poor taxonomic resolution. The taxonomy of North Pacific bryozoans is generally poorly resolved (Soule et al. 2002; Dick and Mawatari 2004), and adequate taxonomy is an absolute prerequisite for other types of studies, whether they deal with ecology, environmental degradation, zoogeography, or biodiversity.

In this paper, we report on cheilostome bryozoans collected intertidally from three sites in the vicinity of Ketchikan, Alaska in September 2003. Though the primary focus of our study is taxonomic, the collection at Ketchikan was made primarily from rock faces and the undersides of intertidal boulders, so as to be comparable to a similar, though more extensive, study conducted in the Kodiak vicinity by Dick and Ross (1988). The local species richness of bryozoans that emerged from the Kodiak study is among the highest documented intertidally anywhere in the world. A goal of the present study was to assess whether this was an unusually high richness, or simply what might be expected in similar habitats at other localities around the North Pacific rim. Ketchikan, located across the Gulf of Alaska from Kodiak and separated by 1500 km of coast and 2° of latitude, provides an additional data point. Finally, our study sought to examine the intertidal bryozoan fauna for the presence of non-native, invasive species. Literally hundreds of cruise ships from many parts of the world stop at Ketchikan every summer, making it a potential site of introductions.

Study area and methods

Collections were made by M.H.D. at three sites accessible by the road system in the vicinity of Ketchikan (55°21'N, 131°42'W), a town of approximately 14,000 year-around residents located on Revillagigedo Island in the south-eastern Alaskan panhandle. The locations and brief descriptions of these collecting sites are given in the following paragraphs. Both the benchflat rocks and the wave-shaped cobbles and slabs on which bryozoans were found at all three sites consisted of green schist from a Permian–Cretaceous accretionary complex (rocks identified by Dr Reishi Takashima, personal communication).

Higgins Point (9 September 2003)

Collecting was conducted along an approximately 100 m stretch of shore 1.5 km SSE of Higgins Point proper. The shore was rocky, consisting of a shallow layer of boulders and cobbles overlying coarse shell-sand, rock sediment, and solid rock benchflat. Although no stream outlets were observed along this stretch of shore, houses at the head of the beach had sewage or graywater outlets in the nearby subtidal zone. Samples consisting of portable rocks heavily encrusted with bryozoans on their undersides were collected close to the water's edge on a –1.5 ft tide, at the top edge of the *Agarum* zone and within the *Rhodomela larix* zone.

Settlers Cove (10 September 2003)

Collecting was conducted along 100–200 m of shore just north of the outlet of Lunch Creek at the Settlers Cove State Recreation Site, 28 km NW of Ketchikan. The shore consisted mostly of beaches of rock- and shell-sand, interspersed with sand and mud flats supporting beds of seagrass, *Zostera marina*. However, there were patches of shore with boulders lying on sediment, and of solid benchflat. There was much freshwater influence from Lunch

Creek, many other small streams, and seepage coming up through the sediment of the beach. The area was generally depauperate in bryozoans; however, some large, stable slabrocks were extensively encrusted on their undersides by a few species. Specimens were obtained at the water's edge on a -1.6 ft tide, by breaking off the outer layer of heavily encrusted rock surfaces.

East Tongass Narrows (11 and 12 September 2003)

The site was located on the east shore of Tongass Narrows toward the south end, about 10 km south of the cruise-ship dock in the Ketchikan city centre, and roughly 200 m north of the Hole-in-the-Wall Marina. A series of irregular, solid-rock outcrops 1–3 m in height surrounded a large, sand-bottomed tidepool. North of the outcrops and tidepool was a stretch of beach with multi-layered rock piles. Bryozoans were abundant on the undersides of solid-rock overhangs; in crevices in the benchrock; on some exposed rock faces; and on the undersides of boulders in small tidepools and rock piles. Some specimens were collected directly from the surfaces of benchrock. In addition, some heavily encrusted, portable rocks were selected for detailed examination, from underneath boulders and within rockpiles both at the water's edge on a -1.5 ft tide, as well as higher on the shore. However, the bulk of the specimens from this site came from small slabs pried from the underside of a heavy slab rock, roughly $0.6 \times 0.3 \times 0.2$ m in dimensions, that lay in a persistent tidepool nearly 2 m above the water's edge.

Rocks were examined by stereoscopic microscope. A Dremel tool with a circular diamond-surfaced cutting bit was used to remove small pieces of rock with attached bryozoans. Several representative specimens of every species encountered were air-dried. For SEM, selected specimens were immersed in a sodium hypochlorite solution to remove soft tissue, rinsed in water, air dried, and mounted with double-sided adhesive tape on aluminum SEM stubs. They were then 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} with ImageCatcher software. In some cases, digital images from light microscopy were taken with a Nikon SMZ1500 stereoscopic microscope system.

Measurements of zooids and zooidal structures were made by stereoscopic microscope with an ocular micrometer at $80\times$ magnification. Measurements are given in the text as the range of values, followed by the average value and sample size (n) in parentheses. Two values are given for sample size; the first and larger value is the number of zooids or structures from which measurements were taken; the smaller value separated by a comma is the number of colonies from which measurements were taken. Thus, a sample size of ($n=15, 3$) means that 15 measurements were made of zooids or structures from three colonies. Wherever possible, measurements were divided evenly among the colonies, so that ($n=15, 3$), for example, generally means five measurements from each of three colonies. Exceptions occurred where more of a particular structure (e.g. vicarious avicularia, ovicells) could be found in one colony than in another.

Some specimens included in this study were collected from subtidal settling plates at Sitka, Alaska by personnel of the Smithsonian Environmental Research Centre (SERC; Edgewater, MD). SEM illustrations are included of some type specimens loaned by the Swedish Museum of Natural History (SMNH) and The Natural History Museum, London (BMNH on old labels; now NHM). Holotypes and some paratypes were deposited at the

Yale Peabody Museum (YPM), Yale University, New Haven, CT; duplicate paratypes of some species were deposited at NHM and the Zoological Institute of the Russian Academy of Sciences (ZIRAS). In lists of type material in the accounts of new species, specimen localities are abbreviated ETN for the East Tongass Narrows site, HP for the Higgins Point, SC for the Settlers Cove site, and KV for Ketchikan vicinity, site unspecified. Locations of the sites and dates of collection are given in the site descriptions above. With one exception, all type specimens encrusted rock.

The higher classification utilized here follows the Interim Classifications of Families and Genera of Cheilostomata (Working Classification for *Treatise*) compiled by D. P. Gordon (unpublished). To conserve space, authors of genera and higher taxa are not included in the References.

In the calloporid genera *Callopora*, *Tegella*, and *Cauloramphus*, mural spines distal and lateral to the orifice can have a different character (taller, thicker, blunter, more erect) than those proximal to the orifice (shorter, thinner, more acuminate, curved, angled over the opesia). We refer to the former as “orificial spines” and the latter as “opesial spines”, though of course the orificial spines are also at the margin of the opesia. At the boundary between the two types, there is sometimes a pair of spines of intermediate character.

We here use the term “rostrum” to apply to the entire membranous frontal side of an avicularium and the term “poster” to refer to the membranous portion proximal to the hinge bar. In this terminology, the rostrum thus comprises the mandible and the poster.

Results

Thirty-one species were found intertidally at Ketchikan (Table I), of which eight are described herein as new. The three collecting sites differed markedly from one another in species richness, which ranged from 10 species at Settlers Cove to 28 species at East Tongass Narrows; Higgins Point was intermediate, with 18 species. Sixteen species, slightly over half the total, were found at more than one site, with the rest (15 species) found only at a single site: 12 at East Tongass Narrows, two at Higgins Point, and one at Settlers Cove. Only nine species were found at all three sites.

Suborder MALACOSTEGINA Levinsen, 1902
Superfamily MEMBRANIPOROIDEA Busk, 1852
Family MEMBRANIPORIDAE Busk, 1852
Genus *Membranipora* de Blainville, 1830
Membranipora villosa Hincks, 1880
 (Figure 1A–F)

Membranipora villosa Hincks 1880a, p 84, Plate 10, Figure 8.

Membranipora villosa: Robertson 1908, p 269, Plate 16, Figures 22, 23, Plate 17, Figures 24, 25; O'Donoghue and O'Donoghue 1923, p 26; 1926, p 29; Soule et al. 1995, p 39, Plate 4D.

Membranipora membranacea: Hincks 1882, p 469; Robertson 1908, p 267, Plate 16, Figures 19, 20; O'Donoghue and O'Donoghue 1923, p 26; Osburn 1950, p 21, Plate 1, Figures 8, 9.

Table I. Species described and/or illustrated in this study, with information on occurrence and relative abundance at the three collecting sites. *Fenestrulina delicia* was not found intertidally at Ketchikan, but is reported from subtidal specimens from Sitka, Alaska. A paralectotype of *Porella columbiana* and a specimen of *Cauloramphus pseudospinifer* (species also not found at Ketchikan) are illustrated, without full descriptions.

Species	East Tongass		
	Narrows	Higgins Point	Settlers Cove
<i>Membranipora villosa</i> Hincks, 1880	C	—	—
<i>Callopora craticula</i> (Alder, 1856)	U	R	R
<i>Cauloramphus magnus</i> Dick and Ross, 1988	C	C	C
<i>Cauloramphus multiavicularia</i> n. sp.	C	C	R
<i>Cauloramphus pseudospinifer</i> Androsova, 1958	—	—	—
<i>Cauloramphus tortilis</i> n. sp.	C	—	—
<i>Tegella aquilirostris</i> (O'Donoghue and O'Donoghue, 1923)	C	—	—
<i>Tegella horrida</i> (Hincks, 1880)	U	R	—
<i>Hincksina longiavicularia</i> Gontar, 1982	C	—	—
<i>Bugula pacifica</i> Robertson, 1905	U	—	—
<i>Bugula pugeti</i> Robertson, 1905	C	—	—
<i>Dendrobeatia lichenoides</i> Robertson, 1900	C	—	—
<i>Cribrilina annulata</i> (Fabricius, 1780)	C	C	U
<i>Cribrilina corbicula</i> (O'Donoghue and O'Donoghue, 1923)	R	—	—
<i>Puellina caesia</i> n. sp.	C	—	—
<i>Celleporella hyalina</i> (L., 1767) species complex	+	+	+
<i>Celleporella reflexa</i> Dick and Ross, 1988	C	C	C
<i>Celleporella nodasakae</i> n. sp.	—	—	C
<i>Porella alba</i> Nordgaard, 1906	U	C	C
<i>Porella donoghueorum</i> n. sp.	C	U	—
<i>Porella columbiana</i> O'Donoghue and O'Donoghue, 1923	—	—	—
<i>Porella acutirostris</i> Smitt, 1867 species complex	C	—	—
<i>Schizoporella japonica</i> Ortmann, 1890	C	C	—
<i>Pacificincola insculpta</i> (Hincks, 1882)	C	—	—
<i>Cryptosula zavajaloviensis</i> Kubanin, 1976	—	R	—
<i>Microporella setiformis</i> O'Donoghue and O'Donoghue, 1923	—	R	—
<i>Microporella neocribroides</i> Dick and Ross, 1988	+	C	C
<i>Microporella ketchikanensis</i> n. sp.	R	R	—
<i>Microporella germana</i> Dick and Ross, 1988	C	C	—
<i>Fenestrulina delicia</i> Winston, Hayward, and Craig, 2000	—	—	—
<i>Fenestruloides blaggae</i> Soule, Soule, and Chaney, 1995	C	U	—
<i>Fenestruloides tongassorum</i> n. sp.	R	—	—
<i>Rhynchozoon tumulosum</i> (Hincks, 1882)	C	C	U
<i>Rhynchozoon glabrum</i> n. sp.	C	C	—
Total species per site	28	18	10
Species found only at site	12	2	1

R, rare (one to three colonies observed); U, uncommon (would be found with moderate to high sampling effort); C, common (would be found with minimal sampling effort); +, relative abundance not determined because of potential confusion with other species in the field.

Membranipora membranacea form *serrata* Hincks 1882, p 469.

Membranipora serrata: Robertson 1908, p 268, Plate 16, Figures 20, 21; O'Donoghue and O'Donoghue 1923, p 26; 1926, p 29.

Membranipora serrilamella Osburn 1950, p 22, Plate 1, Figures 12, 13.

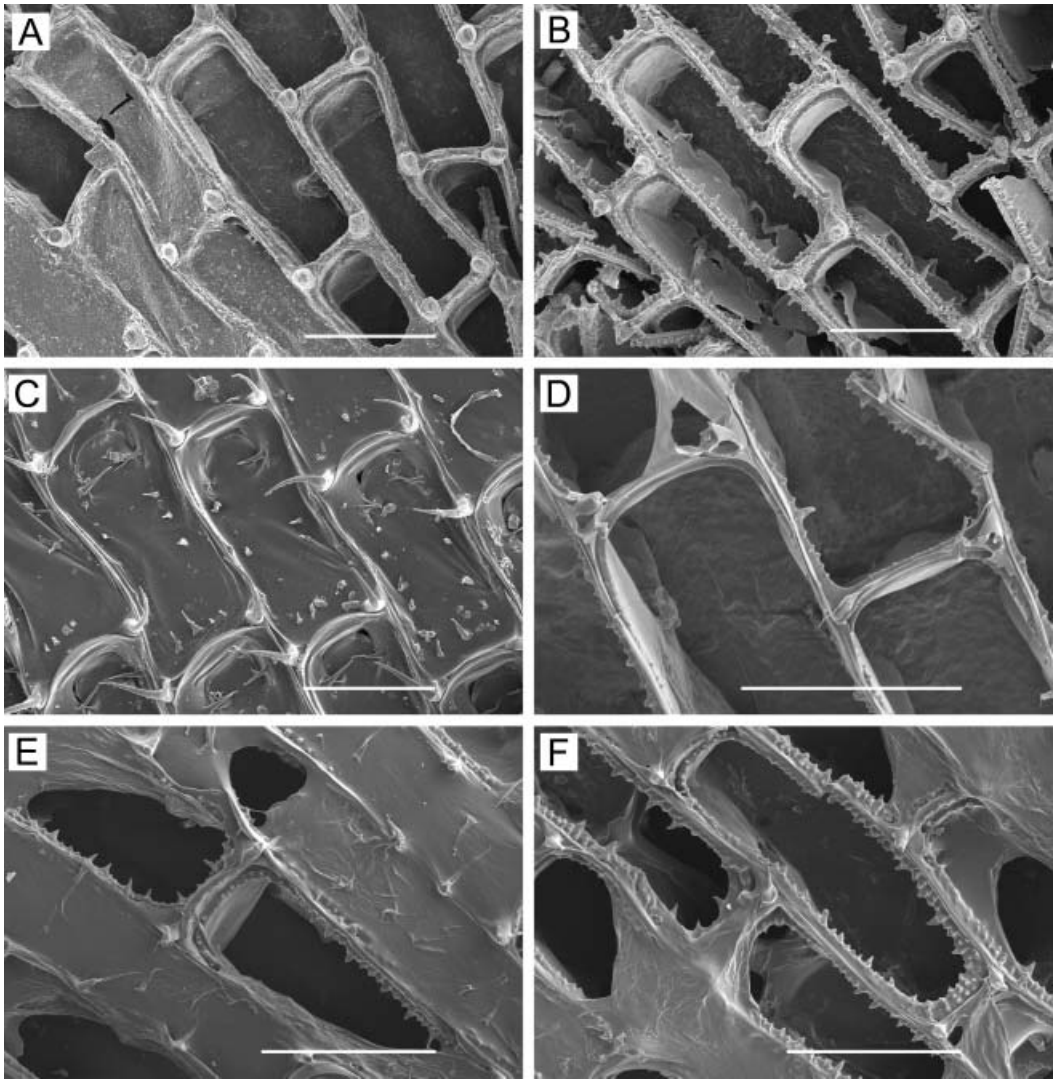


Figure 1. *Membranipora villosa* Hincks. (A) “*Membranacea*” form, weakly bleached; (B) “*serrilamella*” form, bleached; (C) “*villosa*” form; unbleached; note acute chitinous spines at proximal corners and cuticular spines on frontal membranes; (D) “*villosa*” form; same colony as (C) after bleaching, showing weakly denticulate cryptocyst; (E) “*villosa*” form from Sitka, Alaska; weakly bleached specimen with zooids showing both denticulate cryptocyst and cuticular spines on frontal membrane; (F) “*villosa*” form from Sitka, Alaska; same colony as (E), with zooids showing coarse, highly denticulate cryptocyst. Scale bars: 500 μ m (A–C, E, F); 400 μ m (D).

Membranipora serrilamella: Soule et al. 1995, p 39, Plate 4A, B.

Description

Colony. Unilaminar, encrusting, sheet-like, ranging in size from small, circular, young colonies to large expanses of coalesced colonies on laminarian algae, including plants directly accessible low in the intertidal.

Zooids. Elongate-rectangular, 0.53–1.20 mm long (average=0.849 mm, $n=48$, 4) by 0.23–0.41 mm wide (average=0.290 mm, $n=48$, 4); closely appressed, with a narrow rim between them; walls thin and flexible or more heavily calcified and brittle; basal wall uncalcified. Frontal surface completely covered by membrane; with or without acute, short or long, flexible cuticular spines (Figure 1C, E) arising from frontal membrane and along zooidal margins. Cryptocyst lies close below marginal rim, sometimes farther depressed distally; widest around proximal third of zooid and distal end, narrowest in central third; variably developed, consisting of a slight shelf that is smooth or weakly serrate (“*membranacea*” form; Figure 1A), a weakly developed shelf of minute denticles replaced by longer denticles every so often (“*villosa*” form; Figure 1D), or a pronounced shelf with smaller and longer denticles, sometimes with a pronounced denticle in proximal midline (“*serrilamella*” form; Figure 1B). Distal cryptocyst is generally smoother than that more proximally. Distal margin sometimes extended as a raised rim.

Opesia. Differing from shape of zooidal margin by width of narrow cryptocyst; with right-angled corners proximally, or corners rounded at both ends (Figure 1B shows both cases).

Spines. Zooids have a short, blunt, hollow, conical, spine-like knob at each proximal corner (Figure 1A, B, D, F), formed by extension and folding of the marginal wall (Figure 1D), with closure of the fold to give a hollow process; sometimes extended with a long, curved, acute, chitinous projection (“*villosa*” form; Figure 1C).

Avicularia. Lacking.

Ancestrula. Not observed.

Remarks

Three morphologically similar species of *Membranipora* have been reported in the north-eastern Pacific: *M. membranacea* (L.) characterized by a negligible, smooth or finely serrate cryptocyst and lacking frontal cuticular spines; *M. villosa* Hincks characterized by a finely serrate cryptocyst and having numerous cuticular spines on the frontal membrane and zooidal margins; and *M. serrilamella* Osburn, characterized by a markedly serrate, spinous cryptocyst and lacking frontal cuticular spines. Yoshioka (1982) argued that these putative species represent a single species, and that the apparent difference among them are due both to ecophenotypic variation, induced partly by the presence of nudibranch predators, and to astogenetic variation. He concluded that *M. villosa* and *M. serrilamella* are synonyms of *M. membranacea*. However, Soule et al. (1995) retained the name *M. serrilamella*, arguing that it is morphologically distinct from Atlantic *M. membranacea*; furthermore, they did not include *M. villosa* in their synonymy of *M. serrilamella* and provided separate illustrations of the two.

More recently, a study by Schwaninger (1999) supported Yoshioka's results with a phylogeny of *M. membranacea*- and *M. villosa*-like morphs from Friday Harbour, Washington and *M. serrilamella* from Japan. Based on 600 base pairs of the mitochondrial COI gene, her phylogeny showed that single mitochondrial lineages include representatives of all three morphs. Furthermore, the three morphs proved to be genetically indistinguishable at the allozyme level, with no fixed allelic differences among them and

low θ values, indicating free gene flow. Schwaninger thus concluded that the three morphs are conspecific. Unfortunately, she did not show SEM illustrations of the specific morphologies included in her phylogeny. Her definition of non-“*serrilamella*” morphs depended on the presence or absence of frontal cuticular spines, without reference to the nature of the cryptocyst, which has also been a key character in distinguishing among the nominal species reported from the north-eastern Pacific.

There is general agreement among these recent studies that *M. membranacea* (L.) does not occur in the north-eastern Pacific. Yoshioka (1982) noted that the cyphonautes of European *M. membranacea* is larger and differently ornamented than the cyphonautes attributed to the “*membranacea*”–“*serrilamella*”–“*villosa*” morphs in the north-eastern Pacific. Schwaninger (1999) found an average COI divergence of 13% between North Atlantic and North Pacific populations of nominal *M. membranacea*, and concluded that these regions “harbor highly differentiated populations of *M. membranacea*-like morphs that may no longer belong to the same species”. Schwaninger also noted, “there were no obvious differences in adult morphology between these populations”, and continued to refer to Pacific populations as *M. membranacea*. However, Soule et al. (1995) observed differences in zooid morphology between *M. membranacea* they examined in France and *M. serrilamella* in the eastern Pacific, and concluded that these are distinct species.

At Ketchikan, we found colonies identifiable with “*membranacea*”-like (Figure 1A) and “*serrilamella*”-like (Figure 1B) morphologies, both lacking frontal cuticular spines. These are similar to one another in all respects except degree of development of the cryptocyst; the former has a negligible, faintly serrated cryptocyst, whereas the latter has a highly denticulate cryptocyst with long denticles interspersed with more numerous shorter ones. We also found a “*villosa*”-like morph, with thinner, less heavily calcified walls having a weakly denticulate cryptocyst (Figure 1D), and frontal cuticular spines (Figure 1C). Another “*villosa*”-like specimen we examined from Sitka, Alaska has abundant long, frontal cuticular spines (Figure 1E) and more heavily calcified walls than the Ketchikan specimen, yet also shows a “*serrilamella*”-like cryptocyst (Figure 1F). The two “*villosa*”-like morphs have in common a raised distal rim not present in the other morphs, but this may be an ecophenotypic character, either inducible by nudibranch predators in the same manner as the cuticular spines, or correlated with subtidal habitat. The two “*villosa*”-like specimens encrusted laminarian algae continually submerged in a boat harbour, whereas the other morphs encrusted nearshore laminarian algae subject to wave action.

We conclude, from examining admittedly a limited number of specimens from south-eastern Alaska, that there is no suite of characters that can consistently distinguish among the morphs previously reported as separate species in the north-eastern Pacific. Other authors have mentioned similar observations. For example, O’Donoghue (1926) noted, in reference to *M. villosa*, *M. serrilamella*, and *M. membranacea*, “A colony of one ... may contain an area which, if found by itself, might easily be referred to the other”. Similarly, Yoshioka (1982) noted, “...characteristics of all three species can be found in different parts of a single colony”. It is also noteworthy that Osburn (1950) reported the ranges of the three nominal species in the eastern Pacific as virtually identical, from British Columbia to Southern California, with the exception of Robertson’s (1900) records of nominal *M. membranacea* from Yakutat and the Pribilof Islands, Alaska. Here, we consider the “*membranacea*”, “*villosa*”, and “*serrilamella*” morphs in the north-eastern Pacific as synonymous, yet distinct from European *M. membranacea* (L.). Nomenclatural

priority therefore goes to *M. villosa* Hincks, 1880, the earlier description in the eastern Pacific of either of the two morphs (*M. serrilamella* and *M. villosa*) other than *M. membranacea*.

We note, however, that questions remain concerning the identity of *Membranipora* spp. in the north-eastern Pacific. For instance, Osburn (1950, p 21, Plate 1, Figure 9) noted the presence and included an illustration of “tower cells” for nominal *M. membranacea* from the Pacific. These tower zooids are characteristic of European *M. membranacea* (L.) (Hayward and Ryland 1998), and their presence suggests the occurrence of that species in the Pacific, perhaps as an introduced population. Also troublesome are the deep (up to 17%) divergences in three COI lineages within a *Membranipora* population at a single locality, Friday Harbour, Washington (Schwaninger 1999); these divergences are greater than that (13%) between Atlantic and Pacific populations. It is also interesting to note that although *M. serrilamella* has been reported from Japan (Mawatari 1974), *M. villosa* has not. If the two were simply morphs of the same species, one would expect to find both in Japan. However, lack of the *villosa* morph there might be explained by absence (Okutani 2000) of the specific nudibranch predators, *Doridella steinbergae* Lance and *Corambe pacifica* MacFarland and O’Donoghue (Yoshioka 1982), that induce chitinous frontal spines in eastern Pacific populations. This would make sense if *M. serrilamella* had been introduced to Japan from the eastern Pacific, in which case Japanese populations of nominal *M. serrilamella* might not exhibit a defensive response to chemical cues from species of nudibranch predators native to Japan. An introduction would also explain the low genetic divergence between Japanese specimens and one of the clades at Friday Harbour, Washington (Schwaninger 1999). Ultimately, integrated morphological, ecological, and molecular genetic studies will be necessary to resolve the taxonomy of *Membranipora* in the northern Pacific.

Distribution

Pribilof Islands and Yakutat, Alaska (as *M. membranacea*) (Robertson 1900) southward to southern California (Robertson 1908; O’Donoghue and O’Donoghue 1923, 1926; Osburn 1950); southern Hokkaido (as *M. serrilamella*) (Mawatari and Mawatari 1981) southward to Wakayama Prefecture on the Pacific side and Ishikawa Prefecture on the Sea of Japan, Honshu, Japan (as *M. serrilamella*) (Mawatari 1974).

Suborder NEOCHEILOSTOMINA d’Hondt, 1985

Infraorder FLUSTRINA Smitt, 1868

Superfamily CALLOPOROIDEA Norman, 1903

Family CALLOPORIDAE Norman, 1903

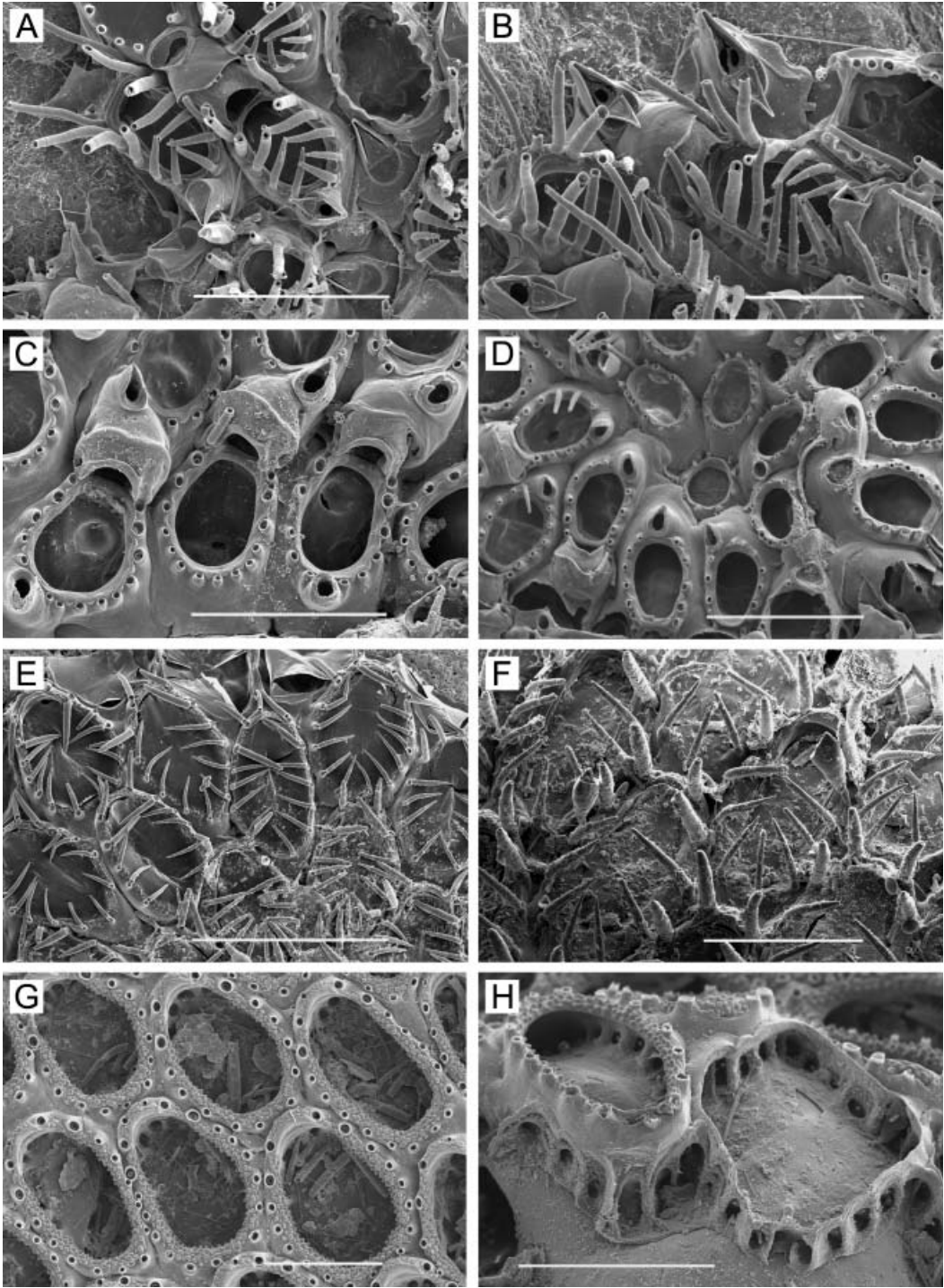
Genus *Callopora* Gray, 1848

Callopora craticula (Alder, 1856)

(Figure 2A–D)

Membranipora craticula Alder 1856, p 144.

Callopora craticula: Osburn 1950, p 67, Plate 6, Figure 7; Kluge 1975, p 344, Figure 171; Mawatari and Mawatari 1980, p 40, Figure 8; Dick and Ross 1986, p 89 (in part); 1988, p 33, Plate 1C.



Description

Colony. Unilaminar, encrusting, sheet-like, whitish to tan in colour; delicate, largest colony observed 4 mm across.

Zooids. Small, 0.30–0.43 mm long (average=0.357 mm, $n=15$, 3) by 0.16–0.26 mm wide (average=0.218 mm, $n=15$, 3); barrel-shaped to oval, proximal end truncate or tapering between adjacent zooids; separated by a groove. Lateral and proximal gymnocyst smooth, sloping, extensive; proximal gymnocyst comprising one-third to two-fifths of zooid length. Cryptocyst negligible, a narrow, smooth, sloping shelf inside mural rim. Opesia oval, often widest proximally, 0.16–0.25 mm long (average=0.190 mm, $n=15$, 3) by 0.10–0.14 mm wide (average=0.120 mm, $n=15$, 3).

Spines. Twelve to 17, arranged as three or four pairs of long, heavy orificial spines, truncate and open at the end, erect or angled distally, sometimes curved laterally; and 7–10 finer, acute opesial spines around proximal half of opesia, angled inward, the tips meeting in the midline (Figure 2A, B); all spines tubular, not flattened. The distalmost pair of opesial spines is intermediate in character, long and open at the end like the orificial spines, but tapering, subacute, the tips meeting in the midline like the more proximal acute spines. In ovicellate zooids, the distalmost pair of orificial spines is often embedded in the lateral ovicell wall on one or both sides; the second pair often abuts or is embedded in the proximal corners of the ovicell (Figure 2C).

Avicularia. Zooids typically have a frontal avicularium with a raised chamber on the gymnocyst close to the proximal opesial margin, the acute, long-triangular mandible pointing proximally (Figure 2A, C); lacking in some zooids; if preceded by an ovicell, this avicularium tends to be larger, the chamber frequently overlapping the distal end of the ovicell, with the mandible pointing distally (Figure 2C). Occasionally, the avicularium occurs on the lateral rather than the proximal gymnocyst. Vicarious avicularia (Figure 2A, B) occur sporadically; these are almost as large as autozooids, with the rostrum bearing an acute, long-triangular mandible extending past the distal end of the chamber.

Ovicell (Figure 2A–C). Raised, hemispherical, imperforate, 0.15–0.16 mm long (average=0.154 mm, $n=10$, 2) by 0.15–0.19 mm wide (average=0.161 mm, $n=10$, 2); with a conspicuous, often decurved transverse ridge across the top marking proximal extent of ectooecium; lumen between ectooecium and endooecium typically filled with calcification in mature zooids (Figure 2C); proximal margin raised as a sharp vertical lip.

Figure 2. (A–D) *Callopora craticula* (Alder): (A) colony margin showing autozooid, ovicellate zooid, and interior vicarious avicularia; unbleached; (B) colony margin, showing ovicellate zooids and marginal vicarious avicularia; unbleached; (C) ovicellate zooids, bleached; (D) ancestrula and surrounding zooids; bleached. (E–H) *Cauloramphus magnus* Dick and Ross: (E) marginal autozooids; unbleached; (F) oblique view of zooids, showing shape and position of pedunculate avicularia; unbleached; (G) brooding zooids, bleached; note crescentic kenozooidal oecium around distal margin of each zooid; (H) marginal zooids, showing pore chambers; bleached. Scale bars: 400 μ m (A, C); 200 μ m (B); 500 μ m (D, F–H); 1 mm (E).

Ancestrula. With nine spines (Figure 2D), initially budding a daughter zooid distally, then two additional zooids, one on each side from junction between ancestrula and first daughter zooid.

Remarks

Callopora craticula formed small colonies growing on rocks and on serpulid worm tubes attached to rocks. Our specimens are similar to most descriptions from other parts of the range. For example, zooids are small, 0.30–0.43 mm at Ketchikan, 0.35–0.45 mm at Kodiak (Dick and Ross 1988), and 0.30–0.38 mm in Britain (Hayward and Ryland 1998); range of spine number is 12–17 at Ketchikan, 11–16 in the Russian Far Eastern seas (Kluge 1975), 12–15 at Kodiak (Dick and Ross 1988), and 12–15 in Britain (Hayward and Ryland 1998). However, Osburn (1950) indicated both larger zooids (0.40–0.55 mm) and more spines (14–18) for eastern Pacific specimens, and Mawatari and Mawatari (1980) indicated more spines (10–19 proximal and two to four distal) for specimens from northern Japan; these records of *C. craticula* may represent other species.

We have examined SEM images, kindly sent by Dr Piotr Kuklinski, of two British specimens of *C. craticula*. One specimen is from the Northumberland Coast, probably a syntype, collected by J. Alder; the other comes from the Norman collection (NHM 1911.10.1.523), labelled as collected by J. Alder from the Durham coast. The spines in these specimens are somewhat more regular than in our material, meaning they are more evenly formed and more regularly angled and tilted to form a neater basket over the opesia. However, the overall arrangement of spines is identical, with acuminate spines meeting in the midline over the proximal half of the opesia; two to four pairs of long, blunt, erect or distally angled spines, with those immediately lateral to the orifice often curved outward; and the distalmost pair of opesial spines of mixed character between the orificial and other opesial spines. As in our material, the distalmost pair of spines is often embedded in the lateral walls of the ovicell.

We can find no diagnostic differences in other characters between Alder's material and ours, such as in the form, size, distribution, and direction of frontal avicularia; form of the gymnocyst and cryptocyst; and form of the ovicell. SEM images of a specimen from Spitsbergen, provided by Dr Piotr Kuklinski, show a similar ancestrula: tatiform with nine spines, initially giving rise to three zooids distally. A questionable character for *C. craticula* has been the occurrence of vicarious avicularia. Although Kluge (1975) and Dick and Ross (1988) reported them, neither Hincks (1880b) nor Hayward and Ryland (1998) mentioned them for *C. craticula* from Britain. However, Hincks (1880b, Plate 19, Figure 7) showed one in his illustration, and a vicarious avicularium is present in the Durham specimen mentioned above (NHM 1911.10.1.523). Therefore, the presence of vicarious avicularia must be regarded as a character of *C. craticula*.

Distribution

This is a circumpolar, arctic-boreal species; Kluge (1975) summarizes many previous records. *C. craticula* has been reported as far south as Scotland and northern England in Britain (Hayward and Ryland 1998), Wood's Hole in the western Atlantic (Osburn 1912; but see Winston et al. 2000), and southern Hokkaido in Japan (Mawatari and Mawatari 1980). In the eastern Pacific, Ketchikan is a little farther south than the previous southernmost record at Frederick Sound (Osburn 1950).

Genus *Cauloramphus* Norman, 1903
***Cauloramphus magnus* Dick and Ross, 1988**
 (Figure 2E–H)

Cauloramphus magnus Dick and Ross 1988, p 36, Plates 2F, 10C, 13B.

Cauloramphus cymbaeformis: Dick and Ross 1986, p 89.

Description

Colony. Unilaminar, encrusting, light brown, forming circular to irregular patches on hard substrates; largest observed 2 cm across.

Zooids. Oval, barrel-shaped, or rounded-hexagonal, sometimes proximally extended, delineated by a shallow groove, 0.60–0.75 mm long (average=0.653 mm, $n=15$, 3) by 0.38–0.48 mm wide (average=0.430 mm, $n=15$, 3). Entire basal wall calcified. Gymnocyst smooth; narrow or obscured if zooids crowded; sometimes evident proximally. Cryptocyst narrow, sloping; widest proximally, covered with coarse conical tubercles (Figure 2G, H) that extend to area of orifice and sometimes on to distal marginal rim. Opesia variable in shape, 0.38–0.54 mm long (average=0.448 mm, $n=15$, 3) by 0.23–0.30 mm wide (average=0.251 mm, $n=15$, 3).

