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Diversity and taxonomy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay, Hokkaido, Japan

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Diversity and taxonomy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay, Hokkaido, Japan

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Abstract

We found 39 cheilostome species among more than 7000 specimens collected at 10 intertidal sites in rocky habitats along the shore of Akkeshi Bay, eastern Hokkaido Island, Japan. These species are herein described in detail and illustrated by scanning electron microscopy. Nine species (23% of total) are described as new (*Electra asiatica*, *Callopora sarae*, *Conopeum nakanosum*, *Cauloramphus cryptoarmatus*, *Cauloramphus multispinosus*, *Cauloramphus niger*, *Stomachetosella decorata*, *Microporella luellae*, and *Celleporina minima*), and 21 species (54%) are reported for the first time from Japan. Species richness ranged from eight to 29 species per study site. A TWINSPAN analysis showed the species fell into nine groups defined by the local pattern of distribution. A cluster analysis of study sites based on similarity of species composition showed three faunistic groups distributed geographically: in Akkeshi Lake, along the eastern-central shore of the bay, and at the mouth of the bay. Species richness in estuarine Akkeshi Lake was low, with a species composition very different from the outer bay. Most cheilostomes were found on rock and shell substrata, but uncommonly occurred on concrete walls, algae, hydroids, tubes of polychaetes, other bryozoans, and anthropogenic debris. Of the 39 species found, 33 (85%) contained embryos during the collecting periods, 2–7 June and 3–6 July 2004. The biogeographical composition of intertidal cheilostomes at Akkeshi Bay included species with Arctic-Boreal (28%), Boreal (59%), and Boreal-Subtropical (13%) distributions. The overall species richness of intertidal cheilostomes was two-thirds that documented intertidally in a comparable study at Kodiak, Alaska, a locality 15° higher in latitude. We attribute the lower richness at Akkeshi to differences in the nearshore marine environment between the two localities.

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

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Introduction

There are several good reasons for studying intertidal bryozoans (Dick et al. 2005). Bryozoans are more readily sampled intertidally than subtidally, and intertidal sites contain a significant subset of the greater diversity of species found on adjacent subtidal shelves, at least at cool-temperate latitudes. For example, the proportion of the total nearshore fauna occurring intertidally is around 32% in the vicinity of Nanaimo, BC (O'Donoghue and O'Donoghue 1923, 1926) and around 26% for Britain (Hayward and Ryland 1998, 1999). Thus intertidal assemblages are speciose enough to be useful for environmental monitoring and zoogeographical comparisons. Finally, as abundant competitors for space in cryptic habitats, bryozoans are important in helping to structure shore communities (Gordon 1972), though their role in this regard has not been well studied.

The diversity and composition of intertidal bryozoan assemblages have been studied at cool-temperate (Dick and Ross 1988; Dick et al. 2005) and subtropical (Dick et al. 2006) localities in the northern Pacific Ocean. These previous studies, as well as data in the monographs of O'Donoghue and O'Donoghue (1923, 1926), have shown that local species richnesses in rock-pile habitats (see Dick and Ross (1988) for definition) in the northeastern Pacific are in the order of 70–80 total species. Maximum richnesses of cheilostome bryozoans, the main group contributing to benthic assemblages, have ranged from 28 to 33 species at single sampling sites in the northeastern Pacific and on Hawaii.

The intertidal assemblage in the cold-temperate northeastern Pacific is similar in composition over broad geographical distances, with the same genera ranking highest in the number of species they contribute to the assemblage. As might be expected, the taxonomic composition of the intertidal assemblage on Hawaii (Dick et al. 2006) is quite different from that of the northeastern Pacific. Although there are indications that the composition of intertidal assemblages may be quite similar between Hawaii and the Indo-West Pacific, no comparable intertidal studies have been conducted in the latter region.

We chose Akkeshi Bay as a study site for several reasons. Previous Russian work suggested that the intertidal bryozoan fauna in this region might be exceptionally rich. Kubanin (1997) provided a regional checklist of 128 bryozoan species documented intertidally along the Russian coasts of the Sea of Japan, Sea of Okhotsk, and Bering Sea, which by way of comparison is a higher number than reported intertidally from Britain (around 79 species). Grischenko (1993, 1994, 2004) reported 63 bryozoan species from the Commander Islands. Furthermore, along the Pacific coast of Hokkaido, there is a confluence of several ocean currents (the Kuroshio from the south, the Oyashio from the north, and the Tsushima from the west) that might transport larvae from several provinces, potentially increasing species richness in the area. Finally, bryozoan alpha-level taxonomy in many parts of the world is in need of considerable revision (Soule et al. 2002; Dick and Mawatari 2004), and it is becoming increasingly evident that intensive local studies facilitate this, since congeners can be compared and similar but distinct species distinguished without the confounding influence of geographical variation.

Reliable alpha-level taxonomy is in turn a prerequisite for drawing reliable conclusions about biogeography. The degree of relationship between the boreal bryozoan faunas of the eastern and western Pacific remains unclear, due both to insufficient sampling and poor taxonomic resolution. Species recently described in the western Pacific have been subsequently found in Alaska (e.g. *Hincksina longiavicularia* Gontar, 1982), and vice versa (e.g. *Cauloramphus magnus* Dick and Ross, 1988). It is unclear whether or not some nominal species reported from both sides are distinct species (e.g. *Porella acutirostris* Smitt, 1868). In some cases, species initially considered to be trans-Pacific have been recognized as separate, sibling species in the eastern and western Pacific. An example is *Cauloramphus pseudospinifer* originally described from the Sea of Japan (Androsova 1958) and subsequently reported from Kodiak, Alaska (Dick and Ross 1988); Dick et al. (2005) later recognized Alaskan material as a new species, *C. multiavicularia*.

There has been no previous intensive local study of intertidal bryozoans in Japan, despite a history of bryozoology in this country beginning with Busk (1884) and followed soon thereafter by Ortmann's (1890) monographic study of Sagami Bay. Information on intertidal occurrences is scattered throughout the literature, including records for Hokkaido or specifically Akkeshi Bay (Silén 1941, 1942; Mawatari 1956, 1963, 1971, 1972, 1973a, 1973b, 1974; Mawatari and Mawatari 1973, 1974, 1980, 1981a, 1981b; d'Hondt and Mawatari 1986; Ikezawa and Mawatari 1993; Suwa and Mawatari 1998; Gordon et al. 2002). At the time we began the present study, 106 bryozoan species had been reported from Akkeshi Bay, including 73 cheilsotomes, 24 cyclostomes, and nine ctenostomes, collectively comprising roughly 60% of the bryozoan species known from the coastal waters around Hokkaido Island. However, few of these records are accompanied by bathymetric, ecological, or local distributional information. This paper is based on a doctoral dissertation presented by Grischenko (2006).

Study area and methods

The environment of Akkeshi Bay

Akkeshi Bay is situated on the northeastern coast of Hokkaido Island (Figure 1), 2° of latitude south of the boundary separating the High and Low Boreal Zones in the western Pacific (Ekaterina Strait, Iturup Island, southern Kuril Islands). The cold Oyashio current flows southward from the Bering Sea along Kamchatka and the Kuril Islands, reaching the southeastern coast of Hokkaido, including Akkeshi Bay. The warm Tsushima current, a branch of the Kuroshio current, weakly influences Akkeshi Bay from the southwest (Uchida et al. 1963).

The bay is about 13 km long by 9 km across, opening to the Pacific Ocean to the south and southeast. It is about 30 m deep at its mouth and becomes gradually shallower towards the inner part, with most of its area less than 20 m in depth (Uchida et al. 1963). Two small islands, Daikokujima and Kojima, are the emergent portions of an undersea ridge less than 5 m deep occupying the eastern half of the mouth of the bay. The bay narrows in the northeastern portion, tapering to a narrow channel connecting it with a shallow, brackish lagoon, Akkeshi Lake, into which flows the Bekambeushi River. Akkeshi Lake is about 5 by 8 km in dimensions; it is 11 m deep at the deepest point, but generally less than 2 m deep. Several tidal flats become exposed at low tide, including artificial Kakijima Island, a flat used for culture of the oyster *Crassostrea gigas* Thunberg.

The tidal pattern at Akkeshi Bay is semidiurnal: the height of high tides is only moderately different between day and night, but morning low waters are lower than afternoon low waters (Saigusa et al. 2000). The annual maximum range in tide level is 1.57 m. The lowest recorded water temperature in Akkeshi Bay was −1.4°C in February 2003, the highest 21.1°C in August 2004. Salinity is relatively constant, about 30 psu; it ranged from 26 psu in June 2003 to 31 psu in August 2004 (Nakamura et al. 2005). Akkeshi Bay is eutrophic; during the spring and autumn, plankton blooms occur and the water column is weakly stratified by phytoplankton (Saito and Hattori 1997).

The shoreline of Akkeshi Bay is varied. The western and northern shores are mostly sandy. The eastern shore consists of exposed capes of solid rock or boulders alternating with sandy beaches, beaches of large cobbles and boulders, and flat rocky platforms. Four main capes are located along this shore: Barasan, Aikappu, Aininkappu, and Mabiro. The capes consist of cliffs, below which lie flat, rocky platforms with crevices and cracks, and aggregated rocks, boulders, and cobbles. The shoreline of Daikokujima Island consists mostly of flat, creviced rocky reefs overlain with boulders and pebbles. In Akkeshi Lake, the tidal flats consist of muddy sand containing shells, gravel, and stones. Artificial Kakijima Island within Akkeshi Bay is surrounded by a border approximately 2–3 m wide consisting of rocks and boulders of portable size, with the interior filled in with oyster shells and sediment.

Collecting sites and collecting

Bryozoans were collected at 10 sites in the Akkeshi Bay complex (Figure 1). The sites were selected because they appeared, upon examination, to support a bryozoan fauna; some sites, such as cobble beaches and stretches of benchrock, were too unstable or exposed to support bryozoans. Two of the sites were located in Akkeshi Lake, six along the rocky eastern shore, and two on Daikokujima Island, each briefly described as follows.

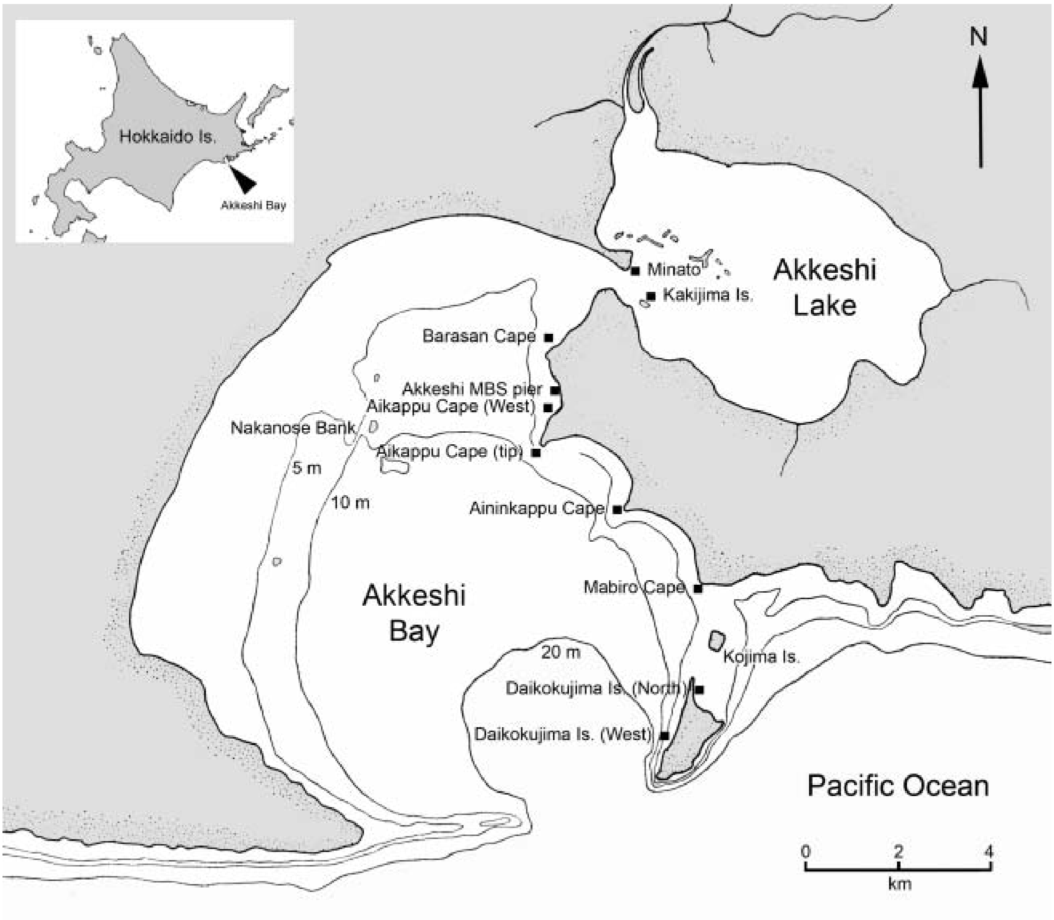

Figure 1. Map of Akkeshi Bay showing the 10 sampling stations (filled squares); 5, 10, and 20 m depth contours are indicated. Inset shows the location of Akkeshi Bay on Hokkaido Island, northern Japan.

- Minato [MIN] (43°02.56′N, 144°51.40′E), western shore of Akkeshi Lake; 4 June 2004; −0.10 m mean lower low water (MLLW) at 09:53 h; exposed beach of mixed sand and mud, with scattered cobbles, boulders, and metallic debris; middle to lower intertidal; specimens collected mostly from flat stones and metal debris, but a few from algae.
- Kakijima Island [KAK] (43°02.33′N, 144°51.44′E), western part of Akkeshi Lake; 4 June 2004; −0.10 m MLLW at 09:53 h; flat, shelly island with an artificial border 2–3 m wide of layered rocks and boulders; *Fucus* sp. and *Laminaria* sp. zones; specimens mostly collected from rocks, but some from shell debris and red algae.
- Barasan Cape [BAR] (43°01.45′N, 144°50.21′E), eastern shore of Akkeshi Bay; 3 July 2004; −0.05 m MLLW at 09:42 h; rocky, creviced reef flat beneath and among a series of arches eroded in the cliff, covered with scattered boulders and cobbles, with abundant shell debris wedged into crevices; zone of *Laminaria* spp.; specimens gathered from rocks and numerous shell fragments.
- Pier of Akkeshi Marine Biological Station [MBS] (43°01.03′N, 144°50.26′E), eastern shore of Akkeshi Bay; 3 June 2004; −0.06 m MLLW at 09:16 h; zone of *Laminaria* spp., with a broad, thick band of encrustation of the bryozoan *Cryptosula zavjalovensis*; specimens were scraped from the vertical concrete surface of the pier. This site was not included in most tabulations of data and other analyses, since the community here comprised a low-diversity fouling community on an artificial substratum.
- Aikappu Cape, west side [ACW] (43°00.46′N, 144°50.15′E), eastern shore of Akkeshi Bay; 2 June 2004; 0.02 m MLLW at 08:39 h; rocky, creviced reef flat with boulders and cobbles, and with pebbles and shell fragments under the boulders and wedged in cracks; zone of *Laminaria* spp.; specimens obtained from rocks and broken shells, and some from the holdfasts of brown algae.
- Aikappu Cape, tip [ACT] (43°00.42′N, 144°50.12′E), eastern shore of Akkeshi Bay; 3 June 2004; −0.06 m MLLW at 09:16 h; prominent rocky reef flat with crevices and pools, overlain with shingles, cobbles, and boulders, with broken shells and gravel under the boulders and wedged into crevices; zone of *Laminaria* spp.; specimens collected from rocks and shell fragments.
- Aininkappu Cape [ANC] (42°59.56′N, 144°51.30′E), eastern shore of Akkeshi Bay; 5 June 2004; −0.10 m MLLW at 10:31 h; prominent rocky reef flat with crevices, pools, caves, and layered boulders and cobbles, with many smaller rocks under the boulders; *Fucus* sp. and *Laminaria* spp. zones; specimens obtained from various rocky surfaces.
- Mabiro Cape [MAC] (42°58.57′N, 144°53.21′E), eastern shore of Akkeshi Bay; 4 July 2004; −0.04 m MLLW at 10:20 h; prominent rocky reef flat with layered boulders and cobbles, with numerous smaller rocks under the boulders; zone of *Laminaria* spp.; specimens collected from rock substrates.
- Daikokujima Island, north side [DIN] (42°57.26′N, 144°52.54′E); 7 June 2004; 0.01 m MLLW at 11:48 h; rocky, creviced reef flat with boulders and cobbles, with smaller rocks underneath the boulders; zone of *Laminaria* spp.; specimens collected from rock substrates.
- Daikokujima Island, west side [DIW] (42°57.00′N, 144°52.08′E); 6 July 2004; 0.09 m MLLW at 11:34 h: rocky, creviced reef flat with boulders; middle to lower intertidal horizons (*Laminaria* spp. zone); specimens collected from rock substrates.
- For some species, additional material was obtained subtidally from Nakanose Bank [NB] (43°00.37′N, 144°46.56′E) in the central region of Akkeshi Bay, at depths of 4–6 m, on 15 July 2003.

Collecting was conducted during cycles of extreme low tides from 2 to 7 June and from 3 to 6 July 2004. Samples were taken from along 10–50 m of shore at each site, beginning up to 1 h before low tide and continuing up to 1.5 h after low tide. We examined the undersides of boulders, pebbles and shells underneath boulders, crevices in reef flat, exposed rock faces, and algae for bryozoans. We either chipped fragments from rocks too large to transport using a hammer and chisel, or carried portable rocks, shell fragments, anthropogenic debris, and algae back to the laboratory at Akkeshi Marine Biological Station for detailed examination.

Laboratory work and data analysis

Bryozoan colonies attached to rocks, shells, and other substrata were cleaned by strong spraying with tapwater, then examined under a stereoscopic microscope. A Dremel tool (Model 395, Type 5; Racine, WI, USA) with a circular diamond-surfaced cutting bit was used to remove small pieces of rock and shell with attached bryozoans. Bryozoan-encrusted pebbles, shells, and fragments removed by Dremel were dried indoors in a warm air stream from an electric heater. Soft or fragile colonies were fixed in 70% alcohol.

For determination of relative abundance, distinct colonies attached to a substratum, as well as separate colony fragments chipped from rocks, were treated equally as "specimens". The number of specimens does not accurately reflect the true number of colonies examined, but likely does reflect an approximate relative abundance. Species with larger colonies would have tended to become fragmented during sampling and thus be counted as several specimens. A high number of specimens of a particular species from a particular site could thus reflect a high number of relatively small colonies, fewer relatively large colonies, or both, and in any case would be proportional to abundance in terms of either number of individuals or colony area.

For scanning electron microscopy (SEM), representative specimens of every species encountered were cleaned in sodium hypochlorite solution, rinsed with tapwater, and dried in air. Dried colonies, bleached or unbleached, were coated with Pd-Pt with a Hitachi-1039 ion sputter coater and examined with a Hitachi S-2380N scanning electron microscope at 15 kV accelerating voltage. Images were stored electronically as TIFF files at a resolution of 500 pixels per inch with Image Catcher software.

Measurements of zooidal characters were made by ocular micrometer with a Nikon SNZ-10 binocular microscope. In the text, measurements are given as ranges, with means and standard deviations in parentheses; unless stated otherwise, the sample size for each measurement was $N=20$ zooids or structures, and usually all measurements were taken from a single colony.

For examination of the distribution of cheilostomes in the study area, a two-way indicator species analysis was performed with TWINSPAN for Windows version 2.3 (Hill 1979; Hill and Smilauer 2005). To examine community subdivisions, we performed a cluster analysis of the sampling sites, using BIODIV software (Baev and Penev 1995). This software also calculated the similarity index on which the clustering was performed, the Sørensen–Chekanovsky similarity coefficient ($C_S=2j/(a+b)$, where j is the number of species common to two samples and a and b are respectively the total number of species in the two samples).

The specimens described herein are deposited in The Natural History Museum (NHM), London. SEM illustrations are included for some type specimens loaned by the Swedish Museum of Natural History (SMNH), Stockholm, and the Zoological Institute of the Russian Academy of Science (ZIRAS), St Petersburg.

The classification of higher taxa follows the Interim Classification of Families and Genera of Cheilostomata (Working Classification for the Treatise) compiled by D. P. Gordon (unpublished). Authors of genera and higher taxa are not included in the Reference section.

Zoogeographical definitions

The boundary between the High and Low Boreal Zones in the Asian Pacific is located at Ekaterina Strait (~46°N) between Iturup and Kunashir Islands, southern Kuril Islands (Ekman 1953; Kussakin 1979). The boundary between the Boreal and Subtropical Zones on the Pacific side of Japan is located near Inubo Cape (~35.7°N). Akkeshi Bay (43°N) is thus situated within the Low Boreal Zone, closer to the boundary separating the High and Low Boreal Zones than that between the Boreal and Subtropical Zones.

We defined categories of zoogeographical distribution for the species encountered in this study as follows. (1) Circumpolar Arctic-Boreal: distributed circumpolarly in the Arctic and extending southward into temperate waters of both the Pacific and Atlantic Oceans. (2) Arctic-Boreal Pacific: distributed along the Eurasian and American sectors of the Arctic region and extending southward into temperate waters of the Pacific, but absent in the Canadian Arctic and northern Atlantic. (3) Amphi-Boreal: primarily distributed in temperate waters in both the Pacific and Atlantic Oceans. (4) Wide Boreal Pacific: distributed in temperate waters of the northern Pacific along the American and Asian coasts and around the north Pacific rim (Aleutian–Commander Island arc). (5) Wide Boreal Asian Pacific: known from the Sea of Okhotsk, along the northern part of the Sea of Japan, the Kuril Ridge, Sakhalin Island, and the Pacific side of Hokkaido Island. (6) Low Boreal Asian Pacific: occurring in the Low Boreal Zone in the Asian part of the northern Pacific, i.e. between Iturup Island (southern Kuril Islands) and Inubo Cape, Honshu. (7) Amphi-Pacific Low Boreal-Subtropical: occurring along the Asian and American coasts within the Low Boreal and Subtropical Zones. (8) Asian Pacific Low Boreal-Subtropical: distributed mostly from Honshu Island, Japan, southward to China and Hong Kong.

Results

Species diversity

Thirty-nine cheilostome bryozoan species, including 14 anascans and 25 ascophorans, were found in this study (Table I). Among these species, nine (23%) are new to science, 21 (54%) are first records for Japan, and 29 (74%) are first records for Akkeshi Bay.

Overall cheilostome species diversity along the eastern coast of Akkeshi Bay was 37 species, with the number of species per site ranging from 19 to 29. The richest locality (29 species) was Aininkappu Cape, with a variety of substrate types including horizontal crevices beneath cliff overhangs and exposed flat reefs overlain by boulders and rock piles. Species diversity in Akkeshi Lake was lower and more variable than along the bay proper; only 15 species were recorded, eight at Minato and 15 on Kakijima Island. Overall diversity on Daikokujima Island was 22 species, with 21 species at the northern site and 16 at the western site.

Species abundance

In all, 7033 specimens were identified. Table I shows the number of specimens collected per species, by sampling site, with species listed in order of decreasing total number of specimens. A species abundance distribution with Log_{10} classes (Gray et al. 2006) showed the following: one species with one individual (2.6% of total species, 0.01% total individuals); six species with 2–10 individuals each (15.4% of species, 0.5% of individuals); 14 species with 11–100 individuals each (35.9% of species, 10.6% of individuals); 17 species with 101–1000 individuals each (43.6% of species, 73.7% of individuals), and one species with>1000 individuals (2.6% of species, 15.2% of individuals).

Table I. Species composition and abundance of cheilostome Bryozoa at intertidal localities examined in Akkeshi Bay.

	Akkeshi Lake		Eastern Coast						Daikokujima		
	MIN	KAK	BAR	MBS	ACW	ACT	ANC	MAC	DIN	DIW	Total
Microporella luellae			117		214	138	290	69	155	89	1072
Cauloramphus spinifer	8	68	151		78	71	222	33	153	77	861
Celleporella hyalina	9	45	98	1	76	68	180	91	182	107	857
Cauloramphus niger	62	202	23		26	35	86	58	110	71	673
Cribrilina annulata	2	46	95		39	75	128	6	28	21	440
Porella acutirostris			31		29	26	211	15	14	4	330
Microporella trigonellata	10	132	105		19	1					267
Cryptosula zavjalovensis		17	30	9	12	31	72	16	47	12	246
Cauloramphus multispinosus		141	16		16	1	36		14	4	228
Pacificincola perforata	4	200									204
Fenestrulina orientalis		32	1		8	2	135	1	3	1	183
Electra korobokkura	102	29	19		1						151
Desmacystis sandalia		32	10	5	8	7	34	10	17	27	150
Raymondcia rigida		1	2		21	14	82	8		1	129
Tegella aquilirostris					7	6	67	14	19	12	125
Hippoporella multiavicularia					2		86	24	6	3	121
Myriozoella plana					9	4	63	4	26	9	115
Cauloramphus magnus							74		25	4	103
Porella belli					1		94				95
Raymondcia klugei							92	1			93
Electra asiatica	50	12	9				10	9			90
Schizoporella japonica		46	29		10						85
Cauloramphus cryptoarmatus			2				80		1		83
Stomachetosella decorata			1		3	9	41	1	2	6	63
Celleporina nordenskjoldi								12	43		55
Parkermavella orientalis			1		5		35				41
Tricellaria occidentalis			3	3	4	4	3	1	18		36
Parasmittina avicularissima							15	11			26
Integripelta novella									23		23
Celleporina minima						5	16				21
Phidolopora elongata						1	17				18
Bugula pacifica		11						1	1		13
Hippoporella kurilensis								1	9		10
Tegella arctica							9				9
Callopora sarae								7			7
Celleporina porosissima						4					4
Callopora craticula						2	1				3
Conopeum nakanosum							2				2
Cheilopora sincera						1					1
Specimens per locality	247	1014	743	18	588	505	2181	393	896	448	7033
Species per locality	8	15	19	4	21	21	29	23	21	16	
Species found only at locality	0	0	0	0	0	2	2	1	1	0	

Unless otherwise indicated, numbers in the table indicate number of colonies or colony fragments counted. Species are listed in order of decreasing abundance. The collection at locality MBS represents a low-diversity fouling assemblage. Locality abbreviations: MIN, Minato; KAK, Kakijima Is.; BAR, Barasan Cape; MBS, Pier, Akkeshi Marine Biological Station; ACW, Aikappu Cape (west); ACT, Aikappu Cape (tip); ANC, Aininkappu Cape; MAC, Mabiro Cape; DIN, Daikokujima Island (north); DIW, Daikokujima Island (west).

Table II. Results of TWINSPAN analysis of distributional groups of intertidal cheilostome bryozoans at Akkeshi Bay.

	Akkeshi Lake		Eastern Coast					Daikokujima	
	MIN	KAK	BAR	ACW	ACT	ANC	MAC	DIN	DIW
Group 1									
Callopora craticula					+	+			
Conopeum nakanosum						+			
Tegella arctica						+			
Porella belli				+		+			
Cheilopora sincera					+				
Celleporina minima					+	+			
Celleporina porosissima					+				
Phidolopora elongata					+	+			
Group 2									
Callopora sarae							+		
Integripelta novella								+	
Hippoporella parva							+	+	
Celleporina nordenskjoldi							+	+	
Group 3									
Cauloramphus magnus						+		+	+
Hippoporella multiavicularia				+		+	+	+	+
Tegalla aquilirostris				+	+	+	+	+	+
Raymondcia klugei						+	+		
Parasmittina avicularissima						+	+		
Myriozoella plana				+	+	+	+	+	+
Group 4									
Tricellaria occidentalis			+	+	+	+	+	+	
Porella acutirostris			+	+	+	+	+	+	+
Stomachetosella decorata			+	+	+	+	+	+	+
Microporella luellae			+	+	+	+	+	+	+
Group 5									
Desmacystis sandalia		+	+	+	+	+	+	+	+
Cryptosula zavjalovensis		+	+	+	+	+	+	+	+
Fenestrulina orientalis		+	+	+	+	+	+	+	+
Cauloramphus multispinosus		+	+	+	+	+		+	+
Raymondcia rigida		+	+	+	+	+	+		+
Group 6									
Bugula pacifica		+					+	+	
Parkermavella orientalis			+	+		+			
Group 7									
Cauloramphus cryptoarmatus			+			+		+	
Cauloramphus niger	+	+	+	+	+	+	+	+	+
Cauloramphus spinifer	+	+	+	+	+	+	+	+	+
Cribrilina annulata	+	+	+	+	+	+	+	+	+
Celleporella hyalina	+	+	+	+	+	+	+	+	+
Group 8									
Electra asiatica	+	+	+			+	+		
Microporella trigonellata	+	+	+	+	+				
Group 9									
Electra korobokkura	+	+	+	+					
Pacificincola perforata	+	+							
Schizoporella japonica		+	+	+					

Locality abbreviations: MIN, Minato; KAK, Kakijima Is.; BAR, Barasan Cape; MBS, Pier, Akkeshi Marine Biological Station; ACW, Aikappu Cape (west); ACT, Aikappu Cape (tip); ANC, Aininkappu Cape; MAC, Mabiro Cape; DIN, Daikokujima Island (north); DIW, Daikokujima Island (west).

Another way to interpret these data is to consider the likelihood of obtaining a specimen of a particular species during collecting. A likelihood of 1% of detecting a particular species (that is, one in 100 specimens) means that in the collection of 7033 specimens in our study, 70 specimens of this species could be expected. Sixteen of the species had a likelihood of detection of less than or equal to 1% (*Stomachetosella decorata* and below in Table I). Five species (*Callopora sarae* and below in Table I) had a likelihood of detection of less than or equal to 0.1%, meaning that between 1000 and 7000 specimens would have to be examined to detect these species.

Species distributions and community subdivisions

An analysis of cheilostome species distribution in Akkeshi Bay with TWINSPAN identified nine distributional groups (Table II). Each group includes species having a similar pattern of distribution, indicated by rows in Table II. Table II suggests that groups of species have similar ecological preferences along environmental gradients, which, however, were not measured in this study. For example, Group 1 includes species restricted to Aininkappu and Aikappu Capes projecting from the central eastern shore of the bay. We speculate that conditions here are intermediate between the exposed environment of the bay mouth and the estuarine environment of Akkeshi Lake. Group 2 contains species occurring only at the southeastern entrance to the bay, where oceanic conditions might prevail. Group 7 contains broadly distributed species, tolerant of conditions ranging from near-oceanic to estuarine.

We also conducted a cluster analysis (Figure 2), which made use of the occurrence of species at the sampling sites (Table I) to group sites of similar species composition. This analysis showed three main clusters having within-group similarity of at least 70%. One cluster contained the Minato and Kakijima Island sites located in estuarine Akkeshi Lake. This cluster was separated from all other sites, probably due to the absence of many species shared among sites in the bay proper. Another cluster contained sites located on Barasan, Aikappu, and Aininkappu Capes along the eastern shore of the bay, with the two inner sites (Barasan Cape and Aikappu Cape West) forming a group, and the outer two sites at the tips of Aikappu and Aininkappu Capes forming another group. The three sites near the bay mouth comprised the third cluster, with the two sites on Daikokjima Island forming a group to the exclusion of Mabiro Cape. The striking congruence of the main clusters with inner, middle, and outer regions of the bay complex strongly suggests that the composition of the intertidal bryozoan assemblages varies along a gradient of environmental parameters from the inner to the outer bay.

Substrata

Most cheilostome bryozoans in the study area (34 species, or 87%) occurred on rocky substrates, including solid rock, the undersides of boulders and cobbles, and pebbles (Table III). Both the undersides of some boulders and many pebbles under larger rocks were covered almost entirely by bryozoan colonies. Several species attained high abundance, either in density or cover, on undersides of boulders, e.g. *Microporella luellae*, *Raymondcia rigida*, *Raymondcia klugei*, *Myriozoella plana*, *Cryptosula zavjalovensis*, and *Hippoporella multiavicularia*. *Tegella aquilirostris*, *Desmacystis sandalia*, and *Cryptosula zavjalovensis* were the only species observed on the upper surface of stable boulders. Twenty-one species (54%) also encrusted shell fragments accumulated beneath and among larger rocks (Table III). Eight species (21%) were found on algae. One species (2.6%), *Celleporina porosissima*, was encountered only on the rhizoids of *Laminaria* sp.

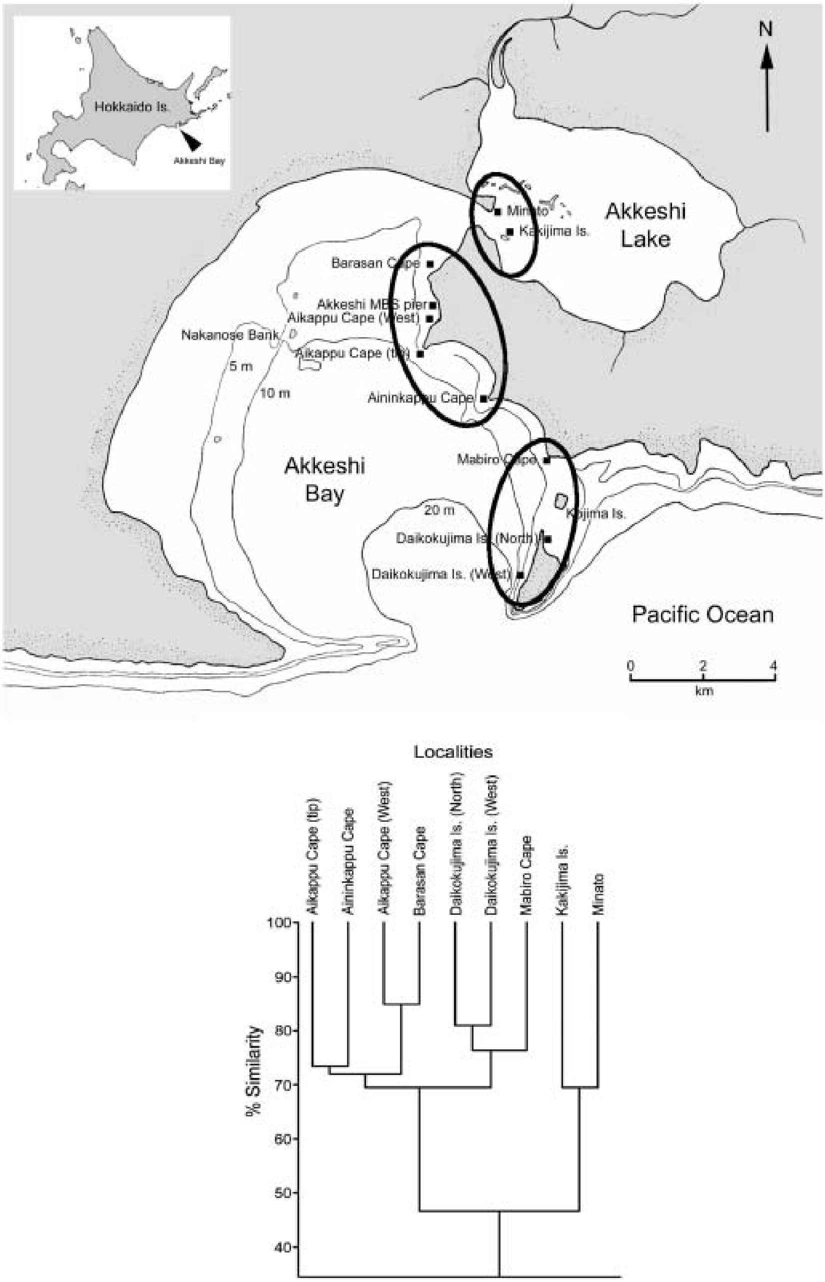

Figure 2. Dendrogram (below) showing similarity of sampling localities based on species presence/absence, and a map (above) showing the geographical distribution of three groups of sampling localities (circled) that are less than 70% similar in species composition between groups.

Other substrata used by bryozoans included hydroids, polychaete tubes, other bryozoans, and anthropogenic debris. The two *Celleporina* species (5.1%), *C. minima* and *C. nordenskjoldi*, occurred on hydroid stolons. *Parkermavella orientalis* (2.6%) was noted on tubes of serpulid polychaetes. One undetermined cyclostome bryozoan, four

Table III. Distribution of cheilostome bryozoans on substrata in Akkeshi Bay.

	Substratum			
Taxon	Rock	Shell	Algae	Other
Cauloramphus multispinosus	228 (100)			
Porella belli	95 (100)			
Raymondcia klugei	93 (100)			
Parasmittina avicularissima	26 (100)			
Integripelta novella	23 (100)			
Phidolopora elongata	18 (100)			
Callopora sarae	7 (100)			
Conopeum nakanosum	2 (100)			
Pacificincola perforata	202 (99.0)	2 (1.0)		
Raymondcia rigida	127 (98.4)	2 (1.6)		
Hippoporella multiavicularia	119 (98.4)	2 (1.7)		*Phidolopora elongata*, 1 (0.9) Cyclostome bryozoan, 1 (0.9)
Myriozoella plana	113 (98.3)			
Fenestrulina orientalis	178 (97.3)	3 (1.6)		*Phidolopora elongata*, 2 (1.1)
Stomachetosella decorata	61 (96.8)	2 (3.2)		
Electra asiatica	87 (96.7)	3 (3.3)	1 (1.1)	
Electra korobokkura	144 (95.4)	6 (4.0)		Metal debris, 1 (0.1)
Tegella aquilirostris	118 (94.4)	1 (0.8)		*Phidolopora elongata*, 4 (3.2) *Cryptosula zavjalovensis*, 1 (0.8) Plastic debris, 1 (0.8)
Cauloramphus cryptoarmatus	78 (94.0)	4 (4.8)		*Phidolopora elongata*, 1 (1.2)
Microporella luellae	1000 (93.3)	62 (5.8)		*Cryptosula zavjalovensis*, 4 (0.4) Plastic debris, 6 (0.6)
Cauloramphus magnus	96 (93.2)	7 (6.8)		
Cauloramphus niger	627 (93.2)	33 (4.9)	3 (0.5)	Plastic debris, 3 (0.5)
Bugula pacifica	12 (92.4)		1 (7.6)	
Porella acutirostris	298 (90.3)	32 (9.7)		
Tegella arctica	8 (89.0)	1 (11.1)		
Schizoporella japonica	74 (87.1)	11 (12.9)		
Desmacystis sandalia	125 (83.3)	9 (6.0)	1 (0.7)	Concrete, 5 (3.3) *Phidolopora elongata*, 5 (3.3) *Flustrellidra akkeshiensis*, 5 (3.3)
Celleporella hyalina	700 (81.7)	102 (11.9)	24 (2.8)	Concrete, 1 (0.1) Plastic debris, 26 (4.0) *Alcyonidium alcilobatum*, 1 (0.1) *Flustrellidra akkeshiensis*, 2 (0.2) *Flustrellidra corniculata*, 2 (0.2)
Cribrilina annulata	355 (80.7)	75 (17.0)	4 (0.9)	*Phidolopora elongata*, 1 (0.2) Plastic debris, 5 (1.1)
Microporella trigonellata	215 (80.5)	52 (19.5)		
Cryptosula zavjalovensis	190 (77.2)	42 (17.1)		Concrete, 9 (3.7) Plastic debris, 5 (2.0)
Parkermavella orientalis	31 (75.6)			*Phidolopora elongata*, 1 (2.4) Polychaete tube, 9 (22.0)
Cauloramphus spinifer	632 (73.4)	173 (20.1)	21 (2.4)	*Phidolopora elongata*, 1 (0.1) Plastic debris, 34 (4.0)
Tricellaria occidentalis	17 (47.2)			Concrete, 1 (2.8) Plastic debris, 1 (2.8) *Flustrellidra akkeshiensis*, 15 (41.7) *Phidolopora elongata*, 1 (2.8) *Bugula pacifica*, 1 (2.8)

Table III. Continued.

	Substratum			
Taxon	Rock	Shell	Algae	Other
Celleporina minima	5 (23.8)			Hydroid stolon, 16 (76.2)
Callopora craticula				*Phidolopora elongata*, 3 (100)
Cheilopora sincera				*Phidolopora elongata*, 1 (100)
Hippoporella parva				*Flustrellidra filispina*, 10 (100)
Celleporina nordenskjoldi				*Flustrellidra filispina*, 34 (61.8) Hydroid stolon, 9 (16.4) *Bugula pacifica*, 12 (21.8)
Celleporina porosissima			4 (100)	
Number of species on substratum	34	21	8	19
Species restricted to substratum	8	0	1	4

Numbers indicate number of colonies observed on a substratum, with percentage of total observations in parentheses.

ctenostome bryozoans (*Alcyonidium alcilobatum* d'Hondt and Mawatari, 1986; *Flustrellidra akkeshiensis* Mawatari, 1971; *F. corniculata* (Smitt, 1872); and *F. filispina* Mawatari, 1971) and three cheilostome species (*Bugula pacifica*, *Cryptosula zavjalovensis*, and *Phidolopora elongata*) were substrates for another 16 (41%) bryozoan species. Large, erect colonies of *Phidolopora elongata* provided a substrate for 11 (28%) cheilostome species. Finally, several species were observed on anthropogenic debris scattered along the intertidal zone. *Electra korobokkura* was found on a piece of abraded metal plate, and eight other species (21%) (*Cauloramphus niger*, *Cauloramphus spinifer*, *Tegella aquilirostris*, *Tricellaria occidentalis*, *Cribrilina annulata*, *Celleporella hyalina*, *Cryptosula zavjalovensis*, and *Microporella luellae*) were repeatedly found on various kinds of plastic debris. Among them, *C. spinifer* was abundant on plastic, forming extensive encrustations occupying considerable space.

Based on the range of substrata used (Table III), some of the cheilostome species of Akkeshi Bay could be classified as clearly stenotopic or eurytopic. Eleven species (28%) were stenotopic, occurring only on a single type of substratum: eight species (21%) were found only on rock (*Cauloramphus multispinosus* to *Conopeum nakanosus*); two species (5.1%), *Callopora craticula* and *Cheilopora sincera*, were found only encrusting the erect bryozoan *Phidolopora elongata*; and one species (2.6%), *Celleporina porosissima*, was found only on algae. Five species (13%) (*Cauloramphus niger*, *C. spinifer*, *Cribrilina annulata*, *Celleporella hyalina*, and *Desmacystis sandalia*) were eurytopic, noted on rock, shells, algae, and sometimes other substrata. The rest of the species fell somewhere in between stenotopy and eurotopy; for example, 15 species (38%) were observed on rock, shell, and sometimes other substrates, but not on algae.

Reproduction

Table IV indicates the presence of embryos in bryozoan colonies during either of the periods of collection (2–7 June and 3–6 July 2004). Of the 39 species found in the study, 33 (85%) contained embryos; among these, the percentage of colonies with embryos was determined for 26 species, and presence or absence only was noted for seven species for which it was difficult to observe embryos in dried specimens. For the same reason, it was unclear whether four of the species contained embryos. Two species (5%), *Cheilopora sincera* and *Bugula pacifica*, lacked embryos or ovicells.

Table IV. Occurrence of embryos in cheilostome bryozoans during either of the collecting periods (2–7 June and 3–6 July 2004) in Akkeshi Bay.

Taxon	Colonies observed	Colonies with embryos	Percentage with embryos
Celleporina nordenskjoldi	55	55	100.0
Celleporina porosissima	4	4	100.0
Callopora sarae	7	6	85.7
Cribrilina annulata	440	365	83.0
Celleporina minima	21	16	76.2
Schizoporella japonica	85	58	68.2
Celleporella hyalina	857	569	66.4
Fenestrulina orientalis	183	121	66.1
Raymondcia rigida	129	85	65.9
Microporella luellae	1072	701	65.4
Hippoporella kurilensis	10	6	60.0
Porella acutirostris	330	182	55.2
Microporella trigonellata	267	146	54.7
Porella belli	95	51	53.7
Stomachetosella decorata	63	33	52.4
Parkermavella orientalis	41	21	51.2
Pacificincola perforata	204	93	45.6
Tegella arctica	9	4	44.4
Phidolopora elongata	18	7	38.9
Tricellaria occidentalis	36	14	38.9
Tegella aquilirostris	125	45	36.0
Callopora craticula	3	1	33.3
Hippoporella multiavicularia	121	38	31.4
Myriozoella plana	115	32	27.8
Integripelta novella	23	5	21.7
Parasmittina avicularissima	26	2	7.7
Bugula pacifica	13	0	–
Cheilopora sincera	1	0	–
Cauloramphus cryptoarmatus	+		
Cauloramphus magnus	+		
Cauloramphus multispinosus	+		
Cauloramphus niger	+		
Cauloramphus spiniferum	+		
Desmacystis sandalia	+		
Cryptosula zavjalovensis	+		
Electra korobokkura	?		
Electra asiatica	?		
Conopeum nakanosum	?		
Raymondcia klugei	?		

+, indicates presence of embryos noted, but frequency not determined; ?, indicates presence of embryos was not determined.

Zoogeography

Table V shows a biogeographical categorization of the known distributions of the intertidal cheilostomes of Akkeshi Bay. Nearly two-thirds of the species (59%) are Boreal, known only from northern temperate waters. Over two-thirds of the Boreal species (38% of total species) are Low Boreal Asian Pacific species. This category may be artificially inflated because all but one of the nine new species described herein are known only from Akkeshi Bay, and some of these may eventually prove to have broader distributions. Over one-quarter of the species (28%) have Arctic-Boreal distributions; all but one of these

Table V. Biogeographical composition of the intertidal cheilostome bryozoan fauna of Akkeshi Bay.

- Arctic-Boreal (28%)
  - Circumpolar Arctic-Boreal (25%)
    - *Porella belli*
    - *Callopora craticula*
    - *Tegella arctica*
    - *Cribrilina annulata*
    - *Porella acutirostris*
    - *Raymondica rigida*
    - *Cheilopora sincera*
    - *Myriozoella plana*
    - *Phidolopora elongata*
    - *Celleporella hyalina*
  - Arctic-Boreal Pacific (3%)
    - *Celleporina nordenskjoldi*
- Boreal (59%)
  - Amphi-Boreal (3%)
    - *Cauloramphus spinifer*
  - Wide Boreal Pacific (13%)
    - *Tegella acutirostris*
    - *Cauloramphus magnus*
    - *Bugula pacifica*
    - *Desmacystic sandalia*
    - *Cryptosula zavjalovensis*
  - Wide Boreal Asian Pacific (5%)
    - *Electra asiatica* n. sp.
    - *Hippoporella multiavicularia*
  - Low Boreal Asian Pacific (38%)
    - *Electra korobokkura*
    - *Conopeum nakanosum* n. sp.[a]
    - *Callopora sarae* n. sp.[a]
    - *Cauloramphus cryptoarmatus* n. sp.[a]
    - *Cauloramphus niger* n. sp.[a]
    - *Cauloramphus multispinosus* n. sp.[a]
    - *Integripelta novella*
    - *Raymondcia klugei*
    - *Parasmittina avicularissima*
    - *Parkermavella orientalis*
    - *Stomachetosella decorata* n. sp.[a]
    - *Hippoporella kurilensis*
    - *Microporella luellae* n. sp.[a]
    - *Microporella trigonellata*
    - *Celleporella minima* n. sp.[a]
- Boreal-Subtropical (13%)
  - Amphi-Pacific Low Boreal-Subtropical (5%)
    - *Tricellaria occidentalis*
    - *Schizoporella japonica*
  - Asian Pacific Low Boreal-Subtropical (8%)
    - *Pacificincola perforata*
    - *Fenestrulina orientalis*
    - *Celleporina porosissima*

[a] New species for which the known distribution is restricted to Akkeshi Bay or Hokkaido Island.

have a circumpolar Arctic distribution, extending into temperate waters in both the Atlantic and Pacific Oceans. The few species (13%) with Boreal-Subtropical distributions all have Akkeshi Bay as the northernmost limit of their range in the Asian Pacific. The two Boreal-Subtropical species (*Tricellaria occidentalis* and *Schizoporella japonica*) with Amphi-Pacific distributions were both likely introduced from Asia to North America in the previous century along with shipments of the Pacific oyster (*Crassostrea gigas*) for culture.

The distributions of some species are problematic. *Porella acutirostris* and *Celleporella hyalina* are listed in Table V as circumpolar Arctic-Boreal species, although it is unclear for both of these whether the Arctic and Boreal forms are conspecific. Although *Cauloramphus spinifer* has been reported from the European Arctic, it is considered by most authors to be an Amphi-Boreal species.

