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Diversity and distribution of intertidal *Microporella* (Bryozoa: Cheilostomatida) from California

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Abstract. Seven species of the cheilostome bryozoan genus *Microporella* were identified across 15 rocky intertidal sites spanning 940 km of the California coast, from Mill Creek in the Montereyan Pacific Transition Region north to Point Saint George in the Mendocinian Region. Colonies of *Microporella* were found encrusting boulders and mollusc shells. Among these species, three are new to science, namely *Microporella dentata* Chowdhury & Di Martino sp. nov., *M. pauciperforata* Chowdhury & Di Martino sp. nov. and *M. rota* Chowdhury & Di Martino sp. nov. Three other species, *M. californica*, *M. setiformis*, and *M. umbonata* have previously been recorded from other localities in California. Finally, *Microporella neocribroides*, originally described from off Kodiak Island, Alaska, and subsequently found in Hokkaido, Japan, was recorded in California for the first time. An additional new species, *M. similis* Chowdhury & Di Martino sp. nov., was identified through the re-examination of museum material previously attributed to *M. cribrosa* and *M. californica*. These newly acquired data allowed for a more comprehensive examination of the distribution of species, intraspecific variability, and potential predator-induced teratologies in certain species, thanks to the availability of numerous colonies from various sites and the re-examination of museum records. Altogether, this study increases the known Recent diversity of *Microporella* in California's waters to a total of 18 species.

Keywords. New species, Microporellidae, Montereyan Pacific Transition Region, Mendocinian Region.

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Introduction

The genus *Microporella* Hincks, 1877 is one of the most distinctive among all cheilostome bryozoans (Taylor & Mawatari 2005). It is characterized by rounded polygonal, often hexagonal zooids with a convex, granular frontal shield with scattered pseudopores and a variably shaped ascopore, transversely D-shaped orifice with or without oral spines, single or paired adventitious avicularia usually placed laterally or distolaterally, and prominent ovicells either with or without pseudoporous ooecium, and with or without a personate structure enclosing or not the ascopore. *Microporella* is cosmopolitan and speciose. To date, 160 species have been described worldwide, including 38 fossil and 122 living species (Bock 2023).

Canu & Bassler (1923: 120) stated: "The coast of California is the Elysium of the genus *Microporella* for a wealth of species occurs there". Indeed, with 13 species thriving in California's waters, *Microporella* is currently one of the most species-rich cheilostome genera in the region. Busk (1856) was apparently the first to report *Microporella* in California, introducing a new species, *M. californica*, originally described as *Lepralia*. Later, Robertson (1908: 282) identified Busk's species across "numerous points on the coast of Southern California". Subsequently, Osburn (1950) examined bryozoan material collected during several Pacific expeditions, including the Allan Hancock Expeditions (1933–1942) that focused mostly on intensive dredging around the islands off Southern California. Osburn also drew from material stored in various museum collections, including the collection in the California Academy of Sciences curated by Robertson. Based on this material, Osburn (1952) identified seven species of *Microporella* from California (USA): *M. californica*, *M. ciliata* (Pallas, 1766), *M. cribrosa* Osburn, 1952, *M. setiformis* O'Donoghue & O'Donoghue, 1923, *M. stellata* (Verrill, 1879), *M. umbonata* Hincks, 1883, and *M. vibraculifera* Hincks, 1883. Soule *et al.* (1995, 2003, 2004) re-examined Osburn's records and made some re-assignments. For instance, colonies previously identified as *Microporella ciliata*, a species once thought to be widely distributed but later found to be a Mediterranean endemic (Kuklinski & Taylor 2008, Di Martino & Rosso 2021), were described as the following new species: *M. catalinensis* Soule, Soule & Chaney, 1995, *M. planata* Soule, Soule & Chaney, 1995, *M. santabarbarensis* Soule, Chaney & Morris, 2004, and *M. wrigleyi* Soule, Chaney & Morris, 2004. In addition, part of the material initially attributed to *M. californica* was re-described as *M. infundibulipora* Soule, Soule & Chaney, 1995; and colonies attributed to *M. umbonata*, a species first described from British Columbia (Hincks 1883), were reassigned to *M. umboniformis* Soule, Soule & Chaney, 1995. No definitive re-assignments were made for records of *M. stellata*, a species originally described from the northeastern Atlantic off the coast of Maine (USA). Soule *et al.* (1995) also synonymized records of *M. californica* in Robertson (1908) with *M. cribrosa*.

Most of the material studied by previous authors was collected by dredge, trawl, or benthic grab and only subordinately by SCUBA diving, and during intertidal surveys focusing on bryozoans encrusting algae and pilings (Osburn 1950; Soule *et al.* 2003).

This paper aims to document the diversity and distribution of species of *Microporella* from 15 rocky intertidal sites (mainly boulder fields) along 940 km of the California coast, describe and illustrate four new species using scanning electron microscopy (SEM), and update the known range of distribution of species previously known from other areas.

Material and methods

Material for this study was collected from 15 rocky intertidal sites that are located in the Oregonian zone, a major coastal biogeographic zone running from Monterey Bay (California) to Cape Flattery (Washington) (Blanchette *et al.* 2008; Toonen *et al.* 2016). Specifically, colonies of *Microporella* were collected from 13 sites located in the Mendocinian Region and two sites located in the Montereyan Pacific Transition Region (see Wilkinson *et al.* 2009 for details on the marine ecoregions of North America). The collecting sites stretch from Mill Creek (southernmost site) to Point Saint George (northernmost site) (see Fig. 1, Table 1). Sampling was undertaken by two of us (I.A.C. and H.L.) between December 2019 and October 2020. Some sites were selected based on Blanchette *et al.* (2008), while new sites were identified using Google Earth, local expert suggestions, and personal experience. Outer-coast samples were collected in the intertidal zone during low tides; tidal levels (Mean Low Water and Mean High Water; see Table 1) are from NOAA (National Oceanic and Atmospheric Administration); environmental parameters (i.e., Sea Surface Temperature, salinity and pH; see Table 1) are from the closest offshore profiling buoys of CeNCOOS (Central & Northern California Ocean Observing System). All numbered specimens herein, other than those on bivalve shells, were found as either partially living or recently dead colonies on the undersides of rocks ranging from 12 to 75 cm in maximum dimension. Bryozoan colonies were sampled

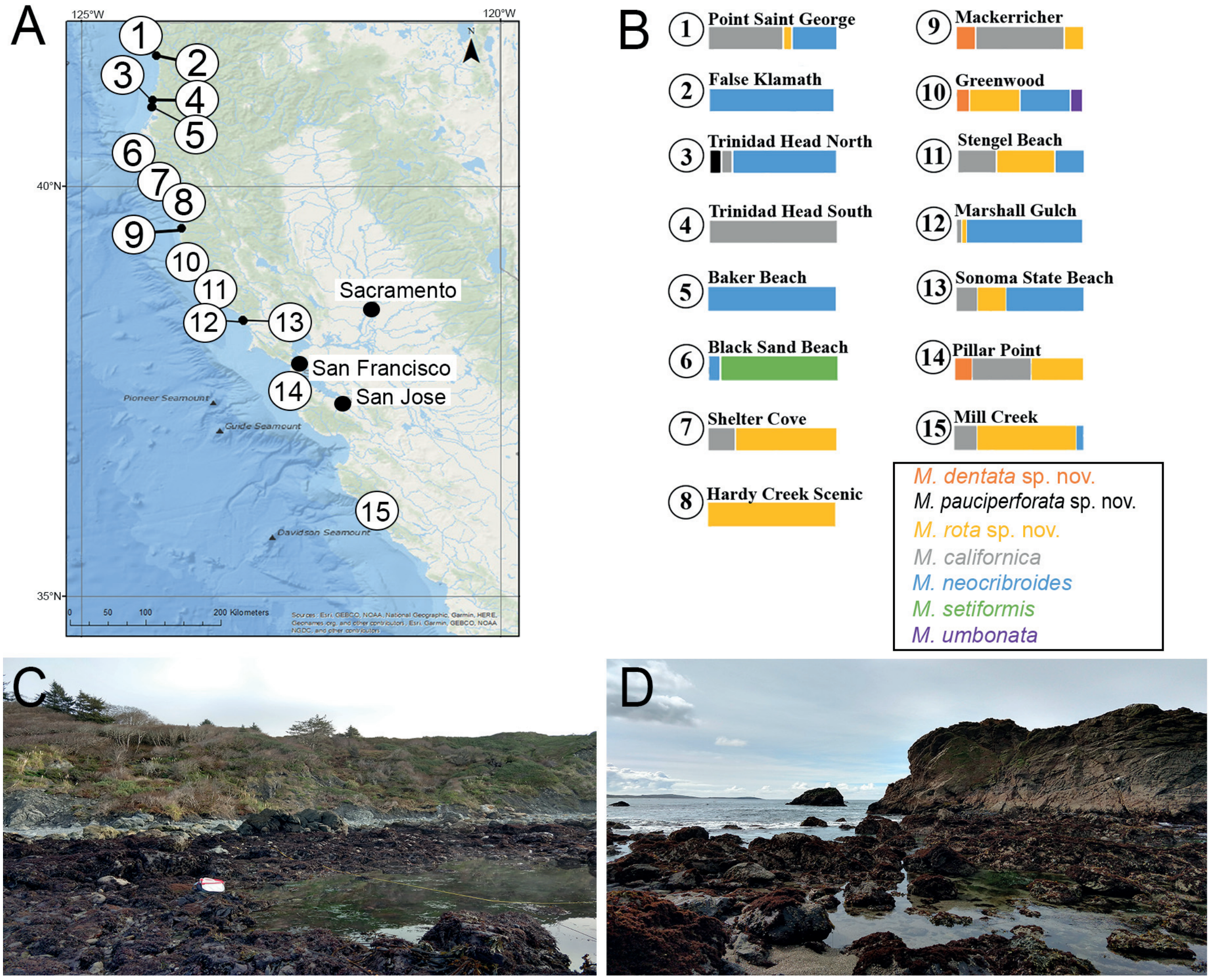

Fig. 1. A. Location of sampling sites along the Californian coastline. **B**. Distributions and relative abundances of species indicated by colour-coded bars. **C–D**. Two sites as examples of the rocky intertidal boulder fields that were sampled for this study. **C**. Palmer's Point. **D**. Marshall Gulch.