Spines (Figure 2E, F). Twelve to 18, including four to six (modal number=4, $n=22$, 4) stout, straight, erect orificial spines and 8–12 thin, acuminate, straight or curved opesial spines, well separated, angled over the opesia but often not meeting in midline.

Avicularia (Figure 2F). Uncommon; arising from outer mural rim on one side of some zooids, between orificial and opesial spines; as long as longest opesial spines; short peduncle expanding to a broad chamber; rostrum at distal end, angled at 45° to long axis.

Ovicell. Embryos brooded inside the distal third to half of maternal zooid; oecium exists as a small kenozooid budded by the maternal zooid and occupying the distal margin of the mural rim (Figure 2G), evident as a raised, crescentic lip in brooding zooids.

Ancestrula. Not observed.

Remarks

Common at all three collecting sites at Ketchikan, this was by far the dominant species of *Cauloramphus* at Settlers Cove, an area of low circulation, high sedimentation, and freshwater seepage. A tendency to occur in these conditions was also noted at Kodiak (Dick and Ross 1988). Specimens at Ketchikan agree well with the original description (Dick and Ross 1988) of *C. magnus* from Kodiak. Zooid size is similar, but opesial measurements are a little smaller and spine number greater at Ketchikan. The diagnostic characters of this species are the narrow, raised mural rim; the narrow cryptocyst covered with coarse, conical tubercles that impart a serrate aspect to the opesial outline; the thin, straight or slightly curved, acuminate proximal spines generally separated from one another by two or more times their width; and avicularia with a short peduncle giving rise to a broad chamber. The

species has an unruly appearance, with the opesial spines somewhat irregular in length, degree of curvature, and orientation; the tips meet at the midline in some zooids but not in others. Colonies are typically fouled with particulate debris.

Distribution

Gulf of Alaska; known from Kodiak (Dick and Ross 1988) and Ketchikan.

Cauloramphus multiavicularia, new species

(Figure 3A–F)

Membranipora spinifera: O'Donoghue and O'Donoghue 1923, p 26 (in part?).

Cauloramphus spinifer: O'Donoghue and O'Donoghue 1926, p 39 (in part?).

Cauloramphus pseudospinifer: Dick and Ross 1988, p 37, Plates 2A, H, 13C.

Diagnosis

Up to seven stout orificial spines, erect or nearly so, well differentiated from tight basket of thinner, more acuminate spines proximal to orifice that angle over opesia, variably meeting in midline. Gymnocyst smooth; cryptocyst sloping, with coarse, rounded tubercles. Basal wall uncalcified in centre. Up to five avicularia per zooid emerging from middle of zooid on either side and around distal margin. Avicularia thin, clavate, pedunculate, often directed nearly horizontally at colony margin.

Type material

Holotype: ETN, unbleached and uncoated (YPM 35832). Paratype 1: ETN, unbleached and uncoated (YPM 35833). Paratype 2: ETN, unbleached and uncoated (NHM 2005.7.11.1). Paratype 3: KV, specimen KE-8 bleached and coated for SEM (YPM 35834). Paratype 4: KV, specimen KE-59 unbleached and coated for SEM (ZIRAS 1/50527). Paratype 5: SC, specimen KE-61, aberrant ecophenotype, lightly bleached and coated for SEM (YPM 35835). Paratype 6: KV, specimen KE-31 bleached and coated for SEM (ZIRAS 2/50527).

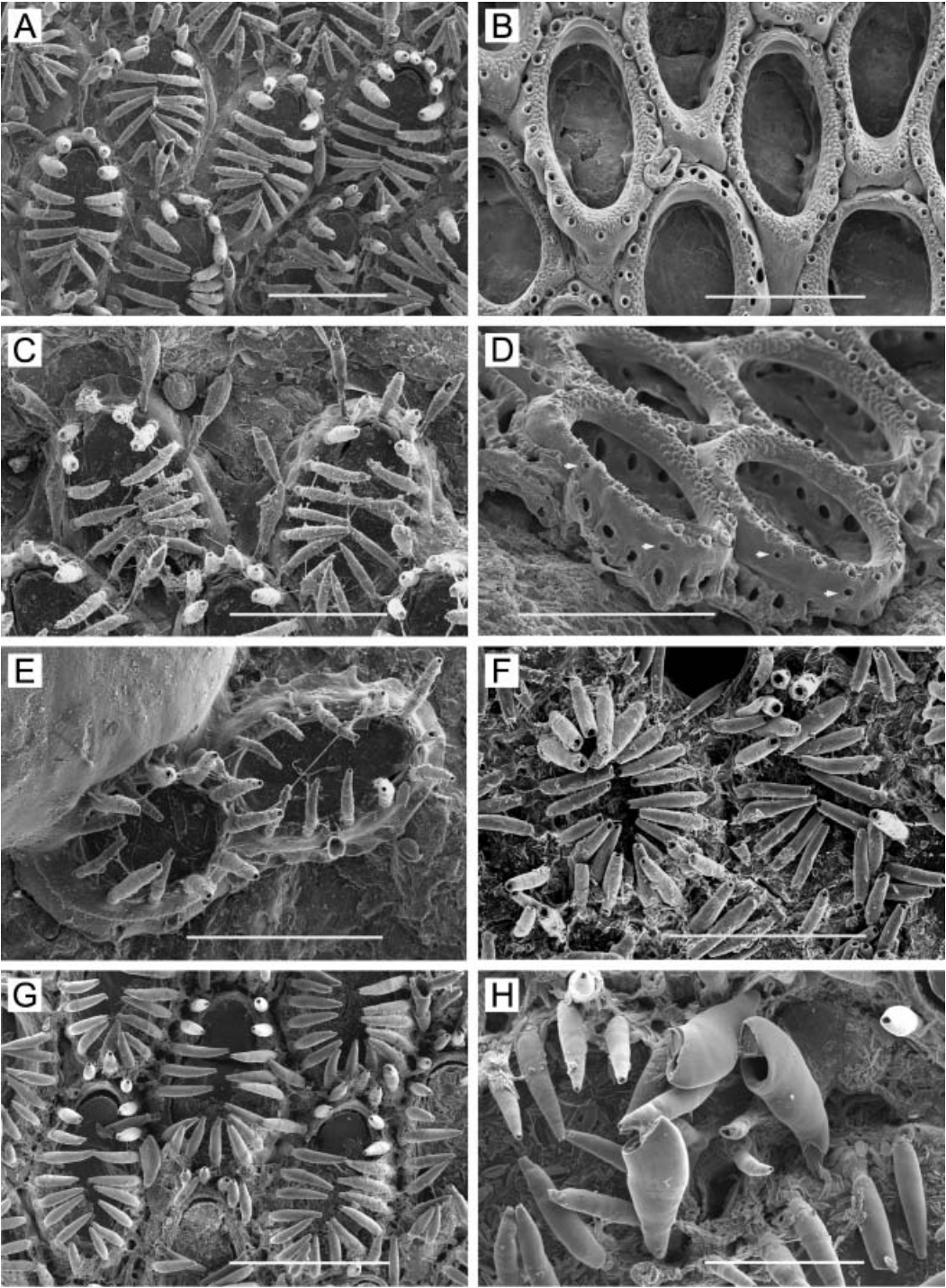
Etymology

The species name derives from Latin meaning “many avicularia”.

Description

Colony. Unilaminar, encrusting, light tan-brown in colour, forming irregular to circular patches tightly adhering to hard substrates; largest observed 2 cm across.

Zooids. Irregularly oval to rounded-hexagonal, variable in size and shape with irregularities in substrate, 0.50–0.87 mm long (average=0.685 mm, $n=15$, 3) by 0.38–0.50 mm wide (average=0.412 mm, $n=15$, 3); closely set, but separated by a distinct groove; proximally



quadrate or tapering to a median or two lateral lobes between adjacent zooids; basal wall with an irregular marginal shelf but uncalcified in centre (Figure 3B). Openings to pore chambers (Figure 3D) unusually small for the genus (compare Figure 3D with Figures 2H and 4D); seen from margin, the circular or irregularly oval openings lie at base of distolateral and distal walls, and are about one-third the height of the wall. Gymnocyst smooth; narrow or obscured if zooids crowded; generally evident proximally. Cryptocyst rounded, sloping inside mural rim; covered with coarse, rounded tubercles (Figure 3B, D). Opesia elliptical to oval, 0.38–0.58 mm long (average=0.495 mm, $n=15$, 3) by 0.25–0.33 mm wide (average=0.274 mm, $n=15$, 3).

Spines (Figure 3A, C). Total 16–23 (mode=18, $n=15$, 3), including five to seven stout, blunt, erect orificial spines (mode=6, $n=15$, 3) and 11–17 (mode=14, $n=15$, 3) slightly curved, acuminate opesial spines angled over proximal two-thirds of opesia, the tips usually meeting nearly horizontally at midline to form a tight basket.

Avicularia (Figure 3A, C). Thin, clavate, 0.20–0.28 mm long (average=0.241 mm, $n=16$, 3); peduncle expanding gradually to a chamber about as thick as thickest spines; often laterally compressed. Avicularia originate from marginal gymnocyst anywhere around the distal margin anterior to the third pair of erect orificial spines, or from either side in the zone between the first and fourth pairs of angled opesial spines; the most avicularia observed on a single zooid was five. Avicularia angle away from zooid to a greater or lesser extent (Figure 3C), sometimes orientated nearly horizontally on marginal zooids, the rostral side facing upward.

Ovicell. Embryos brooded inside the distal part of maternal zooid; oecium exists as a small kenozooid budded by the maternal zooid and occupying the distal margin of the mural rim (Figure 3B), evident as a raised, crescentic lip in brooding zooids.

Ancestrula. 0.38 mm long by 0.30 mm wide, with 12 spines (Figure 3E); periancestrular zooids smaller than subsequent autozooids, but similar in form, often bearing avicularia.

Remarks

In Alaska, this species was previously found at Kodiak by Dick and Ross (1988), who identified it as *C. pseudospinifer* Androsova, 1958. This determination was based largely on a specimen from the Sea of Japan, obtained from the Academy of Sciences in St Petersburg and labelled as *C. pseudospinifera*. After re-examination of that specimen by SEM and comparison with Ketchikan specimens, we believe the two are distinct species; hence, we here describe the Ketchikan material as a new species, *C. multiavicularia*.

Figure 3. (A–F) *Cauloramphus multiavicularia* n. sp.: (A) autozooids with scattered pedunculate avicularia; unbleached; (B) autozooids, bleached; each of the two complete zooids (left and right of centre) is a brooding zooid, having a crescentic kenozooidal oecium around distal margin; (C) colony margin showing autozooids, each with up to three horizontally directed pedunculate avicularia; (D) colony margin, showing pore chambers; note lateral and distal avicularium scars (arrows); bleached; (E) ancestrula and first daughter zooid; unbleached; (F) autozooids of ecophenotypic variant from Settlers Cove, Ketchikan; specimen partially bleached for cleaning. (G, H) *Cauloramphus pseudospinifer* Androsova, from Sea of Japan: (G) group of autozooids; note avicularium lower left; unbleached; (H) enlargement of avicularia; unbleached. Scale bars: 500 μ m (A–D, F, G); 400 μ m (E); 200 μ m (H).

Cauloramphus multiavicularia is similar to *C. pseudospinifera* (Figure 3G, H) in most characters. In both, the smooth gymnocyst is reduced laterally and variably evident proximally; the sloping cryptocyst is covered with coarse, rounded tubercles; spines are similar in number (18–23 in *C. pseudospinifera*, 16–23 in *C. multiavicularia* at Ketchikan), form, and arrangement (e.g. compare Figure 3A with Figure 3G). Both species have the basal wall uncalcified in the centre. Zooid length is similar; *C. pseudospinifera* is 0.5–0.8 mm long (Androsova 1958); *C. multiavicularia* is 0.60–0.80 mm long at Kodiak (Dick and Ross 1988) and 0.50–0.87 mm long at Ketchikan. Both species can have at least two avicularia on the same side of the zooid.

The diagnostic difference between the two species lies in the shape and number of avicularia (compare Figure 3A and C with Figure 3G and H). Androsova (1958) noted for *C. pseudospinifera* that avicularia are rare, usually one or two per zooid when they occur; and similar in form to those of *C. spinifera*, with a short peduncle and a short, rather wide chamber (Figure 3G, H). In *C. multiavicularia*, the avicularia have a long peduncle that expands gradually to a narrow chamber that is often scarcely, if at all, thicker in any direction than the thickest of the orificial spines (Figure 3C). In Ketchikan specimens, avicularia are profuse and especially evident on marginal zooids (Figure 3C), which may have up to five horizontally orientated avicularia per zooid scattered around the lateral and distal margins. In bleached specimens, most marginal zooids show one or more avicularium scars (Figure 3D) around the distal end and one or more scars on each side laterally. Avicularia are less profuse in material from Kodiak (Dick and Ross 1988), though their narrow, pedunculate form is the same as at Ketchikan.

At Settlers Cove, we found one colony (Figure 3F) that appeared to represent yet another *Cauloramphus* species at Ketchikan. All spines are very thick, nearly straight, and blunt. However, zooid size, a sloping cryptocyst with coarse, rounded tubercles, and distal avicularium scars indicate that this specimen is an ecophenotypic variant of *C. multiavicularia*.

Distribution

C. multiavicularia is known only from the vicinities of Kodiak and Ketchikan, Alaska. However, O'Donoghue and O'Donoghue (1923, 1926) described specimens they identified as *C. spinifera* from British Columbia as having avicularia distributed both laterally and distally, with up to six present on some zooids, strongly suggesting that at least part of the material they examined was *C. multiavicularia*.

Cauloramphus tortilis, new species (Figure 4A–D)

Diagnosis

Zooids closely appressed; mural rim moderately wide, rounded, tumid, completely covered with fine tubercles, cryptocystal; gymnocyst not visible. Spines long, straight or nearly so, 9–15 in total, including four orificial and 5–10 opesial spines, tips of the latter not meeting in the midline. Avicularium long, pedunculate, fusiform; arising in stereotyped position at base of distalmost pair of opesial spines on one or both sides; peduncle twisted around spine; rostrum facing away from zooid.

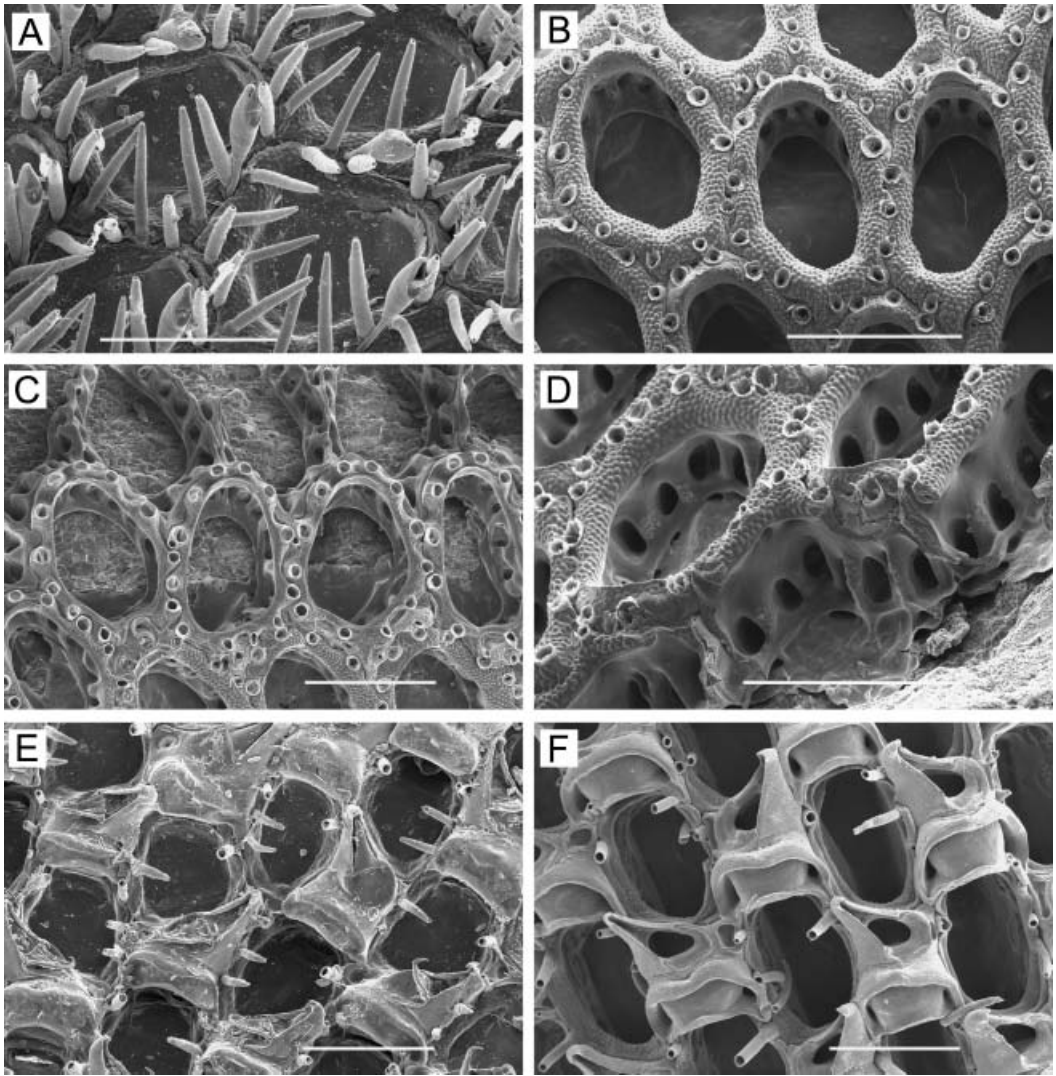


Figure 4. (A–D) *Cauloramphus tortilis* n. sp.: (A) autozooids; unbleached; (B) autozooids, bleached; complete zooid at right is a brooding zooid, with a crescentic kenozooidal oocidium around distal margin; (C) young autozooids near colony margin, showing intermeshing spine bases; bleached; (D) colony margin, showing pore chambers; bleached. (E, F) *Tegella aquilirostris* (O'Donoghue and O'Donoghue): (E) ovicellate zooids; unbleached; (F) ovicellate zooids; bleached. Scale bars: 500 μ m.

Type material

Holotype: ETN, unbleached and uncoated (YPM 35836). Paratype 1: ETN, unbleached and uncoated (NHM 2005.7.11.2). Paratype 2: KV, specimen KE-17 unbleached and coated for SEM (YPM 35837). Paratype 3: KV, specimen KE-10 bleached and coated for SEM (NHM 2005.7.11.3). Paratype 4: KV, specimen KE-37 unbleached and coated for SEM (ZIRAS 1/50528). Paratype 5: KV, specimen KE-54 bleached and coated for SEM (ZIRAS 2/50529).

Etymology

The specific name derives from the Latin *tortilis*, meaning twisted or twined, referring to the twisting of the avicularium laterally around the spine near which it is attached.

Description

Colony. A unilaminar sheet tightly adhering to hard substrates, orangish brown, forming circular to irregular patches; largest observed 2 cm by 3 cm.

Zooids. Tightly appressed to one another, with a line or slight groove between them; rounded-hexagonal, with proximal margin truncate or extending between proximal pair of zooids; 0.53–0.70 mm long (average=0.625 mm, $n=30$, 3) by 0.33–0.58 mm wide (average=0.405 mm, $n=30$, 3). In young, marginal zooids, spine bases bulge from lateral walls, giving zooid a coarsely crenulate outline, intermeshing with spine bases of adjacent zooids (Figure 4C); in older zooids, thickening of mural rim with granulate calcification largely obscures crenulate appearance. Mural rim cryptocystal; broad, rounded, tumid, widest proximally, tapering laterally, narrowest distally, completely and evenly covered by fine-tuberculate granulation (Figure 4B, D); no smooth gymnocyst visible. Opesia regularly to irregularly oval, 0.30–0.50 mm long (average=0.427 mm, $n=30$, 3) by 0.20–0.29 mm wide (average=0.242 mm, $n=30$, 3). Basal wall thinly but completely calcified.

Spines (Figure 4A). Total 9–15 (mode=11, $n=20$, 2), including two pairs erect orificial spines (rarely, five spines), and 5–10 (mode=7, $n=20$, 2) long, tapering, stout, straight or slightly curved opesial spines proximal to orifice; spines separated at base by twice or more their width, angled over opesia, meeting at midline in some colonies but not in others; distalmost pair of opesial spines tends to be longer and thicker than any other spines.

Avicularia (Figure 4A). Approximately as long as longest spines, 0.30–0.38 mm long (average=0.334 mm, $n=12$, 2); clavate, with a narrow peduncle one-third to one-half length of avicularium, expanding to a fusiform chamber of greater width than stoutest spines; membranous frontal portion (mandible and post-mandible) occupying about half the length of the expanded chamber; tip of rostrum with a slight, blunt hook; mandible long-triangular. Avicularium attached immediately proximolateral to base of distalmost (largest) opesial spine, on one or both sides; nearly erect, with peduncle twisted around spine near base (Figure 4A) so that the chamber lies distal or distolateral to the spine, with the mandible facing away from the zooid. In some colonies, most zooids possess one or two avicularia; in others, most zooids lack them.

Ovicell. Embryos brooded inside the distal part of maternal zooid; oecium exists as a small kenozooid budded by the maternal zooid and occupying the distal margin of the mural rim (Figure 4B), evident as a raised, crescentic lip in brooding zooids.

Ancestrula. Not observed.

Remarks

A character that distinguishes *C. tortilis* from most other species reported from Alaska (*C. magnus*, *C. multiavicularia*, *C. spectabilis*, *C. spinifer*, and *C. cymbaeformis*) (Dick and Ross 1988; Osburn 1950; this study), is that of the closely set zooids, with the cryptocystal

exposed frontal surface completely covered with fine tubercles. The only other Alaskan species similar in this regard is *C. variegatus* (see Dick and Ross 1988). In contrast to *C. tortilis*, however, *C. variegatus* has a wider, flatter cryptocyst proximally; the straight, erect orificial spines are markedly thicker than the curved, acuminate opesial spines; the spine bases are often brown; and the avicularium is not long and fusiform.

Distribution

Cauloramphus tortilis is known only from the Ketchikan vicinity.

Genus *Tegella* Levinsen, 1909

***Tegella aquilirostris* (O'Donoghue and O'Donoghue, 1923)**

(Figure 4E, F)

Membranipora aquilirostris O'Donoghue and O'Donoghue 1923 p 28, Plate 2, Figure 16.

Tegella aquilirostris: O'Donoghue and O'Donoghue 1926 p 37, Plate 3, Figure 29; Osburn 1950, p 83; McCain and Ross 1974, p 13, Figure 2b; Mawatari and Mawatari 1980, p 92, Figure 32; Dick and Ross 1986, p 89 (in part); Dick and Ross 1988, p 42, Plate 3A.

Membranipora unicornis: Robertson 1900, p 324.

Membranipora occultata Robertson 1908, p 262, Plate 14, Figures 6–9; not *M. occultata* Waters, 1887.

Membranipora occultata: O'Donoghue and O'Donoghue 1923, p 25.

Tegella robertsoni O'Donoghue and O'Donoghue 1926, p 36.

Description

Colony. Unilaminar, sheet-like, encrusting hard substrates, the margin sometimes raised in folds and frills; roughly circular, up to several centimetres across; often aggregated, covering considerable areas on benchrock faces and beneath overhangs; tan to rich reddish brown in colour, the growing margin often more heavily pigmented.

Zooids. Barrel-shaped, rounded distally, widest in middle, narrower and truncate proximally, 0.50–0.83 mm long (average=0.648 mm, $n=15$, 3) by 0.29–0.48 mm wide (average=0.374 mm, $n=15$, 3); closely appressed, zooidal boundaries indistinct; young zooids with a sharp rim between them. Proximal gymnocyst covered by avicularian chamber; lateral gymnocyst hidden between adjacent zooids; cryptocyst a narrow shelf set below mural rim, smooth or finely tuberculate, extending around entire opesia or absent distally. Opesia occupies roughly two-thirds of zooidal length; round, oval, or rounded-rectangular in shape, 0.33–0.58 mm long (average=0.417 mm, $n=15$, 3) by 0.23–0.38 mm wide (average=0.292 mm, $n=15$, 3).

Spines. A straight, erect tubular spine on one or both sides of orifice, at or near proximolateral flanges of ovicell; if on both sides, one usually stouter than the other; sometimes two straight spines occur on one side and one on the other; young zooids

sometimes have a pair of straight spines on each side. In addition, zooids often have one or two finer, curved, acuminate spines more proximally on one side, arching over opesia.

Avicularia. Each zooid bears a large frontal avicularium with a chamber that is trapezoidal or rectangular in outline, completely covering proximal gymnocyst and connecting through it by several pores, abutting or partly covering ovicell of preceding zooid; rostrum heavy, pointing laterally or distolaterally, sometimes extending around proximolateral margin of opesia, raised at 45° to colony surface, the tip hooked. Avicularian mandible long-triangular, strongly hooked at tip.

Ovicell. Broader than long, 0.28–0.38 mm wide (average=0.319 mm, $n=15$, 3) by 0.15–0.23 mm long (average=0.188 mm, $n=15$, 3); endooecium spherical; partly overgrown by ectooecium, the margin of which comprises a thick, sometimes decurved transverse ridge. Proximal margin of endooecium raised as a lip; a large, transverse lumen between endooecial and ectooecial margins is covered by ectocyst.

Ancestrula. Not observed.

Remarks

We found this species only at the East Tongass Narrows site, where it competed for space with *Schizoporella japonica* on the undersides of rock outcrops. Young colonies can be lighter in colour than astogenetically mature colonies, with the zooids lacking spines and the frontal avicularia smaller, less raised, and not hooked.

Distribution

Boreal North Pacific: California as far south as Santa Barbara (Osburn 1950); Puget Sound (McCain and Ross 1974); British Columbia (O'Donoghue and O'Donoghue 1923, 1926); Kodiak Island, Alaska (Dick and Ross 1988); Commander Islands (Grischenko 1997, 2004), Hokkaido to middle Honshu, Japan (Mawatari and Mawatari 1980); northern Sea of Japan, Sakhalin Island, southern Sea of Okhotsk (Kubanin 1997).

Tegella horrida (Hincks, 1880) (Figure 5A–D)

Membranipora horrida Hincks 1880a, p 82, Plate 10, Figure 6.

Membranipora californiensis Waters 1898, p 681, Plate 49, Figure 14.

Membranipora horrida: Robertson 1908, p 260, Plate 14, Figures 3, 4; O'Donoghue and O'Donoghue 1923, p 24.

Callopora horrida: O'Donoghue and O'Donoghue 1925, p 97; 1926, p 33; Osburn 1950, p 69, Plate 6, Figure 9; Androsova 1958, p 98, Figure 9; Mawatari and Mawatari 1980, p 42, Figure 9.

Tegella robertsonae: Osburn 1950, p 81, Plate 9, Figure 5 (in part).

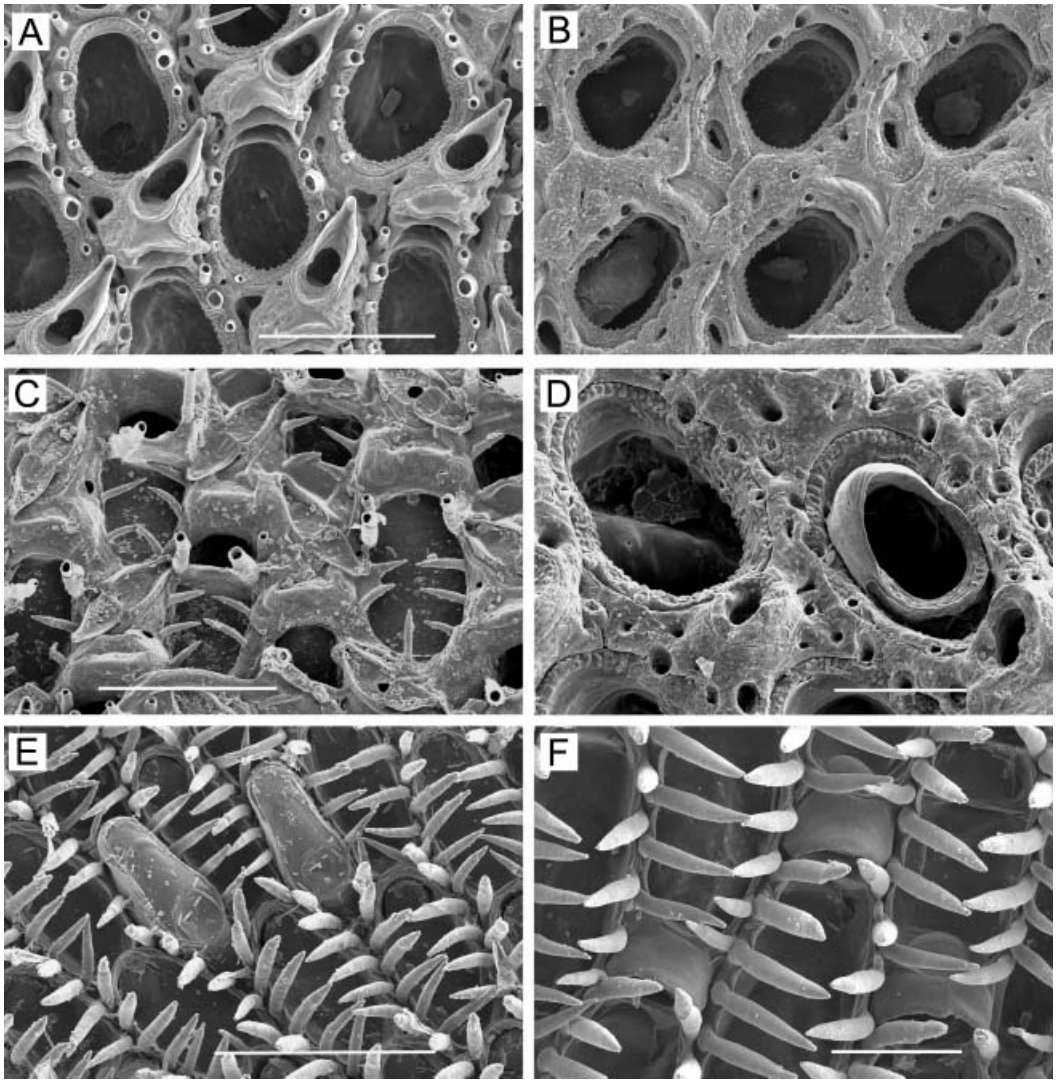


Figure 5. (A–D) *Tegella horrida* (Hincks): (A) group of ovicellate zooids near colony margin, well separated with scattered lacunae between them; bleached; (B) group of heavily calcified ovicellate zooids, the avicularium proximal to opesia completely immersed; bleached; (C) group of ovicellate zooids; unbleached; (D) autozooid (left) and intramural reparative avicularium (right); bleached. (E, F) *Hincksia longiavicularia* Gontar: (E) group of autozooids and spatulate vicarious avicularia; unbleached; (F) several ovicellate zooids; unbleached. Scale bars: 500 μ m (A–C, E); 200 μ m (D, F).

Tegella aquilirostris: Dick and Ross 1986, p 89 (in part).

Tegella horrida: Dick and Ross 1988, p 45, Plate 3D–G.

Description

Colony. Unilaminar, encrusting, sheet-like, tightly adhering to hard substrates; light tan-brown in colour; largest observed 1.5 cm across.

Zooids. Oval, rounded distally, widest proximally; 0.45–0.66 mm long (average=0.559 mm, $n=15$, 3) by 0.28–0.38 mm wide (average=0.321 mm, $n=15$, 3); distinct when young (Figure 5A), separated by a groove, with scattered infundibular pits (incipient kenozooids, connecting to pores) and occasional small lacunae between zooids. Lateral gymnocyst smooth and sloping in young zooids; proximal gymnocyst obscured by chamber of avicularium, ovicell of preceding zooid, or both. With age, groove filled by kenozooidal secondary calcification (Figure 5B), zooidal boundaries indistinct, with external interzooidal (kenozooidal/lacunar) openings remaining; all gymnocyst obscured by heavy, irregular, smooth or finely tuberculate secondary calcification. Cryptocyst steeply sloping, moderately wide proximally, narrow distally, covered with small, sharp conical tubercles. Opesia occupies about three-fifths of frontal length; 0.25–0.40 mm long (average=0.302 mm, $n=15$, 3) by 0.15–0.25 mm wide (average=0.188 mm, $n=15$, 3); oval or rounded-rectangular; well separated from surrounding opesiae. Basal wall completely calcified.

Spines (Figure 5C). Marginal zooids have four to seven (mode=6) straight orificial spines, erect or distally angled, sometimes longer than zooids; most or all of these are lost with age and abrasion. Around mural rim proximal to orifice are three to six short, tapering, acuminate, slightly curved spines angled toward midline. Some spines have an uncalcified ring at the base.

Avicularia. Three types occur. Some zooids have one to three small frontal avicularia arising anywhere around proximal or lateral gymnocyst, rostrum short and raised at 45°, mandible an equilateral triangle pointing toward zooidal margin. Most common type is a large frontal avicularium (Figure 5A–C) with chamber covering most or all of proximal gymnocyst, connecting to it by several pores, and overlapping ovicell of preceding zooid; rostrum moderately raised, often laterally curved, decurved, or both, extending to a greater or lesser extent around proximolateral margin of opesia; mandible elongate, tapering, acute, hooked at tip. With increased secondary calcification (Figure 5B), frontal surface of avicularium comes to lie flush with colony surface. The third type comprises intramural avicularia (Figure 5D) scattered sparsely throughout colony; these are regenerated from autozooids, the autozooidal opesia partly closed with a horizontal lamina from which arises a raised rostrum of varying size, pointing in any direction, with a spatulate or triangular mandible.

Ovicell. Raised, globose, 0.20–0.30 mm wide (average=0.255 mm, $n=15$, 3) by 0.14–0.23 mm long (average=0.173 mm, $n=15$, 3); ectooecium thick, rough, with proximal margin thickened as a transverse ridge (Figure 5A). The two layers nearly meet proximally, the space between them becoming occluded by secondary calcification except for occasional minute pores. With age, ovicell becomes partly or completely immersed by secondary calcification (Figure 5B, C).

Ancestrula. Not observed.

Remarks

This aptly named species is robust; the surface is rough in appearance, often abraded or fouled. We have examined a specimen from the Natural History Museum (London)

labelled “97.5.1.512, *Membranipora horrida* Hincks, California, Pt. of TYPE? material”. Specimens from Ketchikan are clearly conspecific with this specimen. In the NHM specimen, zooids show the characteristic elongate, curved and decurved proximal avicularia, with some having the smaller type; heavy, rough, granulate secondary calcification with kenozooidal/lacunar openings between zooids; widely spaced opesia; up to six orificial spines and two to four short, acuminate opesial spines, with some spines having an uncalcified base. The ovicells in the Californian specimen are smooth, with a slight transverse ridge; similar ovicells are evident in young zooids in our material.

Distribution

This is a boreal North Pacific species, reported from Pacific Grove, California (Robertson 1908) to Kodiak in the western Gulf of Alaska (Dick and Ross 1988); northern Honshu and Hokkaido Islands, Japan (Mawatari and Mawatari 1980); and the Sea of Japan (Androsova 1958).

Superfamily FLUSTROIDEA Fleming, 1828

Family FLUSTRIDAE Fleming, 1828

Genus *Hincksina* Norman, 1903

Hincksina longiavicularia Gontar, 1982

(Figure 5E, F)

Hincksina longiavicularia Gontar 1982, p 547, Plate 1, Figure 3a, b.

Hincksina longiavicularia: Dick and Ross 1988, p 32, Plate 1E.

Hincksina sp.: Dick and Ross 1986, p 89.

Description

Colony. Unilaminar, encrusting, sheet-like, forming circular, bright golden-orange patches on hard substrates; largest observed 10 cm across. Tightly adhering, but sometimes with raised margin attached by radicles, each originating from the basal wall at the distal midline of a zooid, with a branched holdfast.

Zooids. Elongate, barrel-shaped, widest in middle, 0.40–0.55 mm long (average=0.462 mm, $n=15$, 3) by 0.19–0.25 mm wide (average=0.221 mm, $n=15$, 3); distal end of each zooid raised above proximal end of succeeding zooid, often with a sharp, raised lip distal to orifice. Cryptocyst lacking; opesia occupies entire frontal surface.

Spines (Figure 5E, F). Each autozooid surrounded by dense palisade of 10–17 coarse, tapering, acuminate, straight or slightly curved spines, including two pairs of nearly erect orificial spines and 6–13 opesial spines angled inward, tips meeting at midline.

Avicularia. Large, vicarious (Figure 5E), 0.30–0.45 mm long (average=0.370 mm, $n=15$, 3) by 0.14–0.18 mm wide (average=0.159 mm, $n=15$, 3); rostral walls smooth, the end overhanging succeeding zooid; mandible long-spatulate. Avicularia usually occur at a branch point where a zooid in series gives rise to two daughter zooids, one of which

develops as an autozoid, the other as an avicularium. This arrangement is not obligatory; an avicularium occasionally replaces a zoid not at a branch point, and not every branch point has an avicularium.