Taxonomy

Order CHEILOSTOMATA Busk, 1852
Suborder MALACOSTEGINA Levinsen, 1902
Superfamily MEMBRANIPOROIDEA Busk, 1852
Family ELECTRIDAE d'Orbigny, 1851
Genus *Electra* Lamouroux, 1816
Electra korobokkura Nikulina, 2006
(Figure 3)

Electra korobokkura Nikulina 2006, p 23, Figures 1–5.

Material examined

MIN, colony on abraded metal plate (NHM 2006.2.27.1), colony on rock (NHM 2006.2.27.2). Additional material: 149 specimens. Also examined for comparison: *Electra arctica* (Borg, 1931), ZIRAS 36/50535, colony on a pebble sorted from a crab trap Middle Fishery Refrigerator Trawler *Rodino*, 57°36.2′N, 156°09.0′E, Sea of Okhotsk, Western Kamchatka shelf, about 32 km from cape Hayryuzova, depth 78–81 m, coll. 12 September 1992 by A. V. Grischenko.

Description

Colony encrusting, yellowish when alive, forming a thin, irregular network, the largest observed about 2.5 cm across; zooids arranged in anastomosing uniserial branches that expand to lobes two to four zooids across, sometimes more (Figure 3A–C). Zooids oblong, thin-walled, widest in middle, 0.40–0.60 mm long (0.49 ± 0.05 mm), 0.22–0.35 mm wide (0.28 ± 0.03 mm), rounded distally, narrower proximally; separated by a deep groove along lateral margins when anastomosed; lateral walls smooth, vertical to sloping when uniserial; transverse boundary between zooids indistinct. Mural rim raised, sharp. Cryptocyst a narrow, granulated sloping shelf below marginal rim (Figure 3D). Opesia oval to elliptical, 0.25–0.35 mm long (0.31 ± 0.03 mm), 0.14–0.20 mm wide (0.16 ± 0.02 mm), occupying 50–70% of zooidal length. Frontal membrane thin, transparent. Operculum (Figure 3D) semicircular, calcified, of sharply contrasting white colour. Gymnocyst smooth, narrow distally and laterally, elongate and tapering proximally, semicircular in transverse section, sometimes with weak transverse rugae. Proximal to opesia, gymnocyst often rises into a

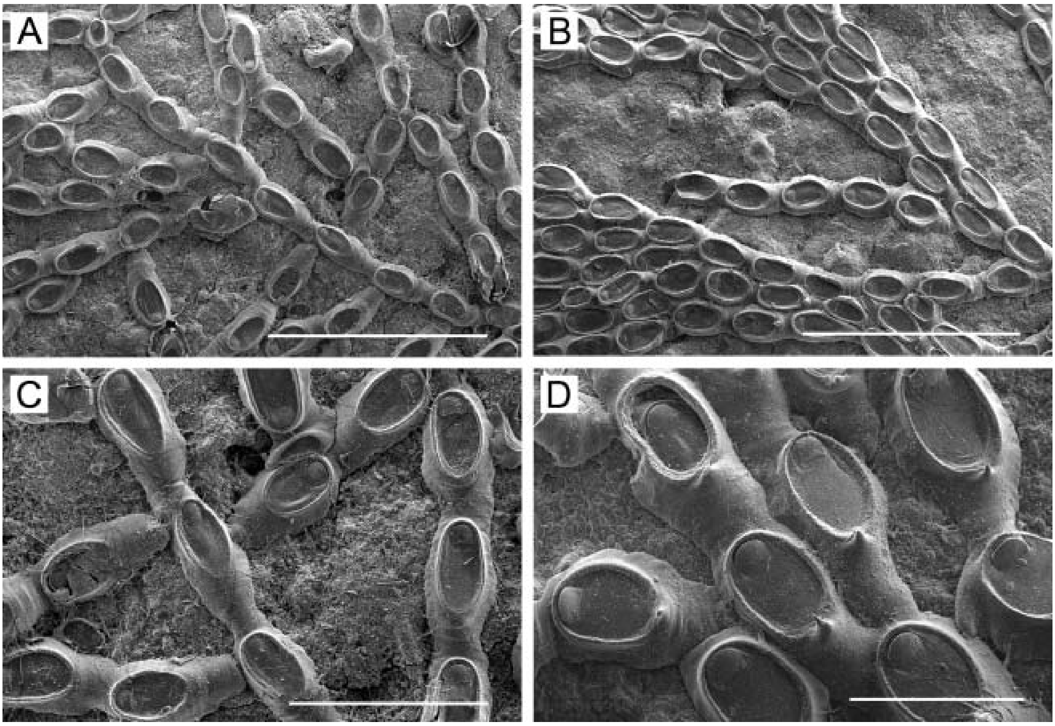

Figure 3. *Electra korobokkura* Nikulina, 2006. (A–C) NHM 2006.2.27.1; (D) NHM 2006.2.27.2. (A) Colony fragment with uniserial branches; (B) colony fragment with anastomosing, multiserial branches; (C) zooids without spinous processes; (D) zooids with spinous processes. All unbleached. Scale bars: 2 mm (A, B); 1 mm (C); 0.5 mm (D).

short, calcified spinous process (Figure 3D). Zooids interconnect via a few minute pores in the basal half of distal wall. Avicularia, lateral spines, ovicells, and hibernacules absent. Ancestrula not seen.

Remarks

Nikulina (2006) recently described this species from Akkeshi Bay. Among congeners, *Electra korobokkura* most closely resembles *Electra arctica* (Borg, 1931) in growth form, as both can form narrowly multiserial branches in portions of colonies. For comparison with *E. korobokkura* (Figure 3), we illustrate a subtidal specimen of what we consider to be *E. arctica*, from the western Kamchatka shelf, Sea of Okhotsk (Figure 4). This specimen illustrates all the characters considered diagnostic by Hansen (1962), who briefly reviewed *E. arctica*: well-developed gymnocyst (Figure 4B–D); enlarged base of proximal spine (Figure 4C, D); well-developed cryptocyst with a crenulated border (Figure 4D); more heavy calcification than in other *Electra* species; operculum heavily calcified, with the proximal border straight (in our specimen, there is intra-colony variation, with some opercula having a concave proximal border) (Figure 4D); the opesial opening restricted or reduced by a closure plate (Figure 4C) in some zooids; and a tendency to form kenozooids (Figures 4B–D) of reduced size among autozooids. Compared to *E. arctica*, *E. korobokkura*

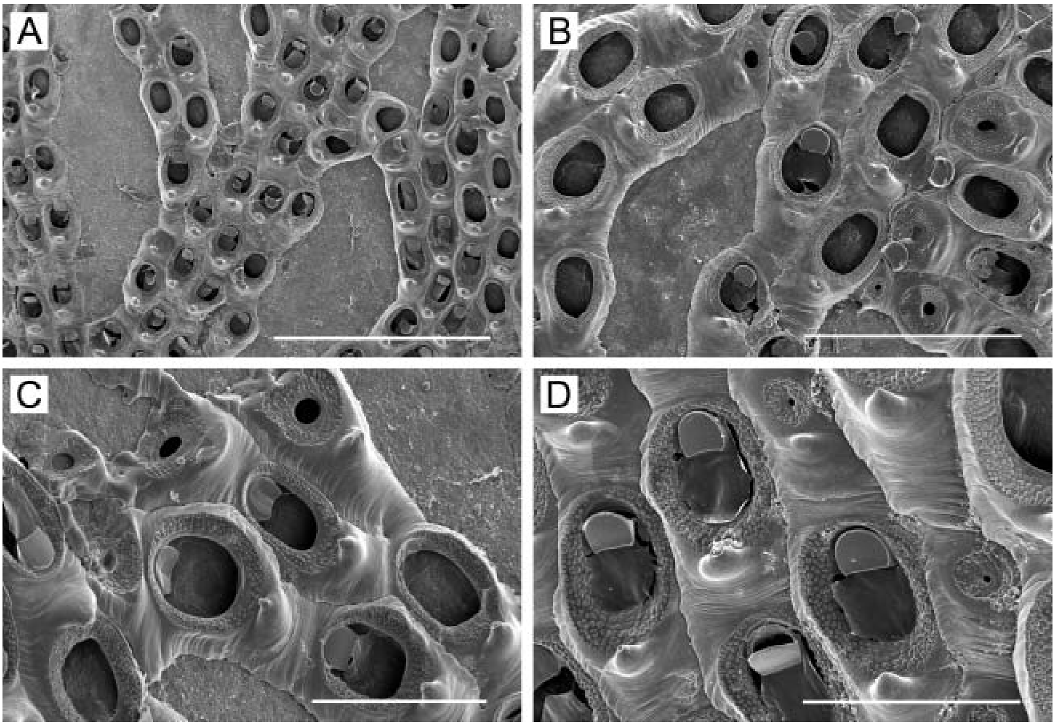

Figure 4. *Electra arctica* Borg, 1931. ZIRAS 36/50535. Colony on rock collected by A. V. Grischenko, 12 September 1992, Sea of Okhotsk, western Kamchatka shelf (57°36.03′N, 156°9.00′E), depth 78–81 m. (A) Portion of colony showing anastomosing, narrowly multiserial branches; (B) autozooids and kenozooids; (C) enlargement of autozooids and kenozooids; (D) autozooids with operculum in place and kenozooids with nearly completely closed aperture. Specimen lightly bleached. Scale bars: 2 mm (A); 1 mm (B); 0.5 mm (C, D).

has a greater tendency to form uniserial branches (compare Figure 3 with Figure 4). Compared to *Electra arctica*, zooids of *Electra korobokkura* appear less heavily calcified; the proximal gymnocyst has the transverse rugae weaker or lacking; the cryptocyst is narrower and much less heavily granulated, leaving a larger opesial opening in relation to overall zooid size; the operculum is less heavily calcified; and the basal chamber of the proximal spine is smaller. Furthermore, the closure plates of kenozooids have a smooth surface in *E. korobokkura* (Nikulina 2006, Figures 2, 3B, 4) whereas in *E. arctica* the closure plates have a broad, granulated component of cryptocystal calcification surrounding the opening (Figure 4C, D). Zooids of the *E. arctica* specimen we illustrate (Figure 4) are 0.42–0.73 mm long (0.57 ± 0.07 mm) by 0.22–0.48 mm wide (0.34 ± 0.06 mm), and the opesia is 0.20–0.33 mm long (0.26 ± 0.03 mm) by 0.12–0.21 mm wide (0.18 ± 0.02 mm). Thus, while the zooids of *E. arctica* are larger than those of *E. korobokkura*, the opesia of the former is roughly the same size or even smaller than that of the latter.

Distribution

Akkeshi Bay is the only known locality. Some previous records of nominal *E. arctica* in the northwestern Pacific (e.g. Mawatari 1956, 1974; Mawatari and Mawatari 1981b) may have included specimens of this species.

Electra asiatica new species

(Figure 5)

Electra crustulenta var. *baltica*: Kubanin 1976, p 31.
Electra baltica: Kubanin 1997, p 121; Grischenko 2002, p 113 (part).
Electra arctica: Nikulina 2006, p 28, Figure 5A–C.

Diagnosis

Colony coherent; opesia large; gymnocyst well developed; cryptocyst moderately well developed, the entire rim crenulate; chitinous spine well developed; base of spine variable in size; chitinized operculum contrasting sharply in colour with the transparent frontal membrane; colony uniserial only near ancestrula, rapidly giving rise to fan-shaped coherent sheets.

Etymology

The species name refers to this species' distribution in the northwestern (Asiatic) Pacific.

Material examined

Holotype: BAC, colony on bivalve shell (NHM 2006.2.27.19). Paratypes: BAC, colony on bivalve shell (NHM 2006.2.27.20); BAC, colony on bivalve shell (NHM 2006.2.27.21); KAI, colony on rock (NHM 2006.2.27.22); MIN, colony on rock (NHM 2006.2.27.23), colony on rock (NHM 2006.2.27.24). Additional material: 84 specimens from Akkeshi and one colony on a barnacle (*Balanus* sp.) fragment, Ptichiy Island (57°10′N, 156°35′E), western Kamchatka shelf, Sea of Okhotsk, lower intertidal, collected by A. V. Grischenko, 6 September 1992.

Description

Colony encrusting, unilaminar, radiating in coherent, fan-shaped lobes (Figure 5A, B) from point of origin, forming circular patches up to 2.8 cm across, whitish or light-yellowish when alive. Zooids oblong hexagonal, barrel-shaped, oval, or subrectangular, rounded distally, 0.45–0.80 mm long (0.56 ± 0.07 mm), 0.21–0.35 mm wide (0.30 ± 0.03 mm), arranged in linear series with almost parallel lateral walls, separated by deep grooves; boundaries between transverse walls indistinct; proximal frontal wall transversely convex. Mural rim raised, sharp. Cryptocyst (Figures 5E, F, H) narrower and nearly vertical distally and laterally, wider and gradually sloping proximally, granulated just inside mural rim, smooth around opesial margin. Basal wall calcified. Opesia oval, elliptical, or rounded-quadrate in outline, 0.25–0.48 mm long (0.36 ± 0.05 mm), 0.16–0.25 mm wide (0.20 ± 0.02 mm), occupying 60–80% of zooidal length. Frontal membrane thin, transparent; operculum strongly chitinized, semicircular, a sharply contrasting bright brown in colour. Gymnocyst (Figures 5C–F) smooth, relatively narrow distally and laterally, usually elongate and tapering proximally, often with minute transverse striations. In most zooids, the gymnocyst proximal to opesia rises to a conspicuous boss bearing a pointed chitinous spine (Figure 5D). Zooids interconnect by three to five circular multiporous septula in each lateral wall and by numerous small pores in basal half of distal wall. Avicularia, lateral spines, ovicells, and hibernacules absent. Small kenozooids

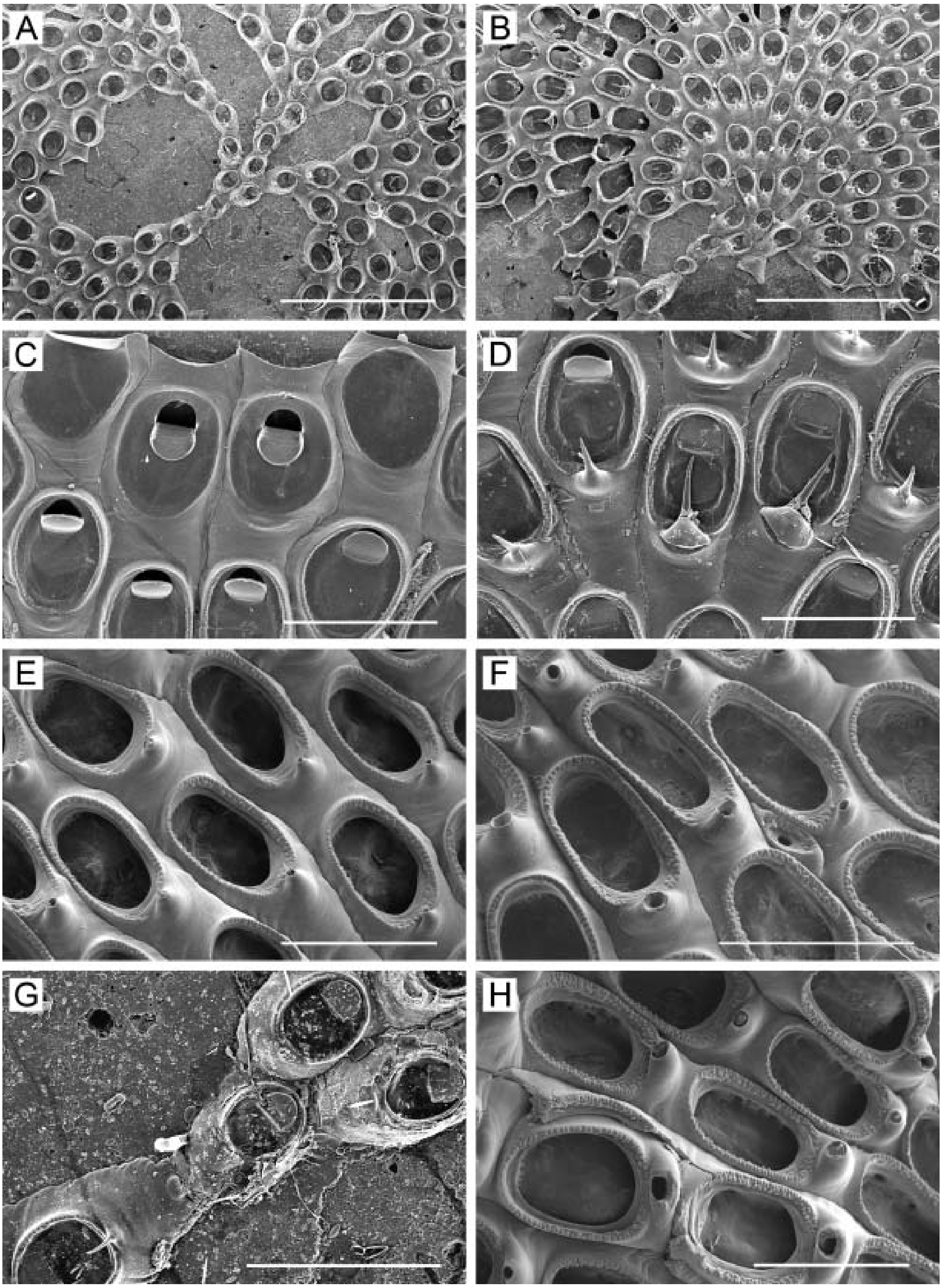

Figure 5. *Electra asiatica* n. sp. (A, G) NHM 2006.2.27.19; (B) NHM 2006.2.27.20; (C, D) NHM 2006.2.27.21; (E, F) NHM 2006.2.27.24. Colony from Ptichiy Island, Sea of Okhotsk (H). (A, B) Colonies radiating in coherent, fan-shaped lobes from the point of origin, unbleached; (C) colony margin with developing zooids, unbleached; (D) astogenetically mature zooids, unbleached; (E) astogenetically mature zooids, bleached; (F) astogenetically mature zooids with a small interzooidal kenozooid (lower right quadrant), bleached; (G) ancestrula and periancestrular zooids; enlargement of ancestrular area seen in panel (A), unbleached; (H) astogenetically mature zooids, bleached. Scale bars: 2 mm (A, B); 0.5 mm (C–H).

(Figure 5F) of irregular shape and size occur sparsely among autozooids; these are completely ringed by a granular cryptocyst and have a small, roughly circular opesia. Ancestrula (Figure 5G) tatiform, small, oval, about 0.40 mm long, 0.28 mm wide; opesia oval, 0.21 mm long, 0.18 mm wide. Ancestrula buds one (Figure 5B) or two (Figure 5A, G) small zooids distally and another proximally (Figure 5A, G) or proximolaterally.

Remarks

Among congeners, *E. asiatica* most closely resembles *E. baltica* (Borg, 1931) in having a similarly coherent colony, a large opesia, and a chitinized operculum contrasting sharply in colour with the transparent frontal membrane. Both species commonly have, proximal to the opesia, a knob terminating in a pointed chitinous spine. However, unlike *E. baltica*, chains of zooids of *E. asiatica* radiate and anastomose only close to the ancestrula, and subsequently form only fan-shaped multiserial sheets that do not diverge again into uniserial chains. In *E. asiatica*, the proximal gymnocyst is more extensive and the opesia is proportionately smaller than in *E. baltica*. Owing to the general similarity between these two species, previous investigators have likely interpreted the differences in zooid size and colony form as intraspecific variation in a single species, *E. baltica*. The records of *E. baltica* by Kubanin (1976, 1997) from numerous localities in the Far Eastern seas appear to be misidentifications of *E. asiatica*; a specimen from the intertidal zone of Ptichiy Island (Figure 5H) proved to be this species.

At Akkeshi, *E. asiatica* is often found growing close to *E. korobokkura* on the same substratum, particularly on dead bivalve shells. *Electra asiatica* has larger zooids than *E. korobokkura* (compare Figure 5C–E, H with Figure 3D at the same scale), a difference readily apparent in specimens close to one another. Nikulina (2006) illustrated and discussed this size difference, but identified the species with larger zooids as *E. arctica*.

Distribution

We consider Kubanin's (1976, 1997) *E. baltica* to be synonymous with *E. asiatica*. To the extent that all of Kubanin's records represent correct identifications of the latter, *E. asiatica* is widely distributed in the northwestern Pacific: southeastern Kamchatka (Kamchatsky, Kronotsky, and Avacha Gulfs); northern and northeastern coast of the Sea of Okhotsk (southwestern Kamchatka; Penzhinskaya, Gizhiginskaya, Yamskaya, and Taujskaya Inlets; Okhotsk; Ayan; Zavyalov Island); southern and southeastern coast of Sakhalin Island (Terpeniya and Aniva Gulfs); northern Sea of Japan (southwestern coast of Sakhalin Island and Moneron Island). Akkeshi Bay is the southernmost known locality.

Genus *Conopeum* Gray, 1848

Conopeum nakanosum new species

(Figure 6)

? *Conopeum reticulum*: Mawatari 1956, p 115, Figure 1e; 1974, p 33, Figure 5.

Diagnosis

Zooids large; opesia about 70–80% of zooidal length; cryptocyst widest proximally, finely tuberculate; gymnocyst hidden; all zooids with a triangular, cone-shaped kenozooid at each distal corner; kenozooids with small, distally facing opesial opening in central depression,

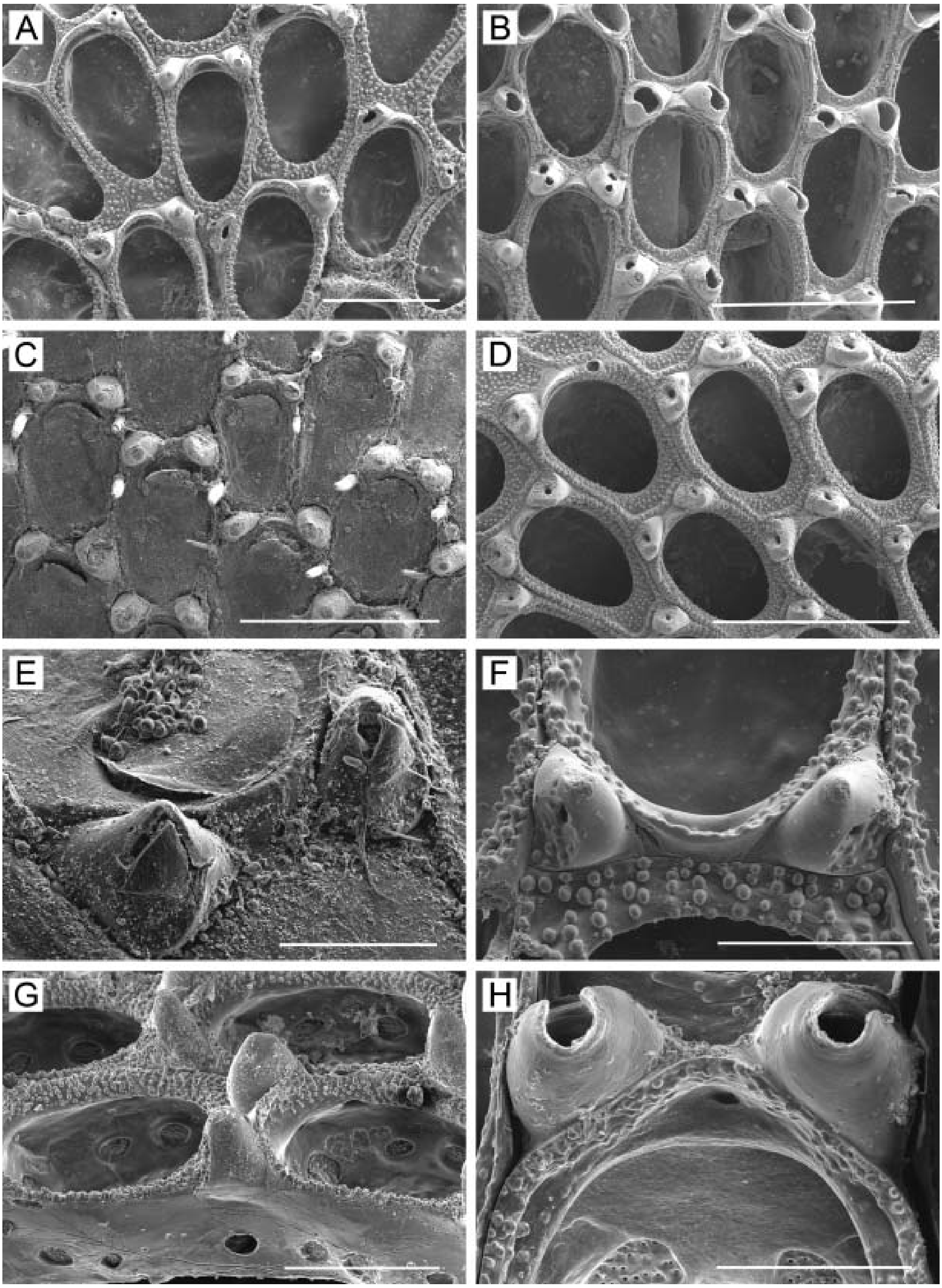

Figure 6. *Conopeum nakanosum* n. sp. (A, F) NHM 2006.2.27.26; (B, D) NHM 2006.2.27.27; (C, E) NHM 2006.2.27.25; (G, H) NHM 2006.2.27.28. (A) Colony margin with differentiating zooids, bleached; (B) zooids with developing angular cone-shaped kenozooids, bleached; (C) mature zooids with erect and curved spines, unbleached; (D) group of mature zooids with granulated cryptocyst, bleached; (E) distally facing triangular avicularia replacing kenozooids, unbleached; (F) distal view of kenozooids, bleached; (G) lateral view of zooids showing multiporous septula, bleached; (H) interior of distal zooidal wall showing developing angular kenozooids and also multiporous septula, bleached. Scale bars: 0.5 mm (A, G); 1 mm (B–D); 0.2 mm (E, F, H).

sometimes transformed into an avicularium with triangular, vertically orientated mandible; two to three spines occasionally present around mural rim. Ovicells absent. Multiporous septula in lateral and transverse wall.

Etymology

The species name refers to Nakanose Bank in Akkeshi Bay, where the holotype specimen was collected subtidally.

Material examined

Holotype: NB, intact colony (NHM 2006.2.27.25). Paratypes: ANC, young intact colony (NHM 2006.2.27.26); NB, five pieces of a single colony (NHM 2006.2.27.27); NB, five pieces of a single colony (NHM 2006.2.27.28). Additional material: one specimen.

Description

Colony encrusting, multiserial, sheet-like, up to 3.5 cm across, greyish when alive, with purple to reddish marginal zone one or two developing zooids deep. Zooids (Figure 6A, B, D) oval, hexagonal, or subquadrangular, widest in middle, 0.67–0.95 mm long (0.81 ± 0.09 mm), 0.40–0.50 mm wide (0.45 ± 0.02 mm), separated by fine sutures between raised lateral walls. Opesia oval, elliptical, or rounded-rectangular; 0.55–0.73 mm long (0.63 ± 0.04 mm), 0.30–0.43 mm wide (0.36 ± 0.03 mm); occupying 70–80% of zooidal length. Cryptocyst (Figure 6A, F) extending around entire opesia; steep and narrow laterally, flatter and wider proximally, reduced distally, finely tuberculate below mural rim. Lateral and proximal gymnocyst hidden between adjacent zooids. Distal gymnocystal wall raised slightly above level of lateral wall into a smooth, narrow, sharp-edged crescentic lip separated from cryptocyst by a transverse, slit-like cavity. At each distal corner is a raised, cone-shaped, subtriangular kenozooid (Figure 6F, H); sharp or blunt on top, smooth except for depressed, finely granulated cryptocystal area distolaterally, surrounding a small, circular to oval opesial opening. Kenozooids at first have this cryptocystal area covered with transparent membrane, but later often become closed to form a pair of knobs, rarely vestigial or lacking. Sometimes kenozooids are transformed into avicularia (Figure 6E) with a distolateral rostral face; mandible triangular with sharp, hooked, vertically orientated tip; such avicularia are rare, developing only in mature regions of the colony. Mural rim often with two or three spines (Figure 6C): a straight, blunt hollow tubular spine on one or both sides of orifice, in line with proximal orificial margin, jointed at base; another finer, curved, acute spine more proximally on one side, slightly arching over opesia. Like the avicularia, the spines tend to appear in mature regions of the colony; many young zooids lack them altogether. Ovicells lacking, but raised mural rim distally with transverse, slit-like cavity below (Figure 6F) may represent kenozooidal ooecium. Four oval multiporous septula (Figure 6G) in each lateral wall and two septula in transverse wall. Ancestrula not observed.

Remarks

In zooidal characters, *C. nakanosum* is very similar to *Conopeum reticulum* (L., 1767), the type species of the genus, especially in having triangular kenozooids at the distal angles of autozooids. However, these two species differ in several characters. In *C. reticulum*, the kenozooids develop predominantly on older zooids, whereas in *C. nakanosum* they occur on all zooids, at all astogenetic stages. With increasing calcification in *C. reticulum*, the pair of kenozooids occasionally comes into contact along the entire distal end of the zooid, forming a single, dumbbell-shaped unit. The kenozooids of *C. nakanosum* are always separated by a raised, crescentic gymnocystal lip. The opesial opening in the central depression of the kenozooids is terminal on the knob and facing upward in *C. reticulum*, whereas it always faces distally or distolaterally in *C. nakanosum*. Finally, zooid size in *C. nakanosum* exceeds that of *C. reticulum*, and the ranges do not overlap: zooids are 0.67–0.95 mm long by 0.40–0.50 mm wide in the former, compared to 0.4–0.6 mm long by 0.2–0.3 mm wide in the latter (Hayward and Ryland 1998).

There has been some confusion over the nature of the distal kenozooids in *Conopeum*, and both Osburn (1950) and Mawatari (1974) were sceptical that these represented vestigial avicularia or ever formed true avicualaria. However, there is no doubt that in *C. nakanosum* the distolateral kenozooids can be replaced by avicularia. This does not occur on every zooid, but usually only among a few zooids in a mature region of a colony. It remains unclear whether the possible occurrence of avicularia in place of the kenozooids should be incorporated into the generic diagnosis of *Conopeum*. Another anascan, *Crassimarginatella leucocypha* Marcus, 1937, described from Brazil and subsequently reported by Mawatari (1952) from the Kii Peninsula, Sea of Japan, is morphologically similar to *C. nakanosum* in having angular kenozooids that can transform into an avicularium (see Marcus 1937, p 46, Plate 8, Figure 20A). The apparent lack of ovicells in the former suggests *Conopeum* rather than the calloporid *Crassimarginatella*. The kenozooids in this species are more extensive than in *C. nakanosum*, with a more central opesial opening, and there has been no mention of spines.

Distribution

Akkeshi Bay is the only known locality for *C. nakanosum*. Mawatari's (1956) short description and illustration of *C. reticulum* from the Kuril Islands (Alaid and Paramushir) and from Hokkaido (Akkeshi Bay and Kushiro) suggest he might have had *C. nakanosum* instead.

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 7)

Membranipora craticula Alder 1856, p 144, Plate 8, Figure 3.

Callopora craticula: Osburn 1950, p 67, Plate 6, Figure 7; Androsova 1958, p 96, Figure 7; Kluge 1962, p 288, Figure 171; 1975, p 344, Figure 171; Gontar 1979, p 235; 1980, p 5; Mawatari and Mawatari 1980, p 40, Figure 8; 1981b, p 45; Dick and Ross 1988, p 33, Plate 1C; Kubanin 1997, p 121; Grischenko 1997, p 160; 2002, p 113; Hayward and Ryland 1998, p 164, Figure 42, C; Dick et al. 2005, p 3696, Figure 2A–D.

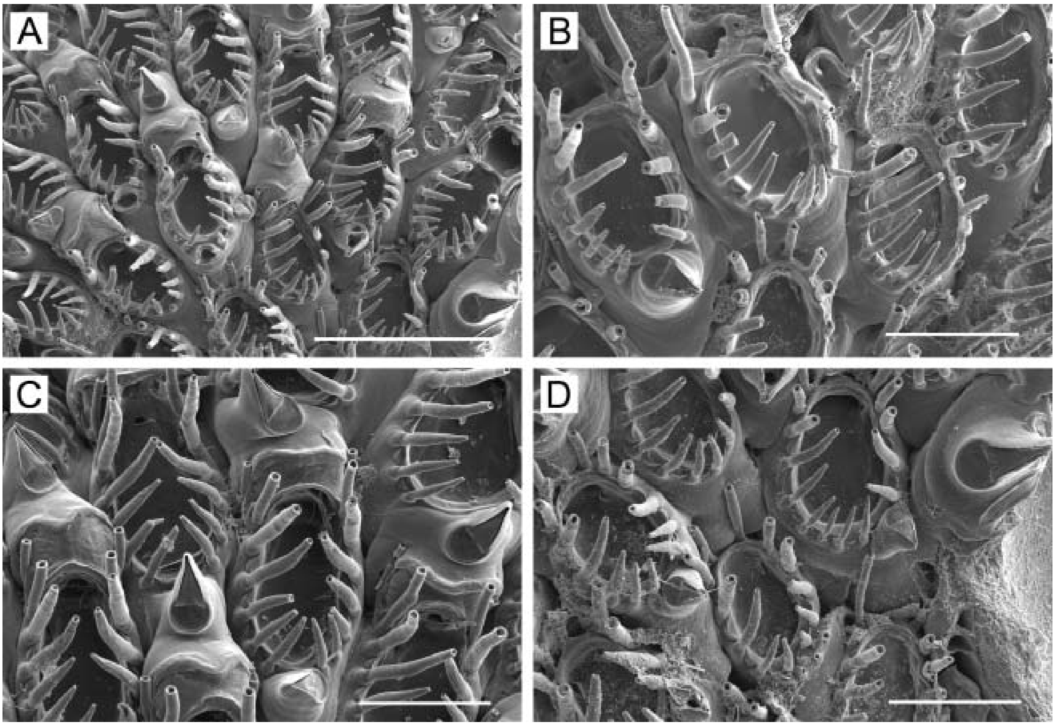

Figure 7. *Callopora craticula* (Alder, 1856). NHM 2006.2.27.29. (A) General view of colony fragment, unbleached; (B) immature zooids near colony margin, unbleached; (C) mature zooids showing ovicells and associated avicularia, unbleached; (D) group of immature zooids and vicarious avicularium on right, unbleached. Scale bars: 0.5 mm (A); 0.2 mm (B–D).

Material examined

ANC, colony encrusting erect bryozoan *Phidolopora elongata* (NHM 2006.2.27.29); ACT, colony encrusting erect bryozoan *Phidolopora elongata* (NHM 2006.2.27.30). Additional material: one specimen.

Description

Colony encrusting, unilaminar, multiserial, more or less circular, small, less than 1 cm across, whitish to yellowish in colour when alive. Zooids (Figure 7A–D) elongate-oval, broadest in middle, narrowing proximally, 0.30–0.45 mm long (0.35 ± 0.04 mm), 0.15–0.25 mm wide (0.20 ± 0.02 mm), separated by deep grooves. Mural rim raised, sharp. Cryptocyst a narrow, smooth, sloping shelf inside marginal rim. Opesia oval, often widest proximally, 0.16–0.21 mm long (0.18 ± 0.02 mm), 0.09–0.14 mm wide (0.11 ± 0.01 mm), 60–70% of zooidal length. Gymnocyst smooth, laterally narrow and sloping, proximally smooth, extensive, tapering, occupying up to 30–40% of zooid length. Spines 12–16 around mural rim; distal three pairs hollow, longer, and vertical; proximal 6–10 spines thinner, acuminate, arched over opesia, converging at or near midline, becoming progressively shorter toward proximal end of zooid. Frontal avicularia with raised chamber on proximal gymnocyst, close to opesial margin, often abutting ovicell of preceding zooid; avicularian chamber with nearly vertical sides, cross-bar complete, mandible long-triangular, usually pointing distally or distolaterally if preceded by ovicell, laterally or proximally if not. Vicarious avicularia (Figure 7D) occur sporadically; almost as large as autozooids, with raised, acute, long-triangular mandible pointing distally. Ovicells (Figure 7A, C) hyperstomial, prominent, globular, imperforate, 0.09–0.14 mm long (0.11 ± 0.02 mm), 0.12–0.16 mm wide (0.14 ± 0.01 mm), with a decurved transverse ridge across top marking proximal extent of ectooecium, separated from proximal ooecial margin by a lunate or quadrate area. Four pore chambers in each lateral wall and three or four single pores in distal wall. Ancestrula not observed.

Distribution

This is a circumpolar, Arctic-Boreal species. Gontar and Denisenko (1989) summarized numerous previous records from the Arctic. In the eastern Atlantic, *C. craticula* extends southward to Scotland and northern England in Britain (Hayward and Ryland 1998), but its occurrence in the western Atlantic is uncertain (Winston et al. 2000). In the eastern Pacific it extends as far south as Ketchikan (Dick et al. 2005). In the western Pacific, it has been recorded from Saint Lawrence Island, Avacha Inlet (Kluge 1961), Commander Islands (Grischenko 1997, 2004), Sea of Okhotsk, Kuril Islands (Gontar 1980), northern Sea of Japan along Primorye and western Sakhalin Islands (Androsova 1958), and from Kushiro, Akkeshi, and Hakodate on Hokkaido, northern Japan (Mawatari and Mawatari 1980, 1981b).

Callopora sarae new species
(Figure 8)

Diagnosis

Opesia 60–85% of zooidal length; 17–25 spines with enlarged, cylindrical bases around mural rim, including three pairs of thick, vertical distal spines (the most proximal pair by far heavier than the rest), 12–17 thin proximal spines arched over opesia, and often one or two additional thin spines present on outer distolateral gymnocyst; avicularia small, on lateral or proximal gymnocyst, usually single, rarely paired, associated with distal half of ovicell in mature zooids; ovicell with a wide transverse tabula; transverse ridge often enlarged into a median knob; proximal ovicell margin raised as a wide lip; zooids interconnect by multiporous septula.

Etymology

The species is named in honour of Sarah Taranto, who collected the holotype specimen.

Material examined

Holotype: MAC, colony on rock (NHM 2006.2.27.4). Paratypes: MAC, colony on rock (NHM 2006.2.27.3); MAC, colony on rock (NHM 2006.2.27.5). Additional material: four specimens.

Description

Colony encrusting, unilaminar, multiserial, irregular in shape, up to 2.1 cm in maximum dimension, whitish to light yellow in colour when alive. Zooids (Figure 8A–F) elongate-oval,

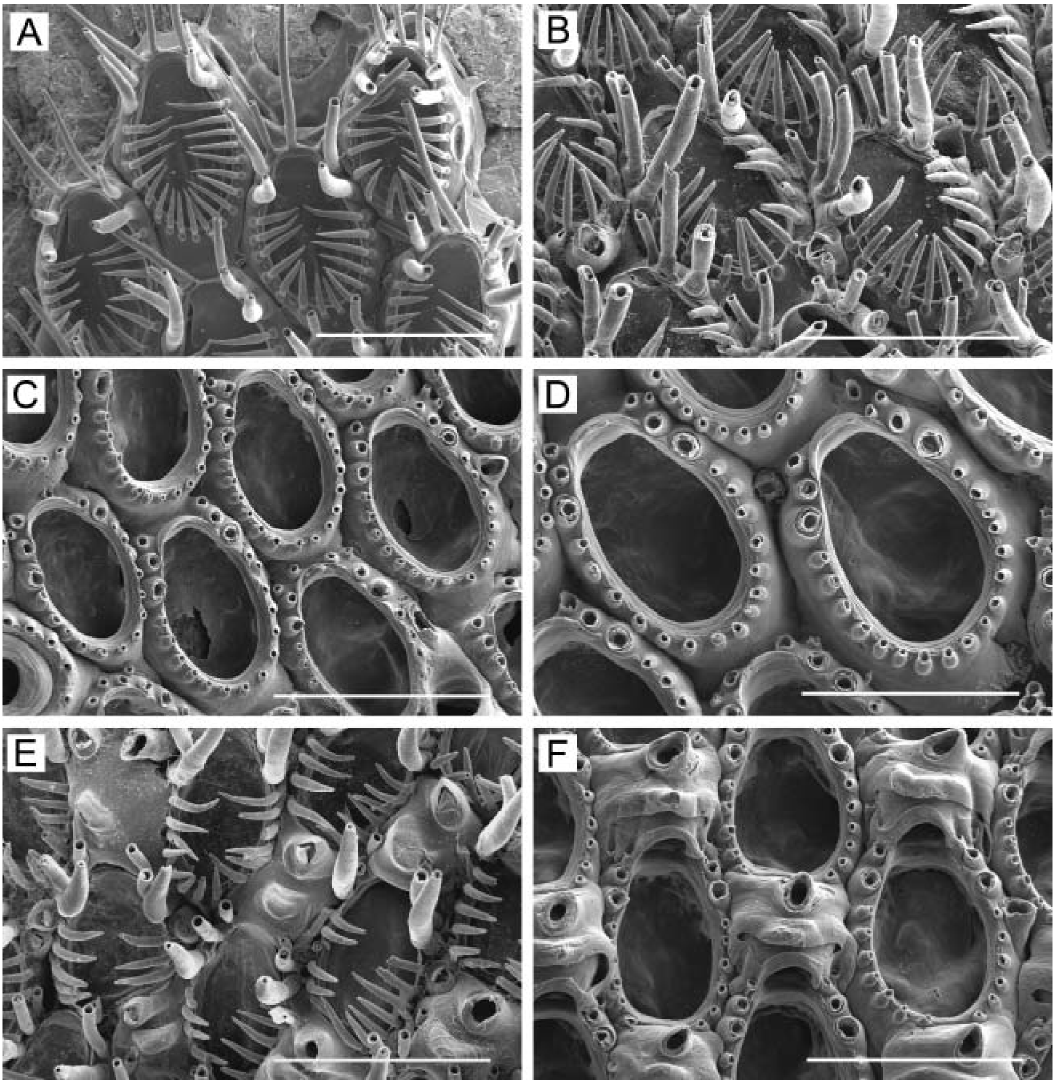

Figure 8. *Callopora sarae* n. sp. (A, E) NHM 2006.2.27.5; (B) NHM 2006.2.27.3; (C, D, F) NHM 2006.2.27.4. (A) Zooids at colony edge, unbleached; (B) immature zooids with spines, lateral and proximal avicularia, unbleached; (C) immature zooids, showing bases of spines and lateral avicularia, bleached; (D) two immature zooids showing bases of additional spines on outer distolateral gymnocyst, bleached; (E) mature zooids with ovicells and associated avicularia, unbleached; (F) mature zooids with heavily calcified ovicells, bleached. Scale bars: 0.5 mm (A–C, E, F); 0.4 mm (D).

hexagonal, or pyriform, 0.38–0.60 mm long (0.50 ± 0.06 mm), 0.20–0.33 mm wide (0.28 ± 0.04 mm), demarcated by deep, narrow grooves when young, more closely appressed when mature. Mural rim raised, sharp, smooth. Cryptocyst reduced, narrow, with parallel horizontal folds, non-granulated, sloping abruptly below marginal rim. Distal and lateral gymnocyst smooth, sloping and narrow; proximal gymnocyst variably developed, occasionally tapering, up to 25% of zooid length, entirely covered by ovicell in mature zooids. Opesia (Figure 8C, D) oval to pyriform, widest in middle or proximally, 0.27–0.38 mm long

(0.33 ± 0.03 mm), 0.16–0.24 mm wide (0.20 ± 0.02 mm), occupying 60–85% of zooidal length. Around mural rim 17–25 spines (Figure 8A, B) with enlarged, cylindrical bases; the three distal pairs thick, hollow, long, vertical, leaning slightly over opesia but curving outwards, their bases heavily calcified and rising above plane of mural rim; proximal 12–17 spines thinner, acuminate, arched over opesia, becoming progressively shorter towards proximal end of zooid; in addition, one or two thin, short tubular spines often present on outer distolateral gymnocyst. Small frontal avicularium (Figure 8C, E, F) with raised chamber occupies outer slope of lateral gymnocyst on one side, usually near middle, sometimes more proximally or on proximal gymnocyst; mandible triangular, with acute, hooked tip, pointing in any direction; rarely avicularia paired, laterally arranged on opposite sides of opesia, or on lateral and proximal gymnocyst; some zooids lack avicularia altogether; ovicellate zooids have a similarly small avicularium on distal half of ovicell, pointing distally or distolaterally. Ovicells (Figure 8F) hyperstomial, prominent, spherical, imperforate, about as long as broad, 0.18–0.23 mm long (0.20 ± 0.02 mm), 0.16–0.28 mm wide (0.21 ± 0.03 mm); outer surface smooth; proximal margin of ectooecium enlarged as a thick transverse ridge, often with a blunt, wide median knob; proximal margin of endooecium a wide, raised lip; between entooecial and ectooecial margins is a transverse, dumbbell-shaped tabula covered by ectocyst; ovicell heavily calcified, entirely covering proximal gymnocyst of zooid beneath and reaching lateral walls of neighbouring zooids, extending between spine bases. Four oval to circular multiporous septula in each lateral wall and two septula in transverse wall. Ancestrula not observed.

Remarks

Callopora sarae is similar to *C. corniculifera* (Hincks, 1882), a Boreal species reported from both sides of the Pacific (see Soule et al. 1995, p 66, Plate 16A, B), in having small lateral avicularia. However, *C. corniculifera* has larger zooids (0.65–0.70 mm long by 0.45–0.50 mm wide); roughly half the number of spines (10–12); and a smaller avicularium situated along the lateral margin only, in line with the proximal orificial margin.

Callopora decidua Dick and Ross, 1988, described from Kodiak, Alaska, also has a high spine number, 14–21, including three pairs of heavy distal spines, as well as small, single or paired lateral avicularia; however, in this species, proximal avicularia are rare unless preceded by an ovicell, and when they occur, the rostrum is long and curved.

Callopora longispinosa Androsova, 1958, distributed in the northwestern Pacific, is similar to *C. sarae* in having two or three pairs of long, stout distal spines, occasionally 1.5–2 times or more the length of the zooid (Grischenko 1997); however, this species differs from *C. sarae* in having fewer proximal spines (four to six); avicularia rare and located on the proximal gymnocyst only; and the spherical ovicells weakly calcified and not associated with avicularia.

Distribution

Akkeshi Bay is the only known locality.

Genus *Cauloramphus* Norman, 1903

Cauloramphus cryptoarmatus new species

(Figure 9)

? *Cauloramphus spiniferus* [sic]: Liu et al. 2001, p 458, Plate 20, Figures 2–4.