Table 1. Summary of sampling sites reporting latitude (Lat.), longitude (Long.), Sea Surface Temperature (SST), salinity (Sal.), pH, and tidal parameters (MLW = low water; MHW = high water; TR = tidal range) at the time of sampling. Montereyan Pacific Transition Region sites are in bold font. NA = not available

Site	Lat. (N)	Long. (W)	SST (°C)	Sal. (‰)	pH	MLW (m)	MHW (m)	TR (m)
1. Point Saint George	41.785	124.255	11.65333	NA	NA	-0.51	2.27	1.76
2. False Klamath	41.594	124.106	10.28389	NA	NA	-0.27	1.79	1.52
3. Trinidad Head North	41.057	124.151	10.545	31.86	7.9	-0.30	2.05	1.75
4. Trinidad Head South	41.056	124.147	10.72778	32.122	7.8384	-0.12	1.59	1.47
5. Baker Beach	41.049	124.128	10.70556	32.118	7.878	-0.24	1.92	1.68
6. Black Sand Beach	40.414	124.397	11.595	NA	NA	-0.34	2.20	1.87
7. Shelter Cove	40.021	124.068	12.82944	NA	NA	-0.24	2.05	1.81
8. Hardy Creek Scenic	39.710	123.808	11.46667	NA	NA	-0.15	1.86	1.71
9. MacKerricher	39.490	123.802	11.1	NA	NA	-0.12	1.84	1.72
10. Greenwood	39.129	123.719	10.775	NA	NA	-0.35	1.31	0.96
11. Stengel Beach	38.715	123.460	11.78444	33.50	NA	-0.36	1.92	1.56
12. Marshall Gulch	38.369	123.075	11.93667	33.637	NA	-0.06	1.63	1.57
13. Sonoma State Beach	38.361	123.070	11.97944	33.07	NA	-0.04	1.69	1.65
14. Pillar Point	**37.495**	**122.496**	**12.31278**	**NA**	NA	**-0.09**	**1.60**	**1.51**
15. Mill Creek	**35.983**	**121.492**	**14.69389**	**NA**	NA	**-0.30**	**1.82**	**1.52**

cutting the rock substrate with Dremel 8220, a rotary hand saw tool with diamond bit blades. A colony of *M. umbonata* was collected incidentally in December 2019 from an intertidal boulder field at Palmer's Point, Trinidad (California).

In preparation for SEM examination, specimens of *Microporella* were placed in a 20–50% household bleach solution to remove organic material, rinsed in tap water, and air-dried for 24 hours. Uncoated specimens were observed and imaged using a FEI Quanta-250 SEM operated at low-vacuum and environmental scanning mode at California State Polytechnic University, Humboldt in Arcata, California, USA. SEM images of *M. umbonata* were taken using a Hitachi TM4000plus Tabletop SEM at the Natural History Museum in Oslo, Norway.

Character measurements were taken from SEM images with the image-processing software ImageJ (https://imagej.nih.gov/).

Type and figured specimens are housed in the Chowdhury and Lee Collection at the Santa Barbara Natural History Museum (SBMNH) under the catalog numbers reported for each species. One specimen, *M. umbonata* NHMO H1940, resides in the zoological collection of the Natural History Museum in Oslo (NHMO), Norway.

Note that in the "Type material" and "Material examined" section of each species, we listed only those colonies / specimens that were studied using SEM and that were later deposited in the aforementioned museum collections. For a complete overview of the richness of species at each site, including also unregistered colonies / specimens examined only with a stereomicroscope, see Table 2 and Fig. 1B.

Table 2. Summary of sampling sites reporting the number of colonies collected for each species of *Microporella* Hincks, 1877. Sites in bold font lie within the marine realm known as the Montereyan Pacific Transition Region, whereas the remaining sites lie in the Mendocinian Region.

Site	***M. dentata*** Chowdhury & Di Martino sp. nov.	***M. pauciperforata*** Chowdhury & Di Martino sp. nov.	***M. rota*** Chowdhury & Di Martino sp. nov.	***M. californica*** (Busk, 1856)	***M. neocribroides*** Dick & Ross, 1988	***M. setiformis*** O'Donoghue & O'Donoghue, 1923	***M. umbonata*** (Hincks, 1883)	**N species**	**N colonies**
1. Point Saint George	–	–	2	18	11	–	–	3	31
2. False Klamath	–	–	–	–	15	–	–	1	15
3. Trinidad Head North	–	1	–	1	9	–	–	3	11
4. Trinidad Head South	–	–	–	1	–	–	–	1	1
5. Baker Beach	–	–	–	–	7	–	–	1	7
6. Black Sand Beach	–	–	–	–	2	20	–	2	22
7. Shelter Cove	–	–	15	4	–	–	–	2	19
8. Hardy Creek Scenic	–	–	3	–	–	–	–	1	3
9. MacKerricher	2	–	2	9	–	–	–	3	13
10. Greenwood	3	–	5	–	5	–	1	4	14
11. Stengel Beach	–	–	6	4	3	–	–	3	13
12. Marshall Gulch	–	–	1	1	10	–	–	3	12
13. Sonoma State Beach	–	–	3	1	21	–	–	3	25
14. Pillar Point	**1**	–	**13**	**16**	–	–	–	**3**	**30**
15. Mill Creek	–	–	**13**	**3**	**1**	–	–	**3**	**17**

For further comparison, the holotypes of *Microporella cribrosa* (SBMNH 668403, previously AHF 80) and *M. umboniformis* (SBMNH 671678, previously AHF 213) were studied and figured using a Zeiss EVO 10 LS SEM at SBMNH. Additional SBMNH non-type material identified by R.C. Osburn as *M. cribrosa* and *M. californica* was also studied and assigned to two new species (i.e., *M. rota* Chowdhury & Di Martino sp. nov. and *M. similis* Chowdhury & Di Martino sp. nov.). Images of putative *Microporella umbonata* from Departure Bay, Vancouver, Canada (NHMUK 1921.11.17.15; O'Donoghue Collection, Natural History Museum London, UK) were made available by Dr P.D. Taylor.

Two of us (I.A.C. and E.D.M.) were responsible for the systematic part of this paper and are to be considered the taxonomic authors for the new species described.

Institutional abbreviations

NHMO = Natural History Museum, Oslo, Norway
NHMUK = Natural History Museum, London, UK
SBMNH = Santa Barbara Museum of Natural History, California, USA

Abbreviations for morphological terms and measurements

AvL = avicularium length
AvW = avicularium width

D = diameter
OL = orifice length
OW = orifice width
OvL = ovicell length
OvW = ovicell width
ZL = autozooid length
ZW = autozooid width

Measurements are given in the text as size ranges and, in parentheses, means ± standard deviations and the number of measurements (N) taken.

Results

Taxonomy

Phylum Bryozoa Ehrenberg, 1831
Class Gymnolaemata Allman, 1856
Order Cheilostomatida Busk, 1852
Superfamily Schizoporelloidea Jullien, 1883
Family Microporellidae Hincks, 1879
Genus *Microporella* Hincks, 1877

Microporella dentata Chowdhury & Di Martino sp. nov.
urn:lsid:zoobank.org:act:B70AFEDB-8620-4902-B464-17A652381A30
Fig. 2, Table 2

Diagnosis

Encrusting *Microporella*; zooids with single or paired avicularia with channelled rostrum; frontal shield tubercular, pseudoporous with indistinct marginal areolae and well developed central umbo; orifice with two prominent condyles and serrated proximal margin; four oral spines; ascopore cribrate, placed in a triangular depression, close to orifice; ovicells umbonate, with conspicuous radiating ridges, imperforate except for marginal pores.

Etymology

Latin '*dentatus*', toothed, alluding to the denticles and prominent condyles present on the proximal margin of the orifice of this species.

Type material

Holotype

USA • 1 colony of 50 zooids, several ovicellate, on inner surface of red abalone shell; California, MacKerricher State Park, Fort Bragg; 39°29′25.764″ N, 123°48′8.748″ W; 2 Feb. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704789.

Paratypes

USA • 2 colonies of 40 zooids each, none ovicellate, on underside of small boulder; California, Greenwood; 39°7′45.0582″ N, 123°43′9.192″ W; 2 Feb. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704790a–704790b.

Description

Colony encrusting, multiserial, unilaminar, forming circular patches, found encrusting red abalone shells (*Haliotis rufescens* Swainson, 1822) or small boulders.

Autozooids rounded hexagonal to rectangular, ZL = 397–607 μm (494±54 μm, N = 20), ZW = 316–522 μm (380±57 μm, N = 20), mean ZL/ZW = 1.30 (Fig. 2A), boundaries marked by grooves between slightly raised vertical walls. Frontal shield convex centrally, tubercular, coarsely granular, marked by radial ridges with circular pseudopores in grooves between ridges, 23–40 circular pseudopores, D = 7–20 μm; up to 10 circular to elliptical, marginal areolae per side, indistinguishable from pseudopores due to similar size.