Ovicell (Figure 5F). Globose, 0.10–0.18 mm long (average=0.126 mm, $n=15$, 3) by 0.13–0.18 mm wide (average=0.155 mm, $n=15$, 3); endozoecial in cystid of succeeding zoid; endooecium covered by lateral flaps of ectooecium growing from each margin and fusing in midline; ovicell not closed by zooidal operculum, but rather by an extension of frontal membrane distal to operculum. In ovicellate zooids, distalmost pair of orificial spines often tilt medially, the tips meeting in the midline to form an arch protecting ovicell.

Ancestrula. One observed; oval, 0.35 mm long by 0.25 mm wide, with 10 (?12) short spines, including four erect orificial spines and six (?eight) thinner opesia spines angled inward; surrounded by seven zooids: one distal, two distolateral, two proximolateral, two proximal.

Distribution

The occurrence of this species at Ketchikan extends the known range in the north-eastern Pacific considerably southward from Kodiak and Prince William Sound (Dick and Ross 1988). On the Asian side, *H. longiavicularia* has been reported from the Kurile Islands (Gontar 1982) and Commander Islands (Grischenko 1997).

Superfamily BUGULOIDEA Gray, 1848

Family BUGULIDAE Gray, 1848

Genus *Bugula* Oken, 1815

***Bugula pacifica* Robertson, 1905**

(Figure 6A, B)

Bugula pacifica Robertson 1905, p 268, Plate 10, Figure 50, Plate 16, Figure 101.

Bugula purpurotincta: Robertson 1900, p 320, Plate 20, Figures 5, 6.

Bugula pacifica: O'Donoghue and O'Donoghue 1923, p 20; 1925, p 100; 1926, p 45; Osburn 1950, p 155, Plate 22, Figure 6, Plate 23, Figure 4; Soule et al. 1995, p 108, Plate 36.

Description

Colony. Erect, branched, flexible; attached by a stalk composed of rhizoids originating from zooids at base of colony; branches biserial (Figure 6A), dichotomously branching, spiralled around a central axis with the frontal sides facing inwards. Branching pattern Type 3 (Harmer 1923; Hayward and Ryland 1998), with axil at bifurcations formed by inner pair of two pairs of zooids flanking branch point. The colonies we collected were young, the largest 1 cm high.

Zooids. Elongate, 0.45–0.90 mm long (average=0.646 mm, $n=15$, 3) by 0.13–0.20 mm wide (average=0.154 mm, $n=15$, 3), tapering proximally and truncate distally; walls thin,

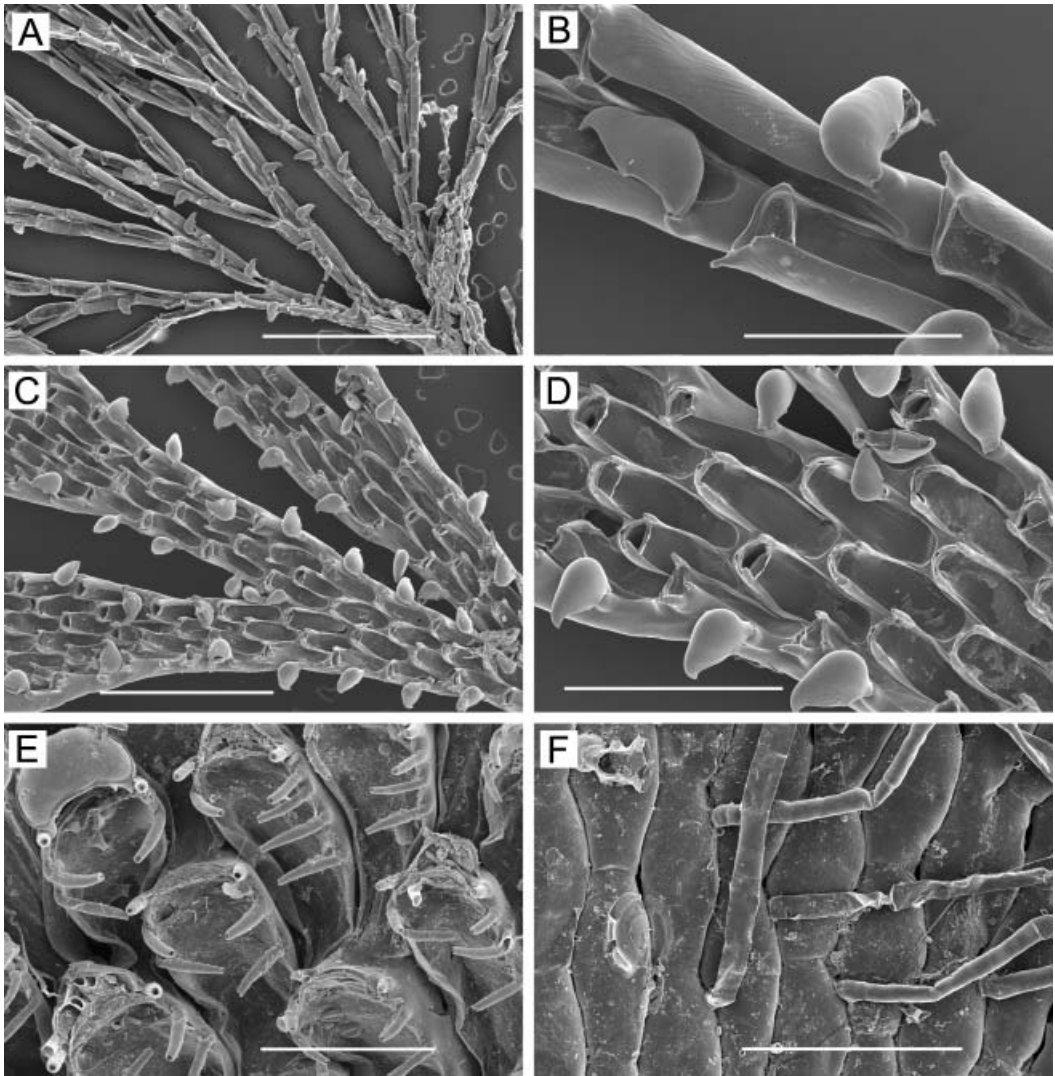


Figure 6. (A, B) *Bugula pacifica* Robertson: (A) general colony view; (B) autozooids and lateral avicularia. (C, D) *Bugula pugeti* Robertson: (C) general colony view; (D) autozooids and lateral avicularia; note smaller avicularium near branch point (near top, right of centre). (E, F) *Dendrobeatia lichenoides* Robertson: (E) autozooids and one ovicellate zooid; (F) abfrontal surface of portion of colony, showing attachment radicles. All specimens unbleached. Scale bars: 2 mm (A, C); 400 μ m (B); 1 mm (D, F); 500 μ m (E).

weakly calcified, flexible, translucent. Opesia occupies nearly entire exposed frontal area, leaving only a small zone of proximal gymnocyst.

Spines (Figure 6B). In our material, two short, spinous projections on outer distal zooidal margin; no spine on inner distal margin.

Avicularia (Figure 6B). Attached by a flexible joint near base of zooid, on lateral wall close to opesial margin; approximately twice as long as deep, 0.16–0.24 mm long

(average=0.215 mm, $n=10$, 1) by 0.08–0.11 mm deep (average=0.101 mm, $n=10$, 1); hooked at end; not occurring on all zooids.

Ovicell. Not observed in our specimens, but in this species a reduced, hood-like ooecium occurs.

Remarks

We found this species only at the East Tongass Narrows site, where it was uncommon in rock crevices.

Distribution

Bugula pacifica is distributed from the Pribilof Islands, Bering Sea (Robertson 1905; Osburn 1950) southward to the Channel Islands off Southern California (Soule et al. 1995). On the Asian side, it has been reported from the Commander Islands (Grischenko 1997, 2004).

***Bugula pugeti* Robertson, 1905** (Figure 6C, D)

Bugula pugeti Robertson 1905, p 271, Plate 10, Figures 53, 54, Plate 11, Figure 55.

Bugula pugeti: O'Donoghue and O'Donoghue 1923, p 21; 1925, p 100; 1926, p 45; Osburn 1950, p 158, Plate 23, Figures 7, 8; Soule et al. 1995, p 115, Plate 39.

Bugula flabellata: Robertson 1900, p 321.

Description

Colony. Erect, branched, flexible, attached by a stalk composed of rhizoids originating from zooids at base of colony; branches in very young colonies and at base of older colonies biserial, soon becoming multiserial (Figure 6C), up to seven to eight zooids wide, dichotomously branching, spiralled around a central axis, with the frontal sides facing inwards.

Zooids. Elongate, 0.49–0.74 mm long (average=0.616 mm, $n=20$, 2) by 0.18–0.23 mm wide (average=0.201 mm, $n=20$, 2); widest in middle, tapering proximally, rounded distally, with a slight median knob that is sometimes open on frontal side; distal end overlapping gymnocyst of succeeding zooid, slightly raised. Walls weakly calcified, translucent. Opesia occupies nearly entire exposed frontal surface, except for narrow band of proximal gymnocyst.

Spines (Figure 6D). Marginal zooids typically with two well-developed, non-jointed spines at outer distolateral margin (the more distal one longer and stouter), and one at inner distal margin; interior zooids have one spine at each distolateral margin; all spines angled distally; very weakly developed in some colonies.

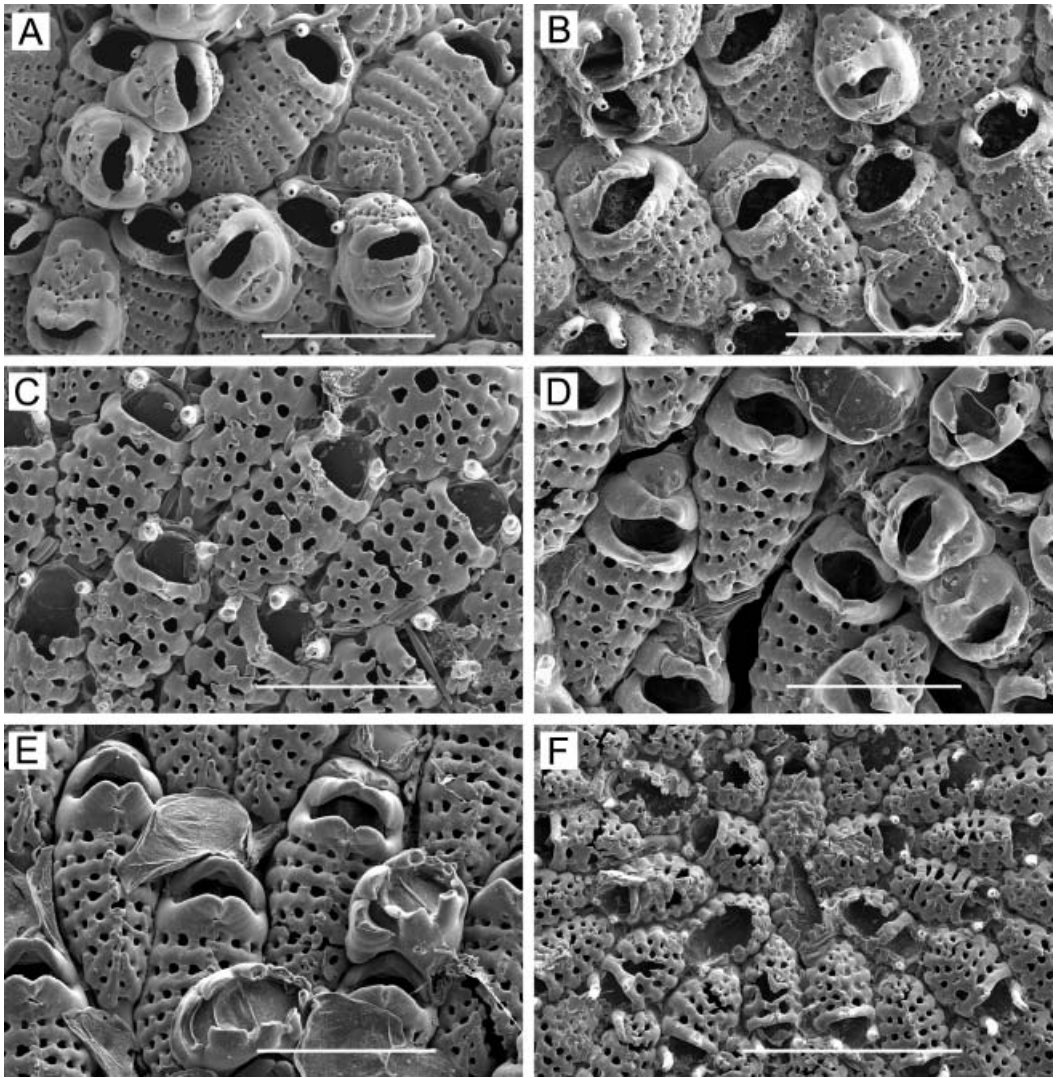


Figure 7. (A, B) *Cribrilina annulata* (Fabricius): (A) autozooids and frontally budded dwarf ovicellate zooids; bleached; (B) autozooids (lower right), ovicellate zooids in primary layer (lower centre and left), and frontally budded dwarf ovicellate zooids (top); bleached. (C–F) *Cribrilina corbicula* (O'Donoghue and O'Donoghue): (C) astogenetically young autozooids; unbleached; (D) ovicellate zooids in primary layer and frontally budded dwarf ovicellate zooids; bleached; (E) ovicellate zooids in primary layer and newly forming dwarf ovicellate zooids with membranous front only (upper left of centre) or with incomplete costae (lower right and centre); note compressed, subspatulate suboral costae; unbleached; (F) ancestrula and surrounding zooids; unbleached. Scale bars: 500 μ m (A–E); 1 mm (F).

Avicularia (Figure 6D). Marginal zooids with a stout avicularium attached by a short peduncle and flexible joint to a knob on lateral wall, close to opesia, near or somewhat proximal to middle of opesia, but not close to proximal end of opesia. Avicularia longer than zooid width, 0.21–0.33 mm long (average=0.281 mm, $n=22$, 2) by

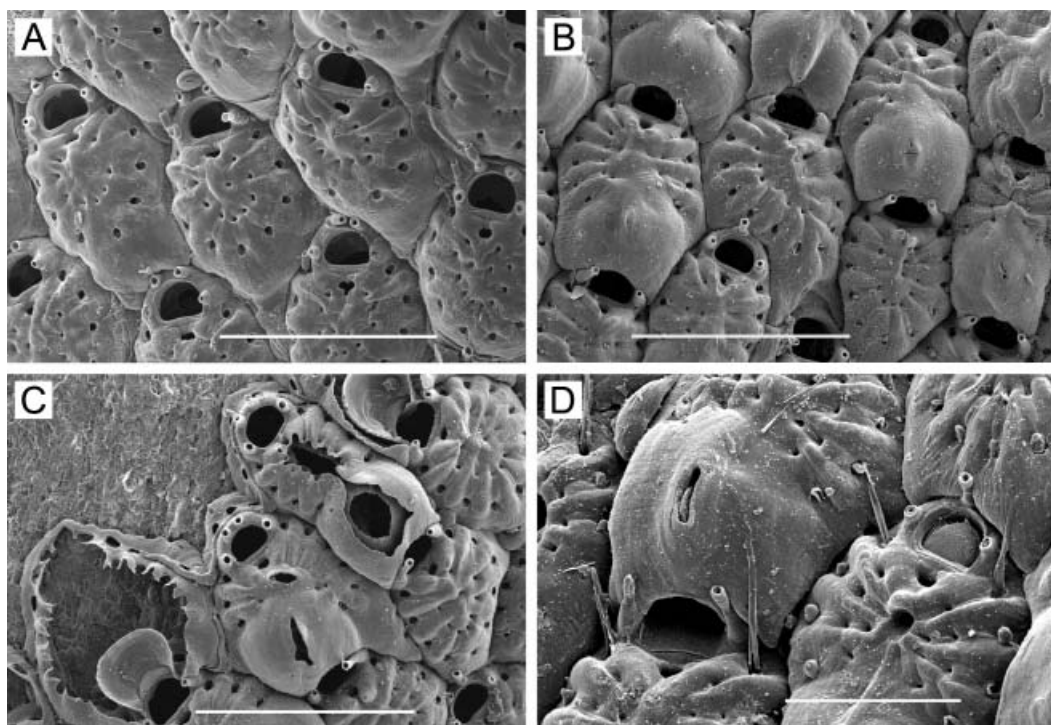


Figure 8. (A–D) *Puellina caesia* n. sp.: (A) group of autozooids; bleached; (B) group of ovicellate zooids; bleached; (C) colony margin showing several stages of ovicell formation; bleached; (D) enlargement showing setiform papillae proximolateral to orifice; unbleached. Scale bars: 400 μ m (A); 500 μ m (B, C); 200 μ m (D).

0.15–0.23 mm deep (average=0.181 mm, $n=22$, 2), somewhat bulbous; frontal margin slightly convex; rostrum hooked at end. Interior zooids lack an avicularium.

Ovicell. Lacking in this species; embryos brooded internally (Robertson 1905).

Ancestrula. Not observed.

Remarks

We observed this species only at the East Tongass Narrows site, where it was common in benchrock crevices and beneath overhangs. Osburn (1950, Plate 23, Figure 7) showed avicularia of two sizes for this species, which Soule et al. (1995) pointed out is contrary to his description. In our specimens, a smaller avicularium is sometimes associated with a zooid proximal to or on one side of a branch point (Figure 6D).

Distribution

The known range is from Sitka, Alaska (Robertson 1905) southward to San Francisco Bay, California (Osburn 1950).

Genus *Dendrobeatia* Levinsen, 1909
***Dendrobeatia lichenoides* Robertson, 1900**
 (Figure 6E, F)

Flustra lichenoides Robertson 1900, p 322, Plate 20, Figures 7, 7a, 8.

Flustra lichenoides: Robertson 1905, p 291, Plate 15, Figures 91, 92, Plate 16, Figure 105; O'Donoghue and O'Donoghue 1923, p 23; 1925, p 100; 1926, p 48.

Dendrobeatia lichenoides: Osburn 1950, p 167, Plate 25, Figure 6; McCain and Ross 1974, p 13; Dick and Ross 1986, p 89; 1988, p 51, Plate 4D; Soule et al. 1995, p 104, Plate 34A–C.

Description

Colony. Recumbent, tan-coloured lobes similar in appearance to some foliose lichens, loosely attached to substrate by radicles (Figure 6F) originating from basal distolateral corner of some zooids; unilaminar, but younger lobes of a colony can overlap older lobes; up to 5–10 cm across.

Zooids. Club-shaped in outline (Figure 6E), rounded distally, widest at orifice, tapering and truncate proximally, each overlapping next distal zooid, 0.60–0.90 mm long (average=0.716 mm, $n=15$, 3) by 0.23–0.35 mm wide (average=0.306 mm, $n=15$, 3). Walls weakly calcified, flexible; adjacent zooids loosely appressed to one another; margins sharp. Opesia occupies entire visible frontal surface; proximal gymnocyst covered by preceding zooid; cryptocyst lacking.

Spines (Figure 6E). A straight, erect or distally angled spine at each distolateral corner and a total of three to six more-or-less curved spines along the lateral margins, paired or unequally distributed, angled over the opesia, with no more than four per side.

Avicularia. Lacking.

Ovicell (Figure 6E). Hyperstomial, globose, smooth, imperforate; broader than long, 0.25–0.33 mm wide (average=0.288 mm, $n=15$, 3) by 0.18–0.25 mm wide (average=0.202 mm, $n=15$, 3).

Ancestrula. Not observed.

Remarks

Aggregated colonies formed extensive mats on the undersides of some boulders at East Tongass Narrows.

Distribution

Known from San Francisco (Robertson 1900, 1905) to Kodiak Island in the Western Gulf of Alaska (Dick and Ross 1988), with a number of records in between; also recorded from several localities around the Commander Islands (Grischenko 1997, 2004).

Infraorder ASCOPHORINA Levinsen, 1909
“Grade” ACANTHOSTEGA Levinsen, 1902
Superfamily CRIBRILINOIDEA Hincks, 1879
Family CRIBRILINIDAE Hincks, 1879
Genus *Cribrilina* Gray, 1848
Cribrilina annulata (Fabricius, 1780)
 (Figure 7A, B)

Cellepora annulata Fabricius 1780, p 436.

Cribrilina annulata: Robertson 1900, p 234; O'Donoghue and O'Donoghue 1923, p 30; 1926, p 50; Osburn 1950, p 177, Plate 28, Figure 7; Kluge 1975, p 470, Figure 247; Hayward and Ryland 1998, p 314, Figure 110; Dick and Ross 1986, p 89; 1988, p 51, Plate 4C.

Description

Colony. Encrusting, forming circular or irregular sheets on hard substrates; pink to reddish in colour; largest observed 1.5 cm across, but generally <0.7 cm; unilaminar, with scattered frontally budded dwarf ovicellate zooids.

Zooids. Autozooids rounded-hexagonal to oval (Figure 7A, B); separated by a groove; 0.35–0.69 mm long (average=0.524 mm, $n=15$, 3) by 0.30–0.53 mm wide (average=0.356, $n=15$, 3); basal wall uncalcified except for marginal shelf.

Frontal wall. Convex, inflated; frontal shield with 12–17 smooth, rounded, tapering costae connected along their lengths, tips meeting at midline, where there is sometimes a slight keel; each costa with a minute pseudopore at the tip; distalmost pair of costae usually thicker than the rest, forming proximal rim of orifice, the fused tips often raised as a suboral mucro; between adjacent costae are a marginal pore and three to six smaller intercostal pores, their diameter less than the intercostal struts between them; 6–12 intercostal pores in a transverse series across zooid at widest point.

Orifice. Orifice of non-ovicellate zooids 0.09–0.12 mm long (average=0.11 mm, $n=15$, 3) by 0.14–0.18 mm wide (average=0.160 mm, $n=15$, 3), rounded distally, broadly concave proximally.

Spines. Usually four (sometimes three) short, stout, erect spines around distal margin of orifice, the middle pair often shorter than lateral pair and sometimes fused as a single broad spine (Figure 7B).

Ovicells. Ovicellate zooids occur in primary layer in some colonies (Figure 7B); smaller than non-ovicellate autozooids, 0.31–0.63 mm long including ovicell (average=0.527 mm, $n=15$, 2) by 0.21–0.38 mm wide (average=0.301 mm, $n=15$, 2), with fewer costae (11–14). Most colonies also have small, frontally budded, dwarf ovicellate zooids (Figure 7A, B) orientated in any direction, 0.20–0.35 mm long including ovicell (average=0.299 mm, $n=18$, 4) by 0.18–0.25 mm wide (average=0.228 mm, $n=18$, 4); frontal shield reduced, with three to four short frontal costae in addition to the pair of heavy costae comprising proximal lip of orifice; orifice proximo-distally compressed. Ovicells of primary and dwarf

zooids similar, the proximal margin formed by a pair of heavy costae fused at the midline, often ending in a blunt point; distal to thickened costae is a cap-like chamber perforated on top with one to four pores (typically two) that sometimes merge with one another. Pseudopores at tips of proximal ovicellar costae appear as additional small perforations.

Avicularia. Lacking.

Ancestrula. Similar in form to autozooid, though smaller, 0.30–0.38 mm long (average=0.349 mm, $n=11$) by 0.20–0.30 mm wide (average=0.247 mm, $n=11$), with four (rarely five) orificial spines. Ancestrula typically first buds a distal zooid, then a pair of distolateral zooids, after which budding continues simultaneously from daughter zooids and proximal half of ancestrula; ultimate complement of periancestrular zooids is six (one distal, two distolateral, two proximolateral, one proximal, with the proximal zooid abutting the ancestrula, but produced by and connecting to the two proximolateral zooids). Variations occasionally occur in initial budding order.

Remarks

Ketchikan specimens show some differences from material described from other parts of the range of this broadly distributed nominal species. For example, there is a tendency for the middle pair of orificial spines to fuse into a single broad spine (Figure 7B), whereas this has not been reported for material from Britain (Hayward and Ryland 1998), high latitudes (Kluge 1975), or Kodiak (Dick and Ross 1988). In Ketchikan specimens, as in material treated by Kluge (1975) and Dick and Ross (1988), a pair of heavy costal spines forms the thick proximal margin of the ovicell, whereas in British material, the homologous pair of spines curve across the frontal surface of the ovicell, forming a transverse rib separate from the thin proximal margin. Finally, the ancestrular budding pattern seen at Ketchikan seems to differ from that of some other populations. For example, Nikulina (2002) illustrated and noted five periancestrular zooids for specimens from the White Sea; the proximal zooid seen in our material is apparently lacking. These kinds of variation perhaps indicate that across its range, nominal *C. annulata* may comprise several cryptic biological species; however, there is no basis at present for considering the Ketchikan material as distinct from *C. annulata* (Fabricius).

We observed colonies of two different reproductive modes at Ketchikan. In the more common mode, the primary layer lacks ovicellate zooids; dwarf zooids are produced early in colony astogeny and tend to be clustered in the centre of small colonies. In the alternative mode, ovicellate zooids occur in the primary layer; dwarf zooids are not produced early on, and if they occur at all, are in more peripheral positions. We were unable to distinguish any other morphological differences between colonies of the two modes.

Distribution

This is considered a circumpolar, arctic-boreal species. Along the Pacific coast of North America, it has previously been reported from Point Barrow, Kodiak, Cordova, and Yakutat, Alaska (Robertson 1900; Osburn 1950; Dick and Ross 1988), as well as British Columbia (O'Donoghue and O'Donoghue 1923, 1926). On the Asian side, it has been reported from as far south as southern Hokkaido Island in Japan (Mawatari and Mawatari 1981), and the northwest coast of the Sea of Japan (Kubanin 1997).

Cribrilina corbicula (O'Donoghue and O'Donoghue, 1923)
(Figure 7C–F)

Membraniporella corbicula O'Donoghue and O'Donoghue 1923, p 30, Plate 3, Figure 20.

Cribrilina corbicula: O'Donoghue and O'Donoghue 1926, p 51; Osburn 1950, p 178.

Description

We found one young colony at Ketchikan; description is based on that specimen and others from SERC settling plates from Sitka, Alaska.

Colony. Unilaminar, with scattered frontally budded dwarf zooids; flexible; golden brown in colour.

Zooids. Oval to spindle-shaped; 0.40–0.64 mm long (average=0.517 mm, $n=20$, 3) by 0.25–0.34 mm wide (average=0.298 mm, $n=20$, 3); loosely appressed, separated by a groove.

Frontal wall. Frontal shield highly convex, composed of 10–14 coarse, somewhat flattened costae that meet at an irregular suture in midline; between adjacent costae on each side are usually two large intercostal pores in addition to marginal pore, thus six pores in transverse series across widest part of zooid; pores variable in shape (irregular, circular, oval, or inverted heart-shaped), their maximum dimension often greater than width of intercostal struts between them. Non-ovicellate zooids have distalmost pair of costae less flattened than the rest, forming proximal margin of orifice, the somewhat acute tips often rising at the midline to form a suboral mucro. Ovicellate zooids in primary layer have suboral costae markedly thickened, their blunt tips either forming a bilobed suboral mucro (Figure 7D) or flattened in the transverse plane, rising as paddle-like projections meeting in the midline (Figure 7E), sometimes quite high.

Orifice. Secondary orifice roughly semicircular in non-ovicellate zooids, 0.10–0.13 mm long (average=0.107 mm, $n=15$, 3) by 0.14–0.19 mm wide (average=0.162 mm, $n=15$, 3), the distal margin a sharp, rounded rim.

Spines. Three to four orificial spines (Figure 7C), the proximal pair stout, cylindrical, erect; the median one or two spines shorter and more acute.

Avicularia. Lacking.

Ovicells. Ovicellate zooids in primary layer (Figure 7D, E) 0.38–0.68 mm long, including ovicell (average=0.556 mm, $n=20$, 3) by 0.18–0.38 mm wide (average=0.288 mm, $n=15$, 3); ovicell formed from two pairs of costae, the proximal pair heavy, often forming a blunt, sometimes bilobed mucro in midline, the distal pair completing the ovicell in a cap-like structure with two to four pores on top (often two are conspicuous). Frontally budded dwarf zooids (Figure 7D, E) occur in mature colonies, 0.25–0.34 mm long, including ovicell (average=0.294 mm, $n=15$, 3) by 0.19–0.23 mm wide (average=0.214 mm, $n=15$, 3). Dwarf zooid and ovicell roughly same size; zooidal shield with five to seven costae, the

suboral pair thickened; two or three pores between adjacent costae. Ovicell has same form as that of ovicellate zooids in primary layer.

Ancestrula. One observed at Ketchikan (Figure 7F); 0.38 mm long by 0.23 mm wide; similar in form to subsequent autozooids, though in our specimen costae of ancestrula and several first- or second-generation zooids incompletely developed. Ancestrula with four orificial spines; first and second generations with two or three oral spines; seven periancestrular zooids (one distal, two distolateral, two proximolateral, two proximal).

Remarks

Cribrilina corbicula has not been reported since the original and subsequent descriptions from British Columbia (O'Donoghue and O'Donoghue 1923, 1926), where it occurred on the seagrass *Zostera marina*. The one colony found at Ketchikan occurred on the alga *Halosaccion glandiforme*; *C. corbicula* thus seems to settle preferentially on plant and algal substrates, though our specimens from Sitka came from settling plates. O'Donoghue and O'Donoghue (1923) noted that *C. corbicula* is "a much larger form than *C. annulata*"; it is unclear what they meant by this, for colonies of *C. annulata* can become as large as those of *C. corbicula*, and zooids are about the same size. Perhaps *C. corbicula* simply appeared larger because of the coarser costae and larger intercostal pores. *Cribrilina corbicula* differs from *C. annulata* in colony colour (golden brown versus pinkish); zooids of *C. corbicula* are less firmly attached to one another and the colony is therefore rather flexible, which may be an adaptation to growing on vegetation. Zooids of *C. corbicula* tend to be narrower in proportion to length, and the raised, paddle-like suboral costae (Figure 7E) often seen in ovicellate zooids are not found in *C. annulata*.

We have examined the type specimen of *C. corbicula* (NHM 1963.12.30.43; locality labelled as "Vancouver Island, O'Donoghue Collection"), which consists of about 20 small colonies on both sides of two fragments of seagrass. Our specimens of *C. corbicula* are indistinguishable from the type in most characters. However, as with *C. annulata*, there seems to be intraspecific variation in life-history traits in *C. corbicula*. Although all the colonies in the type are young, no more than 6–7 mm in diameter, most of them have many ovicellate zooids in the primary layer, beginning as soon as the second generation of daughter zooids from the ancestrula. Our specimen from Ketchikan is of similar size, 6 mm across, but lacks ovicellate zooids altogether. O'Donoghue and O'Donoghue (1923) made no mention of frontally budded dwarf ovicellate zooids for *C. corbicula*, but we observed in the type material one fully formed dwarf zooid on one colony and one forming on another. In mature specimens from Sitka, ovicellate zooids are common in the primary layer, and dwarf zooids are abundant on some colonies. Therefore, presence or absence of dwarf zooids is not a distinguishing character between *C. annulata* and *C. corbicula*.

Distribution

The type locality of *C. corbicula* is Nanaimo, British Columbia (O'Donoghue and O'Donoghue 1923). In addition to the Ketchikan specimen, we have identified specimens from SERC settling plates from Dutch Harbour, Kodiak, Kachemak Bay, Port Valdez, and Sitka in Alaska, and from Puget Sound. Thus this is a boreal species apparently endemic to the north-eastern Pacific, with the known range extending from the eastern Aleutian Islands to Washington State.

Genus *Puellina* Jullien, 1886
***Puellina caesia*, new species**
 (Figure 8A–D)

Puellina setosa: Osburn 1950, p 186, Plate 29, Figure 4 (in part?).

Diagnosis

Lateral and proximal gymnocyst evident, sometimes extensive; frontal shield nearly circular, composed of 10–14 costae; one papilla pore and usually one intercostal pore between adjacent costae; intercostal pores arranged in a circle in centre of frontal shield, inside circle of papilla pores; with a pair of long setiform papillae near orifice; non-ovicellate zooids usually with four (range three to five) orificial spines; ovicell imperforate, smooth, often umbonate or keeled, the ectooecium confluent with frontal wall of next distal zooid; avicularia lacking.

Type material

Holotype: ETN, specimen KE-20 bleached and coated for SEM (YPM 35850). Paratype: ETN, specimen KE-64 unbleached and coated for SEM (YPM 35851).

Etymology

The species name comes from the Latin *caesia*, meaning bluish grey, referring to the colour of the colony when alive.

Description

Colony. Unilaminar, sheet-like, encrusting hard substrates, bluish grey when alive, roughly circular; largest observed 3 cm in diameter.

Zooids. Rounded-hexagonal or barrel-shaped, sometimes tapering proximally between adjacent zooids, separated by a deep groove; 0.34–0.53 mm long (average=0.398 mm, $n=25$, 3) by 0.21–0.35 mm wide (average=0.270 mm, $n=25$, 3); basal wall usually incompletely calcified, with a central lumen of varying size, but in some zooids completely calcified; three to five tiny, horizontally elliptical external openings of pore chambers in distal half of each lateral wall and two in distal wall, with corresponding simple openings in lateral walls of proximal halves of surrounding zooids.

Frontal wall. Convex; gymnocyst smooth, narrow laterally, widest and sometimes extensive proximally; frontal shield nearly circular, 0.20–29 mm long (average=0.235 mm, $n=20$, 2) by 0.19–0.25 mm wide (average=0.223 mm, $n=20$, 2), composed of 10–14 fused costae, sometimes with a low umbo or median ridge where costae meet; costae smooth and unornamented, curving sharply from base to apex. Costal lumen pores (pelmatidia, or pseudopores) lacking. Between bases of each set of adjacent costae is a circular or subcircular papilla pore several times as large as intercostal pores. Emerging from distalmost papilla pore on each side, lateral to proximal margin of orifice, is a long, tapering setiform papilla (Figure 8D). Between adjacent costae is usually a single, tiny, circular

intercostal pore (range zero to two); the intercostal pores are arranged in a circle approximately halfway from base to apex of frontal shield. The distalmost pair of costae is generally shorter and sometimes thicker than the rest; between these and just proximal to orifice lies a circular or laterally elliptical lacuna that is usually larger than any of the other frontal pores.

Orifice (Figure 8A, D). Semicircular, proximal margin straight, 0.05–0.07 mm long (average=0.058 mm, $n=20$, 2) by 0.07–0.11 mm wide (average=0.084 mm, $n=20$, 2); condyles lacking.

Spines (Figure 8A, C). Non-ovicellate zooids usually with four short, erect, tubular spines around distal margin of orifice; about 10% of zooids have three or five spines. Ovicellate zooids have a single pair of spines lateral to orifice, sometimes angled medially, appressed to the proximolateral corners of the ovicell.

Ovicell (Figure 8B–D). Roughly circular in outline, 0.21–0.24 mm long (average=0.224 mm, $n=15$, 2) by 0.23–0.26 mm wide (average=0.234 mm, $n=15$, 3); raised and globose, or subimmersed; surface smooth, with a low umbo or rounded median ridge; imperforate except for one or two minute median pores on top or toward proximal margin, probably remaining from incomplete closure of ectooecium, difficult to detect without SEM. Ectooecium is confluent with frontal shield of next distal zooid.

Avicularia. Lacking in specimens examined.

Ancestrula. Not observed.

Discussion

Puellina caesia n. sp. is similar to what Osburn (1950) described as *Puellina setosa* (Waters, 1899) from the eastern Pacific; characters in common include a similar number of costae; similar zooid measurements; a round frontal shield; a smooth, sometimes extensive proximal gymnocyst; an identical range of oral spine number; an imperforate ovicell often with a longitudinal keel; and no avicularia (Osburn referred to the setiform papillae as “setose avicularia”). There are some differences as well; *P. caesia* has heavier, less distinct costae than figured by Osburn (1950, Plate 29, Figure 4); zero to two rather than one to three intercostal pores in addition to the papilla pores; a larger suborificial lumen; and a larger ovicell.

Soule (1959) declared Osburn’s *P. setosa* as a synonym of *Colletosia radiata* (Moll, 1803), noting that Osburn had overlooked the presence of vicarious avicularia in specimens he identified as *P. setosa*. However, Osburn included in his *P. setosa* specimens ranging from the Galapagos Islands to Puget Sound, which suggests he treated more than one species. Furthermore, his description and illustration of nominal *P. setosa* are so different from those of his *C. radiata*, and his description so similar to our material, that we suspect at least some of the specimens he examined from Washington and Oregon may have been *P. caesia*.

Soule et al. (1995) described a new cribrimorph from California, *Puellina* (*Cribrilaria*) *californiensis*, with which they synonymized Osburn’s (1950) *P. setosa*, in part, and Soule’s (1959) *Colletosia radiata*. They recognized *Puellina* (*Cribrilaria*) *radiata* (Moll, 1803) as a Mediterranean species not occurring in the Pacific.

Puellina caesia differs from *P. setosa* (Waters, 1899) in having more numerous, less well-defined costae, fewer intercostal pores, and a different mode of ovicell formation. The ovicell of *P. caesia* is of Type A (Bishop and Househam 1987), with the ovicell produced during budding of the next distal autozoid and the ectooecium of the ovicell confluent with the frontal wall of that zoid (Figure 8C). Except for occasional minute pores, the ovicell of *P. caesia* is imperforate. The ovicell of *P. setosa* is of Type C, developing separately from the frontal wall of the next distal zoid, and is clearly perforate. *Puellina caesia* is superficially similar to *P. gattyae* (Landsborough, 1852), which has similarly thick, rather indistinct costae; however, the latter has fewer (five to nine) costae and a perforate, Type C ovicell (Bishop and Househam 1987).