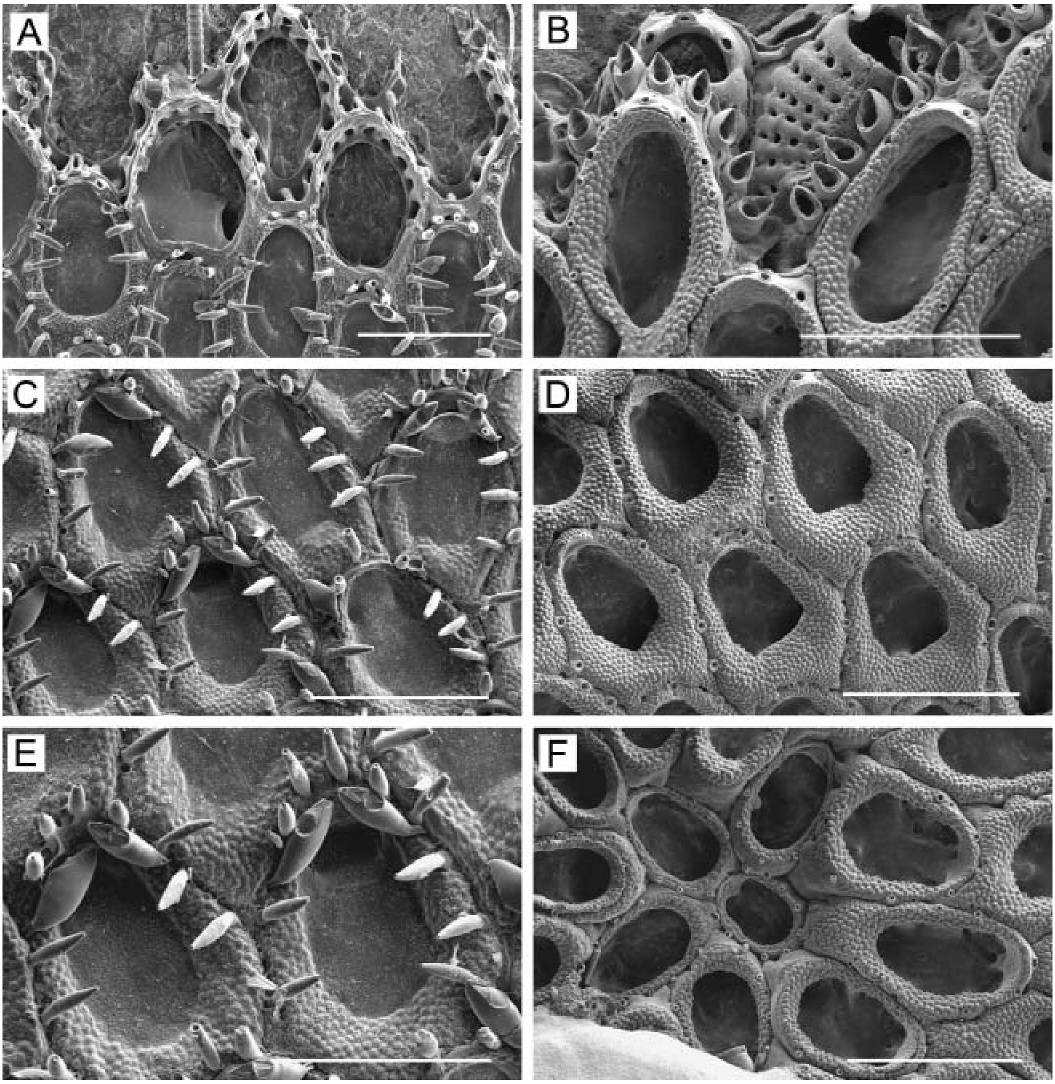

Figure 9. *Cauloramphus cryptoarmatus* n. sp. (A, C, E) NHM 2006.2.27.14; (B, F) NHM 2006.2.27.31; (D) NHM 2006.2.27.13. (A) Colony margin with developing zooids, unbleached; (B) zooids at colony margin in interaction with *Cribrilina annulata*, showing numerous additional avicularia developing along vertical walls from pore chambers, bleached; (C) autozooids, unbleached; (D) autozooids, showing strongly developed granulated cryptocyst, bleached; (E) two zooids showing details of avicularia and spines, unbleached; (F) ancestrula surrounded by periancestrular zooids, bleached. Scale bars: 0.5 mm (A–D, F); 0.4 mm (E).

Diagnosis

Zooids closely appressed; gymnocyst negligible; cryptocyst strongly developed, widest proximally, entirely and uniformly coarsely granulate; 8–10 spines, generally short, not meeting in opesial midline, including two to four straight orificial and four to six thin, curved opesial spines; avicularia commonly paired, originating between orificial and opesial spines, approximately lateral to proximal orificial border, with short, thin pedicel abruptly expanding into curved chamber; non-pedunculate avicularia can arise from pore chambers at colony margin, sometimes in abundance.

Etymology

The species name is from the Greek *kruptos* (hidden) and Latin *armatus* (armed), referring to the occurrence of small marginal avicularia, which are unusual for the genus.

Material examined

Holotype: ANC, colony on rock (NHM 2006.2.27.14). Paratypes: ANC, colony on rock (NHM 2006.2.27.13); ANC, colony on rock (NHM 2006.2.27.31). Additional material: 80 specimens.

Description

Colony unilaminar, encrusting, coherent, irregularly circular in outline, up to 2.2 cm across; light yellow, greyish, or whitish when alive. Zooids (Figure 9A–F) very variable in form: oval, irregularly hexagonal, pyriform, tapering, or irregular; 0.52–0.73 mm long (0.60 ± 0.06 mm), 0.30–0.40 mm wide (0.35 ± 0.03 mm); closely appressed, separated by shallow groove with fine, undulating suture. Mural rim cryptocystal (Figure 9B, D, E); wide, rounded, tumid, entirely covered with uniform, coarse granules; relatively narrow and steep distally, widening laterally, widest proximally; opesiae well separated. Gymnocyst greatly reduced, negligible. Opesia (Figure 9B, D, E) irregularly oval, often with straight proximal margin, widest in middle or more proximally, 0.32–0.40 mm long (0.37 ± 0.02 mm), 0.17–0.27 mm wide (0.20 ± 0.02 mm), occupying 60–75% of zooidal length. Mural rim with 8–10 spines (Figure 9C, E), including three or four hollow, straight, vertically orientated orificial spines, arranged in a semicircle around distal curvature of orifice, that are slightly longer, thicker, and blunter than the rest; and four to six short, thin, acuminate spines curving over opesia. Pedunculate avicularia (Figure 9E) originate from distolateral gymnocyst between orificial and opesial spines, approximately in line with proximal edge of orifice; longer than distal spines, with comparatively short, thin peduncle abruptly expanding into curved chamber; orientated vertically or angling over opesia, with rostral side facing proximolaterally; mandible narrow, elongate-triangular; avicularia commonly paired, sometimes single; rarely zooids lack them altogether. Where colonies of *C. cryptoarmatus* encounter other bryozoan species, zooids at the colony margin can produce numerous (up to nine) small, closely set additional avicularia (Figure 9B), each developing from a pore chamber along the free distal and distolateral walls; these avicularia non-pedunculate, chamber slightly elevated; mandible triangular, with sharp tip. Embryos brooded endozooidally; fertile zooids have a small kenozooidal ooecium (Figure 9D) comprising the mural rim distal to the orifice. Six pore chambers in each lateral wall and two or three in distal wall. Ancestrula (Figure 9F) tatiform, oval, 0.28 mm long, 0.20 mm wide, with large, oval opesia, 0.19 mm long by 0.13 mm wide, with 12 short, hollow spines. Ancestrula (Figure 9F) buds triplet of small zooids distally and distolaterally; eventually surrounded by seven zooids.

Remarks

Cauloramphus cryptoarmatus resembles eastern-Pacific *C. variegatus* (Hincks, 1881) and *C. tortilis* Dick et al., 2005 and Korean *C. korensis* Seo, 2001 in having closely appressed zooids with a broad, cryptocystal mural rim uniformly covered with coarse granules. However, in *C. variegatus*, the bases of the spines are yellowish brown to black in colour (Dick and Ross 1988), and their number, shape, and arrangement are different: there are three pairs of blunt, cylindrical distal spines and two to six much finer, acuminate proximal spines curved over the opesia, with the tips often converging near the midline. *Cauloramphus tortilis* has more and longer spines (9–15 heavy, elongate spines, with strong bases conspicuous after bleaching), and the pedunculate avicularia are as long as the longest spines, with a peduncle that is twisted around the spine near which it originates. *Cauloramphus korensis* is similar in having a coarsely granulated cryptocyst widest proximally (Seo 2001). However, *C. korensis* has dark spines that are brown or violet in colour, fewer total spines (five to nine) and fewer orificial spines (one to three), and the proximalmost opesial spines originating close to the edge of the opesia (see Seo 2001, Figure 1A) rather than at the zooidal margin. Furthermore, the pedunculate avicularium of *C. korensis* is quite curved in the rostral direction, whereas that of *C. cryptoarmatus* is fusiform. Finally, the kenozooidal ooecium of *C. korensis* is larger and more conspicuous than that of *C. cryptoarmatus*. The non-pedunculate marginal avicularia observed in some colonies of *C. cryptoarmatus* have not been reported in the other species just mentioned.

Distribution

Cauloramphus cryptoarmatus is presently known only from Akkeshi Bay.

Cauloramphus magnus Dick and Ross, 1988

(Figure 10)

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

Cauloramphus magnus: Grischenko 1997, p 163; 2004, p 40; Dick et al. 2005, p 3700, Figure 2E–H.

Cauloramphus cymbaeformis: Dick and Ross 1986, p 89.

Cauloramphus spinifer: Kubota and Mawatari 1985a, p 80, Figure 5.

Material examined

ANC, ancestrular colony on rock (NHM 2006.2.27.32), colony on rock (NHM 2006.2.27.54), two extensive colonies on rock (NHM 2006.2.27.33–34); DIN, two colony fragments (NHM 2006.2.27.35). Additional material: 97 specimens; also several colonies on stones from Oshoro Bay, Hokkaido, Sea of Japan.

Description

Colony up to 2.8 cm across, light yellow to tan when alive. Zooids (Figure 10A–F) 0.57–0.80 mm long (0.67 ± 0.07 mm), 0.32–0.48 mm wide (0.39 ± 0.04 mm), separated by a distinct, shallow groove. Cryptocyst (Figure 10E) narrow, sloping, coarsely granulate. Gymnocyst mostly reduced, smooth; occasionally tapering back between preceding zooids. Opesia 0.37–0.53 mm long (0.44 ± 0.04 mm), 0.20–0.30 mm wide (0.26 ± 0.03 mm), with crenulate margin, occupying 70–90% of zooidal length. Around mural rim, 11–18 spines; five or six distal spines hollow, straight, thicker and blunter than the rest; proximal 6–12 spines considerably thinner, sharp, curved, arched over opesia, well separated, occasionally meeting in midline; in some zooids, most proximal spine erect, hollow, thicker and longer than others, similar in length to distal spines. Avicularia (Figure 10D) generally rare, usually single when present, originating from gymnocyst between proximal and distal spines (Figure 10C, D); slightly longer than distal spines, with relatively long, thin pedicel

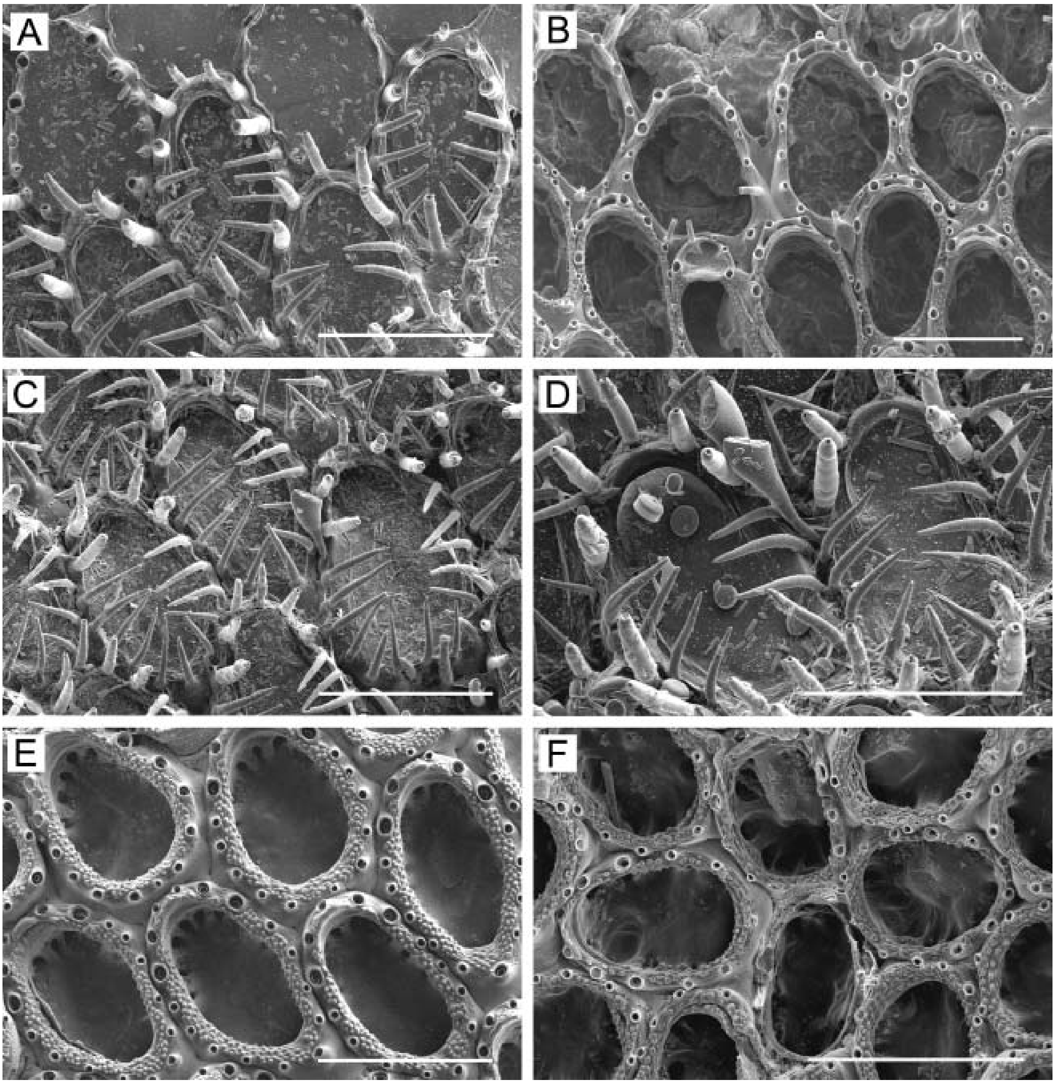

Figure 10. *Cauloramphus magnus* Dick and Ross, 1988. (A, C, D) NHM 2006.2.27.33–34; (B) NHM 2006.2.27.54; (E) NHM 2006.2.27.35; (F) NHM 2006.2.27.32. (A) Colony margin with developing zooids, unbleached; (B) same, bleached; (C) autozooids, unbleached; (D) close up of autozooids showing details of avicularia and spines, unbleached; (E) autozooids, bleached; (F) ancestrula and periancestrular zooids, bleached. Scale bars: 0.5 mm (A–C, E, F); 0.4 mm (D).

gradually expanding into heavy, slightly curved chamber with terminally facing rostrum; mandible triangular, directed laterally. Embryos brooded endozooidally; fertile zooids with a small kenozooidal ooecium (Figure 10E) occupying distal portion of mural rim. Six pore chambers in each lateral wall and three in distal wall. Ancestrula (Figure 10F) tatiform, elongate-oval, 0.42 mm long, with about 16 spines along opesial margin. Ancestrula buds triplet of small zooids distally and distolaterally, each with 8–12 spines; ancestrula surrounded by six zooids.

Remarks

Specimens from Hokkaido agree well with the original description (Dick and Ross 1988) of *C. magnus* from Kodiak Island, Gulf of Alaska. Both zooidal and opesial sizes are similar, but the spine number is greater at Akkeshi (11–18 compared to 11–14); a population from Ketchikan, Alaska (Dick et al. 2005) also had more spines (12–18) than material from the type locality.

Distribution

This is a Boreal Pacific species, reported in the eastern Pacific from Kodiak Island in the western Gulf of Alaska (Dick and Ross 1988) and Ketchikan in southern southeast Alaska (Dick et al. 2005). In the western Pacific, it has been reported from the Commander Islands (Grischenko 1997, 2004), though this material needs reexamination by SEM. We also collected this species at Oshoro Bay (Hokkaido), which is the southernmost known locality for *C. magnus*.

Cauloramphus multispinosus new species

(Figure 11)

Diagnosis

Zooids large, oval, demarcated by groove; opesia large, up to 85% of zooidal length; cryptocyst narrow, granulated; gymnocyst reduced, smooth; 20–26 spines around mural rim; distal spines long, heavy, straight or nearly so; proximal spines very thin, sharp, curved and arched over opesia to meet nearly horizontally at midline; avicularia not observed and may be absent in this species; ancestrula tatiform.

Etymology

The species name refers to the unusually large number of spines.

Material examined

Holotype: KAI, two colonies on rock (NHM 2006.2.27.36). Paratypes: KAI, four colony fragments (NHM 2006.2.27.37); KAI, colony on rock (NHM 2006.2.27.38); KAI, colony on rock (NHM 2006.2.27.39); KAI, ancestrular colony on rock (NHM 2006.2.27.40). Additional material: 221 specimens; also several colonies on stones from Oshoro Bay, Hokkaido, Sea of Japan.

Description

Colony unilaminar, encrusting, coherent, forming extensive irregular patches up to 4 cm in maximum dimension, yellow to tan when alive. Zooids (Figure 11A–F) large, oval or rounded-hexagonal, occasionally tapering or pyriform, 0.55–0.98 mm long (0.75 ± 0.10 mm), 0.37–0.55 mm wide (0.46 ± 0.04 mm), demarcated by a deep, narrow groove. Mural rim sharp and comprises the boundary between smooth gymnocyst and granulated cryptocyst. Cryptocyst (Figure 11D, E) narrow, steep distally and laterally, sloping

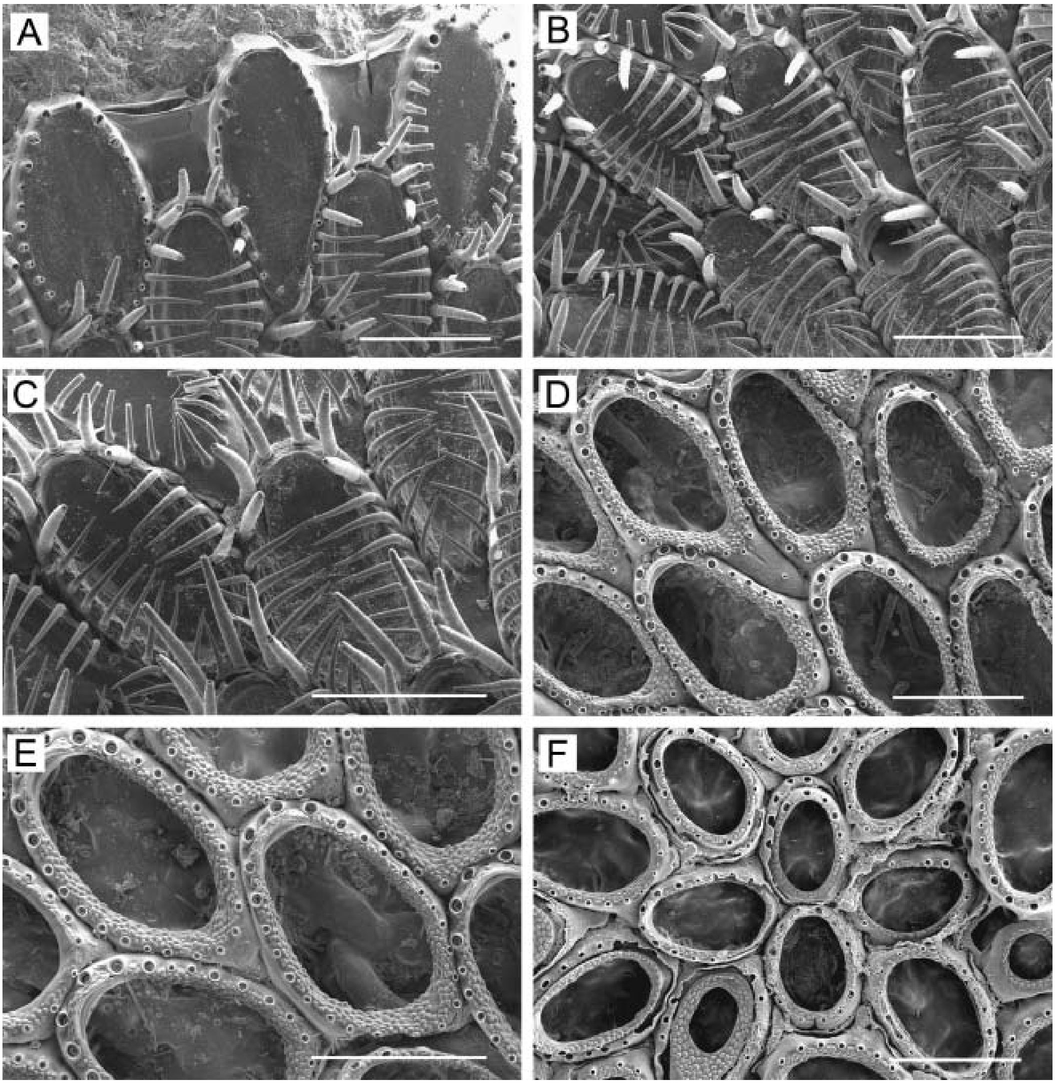

Figure 11. *Cauloramphus multispinosus* n. sp. (A) NHM 2006.2.27.36; (B, C) NHM 2006.2.27.38; (D, E) NHM 2006.2.27.37; (F) NHM 2006.2.27.40. (A) Colony margin with developing zooids, unbleached; (B) group of autozooids, unbleached; (C) close up of zooids showing details of distal erect spines and thin proximal spines strongly curved and arched over opesia, unbleached; (D) autozooids with variable form of proximal gymnocyst, bleached; (E) close up of zooids, unbleached; (F) ancestrula surrounded by periancestrular zooids, bleached. Scale bars: 0.5 mm.

proximally, coarsely granulated. Gymnocyst reduced, narrow, smooth; sometimes evident laterally or elongated proximally, tapering between adjacent zooids. Opesia (Figure 11D, E) oval, widest in middle, 0.50–0.68 mm long (0.57 ± 0.04 mm), 0.27–0.35 mm wide (0.31 ± 0.02 mm), rarely with straight proximal margin, occupying 70–85% of zooidal length. Mural rim with 20–26 spines (Figure 11B, C); three pairs orificial spines straight, very long (up to 0.40 mm), hollow, thick, blunt, with enlarged cylindrical bases, the most proximal pair almost perpendicular or slightly tilted over opesia, the two distal pairs angling slightly forward; 14–20 opesial spines very thin, sharp, strongly curved over opesia, meeting almost horizontally in midline. Avicularia not observed. Embryos brooded endozooidally; fertile zooids have a small kenozooidal ooecium (Figure 11D, E) comprising the sharp mural rim distal to the orifice, usually with a tiny round or slit-like pore in midline. Six pore chambers in each lateral wall and two in distal wall. Ancestrula tatiform, oval, 0.50 mm long by 0.39 mm wide, basal wall with central uncalcified window, opesia large, oval, 0.38 mm long by 0.26 mm wide, surrounded by 16 spines (six hollow distal spines with enlarged bases, 6–10 thin proximal spines, curved over opesia). Ancestrula (Figure 11F) buds triplet of small zooids distally and distolaterally, with 16–20 spines each, and is eventually surrounded by six or seven zooids.

Remarks

Cauloramphus multispinosus is distinguishable from congeners by the large size of zooids; large number of thin, curved spines (up to 26) forming a tight, neat basket; and the apparent absence of avicularia. Northeastern Pacific *C. spectabilis* Dick and Ross, 1988 has up to 24 spines, but differs in having four pairs of heavy orificial spines, thicker opesial spines, long-pedunculate avicularia, and smaller zooids, not exceeding 0.65 mm in length. *Cauloramphus pseudospinifer* Androsova, 1958 has up to 23 spines, but compared to *C. multispinosus*, there is less difference in thickness between orificial and opesial spines; the opesial spines are thicker; and there are thick, pedunculate avicularia (see Dick et al. 2005, Figure 3G, H).

Distribution

Cauloramphus multispinosus is at present known from Akkeshi and Oshoro Bays, Hokkaido.

Cauloramphus niger new species

(Figure 12)

Diagnosis

Zooids closely appressed; mural rim narrow, rounded, largely cryptocystal, covered with conical granules; gymnocyst reduced, evident proximally; 12–19 spines, including four to six vertical orificial spines and 8–13 curved opesial spines angled over opesia; spines light with dark bases in marginal zooids, dark brown to black in older zooids; avicularia single, numerous near colony periphery, longer than distal spines, with short peduncle rapidly expanding into chamber with terminal rostral face; mandible triangular, the tip rounded; kenozooidal ooecium much larger than in other species, granulated.

Etymology

The species name is from the Latin *niger* (dark coloured, black), referring to the colour of the spines.

Material examined

Holotype: DIN, seven colony fragments (NHM 2006.2.27.16). Paratypes: KAI, colony on rock (NHM 2006.2.27.41); KAI, ancestrular colony on rock (NHM 2006.2.27.17). Additional material: 664 specimens.

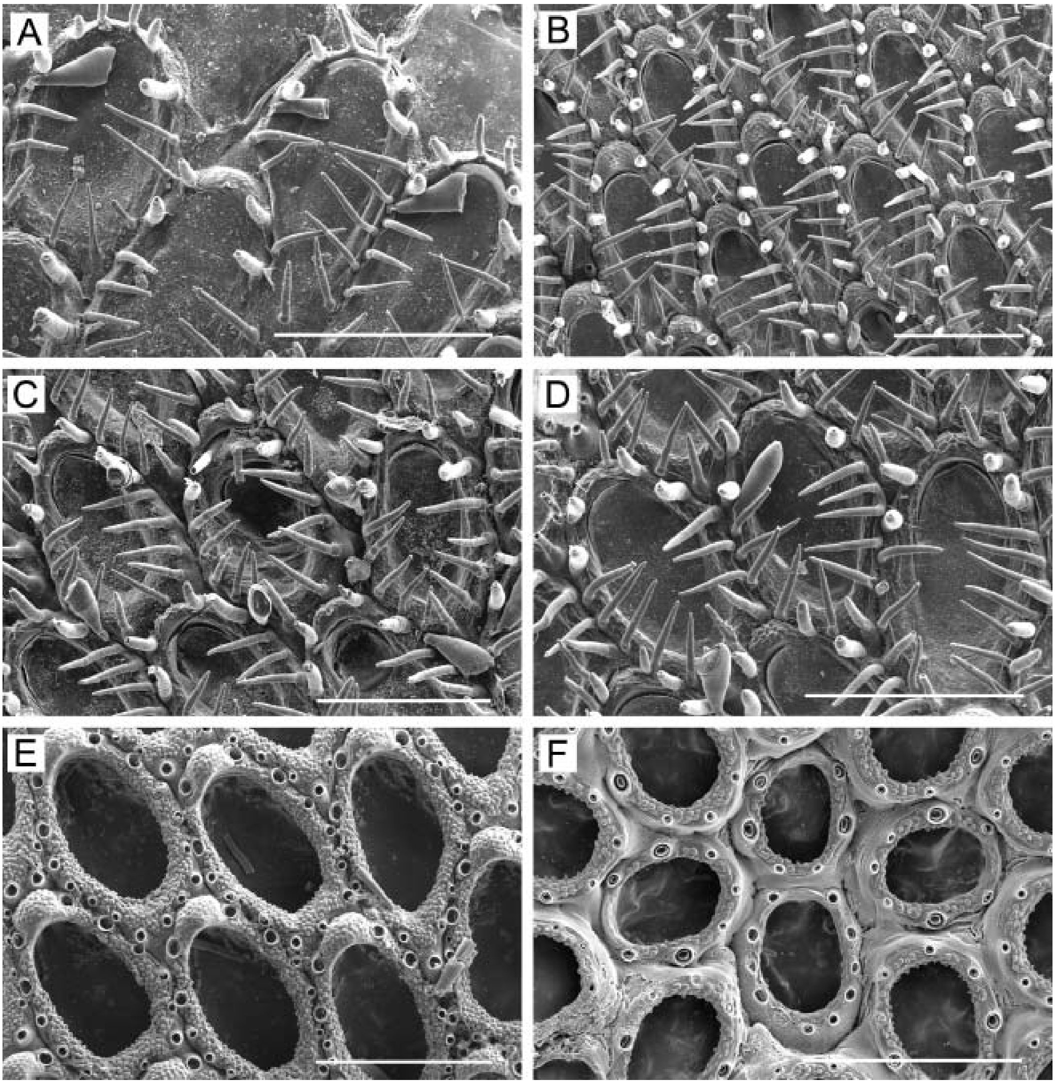

Figure 12. *Cauloramphus niger* n. sp. (A–E) NHM 2006.2.27.16; (F) NHM 2006.2.27.17. (A) Developing zooids at colony margin, unbleached; (B) general view of group of zooids with immersed vestigial ovicells, unbleached; (C) zooids from colony periphery, showing numerous avicularia, unbleached; (D) close up of zooids with avicularia, unbleached; (E) autozooids with immersed ovicells and bases of spines, bleached; (F) ancestrula and periancestrular zooids, bleached. Scale bars: 0.5 mm.

Description

Colony unilaminar, encrusting, coherent, forming irregularly circular patches up to 3 cm across; brown, dark yellow, or grey when alive, with reddish to pink marginal zone one or two developing zooids deep. Zooids (Figure 12A–F) oval to rounded-hexagonal, occasionally tapering proximally, 0.47–0.65 mm long (0.56 ± 0.04 mm), 0.30–0.45 mm wide (0.35 ± 0.03 mm), closely appressed, demarcated by a shallow groove. Mural rim (Figure 12E) narrow, rounded, largely cryptocystal, covered with conical granules. Gymnocyst reduced, smooth, occasionally elongate proximally between adjacent zooids, distinct from granulated mural rim. Opesia (Figure 12E) oval, widest in middle or sometimes proximally, 0.27–0.40 mm long (0.35 ± 0.03 mm), 0.17–0.28 mm wide (0.22 ± 0.02 mm), with crenulate outline due to granulation, occupying 60–80% of zooidal length. Around mural rim, 12–19 spines (Figure 12B–D), light yellowish with dark bases in marginal zooids, rapidly changing to entirely dark brown or black in older zooids, contrasting sharply with yellowish to greyish zooidal walls; two to three pairs of orificial spines long, hollow, thick, blunt, vertically orientated, with enlarged cylindrical bases, occasionally most distal pair reduced in size; 8–13 opesial spines thin, sharp, arched over opesia, occasionally meeting in midline; distance between adjacent opesial spines two to three times or more their basal thickness; in some proximally broadened zooids, one to four most proximal spines are vertically orientated and slightly longer and thicker than the others. Avicularia (Figure 12C, D) single, arising from distolateral gymnocyst between orificial and opesial spines, of same length as or slightly longer than orificial spines; short, thick peduncle rapidly expanding to thick, laterally compressed chamber with terminal rostral face; mandible triangular, the tip rounded, pointing in any direction, but most frequently laterally; avicularia numerous near periphery of colony but may be entirely absent in older areas. Kenozooidal ooecium (Figure 12E) distal to orifice is prominent, cap-like, with granulose surface, occupying entire space between bases of distalmost spines. Six pore chambers in each lateral wall and two in distal wall. Ancestrula (Figure 12F) tatiform, oval, with entirely calcified basal wall, 0.39 mm long by 0.30 mm wide; large, oval opesia 0.28 mm long by 0.20 mm wide; 10 spines around opesial margin. Ancestrula buds triplet of small zooids distally and distolaterally, each with six or seven spines, including two pairs of hollow distal spines with enlarged bases and two or three thin proximal spines curving over opesia.

Remarks

Characters that distinguish *C. niger* from other reported species of this genus are the unusually large kenozooidal ooecium and the dark brown spines. The only other known species of *Cauloramphus* with similarly dark spines is *C. brunnea* Canu and Bassler, 1930, originally described from the Galapagos Islands. However, whereas zooids of *C. niger* are closely appressed, those of *C. brunnea* are separated by a broad groove, so that the opesiae are about as far apart as their width. In addition, the avicularium of the latter species is long-pedunculate, narrowly fusiform, and attached proximal to the middle of the zooid, lateral to the zone of opesial spines. The light yellowish spines with dark bases on marginal zooids of *C. niger* are similar to spines of *C. variegatus* (Hincks, 1881); however, the spines of the latter are never entirely dark brown, and other characters differ as well.

Distribution

Cauloramphus niger is known at present only from Akkeshi Bay.

Cauloramphus spinifer (Johnston, 1832)

(Figure 13)

Flustra spinifera Johnston 1832, p 266, Plate 9, Figure 6.

Cauloramphus spinifer: Osburn 1950, p 55, Plate 5, Figure 9; Mawatari 1956, p 118, Figure 4a; Androsova 1958, p 106, Figure 15; Kluge 1962, p 295, Figure 179; 1975,

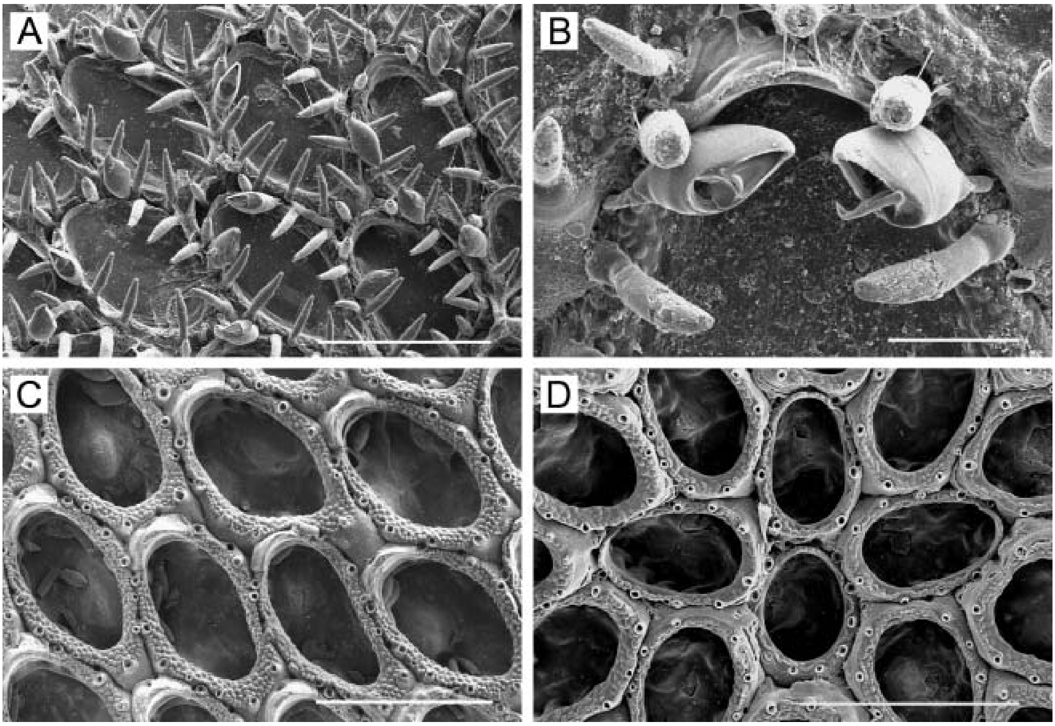

Figure 13. *Cauloramphus spinifer* (Johnston, 1832). (A) NHM 2006.2.27.38; (B) NHM 2006.2.27.41; (C) NHM 2006.2.27.18; (D) NHM 2006.2.27.17. (A) Group of autozooids, unbleached; (B) distal half of zooid, showing avicularia, unbleached; (C) autozooids, bleached; (D) ancestrula and periancestrular zooids, bleached. Scale bars: 0.5 mm (A, C, D); 0.1 mm (B).

p 353, Figure 179; Gontar 1980, p 6; Mawatari and Mawatari 1981a, p 43, Figure 10; 1981b, p 44; Dick and Ross 1986, p 89; Grischenko 1997, p 162; 2004, p 40; Hayward and Ryland 1998, p 172, Figure 48.

Cauloramphus spinifera: Kubanin 1997, p 121.

Cauloramphus spinifer: Dick and Ross 1988, p 39, Plates 2D, E, 13D.

Not *Cauloramphus spinifer*: Kubota and Mawatari 1985a, p 80, Figure 5.

Material examined

ANC, colony on rock (NHM 2006.2.27.13); KAI, ancestrular colony on rock (NHM 2006.2.27.17), colony on rock (NHM 2006.2.27.38), colony on rock (NHM 2006.2.27.41); BAC, two colony fragments (NHM 2006.2.27.18). Additional material: 855 specimens.

Description

Colony unilaminar, encrusting, coherent, more or less circular, up to 2.5 cm across, light tan in colour when alive. Zooids (Figure 13A–D) elongate-oval to irregularly hexagonal, 0.47–0.68 mm long (0.56 ± 0.05 mm), 0.30–0.40 mm wide (0.33 ± 0.03 mm), closely set, separated by a fine groove. Mural rim (Figure 13C) slightly raised; cryptocyst relatively narrow, sloping, granulated; distal and lateral gymnocyst reduced or lacking; proximal gymnocyst narrow or tapering back between adjacent zooids, smooth, distinct from granulated mural rim. Opesia (Figure 13C) oval, commonly widest in middle, sometimes proximally, 0.35–0.43 mm long (0.40 ± 0.03 mm), 0.18–0.25 mm wide (0.22 ± 0.02 mm), with crenulate outline, occupying 80–90% of zooidal length. Around mural rim, 8–13 spines; three (rarely two or four) orificial spines orientated vertically, one in midline and one to each side of orifice, slightly blunter, thicker but not longer than opesial spines; 5–10 opesial spines slightly thinner, more acuminate, angling over opesia; sometimes most proximal spine vertically orientated, thicker, longer, blunter even than distal spines. Avicularia (Figure 13A, B) usually paired, sometimes single or lacking on a zooid, arising from distolateral gymnocyst between orificial and opesial spines, in line with proximal edge of orifice; peduncle short, with expanded portion comprising most of the avicularium; about as long as proximal spines, typically turned inward and angled over opesia, with rostral plane facing proximomedially; mandible elongate-triangular, with hooked tip. Embryos brooded endozooidally; fertile zooids have a smooth, moderately well-developed kenozooidal ooecium (Figure 13C) comprising the sharp mural rim distal to the orifice. Six pore chambers in each lateral wall and two in distal wall. Ancestrula (Figure 13D) tatiform, oval, with fully calcified basal wall, 0.34 mm long by 0.26 mm wide; oval opesia 0.25 mm long by 0.18 mm wide; 12 spines around opesial margin, three distal pairs straight and vertical, six proximal spines thin, curved over opesia; ancestrula buds triplet of small zooids distally and distolaterally, each with 10 or 11 spines.

Remarks

Dick and Ross (1988) discussed diagnostic characters and geographic variation in spine number for *C. spinifer*.

Distribution

This is a circumboreal species extending into the Arctic. In the eastern Atlantic, it is widely distributed in cool-temperate waters, from the White Sea (Gostilovskaya 1978) and Barents Sea (Kluge 1962) southward to the Shetland Isles and northern coast of France. In the eastern Pacific, *C. spinifer* is known from Kodiak Island, Gulf of Alaska; previous records from farther south need to be re-examined (Dick and Ross 1988). In the western Pacific it has been reported from the Gulf of Anadyr and the vicinity of St Lawrence Island in the Bering Sea; Commander Islands; Sea of Okhotsk; Kuril Islands; Sakhalin Island; and Primorye and Gulf of Peter the Great in the northern Sea of Japan (Gontar 1980; Kubanin 1997; Grischenko 1997, 2004). From Japan, *C. spinifer* is known from the Pacific coast of Hokkaido, including Akkeshi, Kushiro, Mori, Muroran, and Shirikishinai, southward to middle Honshu (Mawatari and Mawatari 1981a, 1981b). We have determined material from Oshoro Bay, western coast of Hokkaido, Sea of Japan, identified by Kubota and Mawatari (1985a) as *C. spinifer*, actually to be *C. magnus*.

Genus *Tegella* Levinsen, 1909

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

(Figure 14)

Membranipora aquilirostris O'Donoghue and O'Donoghue 1923, p 170, Plate 2, Figure 16.

Tegella aquilirostris: O'Donoghue and O'Donoghue 1926, p 83, Plate 3, Figure 29; Osburn 1950, p 83; McCain and Ross 1974, p 13, Figure 26; Mawatari and Mawatari 1980, p 92,

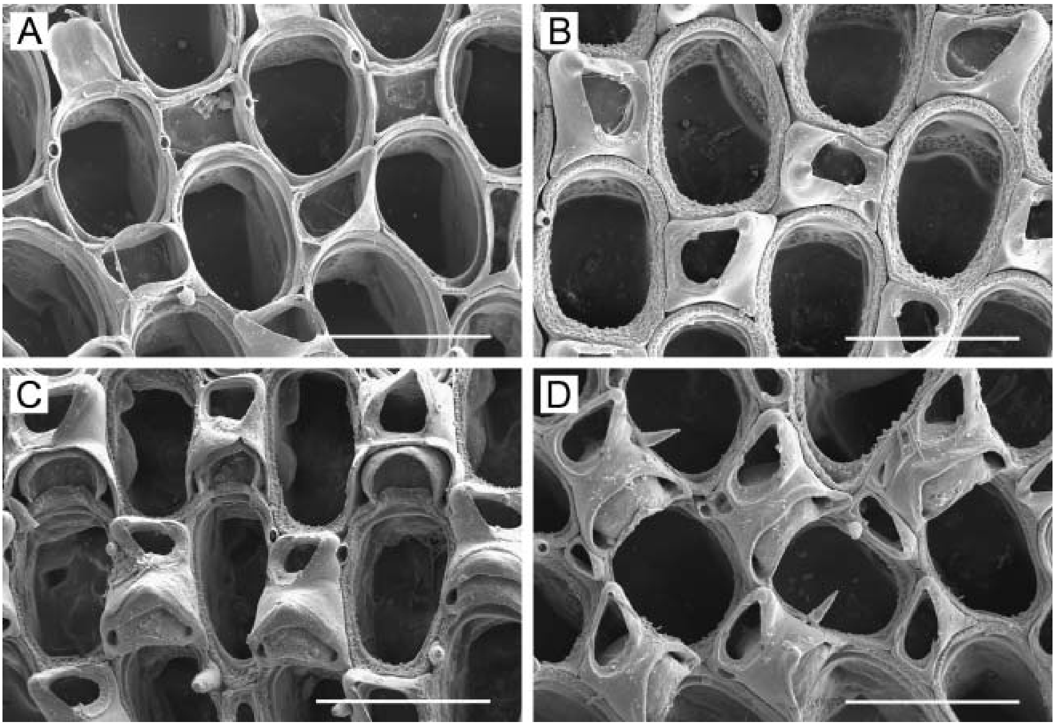

Figure 14. *Tegella aquilirostris* (O'Donoghue and O'Donoghue, 1923). HNM 2006.2.27.42. (A) Developing zooids near colony margin, bleached; (B) immature zooids with large frontal avicularia, bleached; (C) zooids with developing and completed ovicells, bleached; (D) mature zooids, showing ovicells with associated frontal avicularia, and also straight and curved spines, bleached. Scale bars: 0.5 mm.

Figure 32; 1981b, p 46; Dick and Ross 1988, p 42, Plate 3A; Kubanin 1997, p 121; Grischenko 1997, p 159; 2004, p 40; Dick et al. 2005, p 3707, Figure 4E, F.

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

Tegella robertsoni O'Donoghue and O'Donoghue 1926, p 82.

Tegella robertsonae: Osburn 1950, p 81, Plate 9, Figure 5.

Material examined

ACT, four intact colonies (NHM 2006.2.27.42). Additional material: 121 specimens.

Description

Colony unilaminar, encrusting, coherent, subcircular, up to 3.5 cm across, reddish brown in colour when alive. Zooids (Figure 14A–D) oval, barrel-shaped, or quadrangular, widest in middle, 0.55–0.80 mm long (0.65 ± 0.07 mm), 0.26–0.40 mm wide (0.35 ± 0.04 mm), closely appressed even when young (Figure 14A), with adjoining lateral walls forming a sharp rim. Opesia (Figure 14B) oval or rounded-rectangular, 0.33–0.45 mm long (0.39 ± 0.03 mm), 0.21–0.30 mm wide (0.25 ± 0.02 mm), occupying 50–80% of zooidal length. Lateral gymnocyst hidden between adjacent zooids; proximal gymnocyst covered by avicularian chamber. Cryptocyst sloping below mural rim, granulated, extending around entire opesia or absent distally. Usually two spines (Figure 14D) around mural rim comprising a straight, hollow tubular spine on one side, at middle of zooid or near proximolateral flange of ovicell, and another finer, curved, acute spine more proximally, arching over opesia on opposite side; young zooids sometimes with a pair of straight spines on each side. Large frontal avicularium (Figure 14B), with square or transversely rectangular avicularian chamber, occupies entire proximal gymnocyst, abutting or partly covering ovicell of preceding zooid; rostrum heavily calcified, directed laterally or distolaterally, mandible tilted 45° to frontal plane, sometimes extending around proximolateral edge of aperture; mandible triangular, slightly elongate, with acute, hooked tip; rostrum usually hooked upward at tip, in opposite direction to hook of mandible. Ovicell (Figure 14C, D) hyperstomial, prominent, imperforate, broader than long, 0.20–0.26 mm long (0.23 ± 0.02 mm), 0.21–0.31 mm wide (0.26 ± 0.03 mm); endooecium spherical, partly overgrown by ectooecium, margin of which comprises a thick, curved transverse ridge that is often thickened into a blunt median knob; proximal margin of endooecium thickened, continuous with lateral walls; between endooecial and ectooecial margins is a large, transversely lunate tabula covered by ectocyst; laterally within tabula on each side is a deep recess between endooecium and ectooecium. Zooids intercommunicate via four circular or oval multiporous septula in each lateral wall and a crescent-shaped or bilobed zone of pores in distal wall. Ancestrula not observed.

Remarks

Colonies often aggregated, covering considerable areas on benchrock faces and beneath overhangs; those in sheltered microhabitats are often loosely attached, the margin sometimes raised in folds and frills.

Distribution

This is a Boreal Pacific species. In the eastern Pacific there are records from Kodiak Island (Dick and Ross 1988) southward to Ketchikan (Dick et al. 2005), British Columbia (O'Donoghue and O'Donoghue 1923, 1926), Puget Sound (McCain and Ross 1974), and Santa Barbara, California (Osburn 1950). In the western Pacific, *T. aquilirostris* is known from the Commander Islands (Grischenko 1997, 2004); and from the Kuril Islands, Aniva and Terpeniya Gulfs of southeastern Sakhalin Island, the Sea of Okhotsk, and Primorye in the Sea of Japan (Kubanin 1997). In Japan, this species has been found at Akkeshi, Kushiro, and Hakodate on Hokkaido, and also at Kominato and Misaki, Pacific coast of Honshu (Mawatari and Mawatari 1980, 1981b).

Tegella arctica (d'Orbigny, 1851)
(Figure 15)

Reptoflustra arctica d'Orbigny 1851, p 352.

Membranipora arctica: Lorenz 1886, p 85, Plate 7, Figure 1; Nordgaard 1895, p 17; Osburn 1912, p 229, Plate 23, Figures 33, 34, Plate 30, Figure 86.

Membranipora conferta: Hincks 1882, p 249.

Membranipora sophiae: Hincks 1882, p 466, Plate 20, Figure 2.

Callopora arctica: Nordgaard 1918, p 41; 1923, p 9; 1927, p 4; Osburn 1919, p 608.

Tegella sophiae: Canu and Bassler 1920, p 166.

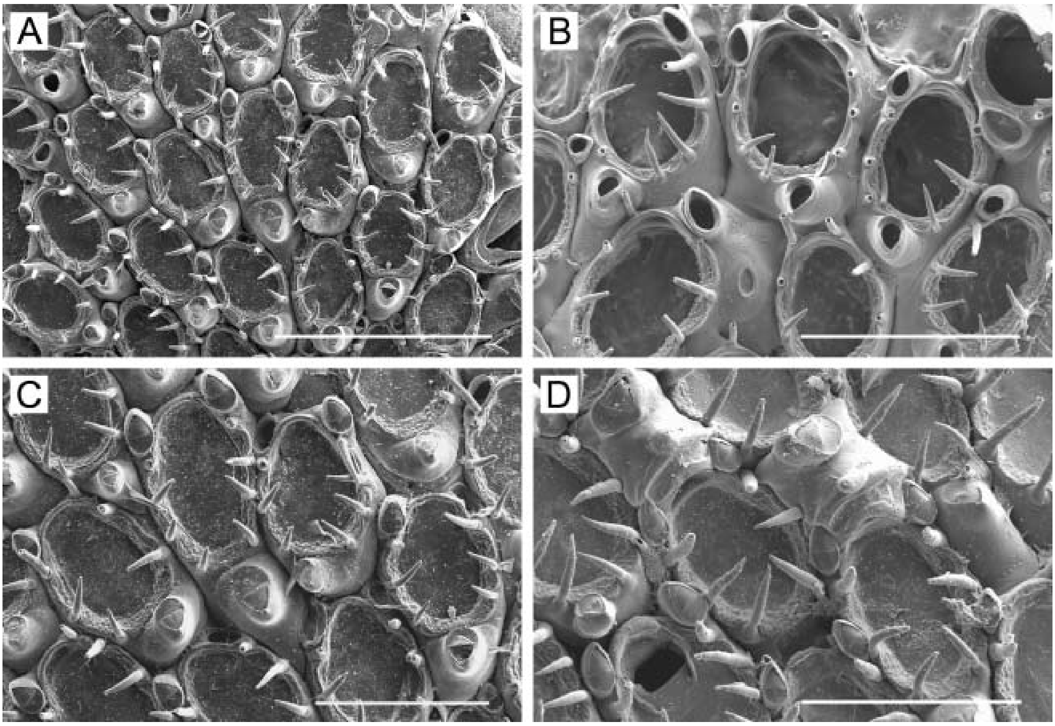

Figure 15. *Tegella arctica* (d'Orbigny, 1851). (A, C) NHM 2006.2.27.44; (B) NHM 2006.2.27.46; (D) NHM 2006.2.27.43. (A) General view of group of autozooids, unbleached; (B) zooids from region near colony margin, bleached; (C) immature zooids with small paired angular and large frontal avicularia, unbleached; (D) mature zooids with ovicells and associated frontal avicularia, unbleached. Scale bars: 1 mm (A); 0.5 mm (B, C); 0.4 mm (D).