Primary orifice transversely D-shaped, OL = 68–102 μm (86±8 μm, N = 20), OW = 84–116 μm (102±8 μm, N = 20), mean OL/OW = 0.84, mean ZL/OL = 5.74; hinge-line straight, serrated, with

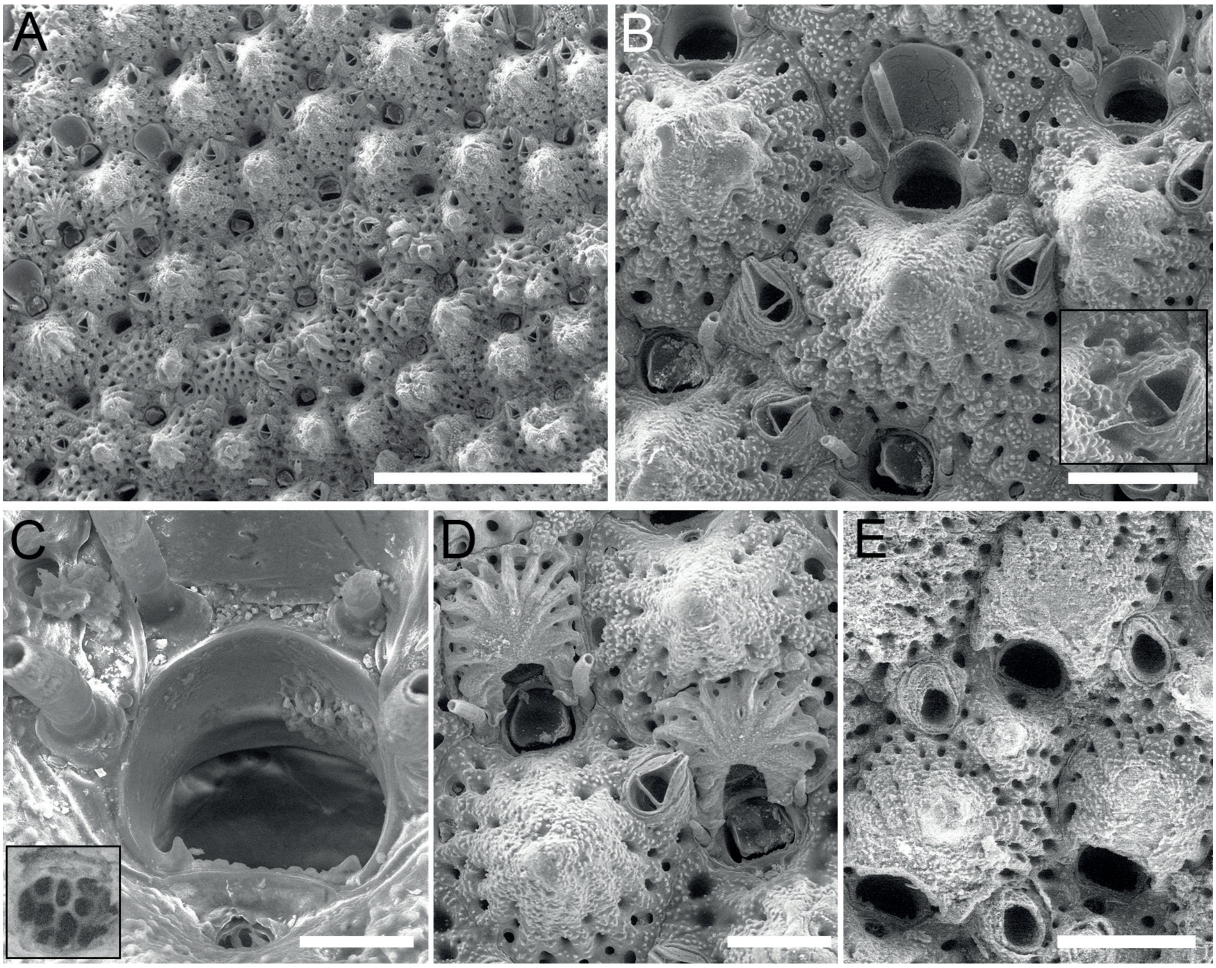

Fig. 2. *Microporella dentata* Chowdhury & Di Martino sp. nov., holotype (SBMNH 704789), MacKerricher State Park, California, USA. **A**. General view of colony. **B**. Group of autozooids, each with four oral spines and avicularia. The insert shows an avicularium with open mandible. **C**. Close-up of orifice with serrated hinge-line and ascopore. **D**. Ovicellate zooids with incomplete, developing ovicells. **E**. Paratype (SBMNH 704790a), Greenwood, California, USA. Ovicellate zooids with complete ovicells. Scale bars: A = 1 mm; B = 200 μm; C = 50 μm; D = 150 μm; E = 250 μm.

pair of sharply triangular condyles at corners (Fig. 2C). Four oral spines; proximalmost pair retained in ovicellate autozooids (Fig. 2B, D).

Ascopore in depressed triangular area outlined by distalmost ridges of frontal shield converging towards the centre (Fig. 2C) and forming the imperforate umbo proximal to ascopore (Fig. 2B); close to orifice, no more than 1–1.5 ascopore widths from proximal margin; ascopore opening 20–31 µm in diameter, cribrate, often obscured by proximal umbo (Fig. 2C, E).

Avicularium usually single, occasionally paired or absent, AvL = 58–112 µm (91±17 µm, N = 20), AvW = 35–55 µm (46±6 µm, N = 20), mean AvL/AvW = 1.98; located distolaterally on either side with rostrum tip at same level as ascopore or more proximally, proximolaterally to frontal umbo; crossbar complete; rostrum sharply triangular, narrowly channelled distally, with open, raised tip, directed distolaterally (Fig. 2B, D). Mandible triangular, slightly longer than rostrum (in Fig. 2B mandible length 90 µm, rostrum length 60 µm).

Ovicell prominent (Fig. 2D–E), rounded-quadrate, OvL = 172–201 µm (186±21 µm, N = 2), OvW = 200–222 µm (211±15 µm, N = 2), mean OvL/OvW = 0.88, overlying frontal shield of next distal zooid, obscuring distal margin of orifice of maternal zooid; imperforate centrally, with a row of pseudopores all around the periphery inside the margin and areolae placed most-laterally; with radial ridges soon after formation but eventually covered by granulated frontal calcification from surrounding zooids and sometimes central, rounded, smooth umbo similar to that on the frontal shield.

Ancestrula not observed.

Remarks

The main character distinguishing this new species from the other species of *Microporella* is the serrated proximal margin of the orifice, which also bears two prominent, triangular condyles. The combination of a serrated orifice with a cribrate ascopore has been observed in *Microporella elegans* Suwa & Mawatari, 1998 from Japan. That species, however, differs in having reticulate pseudopores and avicularia directed laterally (Suwa & Mawatari 1998). *Microporella germana* Dick & Ross, 1988 from Alaska is similar in the shape and position of the avicularium, in having a crenulated proximal oral margin, and in the number of spines; it differs in having an ascopore with lunate opening and smaller condyles (Dick & Ross 1988). Additional similar species with a cribrate ascopore include: *Microporella neocribroides* Dick & Ross, 1988 from Alaska, which differs in having an orifice with smooth proximal margin and less prominent condyles (Dick & Ross 1988); *M. sanmiguelensis* (Soule, Chaney & Morris, 2004) which differs in having all zooids with paired avicularia (Soule *et al.* 2004); *M. santabarbarensis* (Soule, Chaney & Morris, 2004), in which the ascopore is placed at the same level as the adjacent frontal shield rather than in a triangular depression (Soule *et al.* 2004); and *M. serrata* Mawatari & Suwa, 1998 from Japan, in which the ascopore opening is reniform, rather than circular or elliptical (Mawatari & Suwa 1998).

Distribution and ecology

Microporella dentata Chowdhury & Di Martino sp. nov. is known from MacKerricher State Park beach to Pillar Point in California, USA. The colony in Fig. 2 encrusted a red abalone shell (*H. rufescens*), while the remaining colonies encrusted rocks, all in an exposed intertidal boulder field.

Microporella pauciperforata Chowdhury & Di Martino sp. nov.
urn:lsid:zoobank.org:act:B17B841F-E7A3-4548-AFA7-A2B04E5A8674
Fig. 3, Table 2

Diagnosis

Encrusting *Microporella*; zooids with single, small, distally directed adventitious avicularium, proximolateral to orifice, or lacking avicularium; some zooids with avicularium in proximolateral corner of zooid; primary orifice with smooth proximal margin and rounded corners lacking condyles; 2–4 ephemeral oral spines; frontal shield with relatively few pseudopores and distinct, elliptical marginal areolae; ascopore cribrate, close to the proximal margin of the orifice; ovicells rounded-quadrate, imperforate except for marginal pores.

Etymology

Latin '*paucus*', few, plus '*perforatus*', pierced, alluding to the limited number of pseudopores in the frontal shield of this species.

Type material

Holotype

USA • colony of 40 zooids, one ovicellate, on rock; California, Trinidad Head North; 41°3′25.1928″ N, 124°9′4.1826″ W; 7 Feb. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704788.

Description

Colony encrusting, multiserial, unilaminar, forming a subcircular patch; pore chamber windows not observed.

Autozooids (Fig. 3A–B) generally elongate and hexagonal but sometimes irregularly shaped, delineated by narrow grooves and suture lines; ZL = 361–752 µm (523±99 µm, N = 22), ZW = 223–446 µm (323±59 µm, N = 22) µm, mean ZL/ZW = 1.62. Frontal shield (Fig. 3B–C) flat to slightly convex centrally, coarsely granular, with 13–36 circular pseudopores (D = 8–15 µm) sparsely scattered proximal to ascopore; 5–8 circular to elliptical, marginal areolae per side, clearly distinguishable from pseudopores because much larger (D = 20–55 µm).

Primary orifice transversely D-shaped, wider than long; OL = 64–109 µm (86±12 µm, N = 22), OW = 106–149 µm (120±10 µm, N = 22), mean OL/OW = 0.72, mean ZL/OL = 6.08; hinge-line straight, smooth, lacking denticles; proximolateral corners rounded without condyles. Two to four articulated spines visible in some zooids, often hidden by secondary calcification spreading from the distal zooid (Fig. 3F).

Ascopore depressed relative to adjacent frontal shield, transversely elliptical to subcircular, D = 22–35 µm, close to orifice, roughly no more than 0.5–1.5 ascopore widths from proximal margin; ascopore in some zooids outlined by a rim of gymnocystal calcification that also encircles orifice; ascopore opening cribrate (Fig. 3D).

Avicularium usually single but often absent, located laterally on either side, in some zooids at zooidal mid-length, in some others at orifice level (Fig. 3E); AvL = 40–78 µm (52±11 µm, N = 11), AvW = 27–57 µm (40±8 µm, N = 11) µm, mean AvL/AvW = 1.3; crossbar complete; triangular rostrum, usually directed distally but sometimes laterally, slightly depressed relative to adjacent frontal shield; in some zooids, slightly larger avicularium was observed in one of the proximolateral corners, directed proximally or proximolaterally inwards (Fig. 3B). Mandible not observed.