Puellina caesia is intermediate between subgenera *Puellina* (*Puellina*) and *Puellina* (*Cribrilaria*) as defined by Bishop and Househam (1987). The broad proximal gymnocyst, circular frontal shield, lack of avicularia, and two oral spines per ovicellate zoid are all characters of *Puellina* (*Puellina*), whereas the imperforate, Type A ovicell is a character of *Puellina* (*Cribrilaria*). In having this mixture of characters from the two subgenera, *Puellina caesia* is similar to *P. directa* Bishop and Househam, 1987 from Britain, though in other characters the two are distinct. *P. caesia* is unusual among *Puellina* species in having predominantly four orificial spines per non-ovicellate zoid, rather than five or six.

Distribution

The East Tongass Narrows site near Ketchikan, Alaska is the only known locality.

“Grade” HIPPOTHOOMORPHA Gordon, 1989

Superfamily HIPPOTHOOIDEA Busk, 1859 [*nom. transl.* Gordon 1984]

Family HIPPOTHOIDAE Busk, 1859

Genus *Celleporella* Gray, 1848

Celleporella hyalina (Linnaeus, 1767) species complex
(Figure 9A–D)

Description

Colony. White, hyaline, vitreous; coherent; unilaminar when young; multilaminar with age, often several layers thick. At Ketchikan, we collected colonies growing intertidally on rocks, as well as subtidally on mussel shells; largest colony observed 1.5 cm across. Primary layer with autozooids only; male, ovicellate, and autozooids frontally budded in secondary layers.

Zooids. Young, marginal zooids spindle-shaped, 0.48–0.63 mm long (average=0.542 mm, $n=15$, 3) by 0.23–0.28 mm wide (average=0.248 mm, $n=15$, 3), separated by a deep groove, with slit-like lacunae evident between them; autozooids distinct only in young colonies and in marginal budding zone, the distal ends overlapping the proximal ends of subsequent zooids. One or two tiny incipient zooids often arise from pore chambers along either lateral margin. Ovicellate zooids much shorter than autozooids, triangular in shape, generally obscured by surrounding zooids. Male zooids shorter than autozooids but of similar form, often obscured for much of their length by surrounding zooids. Basal wall of autozooids in primary layer either completely calcified, or with an elongate uncalcified area in centre.

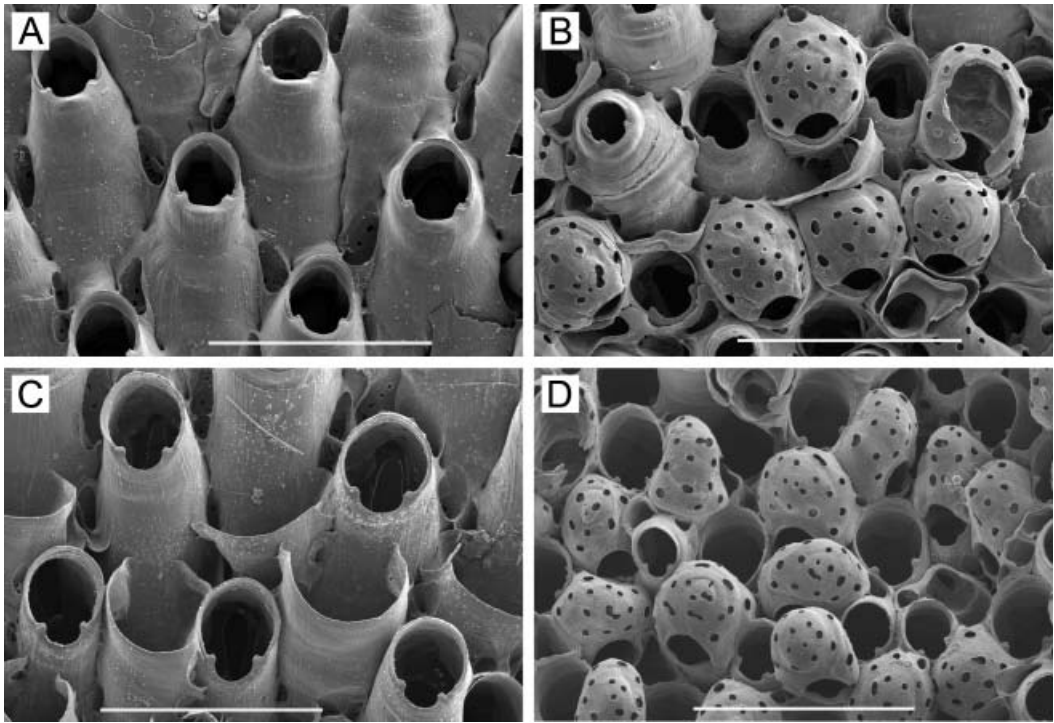


Figure 9. *Celleporella hyalina* (L.) species complex, showing variation between two colonies encrusting a single mussel (*Mytilus edulis*) individual collected subtidally; (A, B) are from one colony, (C, D) are from the other; both specimens bleached. (A) Autozooids near colony margin; (B) autozooids in primary layer (large primary orifices), a frontally budded male zooid (small primary orifice, at left), and frontally budded ovicellate zooids; (C) autozooids near colony margin; (D) autozooids in primary layer (large primary orifices), frontally budded male zooids (small primary orifices), and frontally budded ovicellate zooids. Scale bars: 500 μ m.

Frontal wall. Quite convex, thin, vitreous, translucent, imperforate, with or without irregularly spaced transverse striations or weak ridges; sometimes with a thickening of proximal orificial margin forming a low, transverse umbo.

Orifice. Autozooidal orifice (Figure 9A, C), including proximal sinus, roughly circular or longer than broad, 0.13–0.16 mm long (average = 0.140 mm, $n=15$, 3) by 0.11–0.14 mm wide (average = 0.124 mm, $n=15$, 3), with conspicuous, shelf-like condyles at proximolateral margins delineating a deep, broad, U-shaped proximal sinus that is variably flattened at the bottom. Male orifice (Figure 9B, D) similar in shape, roughly one-half to two-thirds the length and width of the autozooidal orifice. Female secondary orifice, including proximal margin of ovicell, semicircular in frontal view and with a concave proximal margin in distal view.

Spines. Lacking.

Avicularia. Lacking.

Ovicell (Figure 9B, D). Occurring densely in central, frontally budded, fertile zone of colony; thin-walled, prominent, globose, irregular in shape, orientation, and size,

0.18–0.23 mm long (average=0.195 mm, $n=15$, 3) by 0.18–0.26 mm wide (average=0.214 mm, $n=15$, 3); with 12–18 conspicuous pores (average=15, $n=10$, 1) distributed over entire surface.

Ancestrula. Like a small autozooid in form; budding pattern a spiral, with first bud arising distolaterally from ancestrula and each subsequent bud arising from angle between ancestrula and preceding bud.

Remarks

In addition to colonies collected intertidally, we examined several specimens encrusting a mussel (*Mytilus edulis*) shell growing subtidally in a boat harbour near the East Tongass Narrows site. The intertidal distribution of this species was not adequately determined due to difficulty in distinguishing it in the field from multilaminar colonies of *C. reflexa*. Our impression is that *C. hyalina sensu lato* was much less common on intertidal rocks than *C. reflexa*.

Celleporella hyalina (Linnaeus, 1767) has historically been treated as a widely distributed species. For example, Osburn (1952) noted, "It is a truly cosmopolitan species, occurring around the world and from the Arctic ... to the tropics. It has been reported by everyone who has studied Pacific coast Bryozoa, from Alaska to southern California..." Recently, however, morphological, molecular genetic, and mating-compatibility studies (e.g. Hoare et al. 2001; Hughes et al. 2003; Navarette et al. 2003, 2005) have shown that *C. hyalina* (L.) is likely only part of a complex of sibling or cryptic species, with at least 11 major, genetically divergent lineages worldwide. Morris (1980: Text-figure 14) illustrated variation in orifice shapes for nominal *C. hyalina* along the Pacific coast of North America, which might reflect inter-lineage or even interspecific variation.

The specimens from Ketchikan are undoubtedly synonymous with some of the previous records of nominal *C. hyalina* from the north-eastern Pacific. For instance, one of the orifice shapes shown by Morris (1980: Text-figure 14, left) for Alaskan material is similar to that of one of our specimens (Figure 9C); however, this colony (Figure 9C, D) had a distinctly larger orifice (0.15–0.20 mm long, average=0.178 mm, $n=10$, 1; 0.13–0.16 mm wide, average=0.147 mm, $n=10$, 1) than others examined. It is questionable whether any of our specimens are conspecific with *C. hyalina* (L.); measurements of the autozooid and autozooidal orifice are considerably larger than those reported for British material by Morris (1980) and Hayward and Ryland (1999).

Until the taxonomy of the *C. hyalina* species complex is better understood through integrated morphological, molecular, and reproductive-compatibility studies, we simply refer specimens from Ketchikan to this species complex. For the same reason, we include neither synonymies nor distributional data.

Celleporella reflexa Dick and Ross, 1988 (Figure 10A–F)

Celleporella reflexa Dick and Ross 1988 p 83, Plates 6C–H, 12E.

Celleporella hyalina: Dick and Ross 1986 p 89 (in part); Soule et al. 1995, p 183 (in part: Plate 66A, specimen from Canoe Bay, Alaska).

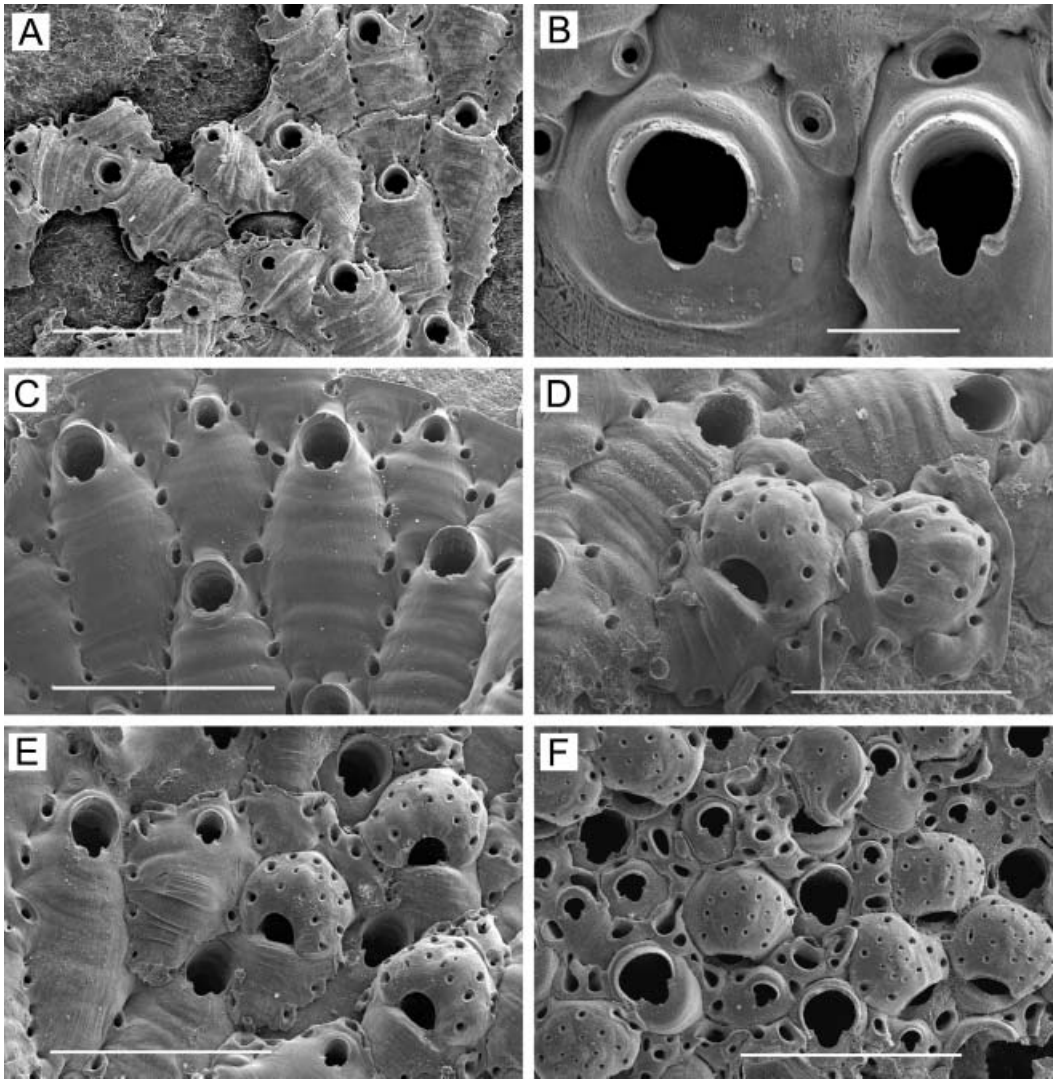


Figure 10. *Celleporella reflexa* Dick and Ross: (A) portion of a colony showing unilaminar, oligoserial growth, with autozooids and male zooids (small orifices) in primary layer; (B) variation in autozooidal orifice shape in two adjacent zooids; elongate orifice shape at right is more typical of specimens from Kodiak, Alaska, the type locality; (C) autozooids and male zooids in primary layer at margin of a coherent colony; note weak transverse ridges; (D) ovicellate female zooids in primary layer (rare at Ketchikan) and autozooids showing typically pronounced transverse ridges; (E) autozooids in primary layer and frontally budded male and female zooids; (F) frontally budded autozooids, male zooids, and female zooids in a colony with a thick secondary layer; note subimmersed ovicells. All specimens bleached. Scale bars: 1 mm (A); 100 μ m (B); 500 μ m (C, E, F); 400 μ m (D).

Description

Colony. Off-white, vitreous; uniserial, oligoserial, broadly multiserial, or a coherent sheet, with a single colony often giving rise to these different morphologies with variations in substrate; initially unilaminar, with autozooids and male zooids in primary layer (Figure 10A, C); subsequently some colonies produce one or more frontally budded layers containing all zooid types (Figure 10F). At Ketchikan, female zooids occurred only

rarely in primary layer (Figure 10D). Encrusting hard substrates; largest colony observed 3 cm across, though aggregations of colonies can cover larger areas.

Zooids. Autozooids distinct in primary layer, separated by a shallow groove, spindle-shaped, widest in middle, tapering proximally, narrowing and rounded distally, 0.50–0.75 mm long (average=0.620 mm, $n=15$, 3) by 0.23–0.35 mm wide (average=0.277 mm, $n=15$, 3); between adjacent zooids are a few slit-like lacunae and up to eight circular, infundibular openings that lead to the pore chambers connecting zooids. Zooidal boundaries obscured in colonies with a thick, frontally budded layer; autozooids can become orientated almost vertically, and the grooves between all zooid types (autozooids, female zooids, male zooids, zooeciules) completely filled with coarsely porous kenozooidal calcification. Ovicellate zooids small, more-or-less triangular in shape (Figure 10D, E), widest at orifice, 0.24–0.40 mm long including ovicell (average=0.346 mm, $n=15$, 3) by 0.21–0.30 mm wide (average=0.250 mm, $n=15$, 3). Male zooids like autozooids in form, similar in size or somewhat to considerably smaller.

Frontal wall. Thin, vitreous, translucent, markedly convex, usually with conspicuous, irregular transverse folds or ridges along the whole length, though sometimes these are scarcely developed. Basal wall with oval uncalcified area in centre.

Orifice. Autozooidal orifice typically longer than broad (Figure 10B, right), 0.11–0.13 mm long (average=0.121 mm, $n=15$, 3) by 0.09–0.10 mm wide (average=0.096 mm, $n=15$, 3). In some colonies, most zooids have an orifice as broad as, or broader than, long (Figure 10B, left); this is especially pronounced in frontally budded autozooids comprising a secondary layer. Orifice typically with a moderately broad, deep U- or rounded V-shaped proximal sinus (Figure 10B) between sharp condyles pointing distally or distomedially and separated from lateral margin by a notch; however there is variation, and in some zooids the condyles are blunt, directed almost medially, and without a discernible notch. Orifice of male zooids similar in shape to that of autozooids, but three-fifths to less than one-half the length. Female secondary orifice D-shaped in frontal view (Figure 10D), broader than long, with a shallowly concave proximal margin evident from a more distal view.

Spines. Lacking.

Avicularia. Lacking.

Ovicell (Figure 10D–F). Globose, raised or partly immersed, 0.18–0.23 mm long (average=0.188 mm, $n=15$, 3) by 0.19–0.28 mm wide (average=0.227 mm, $n=15$, 3), with 10–23 infundibular pores scattered over the surface.

Ancestrula. Oval, smooth, with the orifice similar in shape to that of later zooids; gives rise to one distolateral zooid which in turn buds from the proximolateral margin a zooid that grows back alongside the ancestrula, in the opposite direction.

Remarks

Celleporella reflexa was common underneath boulders at all three collecting sites, attached to rock surfaces, dead mollusc shells, and serpulid tubes. Ketchikan specimens are similar in

most respects to *C. reflexa* described at Kodiak (Dick and Ross 1988). However, at Ketchikan female zooids are rare in the primary layer; most are frontally budded in the groove between autozooids.

In Alaska, multilaminar, coherent colonies of *C. reflexa* can be confused with specimens of the *C. hyalina* species complex. In *C. reflexa*, the autozooidal orifice is conspicuously smaller, typically with sharp, distally or distomedially pointed condyles separated by a notch from the lateral margin; the irregular transverse ridging is more pronounced; the openings to pore chambers along the lateral margins are smaller, more numerous, and infundibular; the basal wall is always incompletely calcified; and the ovicell can become subimmersed. The ancestrular budding patterns of the two species are also quite different. A specimen from Canoe Bay, Alaska, identified and illustrated by Soule et al. (1995, Plate 66A) as *C. hyalina* (L.), appears to be *C. reflexa*, as it shows most of the characters just mentioned.

Distribution

In south-eastern Alaska, this species was previously recorded from the Blashke Islands (Dick and Ross 1988). The known range extends from Ketchikan to the eastern Aleutian Islands.

Celleporella nodasakae, new species (Figure 11A–F)

Diagnosis

Colony strictly unilaminar; growth form uniserial, biserial, oligoserial, aggregated, or coherent, often in same colony; only autozooids and ovicellate female zooids occur; male polymorphs and zoeciules lacking; zooids loosely connected by tubular pore chambers with conspicuous lacunae between them; ovicells with four to five pores, generally around perimeter; autozooidal orifice with a deep, U-shaped sinus and sharp condyles pointing distally, flanked by a notch; proximal margin of female orifice M-shaped, with a U- or rounded V-shaped sinus between triangular, distally directed projections.

Type material

Holotype: SC, specimen KE-26 bleached and coated for SEM (YPM 35839). Paratype 1: SC, specimen KE-24 bleached and coated for SEM (YPM 35840). Paratype 2: SC, specimen KE-119 bleached and coated for SEM (NHM 2005.7.11.4). Paratype 3: SC, specimen KE-57 on bivalve fragment, lightly bleached and coated for SEM (YPM 35841). Paratype 4: SC, specimen KE-32 bleached and coated for SEM (ZIRAS 1/50530). Paratype 5: SC, specimen KE-13 bleached and coated for SEM (NHM 2005.7.11.5).

Etymology

The species is named for Dr Yoshinobu Nodasaka, Hokkaido University School of Dentistry, to whom we are deeply indebted for cheerful assistance with scanning electron microscopy over a period of many years.

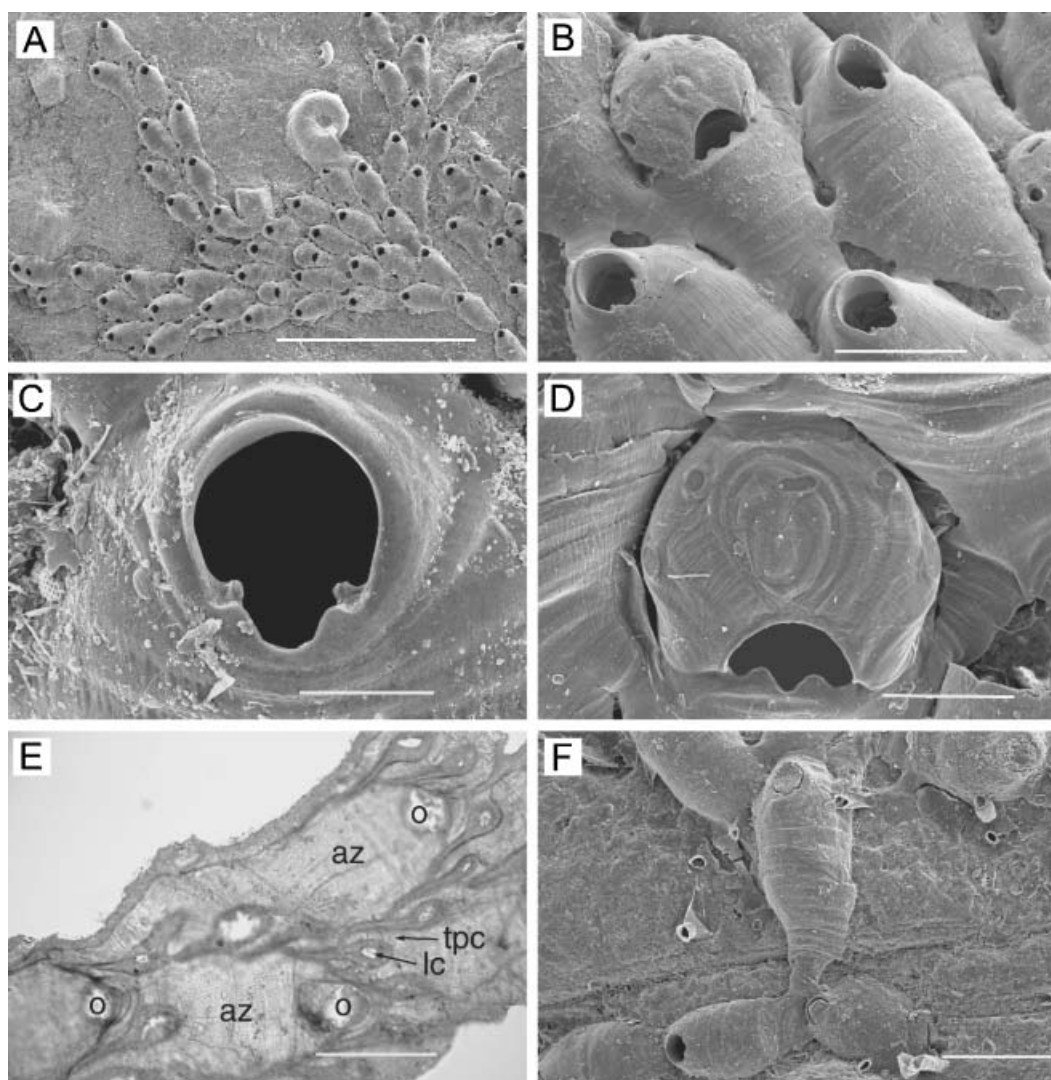


Figure 11. *Celleporella nodasakae* n. sp.: (A) general colony view, showing uniserial branch giving rise to coherent sheet followed by oligoseriate rami; (B) autozooids and an ovicellate zooid; (C) enlargement of autozooidal orifice; (D) enlargement of ovicell and female orifice; (E) photomicrograph of several autozooids from basal side, showing interzooidal connections; az, autozooid; o, orifice; tpc, tubular pore chamber; lc, interzooidal lacuna; (F) ancestrula (bottom, right of centre) and first daughter zooid (bottom, left of centre); from proximal margin of latter is budded a zooid directed perpendicularly. All specimens except (F) were bleached. Scale bars: 2 mm (A); 200 μ m (B); 50 μ m (C); 100 μ m (D); 250 μ m (E, F).

Description

Colony. White, vitreous; strictly unilaminar; at Ketchikan found on rocks and dead bivalve shells. Zooids arranged in branching uniserial, biserial, or oligoseriate series; an anastomosing, aggregated network; or a coherent crust; sometimes a single colony displays most or all of these forms in different parts (Figure 11A). Ovicellate female zooids interspersed with autozooids (Figure 11B); male polymorphs and zoeciules lacking.

Zooids. Autozooids oval or spindle-shaped, sometimes with a cauda one-third to two-fifths of zooid length, tapering to one-third to one-half of zooid width; separated by a groove, more-or-less loosely appressed to one another, with three to five conspicuous lacunae along each lateral margin between coarse tubular connections; 0.33–0.73 mm long (average=0.447 mm, $n=30, 4$) by 0.18–0.28 mm wide (average=0.230 mm, $n=30, 4$). Ovicellate zooids triangular, smaller than autozooids, 0.29–0.49 mm long including ovicell (average=0.380 mm, $n=30, 4$) by 0.13–0.25 mm wide at orifice (average=0.192 mm, $n=30, 4$). Zooids interconnect by two tubular pore chambers distally and four to six along each lateral margin (Figure 11E). Basal wall with a narrow, marginal calcified shelf surrounding the uncalcified centre.

Frontal wall. Thin, vitreous, translucent, imperforate, convex, with transverse striae or weak transverse ridges; umbo lacking in our specimens.

Orifice. Autozooidal orifice (Figure 11C) slightly longer than broad, 0.06–0.09 mm long (average=0.074 mm, $n=30, 4$) by 0.05–0.08 mm wide (average=0.065 mm, $n=30, 4$); proximal margin with a deep, broadly U-shaped sinus flanked by small, sharp, distally or distomedially directed condyles separated by a notch from lateral orificial margin. Female secondary orifice (Figure 11D) semicircular; proximal margin M-shaped, with a U- or rounded V-shaped median sinus flanked by coarse, triangular, distally pointing projections.

Ovicell (Figure 11B, D). Raised, globose, nearly circular in outline, 0.16–0.23 mm long (average=0.185 mm, $n=30, 4$) by 0.16–0.24 mm wide (average=0.204 mm, $n=30, 4$); with four to five pores scattered mostly around the sloping perimeter, generally away from the central area; sculptured with faint concentric growth lines and sometimes a slight umbo.

Spines and avicularia. Lacking.

Ancestrula. One observed (Figure 11F); similar in form to subsequent autozooids, though smaller, 0.30 mm long by 0.20 mm wide. This ancestrula produced one daughter zooid distally, which in turn produced two buds, one distally and the other at the proximolateral margin, directed laterally.

Remarks

We have placed this species in *Celleporella*, rather than *Hippothoa*, because of its coherent growth form in at least parts of colonies, and its tubular pore chambers. *Celleporella nodasakae* is similar in growth form to *C. reflexa* Dick and Ross; both can range from uniserial to narrowly multiserial to coherent, and both can have female zooids in the primary layer. However, compared to *C. reflexa*, *C. nodasakae* has a greater tendency to be uniserial; lacks male zooids and zoeciules; was never observed to become multilaminar; has a distinctly smaller autozooidal orifice; has fewer pore chambers; has fewer, larger interzooidal lacunae; has fewer pores in the ovicell; and has the orifice of ovicellate zooids with a diagnostic, M-shaped proximal margin. The ancestrular budding pattern of *C. nodasakae* is somewhat similar to that of *C. reflexa*; in both species, the ancestrula first buds a distolateral daughter zooid, from which arises another zooid from the proximolateral margin. However, whereas this proximolaterally budded zooid grows back alongside the

ancestrula in *C. reflexa*, it grows laterally or proximolaterally in *C. nodasakae*, away from the ancestrula. We found both species in the Ketchikan vicinity; however, whereas *C. reflexa* occurred at all three collecting sites, *C. nodasakae* occurred only at Settlers Cove, a silty environment with much freshwater influence.

Celleporella nodasakae is similar to *Hippothoa minitumulosa* Morris, 1980, which also ranges from uniserial to coherent in form, displays only unilaminar growth, and lacks male polymorphs (the latter two characters were not specifically mentioned in the original description, but Morris (1980) gave no measurements for male polymorphs, and her figure shows only unilaminar growth). However, compared to *C. nodasakae*, *H. minitumulosa* has smaller zooids with midline tubercles, ovicells with more pores, and a differently shaped female orifice.

Celleporella nodasakae is also similar to *H. santacruzana* Pinter, 1973, in which the ovicell likewise can have a few peripheral pores, and in which the proximal margin of the female orifice has two rounded-triangular projections flanking a median sinus. However, *H. santacruzana* forms only disc-shaped coherent crusts, and male polymorphs occur.

Distribution

Settlers Cove near Ketchikan is the only known locality.

“Grade” UMBONULOMORPHA Gordon, 1989
Superfamily LEPRALIELLOIDEA Vigneaux, 1949
Family BRYOCRYPTELLIDAE Vigneaux, 1949
Genus *Porella* Gray, 1848
Porella alba Nordgaard, 1906
 (Figure 12A, B)

Porella alba Nordgaard 1906, p 25, Plate 3, Figures 43–45.

Porella alba: Hayward 1979, p 77, Figure 2d–f; Hayward and Ryland 1999, p 156, Figure 54; Dick and Ross 1986, p 89; 1988, p 64, Plate 8B, C; Grischenko 1997, p 178, 2004, p 40.

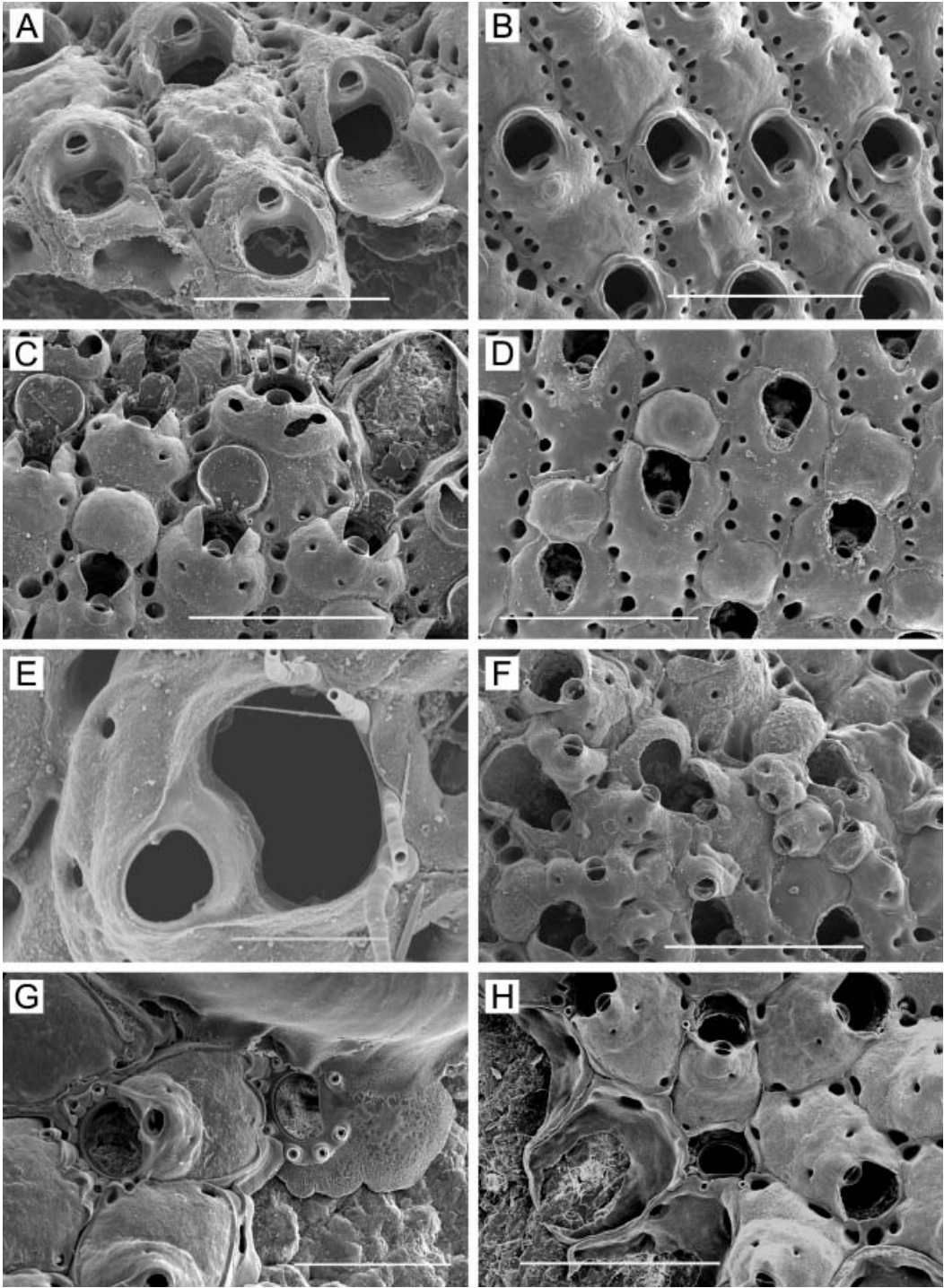
Porella minuta: ?Osburn 1953, p 780, Plate 81, Figure 9; Kluge 1975, p 552, Figure 302.

Description

Colony. Unilaminar, tightly adhering, glistening white in colour, forming circular to irregular patches on hard substrates; largest observed 1.5 cm across.

Zooids. Distinct, separated by a groove flanked by areolar pores; barrel- to spindle-shaped, often tapering proximally, 0.33–0.53 mm long (average=0.420 mm, $n=15$, 3) by 0.23–0.30 mm wide (average=0.263 mm, $n=15$, 3).

Frontal wall. Moderately to markedly convex; heavily calcified at all stages, increasingly thick with age; imperforate except for 7–11 conspicuous, often enlarged, areolae along each lateral margin, frequently with conspicuous ridges or buttresses between them; often with a low, blunt suboral umbo covering avicularian chamber.



Orifice. Primary orifice (Figure 12A) visible only on marginal zooids, rapidly becoming deeply submerged in peristome; semicircular, broader than long, 0.08–0.10 mm long (average=0.086 mm, $n=15$, 3) by 0.08–0.13 mm wide (average=0.104 mm, $n=15$, 3), proximal margin straight, condyles minute, lyrula lacking. Secondary orifice circular, oval, or rounded-quadrangular in outline, surrounded by a thickened rim.

Spines. Lacking.

Avicularia. A median suboral avicularium (Figure 12A) lies at the proximal edge of the peristome in young zooids and within the peristome in older zooids; rostrum nearly circular, angled slightly proximally; mandible semicircular. Avicularian chamber small, crescent-shaped or occasionally globose, originating from a marginal pore on each side; rapidly obscured by increasing calcification.

Ovicell. Initially raised, but immersed with age (Figure 12B) and often indistinguishable from frontal wall of next distal zooid; opening at bottom of peristome, not closed by operculum; imperforate, globose, 0.15–0.23 mm long (average=0.183 mm, $n=15$, 3) by 0.18–0.25 mm wide (average=0.214 mm, $n=15$, 3); proximal margin usually raised and continuous with peristomial rim.

Ancestrula. Not observed.

Remarks

Porella alba is superficially similar to *P. donoghueorum* in having similar colony colour and form, the rostrum and mandible of the suboral avicularium similarly shaped, immersed ovicells, and small zooids. *Porella alba* differs in having roughly twice the number of areolar pores, a pronounced tendency for inter-areolar ridges or buttresses, and a straight rather than a convex, weakly lyrulate proximal orificial margin. *Porella alba* lacks distal spines altogether, whereas these are typically evident in marginal zooids of *P. donoghueorum*; it also lacks the pores in the avicularian chamber that are typical of the latter.

Distribution

Previously recorded at Kodiak, Alaska by Dick and Ross (1988), this is considered a circumpolar, arctic-boreal species (Hayward and Ryland 1999). Ketchikan represents the southern limit of the known range in the north-eastern Pacific. In the north-western Pacific, it has been found as far south as the Commander Islands (Grischenko 1997, 2004) and the Pacific coast of Kamchatka (Kubanin 1997).

Figure 12. (A, B) *Porella alba* Nordgaard: (A) marginal zooids showing shape of orifice and suboral avicularium; (B) group of ovicellate zooids. (C–H) *Porella donoghueorum* n. sp.: (C) group of marginal zooids, with one showing formation of pores in suboral avicularian chamber; (D) several ovicellate zooids; (E) enlargement showing shape of zooidal orifice and suboral avicularium; (F) group of ovicellate zooids with numerous frontally budded avicularia; (G) ancestrula and first daughter zooid; ancestrula partly overgrown by spirorbid worm tube; (H) ancestrula (bottom, centre) and budding pattern of periancestrular zooids. All specimens bleached. Scale bars: 400 μ m (A, H); 500 μ m (B–D, F); 100 μ m (E); 200 μ m (G).

Porella donoghueorum, new species
(Figure 12C–H)

Porella columbiana: Osburn 1952, p 398, Plate 46, Figures 7, 8; Dick and Ross 1988, p 64, Plate 5B, C; Soule et al. 1995, p 253, Plate 95; Grischenko 1997, p 180.

not *Porella columbiana* O'Donoghue and O'Donoghue 1923, p 41, Plate 3, Figure 28; 1926 (as *Smittina columbiana*), p 69.

Diagnosis

Zooids small to moderate in size; frontal wall smooth, with four to five conspicuous areolae along each lateral margin, some becoming occluded with age; marginal zooids with four ephemeral distal spines; rostrum of suboral avicularium elliptical, mandible semicircular; avicularian chamber with two to three conspicuous frontal pores; marginal frontal avicularia variably present; ovicell globose when young, immersed with age.