Tegella arctica: Osburn 1950, p 82, Plate 9, Figure 6; Kluge 1962, p 280, Figure 163; 1975, p 334, Figure 163; Gontar 1980, p 5; Mawatari and Mawatari 1980, p 94, Figure 33; 1981b, p 46; Dick and Ross 1988, p 43, Plate 3B; Kubanin 1997, p 121; Grischenko 1997, p 157; 2004, p 40.

Material examined

ANC, colony on rock (NHM 2006.2.27.43), colony on bivalve shell (NHM 2006.2.27.44), colony on rock (NHM 2006.2.27.45), colony on erect bryozoan *Phidolopora elongata* (NHM 2006.2.27.46). Additional material: five specimens.

Description

Colony unilaminar, encrusting, coherent, irregularly circular, largest about 2 cm across, yellowish when alive. Zooids (Figure 15A–D) oval or oblong, 0.38–0.63 mm long (0.49 ± 0.06 mm), 0.22–0.33 mm wide (0.28 ± zz0.03 mm), separated by a deep, narrow groove. Opesia (Figure 15B) oval, elliptical, widest in middle, 0.17–0.31 mm long (0.25 ± 0.04 mm), 0.14–0.20 mm wide (0.17 ± 0.02 mm), occupying 50–70% of zooidal length. Mural rim (Figure 15B, C) raised, with a sloping, finely granulated cryptocyst. Gymnocyst smooth, sloping and narrow distally and laterally; tapering proximally, occupying up to 20–30% of zooid length. Around mural rim, six to eight spines (Figure 15A–D); distal pair located just proximal to lateral avicularia and in line with orifice, straighter, thicker and more erect than the rest; proximal four to six spines curved, acuminate, arched over opesia. Proximal gymnocyst covered by relatively large frontal avicularium with raised rostrum; mandible triangular, with complete cross-bar, raised at an angle to frontal plane, directed proximally or proximolaterally, not extending laterally around aperture; abutting and covering distal half of ovicell of preceding zooid, in this case pointing distolaterally. Two small paired avicularia located on mural rim lateral to orifice; mandibles triangular, directed distally and raised 45° from frontal plane. Ovicells (Figure 15D) hyperstomial, hemispherical, imperforate, 0.13–0.19 mm long (0.16 ± 0.02 mm), 0.16–0.21 mm wide (0.19 ± 0.02 mm), with thick transverse rib across top that may be thickened into a blunt median knob. Proximal margin raised, with lunate tabula between margin and ridge. Four pore chambers in each lateral wall and two in basal half of distal wall. Ancestrula not observed.

Distribution

Tegella arctica is a circumpolar, Arctic-Boreal species. Kluge (1962, 1975) and Gontar and Denisenko (1989) summarized a number of previous Arctic records. In North America it is known from Point Barrow southward to Frederic Sound, southeastern Alaska (Osburn 1950; Dick and Ross 1988). In the western Pacific, there are records from the Bering Sea near St Lawrence Island, along western Kamchatka (Kluge 1961; Kubanin 1997), the Commander Islands (Grischenko 1997, 2004), the Shantar Archipelago (Kluge 1961), and the Kuril Islands (Gontar 1980) on the Sea of Okhotsk side. In Japan it has previously been found at Akkeshi and Hakodate, Pacific coast of Hokkaido (Mawatari and Mawatari 1980, 1981b).

Superfamily BUGULOIDEA Gray, 1848
Family BUGULIDAE Gray, 1848
Genus *Bugula* Oken, 1815
Bugula pacifica Robertson, 1905
(Figure 16A, B)

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

Bugula pacifica: O'Donoghue and O'Donoghue 1923, p 162; 1926, p 91; Osburn 1950, p 155, Plate 22, Figure 6, Plate 23, Figure 4; McCain and Ross 1974, p 13; Soule et al. 1995, p 108, Plate 36; Grischenko 1997, p 167; 2004, p 40; Dick et al. 2005, p 3712, Figure 6A, B.

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

Bugula pacifica pacifica: Kubanin 1997, p 122.

Not *Bugula pacifica*: Kubanin 1975, p 114, Figure 2b–g.

Material examined

KAI, seven fragments of same colony (NHM 2006.2.27.15). Additional material: six specimens.

Description

Colony (Figure 16A) erect, flexible, dichotomously branched, spiralled around a central axis with basal sides facing outwards. Our specimens small, up to 5.5 cm high, yellow in

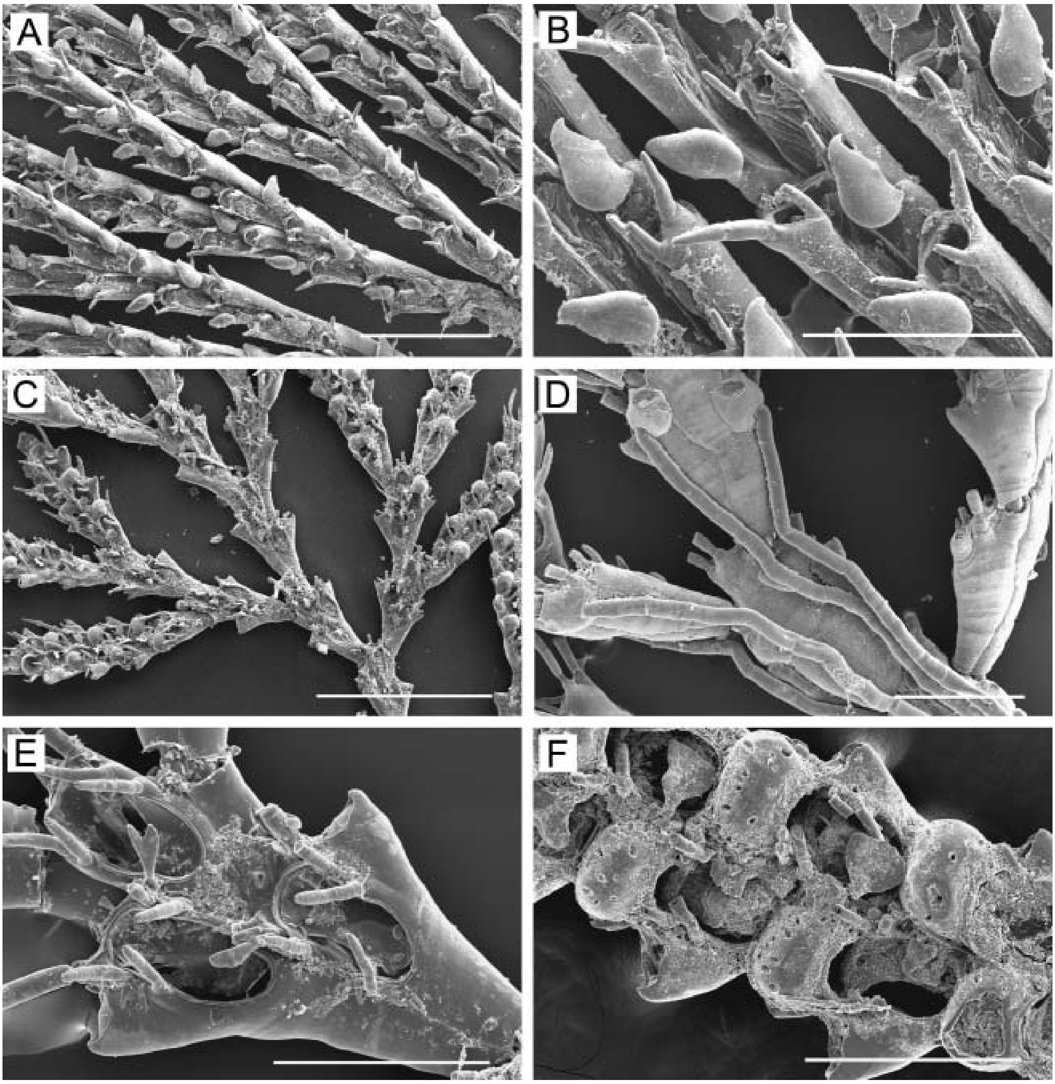

Figure 16. (A, B) *Bugula pacifica* Robertson, 1905. NHM 2006.2.27.15. (A) General view of colony fragment, unbleached; (B) zooids, showing distal spinous projections and avicularia, unbleached. (C–F) *Tricellaria occidentalis* (Trask, 1857). (C) NHM 2006.2.27.48; (D–F) NHM 2006.2.27.49. (C) General view of colony fragment, unbleached; (D) basal surface of branch with kenozooids (rhizoids or radicle fibres), unbleached; (E) internode with immature zooids, unbleached; (F) abraded internode containing mature zooids with ovicells, unbleached. Scale bars: 1 mm (A); 0.5 mm (B, D, F); 2 mm (C); 0.4 mm (E).

colour when alive, attached by a stalk composed of rhizoids originating from zooids at base of colony. Branching dichotomous, with axil at bifurcations formed by inner zooid of each of first pair on either side of branch point (branching pattern type 3; Hayward and Ryland 1998 after Harmer 1923). Zooids (Figure 16B) in biserial series, elongate, narrow, 0.50–1.03 mm long (0.67 ± 0.13 mm), tapering proximally, truncate distally, with thin, flexible, transparent, weakly calcified walls. Opesia occupies nearly entire frontal surface, leaving only a small zone of proximal gymnocyst. One relatively short, spinous projection located on inner distal zooidal margin; two elongate spinous projections on outer distal margin;

distalmost projection strongly thickened, pointing distolaterally, curved away from zooid. Avicularia attached by a flexible joint near base of zooid, on lateral wall close to opesial margin, 0.21–0.27 mm long, with hooked rostrum; not occurring on all zooids. Neither ovicells nor ancestrula present in our material.

Remarks

Androsova (1977) described a new subspecies, *Bugula pacifica nana*, from Aniva Gulf, southern Sakhalin Island, Sea of Okhotsk. In comparison with the nominal subspecies, *B. pacifica pacifica*, this subspecies forms smaller colonies, zooids, and zooidal structures (see Androsova, 1977, p 795). Kubanin (1984a, 1984b, 1997) reported *B. pacifica nana* from Primorye, Peter the Great Gulf, southern coast of Sakhalin Island, and concluded that it is distributed only in Low Boreal Asiatic waters. He suggested that *B. pacifica pacifica* is primarily distributed in the Boreal eastern Pacific, extending to the fringes of the western Pacific, including the Commander Islands. The finding of *B. pacifica pacifica* in Akkeshi Bay shows that this form has a trans-Pacific distribution, although its occurrence in the western Pacific as a relatively recently introduced population cannot be ruled out.

Distribution

Bugula pacifica is a Boreal Pacific species distributed from the Channel Islands off Southern California (Soule et al. 1995) northward to Ketchikan, Alaska (Dick et al. 2005) and the Pribilof Islands, Bering Sea (Robertson 1905; Osburn 1950). On the Asian side, it has previously been reported from the Commander Islands (Grischenko 1997); Akkeshi Bay is the southernmost known locality in the western Pacific.

Family CANDIDAE d'Orbigny, 1851

Genus *Tricellaria* Fleming, 1828

Tricellaria occidentalis (Trask, 1857)

(Figure 16C–F)

Menipea occidentalis Trask 1857, p 102, Plate 4, Figure 4.

Menipea occidentalis: Jelly 1889, p 173; Robertson 1905, p 254, Plate 6, Figures 22–25; Yanagi and Okada 1918, p 409; O'Donoghue and O'Donoghue 1923, p 159; 1925, p 99; Okada and Mawatari 1936, p 59; 1937, p 437.

Menipea compacta Ortmann 1890, p 21.

Menipea compacta dilatata Ortmann 1890, p 21, Plate 1, Figure 2.

Menipea compacta form *triplex* Hincks 1882, p 461; 1884, p 208, Plate 9, Figure 8.

Menipea occidentalis catalinensis Robertson 1905, p 255, Plate 7, Figures 26, 27; Yanagi and Okada 1918, p 409; Okada 1929, p 15, Plate 1, Figure 3; Okada and Mawatari 1937, p 437; Osburn 1950, p 122, Plate 13, Figures 8, 9.

Tricellaria occidentalis: Harmer 1923, p 353; Silén 1941, p 79; Osburn 1950, p 122, Plate 13, Figures 6, 7; Mawatari 1951, p 9, Figures 1–7; Mawatari and Mawatari 1981b, p 49; Kubota and Mawatari 1985a, p 85, Figures 8, 9; Gordon 1986, p 61, Plate 20E; Gordon and Mawatari 1992, p 25, Plates 2F, 6F; Soule et al. 1995, p 86, Plate 26A–C; Kubanin 1997, p 122; Liu et al. 2001, p 498, Plate 30, 6–7; Seo 2005, p 365, Plates 90–92.

Tricellaria occidentalis dilatata Harmer 1923, p 353.

? *Tricellaria inopinata* d'Hondt and Occhipinti Ambrogi 1985, p 36, Figures 2, 3; Dyrynda et al. 2000, p 2001, Figure 2a–d.

Material examined

ACW, two intact colonies (NHM 2006.2.27.47); MBS, intact colony (NHM 2006.2.27.48); ANC, two intact colonies (NHM 2006.2.27.49). Additional material: 31 specimens.

Description

Colony (Figure 16C) bushy, tightly arborescent, composed of dense branches curved and rolled inward. Colony up to 3 cm high, yellow to tan in colour when alive, attached by a bundle of rhizoids (Figure 16D) originating from zooids situated low in colony. Branching dichotomous, regular, branching pattern type 9, with proximal extremity of zooid F and G not in contact (Hayward and Ryland 1998 after Harmer 1923). Most internodes have three zooids, but distal ones with ovicells have five to nine zooids. Internodes connected by strong, tubular chitinous joints, brown in colour; flexible nodes crossing well proximal to opesia of both outer and inner zooids. Zooids in biserial series, alternate, elongate, narrowing proximally, 0.45–0.78 mm long (0.63 ± 0.10 mm), varying significantly in size depending upon their location in internode and in colony. Opesia oval or elliptical, 0.22–0.28 mm long (0.25 ± 0.02 mm), 0.11–0.14 mm wide (0.12 ± 0.01 mm), occupying 30–50% of zooidal length; cryptocyst negligible. Zooids (Figure 16E) typically have six hollow, tubular jointed spines; most proximal pair straight, located near middle of opesia and tilted slightly inward; next pair straight or turned slightly outward; outer distalmost spine strongly calcified, elongate (up to 0.65 mm long), originating from dorsal side of distal zooidal margin; inner distalmost spine often strongly reduced or lacking. In some zooids the external proximal spine is bifid. Axial zooids at bifurcations have six spines: two pairs along distolateral margins of opesia, straight or tilted slightly outwards, and a medialmost pair of tubular, hollow, elongate spines originating from dorsal side of distal wall from closely set, heavily calcified cylindrical bases; these latter two spines are often asymmetrically placed with respect to the midline, with one occupying the midline position and longer and heavier than the other. Scutum attached to inner border of opesia, proximal to middle of opesia, varing in form from spine-like to a broad flabellate process with two to four or more lobes. Non-axial zooids have large lateral avicularium with hooked rostrum; mandible triangular, with hooked tip. Frontal avicularia absent. Ovicells (Figure 16F) globular, smooth, wider than long, 0.16–0.21 mm long (0.18 ± 0.01 mm), 0.20–0.24 mm wide (0.21 ± 0.01 mm), with around 10 small, circular or oval pores. Some zooids situated low in colony have proximally directed kenozooids (rhizoids or radicle fibres) originating from a slight, flattened disc on dorsal or lateral wall, close to nodal joints. Ancestrula not observed.

Remarks

Many characters of *T. occidentalis*, such as presence or absence of lateral avicularia, number of zooids per internode, and size and shape of scuta, may vary considerably even within a single colony (Gordon 1986; Gordon and Mawatari 1992). This variation, noted by Robertson (1905), Yanagi and Okada (1918), Okada (1929), and Osburn (1950), and superbly illustrated by Mawatari (1951), has caused taxonomic difficulties and resulted in descriptions of several varieties of this species. In specimens from Akkeshi, the scutum varies in form from spine-like to a broad flabellate process with two to four or more lobes, which is within the range of variation of *T. occidentalis* (see also Soule el al. 1995).

Dyrynda et al. (2000) concluded that Japanese and some other populations previously reported under the name *Tricellaria occidentalis* Trask are actually *T. inopinata* d'Hondt and Occhipinti Ambrogi, 1985, a fouling species recently described from the Lagoon of Venice. According to Dyrynda et al. (2000), *T. inopinata* is of Pacific origin, is widely distributed along the coasts of western North America and Japan, occurs in Australia and New Zealand, and has been introduced to Britain and the Mediterranean. They note that the original source region of the species in the Pacific, before anthropogenic introductions to other areas, is unknown. Dyrynda et al. (2000) regarded *T. inopinata* as consistently morphologically distinguishable from *T. occidentalis* Trask, which they considered to be restricted to the western coast of North America. However, they considered many of the Pacific records of *T. occidentalis* var. *catalinensis* Robertson, 1905 to be *T. inopinata*. Our material has one of the distalmost pair of spines on axial zooids located in the midline and better developed than the other; zooids occasionally with a bifid spine; and a quite variable scutum, sometimes broad with a spiky margin. According to Dyrynda et al. (2000) these are all characters distinguishing *T. inopinata* from *T. occidentalis*. Unfortunately, these authors did not provide a detailed description and illustrations of the latter, noting that the type description of *T. occidentalis* was inadequate, that the type material was lost, and that they had been able to examine only limited quantities of mostly very old material. Here we retain the name *T. occidentalis*, pending a detailed redescription of *T. occidentalis* Trask as distinct from *T. inopinata* d'Hondt and Occhipinti Ambrogi and clarification of the range of the former.

Distribution

Trask (1857) originally listed *Tricellaria occidentalis* as occurring from Cape Flattery to Santa Barbara, California. It is now a widely distributed, invasive and fouling species occurring in Japan (Mawatari 1951), Australia (Bock 1985), New Zealand (Gordon 1986; Gordon and Mawatari 1992), China (Liu et al. 2001), and Korea (Seo 2005); it has also been reported from the Mediterranean (d'Hondt and Occhipinti Ambrogi 1985; Occhipinti Ambrogi 1991) and Britain (Dyrynda et al. 2000). Records from the western coast of North America exist from British Columbia (Hincks 1882, 1884; O'Donoghue and O'Donoghue 1923) south to Baja California, Mexico (Robertson 1905; Osburn 1950; Soule et al. 1995). In the western Pacific, *T. occidentalis* has been reported from Peter the Great Gulf, Sea of Japan (Kubanin 1997); the coast of South Korea, including the Yellow Sea (Seo 1996, 2005); China (Liu et al. 2001), the Pacific coast of Honshu, Japan (Mawatari 1951); Akkeshi, Muroran, Mori, and Shirikishinai, Pacific coast of Hokkaido (Mawatari and Mawatari 1981b); and Oshoro Bay, Sea of Japan coast of Hokkaido (Kubota and Mawatari 1985a).

Infraorder ASCOPHORINA Levinsen, 1909
Grade ACANTHOSTEGA Levinsen, 1909
Superfamily CRIBRILINOIDEA Hincks, 1879
Family CRIBRILINIDAE Hincks, 1879
Genus *Cribrilina* Gray, 1848
Cribrilina annulata (Fabricius, 1780)

(Figure 17)

Cellepora annulata Fabricius 1780, p 436.

Cribrilina annulata: Robertson 1900, p 326; 1908, p 280; O'Donoghue and O'Donoghue 1923, p 172; 1926, p 96; Osburn 1950, p 177, Plate 28, Figure 7; Androsova 1958,

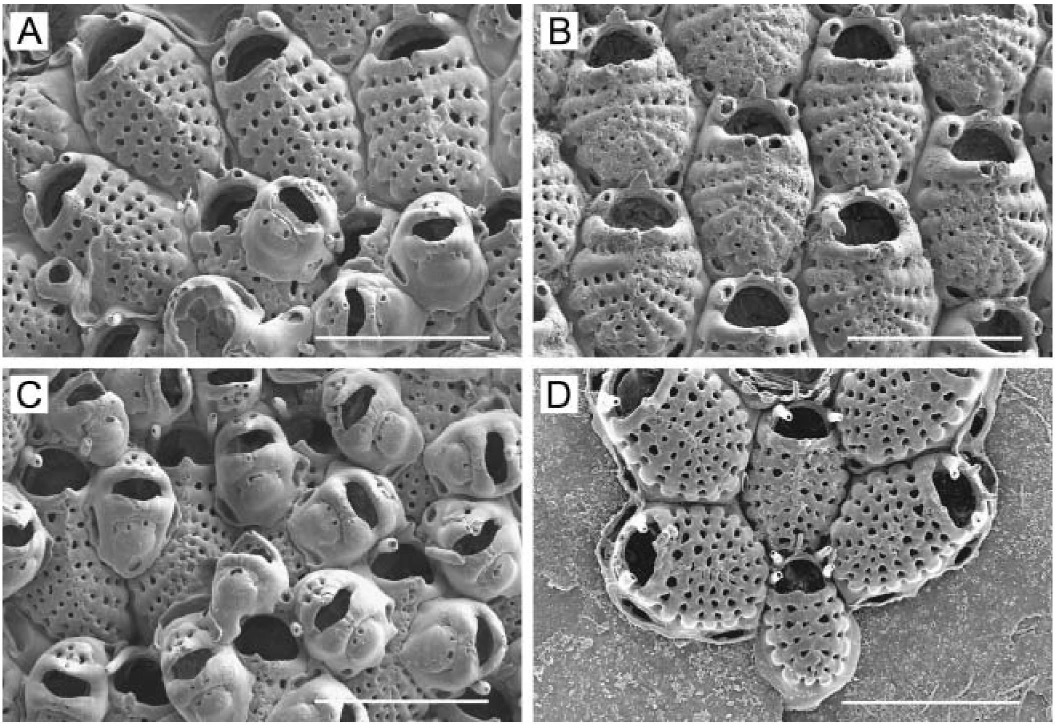

Figure 17. *Cribrilina annulata* (Fabricius, 1780). (A) NHM 2006.2.27.50; (B, C) NHM 2006.2.27.51; (D) NHM 2006.2.27.52. (A) Zooids with developing secondary layer of dwarf zooids, from region nearly colony margin; (B) immature zooids; (C) autozooids densely covered with numerous ovicellate dwarf zooids; (D) ancestrula with periancestrular zooids. Scale bars: 0.5 mm.

p 124, Figure 39; Kluge 1962, p 390, Figure 247; 1975, p 470, Figure 247; Mawatari and Mawatari 1981b, p 49; Kubota and Mawatari 1985b, p 195, Figure 1; Dick and Ross 1988, p 51, Plate 4C; Kubanin 1997, p 123; Grischenko 1997, p 171; 2004, p 40; Hayward and Ryland 1998, p 314, Figure 110; Dick et al. 2005, p 3718, Figure 7A, B.

Material examined

ANC, colony on rock (NHM 2006.2.27.31); DIN, colony on rock (NHM 2006.2.27.50), colony on rock (NHM 2006.2.27.51); BAC, ancestrular colony on bivalve shell (NHM 2006.2.27.52). Additional material: 436 specimens.

Description

Colony encrusting, coherent, forming irregularly circular sheets up to 2.7 cm across; light-yellow, red, or pink when alive; unilaminar, but often with scattered frontally budded dwarf zooids. Autozooids (Figure 17A, B) rounded-hexagonal to oval, 0.51–0.65 mm long (0.56 ± 0.04 mm), 0.30–0.43 mm wide (0.36 ± 0.03 mm), separated by a deep groove. Frontal wall moderately convex, consisting of five to seven pairs of flattened, fused costae, with 6–10 intercostal pores in a transverse series between costae. Distalmost pair of costae wider and heavier than the rest, forming thickened proximal border of secondary orifice, often rising medially to a pointed suboral umbo, sometimes incompletely fused. Secondary orifice oval, 0.09–0.13 mm long (0.10 ± 0.01 mm), 0.15–0.20 mm wide (0.17 ± 0.01 mm), flanked by a pair of hollow, erect spines distolaterally, with a shorter, tapering hollow spine in midline, or sometimes two, occasionally fused. Ovicellate zooids absent in primary layer. Frontally budded dwarf ovicellate zooids (Figure 17A, C), 0.22–0.33 mm long (0.29 ± 0.02 mm), 0.19–0.25 mm wide (0.22 ± 0.02 mm), occupy central region of colony, orientated in any direction; frontal wall reduced, consisting of three or four fused costae, including the pair of heavier subapertural costae comprising proximal lip of longitudinally compressed orifice and an additional one or two others, with a few intercostal pores between them. Ovicell of dwarf zooids derived from two pairs of spines, one pair broadened and thickened to form proximal border of ovicell, the other fused to form cap-like distal wall of ovicell; ovicells of dwarf zooids perforated on top with one to four pores that sometimes merge with one another; pseudopores at tips of thick proximal ovicellar costae appear as additional small perforations. Avicularia lacking. Zooids with two distal and two distolateral basal pore chambers. Ancestrula (Figure 17D) identical in form to autozooid, 0.35 mm long, 0.23 mm wide, with five orificial spines. Ancestrula buds triplet of zooids distally.

Remarks

In the material examined, ovicells were found only on dwarf zooids, usually concentrated densely in the centre of the colony. Dick et al. (2005) noted that differences in the fusion of distal orificial spines, form of the ovicell, and ancestrular budding patterns exist in populations across the range of this putatively circumpolar species and that nominal *C. annulata* may comprise a complex of cryptic species. However, resolution of this issue will require monographic treatment and is beyond the scope of the present study.

Distribution

This is considered a circumpolar Arctic-Boreal species (Kluge 1962, 1975; Gontar and Denisenko 1989). In the eastern Pacific, it has previously been reported from Kodiak, Cordova, Yakutat, and Ketchikan in Alaska (Robertson 1900; Osburn 1950; Dick and Ross 1988; Dick et al. 2005), and from British Columbia (O'Donoghue and O'Donoghue 1923, 1926). On the Asian side, it has been reported from the Commander Islands, southeastern Kamchatka, the Kuril Islands, Sakhalin Island, and Primorye on Peter the Great Gulf (Kluge 1961; Gontar 1980; Grischenko 1997, 2004; Kubanin 1997). In Japan it is known from Akkeshi, Muroran, and Shirikishinai on the Pacific coast of Hokkaido (Mawatari and Matawari 1981b), and from Oshoro Bay on the Sea of Japan side (Kubota and Mawatari 1985b).

Superfamily CATENICELLOIDEA Busk, 1852

Family EURYSTOMELLIDAE Levinsen, 1909

Genus *Integripelta* Gordon, Mawatari, and Kajihara, 2002

Integripelta novella Gordon, Mawatari, and Kajihara, 2002

(Figure 18)

Integripelta novella Gordon, Mawatari, and Kajihara 2002, p 205, Figure 2A, B.

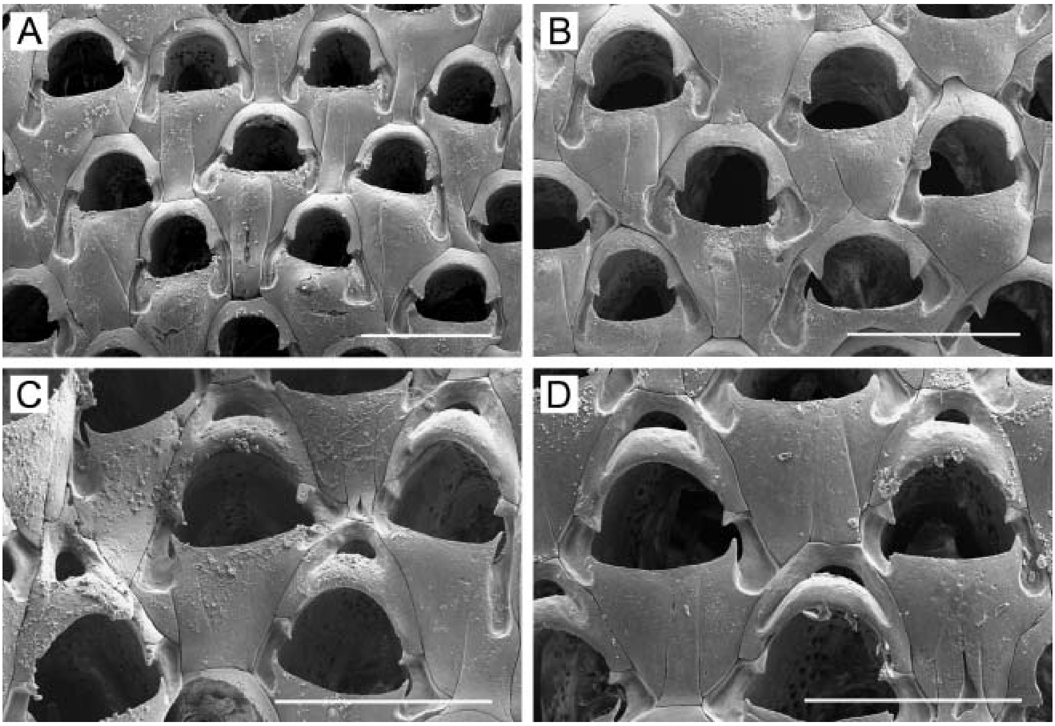

Figure 18. *Integripelta novella* Gordon, Mawatari, and Kajihara, 2002. NHM 2006.2.27.53. (A) General view of colony fragment; (B) immature zooids; (C) maternal zooids showing distal kenozooidal chambers possessing triangular, oval, and crescentic foramens; (D) close up of maternal zooids with foramen varying in size and form. Scale bars: 0.5 mm.

Material examined

DIN, six intact colonies detached from rock (NHM 2006.2.27.53). Additional material: 17 specimens.

Description

Colony unilaminar, encrusting, coherent, forming more or less circular patches with meandering borders, up to 3.5 cm in maximum dimension, dark red or pink when alive. Zooids (Figure 18A–D) roughly hexagonal or irregular, tapering proximally, rounded distally, widest just proximal to orifice, 0.45–0.70 mm long (0.58 ± 0.07 mm), 0.35–0.49 mm wide (0.41 ± 0.04 mm), closely appressed, delineated by a shallow groove and suture line. Frontal wall gymnocystal, smooth-surfaced, slightly convex, mostly without fenestrae, but with a flat, strap-like carina running from proximal zooidal margin nearly to orifice, delineated by sharp borders, sometimes with a slit or foramen in proximal midline; some zooids with low, broad umbo proximal to orifice, occasionally occupying most of frontal wall. Autozooidal orifice hat-shaped, wider than long, 0.16–0.21 mm long (0.19 ± 0.01 mm), 0.23–0.29 mm wide (0.26 ± 0.02 mm), anter semicircular, with sharp indentations in proximolateral corners; proximal rim of poster gently concave, sometimes straight; peristome lacking. Lateral excavations of gymnocyst well developed, extending proximally from orificial indentations on one or both sides for a distance of up to half of zooid length. Zooids dimorphic; orifice of maternal zooids somewhat larger and higher-arched than that of autozooids, though overlapping in size, 0.19–0.23 mm long (0.21 ± 0.01 mm), 0.25–0.32 mm wide (0.29 ± 0.02 mm). Kenozooidal ooecium (Figure 18C, D) caplike, flanked distally by a circular, triangular, or transversely crescentic foramen that varies considerably in size. Interzooidal communications via row of uniporous septula along each lateral wall. Spines and avicularia lacking. Ancestrula not observed.

Remarks

There are some small differences between our material and that from Kamekawa, Hokkaido, the type locality (Gordon et al. 2002). In specimens from Akkeshi, zooids are slightly larger; the ooecial fenestra tends to be larger and more variably shaped; some zooids have a moderately developed frontal umbo; and the strap-like frontal carina can have a slit or fenestra at the proximal end. Our observations add to the range of variation known for this species.

Distribution

Hokkaido Island, Japan. This species was originally described from a tidal flat at Kamekawa (43°03′N, 140°35′E) on the Sea of Japan side of Hokkaido; the record at Akkeshi extends the known range to the Pacific side.

Grade HIPPOTHOOMORPHA Gordon, 1989
Superfamily HIPPOTHOOIDEA Busk, 1859
Family HIPPOTHOIDAE Busk, 1859
Genus *Celleporella* Gray, 1848
Celleporella hyalina (L., 1767) species complex
(Figure 19)

Material examined

ANC, ancestrular colony on rock (NHM 2006.2.27.54); ACT, two intact colonies (NHM 2006.2.27.55); DIN, three intact colonies (NHM 2006.2.27.56); MAC, three colony fragments (NHM 2006.2.27.57); DIW, colony fragment (NHM 2006.2.27.58). Additional material: 847 specimens.

Description

Colony encrusting, coherent, unilaminar when young (Figure 19A), multilaminar, often several layers thick, with age; forming irregularly circular patches up to 2.5 cm across, white to tan in colour when alive. Primary layer consists of autozooids only; male polymorphs, ovicellate female zooids, and autozooids budded frontally in secondary layers. Zooids elongate-elliptical, spindle-shaped, widest in middle, rounded distally, tapering proximally, 0.45–0.78 mm long (0.61 ± 0.09 mm), 0.20–0.30 mm wide (0.25 ± 0.03 mm), separated by a deep groove, with slit-like lacunae and incipient zooeciules evident between young, marginal zooids. Autozooids distinct only in primary layer (Figure 19A) in marginal budding zone and in young colonies; proximal ends of zooids submerged under distal parts of preceding zooids. Frontal wall hemicylindrical, smooth, translucent, convex, rising

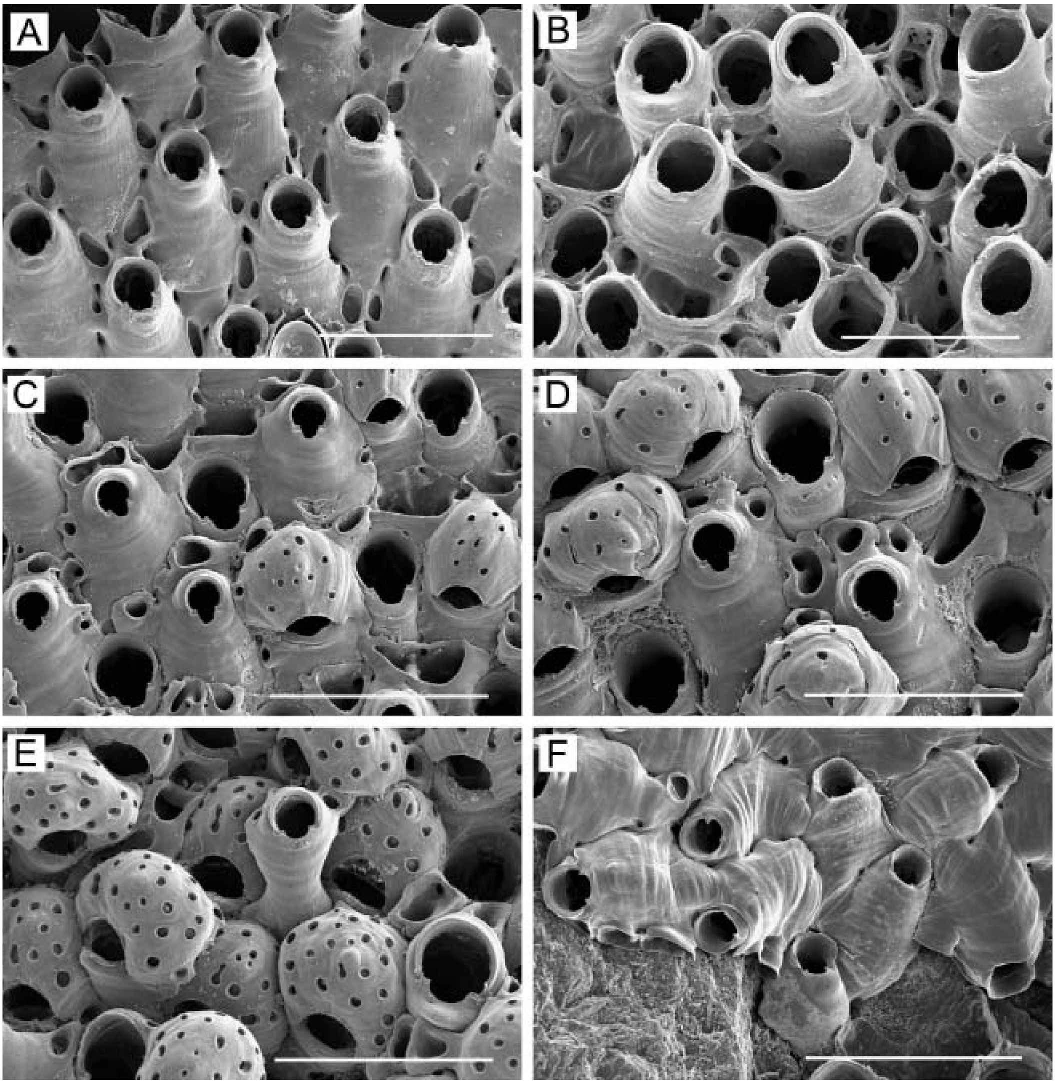

Figure 19. *Celleporella hyalina* (L., 1767) species complex. (A, C–E) NHM 2006.2.27.57; (B) NHM 2006.2.27.55; (F) NHM 2006.2.27.54. (A) Colony margin with developing zooids; (B) autozooids in primary layer; (C, D) autozooids in primary layer (large orifices), frontally budded male zooids (small orifices), and frontally budded ovicellate zooids; (E) central colony region with predominance of ovicellate zooids; (F) ancestrula and periancestrular zooids with spiral budding pattern. Scale bars: 0.5 mm (A–C, F); 0.4 mm (D, E).

distally into lunate suboral umbo. Autozooidal orifice (Figure 19B, D, E), including sinus, roughly circular, longer than broad, 0.11–0.15 mm long (0.13 ± 0.01 mm), 0.10–0.13 mm wide (0.11 ± 0.01 mm), with condylar shelves bearing small condyles pointing distally, distomedially, or medially, often with a notch between condyle and orificial rim; between condylar shelves is a deep, broadly U-shaped proximal sinus. Orifice surrounded laterally and distally by a sharp, thin, raised peristomial rim. Orifice of male zooids (Figure 19C–E) similar in shape to that of autozooidal orifice, but about one-half to one-third the length and width; proximal sinus sometimes appears proportionately longer and narrower in male zooids. Orifice of female zooids (Figure 19C, D) semicircular, broad, with a concave proximal margin. Ovicell (Figure 19C–E) hyperstomial, spherical, smooth, variable in shape, size and orientation, 0.17–0.23 mm long (0.20 ± 0.01 mm), 0.18–0.25 mm wide (0.22 ± 0.02 mm), covered with a variable number of pores, some occluded. Spines and avicularia lacking. Six pore chambers along basal side of lateral wall and two to three in distal vertical wall. Ancestrula (Figure 19F) similar in form to autozooid, though smaller and shorter. Early astogeny a spiral budding pattern, with first zooid budding distolaterally from ancestrula and each following periancestrular bud arising from angle between ancestrula and preceding zooid.

Remarks

Celleporella hyalina (L., 1767) has been considered a cosmopolitan species (Osburn 1952; Androsova 1958; Kluge 1962), distributed around the world from the Arctic to tropical latitudes. Recent studies, however, have suggested that nominal *C. hyalina* likely involves a worldwide complex of similar, perhaps cryptic species (see discussion by Dick et al. 2005, p 3726). Until further data are available from morphological, molecular, and reproductive compatibility studies, we simply refer the material from Akkeshi to the *Celleporella hyalina* (L., 1767) species complex. Variation among some of our specimens (e.g. compare number and distribution of ovicellar pores between Figure 19D and 19E) may be indicative of more than one representative of this species complex at Akkeshhi.

Grade UMBONULOMORPHA Gordon, 1989
Superfamily LEPRALIELLOIDEA Vigneaux, 1949
Family BRYOCRYPTELLIDAE Vigneaux, 1949
Genus *Porella* Gray, 1848
Porella acutirostris Smitt, 1868
(Figure 20)

Porella acutirostris Smitt 1868, p 21, Plate 26, Figures 106, 108; holotype illustrated by Dick et al. 2005, Figure 14E–H.

Porella acutirostris: O'Donoghue and O'Donoghue 1923, p 183; Osburn 1952, p 394, Plate 46, Figure 4; Mawatari 1956, p 129, Figure 10h–k; Androsova 1958, p 163, Figure 93; Kluge 1962, p 453, Figure 300; 1975, p 550, Figure 300; Gontar 1980, p 10; Mawatari and Mawatari 1981b, p 55; Dick and Ross 1988, p 63, Plate 8A; Kubanin 1997, p 123; Grischenko 1997, p 179; 2004, p 41; Dick et al. 2005, p 3738, Figure 14A–D.

Material examined

ACW, colony on rock (NHM 2006.2.27.62); BAC, colony fragment detached from bivalve shell (NHM 2006.2.27.63), three colony fragments on rock (NHM 2006.2.27.64); NB, two young colonies on bivalve shell (NHM 2006.2.27.65). Additional material: 325 specimens.

Description

Colony encrusting, unilaminar, coherent, more or less circular, up to 3 cm across, bright yellow, orange, or tan when alive. Zooids (Figure 20A, B) hexagonal, rectangular, or oval, often tapering proximally, 0.47–0.77 mm long (0.58 ± 0.08 mm), 0.20–0.32 mm wide

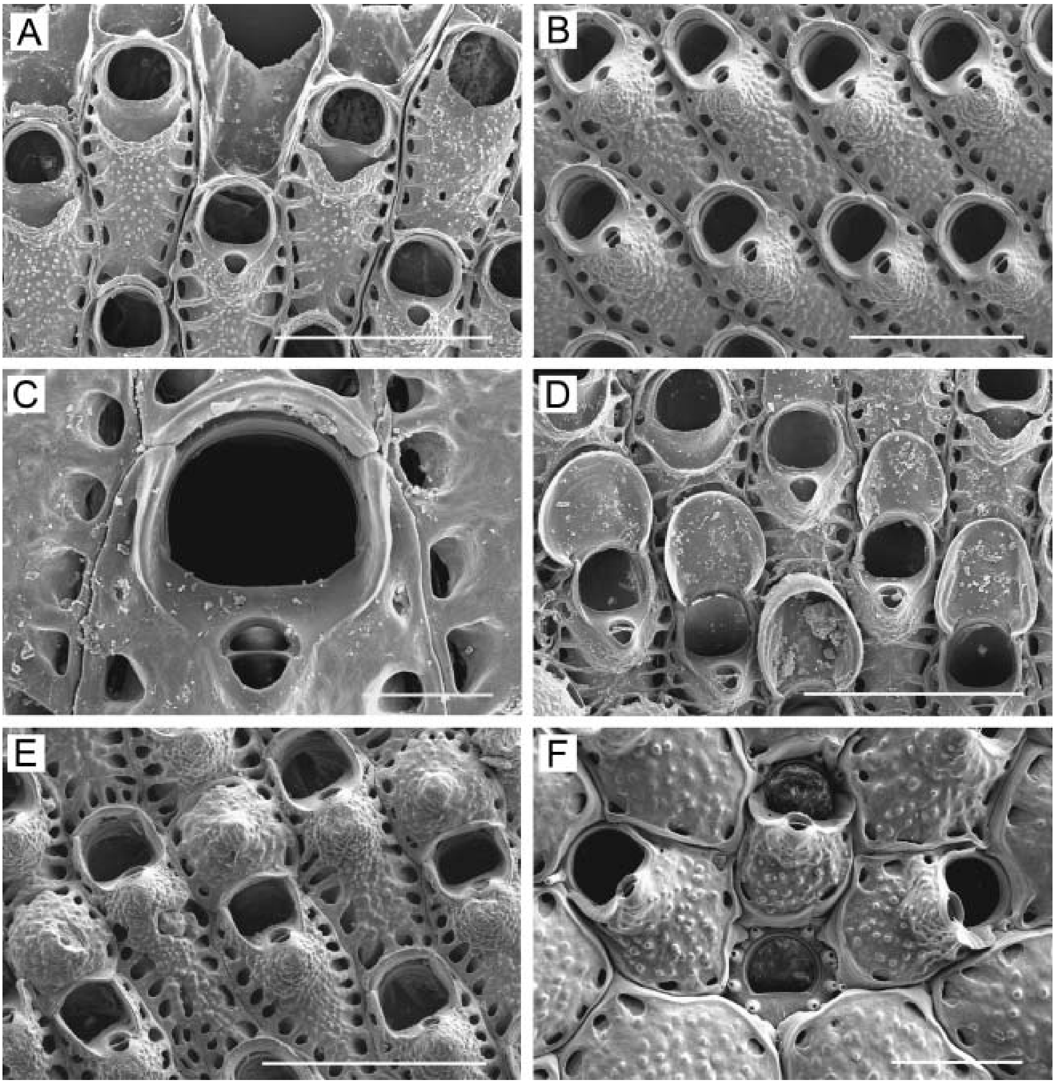

Figure 20. *Porella acutirostris* Smitt, 1868. (A, C, D) NHM 2006.2.27.62; (B) NHM 2006.2.27.64; (E) NHM 2006.2.27.63; (F) NHM 2006.2.27.65. (A) Immature zooids; (B) group of non-ovicellate zooids; (C) enlargement of orifice and suboral avicularium; (D) group of zooids with developing ovicells; (E) group of non-ovicellate zooids and zooids with umbonate ovicells; (F) ancestrula and periancestrular zooids. Scale bars: 0.5mm (A, B, D, E); 0.1mm (C); 0.2 mm (F).

(0.25 ± 0.03 mm), separated by a groove, with a faint suture line between adjacent vertical walls. Frontal wall convex, coarsely granulated, imperforate centrally, with 5–11 conspicuous areolar pores along each lateral margin, separated by short ridges. Primary orifice (Figure 20C) semicircular, broader than long, 0.09–0.12 mm long (0.11 ± 0.01 mm), 0.11–0.15 mm wide (0.12 ± 0.01 mm); proximal margin varying from slightly concave to straight or slightly convex, with an inconspicuous, low, flattened condyle near each proximal corner. Peristome (Figure 20B, C) cormidial, consisting distally of upturned proximal margin of succeeding zooid; this is confluent with sharp, raised lateral flanges that meet avicularian chamber proximally; in ovicellate zooids lateral flanges are confluent with upturned proximal margin of ovicell. Secondary orifice semicircular, or approaching quadrate in non-ovicellate zooids, often markedly quadrate in ovicellate zooids. A median suboral avicularium (Figure 20C) lies on internal slope of peristomial rim, orientated almost vertically, mandible triangular with rounded apex or almost semicircular, cross-bar complete; avicularian chamber (Figure 20D, E) raised from frontal wall, broad, roughly granulated, often umbonate, occupying up to one-half of frontal surface, developing from an areolar pore on each side. Ovicell (Figure 20D, E) hyperstomial, hemispherical, prominent, 0.19–0.24 mm long (0.21 ± 0.02 mm), 0.20–0.29 mm wide (0.24 ± 0.02 mm), imperforate, surface coarsely granulated like frontal wall, sometimes bearing a small, salient central umbo. Interzooidal communication via two multiporous septula in basal half of distal wall of zooid and a single multiporous septulum in each distolateral wall. Ancestrula (Figure 20F) of uncertain shape, obscured by surrounding zooids, with semicircular orifice bearing eight short, hollow spines along lateral margins; surrounded by triplet of small zooids distally and distolaterally and two larger zooids proximally; periancestrular zooids similar to later autozooids, but have one to three hollow ephemeral spines along distal margin of orifice.

Remarks

Dick et al. (2005) discussed the taxonomic status of *P. acutirostris* in some detail, concluding that what has been considered a circumpolar, Arctic-Boreal species may comprise a complex of closely related species in the northern hemisphere, including *P. major* Hincks, 1884 and *P. columbiana* O'Donoghue and O'Donoghue, 1923. Until this species complex is better understood, we simply refer the specimens from Akkeshi to *P. acutirostris* Smitt, 1868. Compared to zooids of specimens at Ketchikan, Alaska, zooids at Akkeshi are somewhat longer; the frontal wall and ovicell more coarsely granulated and appear more heavily calcified; the low but conspicuous lyrula seen in the Ketchikan population is absent; and both the ovicell and frontal wall tend to be umbonate, which is not the case at Ketchikan. However, the differences in morphology between Alaskan populations (Dick and Ross 1988; Dick et al. 2005) might represent geographical variation among conspecific populations.