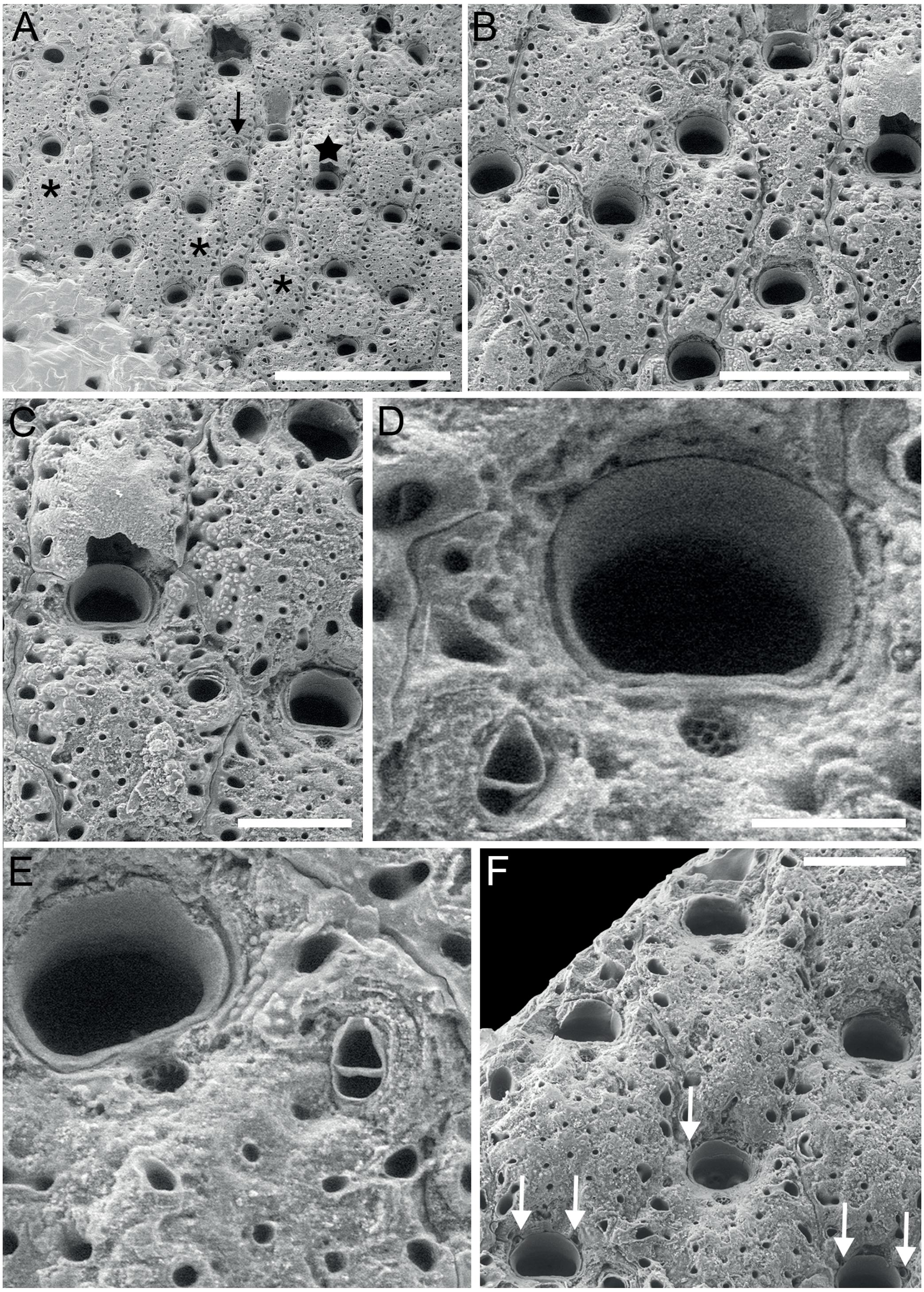

Fig. 3. *Microporella pauciperforata* Chowdhury & Di Martino sp. nov., holotype (SBMNH 704788), Trinidad Head North, California, USA. **A**. General view of the colony showing majority of zooids lacking avicularia (some marked with asterisks), zooid with proximolateral avicularium (arrow), and an ovicellate zooid (star). **B**. Group of autozooids with abraded frontal shields either lacking avicularia, or with small, lateral avicularium distally directed or placed in the proximolateral corner and directed proximally. **C**. Close-up of the ovicellate zooid showing a preserved reticulate ascopore. **D**. Close-up of reticulate ascopore. **E**. Close-up of an avicularium. **F**. Close-up of zooids with evident spine bases (white arrows). Scale bars: A = 1 mm; B = 500 µm; C, F = 200 µm; D = 60 µm; E = 100 µm.

Ovicell prominent, globose, roughly as long as wide, with a rounded-quadrate appearance because narrower than frontal shield of underlying zooid, OvL = 272 µm, OvW = 282 µm (N = 1), OvL/OvW = 0.96; continuous with frontal shield of the distal zooid, obscuring distal margin of orifice (Fig. 3C); calcification finely granular, smoother than the frontal shield, imperforate except for peripheral row of elliptical marginal areolae (12–36 µm, N = 10); peripheral interareolar ridges around margin.

Ancestrula not observed.

Remarks

The main features distinguishing *M. pauciperforata* Chowdhury & Di Martino sp. nov. from other congeners of the NE Pacific are the small, distally directed adventitious avicularia, the relatively flat frontal shield, and subordinately the rounded-quadrate ovicell, although we observed only one. In NW Pacific species of *Microporella* with a cribrate ascopore, the avicularium is usually larger [e.g., AvL 92–137 µm (112±14 µm, N = 20), AvW 39–65 µm (57±7 µm, N = 20) in an unregistered specimen of *Microporella cribrosa* from Korea measured from SEM image pdt4289 made available by Dr P.D. Taylor; AvL 71–91 µm (83±8 µm, N = 5), AvW 35–44 µm (40±4 µm, N = 5) in *M. neocribroides* measured from Dick *et al.* 2005: fig. 19] and directed distolaterally, while the ovicells are globular (e.g., *M. neocribroides* Dick & Ross, 1988) and pseudoporous (e.g., *M. cribrosa* Osburn, 1952) (Osburn 1952; Dick & Ross 1988). In addition to the cribrate ascopore, *M. pauciperforata* resembles both *M. cribrosa* and *M. neocribroides* in having the ascopore close to the proximal margin of the orifice and the latter species in the limited number of pseudopores on the frontal shield. However, *M. pauciperforata* also has very distinct elliptical marginal areolae all along the lateral margins that are lacking in *M. neocribroides*.

The presence of avicularia located proximolaterally is an unusual feature for *Microporella*; this might be induced by the presence of predators and the necessity to repair some boreholes as seen in colonies of *M. hyadesi* (Jullien, 1888) (see Di Martino *et al.* 2020: fig. 6c).

The signs of abrasion on the frontal shield seen in some zooids (Fig. 3B–C) might be due to the high wave action typical of the intertidal environment in which the colony was found. Similar signs of abrasion and/or dissolution were observed in fossil species of *Microporella* from the Florida Tamiami Formation (Di Martino *et al.* 2019). In that case, the cause was unknown.

Distribution and ecology

Microporella pauciperforata Chowdhury & Di Martino sp. nov. is only known from a single specimen from Trinidad Head North in California, USA. The single colony was found encrusting a boulder in a highly exposed intertidal boulder field.

Microporella rota Chowdhury & Di Martino sp. nov.
urn:lsid:zoobank.org:act:15D7C5BF-B963-4A75-96F7-64413ED6A0EE
Fig. 4, Table 2

Diagnosis

Encrusting *Microporella* with interzooidal communications through multiporous septula; zooids with single, large, distolaterally directed adventitious avicularium, with crossbar at same level as ascopore, or lacking avicularium; primary orifice with smooth proximal margin lacking condyles; 2–5 oral spines, obscured in ovicellate zooids; frontal shield tubercular, granular, with reticulate, wheel-like pseudopores and distinct, elliptical marginal areolae; ascopore cribrate without distal projection, lunate in periancestrular zooids, close to orifice, with umbo developing proximally; ovicells globular, granular,