Type material

Holotype: ETN, unbleached and uncoated (YPM 35845). Paratype 1: KV, specimen KE-122 bleached and coated for SEM (YPM 35846). Paratype 2: KV, specimen KE-2 bleached and coated for SEM (YPM 35847). Paratype 3: KV, specimen KE-18 bleached and coated for SEM (YPM 35848). Paratype 4: KV, specimen KE-27 bleached and coated for SEM (NHM 2005.7.11.6). Paratype 5: ETN, unbleached and uncoated (NHM 2005.7.11.7). Paratype 6: HP, unbleached and uncoated (YPM 35849). Paratype 7: ETN, unbleached and uncoated (ZIRAS 1/50531).

Etymology

The species is named in honour of Charles and Elsie O'Donoghue, who contributed much to the knowledge of bryozoans along the Pacific coast of North America.

Description

Colony. Unilaminar, encrusting, white, glistening, forming circular to irregular patches on hard substrates; largest observed 1.5 cm across.

Zooids. Roughly hexagonal, barrel-shaped, or oval; translucent when young, opaque with age; marginal zooids distinct (Figure 12C), separated by a shallow to deep groove flanked by areolar pores; small, 0.28–0.45 mm long (average=0.359 mm, $n=40$, 4) by 0.18–0.33 mm wide (average=0.240 mm, $n=40$, 4).

Frontal wall. Inflated, irregular and convex in young zooids, with four to five large, irregularly shaped areolae along each lateral margin proximal to level of orifice, sometimes with slight marginal ribs between them; wall rapidly thickened by secondary calcification, becoming smoother and flatter in later stages (Figure 12D); areolae diminished in size, with some of them occluded, but still conspicuous.

Orifice. Primary orifice (Figure 12E) more than semicircular, with sides turning inward toward proximal margin; broader than long, 0.06–0.09 mm long (average=0.078 mm, $n=40$, 4) by 0.09–0.15 mm wide (average=0.108 mm, $n=40$, 4); corners rounded; lyrula low, broad, often so reduced it constitutes little more than a convexity; condyles small, rounded. Peristome of young zooids consists of sharp, raised, curved flanges lateral to the orifice, meeting a raised lip or the ovicell margin distally; with age, primary orifice lies deep in peristome. Secondary orifice irregularly oval, interrupted by avicularian rostrum near top of peristome.

Avicularia. Each zooid bears a suboral avicularium; rostrum circular or short-elliptical, tilted in proximal direction at about 45° to colony surface; bisected by a hinge bar; mandible semicircular, pointing proximally. Avicularian chamber broader than long; rectangular or crescentic, developing from an areolar pore on each side; occupying one-third to one-half the length of frontal wall; in later stages completely immersed by secondary calcification. Chamber bears usually two, sometimes three, frontal pores resulting from incomplete closure of the chamber as it forms (Figure 12C). In addition, some zooids have one to three marginal frontal avicularia (Figure 12F), budded from any of the areolae along the zooidal margin; chamber raised, irregular in size and shape, with one or two pores; rostrum and mandible similar in shape to those of suboral avicularium. Frontal avicularia occur sporadically; some colonies lack them altogether, and when present they occur on a few scattered zooids, or in small patches of the colony.

Spines. Marginal zooids have four long, ephemeral distal spines (Figure 12C, E), the bases of which can sometimes be seen in the peristome of older zooids.

Ovicell (Figure 12C, D, F). Globose and distinct in young zooids, overlying the frontal wall of the next distal zooid; broader than long, 0.11–0.18 mm long (average=0.136 mm, $n=40$, 4) by 0.10–0.24 mm wide (average=0.185 mm, $n=40$, 4); smooth, imperforate, the proximal margin upturned as a narrow lip; immersed with age, the top flush with the colony surface.

Ancestrula (Figure 12G, H). Orifice with straight proximal margin, surrounded by eight spines; with a complement of five periancestrular zooids (one distal, two lateral, two proximolateral).

Remarks

O'Donoghue and O'Donoghue (1923) described *Porella columbiana*, a species that they noted is similar in some respects to *P. major* Hincks, 1884. The original description of neither of these species mentions distal spines on marginal zooids, or pores in the chamber of the suboral avicularium. Osburn (1952) erroneously described and illustrated a different species as *P. columbiana*, characterized by having two to four distal spines and a suboral avicularian chamber with "about three small areolar pores". The areolae along the zooidal margin in Osburn's (1952, Plate 46, Figure 7, 8) species are clearly fewer than illustrated by O'Donoghue and O'Donoghue (1923, Plate 3, Figure 28) for *P. columbiana*. Subsequent authors (Dick and Ross 1988; Soule et al. 1995) continued Osburn's (1952) mistaken concept of *P. columbiana*.

Soule et al. (1995) declared a lectotype (NHM 1964.1.2.15) for *P. columbiana* O'Donoghue and O'Donoghue, which we have examined. The box labelled "Lectotype, Pacific coast of N. America, O'Donoghue Collection" contains three colonies on separate bivalve shell fragments, all of which are clearly conspecific with one another and with two other colonies in a wooden depression slide labelled "*Porella columbiana* O'D and O'D, Pac. Coast N. Amer. (Brit. Col.), part 1964.1.2.15)", which we consider as paralectotypes. SEM images (Figure 13A–D) of one of the colonies from the depression slide show that *P. columbiana* is clearly allied with *P. major* and *P. acutirostris* (see Remarks for *P. acutirostris* herein), and not conspecific with what Osburn (1952) and subsequent authors (Dick and Ross 1988; Soule et al. 1995) treated as *P. columbiana*. Osburn's species requires a new name, which we have given as *P. donoghueorum*.

Osburn (1952) and Soule et al. (1995) indicated larger zooids for populations of this species from British Columbia to southern California, as compared to populations from Kodiak (Dick and Ross, 1988) and Ketchikan, Alaska. Furthermore, both Osburn (1952) and Soule et al. (1995) specifically noted the absence of frontal avicularia, which we observed in some of the Ketchikan specimens. Dick and Ross (1988) likewise did not find them in Kodiak specimens. The Alaskan material agrees so well in other characters with material from farther south that we suspect the size difference may reflect a latitudinal cline. As for the frontal avicularia, these were not present in every colony found at Ketchikan, and were sparse or patchily distributed when they did occur, which might explain why previous

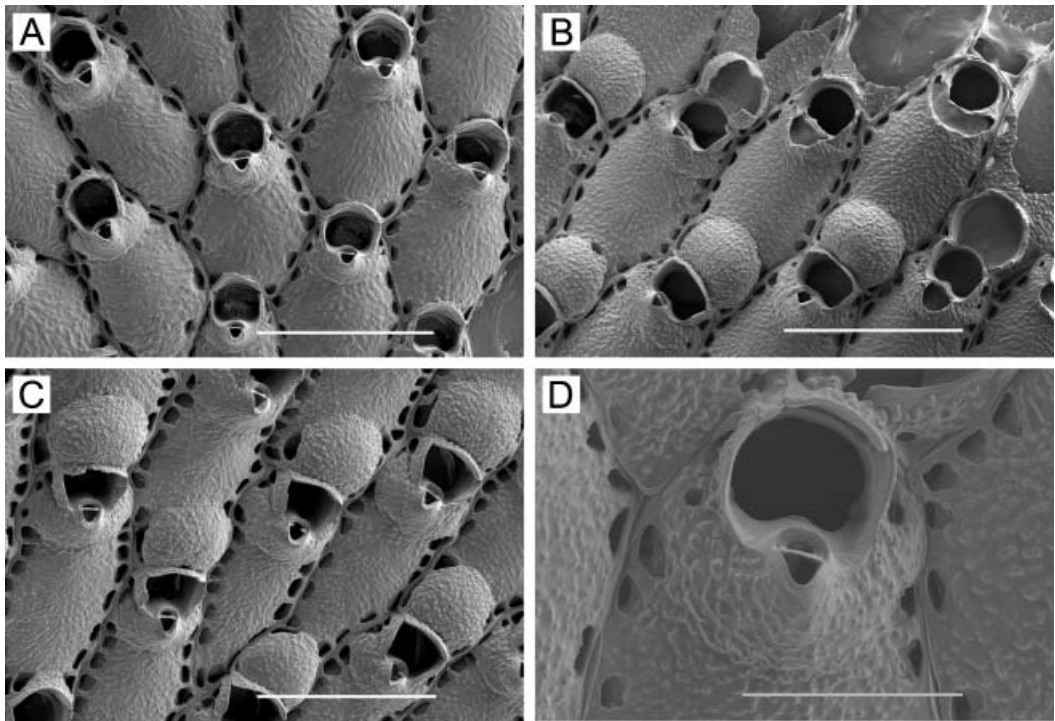


Figure 13. *Porella columbiana* O'Donoghue and O'Donoghue, paralectotype, BMNH 1964.1.2.15; bleached: (A) group of autozooids; (B) zooids near colony margin showing stages in formation of suboral avicularian chamber; (C) group of ovicellate zooids; (D) enlargement of autozooidal orifice showing condyles and weak lyrula. Scale bars: 500 μ m (A–C); 200 μ m (D).

authors missed them. Thus, we consider *P. donoghueorum* a single species from the Gulf of Alaska to southern California.

Distribution

This is a boreal Pacific species, known in the eastern Pacific from Kodiak, Alaska (Dick and Ross 1988) (as *P. columbiana*) southward to Redondo Beach and Santa Monica, California (Osburn 1952) (as *P. columbiana*), and on the Asian side from the Commander Islands (Grischenko 1997) (as *P. columbiana*). Osburn's (1952) record of this or a similar species (as *P. columbiana*) from the Galapagos Islands needs to be re-examined.

***Porella acutirostris* Smitt, 1868 species complex** (Figure 14A–D)

Colony

Description. Unilaminar, encrusting, sheet-like, roughly circular, tightly adhering to hard substrates, light yellow to deep golden-yellow in colour, often with the margin more heavily pigmented; largest observed 5 cm across.

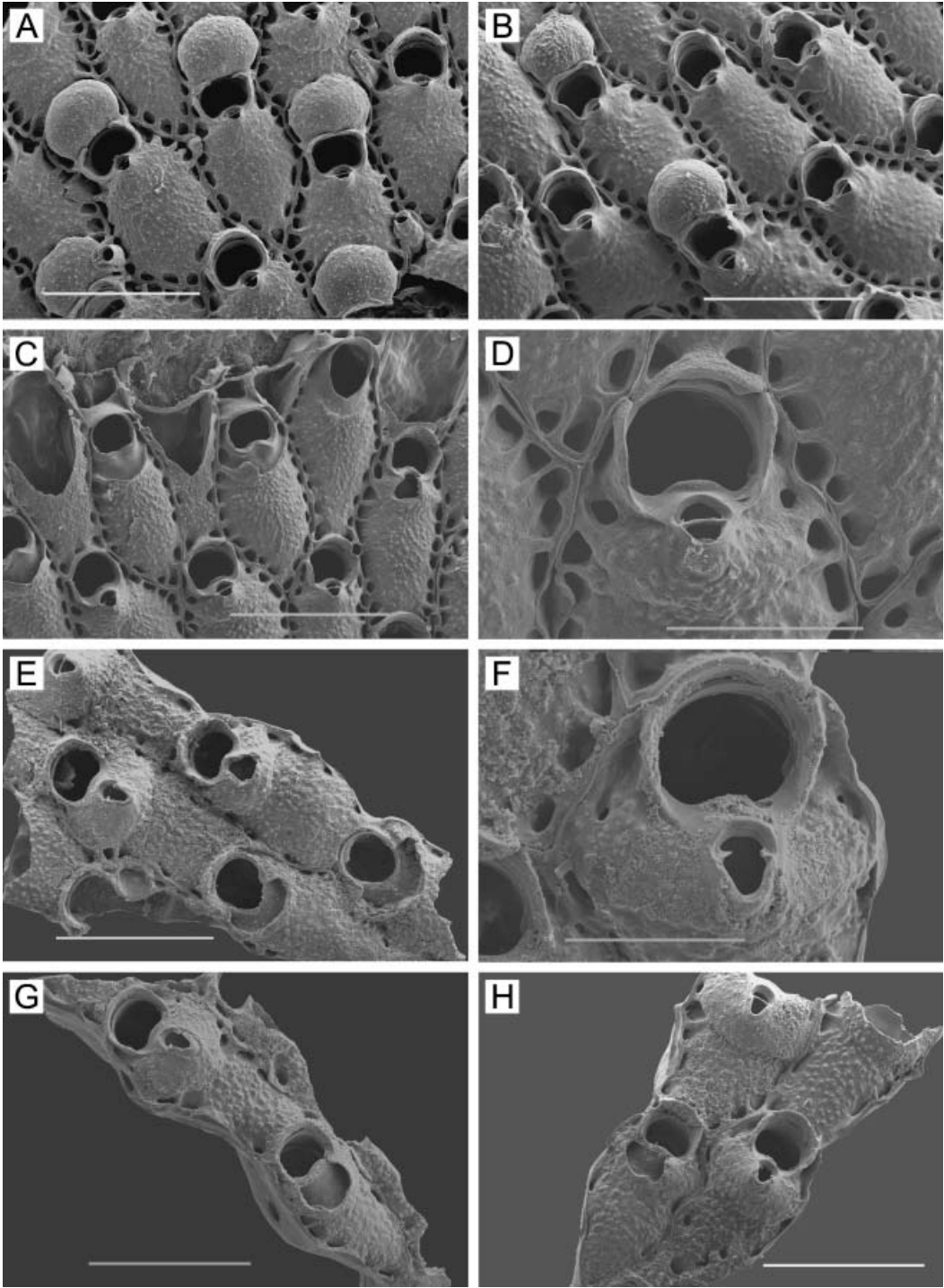
Zooids. Rectangular, barrel-shaped, or rounded hexagonal, sometimes tapering proximally; separated by a groove in which lies a narrow suture line between adjacent rows of areolae; 0.35–0.70 mm long (average=0.515 mm, $n=21$, 4) by 0.21–0.33 mm wide (average=0.260 mm, $n=21$, 4); interconnecting by a pair of multiporous septula in distal wall and a single elliptical multiporous septulum in each distolateral wall; basal wall completely calcified.

Frontal wall. Slightly to markedly convex; finely to coarsely granulated; imperforate, with 6–11 conspicuous areolar openings along each lateral margin, extending lateral to orifice, slit-like, oblong, circular, or irregular in shape.

Orifice. Primary orifice (Figure 14D) semicircular, broader than long, 0.08–0.13 mm long (average=0.091 mm, $n=20$, 4) by 0.10–0.15 mm wide (average=0.115 mm, $n=20$, 4); proximal margin sometimes straight, but usually broadly convex, often rising to a low, broad, rounded lyrula; condyles variable within colonies, often minute, flattened, and scarcely evident, but raised, blunt, and conspicuous in some zooids. Peristome deep enough to obscure primary orifice; bounded proximally by avicularian chamber and laterally by a narrow flange on each side that is confluent distally with raised proximal lip of ovicell or raised proximal margin of succeeding zooid. Secondary orifice semicircular to roughly quadrate.

Spines. Five spines around distal orificial margin in zooids surrounding ancestrula; lacking outside zone of astogenetic change.

Avicularia. Each zooid has a median suboral avicularium (Figure 14D); the chamber arises from an areolar pore on each side, is raised from frontal wall, broader than long, crescentic (Figure 14C), 0.10–0.15 mm long (average 0.121 mm, $n=20$, 4) by 0.15–0.24 mm wide (average=0.199 mm, $n=20$, 4); rostrum partly within peristome, the hinge bar about level



with top of peristomial flanges; rostrum orientated nearly vertically or angled to 45° in proximal direction, mandible a blunt equilateral triangle.

Ovicell (Figure 14A, B). Raised, globose, 0.15–0.20 mm long (average 0.186 mm, $n=20$, 4) by 0.20–0.28 mm wide (average=0.237 mm, $n=20$, 4); imperforate, surface finely or coarsely granulated like frontal wall.

Ancestrula. Ancestrula proper was obscured in Ketchikan specimens, but budding pattern appears to be three zooids distally and distolaterally and a pair of larger zooids proximally. Periancestrular zooids are similar to later autozooids, but have five oral spines.

Remarks

Smitt (1868) originally described *Porella acutirostris* from the European Arctic, with the type locality near Spitsbergen Island ($78^\circ 10'N$, $13^\circ 30'E$). Subsequently, it came to be considered a circumpolar, arctic-boreal species; see Kluge (1975) for many distributional records. The nominal species has been reported as far south as Wood's Hole (Cape Cod) in the north-western Atlantic (Osburn 1912), southern California in the north-eastern Pacific (Osburn 1952), and middle Honshu, Japan in the north-western Pacific (Mawatari and Mawatari 1981). We can find no record of this species from the boreal north-eastern Atlantic; in Europe, it has apparently not been reported south of the Lofoten Islands in the Norwegian Arctic (Nordgaard 1918).

Hincks (1884) described from British Columbia a similar species, *P. major*, which Osburn (1952) listed as a junior synonym of *P. acutirostris*. However, Soule et al. (1995) resurrected *P. major* Hincks, speculating that this is a southern species, distinct from *P. acutirostris* and ranging from British Columbia to southern California in the eastern Pacific. They showed SEM illustrations of Hincks's type of *P. major*, a young, periancestrular colony, and suggested that characters distinguishing *P. major* from *P. acutirostris* include flatter zooids; larger, more numerous areolae; weaker condyles; and a less bulbous avicularian chamber.

To try to clarify the differences between *P. major* and *P. acutirostris*, we examined Smitt's type of *P. acutirostris* (SMNH Type-1752) (Figure 14E–H), which includes two small fragments of *P. acutirostris* (about 3 and 7 mm²) lacking ovicells, as well as a 2 mm² fragment of *Porella peristomata* (Nordgaard, 1905). The primary orifice in the type of *P. acutirostris* (Figure 14F) is very similar to that in the type of *P. major* (Soule et al. 1995, Plate 94B), with similar variation. Some zooids in the *P. acutirostris* type have only a slightly convex proximal orificial margin, whereas others have a low, broad, rounded-truncate lyrula. The degree of development of the condyles is variable, ranging from weak and flattened to rounded and conspicuous. The shape of the avicularian chamber (Figure 14E–H) is likewise variable; in some zooids it is bulbous, but in others it is narrow and sometimes crescentic, as in the type of *P. major*. Some zooids in the type of *P. acutirostris* have the avicularian rostrum narrower in proportion to length than in the type of *P. major*,

Figure 14. (A–D) *Porella acutirostris* Smitt s. l.: (A) group of ovicellate and non-ovicellate zooids; (B) group of ovicellate and non-ovicellate zooids, another colony; (C) zooids at colony margin; (D) enlargement of orifice and suboral avicularium; note condyles (one visible) and low, broad lyrula. (E–H) *Porella acutirostris* Smitt, holotype, SMNH Type-1752: (E) group of autozooids; (F) enlargement of orifice and suboral avicularium; note condyles (one visible) and low, broad lyrula; (G) two autozooids; (H) group of autozooids. All specimens bleached. Scale bars: 500 μ m (A–C, E, G, H); 200 μ m (D, F).

with the mandible long-triangular; however, this is again variable, with other zooids having a wider, equilateral mandible. The types of *P. acutirostris* and *P. major* are similar in the structure of the secondary orifice and in the granulated texture of the frontal wall. Finally, zooid length is similar, 0.43–0.65 mm ($n=20$, 2) in the type of *P. acutirostris* compared to 0.45–0.60 mm given by Soule et al. (1995) for *P. major*.

There are also differences between the type of *P. acutirostris* and that of *P. major*. *Porella acutirostris* has fewer (four to seven on each side), slit-like areolae (Figure 14E, G), whereas those of *P. major* are more numerous (6–10 on each side) and much larger, with the appressed lateral walls showing as a distinct suture line between rows of areolae (Soule et al. 1995, Plate 94A, C, E). The avicularian chamber is proportionately larger in *P. acutirostris*; its external area is generally equal to or greater than twice the area of the primary orifice. The chamber of *P. major* is less than twice the area of the primary orifice. In *P. acutirostris*, the avicularian rostrum tends to be set farther back on the chamber and is thus more separate from the peristome. Finally, an apparent difference is the flatness of the zooids of *P. major* compared to *P. acutirostris*. However, it is unclear whether this character is idiosyncratic to the type specimen of *P. major*, which is a young colony growing on a smooth shell, or an artefact resulting from the back-scattered electron imaging used to examine the uncoated specimen.

Our specimens from Ketchikan are similar to *P. major* in having larger, more numerous areolae with a narrow suture line between rows; an avicularian chamber smaller than twice the area of the primary orifice; and the rostrum tilted farther forward into the peristome, with an equilateral mandible. However, our zooids do not appear as flat as in the type of *P. major*. We cannot at present identify our material with either *P. acutirostris* or *P. major* with certainty. One reason is that there appears to be some clinal variation in relevant characters. A specimen we have from the Bering Sea, for example, shows areolae intermediate between *P. acutirostris* and *P. major*; their number is low as in the former, but they are of larger size, as in the latter. By the same token, Osburn's (1912, Plate 27, Figure 69) illustration of *P. acutirostris* from Wood's Hole in the boreal north-western Atlantic shows 4–10 conspicuous areolae per side, much like those of *P. major*, but with a circular rather than a quadrate secondary orifice even in ovicellate zooids. This suggests either that there is clinal variation in areolae in *P. acutirostris*, or that boreal species distinct from arctic *P. acutirostris* exist in both the Atlantic (e.g. the Woods Hole population) and Pacific (e.g. *P. major*). We note that although *P. major* has previously been reported from the Asian side (Androsova 1958; Gontar 1980), Androsova's species, with tiny, circular areolae and the suboral avicularium with a semicircular mandible, is likely not *P. major* Hincks, in light of the type figured by Soule et al. (1995).

Populations of nominal *P. acutirostris* previously identified around the Pacific rim, e.g. the Kurile Islands (Mawatari 1956), Kodiak, Alaska (Dick and Ross 1988), and Akkeshi, Hokkaido, Japan (Mawatari and Mawatari 1981) have numerous, large areolae characteristic of *P. major*. However, they show variation in some of the same characters that vary within colonies in the types of *P. acutirostris* and *P. major*. For example, these Pacific populations tend to have a straight or broadly convex proximal orificial margin, without occurrence of a rounded-truncate lyrula. In *P. acutirostris* and *P. major*, the proximal orificial margin varies at the other end of a continuum, from being broadly convex to having a rounded-truncate lyrula. Compared to Ketchikan specimens, some specimens from the Bering Sea, Kodiak, and Akkeshi are more heavily tuberculate and have the avicularian rostrum suspended almost vertically in the peristome.

Porella columbiana O'Donoghue and O'Donoghue, 1923 is a nominal species closely related to *P. major* and *P. acutirostris* (compare Figures 13 and 14 herein with Soule et al. 1995, Plate 94). Like the latter two species, *P. columbiana* has a granulated frontal wall and ovicell; lacks oral spines outside the zone of astogenetic change; has a blunt-triangular mandible on the suboral avicularium; and has a somewhat quadrate secondary orifice. The areolae (5–11 per side, most frequently seven or eight) are much like those of *P. major* in size and number (6–10 per side, mode=7); indeed, the two may be synonymous. However, compared to the type of *P. major*, *P. columbiana* has longer, more evenly granulated zooids and a narrower lyrula.

Porella acutirostris, rather than being a circumpolar, arctic-boreal species, likely comprises a complex of morphologically similar species, among which *P. major* and *P. columbiana* may be valid species. Integrated studies using morphological and molecular data will be necessary to adequately resolve this group; until this is done, we simply refer specimens from Ketchikan to the species complex, and include neither synonymies nor distributional data.

“Grade” LEPRALIOMORPHA Gordon, 1989
Superfamily SCHIZOPORELLOIDEA Jullien, 1883
Family SCHIZOPORELLIDAE Jullien, 1883
Genus *Schizoporella* Hincks, 1877
Schizoporella japonica Ortmann, 1890
 (Figures 15A–H, 16A–D)

Schizoporella unicornis var. *japonica* Ortmann 1890, p 49, Plate 3, Figure 35.

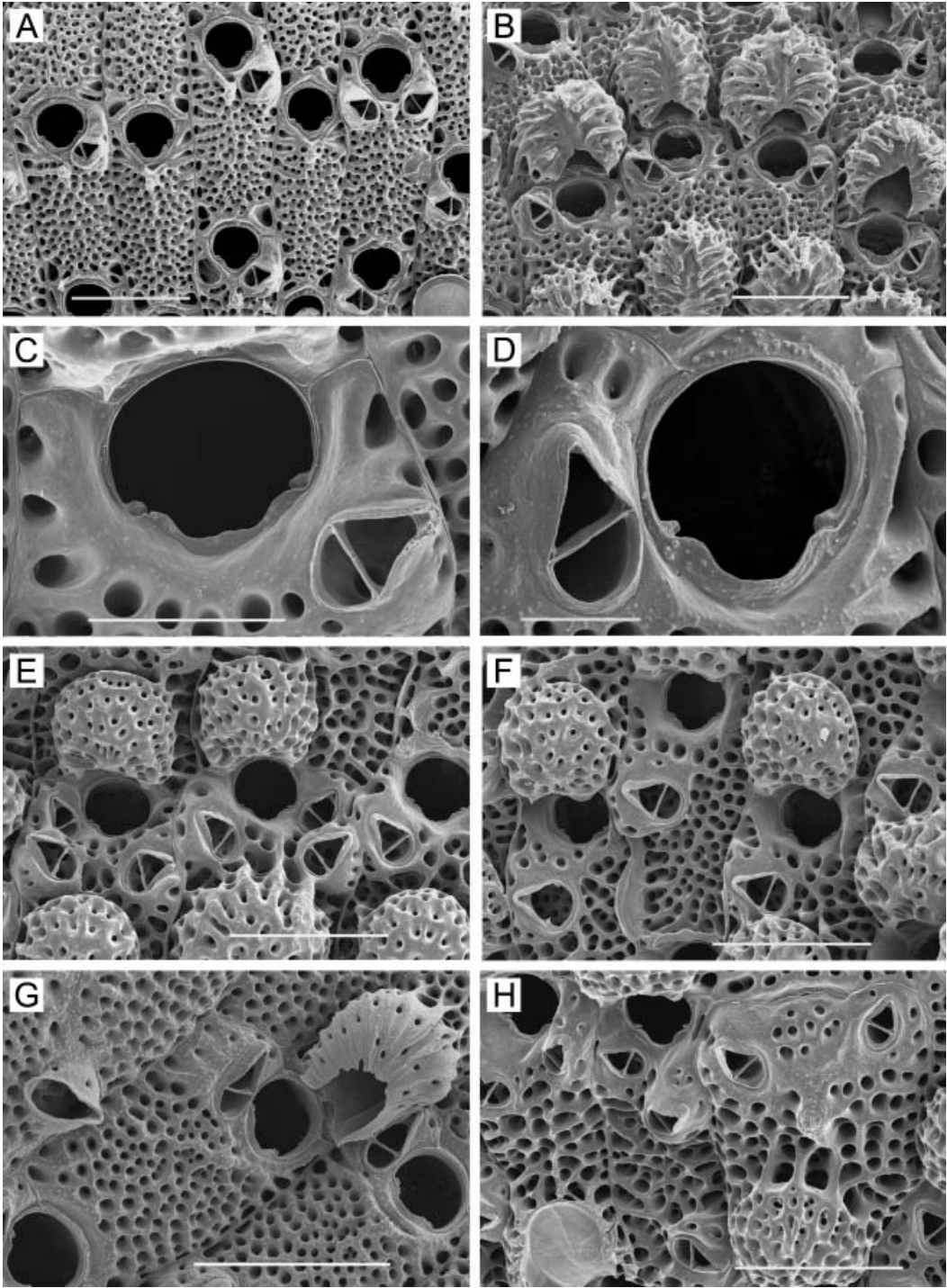
Schizoporella unicornis: Okada 1929, p 20, Text-figure 7; Powell 1970, p 1849, Figures 2, 3; McCain and Ross 1974, p 13, Figure 2c, d; Ross and McCain 1976, p 164, Figures 1–6; Mawatari and Mawatari 1981, p 51; Kubota and Mawatari 1985, p 201, Figure 3A–E; Liu et al. 2001, p 596, Plate 48; Osburn 1952, p 317, Plate 37, Figures 1, 2 (in part?); ?Soule et al. 1995, p 204.

Description

Colony. Encrusting shells, rock substrates, and algae; unilaminar, but sometimes bilayered due to overgrowth of one portion of colony over another, occasionally with foliose lobes free from substrate; whitish, pink, or deep red in colour; colonies to 5 cm or more across.

Zooids. Distinct, delineated by a shallow groove and suture line; approximately rectangular, rounded distally; arranged in columns radiating from centre; quite variable in size, 0.48–0.90 mm long (average=0.648 mm, $n=35$, 3) by 0.25–0.51 mm wide (average=0.364 mm, $n=35$, 3); zooid width increases in a column until zooid at bifurcation point is nearly as broad as long, with daughter zooids again narrow and elongate after bifurcation. In some colonies, there are autozooids with a perforate closure plate over the orifice (Figures 15H, 16D); there can be one or two oral avicularia in the positions they would have occupied had there been an orifice, or an avicularium of the larger type.

Frontal wall. Slightly to moderately convex, with areolar pores along the lateral margins and smaller pseudopores over the entire frontal surface but not extending around distal



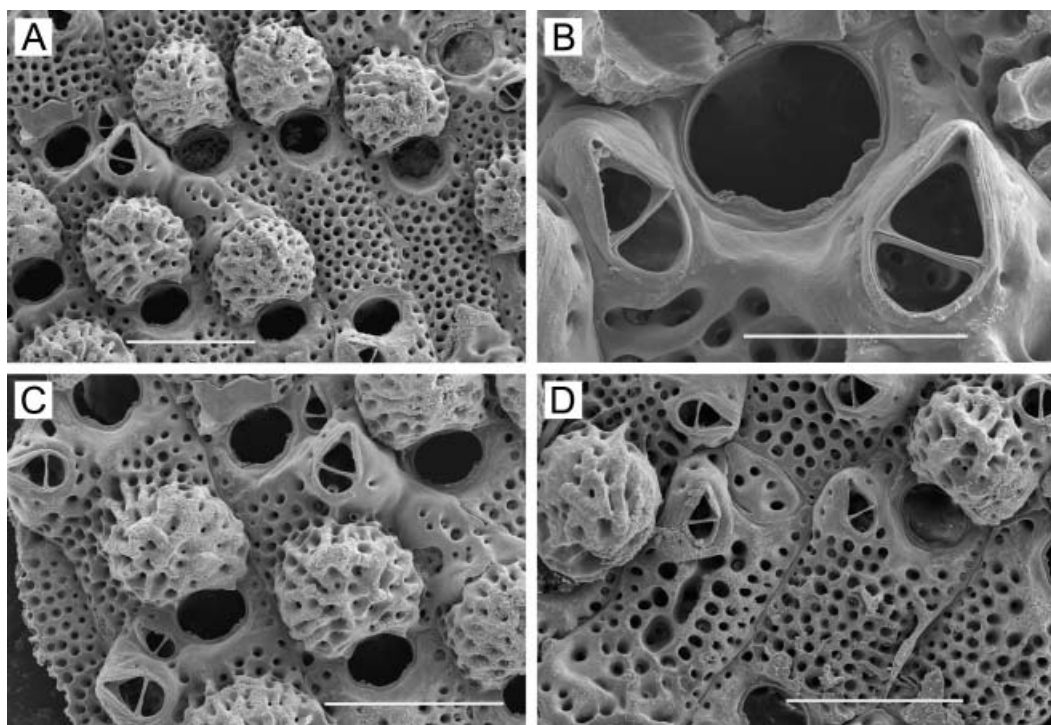


Figure 16. *Schizoporella japonica* Ortmann; portion of Ortmann's (1890) holotype of *Schizoporella unicornis* var. *japonica*; bleached: (A) group of ovicellate zooids; (B) enlargement showing typical orifice shape; (C) zooids (top centre and lower left) with a single oral avicularium and a large frontal avicularium; (D) autozooid (left of centre) with perforate closure plate covering orifice. Scale bars: 500 µm (A, C, D); 200 µm (B).

margin of orifice; frontal smooth or sparsely granulated between pseudopores; often with a small, knob-like, median umbo proximal to orifice; pseudopores become infundibular as frontal wall thickens; in portions of colony crowded with ovicells, thickened frontal wall can become quite reticulate.

Orifice (Figures 15C, D, 16B). Usually broader than long, 0.13–0.16 mm long including sinus (average=0.149 mm, $n=35$, 3) by 0.14–0.19 mm wide (average=0.161 mm, $n=35$, 3); anter semicircular, separated from poster by a stout, blunt condyle on each side, set on a narrow ledge and pointing medially; poster a deep, broad sinus extending between condylar ledges, sloping on the sides and flattened at the bottom. Distal margin of orifice finely tuberculate. Operculum light golden brown, transparent. Orifice usually positioned in midline, but in some zooids is offset to one of the distal corners, with an avicularium in the other.

Figure 15. *Schizoporella japonica* Ortmann; all from Ketchikan: (A) group of non-ovicellate zooids with zero, one, or two oral avicularia; (B) group of ovicellate zooids; (C) enlargement showing typical orifice shape; (D) variant orifice shape; (E) ovicellate zooids (centre and left), each with a single oral avicularium and two larger frontal avicularia; (F) zooids lacking oral avicularia, with a larger frontal avicularium separate from orifice; (G) ovicellate zooid, showing development of primary pores in ovicell; note a frontal avicularium (left) near proximal end of an adjacent zooid; (H) autozooid (right) with perforate closure plate covering orifice. All specimens bleached. Scale bars: 500 µm (A, B, E–H); 200 µm (C); 100 µm (D).

Spines. Lacking.

Avicularia. Oral avicularia may be absent, single, or paired on a given zooid (Figure 15A, B); these lie lateral or proximolateral to orifice, the chamber usually abutting orificial rim; rostrum raised distally at an angle to colony surface, pointing distolaterally or laterally; mandible equilateral or a little longer than broad, acute, without a setose tip. In addition, zooids in some colonies have frontal avicularia similar in form to the oral avicularia, but with a highly raised chamber and a larger rostrum and mandible (Figures 15E, F, 16A–C). The larger type of avicularium can lie close to the orifice, in place of but a little more proximally than an oral avicularium; lie just proximal to an oral avicularium; or occur anywhere along the lateral margin or frontal surface. When near orifice, the large avicularia point distolaterally; in other locations, they generally point laterally (Figure 15F). We have seen zooids with up to four avicularia in all, such as one oral avicularium and three larger avicularia. The large frontal avicularia seem to occur only in zones of a colony producing ovicells, and even then only under growth conditions where the zooids have thickened, highly reticulate frontal walls; many specimens lack these avicularia.

Ovicell (Figures 15B, E–G, 16A, C, D). Raised, conspicuous, resting on the frontal wall of the succeeding zooid; globose, 0.28–0.40 mm long (average=0.341 mm, $n=15$, 3) by 0.28–0.40 mm wide (average=0.344 mm, $n=15$, 3); with scattered small pores over the entire surface and heavy ribs converging from margin toward midline (Figure 15B); with increased secondary calcification, surface can become coarsely rugose (Figures 15E, F, 16A, C, D). Ovicellate zooids can occur sparsely scattered among non-fertile zooids over most of the colony, except in the marginal growth zone, or they can occupy a distinct reproductive band within the colony.

Ancestrula. Not observed.

Remarks

At the East Tongass Narrows Site, aggregations of large, bright-red colonies of *S. japonica* covered square metres of exposed benchrock faces and occupied large portions of the undersides of boulders. Powell (1970) similarly reported collecting “massive colonies” of this species (which he reported as *S. unicornis*) intertidally in the Strait of Georgia, British Columbia and on San Juan Island, Washington.

Many of the records of *Schizoporella unicornis* (Johnston, 1844) along the Pacific coast of North America are likely referable to *S. japonica*. *Schizoporella unicornis* was not reported in early surveys (Robertson 1900, 1908; O’Donoghue and O’Donoghue 1923, 1925, 1926). Osburn (1952) was the first to report it, noting that it was common in bays where oysters from the Atlantic coast had been introduced and thus might have been introduced with the oysters. Later, Powell (1970) found what he identified as *S. unicornis* to be abundant intertidally in the Strait of Georgia, British Columbia, but argued instead that it had been introduced there from Japan in the early to mid-1930s along with the Pacific oyster, *Crassostrea gigas* (Thunberg), rather than from the Atlantic. Ross and McCain (1976) similarly surmised that *S. unicornis* had been present in Washington State as early as 1927 and was abundant in southern Puget Sound by 1943, also likely introduced with the Pacific oyster. However, the two hypotheses concerning the source of nominal *S. unicornis* in the north-eastern Pacific are not mutually exclusive; specimens referred to this species could

comprise more than one species or source population, introduced with oysters from both the Atlantic and Japan at different times.

Recognizing taxonomic problems with *S. unicornis* (Johnston) in the eastern Pacific, Soule et al. (1995, Plate 75) presented SEM illustrations of the Recent lectotype from Britain. Though zooids of the lectotype have a narrower, shallower proximal orificial sinus and smaller condyles than those from Ketchikan, few other characters distinguishing the two are evident in most specimens. However, descriptions of *S. unicornis* from Europe indicate a smaller orifice (0.09–0.12 mm long by 0.10–0.11 mm wide; Hayward and McKinney 2002) than in our material, and the ovicell is imperforate in the centre (Hayward and Ryland 1999; Hayward and McKinney 2002). We have seen no report of *S. unicornis* indicating larger frontal avicularia in addition to the oral avicularia.