Distribution

Smitt (1868) originally described *P. acutirostris* from Spitzbergen. Subsequently, it has come to be considered a circumpolar, Arctic-Boreal species (see Kluge 1962, 1975 and Gontar and Denisenko 1989 for many distributional records), extending as far south as Cape Cod in the northwestern Atlantic (Osburn 1912), the Lofoten Islands in the northeastern Atlantic (Nordgaard 1918), and southern California in the northeastern Pacific (Osburn 1952). In the northwestern Pacific, *P. acutirostris* has been recorded from the southern Chukchi Peninsula, Commander Islands, eastern Kamchatka, Shantar archipelago, Sakhalin Island, Kuril Islands, and Primorye (Kluge 1961; Gontar 1980; Grischenko 1997; Kubanin 1997); in Japan it is previously known from Akkeshi and Hakodate, Hokkaido, southward to middle Honshu (Mawatari and Mawatari 1981b).

Porella belli (Dawson, 1859)

(Figure 21)

Lepralia belli Dawson 1859, p 256.
Porella concinna var. a (*Belli*, Dawson): Hincks 1880, p 324, Plate 46, Figure 2.

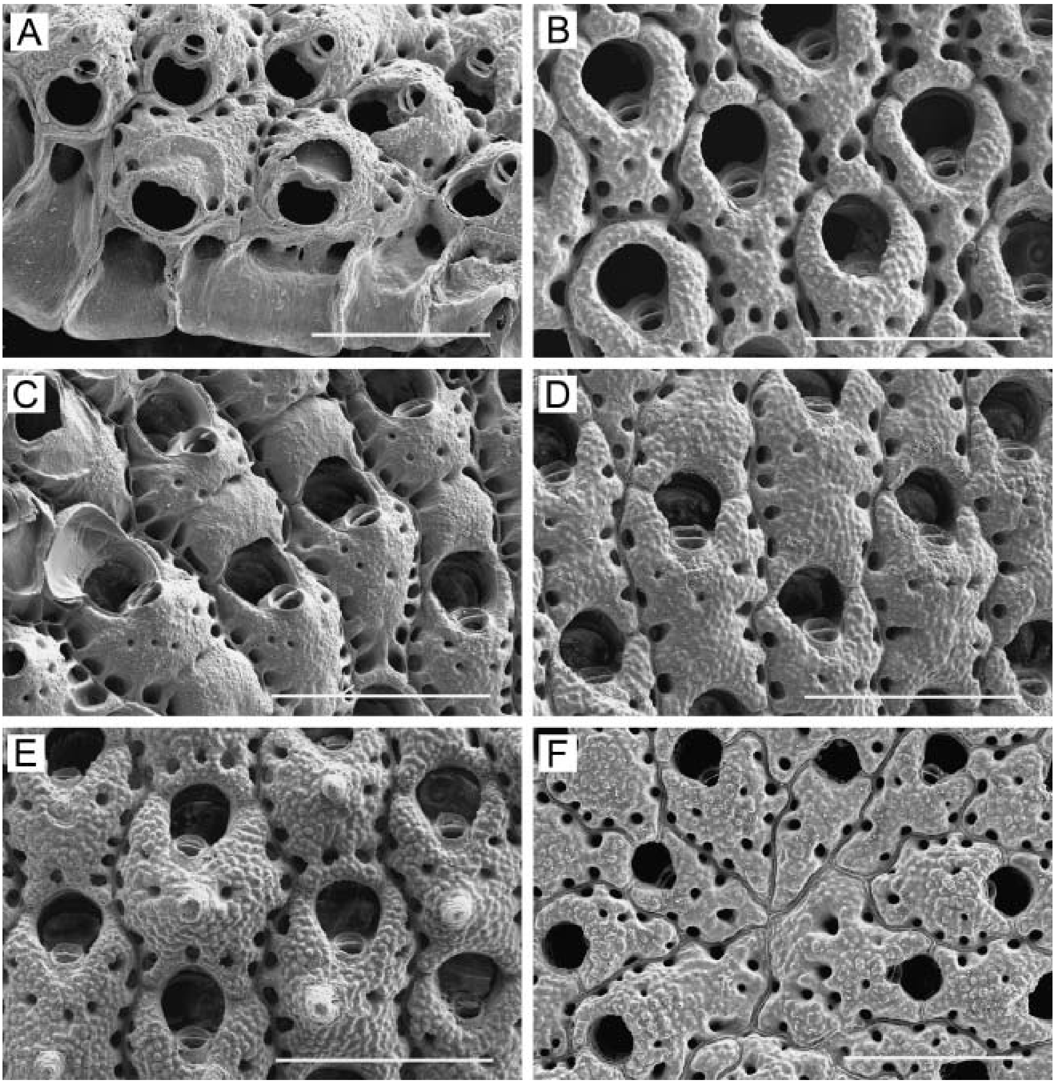

Figure 21. *Porella belli* (Dawson, 1859). (A, F) NHM 2006.2.27.10; (B, D, E) NHM 2006.2.27.9; (C) NHM 2006.2.27.66. (A) Distal view of colony margin with differentiating zooids; (B) immature zooids; (C) zooids with developing and complete ovicells; (D) mature zooids with inflated immersed ovicells; (E) mature zooids with granulose and umbonate frontal walls; (F) ancestrular region. Scale bars: 0.5 mm.

Porella concinna var. *belli*: Kluge 1952, p 158; Gontar and Denisenko 1989, p 353.
Smittina concinna var. *belli*: Androsova 1958, p 155, Figure 84; Kluge 1962, p 432, Figure 283.
Porella concinna belli: Gontar 1980, p 10; 1992, p 146; Grischenko 1997, p 179.
Porella belli: Hayward 1994, p 188, Figure 4c, d; Kubanin 1997, p 123.

Material examined

ANC, eight colony fragments (NHM 2006.2.27.9) and two colonies on rocks (NHM 2006.2.27.10, NHM 2006.2.27.66). Additional material: 85 specimens.

Description

Colony encrusting, unilaminar, coherent, tightly attached to substratum, irregularly circular, up to 2.5 cm across; yellowish, greyish, or off-white when alive. Zooids (Figure 21B–E) hexagonal or rectangular, sometimes tapering proximally, 0.35–0.60 mm long (0.48 ± 0.07 mm), 0.23–0.38 mm wide (0.31 ± 0.04 mm), delineated by a deep groove with a suture line when young, and by deep, undulating lateral groove with age; transverse boundaries indistinct. Frontal wall imperforate centrally, coarsely granulated, with four to seven circular areolar pores along each lateral margin; inflated and convex in young zooids; increasingly thick with age, quite convex, roughly granulose, sometimes with a prominent umbo in suboral or proximolateral region. Primary orifice semicircular, deeply submerged, difficult to measure, but about 0.10–0.13 mm long by 0.12–0.15 mm wide; lyrula low and broad, occasionally lacking in some zooids, which have a slightly convex proximal border; condyles low, tapering distally, located near proximal corners of orifice. Peristome deep, secondary orifice pyriform in outline, 0.11–0.16 mm long (0.14 ± 0.02 mm), 0.12–0.16 mm wide (0.15 ± 0.01 mm), cormidial, its distal half formed by indented proximal margin of succeeding zooid; this is confluent with thick, rounded lateral flanges that meet proximally with sides of suboral avicularian chamber; in ovicellate zooids lateral flanges connect with proximolateral corners of ovicell; suture lines separate contributions of secondary calcification from a zooid and its neighbour that make up the secondary orifice. A large, oval median suboral avicularium lies within peristome, below secondary orifice, orientated vertically or tilted slightly proximally; mandible semicircular, cross-bar complete; avicularian chamber broader than long, lunate, occupying frontal surface from margin to margin, with two to five small pores around chamber margin or in chamber itself; in young zooids chamber is convex, inflated, finely granulated, but with age it becomes immersed and rugose. Ovicell (Figure 21C–E) hyperstomial, spherical, 0.16–0.21 mm long (0.19 ± 0.01 mm), 0.20–0.25 mm wide (0.23 ± 0.02 mm), initially finely granulated, rapidly immersed with thick, roughly granulose calcification from surrounding zooids, becoming flush with colony surface. Oral spines lacking. Two multiporous septula in transverse wall and four circular multiporous septula in each lateral wall. Ancestrular complex (Figure 21F) comprises five zooids radiating from common centre; in the specimen illustrated, the ancestrula proper is completely obscured by periancestrular zooids.

Remarks

The structure of the frontal wall varies considerably in *P. belli* according to substratum. In general, the frontal wall is inflated in young zooids and becomes gradually mucronate with age. Colonies on flat surfaces tend to retain the inflated appearance of the frontal wall, without an umbo, whereas those on irregular substrata may comprise entirely heavily calcified zooids with a strongly mucronate frontal wall.

Distribution

This is a circumpolar, Arctic-Boreal, species. Kluge (1962, 1975) and Gontar and Denisenko (1989) gave many distributional records for the Arctic. In the northern Pacific, *P. belli* has been reported from the Commander Islands (Grischenko 1997; Kubanin 1997), eastern Kamchatka (Kluge 1961), the Kuril Islands (Gontar 1980), Sakhalin Island, and Primorye (Androsova 1958). Akkeshi Bay is the southernmost known locality of *P. belli* in the Asian Pacific.

Family UMBONULIDAE Canu, 1904

Genus *Desmacystis* Osburn, 1950

Desmacystis sandalia (Robertson, 1900)

(Figure 22)

Membranipora sandalia Robertson 1900, p 324, Plate 20, Figures 9, 9a, Plate 21, Figure 10; 1908, p 264, Plate 15, Figures 11–14.

Desmacystis sandalia: Osburn 1950, p 32, Plate 3, Figure 1; Gontar 1981, p 102; Dick and Ross 1988, p 30, Plate 1A; Gordon and Grischenko 1994, p 62, Figures 1–6; Kubanin 1997, p 123; Grischenko 1997, p 173; 2004, p 40.

? *Desmacystis sandalia concinna* Gontar 1982, p 543, Figure 1,1.

Material examined

ACT, two colony fragments (NHM 2006.2.27.59); KAI, colony on rock (NHM 2006.2.27.60). Additional material: 147 specimens.

Description

Colony encrusting, unilaminar, coherent, loosely attaching to substrate, irregularly circular, up to 5 cm across, bright orange or reddish when alive. Zooids (Figure 22B–D)

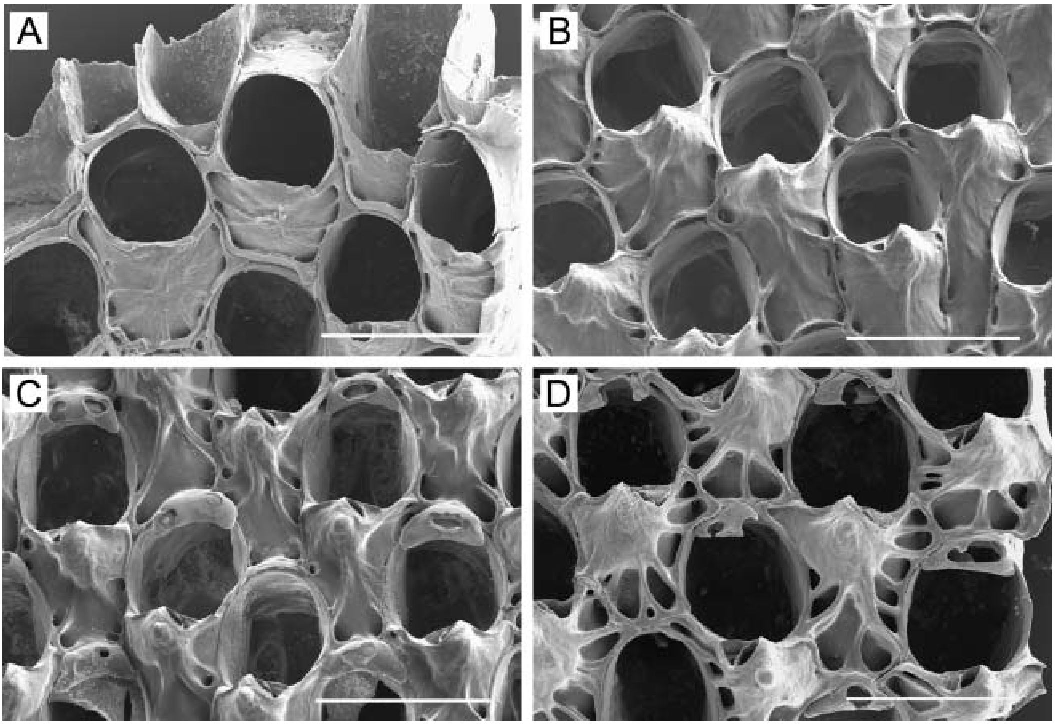

Figure 22. *Desmacystis sandalia* (Robertson, 1900). (A, D) NHM 2006.2.27.59; (B, C) NHM 2006.2.27.60. (A) Colony margin with developing zooids; (B) immature zooids; (C) mature zooids showing transversely elongate vestigial ovicells and relatively smooth frontal walls; (D) mature zooids with frontal shields reinforced by radially arranged ridges of calcification. Scale bars: 0.5 mm.

irregularly hexagonal, or tapering proximally and clavate in shape, rounded distally, thin-walled, 0.60–0.80 mm long (0.71 ± 0.06 mm), 0.32–0.45 mm wide (0.38 ± 0.03 mm), separated by raised vertical walls. Frontal shield cryptocystal, "incomplete", occupying 40–60% of zooidal length; relatively smooth in newly formed zooids, sunken below narrow gymnocystal rim and covered by epitheca, with three to five areolar pores along each lateral margin; with age, reinforced by strong buttresses of calcification running between adjacent areolae toward centre of cryptocyst, meeting proximal and lateral margins of avicularian chamber, often confluent with a heavily calcified median buttress. A suboral avicularium with a raised chamber arises from one of distalmost areolae, asymmetrically placed and overhanging the opesia, rostrum facing obliquely laterally, mandible semicircular to subspatulate, cross-bar complete. Secondary orifice oval to nearly circular, 0.28–0.35 mm long (0.31 ± 0.02 mm), 0.27–0.33 mm wide (0.29 ± 0.02 mm), surrounded by thin, raised gymnocystal margin; with age, orifice can become partially concealed by calcification from adjacent zooids. Ovicell (Figure 22C, D) a small, transversely elongate hood suspended in distal curvature of aperture, with uncalcified central area that is sometimes open at proximal margin. Four small circular multiporous septula in each lateral wall; transverse wall interconnects through numerous pores in basal half, organized into two distinct septular areas. Spines absent. Ancestrula not observed.

Remarks

Gontar (1982) described a new subspecies, *D. sandalia concinna*, on the basis of material from Kunahsir among the southern Kuril Islands. Characters distinguishing this subspecies from the nominal subspecies include strongly calcified ridges on the proximal part of the frontal shield; the occasional presence of a small additional avicularium in the same area; and smaller zooidal dimensions. Grischenko (1997) noted a similar condition of the frontal shield in specimens from the Commander Islands, but did not observe the additional frontal avicularia. Colonies of *D. sandalia* from Akkeshi Bay show considerable variation in the degree of calcification of the frontal shield and avicularian chamber, and in the development of buttresses. Whereas in some colonies zooids have an inflated, relatively smooth frontal shield and reduced, shortened buttresses, in others zooids have a highly mucronate frontal, reinforced by strong buttresses. A parallel variation in characters also occurs during individual zooidal development. Except for the sporadic presence of an additional frontal avicularium, the characters considered diagnostic for *D. sandalia concinna* appear to comprise astogenetic, ecophenotypic, or intra-population variation. It thus remains unclear whether *D. sandalia concinna* represents a valid subspecies.

Distribution

This is a Boreal Pacific species, originally described from Yakutat, Alaska (Robertson 1900) and subsequently reported from the Queen Charlotte archipelago (Osburn 1950), Kodiak Island (Dick and Ross 1988), the Commander Islands (Gordon and Grischenko 1994; Grischenko 1997, 2004; Kubanin 1997), and Kunashir and Shikotan among the southern Kuril Islands (Gontar 1981). Our record from Akkeshi is the first report of *D. sandalia* from Japan and represents the southernmost limit of its known distribution in the western North Pacific.

Grade LEPRALIOMORPHA Gordon, 1989
Superfamily SMITTINOIDEA Levinsen, 1909
Family SMITTINIDAE Levinsen, 1909
Genus *Parasmittina* Osburn, 1952
Parasmittina avicularissima (Gontar, 1982)
(Figure 23)

Parasmittina jeffreisii avicularissima Gontar 1982, p 548, Figures 1, 5a, b.

Material examined

ANC, colony on rock (NHM 2006.2.27.72), colony on rock (NHM 2006.2.27.73), extensive colony on rock (NHM 2006.2.27.74). Additional material: 23 specimens.

Description

Colony encrusting, coherent, unilaminar, but sporadically building up frontally budded layer of irregularly orientated zooids; irregularly circular, largest observed 3.8 cm in maximum dimension; bright yellow when alive, with lemon-yellow membranous growing edge one or two zooids deep. Zooids (Figure 23B, C, E) oval to irregularly hexagonal, rounded distally, 0.40–0.63 mm long (0.49 ± 0.06 mm), 0.27–0.43 mm wide (0.34 ± 0.04 mm), separated by shallow groove, with appressed adjacent vertical walls forming a thick line of calcification flanked by rows of areolar pores. Frontal wall convex, vitreous; smooth, or rugose with coarse granulation; imperforate centrally, with 7–10 conspicuous areolar pores along each lateral margin, separated by short buttresses; with large conical or nodular suboral umbo variable in size, occasionally with one to three additional protuberances scattered elsewhere on frontal surface. Primary orifice (Figure 23B) subcircular, typically slightly longer than broad, 0.10–0.14 mm long (0.12 ± 0.01 mm), 0.10–0.13 mm wide (0.11 ± 0.01 mm), with a low, narrow, truncate lyrula and long, pointed condyles directed proximomedially. Young zooids (Figure 23A) have two short, ephemeral distal spines. Peristome formed by narrow, raised lip proximally and laterally in young zooids, or rarely by two lateral lappets separated by sinus; primary orifice becomes sunken with increased secondary calcification. Zooids with or without a large avicularium (Figure 23A–C), about 0.12–0.15 mm long, lateral to orifice, abutting peristome, the rostrum raised distally, with an acute, slightly long-triangular mandible directed medially, approximately in line with proximal margin of orifice; cross-bar thin, complete; sometimes the lateral-oral avicularium is paired. The lateral-oral avicularium may be replaced by a larger avicularium (Figure 23D, E) of similar shape occupying central or proximal area of frontal wall and pointing distally, distolaterally, or sometimes proximally. Small avicularia (Figure 23D, F), about 0.07–0.10 mm long, pyriform or oval in shape, with semicircular mandible directed laterally or proximally, can also occur anywhere along the proximal or lateral margins proximal to the orifice, with or without the larger, acute types; sometimes an oval avicularium overlaps the margin of an ovicell. Ovicell (Figure 23F, G) spherical, broader than long, 0.20–0.28 mm long (0.24 ± 0.02 mm), 0.23–0.33 mm wide (0.28 ± 0.02 mm), overhanging the orifice; smooth, flattened on top and bearing a single large, circular or transversely elliptical pore; recumbent and sunken in frontal wall of distal zooid, with contributions of ectocystal calcification from that zooid and laterally flanking zooids delineated by raised suture lines; ovicell lacking ornamentation, or with one to three conical, tuberculate processes, one per sector of secondary calcification.

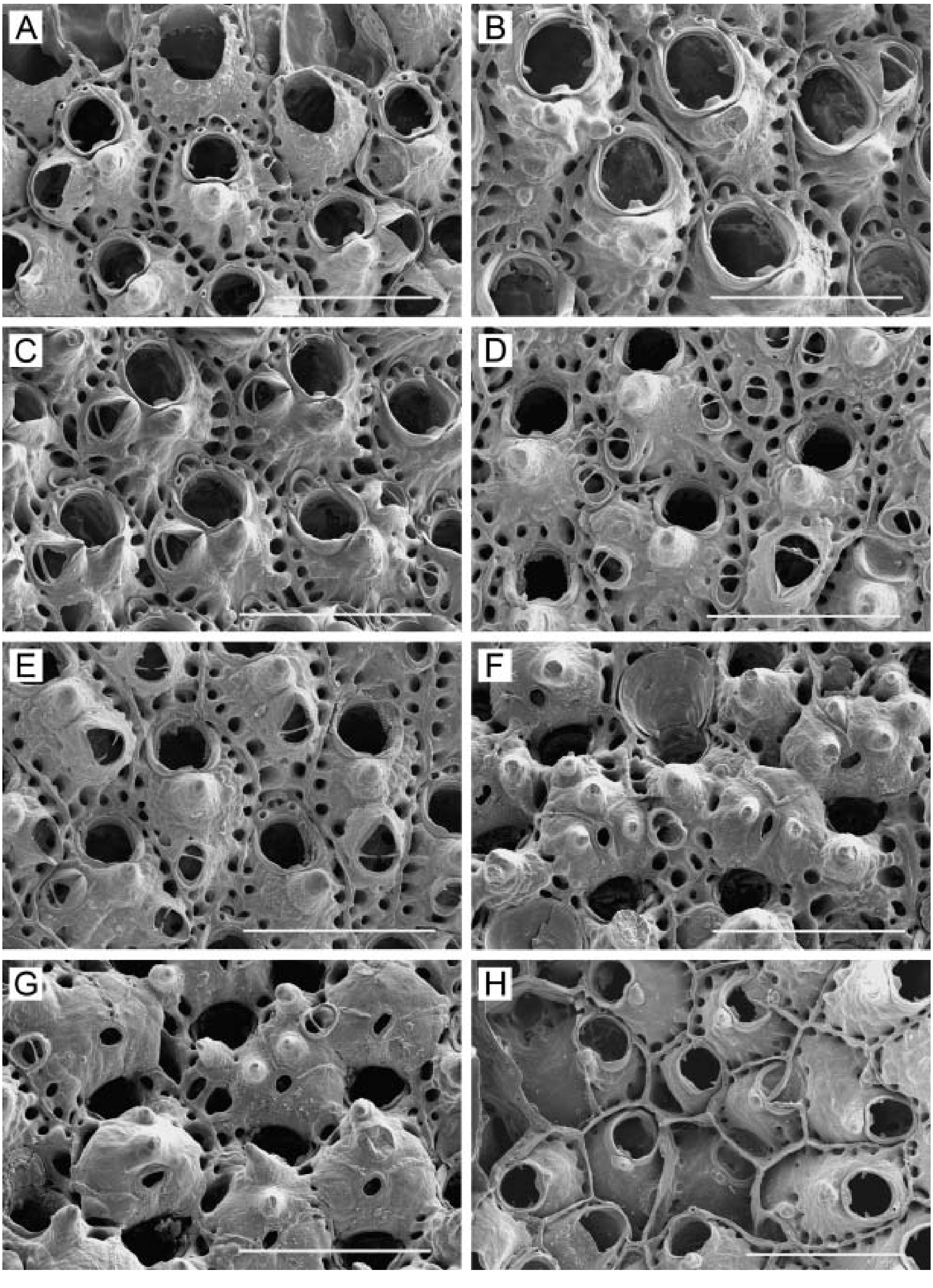

Figure 23. *Parasmittina avicularissima* (Gontar, 1982). (A, H) NHM 2006.2.27.72; (B, C, F, G) NHM 2006.2.27.73; (D, E) NHM 2006.2.27.74. (A) Zooids differentiating at colony margin; (B) immature zooids, showing oral spinescars, lyrula, and condyles; (C) immature zooids with lateral triangular avicularia; (D) autozooids with oval proximo-lateral avicularia and large frontal avicularium directed proximally; (E) autozooids with frontal avicularia directed distally; (F) zooids with developing and completed ovicells; (G) mature zooids with ovicells possessing single pore; (H) ancestrular region. Scale bars: 0.5 mm (A, C–H); 0.4 mm (B).

Interzooidal communication via uniporous septula. Ancestrula not observed; ancestrular region we observed (Figure 23H) appears entirely covered by a frontally budded layer of irregularly orientated zooids.

Remarks

The stable character that distinguishes this species from any other *Parasmittina* reported from the northwestern Pacific, including *P. jeffreysii* (Norman, 1903), *P. trispinosa* (Johnston, 1838), and *P. macroavicularia* (Androsova, 1958), is the presence of only a single, large pore in the ovicell.

Gontar (1982) described and illustrated two types of avicularia in her original description, but only briefly mentioned their arrangement, which we found to be quite variable. Most zooids located marginally or peripherally lack avicularia or have only the lateral-oral avicularium with a triangular mandible pointed medially. In contrast, zooids situated near the colony centre tend to have several different combinations of avicularia, such as: (1) a triangular lateral-oral avicularium on both sides of orifice, mandibles pointing medially; (2) an oval avicularium on each side of the orifice; (3) both triangular and oval avicularia lateral to orifice; (4) a single triangular avicularium located proximally on the frontal wall, with the mandible directed distally, laterally, or proximally; (5) a single oval avicularium lateral to orifice; (6) one or two oval avicularia in the proximal half of the frontal wall; or (7) one oval avicularium lateral to the orifice and another more proximally.

Distribution

Parasmittina avicularissima was originally described from Crabovaya Bay, Shikotan Island, southern Kuril Islands. Akkeshi Bay is the second and southernmost known locality.

Genus *Raymondcia* Soule, Soule, and Chaney, 1995

Raymondcia rigida (Lorenz, 1886), new combination

(Figure 24)

Smittina rigida Lorenz 1886, p 91 (9), t 7, Figures 8, 8a.

Smittina rigida: Androsova 1958, p 152, Figure 80; Kluge 1961, p 137; 1962, p 429, Figure 280; 1975, p 520, Figure 280; Gontar 1980, p 9; Mawatari and Mawatari 1981b, p 53.

? *Lepralia bella* Busk 1860, p 144.

? *Smittina bella*: Powell 1968, p 2304; Mawatari and Mawatari 1981b, p 54; Grischenko 1997, p 181.

Not *Smittina bella*: Osburn 1952, p 403, Plate 47, Figures 4, 5; Mawatari 1956, p 130, Figures 12a–e, 13; Dick and Ross 1988, p 59, Plate 11B.

Material examined

ANC, colony on rock (NHM 2006.2.27.12), colony on rock (NHM 2006.2.27.68), colony on rock (NHM 2006.2.27.69), ancestrular colony on rock (NHM 2006.2.27.70); ACW, colony on rock (NHM 2006.2.27.67); NB, five young colonies on bivalve shell (NHM 2006.2.27.71). Additional material: 124 specimens.

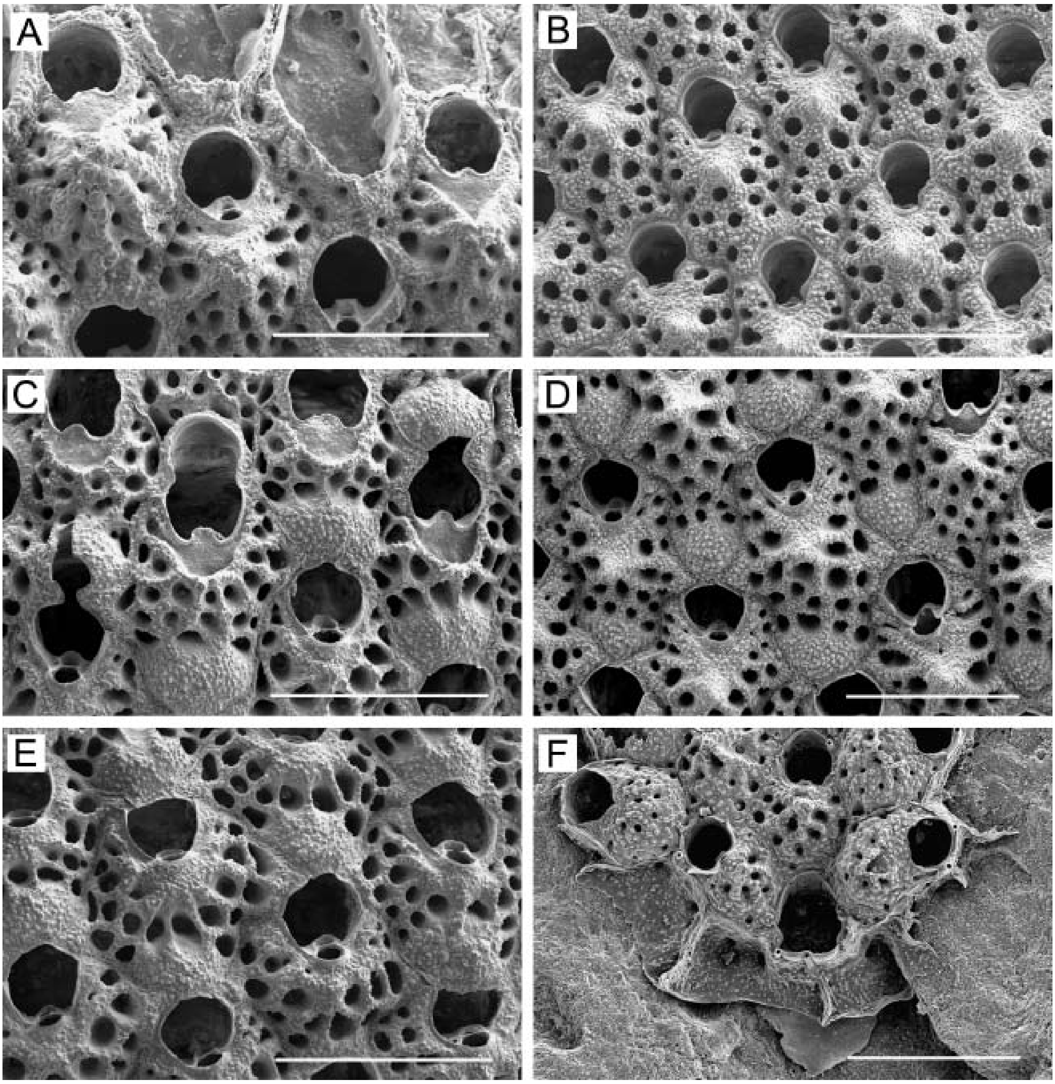

Figure 24. *Raymondcia rigida* (Lorenz, 1886). (A) NHM 2006.2.27.68; (B, D) NHM 2006.2.27.67; (C, E) NHM 2006.2.27.12; (F) NHM 2006.2.27.70. (A) Colony margin with developing zooids; (B) immature zooids; (C) autozooids with developing ovicells; (D) umbonate mature zooids with ovicells covered by merging segments from adjacent zooids; (E) inflated mature zooids; (F) ancestrula with periancestrular zooids. Scale bars: 0.5 mm.

Description

Colony encrusting, unilaminar, coherent, forming circular patches up to 3 cm across, reddish to orange when alive. Zooids (Figure 24A, B) hexagonal, oval, or irregularly rectangular, mostly with indistinct meandering boundaries, 0.43–0.78 mm long (0.59 ± 0.07 mm), 0.33–0.45 mm wide (0.38 ± 0.03 mm), separated by shallow undulating groove with suture line at bottom. Frontal wall slightly to moderately convex, finely granulated, covered with numerous large pores; with age, pores became infundibular. Frontal wall rises into a small or prominent conical median umbo (Figure 24B, D) in suboral or central region. Primary orifice (Figure 24C) round or slightly longer than broad, with wide, variably tall median lyrula; small, sharp lateral condyles evident in some marginal zooids, but usually appear to be lacking (Figure 24A, C). Oral spines lacking outside zone of astogenetic change. Secondary orifice irregularly circular, oval, or pyriform in outline, longer than wide, often constricted proximally; surrounded by thin, smooth, angled rim, 0.14–0.19 mm long (0.16 ± 0.01 mm), 0.13–0.18 mm wide (0.15 ± 0.01 mm); cormidial (Figure 24D), formed distally by proximal margin of succeeding zooid and laterally by extensions of secondary calcification from adjacent zooid on each side. Median suboral avicularium (Figure 24D, E) oval or pyriform in outline, with short-spatulate mandible and complete cross-bar; rising above proximal orificial denticle and lying mostly within peristome, tilted proximally from perpendicular. Avicularian chamber small, semicircular, completely immersed in suboral umbo, often flanked laterally by a minute pore on each side. Ovicell (Figure 24C–E) hyperstomial, spherical, imperforate, broader than long, 0.14–0.20 mm long (0.17 ± 0.01 mm), 0.18–0.23 mm wide (0.20 ± 0.01 mm), rapidly immersed, the top flush with colony surface, finely granulated; outer layer cormidial like secondary orifice, with calcification from the succeeding and lateral zooids, the contributions delineated by sutures on surface. Lateral wall of zooids with two distal and six lateral basal pore chambers. Ancestrula (Figure 24F) modified tatiform, about 0.42 mm long by 0.33 mm wide; rapidly obscured by periancestrular zooids; opesia a little less than half the length of ancestrula, with an undetermined number of opesial spines. Ancestrula buds a small zooid distally and a pair distolaterally; from the latter arise two proximal periancestral zooids. Zooids in zone of astogenetic change with two to four ephemeral oral spines.

Remarks

Soule et al. (1995) established the genus *Raymondcia* for species resembling *Smittina*, but with the secondary orifice and ovicell cormidial, composed of distal and two lateral segments, characters present in our material. Accordingly, we use the new combination *R. rigida* (Lorenz, 1886) herein. *Raymondcia rigida* is similar to *R. macginitiei* Soule et al., 1995 in having a pyriform secondary orifice and the avicularium orientated nearly vertically within the peristiome; however, in the latter species, the orificial denticle is wider than the width of the suboral avicularium, whereas in *R. rigida* it is narrow, about the same width as the avicularium. Although the frontal wall is inflated in *R. macginitiei*, it is distinctly umbonate in *R. rigida*, which also has considerably larger frontal pores. Finally, the most deeply immersed ovicells of *R. rigida* are still a little convex and recognizable, whereas those of *R. macginitiei* became totally immersed.

Distribution

This has been considered a circumpolar Arctic-Boreal species; Kluge (1962, 1975) and Gontar and Denisenko (1989) provided many distributional records. Most of these records need to be re-examined (see Dick and Ross 1988), due to possible confusion with *R. bella* (Busk, 1860), originally described from Shetland, Britain (Hayward and Ryland 1999). On the Asiatic side, the nominal species has been recorded from eastern Kamchatka, the Commander Islands, the Shantar Archipelago, the Kuril Islands, southern Sakhalin Island, Primorye, and Peter the Great Gulf (Androsova 1958; Kluge 1961; Gontar 1980; Grischenko 1997). There is a record of nominal *R. rigida* from Muroran, Hokkaido, Japan (Mawatari and Mawatari 1981b).

Raymondcia klugei (Gontar, 1982)

(Figure 25)

Porella klugei Gontar 1982, p 549, Figure 2-1.

Material examined

ANC, young colony on rock (NHM 2006.2.27.6), two ancestrular colonies on rock (NHM 2006.2.27.7), extensive colony on rock (NHM 2006.2.27.8), colony on rock (NHM 2006.2.27.66). Additional material: 88 specimens.

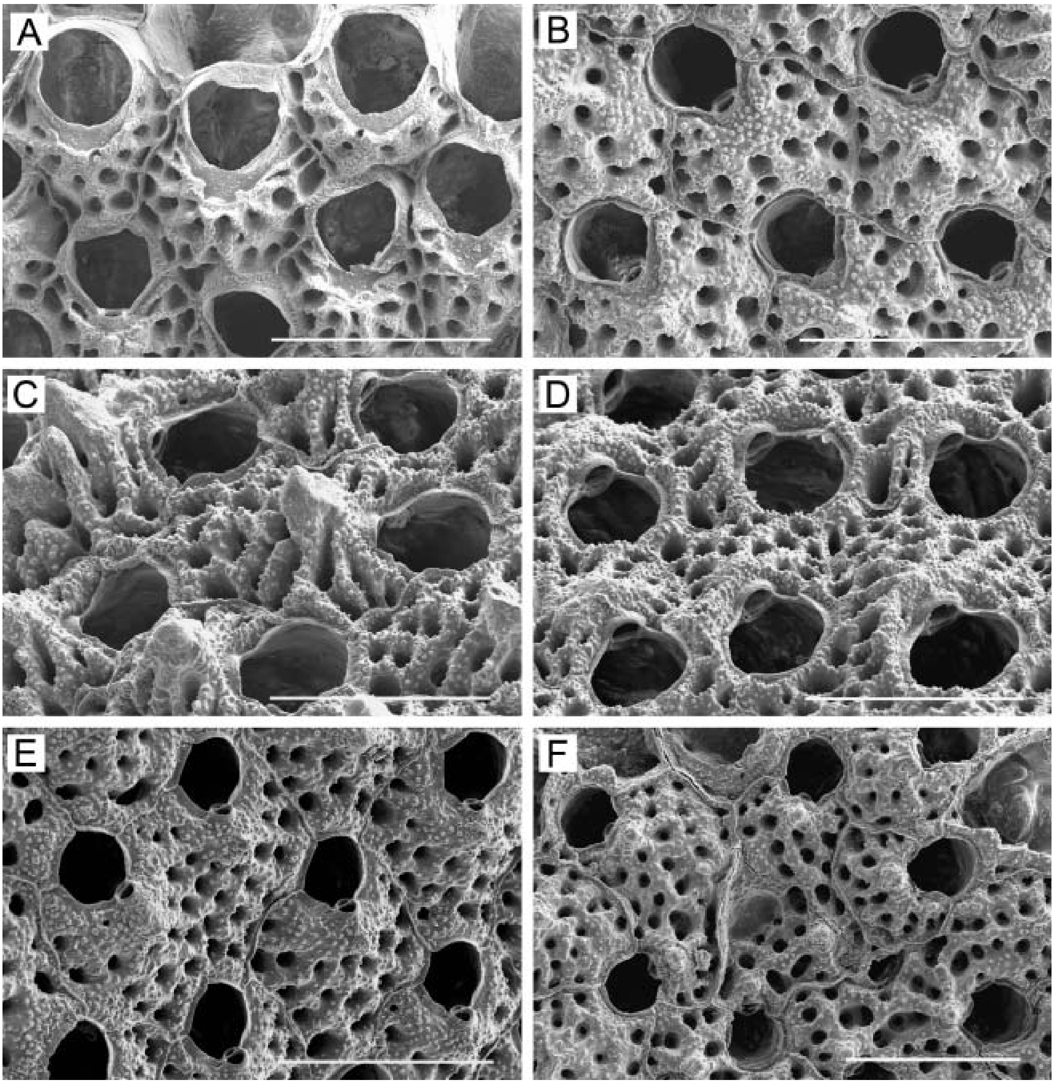

Figure 25. *Raymondcia klugei* (Gontar, 1982). (A, C) NHM 2006.2.27.66; (B) NHM2006.2.27.6; (D) NHM 2006.2.27.8; (E) ZIRAS 2/44556; (F) NHM 2006.2.27.7. (A) Colony margin with developing zooids; (B) immature zooids; (C) mucronate autozooids, lateral view; (D) distolateral view of autozooids showing suboral avicularia tilted inside; (E) autozooids, paratype specimen; (F) ancestrular region. Scale bars: 0.5 mm (A, E, F); 0.4 mm (B–D).

Description

Colony encrusting, unilaminar, coherent, forming circular patches up to 4 cm across; orange, dark red or light violet when alive. Zooids (Figure 25B) hexagonal, oval, or pyriform, 0.47–0.65 mm long (0.57 ± 0.05 mm), 0.30–0.45 mm wide (0.38 ± 0.04 mm), usually with very irregular boundaries, separated by undulating suture line. Frontal wall slightly convex to inflated, finely granulated, with five or six areolar pores along each lateral margin and additional large, infundibuliform pores in the central region. With age, outer pore openings became enlarged and frontal wall appears reticulate, with rounded ridges between pores. In some colonies, frontal wall rises to a prominent, conical median suboral umbo (Figure 25C). Orifice circular to irregularly oval, 0.13–0.17 mm long (0.15 ± 0.02 mm), 0.14–0.19 mm wide (0.17 ± 0.01 mm), with a thin marginal rim; condyles and lyrula lacking. Secondary orifice cormidial, usually comprising four sectors, including contributions of frontal wall from the distal and lateral zooids, with distinct sutures between sectors. With increasing secondary calcification, the low peristome becomes irregular. A small, oval median suboral avicularium (Figure 25B, D, E) abuts the primary orifice; with increasing secondary calcification it comes to lie within peristome, orientated perpendicularly, or nearly so, to colony surface, hidden from frontal view; mandible semicircular, with complete cross-bar. Avicularian chamber small, crescentic, completely immersed with age; avicularium occasionally lacking. Spines and ovicells lacking. Zooids with two distal and four lateral basal pore chambers. Ancestrula not observed; obscured by ancestrular complex (Figure 25F) of heavily calcified zooids smaller than astogenetically mature zooids, often overgrown by layer of irregularly orientated, frontally budded zooids.

Remarks

The taxonomic position of this species is unclear. It does not belong in *Porella*, as originally placed, because that genus is characterized by having an ovicell and an umbonuloid frontal shield with marginal areolae only, although spines and lyrula may be lacking and the condyles greatly reduced (Hayward and Ryland 1999). The cormidial secondary orifice, with contributions from the lateral and distal zooids, is very similar to that of *Raymondcia* (Soule et al. 1995); *Raymondcia* also has a median suboral avicularium. However, characters of *Raymondcia* as the genus is now defined include lyrula, condyles, and ovicell. Although the definitions of some genera (e.g. *Porella*) encompass variation in the presence or degree of development of a lyrula and condyles, inferred loss of the ovicell is problematic; we are not aware of any lepraliomorph genus in which some species have ovicells and others brood internally. Nonetheless, the overall resemblance of *Raymondcia klugei* (Gontar) to *Raymondcia rigida* (Lorenz) is remarkable. Since we were unable to observe embryos internally in any colonies of *R. klugei*, it is unknown whether this species really lacks ovicells and broods internally. As an alternative explanation for the absence of ovicells in our specimens, it might be that conditions in the intertidal zone of Akkeshi Bay are suitable for growth, but not for reproduction. Such a situation would occur, for example, if colonies reproduced only in relatively deep water, but recruits could survive intertidally.

Distribution

This species was originally described from Ivanovskogo Cape, Kunashir Island, southern Kuril Islands. Akkeshi Bay is the second known locality.

Family BITECTIPORIDAE MacGillivray, 1895

Genus *Parkermavella* Gordon and d'Hondt, 1997

Parkermavella orientalis (Androsova and Gontar in Gontar 1982), new combination

(Figure 26)

Schizomavella auriculata orientalis Androsova and Gontar in Gontar 1982, p 549, Figure 2-2.

Material examined

ANC, colony on rock (NHM 2006.2.27.31), intact colony (NHM 2006.2.27.84); ACW, colony on rock (NHM 2006.2.27.83). Additional material: 38 specimens.

Description

Colony unilaminar, encrusting, coherent, forming circular patches up to 3 cm in diameter, bright beige or light orange in colour when alive. Zooids (Figure 26A, B) irregularly hexagonal, barrel-shaped, or rectangular, 0.35–0.53 mm long (0.42 ± 0.05 mm), 0.28–0.45 mm wide (0.36 ± 0.04 mm), separated by fine suture lines between raised adjacent vertical walls. Frontal wall moderately convex to inflated; vitreous, smooth in young zooids, nodulose in mature zooids; imperforate centrally with five to nine conspicuous areolar pores along each lateral margin, separated by short ridges. Primary orifice (Figure 26C) subcircular, 0.10–0.13 mm long (0.11 ± 0.01 mm), 0.10–0.14 mm wide (0.12 ± 0.01 mm); proximal margin with shallow, U-shaped median sinus flanked by broad condylar shelves bearing blunt condyles. Newly budded zooids (Figure 26A) have one or two short, hollow ephemeral spines distal to primary orifice. Secondary orifice cormidial, formed proximally by sharp, elevated flanges of peristome extending from sides of suboral avicularian chamber to distal curvature formed by raised, thickened margin of succeeding zooid; circular in outline in immature zooids, transversely oval in ovicellate zooids; in mature zooids, lateral flanges connect with proximolateral corners of ovicell. Immediately proximal to orificial sinus is a small suboral avicularium (Figure 26B) with complete cross-bar and semicircular mandible directed proximally at an angle to frontal plane; avicularian chamber narrow, crescentic, prominent in immature zooids, becoming immersed and covered by nodules in ovicellate zooids, flanked by a pair of small pores. Ovicellate zooids additionally have paired lateral oral avicularia (Figure 26D, E) directed proximolaterally at an angle to frontal plane, somewhat larger than median avicularium, with complete cross-bar; mandible subspatulate, slightly elongate; rostral opesia triangular distal to cross-bar; lateral avicularia occasionally single or lacking altogether; rarely only one or two lateral avicularia present, with median suboral avicularium absent. Ovicell (Figure 26D, E) hemispherical, recumbent on following zooid, broad, 0.18–0.25 mm long (0.21 ± 0.02 mm), 0.22–0.27 mm wide (0.25 ± 0.01 mm); with concave proximal margin; smooth on top, perforated with 25–30 irregular pores; with age, covered around periphery with heavy nodular secondary calcification. Zooids intercommunicate via uniporous septula. Ancestrula (Figure 26F) similar in form to autozooid, reduced in size, 0.27 mm long, 0.20 mm wide, irregularly hexagonal, with quite convex frontal wall and raised vertical walls; orifice circular, 0.08 mm long, 0.08 mm wide; surrounded by seven zooids.

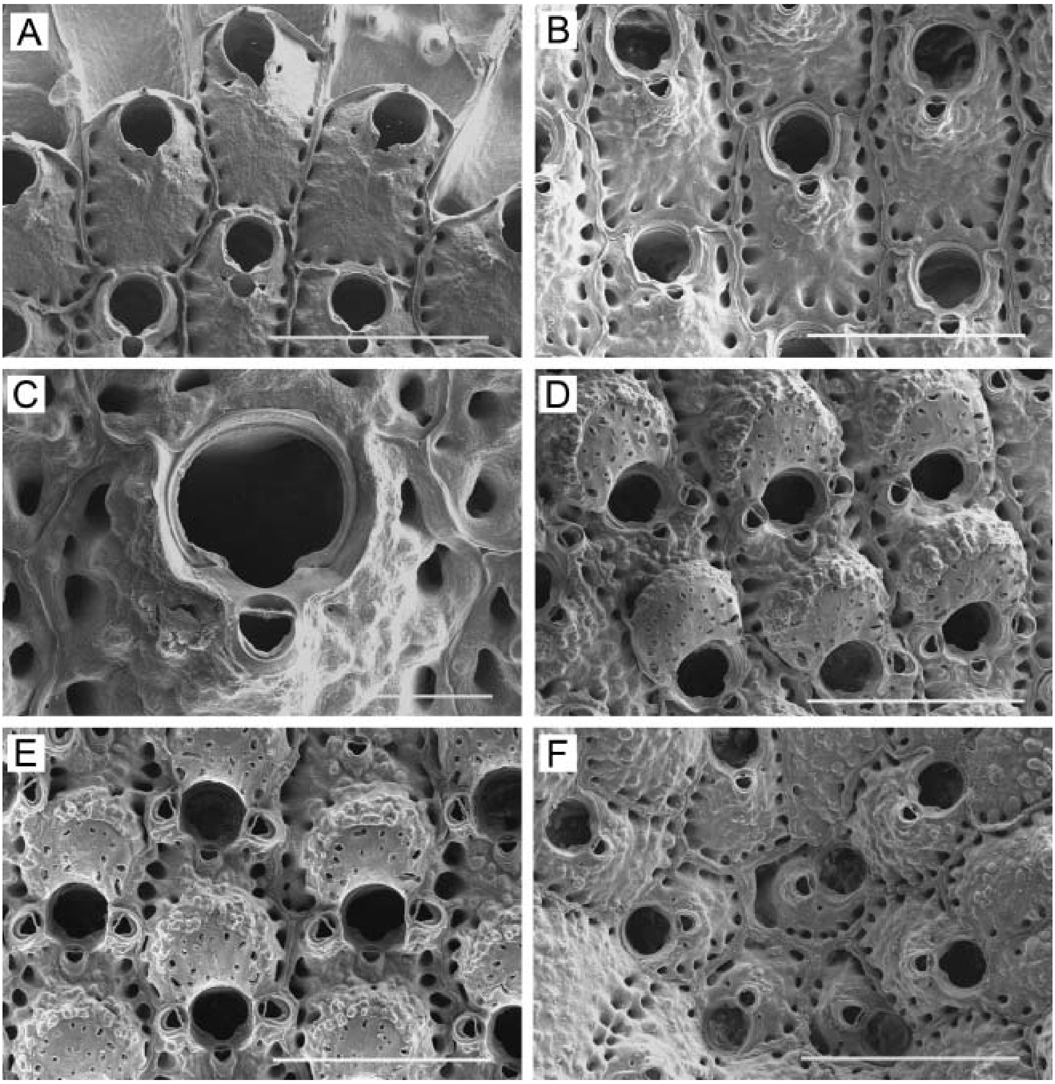

Figure 26. *Parkermavella orientalis* (Androsova and Gontar in Gontar 1982). (A) NHM 2006.2.27.31; (B–E) NHM 2006.2.27.84; (F) NHM 2006.2.27.83. (A) Colony margin with developing zooids; (B) immature zooids; (C) orifice of immature zooid, showing condyles and suboral avicularium; (D) group of mature zooids with ovicells, showing variability in positions of oral avicularia; (E) mature zooids with three oral avicularia; (F) ancestrular region. Scale bars: 0.5 mm (A, B, D–F); 0.1 mm (C).