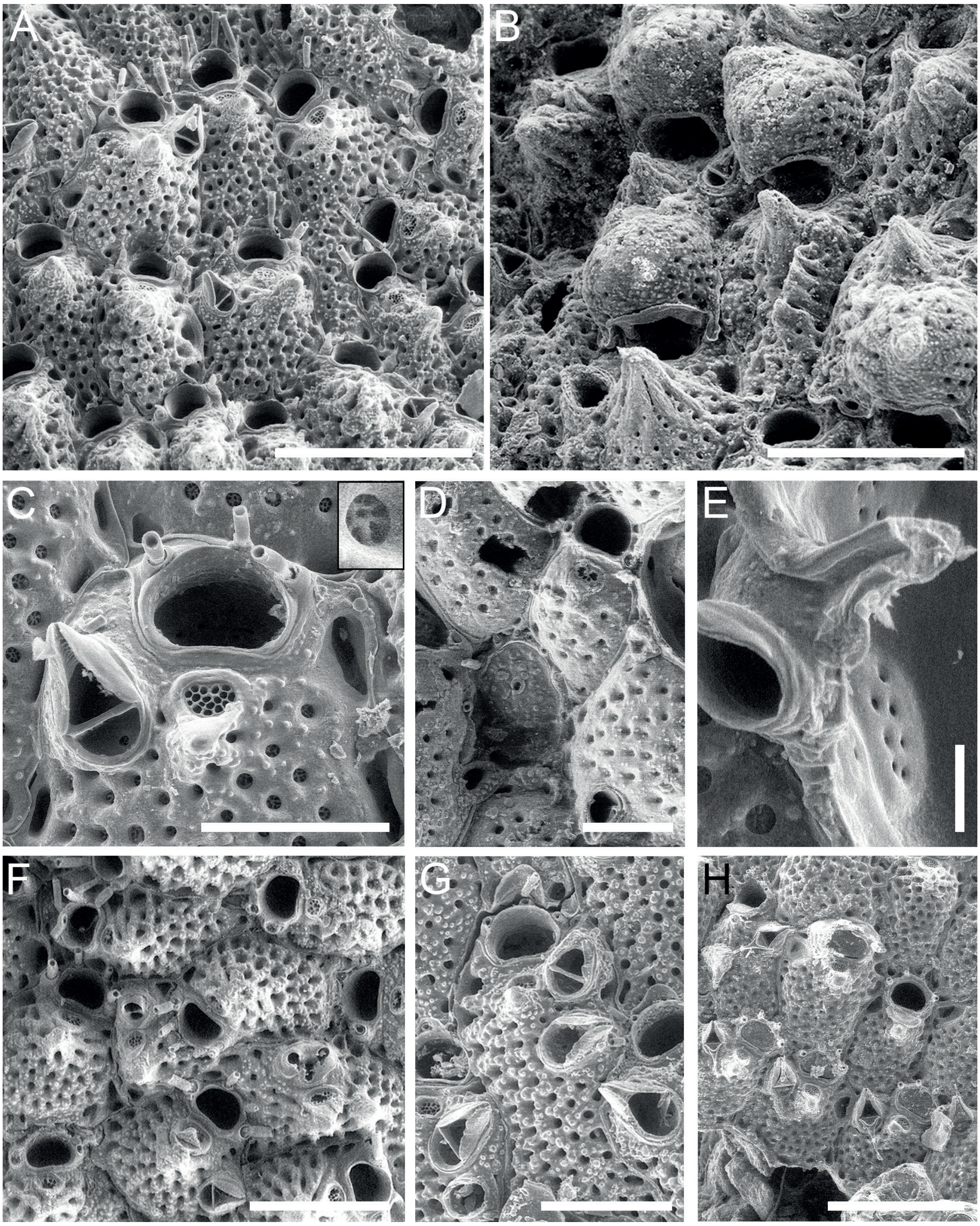

Fig. 4. *Microporella rota* Chowdhury & Di Martino sp. nov., all California, USA. **A, D, F**. Paratype (SBMNH 704769), Pillar Point. **B–C**. Holotype (SBMNH 704766), Shelter Cove. **E, G**. Paratype (SBMNH 704767), Mill Creek. **H**. Paratype (SBMNH 706126), Marshall Gulch. **A**. Group of autozooids with umbonate frontal shield. **B**. Group of ovicellate zooids. **C**. Close-up of the ascopore, reticulate pseudopores (see also insert), and orifice. **D**. Partially overgrown tatiform ancestrula and first budded autozooid lacking an avicularium. **E**. Close-up of multiporous septula. **F**. Aberrant zooids, lacking an orifice but with avicularium and ascopore (seemingly triple in the aberrant zooid at the bottom), formed at the edge of encounter between two colonies. **G**. Autozooid with two avicularia on the same side. **H**. Autozooids having avicularia with preserved mandibles. Scale bars: A–B, F, H = 500 µm; C = 200 µm; D = 150 µm; E = 50 µm; G = 250 µm.

radially ribbed, with pseudopores in radial rows between ribs extending from ovicell periphery but not reaching centre.

Etymology

Latin '*rota*', wheel, alluding to the wheel-like pattern of the pseudopores in the frontal shield of this species. Used as a name in apposition.

Type material

Holotype

USA • colony of 70 zooids, 45 ovicellate, on rock; California, Shelter Cove; 40°1′17.6952″ N, 124°4′4.8684″ W; 17 Oct. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704766.

Paratypes

USA• 1 colony of 40 zooids, none ovicellate, on rock; California, Mill Creek; 35°58′59.0586″ N, 121°29′32.0598″ W; 22 Jul. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704767a • 1 colony of 50 zooids, none ovicellate, on rock; California, Mill Creek; 35°58′59.0586″ N, 121°29′32.0598″ W; 22 Jul. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704767b • 1 colony of 60 zooids, none ovicellate, on rock; California, Mill Creek; 37°29′42.306″ N, 122°29′45.6354″ W; 24 Jul. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704769 • 1 colony of 30 zooids, none ovicellate, on rock; California, Marshall Gulch; 38°22′8.4″ N, 123°4′32.52″ W; 17 Mar. 2020; A. Chowdhury and H. Lee leg.; SBMNH 706126.

Additional material

USA• California, Monterey County, Carmel; 36°31′59. 998169″ N, 121°56′59.989014″ W; unknown leg.; SBMNH 666548 • California, Monterey County, Carmel; 36°31′59. 998169″ N, 121°56′59.989014″ W; 16 Nov. 1948; R.J Menzies leg.; SBMNH 693359.

Description

Colony encrusting, multiserial, unilaminar, forming circular patches, typically found encrusting on rocks of various sizes; elliptical pore chamber windows observed along lateral and distal walls; interzooidal communications through multiporous septula (Fig. 4E).

Autozooids hexagonal, ZL = 345–543 µm (450±55 µm, N = 15), ZW = 241–463 µm (354±76 µm, N = 15), mean L/W = 1.27, boundaries marked by grooves and slightly raised vertical walls. Frontal shield convex centrally, tubercular, finely to coarsely granular, with narrowly elliptical marginal areolae (70–110 µm long) at zooidal corners usually distinguishable from much smaller, circular pseudopores; pseudopores reticulate, with wheel-like pattern (Fig. 4C, see insert for a close-up, E), rarely elliptical, D = 10–30 µm, numbering 21–53, evenly distributed on frontal shield proximal to ascopore (Fig. 4A).

Primary orifice transversely D-shaped (Fig. 4C); OL = 64–106 µm (88±14 µm, N = 15), OW = 116–170 µm (138±14 µm, N = 15), mean OL/OW = 0.64, mean ZL/OL = 5.11; hinge-line straight or slightly concave, smooth, lacking condyles. Two to five articulated oral spines, more commonly three or four, visible in non-ovicellate zooids (Fig. 4A, C, F), but obscured in those with ovicells (Fig. 4B).

Ascopore moderately depressed relative to adjacent frontal shield, transversely elliptical to subcircular, D = 27–79 µm, less than one to roughly one ascopore width from orifice; in some zooids, ascopore outlined by band of gymnocystal calcification; ascopore opening cribrate (Fig. 4C) without any distal projection except in periancestrular zooids in which ascopore is C-shaped (Fig. 4D); pores of ascopore plate circular. In some zooids, low, knobby, rounded or pointed umbo develops proximally to ascopore and becomes robust, rounded, and sometimes ribbed with age and increasing calcification (Fig. 4A–B).

Avicularium usually single (Fig. 4A, C) or absent (Fig. 4H); relatively large, AvL = 85–141 µm (112±17 µm, N = 20), AvW = 45–89 µm (62±12 µm, N = 20), mean AvL/AvW = 1.81; located laterally in zooidal distal half, on either side, with complete crossbar usually at same level as ascopore; rostrum acutely triangular, narrowly channelled distally, mostly directed distolaterally, sometimes laterally or distally, often distally raised. Mandible with setose end (Fig. 4H).

Ovicell globular, prominent (Fig. 4B), OvL = 201–309 µm (256±32 µm, N = 13), OvW = 61–365 µm (313±29 µm, N = 13), mean OvL/OvW = 0.82; overlying frontal shield of next distal zooid, secondary covering confluent with that of shield, obscuring distal part of maternal orifice; calcification finely granular, radially ribbed, with 8–15 circular pseudopores, D = 7–21 µm, arranged in radial rows between ribs extending from ovicell periphery but not reaching centre, which appears imperforate.

Ancestrula tatiform, elliptical, 271 µm long by 180 µm wide (Fig. 4D); opesia surrounded by at least eight spines; first zooid budded distally from ancestrula, similar in appearance to later autozooids but smaller, with most-proximal oral spines at same level as proximal margin of orifice, lacking avicularium, with C-shaped rather than cribrate ascopore (Fig. 4D).

Remarks

Microporella rota Chowdhury & Di Martino sp. nov. is superficially similar to *M. cribrosa* (Fig. 5). Both species share radially ribbed ovicells with pseudopores arranged in radial rows between ribs, extending from ovicell periphery but leaving the centre imperforate. Additionally, they both display a variably developed umbo proximal to the ascopore. Despite these similarities, *M. rota* differs in a sufficiently large number of characters to justify the recognition as a separate species.

In contrast to the holotype of *M. cribrosa* (Fig. 5), colonies of *M. rota* Chowdhury & Di Martino sp. nov. differ in the number of oral spines, ranging from two to five within the same colony (Fig. 4A, F). In the holotype of *M.* cribrosa, spines vary from five to seven and are more robust (Fig. 5B, F) than those in *M. rota*. The proximalmost pair of spines is obscured in ovicellate zooids of *M. rota* (Fig. 4B) but consistently retained in those of *M. cribrosa* (Fig. 5A–B). Ovicellate zooids of *M. cribrosa* also show the development of two wings of calcification proximolateral to the orifice below the proximalmost pair of spines (Fig. 5D), feature absent in *M. rota*.

Further differences lie in the number of avicularia, the morphology of pseudopores, and the ascopore. Paired avicularia are consistently seen in *M. cribrosa* (Fig. 5A), while a single avicularium is typical of *M. rota* Chowdhury & Di Martino sp. nov. In some instances, *M. rota* lacked avicularia, and the corresponding zooids were smaller than those bearing avicularia. Pseudopores exhibit a reticulate, wheel-like pattern in *M. rota* (Fig. 4C), while they are non-reticulate in *M. cribrosa* (Fig. 5C). Moreover, the ascopore in *M. rota* (Fig. 4C) lacks the robust, distal projection observed in the ascopores of *M. cribrosa* (Fig. 5D–E).

Upon SEM examination, two specimens (SBMNH 666548 and SBMNH 693359) identified as *M. cribrosa* by R.C. Osburn were reconfirmed as the new species *M. rota* Chowdhury & Di Martino sp. nov. Two more specimens (SBMNH 668407 and SBMNH 668408) appeared conspecific with *M. cribrosa* sensu Soule *et al.* (1995). Despite some similarities with both *M. rota* and *M. cribrosa*, these specimens have distinct characters that warrant the description of a new species (see below *M. similis* Chowdhury & Di Martino sp. nov.).