As supporting evidence that populations of nominal *S. unicornis* in the north-eastern Pacific originated from Japan, both Powell (1970) in British Columbia and Ross and McCain (1976) in Washington State noted the occurrence of zooids with multiple ovicells, which Powell (1970) also observed in a specimen from Onegawa Bay, north-eastern Honshu, Japan. An obvious question, however, is whether any of these populations is conspecific with *S. unicornis* (Johnston) originally described from Europe. The broad, deep orificial sinus and entirely perforated ovicells of the Ketchikan specimens suggested that they, and thus their putative Japanese source population, might be a different species.

Ortmann (1890) was the first to report nominal *S. unicornis* from Japan. In addition to providing a general description of *S. unicornis*, he erected a new variety, *S. unicornis* var. *japonica*, with the following characters (our translation): “Almost the entire lower lip is taken up by the flat, indistinctly separated sinus. Surface densely checkered-punctured. Avicularium only on one side of the oral opening, often entirely missing.” We have fortuitously been able to examine Ortmann’s (1890) type specimen of *S. unicornis* var. *japonica*, collected by Dr Döderlein, 1882, at Yenoura, Sagami Bay, Honshu Island, Japan, depth unknown (Figure 16A–D). Two of the characters he mentioned—the broad sinus (Figure 16B) and the densely punctured frontal wall (Figure 16C, D)—are correct. However, many zooids in the type have a large frontal avicularium on one side (Figure 16A, C), which Ortmann apparently saw as a single oral avicularium. In fact, some zooids in the type have two oral avicularia, and others have a single oral avicularium in addition to the larger frontal avicularium (Figure 16A, C). In any case, Ortmann’s specimen is virtually indistinguishable from Ketchikan material (compare Figures 15 and 16), which share the coarsely punctured, almost reticulate frontal wall; the orifice broader than long, with a broad, deep sinus flattened at the bottom; strong condyles; perforations over the entire surface of the ovicell, which becomes rugose or reticulate after secondary calcification; the occurrence of large frontal avicularia, often in addition to the oral avicularia; and the sporadic presence of kenozooids with the orifice closed by perforate calcification. This suite of characters is clearly distinct from *S. unicornis* (Johnston), and we here elevate Ortmann’s (1890) *S. unicornis* variety *japonica* to species rank as *S. japonica* Ortmann.

Neither Ortmann (1890) in his original description nor subsequent authors have noted the large frontal avicularia that occur in addition to the oral avicularia in *S. japonica*. Unless one is aware that they occur, these avicularia may simply be misinterpreted as hypertrophied oral avicularia. Illustrations by Powell (1970, Figure 2, lower left) and Ross and McCain (1976, Figures 1 and 2) seem to show avicularia of the larger type. The large frontal avicularia occur only in astogenetic zones containing ovicellate zooids, but in some colonies are lacking even in areas crowded with ovicells. It may be that the large avicularia are ecophenotypically induced, and appear only under a very particular set of

conditions. By the same token, we did not observe in Ketchikan specimens the multiple ovicells on some zooids reported by Powell (1970), McCain and Ross (1974), Ross and McCain (1976), and Kubota and Mawatari (1985).

Soule et al. (1995) identified but did not illustrate *S. unicornis* from California. Although they noted that in their specimens the sinus is wider and the condyles blunter than in the lectotype of *S. unicornis*, they hesitated to consider these species-level differences. However, the orifice they described is suggestive of *S. japonica*. Specimens figured by Liu et al. (2001, Plate 48) as *S. unicornis* from China are clearly *S. japonica*, with the characteristic deep, broad sinus flattened at the bottom. One of their figures (Plate 48, Figure 4) shows an autozooid-derived kenozooid with perforate calcification over the orifice, and the authors note in the figure legend that some oral avicularia can become frontal avicularia. However, some of the illustrations by Liu et al. (2001, Plate 48, Figures 3, 7) show a shape of suboral sinus atypical for *S. japonica*, which may indicate that the material they identified as nominal *S. unicornis* included more than one species.

Distribution

In the western Pacific, *S. japonica* (reported as *S. unicornis*) extends from China (Liu et al. 2001) northward to Akkeshi, Hokkaido Island, Japan (Mawatari and Mawatari 1981). This species was introduced from Japan to the Pacific coast of North America during the 20th century. Previous authors have reported it from British Columbia (Powell 1970) and Washington State (McCain and Ross 1974; Ross and McCain 1976). We have recently observed it on SERC settling plates from Sitka, Alaska; Puget Sound, Washington; Coos Bay, Oregon; and San Francisco, California. The actual range may be much more extensive than indicated here, since this species could have been introduced to several parts of the world. For example, Pacific oysters were transplanted from Japan to Australia in the mid-1900s, and nominal *S. unicornis* (= *S. ?japonica*) was reported in Sydney Harbour in 1975 (Ross and McCain 1976).

Family PACIFICINCOLIDAE Liu and Liu, 1999

Genus *Pacificincola* Liu and Liu, 1999

Pacificincola insculpta (Hincks, 1882)

(Figure 17A–D)

Schizoporella insculpta Hincks 1882, p 251; 1883, p 447, Plate 17, Figure 5.

Schizoporella insculpta: Robertson 1900, p 326; 1908, p 290, Plate 20, Figures 46, 47; O'Donoghue and O'Donoghue 1923, p 36; 1925, p 102; 1926, p 57.

Hippodiplosia insculpta: Osburn 1952, p 341, Plate 40, Figures 1, 2 (in part); McCain and Ross 1974, p 14.

Hippoporina insculpta: Soule et al. 1995, p 179, Plate 64.

Description

Colony. Live colonies orange; primarily unilaminar and encrusting, but capable of rising in irregular, bilaminar lobes and frills; to several centimetres in maximum dimension.

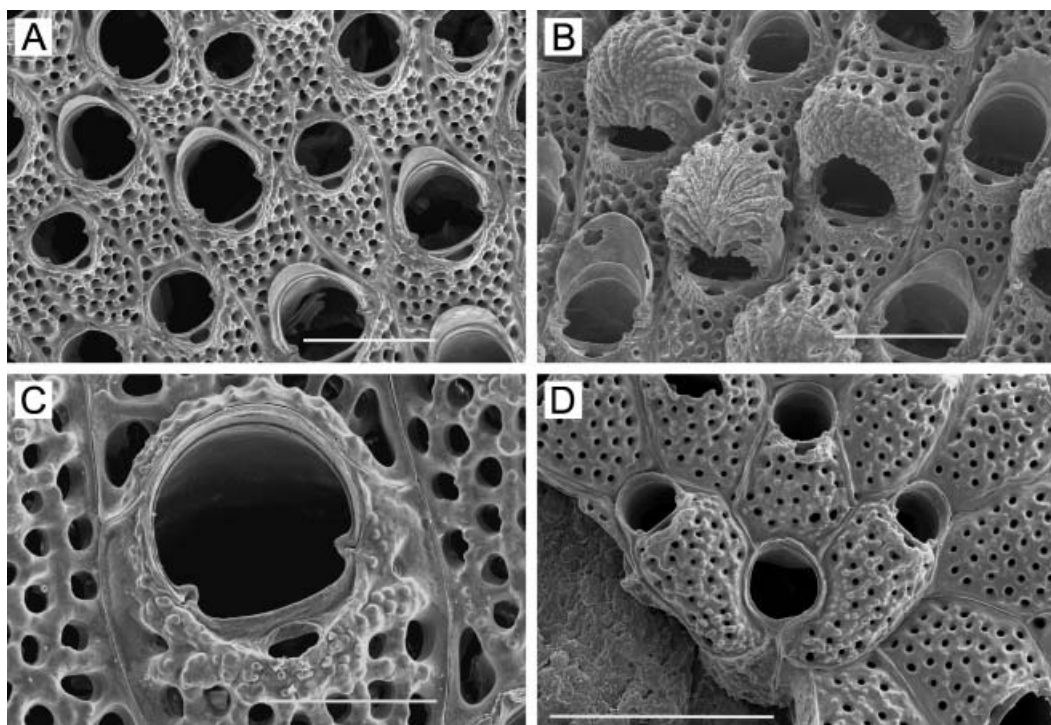


Figure 17. *Pacificicola insculpta* (Hincks): (A) group of zooids showing two orifice sizes; zooids with large orifice are capable of forming ovicells; (B) ovicellate zooids; (C) enlargement of orifice of non-ovicellate zooid, showing suboral umbo and aperture of suboral heterozooid; (D) ancestrula and periancestrular zooids. All specimens bleached. Scale bars: 500 μm (A, B, D); 200 μm (C).

Zooids. Rounded-hexagonal, barrel-shaped, or oval; widest at orifice, narrower proximally, tapering or truncate, 0.58–0.95 mm long (average=0.722 mm, $n=30$, 3) by 0.25–0.45 mm wide long (average=0.341 mm, $n=30$, 3); zooids of two types (Figure 17A), male (terminology of Nielsen 1981) with a smaller orifice, and female with a larger orifice; the latter have an ovicell or the potential to produce one. Young colonies can be composed entirely of non-fertile zooids; as the colony becomes reproductive, it produces a marginal zone of non-fertile interspersed with fertile zooids, the latter producing ovicells.

Frontal wall. Slightly convex; vitreous, texture smooth or finely tuberculate; uniformly perforated with large pores except just proximal to orifice, where there is a raised crescentic arch with a distal cavity covered by ectocyst.

Orifice (Figure 17C). With a semicircular anter separated from a broad poster by prominent, sharp, shelf-like condyles; longer than broad and larger in female zooids, 0.20–0.38 mm long (average=0.275 mm, $n=15$, 3) by 0.23–0.25 mm wide (average=0.241 mm, $n=15$, 3); broader than long and smaller in male zooids, 0.16–0.20 mm long (average=0.183 mm, $n=15$, 3) by 0.18–0.23 mm wide (average=0.200 mm, $n=15$, 3); surrounded by a raised rim; peristome negligible.

Spines and avicularia. Lacking.

Ovicell (Figure 17B). Raised, globose, conspicuous, overlying the frontal wall of next distal zooid; texture finely tuberculate; imperforate, with coarse ridges converging from margin to proximal midline; 0.30–0.50 mm long (average=0.390 mm, $n=15$, 3) by 0.29–0.50 mm wide (average=0.390 mm, $n=15$, 3).

Ancestrula. One observed (Figure 17D), 0.35 mm long by 0.28 mm wide; orifice subcircular; budding a triplet of daughter zooids, one distally and two laterally, with the latter orientated distolaterally but curving proximally around the ancestrula, nearly meeting in the proximal midline.

Remarks

We observed *P. insculpta* only at East Tongass Narrows, where it was commonly attached to algae such as *Rhodomela larix* in crevices. Nielsen (1981) described the morphology and reproduction of this species in detail, but expressed doubts about its placement (Winston 1979; Soule et al. 1995) in the genus *Hippoporina*. Liu and Liu (1999) erected a new family (Pacifincolidae) and genus (*Pacifincicola*) for a group of three Pacific species, including *P. perforata* (Okada and Mawatari, 1937) as the type species of the genus, *P. insculpta* (Hincks, 1882), and *P. mexicana* (Soule et al., 1995). Characters given by Liu and Liu (1999) as defining the family and genus include a bell-shaped orifice; evenly perforate frontal walls; imperforate hyperstomial ovicells with radial ribs; and a subcircular “ascus” present within a suboral umbo. By “ascus”, these authors meant “ascopore”, yet neither does this term correctly reflect the nature of the subcircular opening on the distal face of the suboral umbo. Nielsen (1981) showed this opening in *P. insculpta* to be the aperture of a small heterozoid containing a reduced polypide and connecting to the autozoid by a pair of pore plates; the function of this heterozoid is unknown.

Distribution

Robertson (1908) gave the range of this species as Sitka, Alaska to the Coronados Islands, southern California; however, Osburn (1952) reported it from as far south as Costa Rica, noting that in the southern part of its range zooids were smaller and neater in appearance. Soule et al. (1995) recognized *P. insculpta* as a more northerly species extending from Sitka to southern California, and described a new species, *P. mexicana*, corresponding to Osburn’s southern form, extending from southern California to Costa Rica.

Family CRYPTOSULIDAE Vigneaux, 1949

Genus *Cryptosula* Canu and Bassler, 1925

Cryptosula zavjalovensis Kubanin, 1976

(Figure 18A, B)

Cryptosula zavjalovensis Kubanin 1976, p 33, Figure 1G, H.

Cryptosula zavjalovensis: Grischenko 2004, p 40.

Lepralia reticulata Okada 1929, p 24, Plate 5, Figures 4, 5; not *Lepralia reticulata* MacGillivray, 1842.

Lepralia reticulata: Androsova 1958, p 129, Figure 46.

Lepralia pallasiana: O'Donoghue 1925, p 19, Plate 2, Figure 6.

Cryptosula pallasiana: Dick and Ross 1986, p 89.

Cryptosula okadai Dick and Ross 1988, p 53, Plate 5F.

Cryptosula okadai: Grischenko 1997, p 176.

Description

Colony. Unilaminar, encrusting, sheet-like, brownish orange in colour at Ketchikan; with a sharp, pungent odour when alive or newly dried.

Zooids. Rectangular, barrel-shaped, or roughly hexagonal; distinct, outlined by a shallow groove and a suture line formed by adjacent vertical walls. Two sizes occur in different

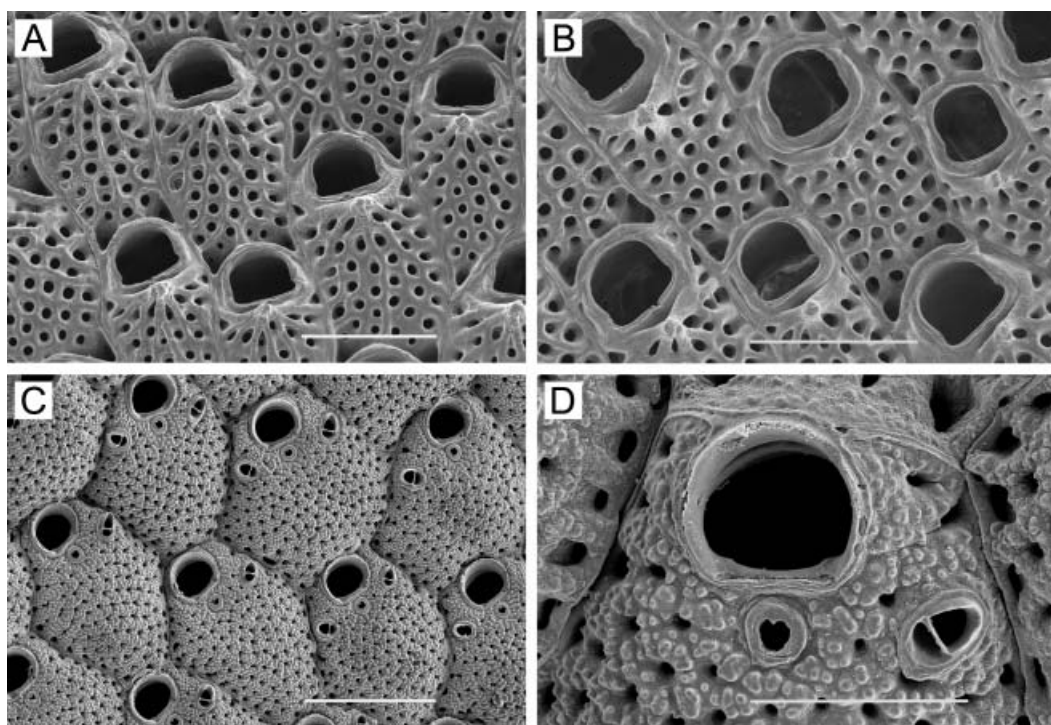


Figure 18. (A, B) *Cryptosula zavjalovensis* Kubanin: (A) group of autozooids with broad-type orifice; (B) group of autozooids, with broader and narrower orifices. (C, D) *Microporella setiformis* O'Donoghue and O'Donoghue: (C) group of autozooids; (D) enlargement of orifice, ascopore, and marginal avicularium. All specimens bleached. Scale bars: 500 μ m (A–C); 200 μ m (D).

astogenetic zones, longer zooids 0.70–1.13 mm long (average=0.833 mm, $n=10$, 1) by 0.30–0.58 mm wide (average=0.404 mm, $n=10$, 1) with a broad orifice (Figure 18A), and shorter zooids 0.58–0.68 mm long (average=0.628 mm, $n=10$, 1) by 0.30–0.45 mm wide (average=0.400 mm, $n=10$, 1) with a narrow orifice (Figure 18B).

Frontal wall. Slightly to quite convex, perforated with large circular pores evenly spaced over the entire surface, but not extending distally around orifice; rising to a slight to tall, blunt, conical umbo proximal to orifice. Frontal wall thickens with age, the pores becoming infundibular and the surface between them granular.

Orifice. Hat-shaped in outline, with a large, semicircular anter constricted from a short, broad poster by long, low condyles; two sizes, the broader type 0.18–0.20 mm long (average=0.184 mm, $n=10$, 1) by 0.20–0.23 mm wide (average=0.215 mm, $n=10$, 1), the narrower type 0.16–0.19 mm long (average=0.178 mm, $n=10$, 1) by 0.16–0.20 mm wide (average=0.181 mm, $n=10$, 1).

Spines and avicularia. Lacking.

Ovicells. Lacking; embryos brooded internally.

Ancestrula. Tatiform, without spines (Dick and Ross 1988), but not observed at Ketchikan.

Remarks

This species was recorded only at Higgins Point, where we found one damaged colony 2 cm across on a boulder. In the Ketchikan specimen, two astogenetic zones are evident: a central area of larger zooids and a marginal area of smaller zooids. Three types of astogenetic zone have been reported for this species. Both Okada (1929) and Dick and Ross (1988) noted in some colonies a marginal zone of autozooids lacking an orifice. Kubanin (1976) noted zones of larger and smaller zooids, but the differences in zooid and orifice size were less pronounced than in the Ketchikan specimen.

Cryptosula zavjalovensis differs from its similar but more southern congener *C. pallasiana* (Moll, 1803) in having a straight rather than a curved proximal margin of the orifice; in lacking pores around the distal curvature of the orifice; and in having zones of marginal zooids without orifices, though such zooids are by no means evident in all colonies of *C. zavjalovensis* and occasionally occur in *C. pallasiana*. In addition, zooids of *C. pallasiana* occasionally have a small, median suboral avicularium (Osburn, 1952), which has not been observed in *C. zavjalovensis*. Finally, a diagnostic character of *C. zavjalovensis* is the intense, pungent odour it exudes. We have noted this odour in live material from Ketchikan, Kodiak, and Dutch Harbour in Alaska; the Commander Islands; and Akkeshi, Hokkaido, Japan. The odour is retained for some time in dried specimens, but gradually fades. No similar odour has been reported for *C. pallasiana*; however, neither had it been reported for *C. zavjalovensis* until noted by Dick and Ross (1988).

Okada (1929) first described this species as *Lepralia reticulata*, which proved to be a junior synonym of *Lepralia reticulata* MacGillivray, 1842. Dick and Ross (1988) renamed the species *Cryptosula okadai*, unaware that Kubanin (1976) had described the same species as *C. zavjalovensis*. Kubanin's name takes priority over *C. okadai* in replacing *L. reticulata* Okada.

Distribution

Extending from the mid-intertidal zone to a depth of at least 40 m (Androsova 1958), *C. zavjalovensis* is one of the most common and widespread bryozoans found intertidally around the north Pacific rim. On the North American side, records exist from Ketchikan (present study), northern Gulf of Alaska, Kodiak Island, eastern Aleutian Islands, and Bering Sea (O'Donoghue 1925; Dick and Ross 1988). On the Asian side, there are records from the Gulf of Anadyr, Commander Islands, Kamchatka, Sea of Okhotsk, and northern mainland of the Sea of Japan (Grischenko 1997, 2004; Kubanin 1997); in Japan, it is patchily abundant at Akkeshi, Hokkaido (our observations) and occurs at Mutsu Bay, northern Honshu (Okada 1929).

Family MICROPORELLIDAE Hincks, 1879**Genus *Microporella*** Hincks, 1877***Microporella setiformis*** O'Donoghue and O'Donoghue, 1923

(Figure 18C, D)

Microporella setiformis O'Donoghue and O'Donoghue 1923, p 32, Plate 3, Figure 21; 1926, p 65, Plate 5, Figure 44.

Microporella setiformis: Osburn 1952, p 385, Plate 44, Figure 8; Soule et al. 1995, p 150, Plate 53.

Description

Colony. Unilaminar, encrusting; white, covered with shiny ectocyst.

Zooids. Irregularly hexagonal, distinct, separated by a deep groove; variable in size and shape, markedly elongate or nearly as wide as long; 0.55–0.80 mm long (average=0.666 mm, $n=11$, 1) by 0.40–0.58 mm wide (average=0.492 mm, $n=11$, 1).

Frontal wall. Convex, rising sharply around margin, flatter on top, even, without umbo, finely granulated; with 10–14 areolar pores along each lateral margin and smaller, slightly infundibular pores over entire surface.

Orifice. As wide as or slightly wider than long, 0.10–0.13 mm long (average=0.122 mm, $n=11$, 1) by 0.13–0.15 mm wide (average=0.138 mm, $n=11$, 1); sides recurve slightly toward proximal margin, which is shallowly concave between small, shelf-like condyles; peristome a low, smooth, rim around curvature of orifice, with a straight hinge shelf along proximal margin.

Ascopore. More-or-less circular, often with a small denticle projecting from the distal margin; surrounded by a flat, smooth collar abutting proximal rim of orifice.

Spines. No spines or spine scars evident in our specimens.

Avicularia. Small, oval; near zooidal margin lateral to ascopore on one or both sides, pointing distolaterally, with a setose mandible roughly three times as long as rostrum.

Ovicell. Not observed.

Ancestrula. Not observed.

Remarks

Microporella setiformis was rare at Ketchikan; we collected two colonies at Higgins Point. Although we observed no spines or spine scars, both Osburn (1952) and O'Donoghue and O'Donoghue (1926) reported this species to have five evanescent oral spines on marginal zooids.

Distribution

Microporella setiformis is a boreal species endemic to the north-eastern Pacific. Osburn (1952) summarized records from numerous localities in British Columbia, Puget Sound, and as far southward as the Channel Islands in Southern California. Ketchikan is the northernmost extent of the known range.

***Microporella neocribroides* Dick and Ross, 1988**

(Figure 19A–D)

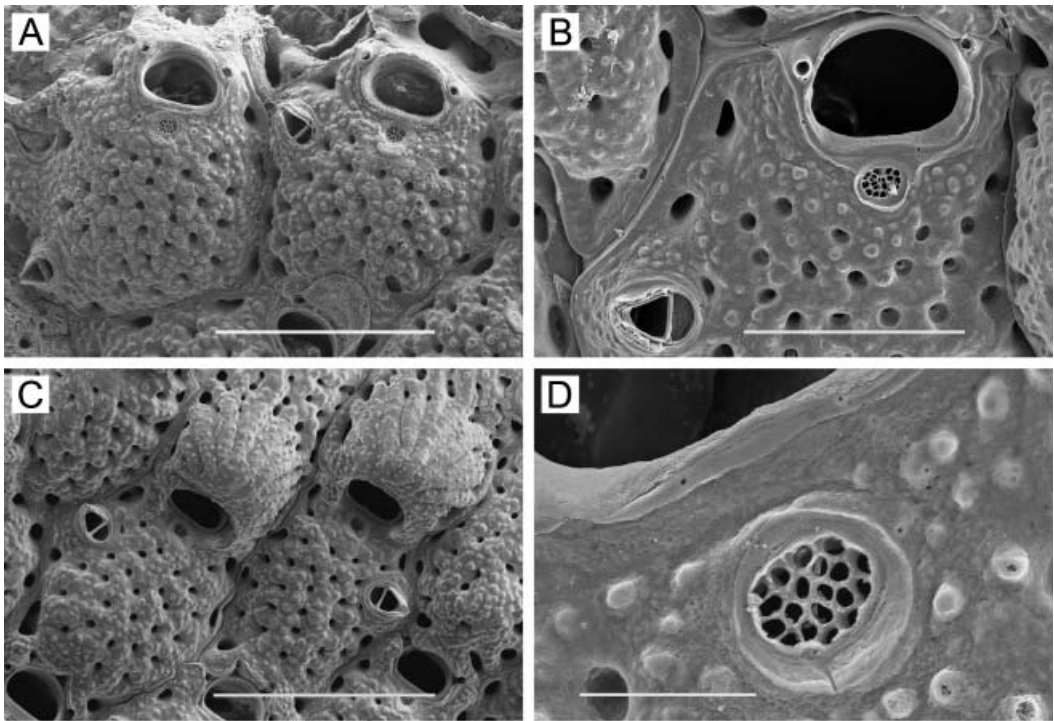


Figure 19. (A–D) *Microporella neocribroides* Dick and Ross: (A) two marginal autozooids; note unusual proximal position of marginal avicularium of zooid at left; (B) enlargement of orifice, ascopore, and marginal avicularium; (C) two ovicellate zooids, each showing a marginal avicularium in typical position; (D) enlargement of ascopore. All specimens bleached. Scale bars: 400 μm (A); 200 μm (B); 500 μm (C); 50 μm (D).

Microporella neocribroides Dick and Ross 1988, p 76, Plate 12C.

Microporella neocribroides: Suwa and Mawatari 1998, p 899, Figure 2.

Microporella ciliata: Dick and Ross 1986, p 89 (in part).

Description

Colony. Unilaminar, encrusting, white with glistening ectocyst, forming circular or irregular patches; largest collected 2 cm across.

Zooids. Vitreous when young, chalky with age; hexagonal to barrel-shaped; varying from elongate to nearly as wide as long; 0.43–0.63 mm long (average=0.553 mm, $n=20, 3$) by 0.28–0.45 mm wide (average=0.361 mm, $n=20, 3$).

Frontal wall. Inflated, quite convex; with 6–10 areolar pores along each lateral margin and perforated over entire surface with smaller pores; surface coarsely granulate between pores; becoming thick and rugose with age, sometimes with a conical umbo proximal to ascopore.

Orifice (Figure 19B). Distinctly broader than long, 0.08–0.11 mm long (average=0.089 mm, $n=20, 3$) by 0.11–0.15 mm wide (average=0.124 mm, $n=20, 3$); proximal margin straight and smooth; proximal corners rounded; condyles slight or lacking.

Ascopore (Figure 19B, D). Transversely elliptical; covered with a cribriform sieve plate; separated from orificial margin by distance approximately equal to or less than ascopore width.

Avicularia (Figure 19A–C). Zooids either lack an avicularium, or have a single one on one side (frequencies: 0=62%, 1=38%), situated anywhere along lateral margin, at or proximal to level of ascopore, with mandible pointing toward margin.

Spines (Figure 19A, B). Marginal zooids usually either lack spines or have a pair of short, weak spines widely separated at distolateral margins of orifice (frequencies: 0=13%, 2=87%; $n=111, 3$); rarely a zooid can have three to four spines.

Ovicell (Figure 19C). Raised, globose, 0.20–0.38 mm long (average=0.291 mm; $n=20, 3$) by 0.28–0.33 mm wide (average=0.301, $n=20, 3$); imperforate except for minute marginal pores; surface granulate like frontal wall; marginal ribbing variable, ranging from absent to moderately developed and converging near proximal margin.

Ancestrula. Not observed.

Discussion

We found this species at all three collecting sites at Ketchikan, but it was most common at Higgins Point, a relatively exposed shore of cobbles and boulders. A similar preference for exposed sites was noted at Kodiak (Dick and Ross 1988). The Ketchikan material is similar in all respects to that originally described at Kodiak (Dick and Ross 1988). Key characters are the cribriform ascopore placed close to the orificial margin; zooids

with no more than one avicularium, which on at least some zooids is located near the middle of the lateral margin; marginal zooids usually with no or two orificial spines; and the orifice with proximal corners rounded, a smooth proximal margin, and condyles weak or lacking. The species has been reported from Hokkaido, Japan (Suwa and Mawatari 1998); there, avicularia tend to be closer to the orifice than is typical for specimens from the eastern Pacific and are also occasionally paired, but other characters indicate *M. neocribroides*.

Distribution

The species has an amphi-Pacific, northern boreal distribution. Other records include Katalla and Kodiak, Alaska (Dick and Ross 1988) and Muroran, Hokkaido, Japan (Suwa and Mawatari 1998). Ketchikan is the southernmost extent of the known range in the north-eastern Pacific.

***Microporella ketchikanensis*, new species**

(Figure 20A–F)

Diagnosis

Frontal wall uniform, non-rugose, with unusually small pores widely and uniformly spaced; zooids with zero to two avicularia, but most (83%) with only one; avicularium situated along lateral margin proximal to level of ascopore, as far back as middle of zooid, mandible directed laterally; rays in ascopore thick, with openings V-shaped or elongate; two to four (mode=4) distal spines on marginal zooids; a small umbo proximal to ascopore and often a heavy, conical umbo on ovicell; ovicell imperforate centrally, with marginal ribbing slight or absent.

Type material

Holotype: ETN, specimen KE-28 bleached and coated for SEM (YPM 35843). Paratype 1: HP, specimen KE-15 bleached and coated for SEM (YPM 35844). Paratype 2: HP, specimen KE-101, bleached and coated for SEM (NHM 2005.7.11.8).

Etymology

The species name derives from the town of Ketchikan, place name of the type locality.

Description

Colony. Unilaminar, forming tightly encrusting, circular or irregular patches on rocks; off-white in colour; covered with glistening ectocyst when alive; largest observed 1 cm across.

Zooids. Roughly hexagonal, barrel-shaped, or oval; distinct at all stages, separated by a groove; 0.40–0.70 mm long (average=0.523 mm, $n=20$, 4) by 0.23–0.45 mm wide (average=0.340, $n=30$, 4). Zooids interconnect by an elongate pore chamber occupying

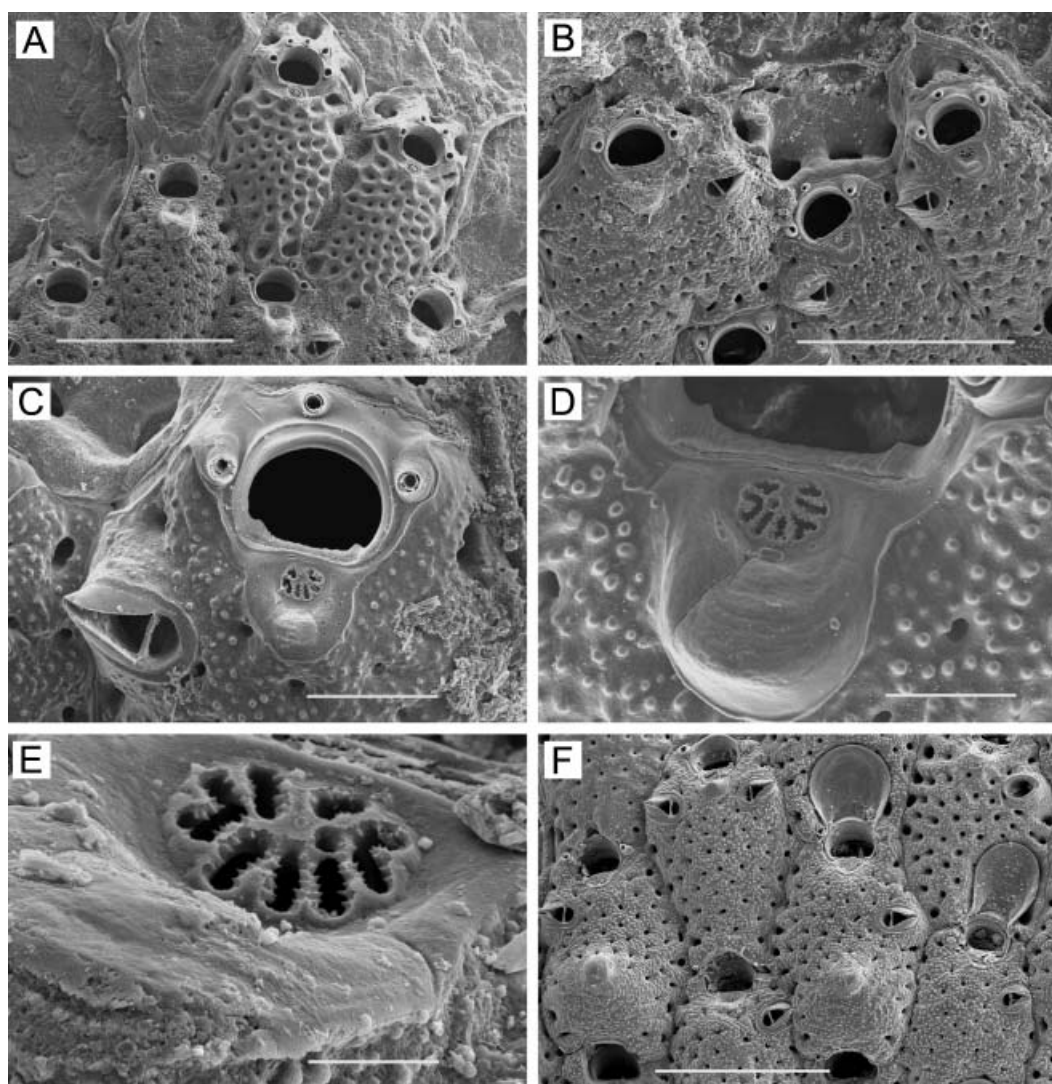


Figure 20. *Microporella ketchikanensis* n. sp.: (A) group of marginal zooids with four to five distal spines per zooid; (B) group of marginal zooids with three distal spines per zooid; (C) enlargement of orifice, ascopore, and marginal avicularium; (D) enlargement of proximal orificial margin and ascopore; (E) enlargement of ascopore; (F) group of zooids, two forming ovicells and two with complete, unribbed, umbonate ovicells; note zooid with rare complement of two marginal avicularia. All specimens bleached. Scale bars: 500 µm (A, B, F); 100 µm (C); 50 µm (D); 20 µm (E).

a third to half the length of each distolateral wall and two to three pore chambers in basal half of distal wall.

Frontal wall. Markedly convex, inflated, margins rising steeply; five to eight circular areolae along each lateral margin; frontal wall with tiny, evenly and widely spaced pores over the entirety; pores do not become infundibular with frontal thickening; surface between pores finely granulate. Immediately proximal to ascopore, most zooids have a low, knob-like umbo that is often covered by the smooth calcification surrounding the ascopore.

Orifice (Figure 20C). Semicircular, broader than long, 0.08–0.10 mm long (average=0.086, $n=15$, 3) by 0.09–0.12 mm wide (average=0.110 mm, $n=15$, 3); proximal margin straight, serrated, each corner with a conspicuous condyle that is shelf-like or triangular in outline.

Ascopore (Figure 20C–E). Sometimes circular, usually transversely elliptical; distance from proximal margin of orifice less than or equal to ascopore width; distal ascopore margin usually with vestige of a median projection, connected to remaining circumference of ascopore by thick rays covered with minute spinules, with width of rays almost as great as width of openings; openings in sieve plate elongate, V-shaped, or irregular.

Spines (Figure 20A–C). Marginal zooids have two to four (rarely five) long, erect distal spines (frequencies: two=20%, three=27%, four=53%, $n=49$, 3), two of them lateral to orifice, the other one or two centred between; spines lost with age.

Avicularia (Figure 20A–C, F). Zooids have zero to two avicularia (frequencies per zooid: zero=16.7%, one=82.8%, two=0.5%; $n=198$, 3), situated close to lateral zooidal margin, just proximal to level of ascopore, the mandible pointing perpendicularly to margin; rostrum raised from colony surface; mandible long-triangular, with a setose tip as long as the mandible proper.

Ovicell (Figure 20F). Globose, 0.25–0.33 mm long (average=0.285 mm, $n=13$, 3) by 0.25–0.33 mm wide (average=0.301 mm, $n=13$, 3); raised at first but becoming subimmersed in frontal calcification of succeeding zooid; marginal ribbing weakly developed or absent; surface granulate like surrounding frontal wall; imperforate except for a few minute pores around margin; often with a thick, blunt umbo on top.

Ancestrula. Not observed.

Remarks

Microporella ketchikanensis was rare at Ketchikan; we identified only three colonies among numerous *Microporella* specimens examined. This species is superficially similar to *M. neocribroides*; both have predominantly a single avicularium positioned along the lateral margin proximal to the ascopore and pointing laterally. However, there are several diagnostic differences. *M. ketchikanensis* has a high frequency (80%) of zooids with three or four spines, whereas *M. neocribroides* has predominantly two spines (87%). The orifice of *M. ketchikanensis* has sharp proximal corners with prominent condyles, and a serrated proximal margin, like that of *M. germana*; in contrast, the orifice of *M. neocribroides* has rounded corners with condyles weak or lacking, and a smooth proximal margin. The ascopore sieve plates of the two species are different. Finally, at all stages of calcification, the frontal wall of *M. ketchikanensis* remains even in appearance and finely granulate, and the pores remain small; that of *M. neocribroides* is more rugose with larger pores at all stages, but especially with advanced calcification.