Remarks

Gordon and d'Hondt (1997) established the genus *Parkermavella* for *Schizomavella*-like species that differ from *Schizomavella* in having an imperforate frontal shield and only marginal areolae. Characters of *Parkermavella* include a proximal oral sinus; articulated oral spines distally; one or more adventitious avicularia near the orifice or elsewhere on the frontal surface; and a prominent or subimmersed ovicell with smooth ectooecial calcification, many perforations that may be rimmed, and secondary calcification sometimes encroaching around the distal margin. The species of Androsova and Gontar treated here lacks frontal perforation and has most of the other characters of *Parkermavella*, and therefore belongs in that genus.

Gontar (1982) originally described this species as subspecies *orientalis* of *Schizomavella auriculata* (Hassall, 1842). However, the nominal subspecies never has more than a single median avicularium associated with the orifice, and also differs in orifice shape and in having numerous frontal pores; it is distributed in the northeastern Atlantic from Scotland to Gibraltar (Hayward and Ryland 1999). On the basis of these differences in morphology and range, we here elevate Gontar's subspecies to species rank as *P. orientalis* (Androsova and Gontar, 1982).

Parkermavella orientalis is very similar to *S. triavicularia* Soule, Soule, and Chaney, 1995, described from the Santa Barbara Channel, which likewise has a single median suboral avicularium in non-ovicellate zooids and an additional pair of lateral oral avicularia in ovicellate zooids. *Parkermavella orientalis* differs from the latter in several characters: (1) it lacks frontal pores, with well-developed areolar pores instead; (2) developing zooids near the colony margin have one or two ephemeral distal oral spines, whereas *S. triavicularia* has three spines; (3) the median suboral avicularium is closer to the suboral sinus than in *S. triavicularia*; and (4) ovicellate zooids have dimorphic suboral avicularia, with the lateral avicularia larger than the median one, and with more elongate mandibles; the median and lateral avicularia are similar in size and form in mature zooids of *S. triavicularia*.

The remarkable overall similarity of *S. triavicularia* and *P. orientalis* dispels misgivings one might have in accepting genera with and genera without a perforate frontal shield in the same family. *Schizomavella triavicularia*, which is evenly perforated, is otherwise so similar to *S. orientalis*, which is not, that there is little doubt the two are closely related; the similarity extends to both species having a pair of small pores flanking the avicularian chamber. Although convergence is a possibility, we conclude that the secondary loss of frontal perforation in *Parkermavella* is a more likely explanation. The small pores that flank the avicularian chamber are actually primary perforations in the frontal shield, as indicated by their presence in the forming shield in marginal zooids (Figure 26A), and in this sense, the frontal pores can be viewed as having been severely reduced in number, rather than lost entirely.

Distribution

This species was originally described from Crabovaya Bay, Shikotan Island, Kuril Islands, and also recorded from Zelenyy Island, Habomai Islands (Small Kuril Achipelago). Akkeshi Bay is the third known locality.

Superfamily SCHIZOPORELLOIDEA Jullien, 1883

Family SCHIZOPORELLIDAE Jullien, 1883

Genus *Schizoporella* Hincks, 1877

Schizoporella japonica Ortmann, 1890

(Figure 27)

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

Schizoporella japonica: Dick et al. 2005, p 3742, Figures 15A–H, 16A–D (illustration of holotype).

Schizoporella unicornis: Okada 1929, p 20, Text figure 7; Osburn 1952, p 317, Plate 37, Figures 1, 2; 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 1981b, p 51; Kubota and Mawatari 1985b, p 201, Figure 3A–E; Liu et al. 2001, p 596, Plate 48; Soule et al. 1995, p 204.

Material examined

KAI, colony on rock (NHM 2006.2.27.39), colony on rock (NHM 2006.2.27.85); BAC, ancestrular colony detached from bivalve shell (NHM 2006.2.27.86), extensive colony detached from bivalve shell (NHM 2006.2.27.87), extensive colony on bivalve shell (NHM 2006.2.27.88). Additional material: 80 specimens.

Description

Colony encrusting, unilaminar, occasionally with bilaminar overgrowth of one portion of colony by another, forming extensive irregularly circular patches up to 5.5 cm across, red to bright orange when alive. Zooids (Figure 27A, B) rectangular to hexagonal, 0.52–0.73 mm long (0.63 ± 0.05 mm), 0.30–0.43 mm wide (0.38 ± 0.03 mm), separated by shallow grooves. Frontal wall weakly to moderately convex, uniformly perforated from margin to margin with small circular pores except in suboral area, with seven to nine larger areolar pores along each lateral margin. Frontal pores become infundibular with development of calcification in mature zooids. Usually frontal wall rises into a small conical median umbo proximal to orifice. Orifice (Figure 27B, E) broader than long, 0.11–0.15 mm long (0.13 ± 0.01 mm), 0.15–0.17 mm wide (0.16 ± 0.01 mm); sinus broadly U-shaped, flattened on bottom; conspicuous condylar shelves bearing blunt condyles. Oral avicularia (Figure 27B) situated lateral or proximolateral to orifice, close to condylar shelf; mandible elongate-triangular, with acute tip, directed distolaterally to distally, cross-bar complete; chamber comparatively small, narrow, smooth, with one to three minute pores laterally around base. Oral avicularia usually single (Figure 27B), often absent (Figure 27C), occasionally paired. Additionally, some colonies have zooids with large frontal avicularia (Figure 27D, E) similar in form to oral avicularia, but with a highly raised, smooth chamber. Position of frontal avicularia variable; they can lie close to orifice, but a little more proximal than oral avicularium, on opposite side; just proximal to oral avicularium on same side; along zooidal lateral margin; or centrally on frontal surface. Large avicularia close to orifice point distolaterally; those in central or lateral region of frontal wall point distally or laterally. Large frontal avicularia developed predominantly in mature zones of colony, among zooids with complete ovicells. Ovicell (Figure 27C, D) hemispherical, prominent, 0.30–0.35 mm long (0.32 ± 0.02 mm), 0.29–0.36 mm wide (0.33 ± 0.02 mm), lying on frontal wall of daughter zooid and partially overhanging zooidal orifice; rugose, with heavily calcified, finely granulated radiating ribs, evenly perforated by numerous small pores, with larger round to slit-like pores around base. Occasionally ovicell has a small, knob-like central umbo. Ovicellate zooids can be sparsely distributed among non-fertile zooids or concentrated as a reproductive band within colony. Zooids intercommunicate via three to five distal and six lateral basal pore chambers. Ancestrula (Figure 27F) oval, imperforate, 0.33 mm long, 0.28 mm wide, with eight spines around D-shaped orifice (0.13 mm long, 0.15 mm wide) with straight proximal margin. Ancestrula buds three small zooids distally; surrounded by seven zooids.

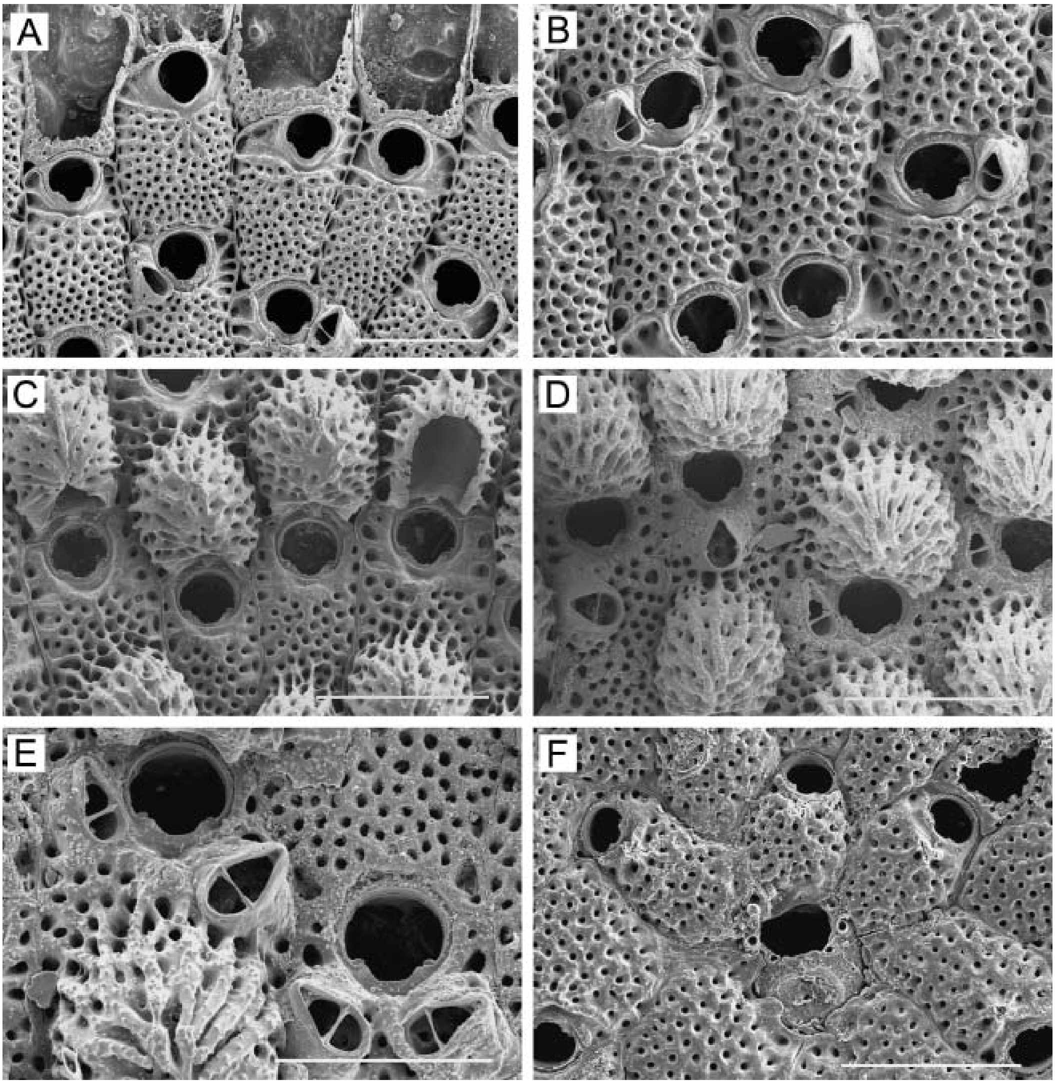

Figure 27. *Schizoporella japonica* Ortmann, 1890. (A, D–G) NHM 2006.2.27.87; (B, C) NHM 2006.2.27.85; (H) NHM 2006.2.27.86. (A) Developing zooids at colony margin; (B) immature zooids; (C) zooids with developing ovicells; (D) mature zooids with oral and frontal avicularia directed laterally and distally; (E) mature zooids, showing details of orifice and avicularia; (F) ancestrular region. Scale bars: 0.5 mm (A–D, F); 0.4 mm (E).

Remarks

Ortmann (1890) reported nominal *S. unicornis* (Johnston, 1844) from Japan, and additionally erected a new variety, *S. unicornis* var. *japonica*. Dick et al. (2005) recently examined Ortmann's type specimens and elevated variety *japonica* to species rank, as *S. japonica*.

Distribution

In the western Pacific, *S. japonica* (reported as *S. unicornis*) extends from China (Liu et al. 2001) northward to Hokkaido Island, where it has previously been recorded at Akkeshi, Muroran, and Shirikishinai on the Pacific side (Mawatari and Mawatari 1981b) and at Oshoro Bay on the Sea of Japan (Kubota and Mawatari 1985b).

Schizoporella japonica was introduced on Pacific oysters (*Crassostrea gigas*) from Japan to the Pacific coast of North America during the 20th century; it is now widely distributed from San Francisco, California to southeastern Alaska (Powell 1970; McCain and Ross 1974; Ross and McCain 1976; Dick et al. 2005). As mentioned by Dick et al. (2005), the actual range of *S. japonica* may be much more extensive, since this species could have been introduced on oysters to other parts of the world as well.

Family STOMACHETOSELLIDAE Canu and Bassler, 1917
Genus *Stomachetosella* Canu and Bassler, 1917
Stomachetosella decorata new species
(Figure 28)

Diagnosis

Frontal wall moderately convex, finely granulated, with a small central umbo; covered uniformly with small pores when young, with large marginal pores when mature. Primary orifice semicircular, with straight or slightly convex proximal margin. Secondary orifice cormidial, with raised, complete peristome having a short mid-proximal sinus. Ovicell hyperstomial, broad, rapidly submerged with secondary calcification, granulose, without pores, with a small, central nodule.

Etymology

The species name refers to the frontal wall decorated with nodular umbones in mature zooids.

Material examined

Holotype: ANC, colony on rock (NHM 2006.2.27.89). Paratypes: ACW, colony on rock (NHM 2006.2.27.90); BAC, young colony on bivalve shell (NHM 2006.2.27.91); ANC, young colony on rock (NHM 2006.2.27.92). Additional material: 59 specimens.

Description

Colony encrusting, unilaminar, coherent, irregularly circular; maximum dimension observed was 1.7 cm; red when alive. Zooids (Figure 28A–E) hexagonal, oval, or rectangular, 0.42–0.63 mm long (0.53 ± 0.06 mm), 0.30–0.43 mm wide (0.35 ± 0.04 mm), separated by raised adjacent vertical walls. Frontal wall moderately convex, finely granulated; when young, covered sparsely and uniformly from margin to margin with small pores, with a small, sharp central umbo (Figure 28B, C) or two or three scattered umbones (Figure 28E); with age and secondary calcification, central umbo becomes stout and prominent, central pores reduced in number, marginal pores enlarged, infundibular, often occluded along margins. Primary orifice (Figure 28A) semicircular, broad, about 0.12–0.14 mm long, 0.15–0.16 mm wide; proximal margin straight to slightly convex, condyles and sinus lacking, deeply submerged, visible only in developing zooids near colony margin. Secondary orifice cormidial (Figure 28C); irregularly circular, transversely oval, or rounded-triangular, 0.12–0.16 mm

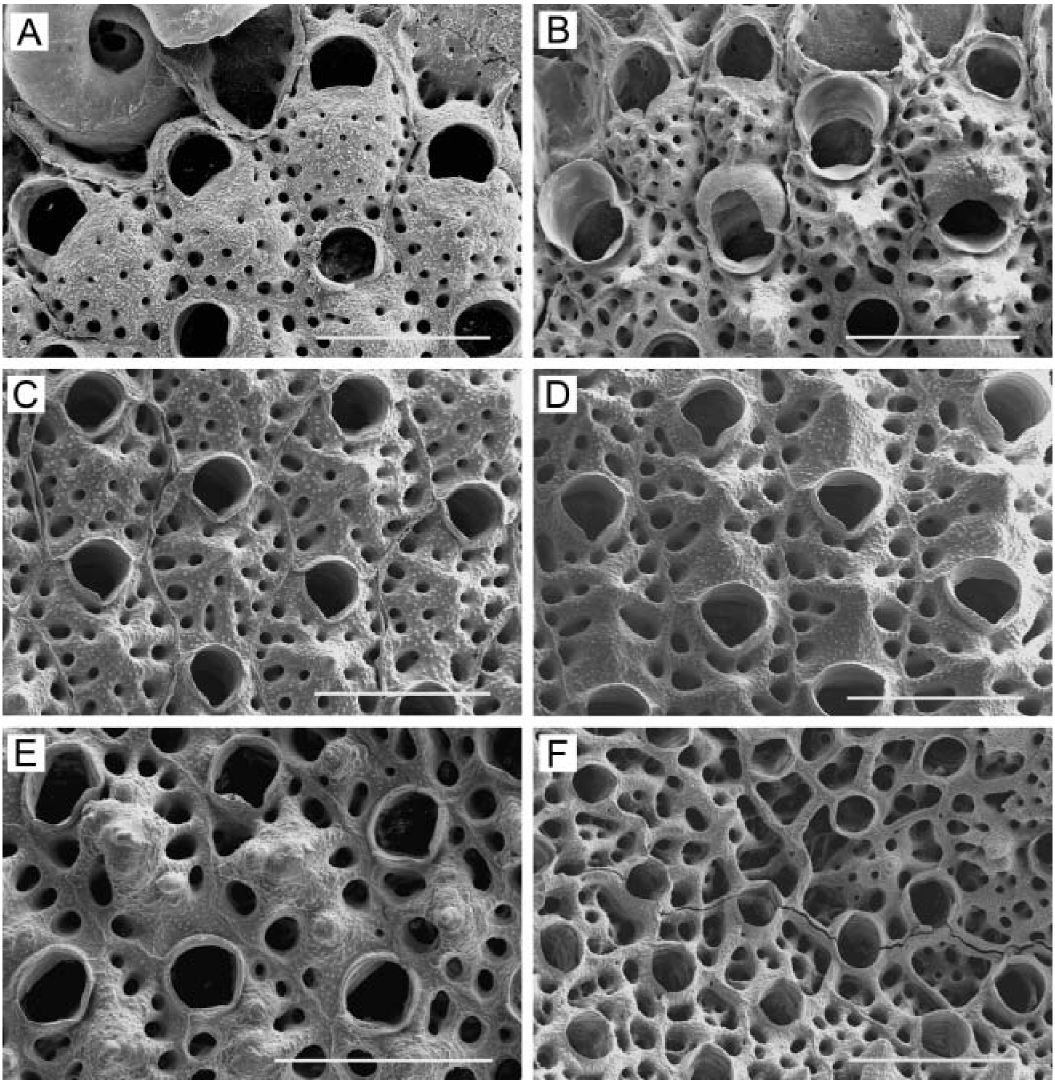

Figure 28. *Stomachetosella decorata* n. sp. (A) NHM 2006.2.27.92; (B, E, F) NHM 2006.2.27.90; (C, D) NHM 2006.2.27.89. (A) Colony margin with developing zooids; (B) zooids with developing ovicells close to colony edge; (C) immature zooids; (D) mature zooids with immersed ovicells; (E) mature zooids with immersed ovicells, infundibular occluded frontal pores and scattered umbones; (F) ancestrular region. Scale bars: 0.5 mm.

long (0.15 ± 0.01 mm), 0.14–0.19 mm wide (0.16 ± 0.01 mm); peristome complete, raised, consisting of sharp, curved lateral flanges meeting distally with raised proximal margin of distal zooid; with a short mid-proximal sinus. Ovicell (Figure 28B) hyperstomial, broad, rapidly submerged (Figure 28D) with secondary calcification, 0.15–0.20 mm long (0.18 ± 0.01 mm), 0.19–0.26 mm wide (0.22 ± 0.02 mm), granulose, imperforate, often with a small nodule in central position. Interzooidal communication via pore chambers. Ancestrula proper not observed; obscured by small, possibly frontally budded zooids (Figure 28F) that are irregular in form.

Remarks

The genus *Stomachetosella* has moderately high diversity in the northwestern Pacific. According to previous reports (Androsova 1958; Kluge 1962; Gontar 1980; Grischenko 1997), at least eight species have been recorded in this region, including *S. cruenta* (Busk, 1854), *S. sinuosa* (Busk, 1960), *S. limbata* (Lorenz, 1886), *S. magniporata* (Nordgaard, 1906), *S. incerta* (Kluge, 1929), *S. pachystega* (Kluge, 1929), *S. tuberculata* Androsova, 1958, and *S. sienna* Dick and Ross, 1988. *Stomachetosella decorata* n. sp. can be distinguished from all of these congeners by the frontal umbo in combination with large, occluded pores, and the broad, submerged ovicell with a small, central umbo.

In the northern hemisphere, only one species of *Stomachetosella*, *S. distincta* Osburn, 1952, described from the Beaufort Sea near Point Barrow, Alaska, has a similarly umbonate ovicell and frontal wall. However, the distribution of frontal pores is different in *S. distincta*; its primary orifice has a sinus; and zooid size is significantly larger (0.65–0.85 mm long, 0.45–0.65 mm wide) and not overlapping with *Stomachetosella decorata* n. sp.

The form of the secondary orifice of *S. decorata* is almost identical to that of *S. sinuosa* (Busk, 1860), previously reported from Akkeshi Bay (Mawatari and Mawatari 1981b). The latter also has a sinuate, peristomial secondary orifice and immersed hyperstomial ovicells; however, the primary orifice is sinuate, rather than straight or slightly convex, and the ovicell has a central pore.

Distribution

Stomachetosella decorata is known only from Akkeshi Bay.

Family MYRIAPORIDAE Gray, 1841
Genus *Myriozoella* Levinsen, 1909
Myriozoella plana (Dawson, 1859)
(Figure 29)

Lepralia plana Dawson 1859, p 256.

Myriozoella plana: Osburn 1952, p 516, Plate 64, Figures 1, 2; Kluge 1952, p 154; Mawatari and Mawatari 1981b, p 51; Dick and Ross 1988, p 91, Plate 6J.

Myriozoella planum: Mawatari 1956, p 135.

Myriozoum crustaceum Smitt 1868, p 114, Plate 25, Figures 88–91.

Myriozoum crustaceum: Robertson 1908, p 295, Plate 21, Figure 54; Kluge 1929, p 19; Okada 1933, p 216.

Myriozoella crustacea: Androsova 1958, p 144, Figure 70; Gontar 1980, p 11; Kubanin 1997, p 124; Grischenko 1997, p 186; 2004, p 40.

Schizoporella crustacea: Okada 1929, p 20, Plate 1, Figure 6, Plate 4, Figure 5; Kluge 1962, p 478, Figure 321; 1975, p 580, Figure 321.

Material examined

ANC, colony on rock (NHM 2006.2.27.66), two colonies on rock (NHM 2006.2.27.79), ancestrular colony on rock (NHM 2006.2.27.82); DIN, five colonies on rock (NHM 2006.2.27.80), colony on rock (NHM 2006.2.27.81). Additional material: 105 specimens.

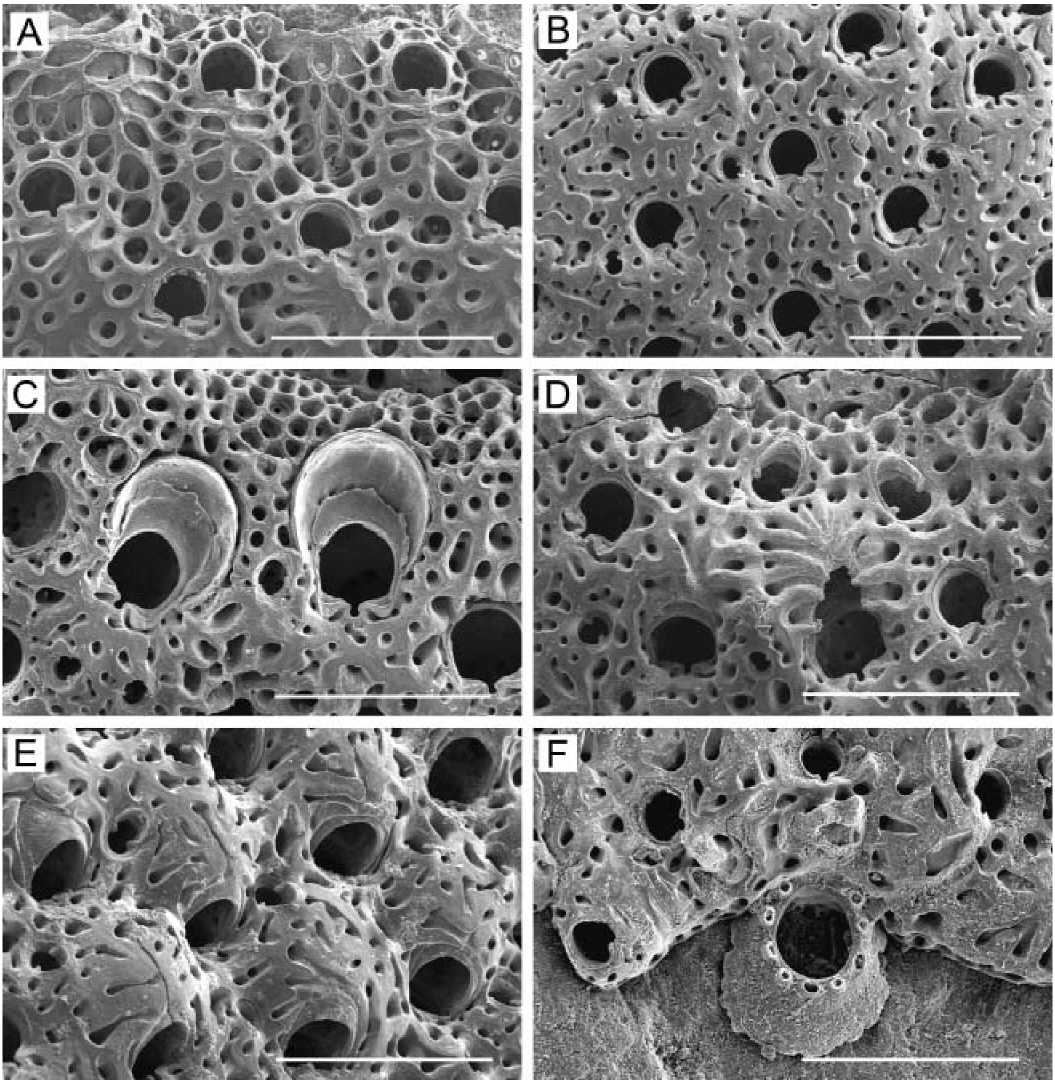

Figure 29. *Myriozoella plana* (Dawson, 1859). (A) NHM 2006.2.27.79; (B–E) NHM 2006.2.27.81; (F) NHM 2006.2.27.82. (A) Differentiating zooids near colony margin; (B) immature zooids; (C) two zooids with developing ovicells; (D) zooids with almost completed ovicell flanked distally by three vicarious avicularia; (E) mature zooids with deeply immersed ovicells; (F) ancestrula and periancestrular zooids. Scale bars: 0.5 mm.

Description

Colony encrusting, coherent, unilaminar at first but bilaminar or multilaminar with age, forming characteristic circular layers of zooids, with each successive layer forming a smaller concentric circle over previous one; up to 5.5 cm across; white, yellowish, or greyish when alive. Zooids (Figure 29A) oval or hexagonal, 0.42–0.60 mm long (0.51 ± 0.04 mm), 0.35–0.43 mm wide (0.39 ± 0.03 mm), with indistinct boundaries even in early stages. Frontal wall well calcified, convex in young zooids, sparsely perforated by tubular alveoli with small pores at the bottom, giving a reticulate appearance; with age, pore openings enlarged, some occluded; frontal surface becomes thick, regular; zooidal boundaries completely obscured

(Figure 29B, C). Some zooids have one or two frontal umbones. Orifice (Figure 29A–C) semicircular, 0.09–0.13 mm long (0.10 ± 0.01 mm), 0.10–0.15 mm wide (0.12 ± 0.01 mm), with straight proximal margin bisected by deep, narrow median sinus. With developing calcification, orifice becomes submerged and surrounded by shallow, sloping peristome. Operculum a rich brown colour, in sharp contrast to lighter frontal walls of zooid. On each side of orifice is a slightly raised chamber bearing an avicularium (Figure 29B) on distal side; semicircular mandible orientated at angle to colony surface and pointing proximally or laterally. Vicarious avicularia (Figure 29D) scattered throughout colony; mandible semicircular to subspatulate, larger than operculum of autozooids and orientated in any direction. Ovicell (Figure 29C, E) hyperstomial, 0.22–0.30 mm long (0.27 ± 0.02 mm), 0.25–0.32 mm wide (0.29 ± 0.02 mm), convex, imperforate, deeply immersed, covered with thick radial to reticulate calcification from surrounding zooids. Zooids communicate via numerous uniporous septula along basal wall. Ancestrula tatiform, nearly circular, 0.35 mm long, 0.33 mm wide, with uncalcified basal wall; opesia oval, 0.18 mm long, 0.14 mm wide, with nine spines around margin. Ancestrula (Figure 29F) buds triplet of small zooids distally and distolaterally.

Remarks

This species has appeared in the northern literature under the names *M. plana* and *M. crustacea*. Osburn (1952) discussed the controversy surrounding the names, noting that some authors had preferred *M. crustacea* Smitt, 1868 because of the inadequacy of Dawson's (1859) original description of *M. plana*. Osburn argued convincingly that there is little doubt that *M. plana* represents the same species as *M. crustacea*, and that the former thus has priority.

Distribution

This is a circumpolar, Arctic-Boreal species widely distributed in the northern Pacific; Kluge (1962, 1975) and Gontar and Denisenko (1989) gave many distributional records. It has been reported from Alaska from the Pribilof Islands (Osburn 1952), Unalaska Island (Kluge 1961), Kodiak Island (Dick and Ross 1988), Orca, Yakutat, and Juneau (Robertson 1900). On the Asian side, records exist from the Commander Islands, eastern Kamchatka, Shantar Archipelago, Sakhalin Island, Kuril Islands, and Primorye (Kluge 1961; Gontar 1980; Grischenko 1997; Kubanin 1997). In Japan, it has previously been reported only from Shirikishinai, Pacific coast of Hokkaido (Mawatari and Mawatari 1981b).

Family PACIFICINCOLIDAE Liu and Liu, 1999

Genus *Pacificincola* Liu and Liu, 1999

Pacificincola perforata (Okada and Mawatari, 1937)

(Figure 30)

Mucronella perforata Okada and Mawatari 1937, p 442, Plate 1, Figure 8, Text figure 4A–C.

Hippoporina perforata: Huang et al. 1990, p 744, Figure 8, c.

Pacificincola perforata: Liu and Liu 1999, p 340, Text figure 1a–c, Plate 1, Figures 1–5; Liu et al. 2001, p 572, Plate 44, Figures 1, 2.

Hippodiplosia insculpta: Kubanin 1975, p 123, Figure 3b, c (not *Schizoporella insculpta* Hincks, 1882).

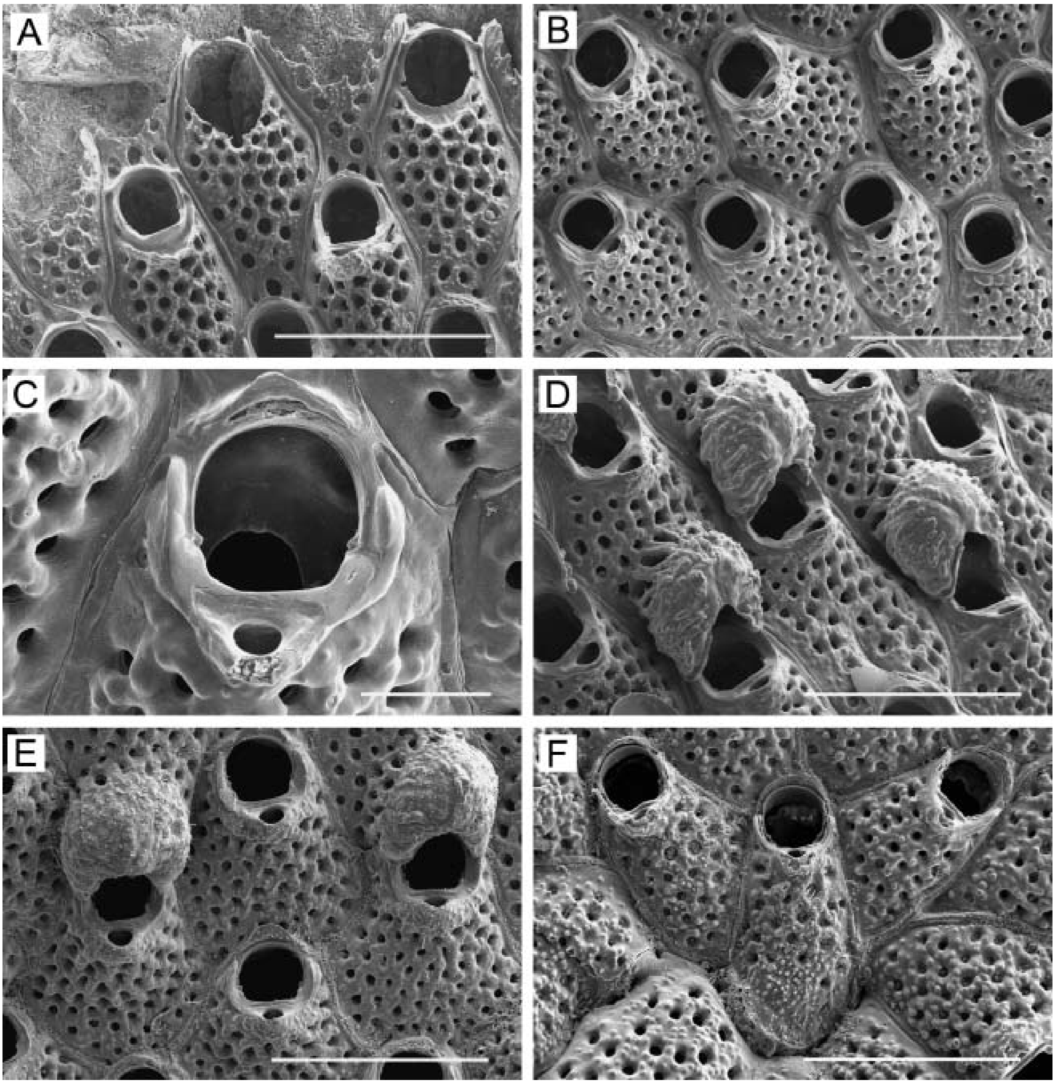

Figure 30. *Pacificincola perforata* (Okada and Mawatari, 1937). (A, D) NHM 2006.2.27.75; (B, C, F) NHM 2006.2.27.76; (E) NHM 2006.2.27.60. (A) Colony edge with differentiating zooids; (B) immature zooids; (C) orifice of immature zooid, showing minute sharp condyles and suboral umbo with central cavity; (D) zooids with developing ovicells; (E) two mature zooids with completed ovicells; (F) ancestrula and periancestrular zooids. Scale bars: 0.5 mm (A, B, D, E); 0.1 mm (C); 0.4 mm (F).

Material examined

KAI, colony on rock (NHM 2006.2.27.60), colony on rock (NHM 2006.2.27.75), young colony detached from bivalve shell (NHM 2006.2.27.76). Additional material: 201 specimens.

Description

Colony encrusting, unilaminar, coherent, forming delicate crusts of very irregular form with meandering margins, up to about 3 cm in maximum dimension, light yellow when alive.

Zooids (Figure 30A, B, E) hexagonal, ovoid, or irregularly rectangular, widest in middle, 0.40–0.60 mm long (0.53 ± 0.06 mm), 0.25–0.43 mm wide (0.33 ± 0.05 mm), rounded distally, demarcated by a groove and fine suture line. All zooids of one type; non-fertile and fertile zooids similar in size and in size and form of orifice. Frontal wall convex, vitreous, texture smooth or granulated, uniformly perforated with circular pores, except for suboral area; with age, pores become infundibular and the frontal wall appears reticulate; proximal to orifice is a heterozooidal chamber (Figure 30C) appearing as a raised, crescentic arch or umbo, with a median distal cavity covered by membrane. Primary orifice (Figure 30C) roughly circular or broader than long, 0.10–0.14 mm long (0.12 ± 0.01 mm), 0.10–0.15 mm wide (0.13 ± 0.01 mm); with a high, semicircular anter separated from narrower, shorter poster by a pair of small condyles pointing proximomedially; proximal orificial margin straight. Peristome low; orifice flanked laterally by low, sharp, curved peristomial flanges extending distally from umbo, connecting with proximal corners of ovicell or raised proximal margin of distal zooid, sometimes present as distinct lateral lappets. Ovicell (Figure 30D, E) globose, prominent, 0.19–0.25 mm long (0.22 ± 0.02 mm), 0.20–0.27 mm wide (0.23 ± 0.02 mm), recumbent on frontal wall of distal zooid and partially overhanging orifice; imperforate, with smooth or slightly nodular central area and short, finely tuberculate radiating ribs around periphery, with series of slit-like pores around distal margin. Spines and avicularia lacking. Zooids intercommunicate via multiporous septula. Ancestrula (Figure 30F) similar to later zooids but elongate-oval, 0.45 mm long, 0.23 mm wide, inflated frontal wall finely granulated and perforated with numerous pores; ancestrular orifice roughly circular, 0.10 mm long, 0.09 mm wide, with reduced peristomial rim and small suboral opening; ancestrula buds quartet of smaller zooids, two distolaterally and two laterally; surrounded by seven zooids.

Remarks

Pacificincola perforata (Okada and Mawatari, 1937) was originally described from Onagawa Bay on the Pacific side of northern Honshu. It was subsequently reported (as *Hippodiplosia insculpta*) from the Peter the Great Gulf (Kubanin 1975) and (as *Hippoporina perforata)* from the Hong Kong vicinity (Huang et al. 1990). Liu and Liu (1999) used *P. perforata* from the coastal waters of China as the type species for the new genus *Pacificincola* and a new family, Pacificincolidae.

Pacificincola perforata most resembles its congener *P. insculpta* (Hincks, 1882) in having a similar, crescentic proximal suboral arch with a central cavity covered by membrane, and prominent spherical ovicells with radiating ribs. However, *P. perforata* differs from the latter in the following characters: (1) non-fertile and fertile zooids of *P. perforata* are all of the same type, whereas they are dimorphic in *P. insculpta*; (2) zooids of *P. perforata* are mostly distinctly hexagonal, widest in the middle, whereas zooids of *P. insculpta* are widest at the orifice, and tapering or truncate; (3) the lateral peristomial lobes, peculiar to *P. perforata*, are absent in *P. insculpta*, where the secondary orifice is a continuous rim; (4) the condyles are minute in *P. perforata*, but larger, prominent and shelf-like, in *P. insculpta*; (5) ovicells of *P. perforata* have reduced peripheral ribbing, in contrast to the well-developed ribs on ovicells of *P. insculpta*; and (6) the ancestrula of *P. perforata* is similar to later autozooids and buds four daughter zooids, whereas that of *P. insculpta* is tatiform and buds three daughter zooids (see Nielsen 1981, p 108, Figures 14, 15); and (7) colonies of *P. perforata* are always encrusting and tightly attaching to the substrate, whereas those of *P. insculpta* are initially unilaminar but then rise in irregular, bilaminar lobes and frills.

Distribution

This species ranges from Akkeshi Bay on the Pacific side of Hokkaido and Peter the Great Gulf, Sea of Japan (Kubanin 1975) southward to Onagawa Bay, Honshu (Okada and Mawatari 1937), Hong Kong (Huang et al. 1990), and China (Liu and Liu 1999).

Family CHEILOPORINIDAE Bassler, 1936

Genus *Cheilopora* Levinsen, 1909

Cheilopora sincera (Smitt, 1868)

(Figure 31)

Discopora sincera Smitt 1868, p 28, 177 (part), Plate 27, Figures 178–180.
Mucronella sincera: Nordgaard 1895, p 29, Plate 1, Figure 6.
Eschara sincera: Nordgaard 1905, p 168, Plate 3, Figures 12–14.
Cheilopora sincera: Nordgaard 1912, p 21; Androsova 1958, p 174, Figure 105; Kluge 1962, p 562, Figure 396; 1975, p 684, Figure 396.
Cheiloporina sincera: Gontar and Denisenko 1989, p 357; Gontar 1996, p 46.
Cheilopora sincera var. *orientalis* Kluge 1952, p 162, Text figure 15.
Cheilopora orientalis: Kluge 1961, p 142.

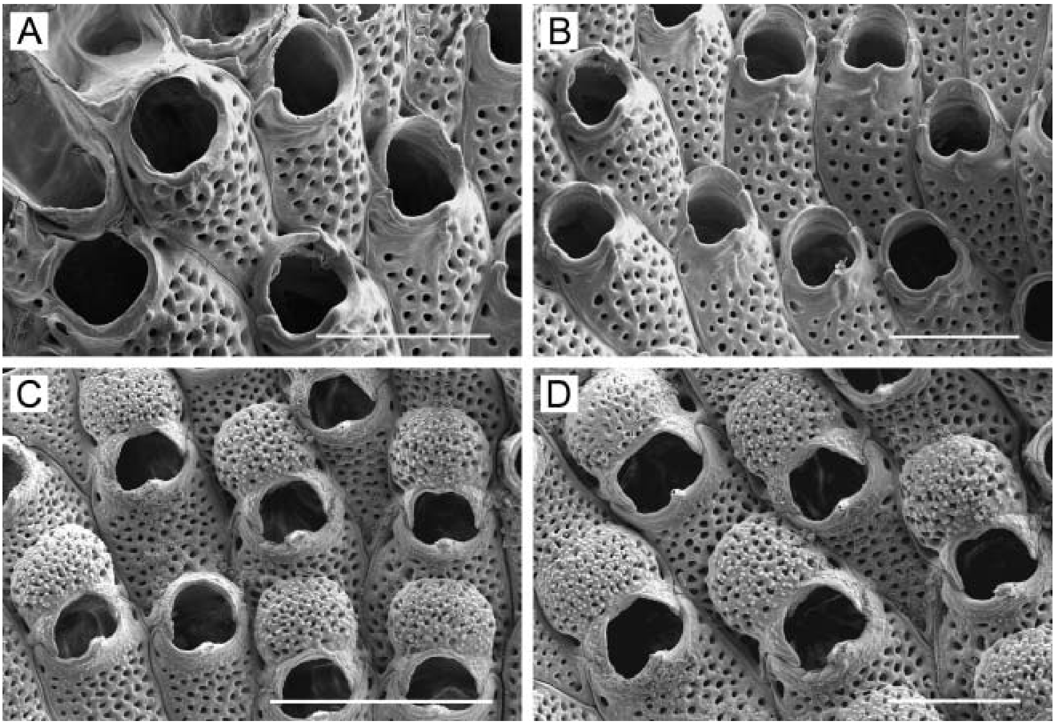

Figure 31. *Cheilopora sincera* (Smitt, 1868). (A, B) NHM 2006.2.27.77; (C, D) NHM 2006.2.27.78. (A) Zooids differentiating at colony margin; (B) immature zooids; (C, D) mature zooids with ovicells. Scale bars: 0.5 mm (A, B, D); 1 mm (C).

Material examined

ACT, colony on the erect bryozoan *Phidolopora elongata* (NHM 2006.2.27.77); NB, colony fragment (NHM 2006.2.27.78).

Description

Colony initially encrusting, unilaminar, sheet-like, later rising in erect, meandering expansions, reaching 2 cm in maximum dimension, bright yellow in colour when alive. Zooids (Figure 31A, B) hexagonal, barrel-shaped, or rectangular, rounded distally, 0.53–0.93 mm long (0.73 ± 0.10 mm), 0.33–0.48 mm wide (0.39 ± 0.04 mm), delineated by narrow incision between adjacent vertical walls. Frontal wall moderately to markedly convex, smooth, uniformly perforated with small pores over entire surface, except for peristome; marginal zooids with an imperforate zone along each lateral margin. Orifice (Figure 31A) semicircular or rounded-quadrate in immature zooids, irregularly semicircular to rounded-quadrate in ovicellate zooids, 0.18–0.25 mm long (0.21 ± 0.02 mm), 0.19–0.25 mm wide (0.22 ± 0.02 mm), without oral spines, lyrula, or condyles. Peristome raised, continuous; cormidial, formed distally by raised, proximal wall of distal zooid, proximally by thick, raised, arcuate rim with a sharp median tooth (Figure 31B, C) and distolateral prominences. Avicularia and ovicells not seen in immature intertidal material. Interzooidal communications via multiporous septula. Ancestrula not observed.

In an ovicellate colony collected subtidally, zooids 0.67–1.10 mm long (0.87 ± 0.13 mm), 0.45–0.63 mm wide (0.52 ± 0.06 mm); orifice 0.21–0.27 mm long (0.23 ± 0.02 mm), 0.22–0.31 mm wide (0.27 ± 0.03 mm); in ovicellate zooids, proximal peristomial rim overlaps proximolateral lappets of ovicell; sides of peristome finely granulated externally; median suboral tooth prominent, thin and hollow, or stout and blunt. Ovicells (Figure 31C, D) hyperstomial, globose, overlying frontal wall of distal zooid; broad, 0.27–0.35 mm long (0.32 ± 0.02 mm), 0.40–0.45 mm wide (0.43 ± 0.02 mm); granulated, uniformly perforated with many small pores; with large, oblong or slit-like basal openings in frontal wall of distal zooid, flanking ovicell on each side proximolaterally. Similar openings often occur at proximolateral edge of peristome of maternal zooid.

Remarks

Despite the apparent absence of lateral oral avicularia in our material, other characters confirm the identification of *Cheilopora sincera*. These characters include the convex, uniformly perforated frontal wall; cormidial secondary orifice with a well-developed median suboral tooth; and narrow slits at the base of the ovicell proximolaterally. In the absence of avicularia and the rounded-quadrangular outline of the secondary orifice, especially in mature zooids, Akkeshi specimens resemble *Cheilopora inermis* (Busk, 1880), previously recorded on the Pacific side of Hokkaido near Shirikishinai (Mawatari and Mawatari 1981b). However, the frontal shield of *C. inermis* is always flat (see Kluge 1962, p 563, Figure 398), whereas that of *C. sincera* is convex, especially in ovicellate zooids; the proximal margin of the peristome is only gently convex in *C. inermis*, whereas in *C. sincera* the median suboral tooth is usually prominent.

Kluge (1952) described a new variety, *C. sincera orientalis*, based on material collected from the Chukchi Sea near Bering Strait. Subsequently, he reported the same form from Avacha Inlet, eastern Kamchatka, elevated to the rank of species as *C. orientalis* (Kluge

1961). Kluge's primary justifications for elevating that taxon to species rank were the form of the suboral tooth (a wide, inflated process instead of a sharp tooth) and the occurrence of bilaminar colony form. However, Androsova (1958) described and illustrated the form and size of the suboral process in *C. sincera* as a significantly variable character that can be sharp, blunt, straight, cone-like, long or short, wide or narrow, or sometimes forked or entirely absent. Furthermore, colonies of *C. sincera* from the Ust' Khayryuzovo area, western Kamchatka shelf, Sea of Okhotsk, can be quite variable in form (A. V. Grischenko, unpublished data). Some colonies encrusting the internal concave surface of dead shells of *Chlamys* sp. bivalves can be loosely attached with elevated margins, or even produce small, bilamellar frills and folds. Hence, *C. orientalis* falls within the range of variation of *C. sincera*, and we here consider it as a junior synonym of *C. sincera*.

Distribution

This is a circumpolar, Arctic-Boreal species; Kluge (1962, 1975) and Gontar and Denisenko (1989) provide detailed records for the Arctic. In the northwestern Pacific, *C. sincera* has been reported from eastern Kamchatka, the southern Kuril Islands, western and southern Sakhalin Island, the Shantar Archipelago (Kluge 1961), and Primorye (Androsova 1958); Akkeshi Bay is the southernmost known locality on the Asian side. Osburn (1952) expressed the opinion that *C. praelucida* (Hincks), described from British Columbia, is likely synonymous with *C. sincera* (Smitt), but he hesitated to make a formal synonymy without examining type material. O'Donoghue and O'Donoghue (1926) also reported *C. praelucida* from British Columbia.