The presence of a variably developed umbo proximal to the ascopore, becoming robust and pointed with age, has been observed in other species of *Microporella* including some of the species described here. The development of the umbo has been interpreted either as a protection for the ascopore from

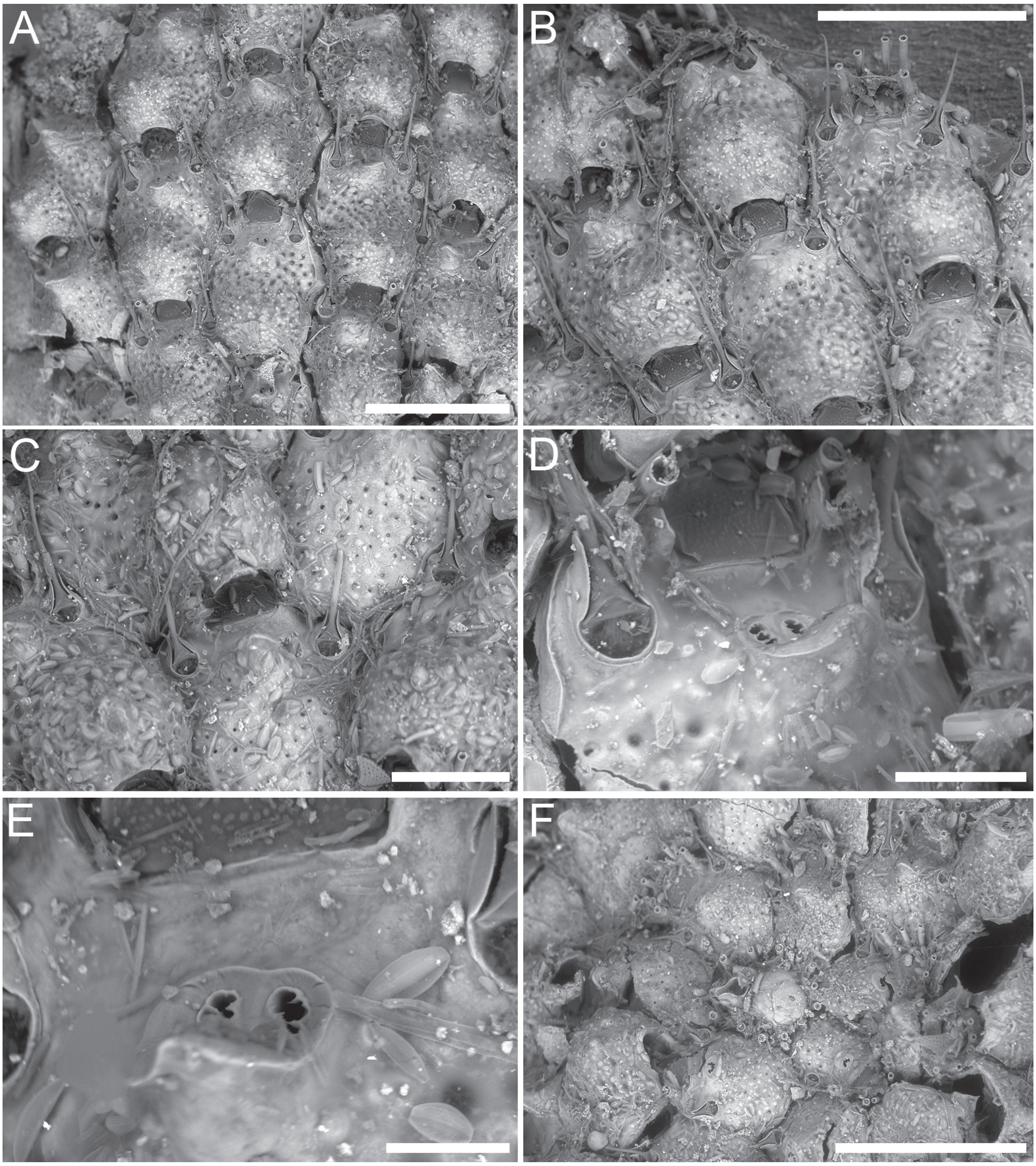

Fig. 5. *Microporella cribrosa* Osburn, 1952, holotype (SBMNH 668403) (previously AHF 80), Corona del Mar (36°31′59.998169″ N, 121°56′59.989014″ W), Newport Harbor, Orange County, California, USA. **A**. Group of ovicellate zooids with two oral spines visible and paired avicularia with setiform mandibles. **B**. Group of zooids, most ovicellate, with umbones hiding the ascopore; one zooid showing five robust oral spines. **C**. Close-up of frontal shield and ovicells showing the simple (i.e., non-reticulate) pseudopores. **D–E**. Close-ups of ascopore showing well-developed distal projections and radial denticulations converging towards the centre giving to the lunate aperture a reticulate appearance. **F**. Tatiform ancestrula, seemingly regenerated as a kenozooid with adventitious avicularium, and early astogeny with zooids showing up to 7 oral spines. Scale bars: A–B, F = 500 µm; C = 200 µm; D = 100 µm; E = 50 µm.

obliteration by secondary calcification or as an environmental effect to protect the colony from sediment deposition and consequent abrasion (Soule *et al.* 1995; Di Martino & Rosso 2021).

Aberrant features were evident in some zooids, such as the presence of two avicularia budded on the same side of the zooid (Fig. 4G). This condition is previously known in *Microporella* but quite uncommon. Taylor & Mawatari (2005: fig. 4G) documented an instance in *Microporella* sp. that appeared to have resulted from damage and regeneration; Dick *et al.* (2005: fig. 21E–F) documented several zooids with two avicularia on the same side in a single unidentified colony, with no signs of damage and regeneration, as was the case for our specimen.

Another aberrant feature was zooids lacking an opening but bearing an avicularium and one or more malformed ascopores at the edge of encounter between two colonies (Fig. 4F).

Distribution and ecology

We detected *Microporella rota* Chowdhury & Di Martino sp. nov. at ten sites, spanning from Cape Flattery to Monterey Bay. Colonies were found encrusting on boulders and shells (e.g., red abalone, clam, and mussel). Furthermore, upon examining some museum specimens previously identified as *M. cribrosa* by Osburn (specifically, specimens SBMNH 666548 and SBMNH 693359), the presence of this species was confirmed at an additional site in Carmel Bay.

Microporella similis Chowdhury & Di Martino sp. nov.

urn:lsid:zoobank.org:act:FD102F85-A00A-44F7-BD69-744CF802D773

Fig. 6, Table 2

Microporella cribrosa – Soule *et al.* 1995: 144, pl. 50 figs a–c.

Diagnosis

Encrusting *Microporella* with interzooidal communications through multiporous septula; zooids with paired, rarely single, distolaterally directed adventitious avicularia, with crossbar at same level as ascopore; primary orifice with smooth, straight proximal margin, and small condyles at corners; 5–7 robust oral spines, two or none retained in ovicellate zooids; frontal shield tubercular, smooth, with reticulate pseudopores and distinct, elliptical marginal areolae; ascopore delicately cribrate with thin distal projection and eight-shaped/trifoliate pores, close to orifice, with proximal, smooth umbo, becoming squared and curved inwards; ovicells prominent, large, with numerous, well defined radial ribs, few pseudopores in grooves between ribs, and central to proximal smooth, imperforate, umbonate area.

Etymology

Latin '*similis*', similar, alluding to the resemblance of this species to both *Microporella cribrosa* and *M. rota* Chowdhury & Di Martino sp. nov.

Type material

Holotype

USA• colony of ca 100 zooids, several ovicellate, detached from the substrate; California, Los Angeles County, Velero 1232–41, 5 miles from San Pedro Breakwater; depth 35 m; 33°38′15″ N, 118°12′15.00012″ W; 15 Feb. 1941; T.B. Scanland leg.; SBMNH 704271.

Paratypes

USA• 1 colony of 30 zooids, several ovicellate, detached from the substrate; California, Orange County, Laguna Beach; 33°32′31.2″ N, 117°47′16.8″ W; Allan Hancock Foundation leg.; SBMNH 702583 • 1 colony of 40 zooids, none ovicellate, on echinoid spine; California, Los Angeles County, Channel Islands, Santa Catalina Island; 33°27′00″ N, 118°25′0.00012″ W; 27 Aug. 1972; Allan Hancock Foundation leg.; SBMNH 703675 (slide 2).

MEXICO • 1 colony of 70 zooids, several ovicellate, detached from the substrate; Mexico, Bahia California (Norte), Bahia Todos Santos; 31°47′59.997254″ N, 116°41′59.989014″ W; depth 25–30 m; 2 Jul. 1938; J.Q. Burch leg.; SBMNH 668408.

Additional material

USA• 1 colony of 40 zooids, several ovicellate, detached from the substrate; California, Marin County, Dillon Beach; 38°15′00″ N, 122°56′59.989014″ W; R.J. Menzies leg.; SBMNH 668407 • 1 colony of ca 100 zooids, several ovicellate, detached from the substrate; California, Monterey County, Lighthouse Point; 36°37′59.97864″ N, 121°56′22.92″ W; intertidal; Nov. 1940; Allan Hancock Foundation leg.; SBMNH 673403 • 1 colony of 60 zooids, several ovicellate, detached from the substrate; California, Ventura County, Channel Island, San Nicolas Island; 33°14′57.99984″ N, 119°29′57.99984″ W; 26 Aug. 1976; Allan Hancock Foundation leg.; SBMNH 695087.

Description

Colony encrusting, multiserial, unilaminar; interzooidal communications through multiporous septula (Fig. 6F).

Autozooids hexagonal, ZL = 398–563 µm (475±37 µm, N = 20), ZW = 259–467 µm (378±51 µm, N = 20), mean L/W = 1.26, boundaries marked by deep grooves (Fig. 6A). Frontal shield flat to slightly convex, tubercular, smooth, with elliptical marginal areolae (30–60 µm long) at zooidal lateral corners usually distinguishable from much smaller, circular pseudopores; pseudopores reticulate (Fig. 6L), D = 10–25 µm, numbering 20–30, evenly distributed on the frontal shield proximal to ascopore.

Primary orifice transversely D-shaped; OL = 75–97 µm (83±7 µm, N = 9), OW = 114–160 µm (138±14 µm, N = 15), mean OL/OW = 0.60, mean ZL/OL = 5.70; hinge-line straight, smooth, with small triangular condyles at corners (Fig. 6D). Five to seven robust, long (190–260 µm), articulated, oral spines visible in non-ovicellate zooids (Fig. 6A, C, E, G); two spines or none visible in ovicellate zooids (Fig. 6A, I–J); proximalmost pair of spines thicker, placed almost at level with the proximal margin of orifice (Fig. 6B, D); spines indenting proximal margin of distal zooid and becoming embedded until completely obliterated by frontal shield calcification (Fig. 6D, J).

Ascopore (Fig. 6B, K) moderately depressed or at level with adjacent frontal shield, transversely elliptical, D = 27–81 µm, less than one ascopore width from orifice; ascopore opening delicately cribrate with thin distal projection expanding proximally; pores of ascopore plate eight-shaped or trifoliate; smooth, low, knobby, rounded umbo developing proximally to ascopore, sometimes becoming quadrangular and curved inwards (Fig. 6I), hiding ascopore. In some zooids multiple umbones forming on frontal shield with age (Fig. 6E).