Microporella ketchikanensis is also similar to *M. germana* in having a high frequency of zooids with only one avicularium (83% and 70%, respectively). However, the latter has a much higher frequency of zooids with two avicularia (28% compared to 0.5% in *M. ketchikanensis*), and the orientation of the avicularia is different. Those in *M. ketchikanensis*

tend to be orientated with the long axis nearly perpendicular to the lateral margin and are set farther proximally, in some cases as far back as the middle of the zooid. Those in *M. germana* tend to point distolaterally, and at slightly different angles if there are two of them; they are generally closer to the orifice. The rays in the ascopore are complete and much coarser in *M. ketchikanensis* than in *M. germana*, which has fine, often incomplete rays. Finally, *M. germana* has larger pores and the frontal wall becomes more rugose with age compared to *M. ketchikanensis*.

Distribution

Ketchikan is the only known locality.

Microporella germana Dick and Ross, 1988 (Figure 21A–D)

Microporella germana Dick and Ross 1988, p 74, Plate 12A, B.

Microporella ciliata: Dick and Ross 1986, p 89 (in part); ?Kluge, 1975, p 629, Figure 361.

Description

Colony. Unilaminar, forming tightly encrusting, circular or irregular colonies on rocks, shells, and serpulid tubes; off-white in colour; covered with glistening ectocyst when alive; largest observed 2.2 cm across.

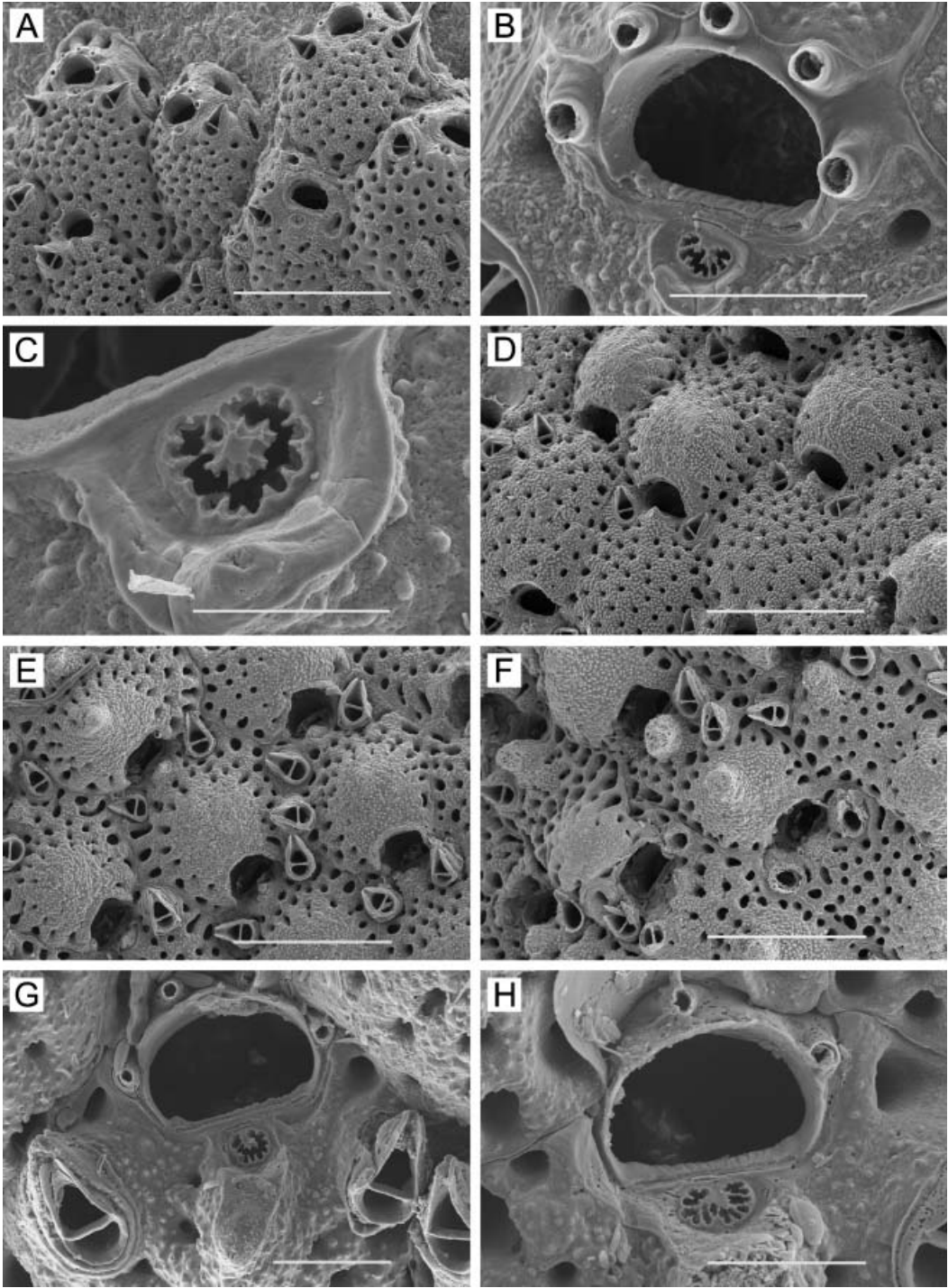
Zooids. Roughly hexagonal or oval, distinct at all stages, separated by a shallow groove; 0.43–0.73 mm long (average=0.556 mm, $n=20$, 4) by 0.25–0.43 mm wide (average=0.366 mm, $n=20$, 4).

Frontal wall. Moderately convex, granular, often with a small, blunt umbo immediately proximal to ascopore; six to eight areolar pores along each lateral margin; frontal wall uniformly perforated with smaller pores over entire surface; pore openings can become enlarged as frontal wall thickens.

Ascopore (Figure 21B, C). Small, wider than long; separated from proximal margin of orifice by a distance less than or equal to ascopore width; surrounded by a zone of smooth calcification that often extends on to distal surface of umbo; distal ascopore margin with an irregular or club-shaped median projection ending in sharp denticles; rest of margin with sharp denticles that sometimes connect with median projection by thin rays.

Orifice (Figure 21B). Semicircular, broader than long, 0.07–0.11 mm long (average=0.086 mm, $n=20$, 4) by 0.10–0.15 mm wide (average=0.119 mm, $n=20$, 4); proximal margin straight, serrated, with a blunt-triangular condylar shelf at each corner.

Spines (Figure 21A, B). Marginal zooids with four to six erect spines around distal margin of orifice (frequencies: four=43%, five=52%, six=5%; $n=42$, 3); spine scars often evident on other non-ovicellate zooids.



Avicularia (Figure 21A, D). Zero to two per zooid (frequencies: zero=2%, one=70%, two=28%; $n=83$, 3), located lateral or proximolateral to ascopore, often close to orifice, pointing distolaterally; if paired, one usually points at a slightly different angle from the other relative to long axis of zooid. Rostrum raised, mandible long-triangular, with setose tip about as long as mandible proper.

Ovicell (Figure 21D). Globose, 0.18–0.33 mm long (average=0.239 mm, $n=15$, 3) by 0.20–0.33 mm wide (average=0.265 mm, $n=15$, 3); partly immersed in frontal wall of succeeding zooid; surface granular like frontal wall and confluent with frontal wall of succeeding zooid; coarse ribs variably developed around margin, extending toward centre; scattered minute pores around periphery between ribs; central area imperforate except for occasional isolated pores.

Ancestrula. Not observed.

Remarks

Specimens at Ketchikan are very similar in zooidal measurements, morphology, and avicularium frequencies to material from Kodiak, Alaska, the type locality (Dick and Ross 1988). The only noteworthy difference is in spine frequencies: zooids in the Kodiak population have three to five spines, with the modal number four; those at Ketchikan have four to six spines, with the modal number five.

At East Tongass Narrows, we collected a colony of *Microporella* (here termed *Microporella* form A (Figure 21E–H), growing on a large serpulid worm tube, that has a few zooids in the interior of the colony with three avicularia per zooid (Figure 21E): one lateral to the ascopore and angled distolaterally; the second on the same side proximal to the first and angled distolaterally or laterally; and the third on the opposite side lateral to the ascopore, angled distolaterally. Other zooids have only two avicularia, but both on the same side (Figure 21F). In addition, some zooids have exceptionally heavy suboral umbones (Figure 21F), and the ovicells are umbonate (Figure 21E, F). This specimen is unusual, because autozooids with two frontal avicularia on the same side are quite rare in *Microporella*. In their overview of this genus, Taylor and Mawatari (2005) observed only two cases of an autozooid with this condition among all the material they examined, and one of these cases resulted from reparative growth of a damaged frontal shield.

We consider this specimen to be an aberrant, perhaps mutant form, and in any case hesitate to describe it as a distinct species without more material. In many respects, it has an admixture of characters occurring in *M. germana* and *M. ketchikanensis*, and we suggest the possibility that it might be a hybrid between the two. Observations that support this idea are as follows: (1) Zooids at the growing margin have zero to two avicularia; when two are present, they are on opposite sides in the normal fashion and are angled in slightly

Figure 21. (A–D) *Microporella germana* Dick and Ross: (A) group of marginal zooids; (B) enlargement of orifice and ascopore; (C) enlargement of ascopore; (D) group of ovicellate zooids; (E–H) *Microporella* form A, all from one colony; (E) group of ovicellate zooids; note zooid (upper right) with a marginal avicularium on one side and two on the other; (F) group of ovicellate zooids, with two zooids (top and bottom, left of centre) each having two marginal avicularia on same side; (G) enlargement of orifice, ascopore, and marginal avicularia; form of ascopore is like that of *M. germana* (compare with C); (H) enlargement of orifice and ascopore; form of ascopore is like that of *M. ketchikanensis* (compare with Figure 20D). All specimens bleached. Scale bars: 500 μ m (A, D–F); 100 μ m (B, G, H); 50 μ m (C).

different directions, as is typical for *M. germana*; however, they also tend to be situated somewhat more proximally than is typical for that species, but more typical of *M. ketchikanensis*. (2) The colony has a mixture of ascopore types, some like *M. germana* (Figure 21G), some like *M. ketchikanensis* (Figure 21H), and some of intermediate form. (3) Zooids have four (80%) or five (20%) distal spines, frequencies more similar to *M. germana* (95% of zooids have four or five spines) than to *M. ketchikanensis* (80% of zooids have three or four spines). However, modal spine number is four (mode in *M. ketchikanensis*) rather than five (mode in *M. germana*). (4) A prominent umbo proximal to the ascopore and on the ovicell are more characteristic of *M. ketchikanensis* than of *M. germana*. (5) The occurrence of two avicularia on the same side may be viewed as a superposition of developmental information of *M. germana* and *M. ketchikanensis* involved in producing avicularia. Roughly 98% of zooids of *M. germana* produce one or two avicularia; 83% of zooids of *M. ketchikanensis* produce one avicularium. Combination of a developmental signal to produce an avicularium on each side lateral to the ascopore (*M. germana*) with that to produce a single avicularium farther proximally on one side (*M. ketchikanensis*) would give the observed pattern of two avicularia on one side and one on the other. Similarly, combination of a developmental signal to produce a single avicularium on one side (*M. germana*) with that to produce a single avicularium farther back on the same side (*M. ketchikanensis*) would give the observed pattern of two avicularia on the same side. This type of superposition should also produce zooids with four avicularia (two on each side); however, as only 0.5% of zooids of *M. ketchikanensis* have two avicularia, this would be a rare event.

Distribution

The known range of *M. germana* extends from Ketchikan (present study) around the Gulf of Alaska and Alaska Peninsula to Dutch Harbour, Alaska (Dick and Ross 1988).

Genus *Fenestrulina* Jullien, 1888

***Fenestrulina delicia* Winston, Hayward, and Craig, 2000**

(Figure 22A–D)

Fenestrulina delicia Winston, Hayward, and Craig 2000, p 417, Figures 13–15.

Description

Colony. Unilaminar, encrusting, forming small, whitish, circular patches; material examined comprised ovicellate colonies <0.5 cm in diameter.

Zooids. Rounded-hexagonal to oval, often irregular, varying considerably in size and shape, 0.53–0.78 mm long (average=0.619 mm, $n=15$, 3) by 0.28–0.45 mm wide (average=0.348 mm, $n=15$, 3); with smooth lateral walls sloping inward, leaving a deep fissure between some zooids, the margin of the lateral gymnocyst forming a sharp border with frontal wall, sometimes encroaching onto it.

Frontal wall. Smooth, slightly inflated, highest at or slightly proximal to ascopore, with large stellate pores in two to three rows between ascopore and orifice, one or two rows along lateral margins, and one row along proximal margin; asymmetrical zooids may have

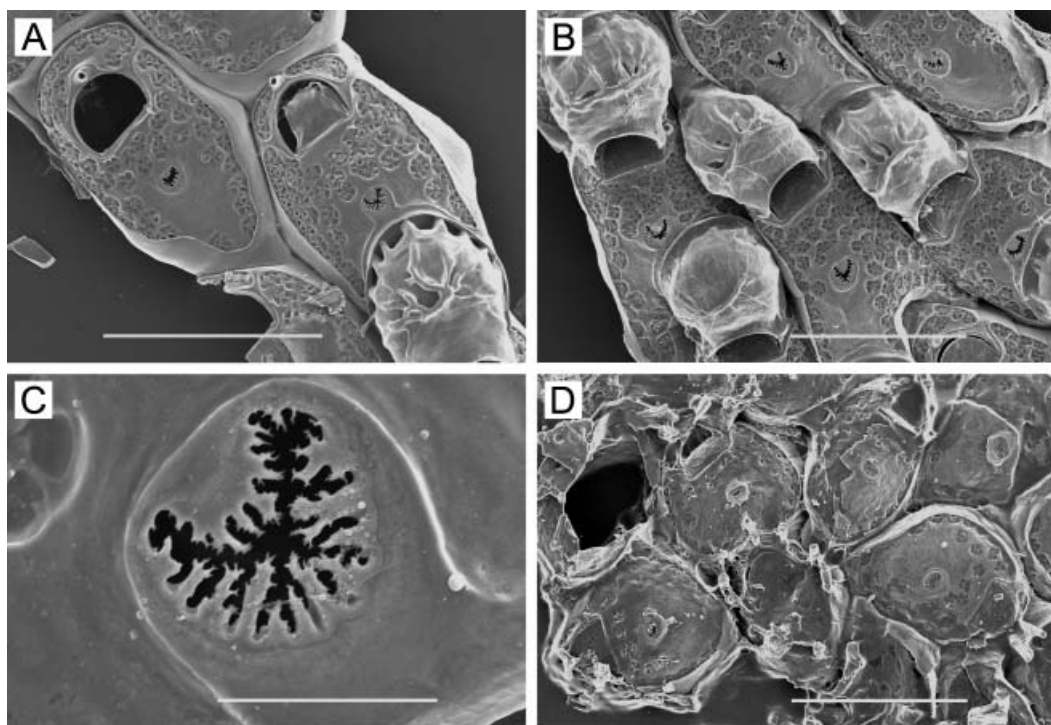


Figure 22. *Fenestulina delicia* Winston, Hayward, and Craig; subtidal specimens from Sitka, Alaska: (A) two complete autozooids and part of an ovicell; lightly bleached for cleaning; (B) group of ovicellate zooids; lightly bleached for cleaning; (C) enlargement of ascopore from zooid at right in Figure 22A above; (D) tatiform ancestrula and periancestrular zooids; unbleached. Scale bars: 500 μ m (A, B, D); 50 μ m (C).

up to four rows along one of the lateral margins; frontal wall imperforate in the area between ascopore and proximal zooidal margin.

Orifice (Figure 22A). Semicircular, usually wider than long, 0.10–0.13 mm long (average = 0.116 mm, $n=15$, 4) by 0.11–0.16 mm wide (average = 0.138 mm, $n=15$, 4); proximal margin straight and smooth, with a minute triangular condyle present near corner on each side; orifice subterminal, with a row of stellate pores distal to orifice, visible in a single transverse panel or a pair of panels sharply delineated by a border of smooth calcification.

Ascopore (Figure 22C). Separated from orifice by 2.5–3.5 ascopore widths; surrounded by a slightly raised border; irregular in size and shape, blunt V-shaped to U-shaped, 0.05–0.08 mm wide; both proximally directed tabula and proximal margin deeply serrated, with irregularly branched processes terminating in tiny points; fractal in appearance.

Spines. Non-ovicellate zooids with one to four orificial spines, but most frequently with a single spine scar evident in midline (Figure 22A); ovicellate zooids with a short spine on each side lateral to orifice, outside proximolateral margins of ovicell (Figure 22B).

Ovicell (Figure 22A, B). Raised, hemispherical, conspicuous; narrower than zooid width, usually longer than broad, 0.28–0.35 mm long (average = 0.316 mm; $n=15$, 3) by

0.23–0.30 mm wide (average=0.264 mm, $n=15$, 3); with a raised border and large pores around margin; distal three-fifths coarsely rugose with thick ribs running between marginal pores to top, where they merge with an irregular transverse fold; sometimes with two to three slit-like pores on top between ribs; proximal to transverse fold, ovicell is narrower and smooth, extending part-way along each side of orifice. Older ovicells can become entirely rugose, with a smooth, raised lip along the proximal margin. Operculum fits to opening of secondary orifice formed by ovicell margin, and can cover either primary or secondary orifice.

Avicularia. Lacking.

Ancestrula (Figure 22D). Tatiform, with 10 spines around opesia margin, surrounded by six periancestrular zooids (one distal, two distolateral, two proximolateral, one proximal).

Remarks

Although we did not find this species intertidally at Ketchikan, it occurred on SERC settling plates at Sitka, Alaska; we include it here to eliminate potential confusion with the two species of *Fenestruloides* that occurred intertidally at Ketchikan. *Fenestrulina delicia* was first recognized (Craig 1994) and described (Winston et al. 2000) only recently from the Gulf of Maine. Our specimens agree in virtually all characters with Atlantic *F. delicia*, e.g. the ovicell strongly ribbed distally and smooth proximally; a pair of spines flanking the proximolateral corners of the ovicell; some zooids with only a single median distal spine; the smooth, sloping vertical walls forming a sharp border with the frontal surface; bordered panels distal to the orifice; and a tatiform ancestrula.

Fenestrulina delicia is very similar to *F. sinica* Liu, Yin, and Ma, 2001. Indeed, we would consider them synonymous, except that the ancestrula of *F. sinica* was described as resembling later autozooids, whereas that of *F. delicia* is tatiform. *Fenestrulina delicia* also resembles *F. farnsworthi* Soule, Soule, and Chaney, 1995, which has a tatiform ancestrula (12 spines) and zooids with a sharp border between the smooth vertical walls and frontal wall. However, *F. farnsworthi* has much smaller zooids, only one or two rows of pores between ascopore and orifice, a mostly imperforate frontal wall, and five to seven long distal spines.

The recent, nearly contemporaneous discovery of *F. delicia* in boreal waters of the western Atlantic and eastern Pacific suggests it might be a species introduced to one or both of these regions within the past few decades. Alternatively, occurrence of a similar species (*F. sinica*) in China and a morphologically similar population of uncertain identity that we have found at Akkeshi, Japan might indicate that *F. delicia* and *F. sinica* belong to a species complex in the northern Hemisphere that has previously gone undetected due to misidentification as *Fenestrulina malusii* (Audouin 1826), a species until recently regarded as cosmopolitan (see discussion in Soule et al. 1995, p 156).

Distribution

Fenestrulina delicia is a boreal species known from Maine in the north-western Atlantic, and from the northern Gulf of Alaska to San Francisco, California in the Pacific. We have

identified specimens on SERC settling plates from Valdez and Sitka, Alaska; Coos Bay, Oregon; and San Francisco.

Genus *Fenestruloides* Soule, Soule, and Chaney, 1995
Fenestruloides blaggae Soule, Soule, and Chaney, 1995
 (Figure 23A–F)

Fenestruloides blaggae Soule, Soule, and Chaney 1995, p 169, Plate 60.

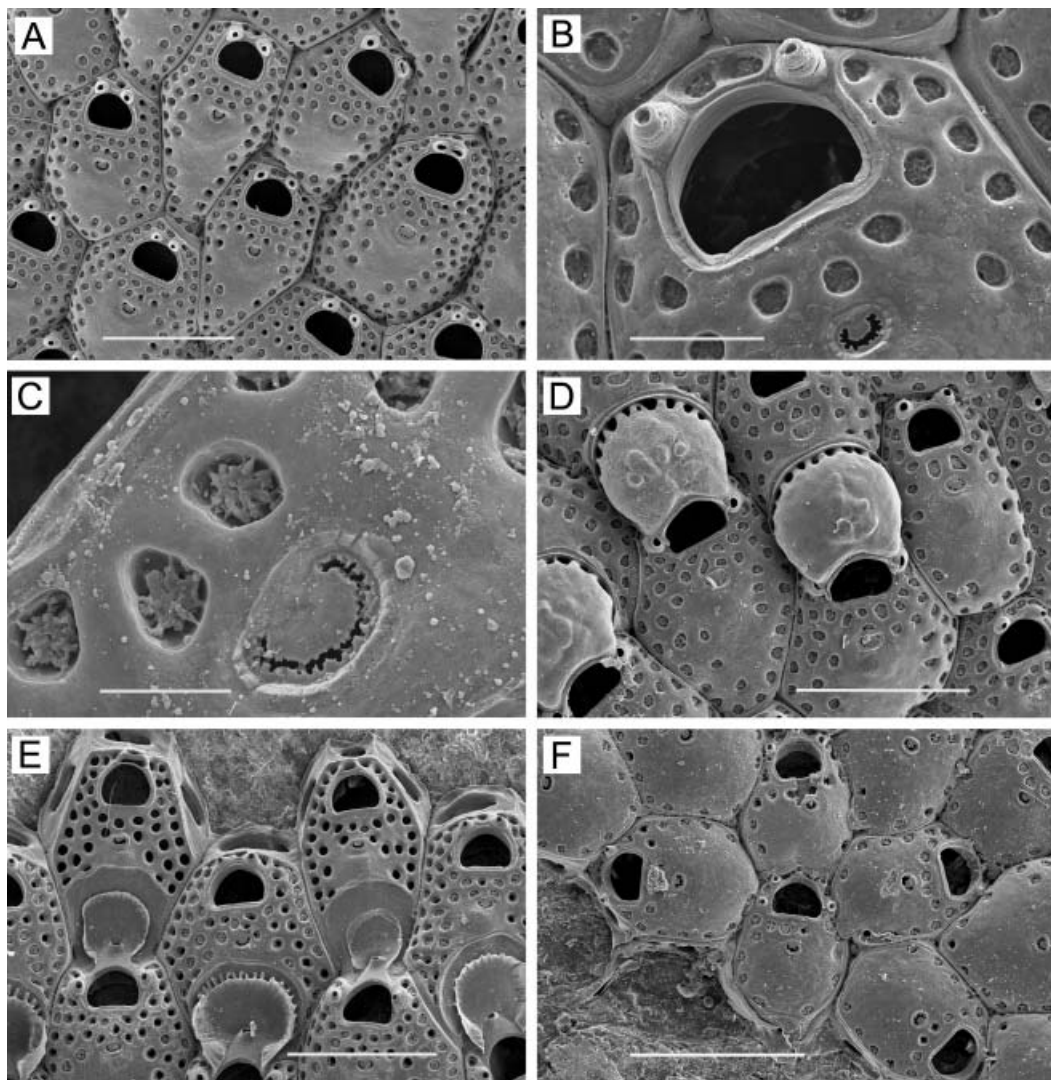


Figure 23. *Fenestruloides blaggae* Soule, Soule, and Chaney: (A) group of autozooids; (B) enlargement of orifice and ascopore; (C) enlargement of stellate pores and ascopore; note that ascopore has narrower opening than in (B); also note incisions around margin of ascopore depression; (D) two ovicellate zooids; knobs on ovicells are variable, and some ovicells are smooth; (E) marginal zooids, showing pore chambers and stages of ovicell formation; (F) ancestrula (lower centre) and surrounding zooids. All specimens bleached. Scale bars: 500 μ m (A, D–F); 100 μ m (B); 50 μ m (C).

Description

Colony. Vitreous when young, chalky white with age; unilaminar, encrusting, sheet-like, circular to irregular; largest observed 5 cm across.

Zooids. Regularly or irregularly hexagonal, distinct, separated by a groove and a sharp incision, 0.43–0.66 mm long (average=0.573 mm, $n=15$, 3) by 0.30–0.46 mm wide (average=0.379 mm, $n=15$, 3).

Frontal wall. Inflated, convex, with a slight to pronounced umbo proximal to, but independent of, ascopore; one or two (occasionally three) rows of stellate pores between ascopore and orifice, usually two to three (range one to four) rows along lateral margins, and a single row along proximal margin and distal to orifice; median area between umbo and proximal margin of zooid is imperforate.

Orifice (Figure 23B). Semicircular; 0.08–0.13 mm long (average=0.099 mm, $n=15$, 3) by 0.11–0.14 mm wide (average=0.131 mm, $n=15$, 3); proximal margin straight, slightly depressed at corners, condyles scarcely evident; orifices of ovicellate zooids tend to be broader than those of non-ovicellate zooids.

Ascopore (Figure 23B, C). Ascopore 0.04–0.06 mm across, depressed slightly from frontal surface, with a few sharp incisions around margin of depression; with a broad, proximally directed shelf; opening crescentic, narrow, with denticulate proximal and distal margins.

Spines (Figure 23A, B, D). Non-ovicellate zooids with two (occasionally one) short, conical spinous projections along distal orificial rim; long spines not observed; ovicellate zooids with a pair of stubby spines visible lateral to orifice, outside proximolateral extensions of ovicell; zooids forming ovicells also show the extended base of a median spine (see below).

Avicularia. Lacking.

Ovicell (Figure 23D). Raised, globose, imperforate, 0.31–0.40 mm long (average=0.353 mm, $n=15$, 3) by 0.30–0.39 mm wide (average=0.335 mm, $n=15$, 3); surface texture smooth; ovicell smooth, slightly rugose, or with pronounced, rounded lumps on top; surrounded by a raised border, with numerous pores around base; proximal margin concave, with a narrow horizontal border. In incompletely formed ovicells, a conical structure is evident distal to the zooidal orifice; this appears to be the extended base of a median distal spine (removed by bleaching) that is enveloped by the fully formed ovicell.

Ancestrula (Figure 23F). A small version of subsequent zooids, first budding a zooid similar to it in size distally, then a pair of zooids distolaterally, and finally three to four larger zooids proximally and proximolaterally. Ancestrula with five distal spines; first-generation periancestrular zooids with two to four distal spines; subsequent generations with normal complement of one or two. Zooids for several generations from ancestrula have only a single row of pores between ascopore and orifice, and a single row of marginal pores.

Remarks

Soule et al. (1995) described three similar new species of *Fenestruloides* (*F. eopacifica*, *F. blaggae*, and *F. miramara*) from California, but indicated that the differences among them are slight and that they might be synonymous. If this proves to be the case, the name *F. eopacifica* will take page priority. Ketchikan specimens have the following characters in common with *F. blaggae*: the ascopore separate from the umbo; ovicells often rugose or lumpy; spine number usually two; predominantly two rows of pores between ascopore and orifice; and the ascopore slightly depressed, with unusual incisions around the margin (compare Soule et al. 1995, Plate 60D with Figure 23C herein). The extended, conical base of a median distal spine on zooids forming ovicells, not mentioned in the original description but evident in our material, might also be a diagnostic character; *F. tongassorum* (following species), for example, does not show this character.

Distribution

The only previous record of *F. blaggae* is the holotype from Carmel, California. Our specimens extend the known range from north-central California to south-eastern Alaska.

***Fenestruloides tongassorum*, new species**
(Figure 24A–D)

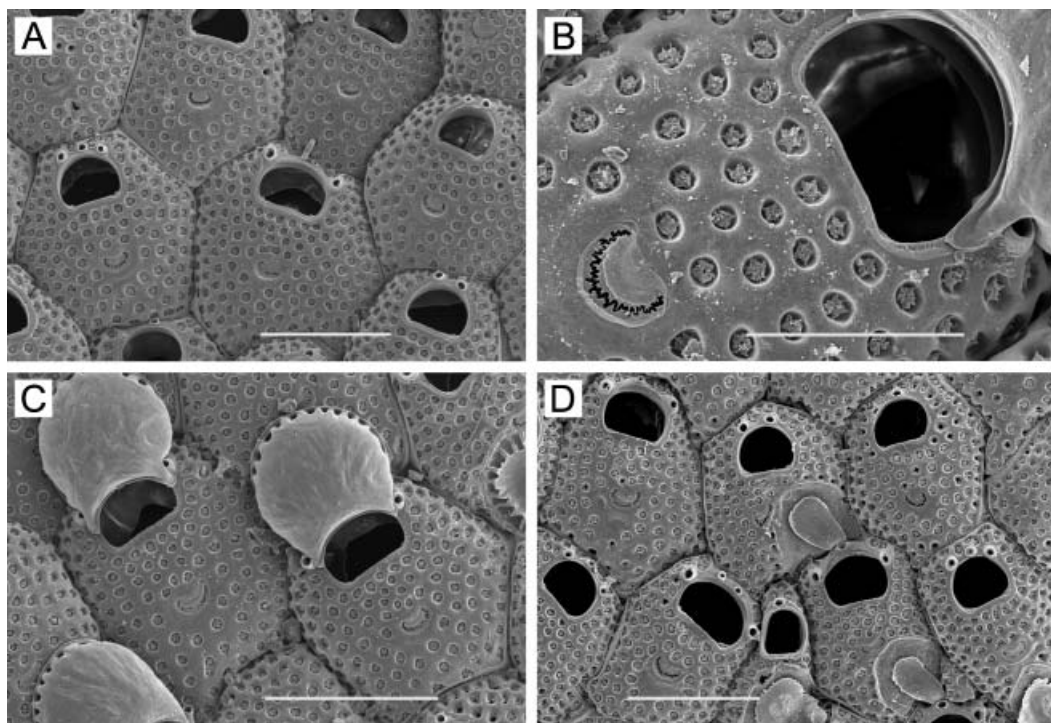


Figure 24. *Fenestruloides tongassorum* n. sp.; holotype: (A) group of autozooids; (B) enlargement of orifice and ascopore of ovicellate zooid; (C) ovicellate zooids; (D) group of zooids, showing small orifices with closely set distal spines indicative of non-ovicellate zooids, and large orifices with widely set distal spines indicative of zooids that have the potential to form an ovicell. Specimen bleached. Scale bars: 500 μm (A, C, D); 200 μm (B).

Fenestruloides morrisae Soule, Soule, and Chaney 1995, p 163, Plate 57 (in part?).

Fenestrulina ?porosa Canu and Bassler 1923, p 117, Plate 37, Figure 4.

Diagnosis

Zooids markedly inflated; frontal wall completely covered with stellate pores except for small area proximal to ascopore; conspicuous umbo lacking; ascopore broader than deep, the opening narrow, crescentic, crenulate; orifice subterminal, broader than long, with one or two rows of pores distal to it; two orifice types, that of ovicellate zooids broader than that of non-ovicellate zooids, with two stout, widely separated spines and one or two finer spines in between; non-ovicellate zooids have one to three fine spines close together. Ovicell smooth, imperforate, globose.

Type material

Holotype: ETN, specimen KE-58 bleached and coated for SEM (YPM 35842).

Etymology

The species name derives from the word *Tongass*, name of a clan of Tlingit Indians from the Ketchikan vicinity, now also applied to the surrounding Tongass National Forest.

Description

Colony. Unilaminar, encrusting, sheet-like; porcellaneous, whitish in colour.

Zooids. Distinct, separated by a groove and deep incision; regularly to irregularly hexagonal or barrel-shaped; quite variable in size and shape, 0.55–0.71 mm long (average=0.641 mm, $n=15$, 1) by 0.31–0.58 mm wide (average=0.465 mm, $n=15$, 1).

Frontal wall. Highly convex, inflated; with a slightly raised, crescentic area around proximal margin of ascopore; frontal wall entirely perforated with somewhat regular columns and rows of stellate pores except for a small area proximal to ascopore; four rows of pores between ascopore and orifice.

Orifice (Figure 24B). Subterminal, with one or sometimes two rows of pores distal to it; semicircular, broader than long, of two sizes (Figure 24D): wider in ovicellate zooids or those that can produce ovicells, 0.13–0.16 mm long (average=0.146 mm, $n=10$, 1) by 0.19–0.24 mm wide (average=0.212 mm, $n=10$, 1), narrower in non-ovicellate zooids, 0.13–0.15 mm long (average=0.135 mm, $n=10$, 1) by 0.16–0.19 mm wide (average=0.174 mm, $n=10$, 1); proximal margin straight or slightly convex, smooth, corners depressed, with a flattened condyle scarcely evident at each corner.

Ascopore (Figure 24B). Located roughly halfway between orifice and proximal zooidal margin, thus closer to proximal than to distal zooidal margin; 0.05–0.6 mm long by 0.08–0.10 mm deep; proximally directed shelf smooth; opening narrow, broadly

crescentic, crenulate, with denticles of shelf and proximal margin meshing between one another.

Spines. All spines short; non-ovicellate zooids (Figure 24A, D) with one to three spines equal in size close together along distal margin of orifice (frequencies: one=14%, two=62%, three=24%; $n=29$, 1); ovicellate zooids (Figure 24C), or those with potential to form ovicells (Figure 24A, D), have two thicker spines widely separated at distolateral corners of orifice, with one or two thinner spines between them; the thicker spines come to lie outside to the proximolateral extensions of the ovicell.

Ovicell (Figure 24C). Raised, globose, conspicuous, 0.30–0.36 mm long (average=0.330 mm, $n=12$, 1) by 0.31–0.35 mm wide (average=0.326 mm, $n=12$, 1); proximal margin with a narrow horizontal border; imperforate, the surface smooth in texture but slightly irregular; with small pores around sharp, slightly raised margin.

Avicularia. Lacking in our specimens.

Ancestrula. Not observed.

Remarks

Fenestruroides tongassorum is similar to *F. morrisae* Soule, Soule, and Chaney, 1995. However, the original description of *F. morrisae* seems to include two species, one tropical and the other more northern in distribution. The holotype of *F. morrisae* (Revillagigedo Islands off western Mexico, 19°N) has zooids with an orifice about as long as broad, and with the ascopore situated in the distal half of the zooid; an avicularium is also present. Our specimens resemble those of nominal *F. morrisae* from the Gulf of California and the Channel Islands off southern California (Soule et al. 1995, Plate 57B–D) more than they do the holotype from farther south (Soule et al. 1995, Plate 57A). The Ketchikan specimens have in common with the Gulf and Channel Island specimens orifices clearly broader than long; a larger orifice in ovicellate than in non-ovicellate zooids; large and small spines on ovicellate zooids; and the ascopore closer to the proximal than the distal zooidal margin. The main difference is a more flattened ovicell in the Gulf and Channel specimens. It is unclear whether the Ketchikan specimens are conspecific with nominal *F. morrisae* from the Gulf of California and the Channel Islands; in any case, we describe our material as new because we consider it distinct from the holotype of *F. morrisae*.

Fenestruroides tongassorum differs from nominal *Fenestruroides porosa* (Canu and Bassler) from Kodiak, Alaska (Dick and Ross 1988) in that the latter has a smaller, more open ascopore that is closer to the distal than the proximal zooidal margin; a smaller orifice; a larger ovicell; sometimes a large umbo; and fewer (two to three) rows of pores between ascopore and orifice. *Fenestruroides tongassorum* is similar to *F. porosa* (Canu and Bassler) in having ovicellate zooids with larger orifices than non-ovicellate zooids, three to four rows of pores between ascopore and orifice, and no conspicuous umbo; the latter differs in having a smaller, more open ascopore situated near the middle of the zooid. Soule et al. (1995) noted lack of spines in *F. porosa* (Canu and Bassler) as a character distinguishing that species from *F. morrisae*, but this is an error; Canu and Bassler (1923) mentioned two spines, and their illustration shows two to three spines, for *F. porosa*.

Distribution

Pending resolution of the question of identity with populations from the Gulf of California and the Channel Islands, we consider the Ketchikan vicinity to be the only known locality for *F. tongassorum*.

Superfamily CELLEPOROIDEA Johnston, 1838
Family PHIDOLOPORIDAE Gabb and Horn, 1862
Genus *Rhynchozoon* Hincks, 1895
Rhynchozoon tumulosum (Hincks, 1882)
 (Figure 25A–H)

Schizoporella tumulosa Hincks 1882, p 252; 1883, p 447, Plate 18, Figure 2.

Schizoporella tumulosa: Robertson 1908, p 293, Plate 20, Figure 53; O'Donoghue and O'Donoghue 1923, p 37, 1926, p 56 (in part?).

Rhynchozoon tumulosum: Osburn 1952, p 458, Plate 54, Figures 4–5, 12.

Rhynchozoon rostratum: Soule and Soule 1964, p 33 (in part); Dick and Ross 1988, p 84, Plate 6I.