Family CRYPTOSULIDAE Vigneaux, 1949

Genus *Cryptosula* Canu and Bassler, 1925

Cryptosula zavjalovensis Kubanin, 1976

(Figure 32)

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

Cryptosula zavjalovensis: Kubanin and Tarasova 1985, p 109; Kubanin 1997, p 125; Grischenko 2004, p 40; Dick et al. 2005, p 3749, Figure 18A, B.

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

Lepralia reticulata: Okada 1933, p 215; Androsova 1958, p 129, Figure 46; Kluge 1961, p 131; Gontar 1978a, p 61; 1978b, p 13; Mawatari and Mawatari 1981b, p 52.

Lepralia pallasiana: O'Donoghue 1925, p 19, Plate 2, Figure 6; not *Eschara pallasiana* Moll, 1803.

Eurystomella reticulata: Gontar 1980, p 9; 1981, p 102.

Eurystomella zavjalovensis: Gontar 1992, p 131.

Cryptosula okadai Dick and Ross 1988, p 53, Plate 5F; Grischenko 1997, p 176.

Cryptosula pallasiana: Dick and Ross 1986, p 89.

Material examined

KAI, ancestrular colony on rock (NHM 2006.2.27.60); MBS, five colony fragments (NHM 2006.2.27.61). Additional material: 240 specimens.

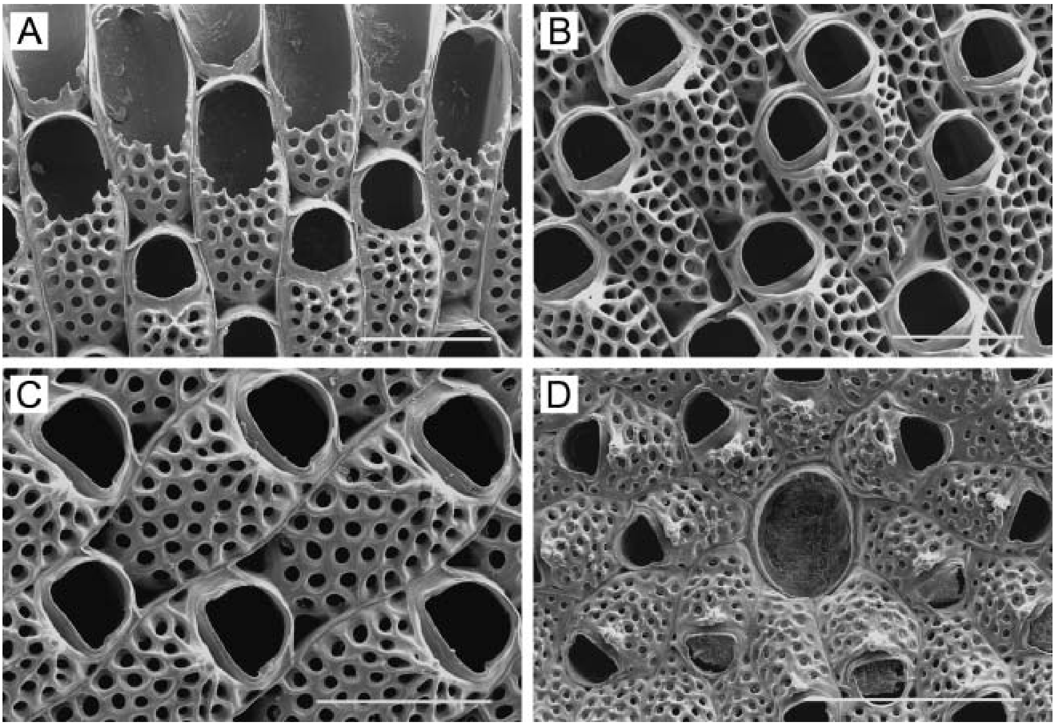

Figure 32. *Cryptosula zavjalovensis* Kubanin, 1976. (A–C) NHM 2006.2.27.61; (D) NHM 2006.2.27.60. (A) Colony margin with developing zooids; (B) group of zooids, showing small and large orifices; (C) heavily calcified autozooids; (D) ancestrula and radially arranged periancestrular zooids. Scale bars: 0.5 mm (A–C); 1 mm (D).

Description

Colony encrusting, unilaminar, coherent, irregularly circular, up to 4 cm across. Living colonies bright yellow, tan, or brownish in colour and exude a foul, pungent odour. Zooids (Figure 32A–C) subrectangular to roughly hexagonal, rounded distally, 0.67–0.95 mm long (0.80 ± 0.08 mm), 0.28–0.45 mm wide (0.37 ± 0.05 mm), delineated by a fine suture formed by raised adjacent vertical walls. Frontal wall cryptocystidean, convex, perforated with large, uniform pores covering entire surface; with age pores become infundibular and the frontal wall reticulate, with rounded ridges between pores; frontal wall rises to suboral umbo (Figure 32B, C) varying from low, conical bulge to tall, costate process. Orifice (Figure 32C) hat-shaped in outline, 0.16–0.21 mm long (0.19 ± 0.01 mm), 0.17–0.26 mm wide (0.22 ± 0.02 mm); large, semicircular anter delineated from short, broad poster by long, low, wedge-shaped condyles. Peristome lacking. Area of smooth frontal wall lacking pores borders orifice proximally and laterally. Spines, avicularia, and ovicells lacking. Zooidal communication via multiporous septula. Occasionally scattered kenozooids present, similar to autozooids but lacking orifice. Ancestrula (Figure 32D) tatiform, oval, 0.53 mm long by 0.44 mm wide, with large opesia occupying almost entire frontal surface, 0.49 mm long by 0.38 mm wide, without spines; basal wall contains uncalcified window. Ancestrula buds triplet of smaller zooids distally; surrounded by eight zooids.

Remarks

This species and its convoluted synonymy were discussed by Dick and Ross (1988) and Dick et al. (2005). *Cryptosula zavjalovensis* is patchily abundant in Akkeshi Bay. It is one of the main components of the fouling community on the vertical cement surfaces of the pier of the Akkeshi MBS, where layers of zooids form a thick crust, with free spaces or slits between layers. These spaces provide a habitat for other benthic invertebrates, mainly spirorbid worms, but also small isopod and amphipod crustaceans and errant polychaetes. The external surface of living colonies of *C. zavjalovensis* remains largely free from encrusting epizoonts, perhaps due to allelopathic activity of the substance responsible for the unpleasant, pungent odour.

Distribution

A Boreal Pacific species, this is one of the most common and widespread bryozoans found intertidally around the north Pacific Rim, extending from the mid-intertidal zone to a depth about 40 m (Androsova 1958). On the North American side it has been reported from the eastern Aleutian Islands, Bering Sea, northern Gulf of Alaska, Kodiak Island, and Ketchikan, Alaska (O'Donoghue 1925; Dick and Ross 1988; Dick et al. 2005). On the Asian side there are records from numerous localities, including the Gulf of Anadyr, Kamchatka, Commander Islands, Sea of Okhotsk, Kuril Islands, Sakhalin Island, Primorye, and northern sector of the Sea of Japan (Androsova 1958; Kluge 1961; Gontar 1980; Kubanin 1997; Grischenko 1997, 2004). In Japan, *C. zavjalovensis* has been previously reported from Shirikishinai, southern Hokkaido (Mawatari and Mawatari 1981b), and Mutsu Bay, northern Honshu (Okada 1929).

Family MICROPORELLIDAE Hincks, 1879

Genus *Fenestrulina* Jullien, 1888

Fenestrulina orientalis Liu, Liu, and Sun, 2003

(Figure 33)

Fenestrulina orientalis Liu, Liu, and Sun 2003, p 209, 221, Plate 4, Figures 3–5.

Fenestrulina orientalis: Liu et al. 2001, p 671, 815, Plate 70, Figures 4–6.

? *Microporella malusii*: Okada 1929, p 27, Text figure 12; Androsova 1959, p 50, 65, Plate 2, Figure 13; not *Cellepora malusii* Audouin, 1826.

? *Fenestrulina malusii*: Mawatari and Mawatari 1981b, p 53; Huang et al. 1990, p 748. Not *Cellepora malusii* Audouin, 1826.

Material examined

ANC, young colony on rock (NHM 2006.2.27.11), colony on rock (NHM 2006.2.27.12). Additional material: 181 specimens.

Description

Colony encrusting, unilaminar, coherent, more or less circular, up to 2 cm in diameter, pale yellow to whitish when alive. Zooids (Figure 33A, B) rounded-hexagonal to oval, 0.50–0.73 mm long (0.58 ± 0.06 mm), 0.35–0.53 mm wide (0.40 ± 0.04 mm), separated by a deep groove between smooth, inward-sloping, lateral walls. Frontal wall moderately

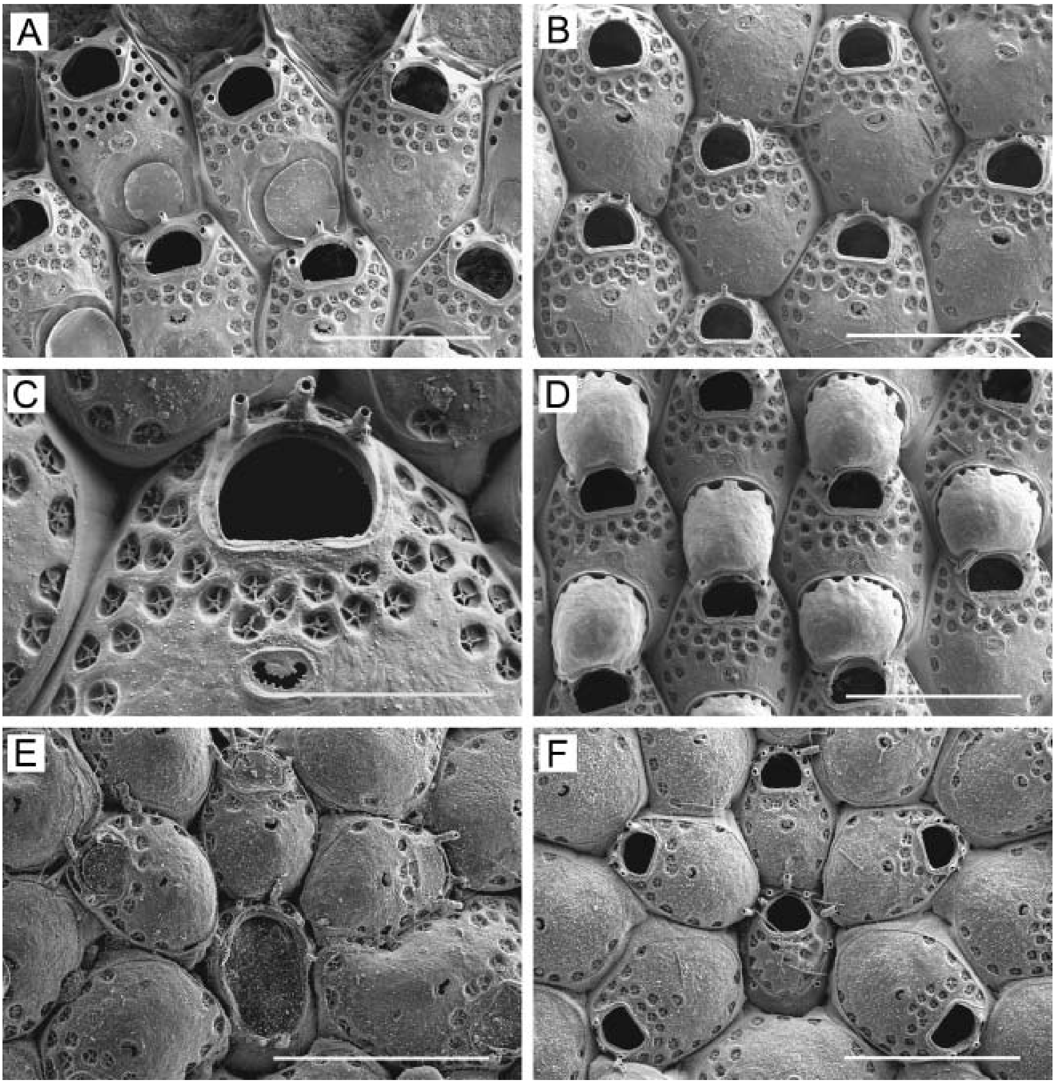

Figure 33. *Fenestrulina orientalis* Liu, Liu, and Sun, 2003. (A–D, F) NHM 2006.2.27.12; (E) NHM 2006.2.27.11. (A) Colony margin with differentiating zooids; (B) immature zooids; (C) distal half of immature zooid, showing orifice with oral spines and ascopore; (D) mature zooids with completed hemispherical ovicells; (E) tatiform ancestrula and periancestrular zooids; (F) modified ancestrula with acquired frontal shield, surrounded by periancestrular zooids. Scale bars: 0.5 mm (A, B, D–F); 0.2 mm (C).

convex, thin, translucent, smooth and imperforate in central area proximal to ascopore; stellate pores in a single marginal row in proximal half of zooid, two or three marginal rows in distal half, and two rows between ascopore and orifice. Orifice (Figure 33C) semicircular, curving slightly inward at proximolateral corners; broader than long, 0.10–0.12 mm long (0.11 ± 0.01 mm), 0.12–0.16 mm wide (0.14 ± 0.01 mm), with straight proximal margin. Non-ovicellate marginal zooids have three short, hollow spines (Figure 33A–C) closely set around distal curvature of orifice; ovicellate zooids also have three spines, the lateral two are more widely separated than in zooids that will not produce an ovicell and remain close to proximal corners of ovicell. Ascopore separated from proximal border of orifice by a distance about equivalent to length of zooidal orifice; crescentic, with a denticulate edge, located on a small, oval, elevated prominence which sometimes coincides with highest point of frontal wall, but more often lies on its distal slope. Ovicell (Figure 33D) hemispherical, prominent, conspicuous, 0.22–0.28 mm long (0.25 ± 0.01 mm), 0.24–0.30 mm wide (0.27 ± 0.02 mm), smooth, without ribs, imperforate except for large marginal pores inside raised border. No avicularia. Zooids communicate via two distal and two distolateral basal pore chambers. Ancestrula (Figure 33E) tatiform, oval, 0.33 mm long, 0.25 mm wide, with smooth, narrow gymnocyst and large, oval opesia, 0.22 mm long, 0.16 mm wide, surrounded by 10 short, jointed hollow spines. The ancestrula becomes modified (Figure 33F) by formation of a frontal shield and loss of spines proximal to level of orifice, thereby coming to resemble periancestrular zooids. Ancestrular orifice irregularly oval, 0.09 mm long, 0.11 mm wide, with slightly concave proximal margin. Frontal wall convex, smooth, with only one row of stellate pores along periphery; slit-like ascopore on small oval prominence at highest point of frontal wall. Ancestrula buds triplet of zooids distally, eventually surrounded by six zooids; periancestrular zooids with three to five oral spines.

Remarks

Specimens from Akkeshi Bay agree well with the original description and illustrations of *F. orientalis* (Liu et al. 2003). Many previous records of *Fenestrulina* from the northwestern Pacific (e.g. Androsova 1959; Kluge 1961; Gontar 1980; Mawatari and Mawatari 1981b; Kubanin 1997; Grischenko 1997) were nominal *F. malusii* (Audouin, 1826), which has been long considered a widely distributed, cosmopolitan species. However, Soule et al. (1995) determined that *F. malusii* does not occur in the eastern Pacific, at least, and that previous records of that species there actually comprised a complex of two genera and several species. According to Hayward and McKinney (2002), *F. malusii* occurs throughout the Mediterranean and northwards to the British Isles and western Norway.

The date of original description of this species is ambiguous, and we were not able to resolve this ambiguity. In their monograph, Liu et al. (2001) included "*Fenestrulina orientalis* Liu et Liu, 2001" and listed "Liu & Liu, 2001: 13, pl. 5, figs. 3–5" as the citation in the synonymy. However, Liu et al. (2001) did not list Liu and Liu (2001) among the monograph's references. Furthermore, in a separate paper whose title indicated "seven new species" of microporellids, Liu et al. (2003) reported "*Fenestrulina orientalis* Liu sp. nov." in the portion of the paper written in Chinese, and "*Fenestrulina orientalis* sp. nov." in the portion of the paper containing an English translation; this paper contained no reference to Liu and Liu (2001), which indeed we have not been able to locate. We thus consider the authorship and date of *Fenestrulina orientalis* to be Liu, Liu, and Sun, 2003.

Distribution

Liu et al. (2003) originally described *Fenestrulina orientalis* from China, but other authors had previously reported it from the Yellow Sea (as *Microporella malusii* or *Fenestrulina malusii*) (Androsova 1959). Some records of *F. malusii* from Japan, e.g. from Akkeshi, Muroran, Shirikishinai, northern to middle Honshu (Mawatari and Mawatari 1981b) and Mutsu Bay (Okada 1929), may represent *F. orientalis*.

Genus *Microporella* Hincks, 1877
Microporella luellae new species
(Figure 34)

Diagnosis

Frontal wall inflated, uniformly perforated with numerous small pores. Primary orifice rounded-semicircular, with straight proximal margin. Two widely separated oral spines. Single avicularium situated anywhere along lateral margin, mandible triangular, pointed

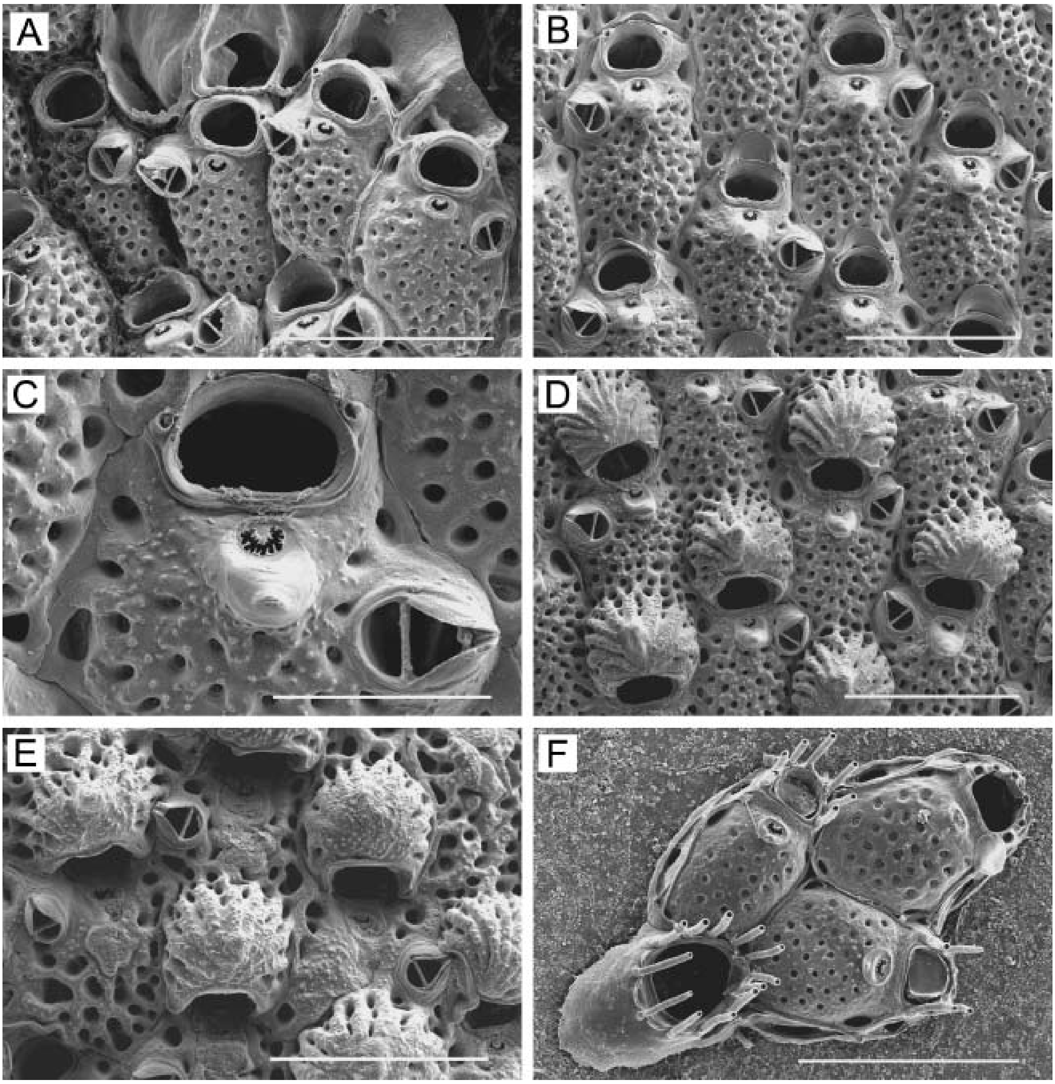

Figure 34. *Microporella luellae* n. sp. (A, E) NHM 2006.2.27.94; (B–D) NHM 2006.2.27.93; (F) NHM 2006.2.27.52. (A) Colony margin with developing zooids; (B) immature zooids; (C) distal half of immature zooid, showing orifice, ascopore, and avicularium; (D) mature zooids with radially ribbed ovicells; (E) heavily calcified mature zooids; (F) ancestrula and periancestrular zooids. Scale bars: 0.5 mm (A, B, D–F); 0.2 mm (C).

distolaterally or laterally, cross-bar complete. Ascopore crescentic, with denticulate edge, located on elevated oval prominence, just distal to prominent conical umbo. Ovicell raised, hemispherical, imperforate centrally, often umbonate, with radial ribs and pores around base. Ancestrula tatiform with 12 spines, budding a pair of zooids distolaterally.

Etymology

Named in honour of Luella Taranto, who greatly helped with collecting during July 2004.

Material examined

Holotype: DIN, four colony fragments (NHM 2006.2.27.93). Paratypes: DIW, two colony fragments (NHM 2006.2.27.94); BAC, ancestrular colony on bivalve shell (NHM 2006.2.27.52). Additional material: 1065 specimens.

Description

Colony encrusting, unilaminar, coherent, irregularly circular, up to 4 cm across; bright orange, pink, or beige in colour when alive. Zooids (Figure 34A, B, D) hexagonal, oval, or somewhat irregular in shape, 0.50–0.73 mm long (0.57 ± 0.06 mm), 0.27–0.43 mm wide (0.36 ± 0.04 mm), separated by deep groove and fine, meandering suture line. Frontal wall moderately to markedly convex, finely granulated, uniformly perforated from margin to margin with small, round pores, except in suboral area. Orifice (Figure 34C) broadly semicircular, with rounded proximolateral corners, 0.09–0.11 mm long (0.10 ± 0.01 mm), 0.12–0.16 mm wide (0.15 ± 0.01 mm), proximal margin straight. No condyles. Two widely separated, short, hollow oral spines along distolateral corners of orifice in immature zooids; some zooids have only one spine or lack them altogether. Ascopore (Figure 34C) crescentic, with a finely denticulate edge, not closed by connecting rays; close to proximal border of orifice, separated from it by a distance about equivalent to distance across short axis of ascopore; located on elevated oval prominence; proximal side of prominence developed into small, smooth, conical umbo. Zooids have a single avicularium (Figure 34A–E), rarely a pair of them, and many zooids lack them altogether; avicularium lateral or proximolateral to ascopore, raised from frontal wall, directed laterally or distolaterally, end of rostrum with narrow channel, cross-bar complete; mandible sharp, elongate-triangular with setiform tip; avicularian chamber with smooth surface. Ovicell (Figure 34D, E) hemispherical, prominent, 0.21–0.26 mm long (0.23 ± 0.01 mm), 0.25–0.32 mm wide (0.29 ± 0.02 mm), radially ribbed, finely granulated, often umbonate, imperforate except for outer margin; proximal margin with a smooth rim or upturned lip. Lateral wall of zooids with two or three distal and two distolateral basal pore chambers. Ancestrula (Figure 34F) tatiform, elongate-oval, 0.35 mm long, 0.23 mm wide, with large, elliptical opesia, 0.18 mm long, 0.15 mm wide, surrounded by 12 spines; ancestrula buds two zooids distolaterally. Periancestrular zooids with six or seven long, tubular oral spines.

Remarks

The genus *Microporella* has been well studied around Hokkaido (Mawatari and Mawatari 1981b; Mawatari et al. 1991), including a recent revision incorporating new taxonomic characters (Suwa and Mawatari 1998). Eight species have previously been reported from

Hokkaido: *M. orientalis* Harmer, 1957; *M. echinata* Androsova, 1958; *M. neocribroides* Dick and Ross, 1988; *M. borealis* Suwa and Mawatari, 1998; *M. elegans* Suwa and Mawatari, 1998; *M. formosa* Suwa and Mawatari, 1998; *M. pulchra* Suwa and Mawatari, 1998; and *M. trigonellata* Suwa and Mawatari, 1998. It is surprising that previous investigators did not detect *M. luellae*, which we found to be exceptionally abundant in Akkeshi Bay.

Microporella luellae is similar in many characters to *M. neocribroides* Dick and Ross, 1988, previously reported intertidally from Densin-Hama, Muroran, southern Hokakido. The two widely separated oral spines distinguish *M. luellae* and *M. neocribroides* from all other congeners reported around Hokkaido. However, in *M. luellae*, the ascopore is always crescentic, with a denticulate edge, and is located on an elevated oval prominence. Except for developing and heavily calcified zooids, the proximal side of this prominence is developed into a small, conical umbo. In *M. neocribroides*, the ascopore is transversely elliptical and covered with a cribriform plate with 10–20 round pores (Suwa and Mawatari 1998, p 899, Figure 2; Dick et al. 2005, p 3753, Figure 19D); only occasionally is there an umbonate process proximal to the ascopore. Another difference is that the ovicell is often umbonate in *M. luellae*, but rarely so in *M. neocribroides*.

Distribution

Microporella luellae is presently known only from Akkeshi Bay.

Microporella trigonellata Suwa and Mawatari, 1998
(Figure 35)

Microporella trigonellata Suwa and Mawatari 1998, p 913, Figure 7A–M.

Material examined

KAI, colony on rock (NHM 2006.2.27.41); BAC, ancestrular colony on bivalve shell (NHM 2006.2.27.52), two colonies on bivalve shell (NHM 2006.2.27.95), intact colony (NHM 2006.2.27.96). Additional material: 262 specimens.

Description

Colony encrusting, unilaminar, coherent, irregularly circular, up to 2.5 cm across, light beige when alive. Zooids (Figure 35A, B) hexagonal to oval, 0.48–0.75 mm long (0.62 ± 0.07 mm), 0.33–0.47 mm wide (0.39 ± 0.04 mm), delineated by a deep groove and fine suture. Frontal wall markedly convex when young, slightly convex with age, finely granulated, evenly perforated with small, round pores over entire surface, except for suboral area. Orifice (Figure 35C) semicircular, broader than long, 0.09–0.12 mm long (0.11 ± 0.01 mm), 0.12–0.15 mm wide (0.14 ± 0.01 mm), with straight proximal margin and rounded proximolateral corners; condyles lacking. Four (rarely, three) to six hollow oral spines (Figure 35A–C) located along curvature of orifice in immature zooids; most proximal pair, with enlarged, cylindrical bases, is retained close to proximolateral corners of ovicell in reproductive zooids. Ascopore (Figure 35C) separated from proximal border of orifice by a distance slightly greater than ascopore width; crescentic, with a crisply denticulate margin, raised on an oval or circular prominence; proximal to ascopore is a sharp, smooth, conical umbo. Avicularium (Figure 35B, C) single, located lateral or proximolateral to ascopore, the chamber with smooth surface; rostrum raised from frontal

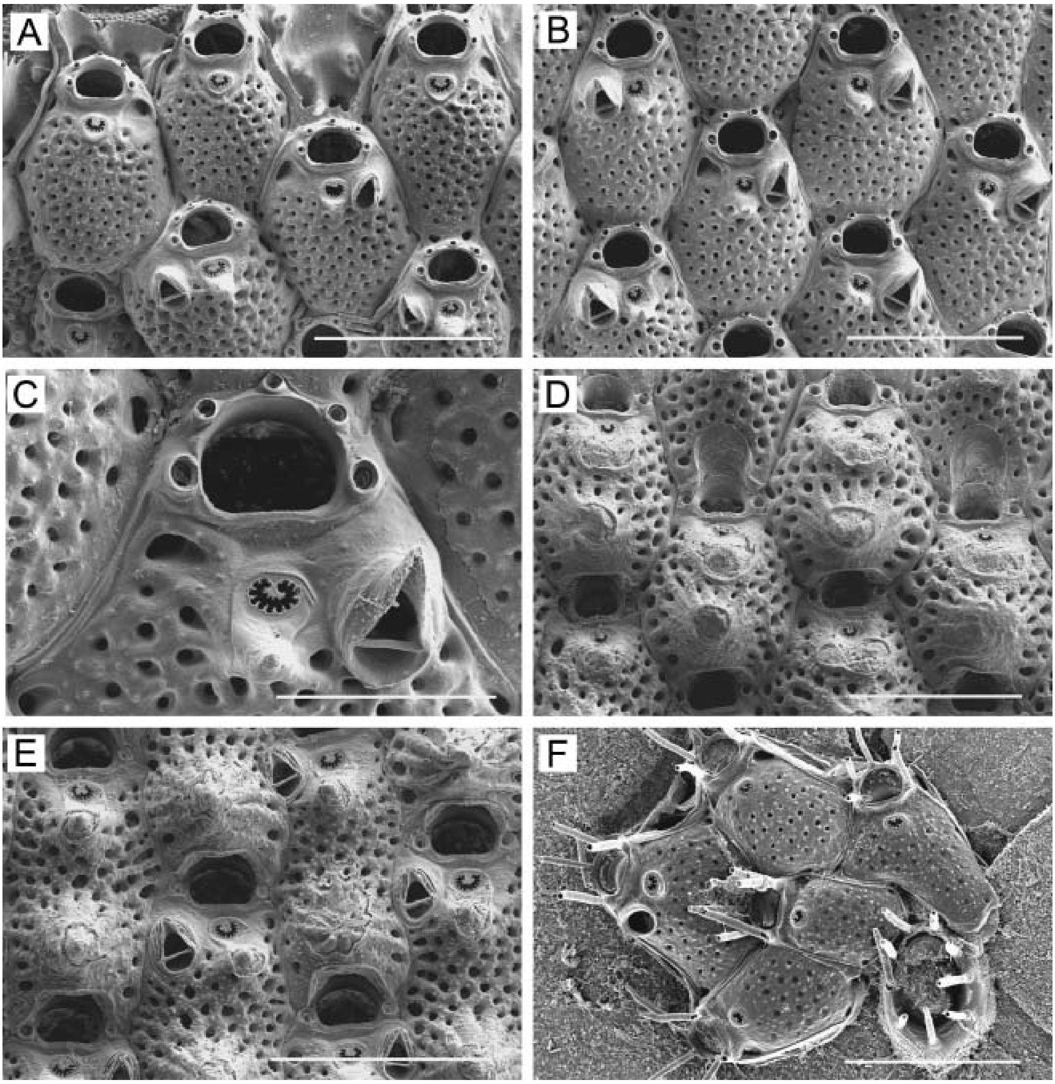

Figure 35. *Microporella trigonellata* Suwa and Mawatari, 1998. (A, E) NHM 2006.2.27.96; (B–D) NHM 2006.2.27.95; (F) NHM 2006.2.27.52. (A) Colony margin with developing zooids; (B) immature zooids; (C) distal half of immature zooid, showing orifice, ascopore, and avicularium; (D) mature zooids; (E) heavily calcified, abraded mature zooids; (F) ancestrula and periancestrular zooids. Scale bars: 0.5 mm (A, B, D–F); 0.2 mm (C).

wall, directed distally or distolaterally, with a narrow channel at the tip; cross-bar complete; mandible elongate-triangular, acute, with setiform tip. Zooids occasionally have two avicularia, or lack them altogether. Ovicell (Figure 35D, E) hemispherical, prominent, broad, 0.20–0.27 mm long (0.24 ± 0.02 mm), 0.25–0.34 mm wide (0.30 ± 0.03 mm), finely granulated, often umbonate, radially ribbed, with pores of varying size around margin, some occluded; indented proximal margin with a smooth rim. Zooids interconnect by three distal and two distolateral basal pore chambers. Ancestrula (Figure 35F) tatiform, oval, 0.37 mm long, 0.28 mm wide, with large oval opesia 0.25 mm long, 0.16 mm wide, surrounded by nine spines. Ancestrula buds two daughter zooids distolaterally, each with five or six tubular oral spines.

Remarks

Our material generally agrees with the original description, except that in contrast to Suwa and Mawatari (1998), we did not observe blunt condyles occasionally present at the proximolateral corners of the orifice. Also, ancestrulae of *M. trigonellata* from Akkeshi Bay are larger than indicated for the type material.

Distribution

Suwa and Mawatari (1998) recently described this species from Deshin-Hama, Muroran, on the Pacific coast of Hokkaido; Akkeshi Bay is the second known locality.

Superfamily CELLEPOROIDEA Johnston, 1838
Family CELLEPORIDAE Johnston, 1838
Genus *Celleporina* Gray, 1848
Celleporina minima new species
(Figure 36)

Diagnosis

Colony small, pisiform, up to 6 mm in diameter. Colony surface very irregular, with numerous knob-like lobes. Zooids erect, cylindrical, haphazardly orientated. Distal pores encircle an oval orifice with a V-shaped sinus. Orifice flanked by paired lateral avicularia on columnar chambers that are straight or curved inward, narrowing terminally, with a small, oval rostrum angled to plane of orifice, the semicircular mandible pointing laterally. Zooids with completed avicularia have a narrow, transverse, slit-like fold in proximal peristomial lip. Vicarious avicularia rare; with broadly spatulate mandible. Ovicell hyperstomial, globose, recumbent on neighbouring zooids; tabula small; circular, semicircular, or roughly triangular, with slit-like, radially arranged pores.

Etymology

The species name refers to the small size of colonies, which can be mature at a few millimetres in diameter.

Material examined

Holotype: ACT, five colonies detached from hydroid stolon (NHM 2006.2.27.97). Paratype: ANC, eight colonies detached from hydroid stolon (NHM 2006.2.27.98). Additional material: eight specimens.

Description

Colony (Figure 36A) pisiform, small, up to 6 mm in diameter, with multilayered arrangement of zooids, one over other, light pink when alive. Surface of colony very irregular with knob-like lobes. Zooids (Figure 36B) erect, cylindrical, 0.23–0.30 mm across (0.26 ± 0.02 mm), haphazardly orientated. Frontal wall convex, smooth, with a row of areolar pores; pore openings carried around orifice and encircling it. In some zooids, frontal wall rises to a small, wide umbo proximal to orifice. Primary orifice (Figure 36D) oval,

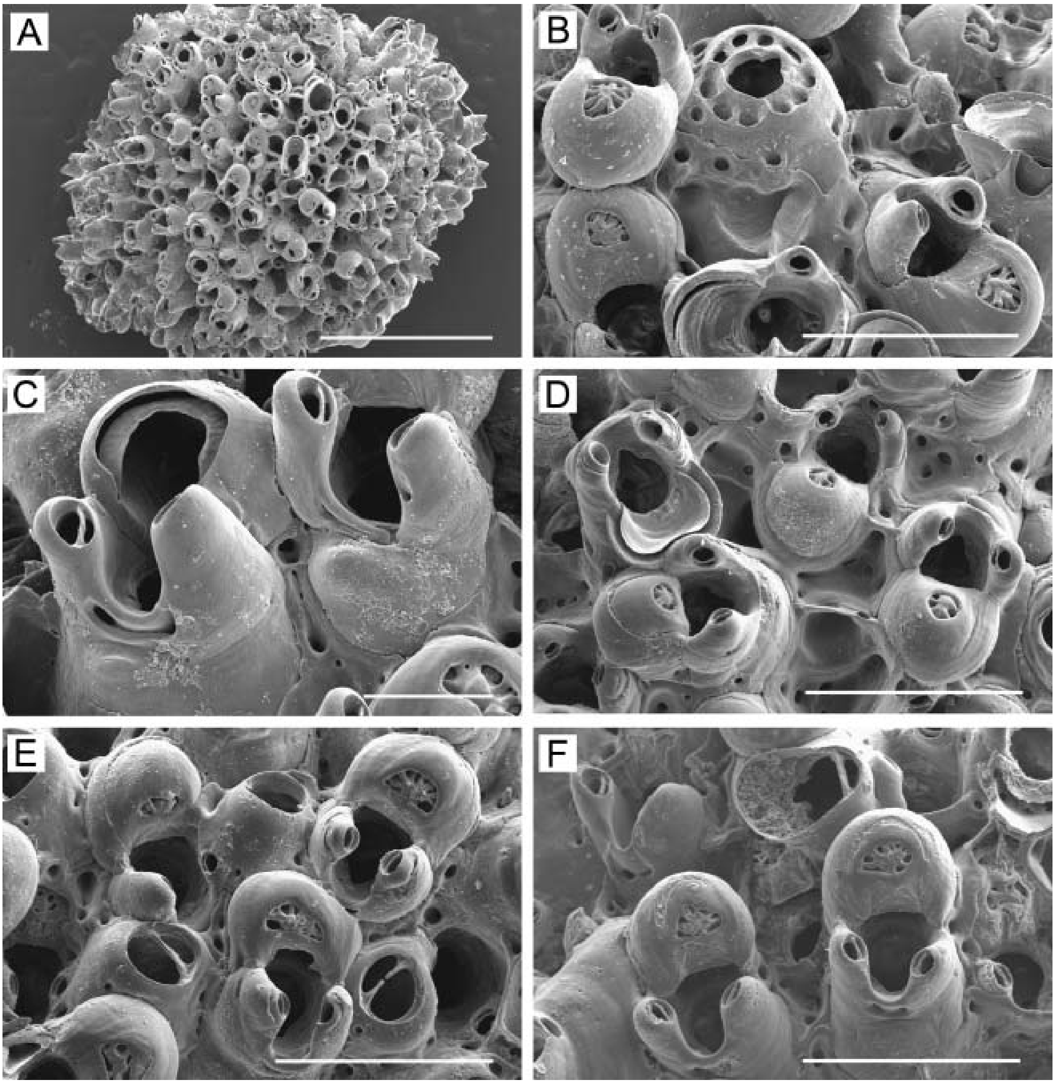

Figure 36. *Celleporina minima* n. sp. (A–C, F) NHM 2006.2.27.97; (D, E) NHM 2006.2.27.98. (A) General view of colony; (B) immature zooid surrounded by ovicellate zooids; (C) two zooids with developing ovicells, showing avicularian columns and external transversal slit-like fold in proximal peristomial lip; (D) zooids with developing and completed ovicells, showing form of primary orifice with deep proximal sinus; (E, F) ovicellate zooids surrounded by vicarious avicularia. Scale bars: 2 mm (A); 0.5 mm (B, D–F); 0.2 mm (C).

0.11–0.15 mm long (0.13 ± 0.01 mm), 0.10–0.14 mm wide (0.12 ± 0.01 mm), with small, flattened condyles and deep, V-shaped proximal sinus. Secondary orifice (Figure 36C–E) formed by peristomial lip proximally and by lateral columnar avicularia laterally. Avicularian columns (Figure 36C) on each side lateral to orifice long, stout, wide at base, tapering distally, with a small, round or oval, terminal rostrum tilted at an angle to the orificial plane and with a complete cross-bar, the semicircular mandible directed laterally; columns straight or curved inward, often submerged in sub-surface zooids. Development of avicularia accompanied by formation of narrow, transverse slit-like fold (Figure 36C) in proximal peristomial lip. Vicarious avicularia rare, scattered over colony surface, about 0.13–0.25 mm long, with complete cross-bar and semicircular (Figure 36E) to broadly spatulate (Figure 36F) mandible; rostral opesia large. Ovicell (Figure 36B, D–F) hyperstomial, globose, 0.18–0.23 mm long (0.20 ± 0.01 mm), 0.24–0.30 mm wide (0.26 ± 0.02 mm), recumbent on neighbouring zooids, initially prominent, subimmersed with age; tabula small; circular, semicircular, or roughly triangular, with slit-like, radially arranged pores. Ancestrula and early astogeny not observed.

Remarks

Celleporina minima n. sp. is similar to the Arctic-Boreal species *C. nordenskjoldi* in having a pisiform colony, columnar lateral avicularia, and globular, recumbent ovicells. However, colonies of *C. minima* are always smaller and can have ovicellate zooids at a diameter of just a few millimetres. Avicularian columns of *C. minima* tend to be curved inward, narrow terminally, with the rostrum angled to the orificial plane and the mandible directed laterally. The avicularian columns of *C. nordenskjoldi* are long and stout, do not narrow terminally, and are usually straight or only slightly curved inward; the mandible is directed distolaterally. Though the ovicells are quite similar in form in these two species, the tabula is much smaller in *C. minima*, its diameter one-third to one-half the width of the proximal orifical margin; the tabula in *C. nordenskjoldi* is usually nearly as wide as the proximal margin of the ovicell.

Distribution

Akkeshi Bay is the only known locality.

Celleporina nordenskjoldi (Kluge, 1929)
(Figure 37)

Cellepora nordenskjoldi Kluge 1929, p 22.

Cellepora nordenskjoldi: Kluge 1962, p 552, Figure 386; 1975, p 672, Figure 386; Androsova 1958, p 179, Figure 109; Mawatari and Mawatari 1981b, p 56.

Costazia nordenskjoldi: Osburn 1952, p 508, Plate 63, Figures 6, 7.

Celleporina nordenskjoldi: Morris 1979, p 478, Text figures 1, 3b, Table 1; Gontar 1980, p 14; Kubanin 1997, p 125.

Celleporina nordenskjoldii [sic]: Grischenko 1997, p 190; 2004, p 41.

Material examined

DIN, four colonies (NHM 2006.2.27.99) and another four colonies (NHM 2006.2.27.101), all detached from ctenostome bryozoan *Flustrellidra filispina*, six colonies detached from hydroid stolon (NHM 2006.2.27.100). Additional material: 41 specimens.

Description

Colony pisiform or ovoid in shape, with multilayered arrangement of zooids, one over the other; up to 9 mm in diameter, orange when alive. Colony surface irregular, undulating, with numerous knob-like lobes. Zooids (Figure 37A, B) cylindrical, erect, 0.29–0.36 mm

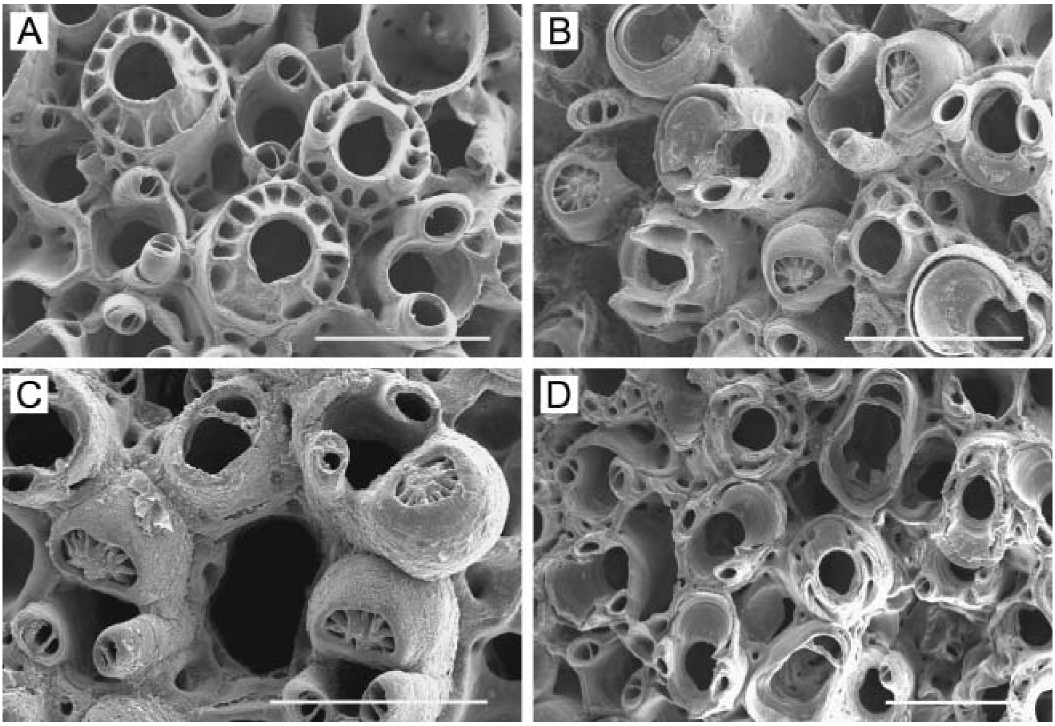

Figure 37. *Celleporina nordenskjoldi* (Kluge, 1929). (A) NHM 2006.2.27.101; (B, D) NHM 2006.2.27.99; (C) NHM 2006.2.27.100. (A) Immature zooids, showing form of primary orifice; (B) zooids with developing and completed ovicells; (C) three ovicellate zooids and vicarious avicularium; (D) two large vicarious avicularia surrounded by zooids with developing ovicells. Scale bars: 0.5 mm.

across (0.32 ± 0.02 mm), with haphazard orientation. Frontal wall arched, smooth, with marginal areolar pores; pore openings carried around orifice and encircling it. Primary orifice (Figure 37A) irregularly oval, 0.12–0.18 mm long (0.15 ± 0.01 mm), 0.12–0.15 mm wide (0.13 ± 0.01 mm), with flattened condyles and rather shallow, broadly V-shaped proximal sinus; located deep within peristome. Peristome (Figure 37B, C) consists of peristomial lip proximally and paired avicularian columns laterally that are long, stout, straight or only slightly curved inward, often becoming submerged with age; rostrum terminal, oval, slightly angled to plane of orifice, cross-bar complete, semicircular mandible directed distolaterally. Vicarious avicularia (Figure 37C, D) rare, scattered over colony surface, up to about 0.5 mm long, with complete cross-bar, mandible broadly spatulate, rostral opesia large. Ovicell (Figure 37B, C) globose, broader than long, 0.22–0.25 mm long (0.24 ± 0.01 mm), 0.25–0.30 mm wide (0.28 ± 0.02 mm), initially prominent, subimmersed with age. Tabula relatively large, semicircular to transversely oval, bordered with radially arranged slit-like pores, its diameter nearly as wide as proximal margin of ovicell. Ancestrula and early astogeny not observed.

Distribution

Celleporina nordenskjoldi is distributed along the Eurasian and American sectors of the Arctic region and extends into the Boreal Pacific, but appears to be absent in the Canadian Arctic and northern Atlantic. It has been reported along the Eurasian Arctic in the Laptev, East-Siberian, Chukchi Seas (Kluge 1962, 1975; Gontar and Denisenko 1989), and from the Beaufort Sea near Point Barrow, Alaska (Osburn 1952; Morris 1979). In the northwestern Pacific, *C. nordenskjoldi* has been recorded from eastern Kamchatka, the Commander Islands, the Kuril Islands, the Shantar Archipelago, Sakhalin Island, Primorye, Peter the Great Gulf (Kluge 1961; Gontar 1980; Kubanin 1997; Grischenko 1997), and Akkeshi and Muroran along the Pacific coast of Hokkaido, Japan (Mawatari and Mawatari 1981b).

Celleporina porosissima Harmer, 1957

(Figure 38)

Celleporina porosissima Harmer 1957, p 906, Plate 62, Figures 3, 16, 17.

Celleporina porosissima: Voigt and Cook 1983, p 53, Plates 1–3; Ikezawa and Mawatari 1993, p 1031, Figure 2A–L.

? *Myriozoum marionense* var. *irregulatum* Okada 1923, p 231, Figures 27–31.

? *Myriozoum marionensis irregulatum*: Okada 1934, p 19; Okada and Mawatari 1935, p 142, Plate 10, Figure 5.

Material examined

ACT, four colonies detached from undetermined red algal rhizoid (NHM 2006.2.27.102).