Avicularia more often paired (Fig. 6A, D, H), sometimes single (Fig. 6D–E); in two zooids third avicularium was observed at zooidal mid-length, budded from one of lateral areolae (Fig. 6J, see arrow); relatively large, AvL = 77–115 µm (95±17 µm, N = 20), AvW = 56–80 µm (69±6 µm, N = 20), mean AvL/AvW = 1.38; located laterally in zooidal distal half, on either side, with thin complete crossbar usually at same level as ascopore; rostrum acutely triangular, narrowly channelled distally, directed

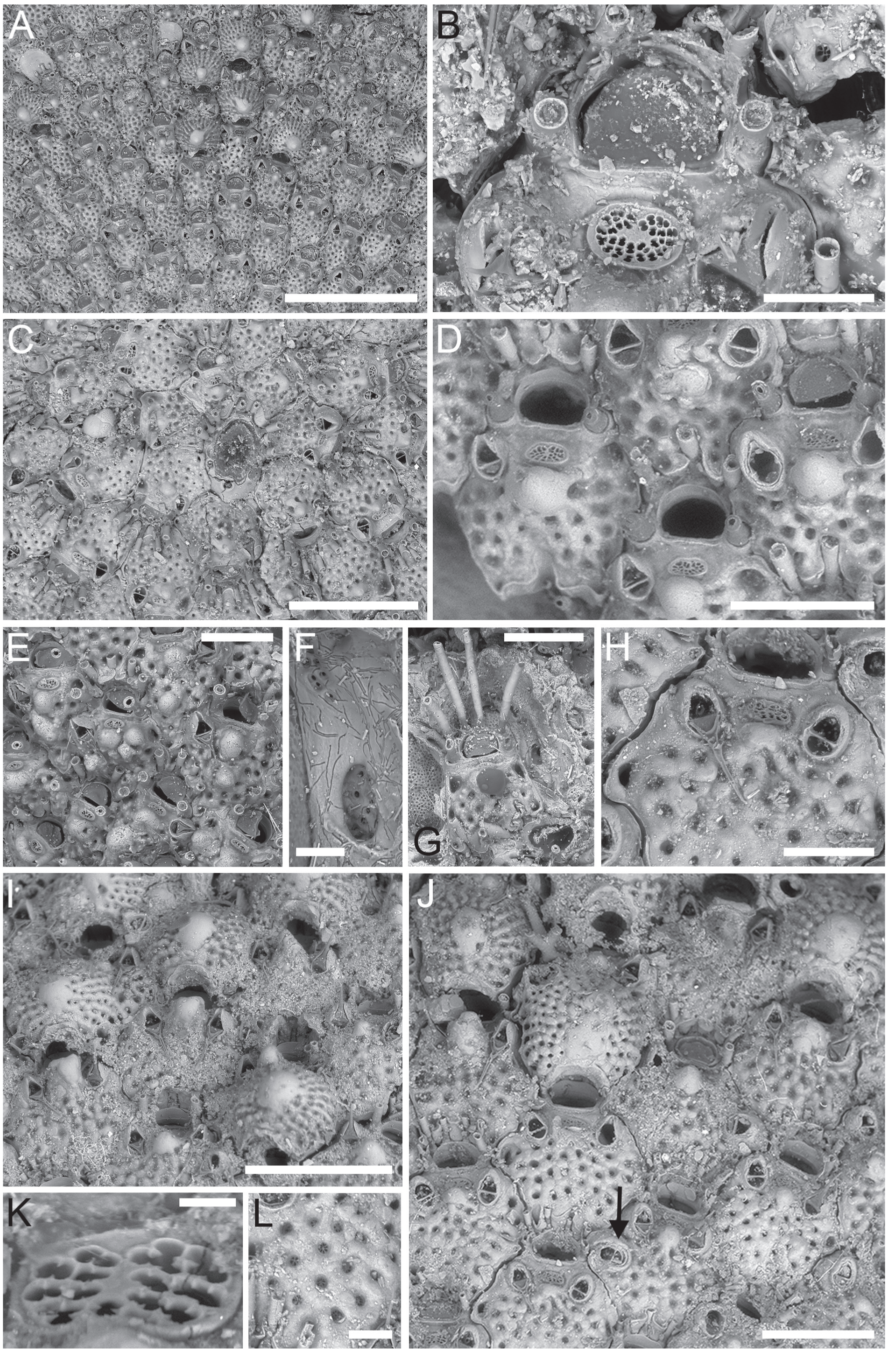

Fig. 6. *Microporella similis* Chowdhury & Di Martino sp. nov. **A–C**. Holotype (SBMNH 704271), Velero 1232–41, 5 miles from San Pedro Breakwater, California, USA. **D**. Paratype (SBMNH 702583), Laguna Beach, California, USA. **E–G**. Paratype (SBMNH 703675), Santa Catalina Island, California, USA. **H–L**. Paratype (SBMNH 668408), Bahia Todos Santos, Mexico. **A**. Group of autozooids, some ovicellate. **B**. Close-up of ascopore. **C**. Ancestrula and periancestrular zooids. **D**. Close-up of autozooids showing the orifice. **E**. Autozooids with multiple umbones on the frontal shield. **F**. Close-up of multiporous septula. **G**. Close-up of a young autozooid at colony growing edge showing the length of oral spines. **H**. Close-up of an open mandible. **I**. Ovicellate zooids with quadrangular umbo. **J**. Group of zooids, one showing a third avicularium (see arrow). **K**. Close-up of ascopore. **L**. Close-up of reticulate pseudopores. Scale bars: A = 1 mm; B = 100 µm; C, I = 500 µm; D = 250 µm; E, G = 200 µm; F = 50 µm; H = 120 µm; J = 300 µm; K–L = 20 µm.

distolaterally, distally raised. Mandible long (120–150 µm), with setose end, and pair of basal hooks (Fig. 6H).

Ovicell globular, prominent (Fig. 6A, I–J), large, OvL = 286–335 µm (306±18 µm, N = 6), OvW = 338–430 µm (384±37 µm, N = 6), mean OvL/OvW = 0.80; occupying frontal shield of next distal zooid up to the proximal margin of avicularia; calcification smooth, radially ribbed, with about 20 well defined ribs, and five circular pseudopores, D = 5–20 µm, arranged in radial rows between ribs, extending from ovicell periphery but not reaching centre, which is occupied by more or less raised, smooth and imperforate umbo; in some ovicells umbo more proximally placed (Fig. 6J).

Ancestrula tatiform (Fig. 6C), elliptical, 370 µm long by 260 µm wide, with 10 circumopesial spines, arranged seven distolaterally closely spaced and three proximally widely spaced, indenting opesia outline which appears undulate, opesia 260 µm long by 185 µm wide, surrounded by seven zooids; first two zooids budded distolaterally, lacking avicularia.

Remarks

Microporella similis Chowdhury & Di Martino sp. nov. is similar to both *M. cribrosa* (Fig. 5) and *M. rota* Chowdhury & Di Martino sp. nov. (Fig. 4). Like *M. cribrosa*, it has robust spines ranging from five to seven and typically has paired avicularia; like *M. rota*, it has reticulate pseudopores. Nonetheless, there are notable distinguishing traits. Despite having a cribrate ascopore as the two aforementioned species, the one in *M. similis* differs from that of *M. rota* in having a distal projection expanding mid-proximally and a different shape of the cribrate plate pores, wich are mostly eight-shaped as well as trifoliate in *M. similis* but simply rounded in *M. rota*. In comparison to *M. cribrosa*, *M. similis* has a more delicate distal projection. Additionally, the frontal shield and ovicell surface of *M. similis* are tubercular and smooth, while in the other two species they are tubercular but also finely to coarsely granular. Ovicells of *M. similis* are larger, displaying a higher number of better defined ribs, while a lower number of pores are present in the grooves between ribs. In ovicellate zooids, the proximalmost pair of spines may either be retained, as observed in *M. cribrosa*, or obliterated, as seen in *M. rota*. The presence of a distinct, quadrangular umbo is another characteristic that sets this species apart.

Soule *et al.* (1995) reassigned to *M. cribrosa* specimens previously identified as *M. californica* by Robertson (1908). However, upon reviewing the description and illustration provided by Robertson (1908: 281, pl. 18 figs 32–34), particularly noting the depiction of the cribrate ascopore with delicate distal projection, it is likely that those specimens actually belong to *M. similis* Chowdhury & Di Martino sp. nov.

Following the SEM examination of the holotype of *Microporella cribrosa*, it becomes evident that it represents a complex of species. This evidence prompts the need for a comprehensive re-evaluation of prior records attributed to *M. cribrosa*, which may lead to the identification of additional colonies belonging to both *M. rota* Chowdhury & Di Martino sp. nov. and *M. similis* Chowdhury & Di Martino sp. nov., as well as potentially revealing the existence of more previously unidentified species. This might imply a more restricted distribution for *M. cribrosa*, suggesting also that it may not be among the commonest species of *Microporella* in California as previously thought, a notion supported by our sampling where we did not encounter any specimens of this particular species.

Distribution and ecology

To date, *Microporella similis* Chowdhury & Di Martino sp. nov. was recorded at three Pacific sites, two in California (USA) waters (i.e., Dillon Beach and San Pedro Bay) down to 126 m depth (Soule *et al.* 1995), and one in Mexican waters (i.e., Bahia Todos Santos) at 25–30 m depth. Studied specimens are usually detached from the substrate except in one instance in which the colony was encrusting an echinoid spine.

Microporella californica (Busk, 1856)
Fig. 7, Table 2

Lepralia californica Busk, 1856: 310, pl. 11 figs 6–7.

Microporella californica – Osburn 1952: 381, pl. 44 fig. 2. — Dick & Ross 1988: 73, pl. 9 fig. c. — Soule *et al.* 1995: 139, pl. 48 figs a–c.

Material examined

USA • 1 colony of 40 zooids, 10 ovicellate, on rock; California, Pillar Point; 37°29′42.306″ N, 122°29′45.6354″ W; 24 Jul. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704770 • 1 colony of 56 zooids, 13 ovicellate, on rock; California, Point Saint George; 41°47′7.588″ N, 124°15′18.8568″ W; 8 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704773a • 1 colony of 60 zooids, none ovicellate, on rock; California, Point Saint George; 41°47′7.588″ N, 124°15′18.8568″ W; 8 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704773b • 1 colony of 30 zooids, none ovicellate, on rock; California, Point Saint George; 41°47′7.588″ N, 124°15′18.8568″ W; 8 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704773c • 1 colony of 20 zooids, none ovicellate, on rock; California, Point Saint George; 41°47′7.588″ N, 124°15′18.8568″ W; 8 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704773d • 1 colony of 80 zooids, 40 ovicellate, on rock; California, Trinidad Head South; 41°3′22.960″ N, 124°8′47.562″ W; 3 Apr. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704774.