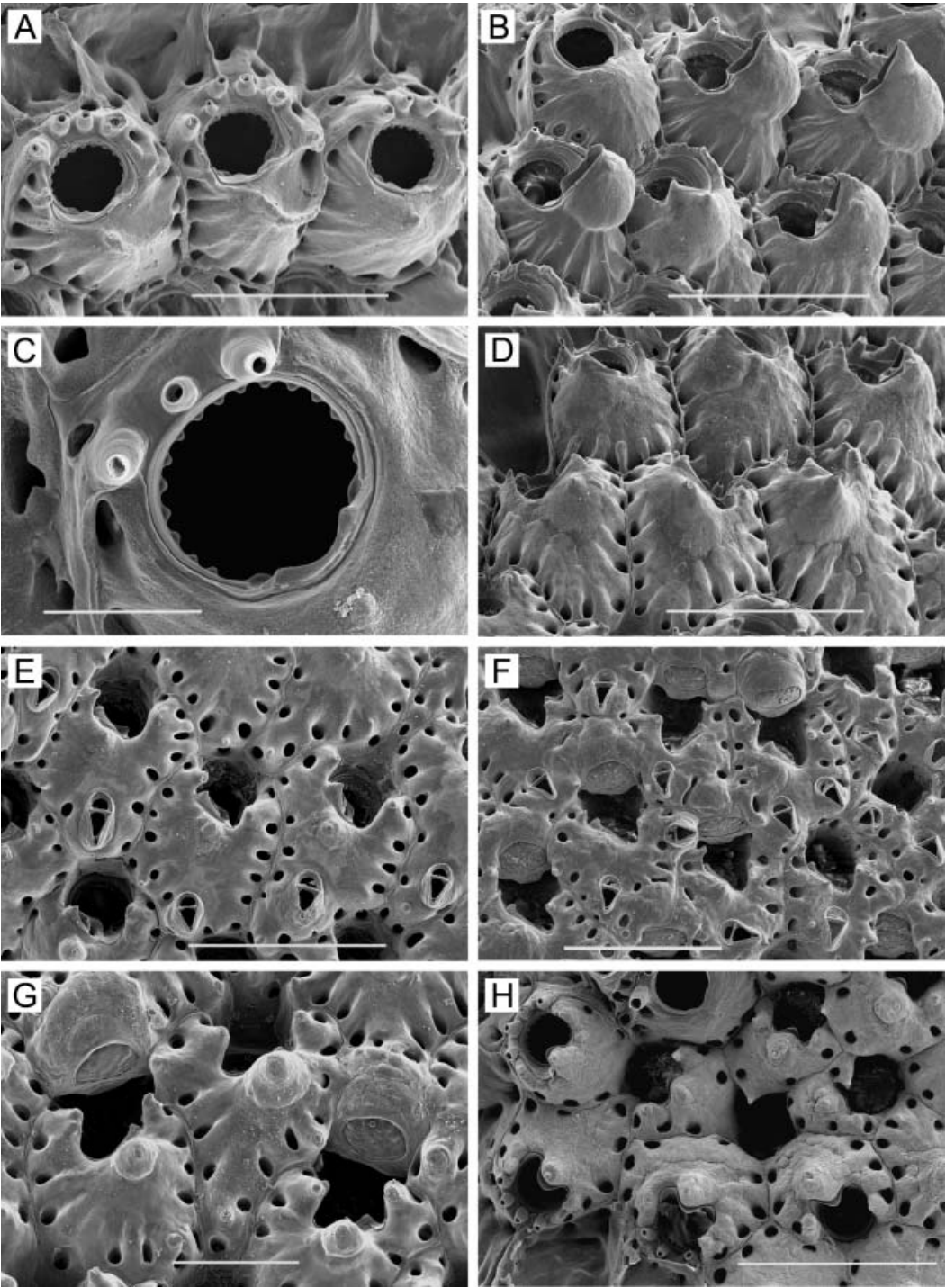
Description

Colony. Tan to light brown in colour; encrusting, unilaminar, occasionally multilaminar through frontal budding or overgrowth of older layers; circular or irregular; largest observed 2.5 cm across.

Zooids. Irregularly hexagonal; marginal zooids 0.40–0.58 mm long (average=0.460 mm, $n=15$, 3) by 0.28–0.43 mm wide (average=0.335 mm, $n=15$, 3); young zooids delineated by a deep groove with a calcified line formed by appressed marginal walls between adjacent rows of areolae; zooidal boundaries later become indistinct. Zooids interconnect by unusual raised, disk-like dietellae scattered irregularly around the distolateral and distal walls, each with a single tiny pore in the centre. Basal wall completely calcified, often with several irregularly distributed white punctae up to 0.05 mm in diameter.

Frontal wall. Shiny, vitreous; initially markedly convex, inflated, occasionally smooth but usually weakly to strongly costate (Figure 25A, B) between the 11–19 (average=14.4, $n=24$, 3) large areolar pores in total around the margin; the costal ridges of the primary layer soon become thickened by finger-like projections of secondary calcification (Figure 25D) growing centripetally over them. Frontal wall at intermediate stage of calcification convex, heavily costate; proximal to orifice is a variably developed umbo that can be tall or short, cylindrical or conical, sharp or blunt. Frontal wall at late stage heavily calcified, flatter and irregular, often with only traces of costal ridges remaining around margin, but generally somewhat rugose, irregular.

Orifice. Primary orifice (Figure 25A, C) slightly broader than long, 0.10–0.14 mm long (average=0.118 mm, $n=15$, 3) by 0.11–0.14 mm wide (average=0.125 mm, $n=15$, 3),



with a shallow, curved proximal sinus between a pair of triangular projections, flanked on each side by a conspicuous, rounded condyle; orificial margin beaded with 14–19 (average=16.5, $n=22$, 3) regularly spaced, rounded denticles. With increased frontal calcification, primary orifice lies deep in peristome; secondary orifice (Figure 25E–G) irregular in shape, with a process at margin on each side, sharp and cylindrical or stout and blunt, angled toward orifice to a variable extent; with a broad pseudosinus between projection on one side and base of avicularian rostrum within the peristome.

Avicularia. Three types occur. One is the asymmetrically positioned suboral avicularium, which arises initially as a bulbous chamber (Figure 25B) from an areolar pore lateral to proximal margin of orifice, on one side or the other; rostrum directed laterally toward side of origin and tilted in frontal direction, with a hooked end; mandible long-triangular with a small hook at end. As frontal wall thickens, avicularian chamber becomes completely immersed, covered by the umbo, and avicularium comes to lie completely in peristome. In addition to suboral avicularium, zooids can have a single frontal avicularium along proximal zooidal margin (Figure 25E), equal to or larger than suboral avicularium in size, with a non-hooked rostrum angled upward from the frontal surface, the mandible long-triangular, pointing proximally or sometimes laterally. Zooids can have a third type of avicularium; this is a frontal avicularium occurring anywhere along the lateral margins (Figure 25F), one or two per zooid. These lateral avicularia are less than or equal in size to the proximal avicularia and have an equilateral or long-triangular mandible usually directed perpendicular to zooidal margin. In heavily calcified zooids, chamber of frontal avicularia (proximal and lateral) can become completely immersed, the rostrum scarcely raised above the frontal surface. The complement of avicularia is variable; zooids within the same colony can have (in addition to the suboral avicularium) no frontal avicularia, only the proximal avicularium, the proximal and one or more lateral avicularia, or one or more lateral avicularia and no proximal avicularium.

Spines. Marginal zooids have two to five stout distal spines sometimes longer than zooid itself; in some colonies, most zooids have only two spines (Figure 25B), whereas in others, zooids with three to five spines are common (Figure 25A, C). Spines are ephemeral and restricted to marginal zooids; colony fragments without marginal zooids appear to lack them altogether.

Ovicell (Figure 25F, G). Broader than long; 0.13–0.20 mm long (average=0.164 mm, $n=22$, 3) by 0.14–0.25 mm wide (average=0.197 mm, $n=22$, 3), immersed to the level of the colony surface, the globose top exposed at first but later weakly covered by frontal calcification from surrounding zooids; proximal face of ovicell lies in peristome and has a lumpy panel of exposed endooecium that is semicircular, blunt-triangular, transversely

Figure 25. *Rhynchozoon tumulosum* (Hincks): (A) marginal zooids before or in initial stage (centre zooid) of formation of suboral avicularian chamber; (B) group of marginal zooids showing bulbous suboral avicularian chamber; (C) enlargement of orifice; (D) zooids near colony margin exhibiting centripetal growth of inter-areolar extensions of secondary calcification; (E) well-calcified zooids, each with a proximal frontal avicularium; some adjacent zooids (top) lack a proximal avicularium; (F) well-calcified ovicellate zooids with proximal frontal avicularium, and several with an additional lateral frontal avicularium; (G) enlargement showing ovicells; (H) secondary orifice of ancestrula (just right of centre); primary orifice is obscured within peristome formed by the proximal margins of five periancestrular zooids. All specimens bleached. Scale bars: 400 μ m (A); 500 μ m (B, D–F, H); 100 μ m (C); 250 μ m (G).

elliptical, or circular in shape, completely or incompletely bordered by ectooecium along the proximal margin. In fertile colonies, many zooids leave space for an ovicell before the ovicell develops; the result is a large secondary orifice that will be reduced in size when the ovicell forms.

Ancestrula. Roughly 0.40 mm in length and width; flattened; orifice semicircular with a straight proximal margin and about 15 rounded denticles around the curvature; possibly with several pairs of spines surrounding orifice, though if present these are obscured by periancestrular zooids in our specimens. Ancestrula surrounded by three zooids distally and distolaterally and a pair of larger zooids proximally (Figure 25H). Form of periancestrular zooids is similar to that of later zooids; they have three or more thick distal spines; however, many zooids within four generations from the ancestrula lack a suboral (or any other) avicularium. Ancestrula is rapidly overgrown by periancestrular zooids and difficult to observe.

Remarks

Hincks (1882) described this species from Cumshewa Harbour, Queen Charlotte Islands; the type locality is thus only about 250 km south of Ketchikan. Hincks's (1882, 1883) descriptions and illustration accord well with our specimens, indicating an orifice that is broader than long; occurrence of more than two distal spines (shown in Hincks 1883, Figure 2b but not mentioned in his descriptions), conspicuous frontal costation, and the occurrence of the proximal frontal avicularium (though Hincks 1883, Figure 2 shows this avicularium positioned more distally). Robertson (1908) provided an additional description and illustration of *R. tumulosum*; she indicated young zooids having "tubelike ridges" radiating from the margin toward the centre, and her illustration shows an orifice similar to that of Hincks's illustration. Unlike Hincks, she noted "avicularia scattered profusely over the whole surface of old colonies".

We have examined (Dick and Mawatari 2005) a NHM specimen labelled "1886.3.6.49. *Schizoporella tumulosa* Hincks, Queen Charlotte Islands, Canada, Pt. of type", with the colony of interest indicated by an arrow in India ink, presumably done by Hincks. This colony, which lacks ovicells, shows the same suite of other characters as our specimens, and we are thus confident that our material is *R. tumulosum* (Hincks).

Earlier, Busk (1856) had described a similar species, *R. rostratum*, from Mazatlán, Mexico. This species was not noted again until Hastings (1930) wrote a few descriptive remarks and provided illustrations for specimens she identified as *R. rostratum* from Panama, Colombia, and the Galapagos. She indicated an orifice with a shallow proximal sinus and small condyles, and mentioned only one frontal avicularium per zooid. Osburn (1952) distinguished between *R. tumulosum* and *R. rostratum* on the basis of the former having a distinctly "schizoporellidan" sinus and strong frontal costae, as compared to the latter having a shallower sinus and only weak marginal costation. Osburn (1952) considered *R. tumulosum* to be distributed from British Columbia southward to the San Benito Islands, Baja California, and *R. rostratum* to be distributed from Point Conception, California southward to the Galapagos Islands. He thus viewed the two species as overlapping from Point Conception to middle Baja California.

After re-examining Osburn's specimens and additional material from the eastern Pacific, Soule and Soule (1964) declared *R. tumulosum* a junior synonym of *R. rostratum*, although they then curiously indicated the range for *R. rostratum* to be from southern California to

the Galapagos, ignoring the records of *R. tumulosum* extending as far north as British Columbia. The Soules reported two to four oral spines for *R. rostratum* and noted that Osburn had overlooked the spines present in some of the specimens in the Hancock collections he had identified as *R. tumulosum*. Indeed, no previous authors had described spines for either *R. rostratum* or *R. tumulosum*, perhaps due to the ephemeral nature of the spines.

We consider it unlikely that *R. tumulosum* and *R. rostratum* are synonymous, partly because of the high-boreal to tropical distribution required by synonymy, and also because Hastings (1930) indicated for *R. rostratum* a characteristic faintly greenish colour strongly contrasting with the opaque white of the endooecial panel of the ovicell and the frontal processes. Hastings's illustrations (1930, Plate 14, Figures 93–96) also indicate an uncinat process within the peristome at the base of the avicularian rostrum, which Osburn (1952) mentioned as a character diagnostic for *R. rostratum*; our specimens lack this process. We have not examined tropical specimens of *R. rostratum*.

Distribution

Dick and Ross (1988) found a single *Rhynchozoon* specimen at Kodiak that was similar to *R. tumulosum* in Osburn's Hancock collections, but that they identified as *R. rostratum* because of the synonymy (Soule and Soule 1964). We have examined an additional specimen from Kodiak in which zooids are heavily costate, with three stout spines on many of the marginal zooids, characters indicative of *R. tumulosum*. In specimens from California, Robertson (1908) noted "tube-like ridges radiating toward the middle" in younger zooids, similarly suggestive of *R. tumulosum*. She noted this species as abundant in dredgings from San Pedro to San Diego. We consider the range of *R. tumulosum* to extend from the western Gulf of Alaska to California.

***Rhynchozoon glabrum*, new species** (Figure 26A–F)

Diagnosis

Marginal zooids smooth or weakly costate, usually with two (rarely three) distal spines; with increased calcification, frontal wall becomes increasingly smooth and regular, rather than costate or rugose; with a tall or short, conical frontal umbo; orificial margin beaded with 15–26 rounded denticles; secondary orifice with one or two conical or finger-like projections at margin; three types of avicularia: suboral avicularium lying within peristome at later stages, proximal marginal avicularium, and one to three lateral marginal avicularia; both of the latter two types can be absent, or occur with or without the other.

Type material

Holotype: ETN, unbleached and uncoated (YPM 35852). Paratype 1: ETN, unbleached and uncoated (NHM 2005.7.11.9). Paratype 2: ETN, specimen Rhy-4a bleached and coated for SEM (YPM 35853). Paratype 3: HP, specimen Rhy-2a bleached and coated for SEM (ZIRAS 1/50532). Paratype 4: HP, specimen Rhy-6a bleached and coated for SEM (YPM 35854). Paratype 5: HP, specimen Rhy-1a bleached and coated for SEM (NMH 2005.7.11.10).

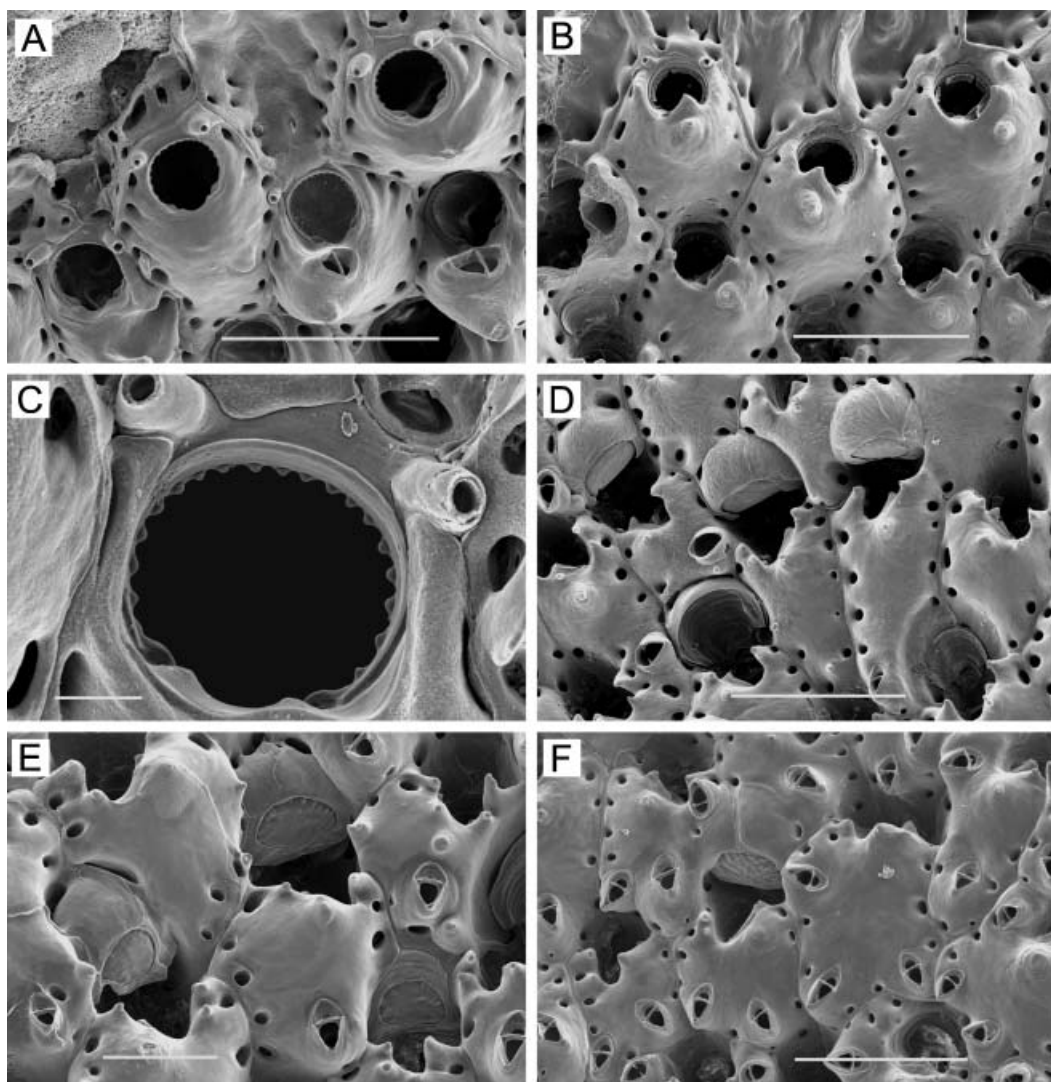


Figure 26. *Rhynchozoon glabrum* n. sp.: (A) group of marginal zooids showing suboral avicularian chamber at several stages of formation; (B) group of marginal zooids with bulbous suboral avicularian chamber; (C) enlargement of orifice; (D) group of ovicellate zooids showing stages of ovicell formation, beginning with extension of endooecium (lower right) into space left for ovicell during development of distal zooids; note that some zooids have a proximal marginal avicularium, whereas others lack one; (E) enlargement showing ovicells; (F) group of zooids with up to three marginal avicularia each. All specimens bleached. Scale bars: 500 µm (A, B, D, F); 50 µm (C); 250 µm (E).

Etymology

The species name derives from the Latin *glaber*, meaning smooth.

Description

Colony. Light tan or light chocolate- to violet-brown in colour; encrusting; unilaminar; multilaminar colonies were not observed; roughly circular; largest found 2.8 cm across.

Zooids. Irregularly hexagonal; marginal zooids 0.40–0.63 mm long (average=0.502 mm, $n=15$, 2) by 0.33–0.43 mm wide (average=0.349 mm, $n=15$, 2); young zooids delineated by a groove with a sharp incision at bottom; zooidal boundaries indistinct at later stages; basal wall completely calcified, often with several irregularly distributed white punctae up to 50 μm in diameter. Zooids interconnect by unusual raised, disk-like dietellae scattered irregularly around the distolateral and distal walls, each with a single tiny pore in the centre.

Frontal wall. Shiny, vitreous; in marginal zooids markedly convex, inflated, smooth or weakly costate (Figure 26A, B) between the 9–16 (average=11.8, $n=24$, 3) areolar pores in total around margin, rapidly becoming thickened by a heavy layer of smooth calcification, without costation (Figure 26B). Frontal wall increasingly smooth at intermediate and later stages of calcification, without ridges or irregularities, with a variably developed conical umbo that can be tall or short, blunt or sharp.

Orifice. Primary orifice (Figure 26C) slightly broader than long; 0.11–0.13 mm long (average=0.127 mm, $n=15$, 2) by 0.11–0.15 mm wide (average=0.135 mm, $n=15$, 2), with a shallow, curved proximal sinus between a pair of triangular projections, flanked on each side by a conspicuous, rounded condyle; orificial margin beaded with 15–26 (average=19.1, $n=21$, 4) regularly spaced, rounded denticles. With increased frontal calcification, primary orifice lies deep in peristome. Secondary orifice (Figure 26D–F) irregular in shape; typically there is one process on the orificial rim on the same side as the suboral avicularium and two processes on the opposite side; sometimes two processes on each side; the processes vary from sharp and conical to cylindrical and finger-like, but are not developed as heavy tubercles. Frequently there is a broad pseudosinus between the lateral projection on one side and the base of the suboral avicularium, which lies within the peristome.

Avicularia. Three types occur. One is the asymmetrically positioned suboral avicularium, which arises initially as a bulbous chamber (Figure 26A, B) from an areolar pore lateral to proximal margin of orifice, on one side or the other; rostrum directed laterally toward side of origin and tilted in frontal direction, with a hooked end; mandible long-triangular with a small hook at end. As frontal wall thickens, avicularian chamber becomes completely immersed, covered by the umbo, and avicularium comes to lie completely in peristome. In addition to suboral avicularium, zooids can have a single frontal avicularium along proximal zooidal margin (Figure 26E), equal to or larger than suboral avicularium in size, with a non-hooked rostrum angled upward from the frontal surface, the mandible long-triangular, pointing proximally or sometimes laterally. At later stages, this avicularium can appear separate from the margin, positioned toward the centre of the frontal wall, surrounded by secondary calcification. Zooids can have a third type of avicularium; this is a frontal avicularium (Fig. 26F) occurring anywhere along the lateral margins, one to three per zooid, equal to or smaller than the proximal frontal avicularium in size, with an equilateral or long-triangular mandible usually directed perpendicular to zooidal margin. In heavily calcified zooids, chamber of frontal avicularia (proximal and lateral) can become completely immersed, the rostrum scarcely raised above frontal surface. The complement of avicularia is variable; zooids within the same colony can have (in addition to the suboral avicularium) no frontal avicularia, only the proximal marginal avicularium, the proximal and one or more lateral avicularia, or one or more lateral avicularia and no proximal avicularium.

Spines. Marginal zooids usually have two distal spines (Figure 26A–C), or rarely three. Spines sometimes longer than the zooid itself. Spines are ephemeral and restricted to marginal zooids; colony fragments without marginal zooids appear to lack them altogether.

Ovicell (Figure 26D–F). Broader than long, 0.13–0.23 mm long (average = 0.180 mm, $n=22$, 4) by 0.20–0.28 mm wide (average = 0.237 mm, $n=22$, 4), the globose top exposed at first, but later weakly covered by frontal calcification from surrounding zooids; proximal face of ovicell lies in peristome and has a lumpy panel of exposed endooecium that is semicircular, blunt-triangular, transversely elliptical, or circular in shape, completely or incompletely bordered by ectooecium along the proximal margin. In fertile colonies, many zooids leave space for an ovicell before the ovicell develops; the result is a large secondary orifice that will be reduced in size when the ovicell forms.

Ancestrula. Not observed.

Remarks

Rhynchozoon glabrum overlaps in many characters with *R. tumulosum*. Primary orifice shape and ovicell form are indistinguishable; both species can have two spines on marginal zooids; both can have a tall frontal umbo proximal to the orifice; and both show some variability in the development of inter-areolar ridges on young, marginal zooids.

In a study of variation in the 16S mitochondrial ribosomal RNA gene among seven *Rhynchozoon* colonies at Ketchikan, Dick and Mawatari (2005) found two clades separated by 2.4% genetic distance ($K2P + \Gamma$). This permitted discrimination of morphological differences between the two lineages, which correspond to *R. glabrum* (Form A) and *R. tumulosum* (Form B). The two lineages are consistently distinguishable by a suite of morphological characters (Dick and Mawatari 2005) that includes degree of frontal costation, range of spine number, number of beads on primary orifice, number of areolar pores, and peri-orificial sculpturing. Considered together, these characters usually allow a particular specimen to be identified. *Rhynchozoon tumulosum* tends to have more areolar pores and fewer orificial beads, though the ranges overlap considerably. Most marginal zooids of *R. tumulosum* have inter-areolar ridges early on (Figure 25A, B), whereas most marginal zooids of *R. glabrum* lack them (Figure 26A, B). In *R. tumulosum*, inter-areolar ridges are strengthened by fingerlike extensions of centripetal secondary growth over the primary frontal wall (Figure 25D), leaving zooids slightly to markedly ridged at an intermediate stage of calcification (Figure 25E, G) and with an irregular surface in advanced calcification (Figure 25F); these finger-like extensions were not observed in *R. glabrum*. In *R. glabrum*, the frontal wall becomes increasingly smooth and regular with increased calcification (Figure 26D–F). Marginal zooids in *R. tumulosum* can have two to five distal spines (Figure 25A–C), although some colonies have zooids with predominantly two spines (Figure 25B); zooids with more than two distal spines are rare in *R. glabrum* (Figure 26A–C). Zooids of both species can either have or lack a single, proximal frontal avicularium, and can produce additional lateral frontal avicularia. However, the tendency to produce the lateral avicularia seems more pronounced in *R. glabrum* than *R. tumulosum*.

Distribution

A colony we have identified as *R. glabrum* is present on the same slide as Hincks's (1882) type colony of *R. tumulosum* (NHM 1886.3.6.49) from the Queen Charlotte Islands,

British Columbia (Dick and Mawatari 2005). The known range of *R. glabrum* thus extends from Ketchikan to the Queen Charlotte Islands; however, previous records of *R. tumulosum* from farther south may have included this species.

Discussion

Earlier reports seemed to indicate an unimpressive species richness of intertidal bryozoans. A scattering of reports dealing specifically with intertidal bryozoans at local scales indicated only modest diversities. Kubanin (1976), for example, reported only eight species, all cheilostomes, in a paper on the intertidal bryozoans of Zav'yalov Island in the Sea of Okhotsk. Rao and Ganapati (1985) found 22 bryozoan species in a series of transects across rocky intertidal in the Bay of Bengal.

In the past quarter century, it has become increasingly apparent that local diversities of intertidal bryozoans are higher than previously appreciated, and that the Bryozoa might, in fact, be one of the most speciose components of the macrofauna on certain types of coralline and rocky shores worldwide. What is interesting is that several studies from various parts of the world converge on remarkably similar estimates of local species richness of intertidal bryozoans, roughly 70–80 species, regardless of considerable differences in species composition and in the surrounding total regional diversities. Gordon (1980) identified 72 bryozoan species encrusting intertidal rocks and algae along several kilometres of coast in New Zealand (latitude 36°S). Dick and Ross (1988) identified 57 cheilostome species and estimated 74 bryozoan species overall among layered cobbles along a span of 11 km at Narrow Strait (57°N), Gulf of Alaska; as many as 25 species were observed on the undersides of single intertidal slabrocks of portable size. Somewhat ironically, an identical estimate for British Columbia lay buried in early systematic monographs by O'Donoghue and O'Donoghue (1923, 1926). Among 228 species and varieties of bryozoans collected subtidally and intertidally, mostly within about 20 miles of Nanaimo, these authors had also indicated a total of 74 taxa (32% of total) as occurring intertidally. Other studies gave more divergent estimates of species richness. 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 quantitative survey at a high-latitude site (eastern Murman, 69°N), Denisenko (1984) found 36 species intertidally. Recently, Grischenko (2004) reported an intertidal diversity of 63 bryozoan species in the Commander Islands off the Kamchatka Peninsula.

Likewise, little attention was paid to regional diversities of intertidal bryozoans. Ryland (1962) published a small identification guide to the common intertidal bryozoans on British shores that included a checklist of 29 species. This paper provided no indication of the local diversities that might be expected, and gave the impression of a rather low regional diversity. Regional systematic monographs contain relevant data, but these data are generally buried in species accounts; information on which species occur intertidally must be extracted piecemeal by going through entire monographs, species by species. In some cases, this tedious exercise indicates low regional intertidal bryozoan diversities. For example, among 340 bryozoan species and subspecies from the Far Eastern seas of the former USSR, Kluge (1975) recorded only 36 taxa (11% of total) as occurring intertidally.

A few recent studies, which vary considerably in geographical scope and sampling effort, have given estimates of regional diversities of intertidal bryozoans that are probably more accurate than that of Kluge (1975). One of the most comprehensive is the checklist of

Kubanin (1997). Based on material collected from 23 expeditions to the Russian sectors of the Sea of Japan, Sea of Okhotsk, and Bering Sea over a period of nearly three decades, this checklist includes 128 species of bryozoans occurring intertidally. The monographs by Hayward (1985) and Hayward and Ryland (1985, 1998, 1999) encompass 300 bryozoan species from the waters around Britain; among these, 79 species (26% of total) are indicated as occurring intertidally. Another 16 species are listed as occurring in estuaries or on pilings and docks, and thus might also comprise intertidal species. To the extent that this estimate is accurate, it reflects a comparatively low regional diversity, as it is similar to local diversities observed in some other parts of the world.

At Ketchikan, single-site cheilostome diversities at East Tongass Narrows (ETN), Higgins Point (HP), and Settlers Cove (SC) were 28, 18, and 10 species, respectively. At Ketchikan, all three sites were in the infralittoral fringe, at about the same intertidal height. Two of the collecting sites at Ketchikan (ETN and HP) had a single-site diversity within the range detected at infralittoral fringe sites in a comparable study by Dick and Ross (1988) at Kodiak, Alaska. There, diversities at nine sampling sites in the infralittoral fringe ranged from 17 to 33 cheilostome species. At Kodiak, midlittoral sites had a lower range of diversity (7–19 species), attributable to increasingly stressful conditions for marine organisms higher in the intertidal zone. While the difference in richness between ETN (28 species) and HP (18 species) at Ketchikan might be primarily correlated with substrate complexity and degree of exposure, the low richness at SC (10 species) was likely related to high sedimentation and low salinity due to the numerous freshwater outlets there.

With further sampling, the overall species richness of intertidal bryozoans detected at Ketchikan will likely prove to be as great as that at Kodiak (74 species; Dick and Ross 1988) and the Nanaimo, British Columbia vicinity (74 species; O'Donoghue and O'Donoghue 1923, 1926). At Ketchikan, some species were detected uniquely at each site (ETN, 12 species; HP, two species; SC, one species), which suggests that sampling at additional sites, especially species-rich sites, will continue to add new species to the cumulative local richness until an asymptote is reached. Though there is no guarantee that this asymptote will be similar to that at Kodiak and Nanaimo, the range of single-site diversities at Ketchikan similar to that observed at Kodiak suggests that this might be the case. Another indication that additional species are likely to be found intertidally at Ketchikan is that, among the 57 cheilostome species found intertidally at Kodiak, at least 18 species have a distribution extending farther south than Ketchikan, and thus might reasonably be expected to occur intertidally there. By the same token, some of the species reported intertidally at Nanaimo, British Columbia (O'Donoghue and O'Donoghue 1923, 1926), but not found by us at Ketchikan, have a distribution extending to the north of Ketchikan.

The cheilostome assemblages at Kodiak and Ketchikan are quite similar in composition. Table II lists species in the genera ranked first or second in terms of species richness at the two localities. Of the five genera ranked first or second at either locality, three (*Microporella*, *Cauloramphus*, and *Porella*) fall into the top two rankings at both. Species in genera in the top two rankings at Kodiak comprise 32% of the total species richness of intertidal cheilostomes; those at Ketchikan comprise 42%. An interesting question is why some of the same genera are predominant contributors to species richness at both localities. Part of the answer is that the assemblages at the two sites are historically and biologically related; that is, for each of the genera in the first two ranks at either locality, at least two species (Table II) co-occur at the two localities. Populations of these species are linked by past and/or present gene flow between the two localities. However, there is also geographical

Table II. Comparison of the most species-rich genera among the intertidal cheilostome bryozoan assemblages at Kodiak (Dick and Ross 1988) and Ketchikan (present study), Alaska.

Kodiak, Alaska	Rank	Ketchikan, Alaska	Rank
<i>Microporella germana</i>	2	<i>Microporella germana</i>	1
<i>Microporella neocribroides</i>		<i>Microporella neocribroides</i>	
<u><i>Microporella alaskana</i></u>		<i>Microporella setiformis</i>	
<u><i>Microporella californica</i></u>		<i>Microporella ketchikanensis</i>	
<i>Cauloramphus magnus</i>	1	<i>Cauloramphus magnus</i>	2
<i>Cauloramphus multiavicularia</i>		<i>Cauloramphus multiavicularia</i>	
<u><i>Cauloramphus variegatus</i></u>		<i>Cauloramphus tortilis</i>	
<i>Cauloramphus spectabilis</i>			
<i>Cauloramphus spinifer</i>			
<i>Porella acutirostris</i>	1	<i>Porella acutirostris</i>	2
<i>Porella alba</i>		<i>Porella alba</i>	
<i>Porella donoghueorum</i>		<i>Porella donoghueorum</i>	
<u><i>Porella concinna</i></u>			
<i>Porella immersa</i>			
<i>Celleporella hyalina</i> s.l.		<i>Celleporella hyalina</i> s.l.	2
<i>Celleporella reflexa</i>		<i>Celleporella reflexa</i>	
		<i>Celleporella nodasakae</i>	
<i>Tegella aquilirostris</i>	2	<i>Tegella aquilirostris</i>	
<i>Tegella horrida</i>		<i>Tegella horrida</i>	
<u><i>Tegella armifera</i></u>			
<u><i>Tegella arctica</i></u>			

The two highest-ranked genera in terms of species richness include five and four species at Kodiak, four and three species at Ketchikan. Taxa in bold co-occur at the two localities. Underlined taxa at Kodiak have a distribution known to extend to the south of Ketchikan, and thus could also occur there.

replacement of species in these genera; for example, *Cauloramphus spectabilis* and *C. spinifer* at Kodiak are replaced by *C. tortilis* at Ketchikan.

Historical and biological relatedness still does not address why some genera predominate in the intertidal assemblages. Two hypotheses can be put forth. One is that certain genera have high intertidal species richness because they are also regionally the most speciose clades. If the proportion of species that evolutionarily adapt to survive in intertidal conditions is roughly the same across all clades, then the most speciose clades will contribute more species to the intertidal fauna. If this hypothesis is true, then the species richness of clades intertidally will be proportional to the overall species richness of the clades in the region under consideration. The alternative hypothesis is that genus-level characters of some genera somehow preadapt species of those genera to be able to extend their existence into the intertidal zone. If this is the case, then some clades will be disproportionately rich intertidally, relative to their overall species richness in the region under consideration.

It is beyond the scope of this discussion to do more than call attention to these hypotheses, except to note that three types of data are needed to address them: (1) reasonably complete and accurate knowledge of local or regional intertidal species composition; (2) knowledge of the overall regional species composition, including subtidal taxa; and (3) accurate species-level taxonomy.

At present, knowledge of North Pacific bryozoans is deficient in all three categories. Although there are several earlier monographic reports from the north-eastern Pacific

(Robertson 1905, 1908, 1910; O'Donoghue and O'Donoghue 1923, 1926; Osburn, 1950, 1952, 1953), recent surveys in the region have found high percentages of new species both intertidally and subtidally (e.g. Dick and Ross 1988: 25% new species among 57 intertidal cheilostomes; Soule et al. (1995): 35% new species among 119 mostly subtidal species; present study: 26% new species among 31 intertidal cheilostomes). We expect that examination of material from poorly collected areas, such as shelf and shelf-slope areas around Alaska, will discover hundreds of undescribed species.

Soule et al. (2002) and Dick and Mawatari (2004) recently discussed some of the problems with the alpha-level taxonomy of bryozoans. These problems are related to the preconception by earlier workers that species tend to have broad geographic ranges (cosmopolitanism), as well as to a historical lack of adequate description and illustration of common, putatively widely distributed nominal taxa. Although the advent of SEM has facilitated documentation and allowed examination of characters difficult to observe with light microscopy, some taxa test the limits of a morphological species concept. Genetic studies making use of DNA sequence data combined with morphological analyses will be necessary to resolve these difficult taxa. An example is the *Celleporella hyalina* (L.) species complex worldwide, for which integrated genetic and morphological studies are under way (Hoare et al. 2001; Hughes et al. 2003; Navarette et al. 2003, 2005). An example from our study for which an integrative approach would be very useful is the *Porella acutirostris* species complex, which includes *P. acutirostris* from the European Arctic, *P. major* and *P. columbiana* from the north-eastern Pacific, and morphologically variant populations in other parts of the northern hemisphere. Genetic data will also be useful in establishing degree of relatedness between species in the north-eastern Pacific and their sister populations or species on the Asian side, e.g. *Cauloramphus multiavicularia* and *C. pseudospinifera*.

One of the goals of this study was to examine the intertidal cheilostome fauna at Ketchikan for the presence of introduced, non-native species. Of the 31 cheilostomes found, we consider only *Schizoporella japonica* to be unambiguously an introduced species. The probable arrival of *S. japonica* (previously reported as *S. unicornis*) to the north-eastern Pacific on Pacific oysters from Japan has been previously well discussed (Powell 1970; McCain and Ross 1974; Ross and McCain 1976). *Fenestrulina delicia*, recently originally described from Maine (Winston et al. 2000), is possibly another introduced species. We report it for the first time from the north-eastern Pacific Ocean, and one explanation for its nearly contemporaneous discovery in both the north-western Atlantic and north-eastern Pacific is that it was introduced to both regions in the past few decades.

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