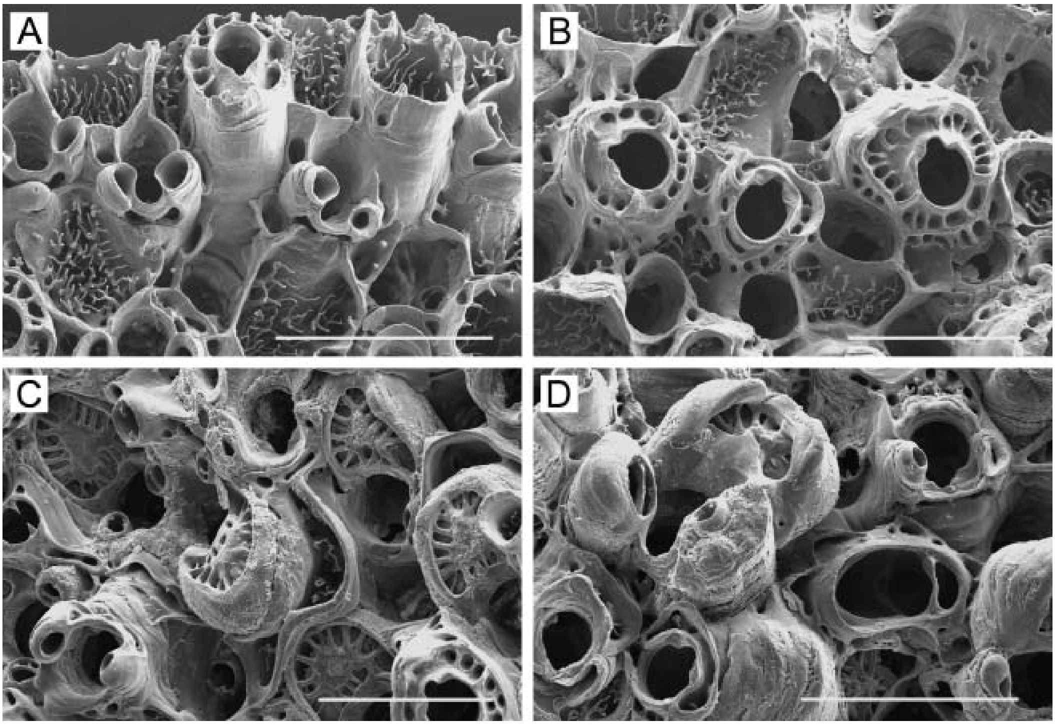

Figure 38. *Celleporina porosissima* Harmer, 1957. NHM 2006.2.27.102. (A) Developing zooids at colony margin; (B) immature zooids, showing form of primary orifice; (C) abraded mature zooids with subimmersed ovicells; (D) heavily calcified and abraded zooids and vicarious avicularium. Scale bars: 0.5 mm.

Description

Colony encrusting, discoid, domed; a typical colony measured 1.5 by 1.2 by 0.2 cm; with multilayered arrangement of zooids, one over the other; light orange when alive. Colony surface undulating, with many knob-like lobes. Zooids at colony margin (Figure 38A) decumbent. As colony rises from substrate, zooids (Figure 38B) become erect, cylindrical, 0.28–0.38 mm across (0.33 ± 0.03 mm), haphazardly orientated. All zooids have numerous spinous processes within the zooidal cavity (Figure 38A, B). Frontal wall of decumbent zooids smooth, convex, with a few marginal pores and imperforate central area; in erect zooids, pores carried towards orifice by tubular extensions and form ring around peristome. Primary orifice (Figure 38B) oval, 0.12–0.18 mm long (0.15 ± 0.01 mm), 0.11–0.16 mm wide (0.14 ± 0.01 mm), submerged with age by peristome, with flattened condyles on condylar shelves and deep, U-shaped proximal sinus. Orifice of non-ovicellate zooids encircled by narrow peristomial lip; peristome enclosed by thickened proximal orificial lip and columnar lateral orificial avicularia, one on each side lateral to orifice, rarely single or absent; avicularian column stout, curved inward, often submerged with age; rostrum circular, terminal, angled almost perpendicular to orificial plane, with a complete cross-bar; semicircular mandible directed in a lateral direction. Vicarious avicularia (Figure 38D) scattered over colony surface, numerous in central colony region, 0.13–0.29 mm long, with spatulate mandible; cross-bar complete, rostral opesia large, sometimes with extensive palatal shelf and high rostral rim. Ovicell (Figure 38C, D) globose, 0.24–0.33 mm long (0.29 ± 0.02 mm), 0.29–0.39 mm wide (0.34 ± 0.03 mm), initially prominent, subimmersed with age; tabula semicircular, crescentic, or triangular, extensive, occupying nearly entire frontal surface of ovicell, bordered with radially arranged slit-like pores; secondary calcification results in a distinct border surrounding tabula. Ancestrula and early astogeny not observed.

Remarks

Okada (1923) was apparently the first person to collect this species, but described his material from the Korea Strait as a new variety, *irregulatum*, of *Myriozoum marionense* Busk, 1884. Harmer (1957) recognized Okada's form as different from *M. marionense*, and on the basis of specimens from Japan described it as a new *Celleporina*. A key diagnostic character is the common occurrence in young zooids of several rows of pores distal to the orifice, which was well illustrated by Ikezawa and Mawatari (1993, Figure 2A, C) in their redescription of *C. porosissima*; these authors also described the early astogeny. The deep-water specimens described by Okada (1923) formed colonies with erect, cylindrical, anastomosing branches, whereas Harmer (1957) described colonies as "small pleurilaminar crusts", and Ikezawa and Mawatari (1993) described them as "encrusting, discoidal, domed". Although Harmer (1957) attributed this difference in growth form to his specimens possibly having been in an initial stage of growth, the difference raises the question whether *Celleporinna porosissima* is indeed synonymous with Okada's (1923) *Myriozoum marionense* var. *irregulatum*.

Distribution

Originally collected from depths of 90–200 m in the Korea Strait (if Harmer's 1957 synonymy is valid), this species has been reported from the vicinity of Shimoda, Shizuoka Prefecture as colonies attached to seaweeds (Okada 1934), and from Oshoro Bay, Hokkaido, as colonies on fronds of *Laminaria religiosa* (Ikezawa and Mawatari 1993). Akkeshi Bay is the northernmost known locality.

Family HIPPOPORIDRIDAE Vigneaux, 1949

Genus *Hippoporella* Canu, 1917

Hippoporella kurilensis (Gontar, 1979)

(Figure 39)

Hippoponella kurilensis Gontar 1979, p 240, Figure 3.

? *Hippoponella parva* Androsova 1958, p 143, Figure 69.

? *Hippoponella parva*: Kluge et al. 1959, p 212; Kluge 1961, p 136; Gontar 1978b, p 14; 1980, p 13; 1992, p 191; Grischenko 1997, p 182; 2002, p 116; 2004, p 41.

? *Hippoporella parva*: Kubanin 1997, p 124.

Material examined

DIN, six colonies detached from erect ctenostome bryozoan *Flustrellidra filispina* (NHM 2006.2.27.103); additional material, four specimens; paratype examined, ZIRAS 2/43720, colony encrusting erect bryozoan *Microporina articulata*, Simushir Island, Polanskogo Cape, depth 20 m, rocky bottom, collected by V. I. Lukin, 10 September 1970.

Description

Colony encrusting, unilaminar, coherent, more or less circular, largest observed 1.2 cm across, beige to orange in colour when alive. Zooids (Figure 39A, B) hexagonal to oval, rounded distally, 0.35–0.55 mm long (0.45 ± 0.05 mm), 0.27–0.38 mm wide (0.33 ± 0.03 mm); newly budded zooids (Figure 39A) demarcated by groove and fine suture line; boundaries indistinct between heavily calcified zooids. Frontal wall moderately to markedly convex, tessellate, dimpled, imperforate except for two or three areolar pores along each lateral margin. Primary orifice (Figure 39A, C) elongate-semicircular, occupying about one-third length of frontal wall, 0.12–0.15 mm long (0.13 ± 0.01 mm), 0.10–0.14 mm wide (0.12 ± 0.01 mm), with straight to slightly concave proximal margin; condyles well developed as rounded-triangular projections located about one-third of distance from proximal to distal margin, separating semicircular anter from shorter, broader poster. Five or six long, hollow oral spines (Figure 39A) with enlarged bases occupy distal curvature of primary orifice of marginal zooids; with age, three or four distal spines become covered by secondary calcification and only most proximal pair remains lateral to orifice, in mature zooids lying close to proximolateral corners of ovicell. Primary orifice evident only in newly budded zooids, becoming rapidly submerged and surrounded by shallow, sloping peristome. Secondary orifice oval to irregularly circular; cormidial, bounded proximally by avicularian chamber, laterally and distally by contributions of calcification from lateral and distal zooids. A relatively large median suboral avicularium (Figure 39B, D) lies within peristome, just below secondary orifice, often orientated slightly obliquely to longitudinal axis and usually tilted proximally; rostrum oval, cross-bar complete, mandible semicircular, rostral margin proximal to hinge bar even or with small prominences. Avicularian chamber fusiform along long axis, evident in young zooids, completely submersed with increased calcification. Some zooids have hypertrophied suboral avicularium (Figure 39C), about 0.19 mm long, comparable to orifice in size, with

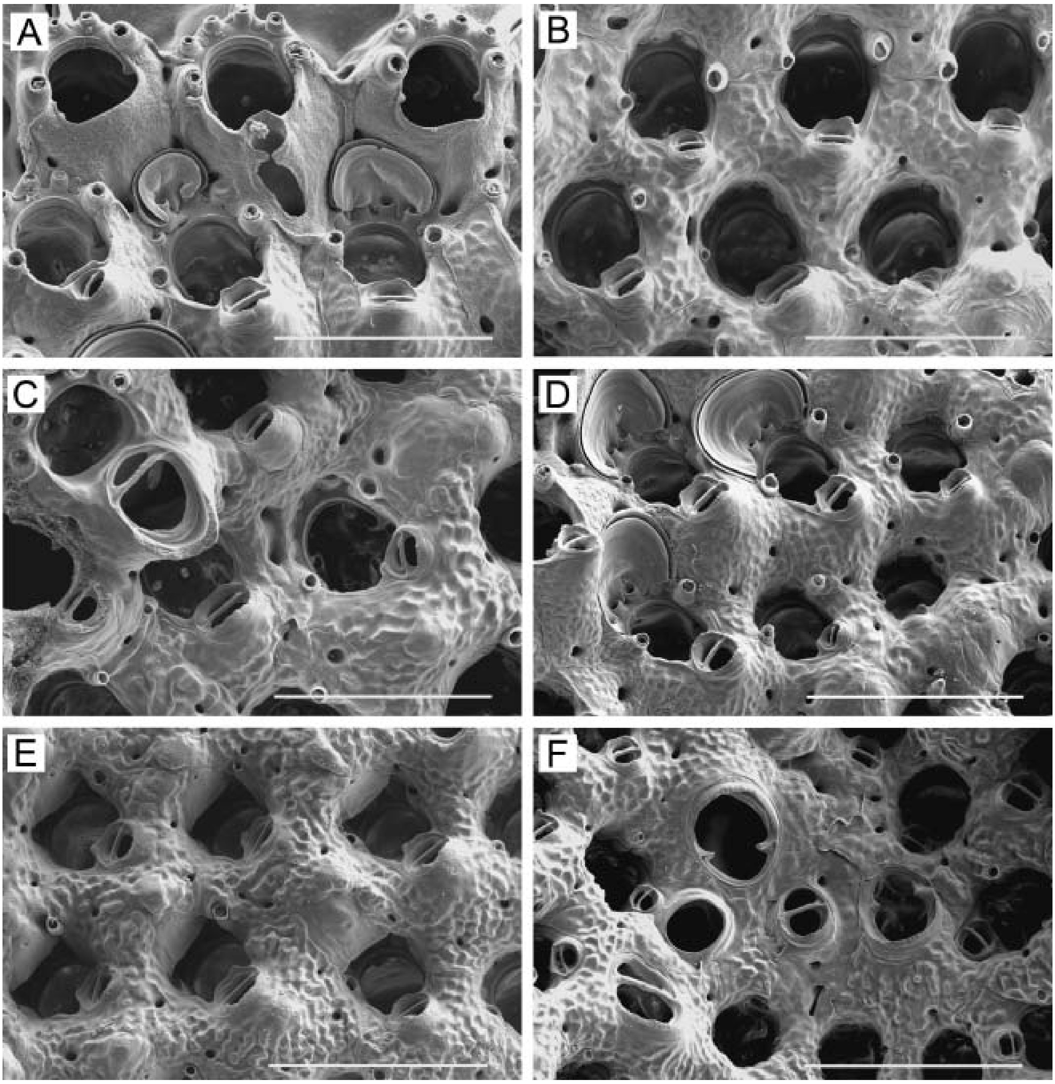

Figure 39. *Hippoporella kurilensis* (Gontar, 1979). NHM 2006.2.27.103. (A) Colony margin with developing zooids; (B) immature zooids; (C) zooids near colony margin, one with hypertrophied suboral avicularium; (D) zooids with developing ovicells; (E) mature zooids with immersed ovicells; (F) ancestrular region covered with large adventitious avicularia. Scale bars: 0.4 mm (A–C); 0.5 mm (D–F).

short-spatulate mandible tilted proximally, almost parallel with frontal plane. Oval frontal avicularia (Figure 39F) with semicircular mandible sometimes occur in proximal half of strongly calcified zooids; oval adventitious avicularia 0.17–0.21 mm long, with semispatulate mandible (Figure 39F), occupy older regions of colony. Ovicell (Figure 39D, E) hyperstomial, globose, 0.17–0.21 mm long (0.19 ± 0.01 mm), 0.20–0.25 mm wide (0.22 ± 0.01 mm), proximal margin straight or nearly so; rapidly submerged and often covered with contributions of secondary calcification from distal and lateral zooids, indicated by fine suture lines; with a smooth proximal tabula having a minute median pore near top. Zooids interconnect by multiporous septula. Ancestrula not observed; Ancestrular region with numerous large adventitious avicularia.

Remarks

Gontar (1979) originally described *H. kurilensis* from subtidal material collected near Cape Polyanskogo, Simushir Island, Kuril Islands, and later reported the species from near Makanrushi, Onekotan, Harimkotan, Ekarma, Raschua, Ketoy, Chiproy, Broutona, Urup, and Shikotan Islands of the Kuril Ridge (Gontar 1980). Material from Akkeshi Bay is quite similar to the paratype specimen (ZIRAS 2/43720).

Hippoporella kurilensis shares many characters with its Asian Pacific Boreal congener *H. parva* (Androsova 1958). The latter is known from the northern part of the Sea of Japan, the coastal waters of southwestern Sakhalin Island, near Moneron Island, and Zolotoy and Uspeniya Capes, northern Primorye (Androsova 1958); Paramushir, Makanrushi, Onekotan, Simushir, Chiproy, Urup, Iturup, Shikotan, and Zelenyy Islands along the Kuril Ridge (Gontar 1978b, 1980, 1992), and the shelf zone of the Commander Islands (Grischenko 1997, 2004).

Both *H. kurilensis* and *H. parva* have a tessellated, dimpled frontal wall with a few marginal areolae, and a large suboral avicularium with an undulating proximal rostral margin, complete cross-bar, and semicircular mandible orientated obliquely to the longitudinal axis and tilted slightly proximally. Additionally, both species have the orifices of marginal zooids surrounded by long spines with strong bases, the most proximal of which are more heavily calcified. The ovicells are also similar, with a smooth frontal surface rapidly immersed with secondary calcification.

Although Gontar (1979) did not clarify the differences between her new species and *H. parva*, they evidently include the presence of small adventitious avicularia on the frontal wall of heavily calcified zooids of *H. kurilensis*; an often enlarged suboral avicularium tilted proximally to colony plane and variable in size in *H. kurilensis*; and five or six oral spines in marginal zooids of *H. kurilensis*, compared to four to eight in *H. parva*.

Examination of material of *H. parva* from the Commander Islands has demonstrated that the size of suboral avicularium may vary significantly in some colonies. Furthermore, the number of oral spines known for *H. kurilensis* falls within the range for *H. parva*. The status of *H. kurilensis* as a species distinct from *H. parva* is thus unclear, especially considering their overlapping distribution along most of the Kuril Islands. Since we have not been able to examine the type material of *H. parva* for comparison and thus cannot adequately address this taxonomic problem here, we retain the name *H. kurilensis* for the Akkeshi specimens, pending further study.

Distribution

Hippoporella kurilensis is known from the majority of the Kuril Islands, and from Akkeshi Bay.

Hippoporella multiavicularia (Androsova, 1958)

(Figure 40)

Hippoponella multiavicularia Androsova 1958, p 143, Figure 68.

Hippoponella multiavicularia: Kluge et al. 1959, p 212; Kluge 1961, p 136; Gontar 1980, p 13; 1992, p 191.

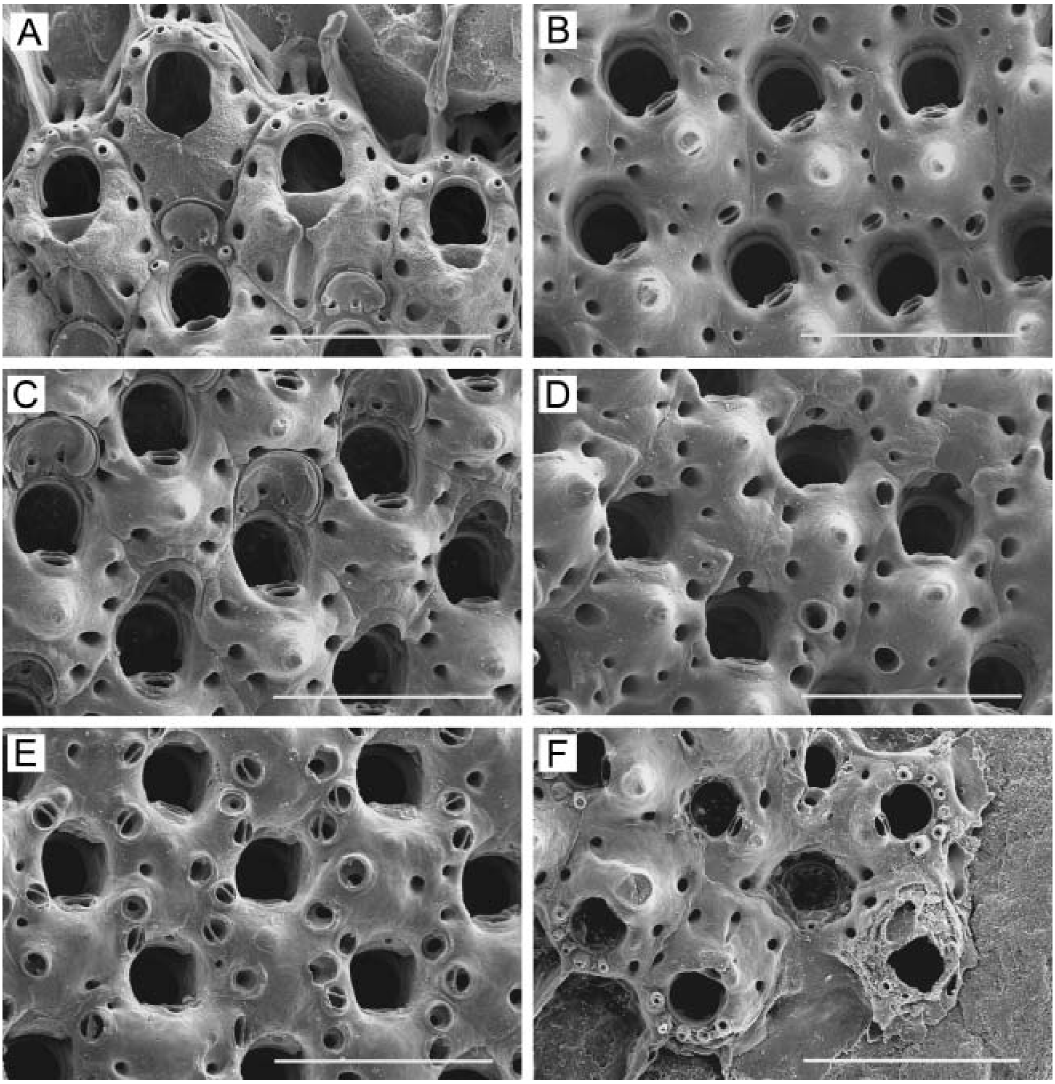

Figure 40. *Hippoporella multiavicularia* (Androsova, 1958). (A–D) NHM 2006.2.27.104; (E) NHM 2006.2.27.105; (F) NHM 2006.2.27.106. (A) Colony margin with developing zooids; (B) immature zooids; (C) zooids with developing ovicells; (D) zooids with submerging ovicells possessing central pore in ectooecium; (E) heavily calcified mature zooids with numerous small avicularia; (F) ancestrula and periancestrular zooids. Scale bars: 0.5 mm.

Material examined

ANC, colony on rock (NHM 2006.2.27.104), colony on rock (NHM 2006.2.27.105), ancestrular colony on rock (NHM 2006.2.27.106). Additional material: 118 specimens.

Description

Colony encrusting, unilaminar, coherent, more or less circular; largest observed 1.4 cm in maximum dimension; bright orange to pink when alive. Zooids (Figure 40A, B) hexagonal, rhombic, or irregularly oval, rounded distally, 0.32–0.53 mm long (0.45 ± 0.06 mm), 0.27–0.45 mm wide (0.36 ± 0.04 mm), demarcated by shallow groove with fine suture line. Frontal wall moderately to markedly convex, translucent, smooth, imperforate except for three or four areolar pores along each lateral margin, rising distally to suboral umbo that varies from a small, low nodule to a tall, conical projection, sometimes rounded in mature zooids. Primary orifice (Figure 40A) hat-shaped, slightly longer than broad, 0.10–0.14 mm long (0.12 ± 0.01 mm), 0.10–0.13 mm wide (0.11 ± 0.01 mm), with straight to slightly concave proximal margin; blunt condyles are swellings in internal rim around anter, separating long-semicircular anter from short, broad poster. Four hollow ephemeral oral spines (Figure 40A), more proximal pair with enlarged bases, located along distal margin of orifice of marginal zooids. Primary orifice evident only in developing zooids near colony margin; with development of secondary calcification, it becomes submerged and surrounded by shallow, sloping peristome. Secondary orifice (Figure 40B) similar in shape to primary orifice, long-semicircular in outline; cormidial, bounded proximally by avicularian chamber, distally and laterally with contributions of calcification from distal and lateral zooids. A circular suboral avicularium (Figure 40B, C) lies within peristome, below secondary orifice, orientated perpendicularly to colony surface or tilted slightly proximally; mandible semicircular, cross-bar complete; avicularian chamber small, broader than long, smooth, inflated in young zooids and submersed by umbo in older zooids. One to five small, circular adventitious avicularia (Figure 40E) with semicircular mandible occupy frontal surface of many zooids; these tend to occur on proximal half of frontal wall in immature zooids and lateral slopes of suboral umbo in ovicellate zooids; often interzooidal in position, surrounding secondary orifices. Ovicell (Figure 40C–E) hyperstomial, globose, broad, smooth, 0.15–0.20 mm long (0.17 ± 0.01 mm), 0.16–0.23 mm wide (0.19 ± 0.01 mm), with a large, circular pore close to slightly concave proximal margin of ectooecium; rapidly submerged (Figure 40D, E), with contributions of secondary calcification from frontal walls of distal and lateral zooids delineated by fine sutures. Zooids interconnect by multiporous septula. Ancestrula (Figure 40F) 0.07 mm long, 0.10 mm wide, orifice semicircular with straight proximal margin, surrounded by 10 spines; ancestrula buds three zooids distally and distolaterally, with another three larger zooids proximolaterally and proximally; periancestrular zooids with suboral avicularia only, and with five or six spines around distal curvature of orifice.

Remarks

The hat-shaped primary orifice surrounded by four spines with strong bases, the vertically orientated suboral avicularium, and the presence of numerous adventitious avicularia characterize this species. Specimens from Akkeshi Bay agree well with the original description of *H. multiavicularia*, except for fewer and differently arranged adventitious avicularia, which occasionally cover the entire frontal surface and number up to 10 per zooid in the type material. Androsova (1958) also did not mention a pore near the proximal margin of the ovicell; however, this is difficult to observe without SEM.

This species is close to *H. fastigatoavicularis* (Kluge, 1955), which is common subtidally in Akkeshi Bay (Mawatari and Mawatari 1981b) in having a similarly shaped secondary orifice, and in the presence of suboral and numerous adventitious avicularia. However, all avicularia, including the suboral avicularium, of *H. fastigatoavicularis* are very small and lie in the plane of the frontal wall. *Hippoporella fastigatoavicularis* also has more regularly hexagonal zooids, with small umbones flanking the orifice laterally, in addition to the conical suboral umbo.

Another congener, *H. kurilensis* (Gontar, 1979), has marginal zooids with very similar morphology. In contrast to four spines in *H. multiavicularia*, *H. kurilensis* has five or six oral spines, with a pair of them remaining in ovicellate zooids. The frontal wall in *H. kurilensis* is convex and tessellated; adventitious avicularia are normally lacking, only occasionally present in heavily calcified zooids from the central region of the colony; and the relatively large suboral avicularium is orientated slightly obliquely to the longitudinal axis and usually tilted proximally. Complete ovicells of *H. kurilensis* are often not entirely covered by secondary calcification.

Distribution

This species was originally described from coastal waters off southern Sakhalin Island in the northern part of the Sea of Japan; it has also been recorded from Primorye (Androsova 1958; Kluge et al. 1959; Kluge 1961). Gontar (1980, 1992) reported it from Paramushir, Shikotan, and Zelenyy among the Kuril Islands. *Hippoporella multiavicularia* also occurs in the shelf zone of the Commander Islands (A. V. Grischenko, unpublished data).

Family PHIDOLOPORIDAE Gabb and Horn, 1862
Genus *Phidolopora* Gabb and Horn, 1862
Phidolopora elongata (Smitt, 1868)
(Figure 41)

Retepora cellulosa forma *notopachys* var. *elongata* Smitt 1868, p 36, Plate 28, Figures 226–332.
Retepora wallichiana: Hincks 1877, p 107, Plate 11, Figures 9–13; 1884, p 55.
Retepora elongata: Androsova 1958, p 117, Figure 107; Kluge 1961, p 142; 1962, p 527, Figure 368.
Phidolopora elongata: Hansen 1962, p 45; Cuffey and Turner 1987, p 67; Kubanin 1997, p 125; Grischenko and Ivanyushina 2002, p 32, Text figure 2.
Phydolopora elongata [sic]: Gontar 1980, p 13; 1990, p 133; 1992, p 188; 1993, p 202; 1996, p 46; Gontar and Denisenko 1989, p 357; Grischenko 1997, p 188.
? *Retepora pacifica* Robertson 1908, p 310, Plate 24, Figures 81–84.
? *Retepora pacifica*: O'Donoghue and O'Donoghue 1923, p 189.
? *Phidolopora pacifica*: Canu and Bassler 1923, p 154, Plate 39, Figures 1–7; O'Donoghue and O'Donoghue 1925, p 106; 1926, p 118; Osburn 1952, p 448, Plate 53, Figures 1, 2; Soule et al. 1995, p 277, Plate 106A–E.

Material examined

ANC, 10 colony fragments (NHM 2006.2.27.107), three colony fragments (NHM 2006.2.27.108), two young colonies on rock (NHM 2006.2.27.109) Additional material: three specimens; holotype, SMNH-1316, Svalbard, Hinlopen Strait, Waigatsöarna.

Description

Colony (Figure 41A) erect, orange in colour when alive, consisting of fenestrate bilaminar sheets, complexly folded and fused into rigid three-dimensional meshwork, largest observed 11 × 8 × 4.5 cm in dimensions, rising from rounded base attached to substratum by kenozooids. Branches range from three to 11 zooids wide between fenestrulae. All

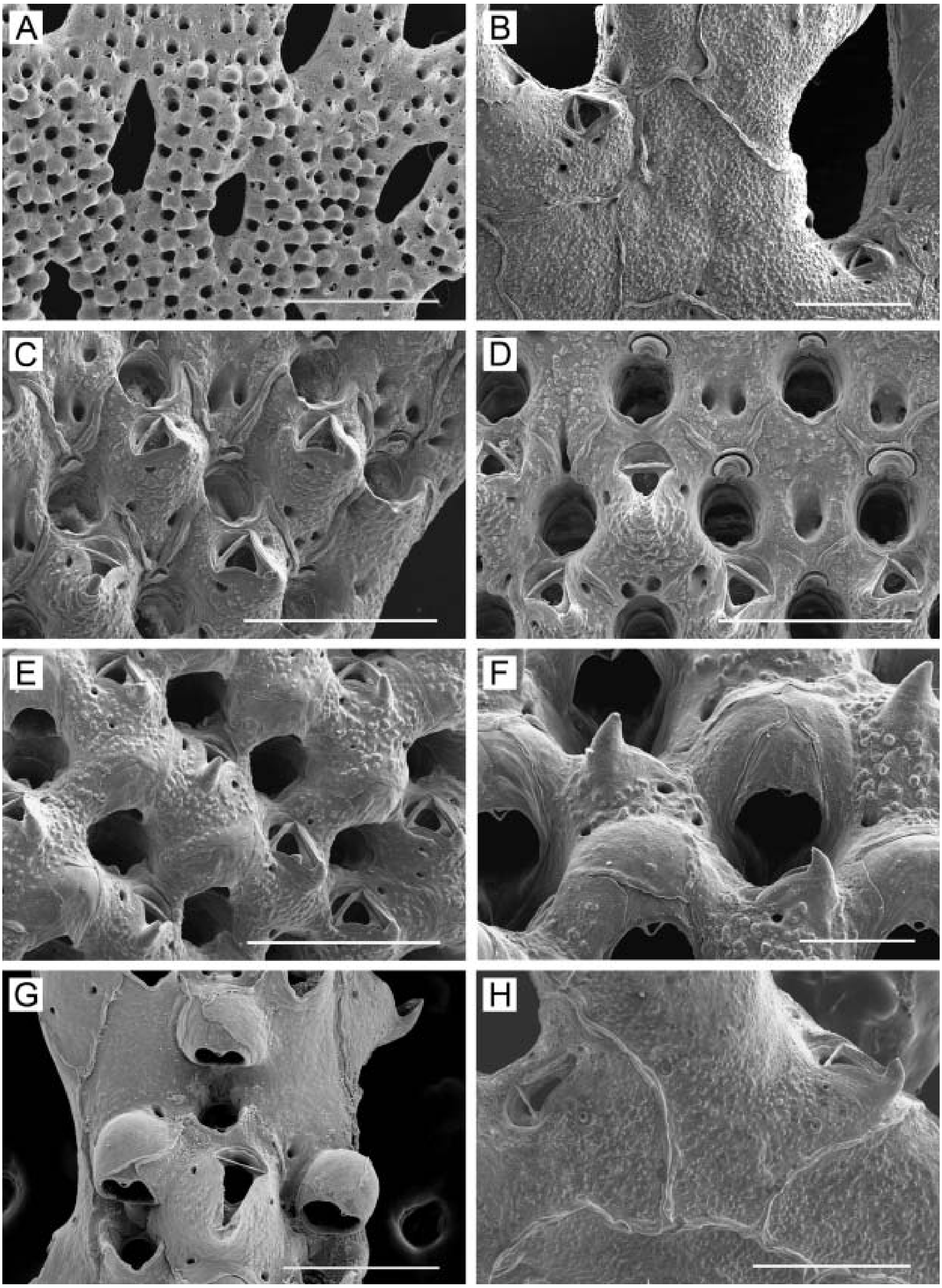

Figure 41. *Phidolopora elongata* (Smitt, 1868). (A, F) NHM 2006.2.27.108; (B–E) NHM 2006.2.27.107; (G, H) SMNH-1316. (A) General view of colony fragment; (B) dorsal surface of colony, showing kenozooids and avicularia in abfrontal axils of fenestrulae; (C) immature zooids; (D) zooids with developing ovicells; (E) mature zooids; (F) close up of ovicells, showing details of denticles in middle of proximal margin; (G) mature zooids with ovicells possessing peculiar sharp denticle; (H) dorsal colony surface with kenozooids and avicularia in abfrontal axils of fenestrulae. Scale bars: 2 mm (A); 0.5 mm (B–E, G, H); 0.2 mm (F).

feeding zooids open on one surface of a sheet; opposite surface consists of kenozooids. Fenestrulae elongate-oval or irregularly rhombic in shape, 0.7–1.9 long by 0.3–0.9 mm wide. Zooids (Figure 41C) hexagonal, rhombic, or oval, 0.48–0.70 mm long (0.59 ± 0.07 mm), 0.24–0.38 mm wide (0.31 ± 0.04 mm). Newly budded zooids delineated by raised vertical walls; in older regions of colony, boundaries between zooids occluded by secondary calcification or represented by fine sutures. Frontal wall slightly convex to inflated in young zooids, markedly convex in mature zooids, finely granulated, imperforate except for two or three pores along each proximolateral margin. Primary orifice (Figure 41D) long-semicircular, with beaded rim, 0.10–0.13 mm long (0.11 ± 0.01 mm), 0.09–0.13 mm wide (0.11 ± 0.01 mm); proximal margin straight, with shallow but distinct U-shaped sinus flanked by condylar shelves bearing low, blunt condyles. With age, primary orifice submerged in peristome; secondary orifice with median pseudosinus. Two short, hollow, ephemeral oral spines with enlarged bases frequently present at distolateral edges of primary orifice in marginal zooids. Large frontal avicularium (Figure 41C–E), 0.14–0.20 mm long, with raised, beak-shaped rostrum, occupies central part of frontal wall in many zooids; cross-bar complete, rostral opesia triangular to oval in shape; mandible long-triangular, with acute tip, directed proximally or proximolaterally; avicularian chamber broad, conical, very prominent in immature zooids, inflated in ovicellate zooids (Figure 41D) by general thickening of frontal wall owing to secondary calcification, coarsely granulated, with two or three small pores flanking its base. Single transversely orientated avicularium occupies proximal abfrontal axils of fenestrulae (Figure 41B), 0.15–0.18 mm long, with short, equilaterally triangular mandible; one or two pairs of circular pores flank rostrum. Ovicell (Figure 41F) hyperstomial, spherical, smooth, often forming a hood overhanging orifice, 0.18–0.23 mm long (0.20 ± 0.01 mm), 0.20–0.25 mm wide (0.22 ± 0.01mm), with incompletely calcified ectooecium having fine concentric striae; proximal edge of ovicell often with slight median denticle. Ovicell rapidly immersed (Figure 41E) by secondary calcification from distal and lateral zooids covering most of its surface, with fine sutures delineating calcification from different zooids. Dorsal surface of colony (Figure 41B) shows outlines of kenozooids of irregular form and size, recognizable by sutures indicating raised vertical walls; kenozooids inflated, roughly granulated, with a few sparse circular pores on the surface; avicularia lacking dorsally except for those in axils of fenestrulae. Ancestrula and early astogeny not observed.

Remarks

Specimens from Akkeshi Bay are similar in many characters to the type specimen of *P. elongata* (SMNH-1316, many fragments) (Figure 41G, H). Both have rhombic zooids with a submerged, rounded primary orifice having a shallow median sinus and encircled by peristome bearing a proximal pseudosinus. Large frontal avicularia are similar in form and position; the ovicells have, on the proximal margin, a median denticle that is often incompletely closed. There are some differences; specimens from Akkeshi Bay have 3–11 zooids comprising branches between fenestrulae, the type of *P. elongata* three to seven. This may be ecophenotypic variation, as depth-dependent variation in branch width occurs in *P. elongata* from the Commander Islands region; colonies from depths of 1–25 m have twice the number of zooids per branch than those from depths of 65–165 m (A. V. Grischenko, unpublished data). Another is that the abfrontal avicularian mandibles are larger with a long-triangular mandible in the type of *P. elongata*, versus smaller, with an equilateral mandible in specimens from Akkeshi.

A congener, *P. pacifica* (Robertson, 1908), is known from the eastern Pacific, reported from Alaska, Puget Sound, and the coast of California (Robertson 1908); British Columbia (O'Donoghue and O'Donoghue 1923, 1925, 1926); and from the Santa Barbara Channel to Mexico and the Galapagos Islands (Soule et al. 1995). Soule et al. (1995) illustrated this species for the first time using SEM. *Phidolopora pacifica* appears to be similar to *P. elongata* in the shape of the orifice and the ovicell with a median denticle, which was also illustrated in line drawings by Robertson (1908) and Osburn (1952). However, *P. pacifica* seems to form more pronounced lappets flanking the peristomial pseudosinus, and the abfrontal avicularium appears to differ somewhat in shape and orientation. Unfortunately, Robertson's types of *P. pacifica* were mixed with other specimens, and neotypes will eventually have to be selected; in any case, we here consider this species as valid. Records of *P. pacifica* from Mexico and the Galapagos Islands (Osburn 1952; Soule et al. 1995) need re-examination.

Many large, erect colonies of *P. elongata* were found growing in horizontal crevices in solid rock at the base of a cliff overhang at Aininkappu Cape; these were inhabited by a number of benthic organisms, including ascidians, sabellid and spirorbid polychaetes, sponges, crustaceans, sipunculids, holothurians, nemerteans, and ophiuroids. A similar hermatypic growth form of this species, supporting a rich associated fauna, occurs below cliffs in the Commander Islands (Grischenko and Ivanyushina 2002).

Distribution

Phidolopora elongata is considered a circumpolar Arctic-Boreal species; Kluge (1962, 1975) and Gontar and Denisenko (1989) gave many distributional records. In the northern Pacific, it has been previously reported from the Bering Sea near the Commander Islands (Kluge 1961; Grischenko 1997; Grischenko and Ivanyushina 2002), along the Kuril Islands (Gontar 1980, 1993), and in Tatar Strait in the northern Sea of Japan (Kluge 1961). Akkeshi Bay is the southernmost known locality for this species in the western North Pacific.

Discussion

Some early researchers (Gurjanova 1935; Deryugin 1939) noted the abundance and appreciable role of bryozoans in intertidal communities along the coast of northeastern Asia (i.e. the northwestern Pacific Ocean and the Bering, Okhotsk, and Japan Seas). Subsequently, a considerable amount of information accumulated on the component bryozoan species of these communities, through regional faunistic surveys (Androsova 1958, 1971, 1976; Kluge 1961, 1975; Kubanin 1975, 1997; Izyumova 1977; Gontar 1978a, 1978b, 1980, 1981, 1989), limited intertidal studies (Androsova et al. 1974; Kubanin 1976, 1987, 1996; Izyumova and Kubanin 1978), or other studies, e.g. Gordon et al. (2002), d'Hondt and Mawatari (1986), Mawatari (1986, 1988), Ikezawa and Mawatari (1993), and Suwa and Mawatari (1998); also see Introduction.

Recent summary publications indicated a high overall diversity of intertidal bryozoans in the region. Kubanin (1997) tabulated 128 intertidal bryozoan species along the northeastern coast of Asia from the Bering Strait southwards to Peter the Great Gulf. Grischenko (2004) listed 49 cheilostomes and 63 bryozoan species overall occurring in the intertidal zone of the Commander Islands. Our study at Akkeshi adds 23 species to Kubanin's (1997) list of intertidal bryozoans of the region, suggesting that this list was far from complete.

Several studies of intertidal bryzoans on suitable rocky shores (usually semi-protected, usually a habitat of layered boulders) in the North Pacific (Table VI) have indicated both ranges of single-site diversity and values of total local diversity. Estimates of diversity will increase with increasing sampling effort, and this is evident in Table VI: sampling effort was similar for Ketchikan and Hawaii, and these studies both found a cheilostome diversity of around 30 species. Likewise, sampling effort was similar for our study at Akkeshi and that at Kodiak; however, the cheilostome diversity measured at Akkeshi was only two-thirds that at Kodiak (39 and 57 species, respectively). Considering the similar, substantial sampling efforts in these two localities, the difference in diversity is likely not an artefact, and raises the question why the diversity at Akkeshi is lower.

In fact, we expected on biogeographic grounds that Akkeshi Bay would have a higher diversity than Kodiak. Akkeshi is situated just 2° of latitude south of the boundary separating the High and Low Boreal Zones in the western Pacific (Ekaterina Strait, Iturup Island, south Kuril Islands). The cold Oyashio current flows southward from the Bering Sea along Kamchatka and the Kuril Islands, reaching the southeastern coast of Hokkaido, including Akkeshi Bay. The warm Tsushima current, a branch of the Kuroshio current, weakly influences Akkeshi Bay from the southwest (Uchida et al. 1963). The transitional biogeographic position of Akkeshi Bay and also the influences of both cold and warm currents should be conducive for the dispersal there of species from the Arctic, Boreal, and Subtropical regions, and hence for enrichment of the fauna. Aside from this argument, one might expect higher bryozoan diversity at Akkeshi than at Kodiak due simply to the latitudinal gradient of increasing diversity from the poles to the tropics that is apparent for many animal phyla (Fisher 1960), including marine bryozoans (Dick and Ross 1988). Akkeshi (43°N) is considerably farther south than Kodiak (58°N).

We speculate that the unexpectedly low diversity of intertidal bryozoans between Akkeshi and Kodiak is due to differences in the environments of the two study areas and correlated ecological differences. Specifically, the difference in diversity may be due to differences in (1) the diversity of the bryozoan source community available for colonization of the intertidal, (2) the extent of the intertidal zone available for colonization by bryozoans, and (3) the diversity of habitats and microhabitats inhabited by bryozoans.

Table VI. Comparison of the species richness of intertidal bryozoans at six localities in the North Pacific.

Locality (study)	Sampling stations	Cheilostome species Per site (range)	Cheilostome species Total	Total species	Study
Nanaimo, BC	–	–	–	74[a]	O'Donoghue and O'Donoghue (1923, 1926)
Ketchikan, Alaska[b]	3	10–28	31	–	Dick et al. (2005)
Kodiak, Alaska[c]	11	9–33	57	74[d]	Dick and Ross (1988)
Commander Islands	13	1–37	49	63	Grischenko (1993, 1994, 2004)
Akkeshi, Japan	10	8–29	39	49[e]	This study
Island of Hawaii	4	0–28	28	31	Dick et al. (2006)

[a] Includes species recorded intertidally on all substrata, mostly within about 30 km of Nanaimo, BC. [b] The number of ctenostome and cyclostome species occurring intertidally was not estimated in this study. [c] The 14 collecting stations reported by Dick and Ross (1988) are here condensed to 11 sites, because in two cases, two or three sampling stations were located at different intertidal heights at the same site. [d] Includes a rough estimate of the number of ctenostome and cyclostome species present, without identification to species. [e] Includes at least five ctenostome and five cyclostome species observed, but not identified to species.

Most intertidal bryozoan species are not restricted to the intertidal zone, but also occur subtidally and reach the upper limit of their depth range in the intertidal (Dick et al. 2005). Although intertidal bryozoan populations reproduce and can directly repopulate the intertidal zone, it might also be the case that species that are collected rarely intertidally represent relatively temporary incursions into the intertidal zone of species whose optimal habitat is subtidal. If this were the case, then the diversity of intertidal bryozoans at a site might be directly related to the species diversity on the adjacent subtidal shelf. We believe that the nearshore shelf areas at Akkeshi Bay and Kodiak may differ significantly in bryozoan diversity, although the subtidal bryozoan assemblages have not been adequately studied at these localities and confirmatory data are thus lacking.

The highest diversity of marine bryozoans occurs in the 0–100 m depth interval, that is, in nearshore shelf areas, although diversity is also high at 200 m (Ryland 1970; Gordon 1999). The width of the adjacent shelf zone is much narrower at Akkeshi than at Kodiak. At Akkeshi, the 200 m depth contour lies about 30 km from the mouth of the bay. At Kodiak, the 200 m depth contour lies about 100 km from the eastern entrance of Narrow Strait, where bryozoans were studied intertidally (Dick and Ross 1988).

Furthermore, few marine bryozoan species are capable of living on sandy or muddy bottoms; most species require a hard substratum such as rocks or shells on which to attach. The bottom of Akkeshi Bay and the adjacent shelf is mostly sandy and muddy; encrusting bryozoans can exist there only on scattered "islands" of substratum comprising isolated banks, scattered boulders, anthropogenic debris, and mollusc shells. At Kodiak, both the nearshore zone close to the intertidal study area of Dick and Ross (1988) and the vast adjacent shelf have mostly a rocky bottom. The Kodiak shelf, with a much greater area of substratum available to encrusting bryozoans, should thus also have much higher overall subtidal species diversity through a simple species–area relationship (MacArthur and Wilson 1967), and consequently more species available for incursion into the intertidal than Akkeshi Bay.

There is some evidence to support this speculation. At Akkeshi, three (8%) of the 39 species found intertidally were extremely rare, collected as one to three colonies per species. At Kodiak, with sampling effort similar to that at Akkeshi, 13 (23%) of the 57 species found intertidally were collected only as one to three colonies each (Dick and Ross 1988). This higher proportion of extremely rare species in the intertidal would be expected if subtidal diversity were much higher and if intertidal diversity were positively influenced by occasional incursions into the intertidal of some proportion of the overall complement of subtidal species.

Another difference between Kodiak and Akkeshi lies in the former locality having a more extensive intertidal zone available for bryozoans. The annual tidal range at Kodiak is 4.18 m, compared to 1.57 m at Akkeshi. This means that both the overall area of the intertidal zone and the areas of particular sub-zones, such as the infralittoral fringe, are considerably greater at Kodiak than at Akkeshi. This greater area should entail a greater number of species, again through a species–area relationship.

In addition to being less extensive, the intertidal zone at Akkeshi probably includes a lower diversity of habitats and possibly microhabitats than at Kodiak, which would also theoretically lower overall species diversity. Our cluster analysis showed the sampling sites forming three main species assemblages (outer Akkeshi Bay, inner Akkeshi Bay, and Akkeshi Lake) that were less than 70% similar to one another. The distribution of these assemblages from the outer to the inner bay suggests that some factor or combination of factors (e.g. degree of wave exposure, salinity, degree of sedimentation) varying from the outer to the inner bay influences the species composition of the assemblages. A cluster analysis of collecting sites at Kodiak (Dick and Ross 1988) showed a more complex pattern that suggested that degree of wave exposure, shore composition (reef flat versus layered boulders), and possibly proximity to the outlets of estuaries influenced species composition. The shoreline at Kodiak is less steep, and two of the sampling sites located in the infralittoral fringe comprised extensive rocky reef-flats exposed for tens of metres from the water's edge at low tide, with a complex structure of tidepools and overlying boulders. Extensive rocky reef flats of this type are not present in Akkeshi Bay.

Among the 39 cheilostome species found at Akkeshi, nine (23%) proved to be undescribed. This proportion of new species is not exceptionally high compared to other intensive studies conducted in local areas in the last two decades: 25% new among 59 species at Kodiak (Dick and Ross 1988); 35% new among 119 species in the eastern Pacific (Soule et al. 1995); 26% new among 31 species at Ketchikan (Dick et al. 2005); 22% new among 92 species at Vanuatu (Tilbrook et al. 2001); 40% new among 178 species in the Solomon Islands (Tilbrook 2006); 31% new among 31 species on the Island of Hawaii (Dick et al. 2006). Interestingly, 80 years ago O'Donoghue and O'Donoghue (1923, 1926) found 26% new among 204 species they reported from the vicinity of Nanaimo, BC, so the rate of description of new species from intensive local studies in the Pacific does not appear to be reaching an asymptote. To put these numbers into context, we note that Hayward and McKinney (2002) reported only 5% new among the 106 species included in their study of the northern Adriatic; this low value reflects a greater cumulative taxonomic effort in the Mediterranean. The high proportion of new species in recent studies in the Pacific is attributable to generally low previous taxonomic effort throughout much of the region, an increase in taxonomic resolution due to the now-routine use of scanning electron microscopy, and a paradigm shift in how taxonomists view geographic variation (Soule et al. 1995; Dick and Mawatari 2004).

In addition to changing our estimate of total bryozoan species diversity, intensive studies in local areas around the Pacific are also identifying speciose clades whose diversity had gone unrecognized in part due to the lumping of multiple, distinct species as geographical variants of putatively widely distributed species. A number of genera in the Pacific are proving much more speciose than was indicated a few decades ago; examples include *Parasmittina* (Soule and Soule 1973; Tilbrook 2006) and *Rhynchozoon* (Hayward 1988; Ryland and Hayward 1992; Tilbrook 2006). The genus *Cauloramphus* provides another example. As of the early 1980s, ten recent species of this genus had been reported from all of the Pacific Ocean, Sea of Japan, Bering Sea, Sea of Okhotsk, and Arctic Ocean (Osburn 1950; Androsova 1958; Kluge 1962, 1975; Kubanin 1975; Mawatari and Mawatari 1981a). Subsequently, another six new species were reported from the Pacific, including two at Kodiak (Dick and Ross 1988), another two at Ketchikan (Dick et al., 2005), and one each from California and Korea (Soule et al. 1995; Seo 2001). Our discovery of five species of *Cauloramphus* intertidally in the relatively small area of Akkeshi Bay, including three new species (*C. cryptoarmatus*, *C. niger*, and *C. multispinosus*) suggests that there are still many undescribed species of *Cauloramphus* in the North Pacific and that this genus may prove to be one of the most speciose among anascan genera in the region.

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