Description

Colony encrusting, multiserial, unilaminar, forming subcircular patches, typically encrusting rocks of variable size (Fig. 7A); three distal pore chamber windows visible at colony margin (Fig. 7G).

Autozooids hexagonal, rectangular, or irregularly polygonal, ZL = 415–789 µm (611±88 µm, N = 20), ZW = 258–539 µm (414±69 µm, N = 20), mean L/W = 1.48, boundaries marked by grooves (Fig. 7B–C). Frontal shield convex centrally, nodular, finely granular, sometimes with blunt umbo proximal to ascopore; with numerous (26–47), circular pseudopores, D = 6–12 µm; marginal areolae only slightly larger than pseudopores.

Primary orifice transversely D-shaped, OL = 91–130 µm (110±12 µm, N = 20), OW = 118–167 µm (144±14 µm, N = 20), mean OL/OW = 0.76, mean ZL/OL = 5.55; hinge-line straight, smooth, with minute trapezoidal to rectangular condyles close to lateral corners (Fig. 7E–F). Four, occasionally five, distal oral spines (Fig. 7D, G), becoming obscured by secondary calcification later in ontogeny, or by ovicell; spine base dark brown.

Ascopore depressed relative to adjacent frontal shield, close to orifice, no more than 1–2 ascopore widths from proximal margin, outlined by narrow, raised rim of gymnocystal calcification (Fig. 7F); ascopore opening transversely C-shaped, D = 30–35 µm, with small, denticulate, distal projection and radial denticulation.

Avicularia usually paired but sometimes single, AvL = 63–110 µm (78±12 µm, N = 20), AvW = 27–48 (38±5 µm, N = 20) µm, mean AvL/AvW = 2.05; flanking orifice at same level as ascopore (Fig. 7E); rostrum triangular, acute with distal channel, raised distally, directed distally or slightly distolaterally, crossbar complete. Mandible not observed.

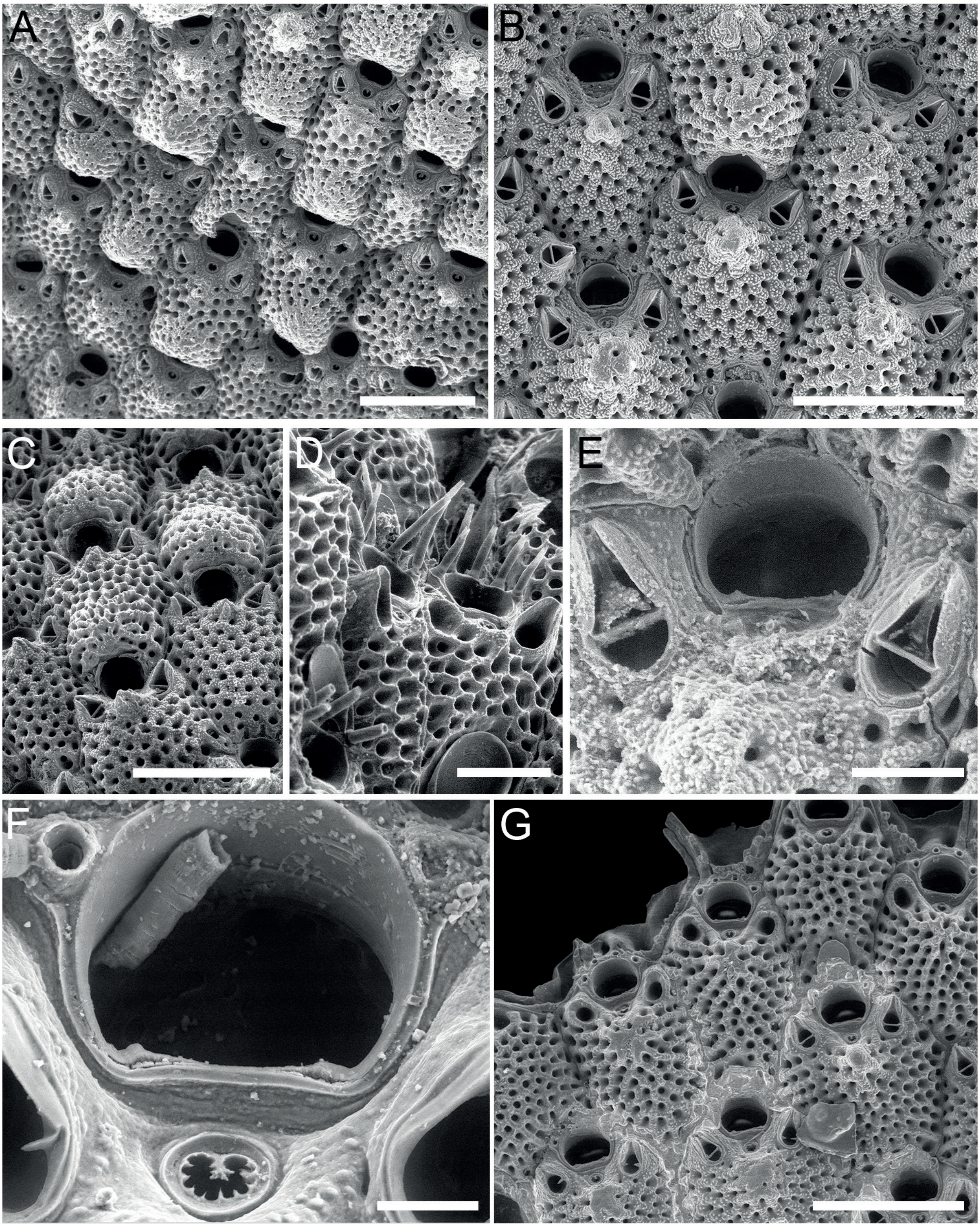

Fig. 7. *Microporella californica* (Busk, 1856) (SBMNH 704770), Point Saint George, California, USA. **A**. Group of zooids, most ovicellate. **B**. Close-up of autozooids with paired avicularia, one zooid ovicellate. **C**. Ovicellate zooids with acute frontal shield umbones hiding the ascopore. **D**. Autozooids with oral spines intact. **E**. Close-up of an orifice, with oral spine bases obliterated by secondary calcification, and avicularia. **F**. Close-up of the ascopore and orifice with condyles. **G**. Incomplete autozooids showing distal pore chamber windows. Scale bars: A–C, G = 500 µm; D = 200 µm; E = 100 µm; F = 50 µm.

Ovicell globular, wider than long, OvL = 153–288 µm (215±33 µm, N = 20), OvW = 228–395 µm (335±43 µm, N = 20), mean OvL/OvW = 0.64, overlying frontal shield of next distal zooid, sometimes slightly obscuring distal margin of maternal orifice; secondary calcification continuous with that of next distal zooid but more finely granular, with 21–32 circular, evenly distributed pseudopores, 5–17 µm in maximum diameter (Fig. 7A–C).

Ancestrula not observed.

Remarks

Microporella californica is a very well-known species, described over the years by numerous taxonomists, who have helped highlight its intraspecific variability. One of the most variable features seems to be the number of distal oral spines; Busk (1856) reported four in the original description, Dick & Ross (1988) three to five, Hincks (1883) six, and Osburn (1952) five to seven. However, caution must be exercised regarding the higher spine count reported by Osburn (1952), as it might stem from a potential misidentification of the species. A preliminary examination of specimens from SBMNH assigned to *M. californica* by Osburn, revealed the presence of several colonies of *M. cribrosa* and *M. similis* Chowdhury & Di Martino sp. nov.

The degree of development of the umbo proximal to the ascopore is also highly variable and probably linked to the environment, as seen in other species in this study.

Distribution and ecology

This species occurs along the Pacific coast from California to Alaska, from the intertidal zone down to 150 m depth. Colonies encrust shells, rocks, and sometimes algae (Osburn 1952; Dick & Ross 1988; Soule *et al.* 1995).

Microporella neocribroides Dick & Ross, 1988
Fig. 8, Table 2

Microporella neocribroides Dick & Ross, 1988: 76, pl. 12 fig. c.

Microporella neocribroides – Dick *et al.* 2005: 3753, fig. 19a–d.
Microporella cribrosa – Suwa & Mawatari 1998: 899, fig. 2.

Material examined

USA • 1 colony of 60 zooids, two ovicellate, on rock; California, Greenwood; 39°7′45.0582″ N, 123°43′9.192″ W; 22 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704691 • 1 colony of 40 zooids, none ovicellate, on rock; California, Stengel Beach; 38°42′55.6884″ N, 123°27′34.7616″ W; 23 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704692a • 1 colony of 30 zooids, 13 ovicellate, on rock; California, Stengel Beach; 38°42′55.6884″ N, 123°27′34.7616″ W; 23 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704692b • 1 colony of 20 zooids, 11 ovicellate, on rock; California, Stengel Beach; 38°42′55.6884″ N, 123°27′34.7616″ W; 23 Jun 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704692c.

Description

Colony encrusting, multiserial, unilaminar, forming subcircular patches, typically inhabiting rocks of various size and bivalve shells (mussels and clams).

Autozooids hexagonal, rectangular, or irregularly polygonal, ZL = 377–540 µm (470±48 µm, N = 20), ZW = 272–439 µm (348±45 µm, N = 20), mean L/W = 1.30; boundaries marked by grooves between slightly raised vertical walls. Frontal shield flat to convex centrally, often ribbed, finely granular, with reduced number of sparse, circular pseudopores (D = 9–15 µm), and 6–14 circular to elliptical, marginal areolae clearly distinguishable due to their larger size (D = 25–45 µm) (Fig. 8A–D).

Primary orifice transversely D-shaped, OL = 55–116 µm (82±16 µm, N = 20), OW = 100–136 µm (113±10 µm, N = 20), mean OL/OW = 0.73; mean ZL/OL = 5.73; hinge-line straight, smooth, without condyles or denticles (Fig. 8E). Two oral spines observed in some zooids, absent or obscured by secondary calcification in some others (Fig. 8A).

Ascopore depressed relative to adjacent frontal shield, within one ascopore width or less from orifice, outlined proximally by rim of gymnocystal calcification that is confluent with lateral peristomial flanges; ascopore circular or transversely elliptical, opening 21–37 µm in width, cribrate (Fig. 8E).

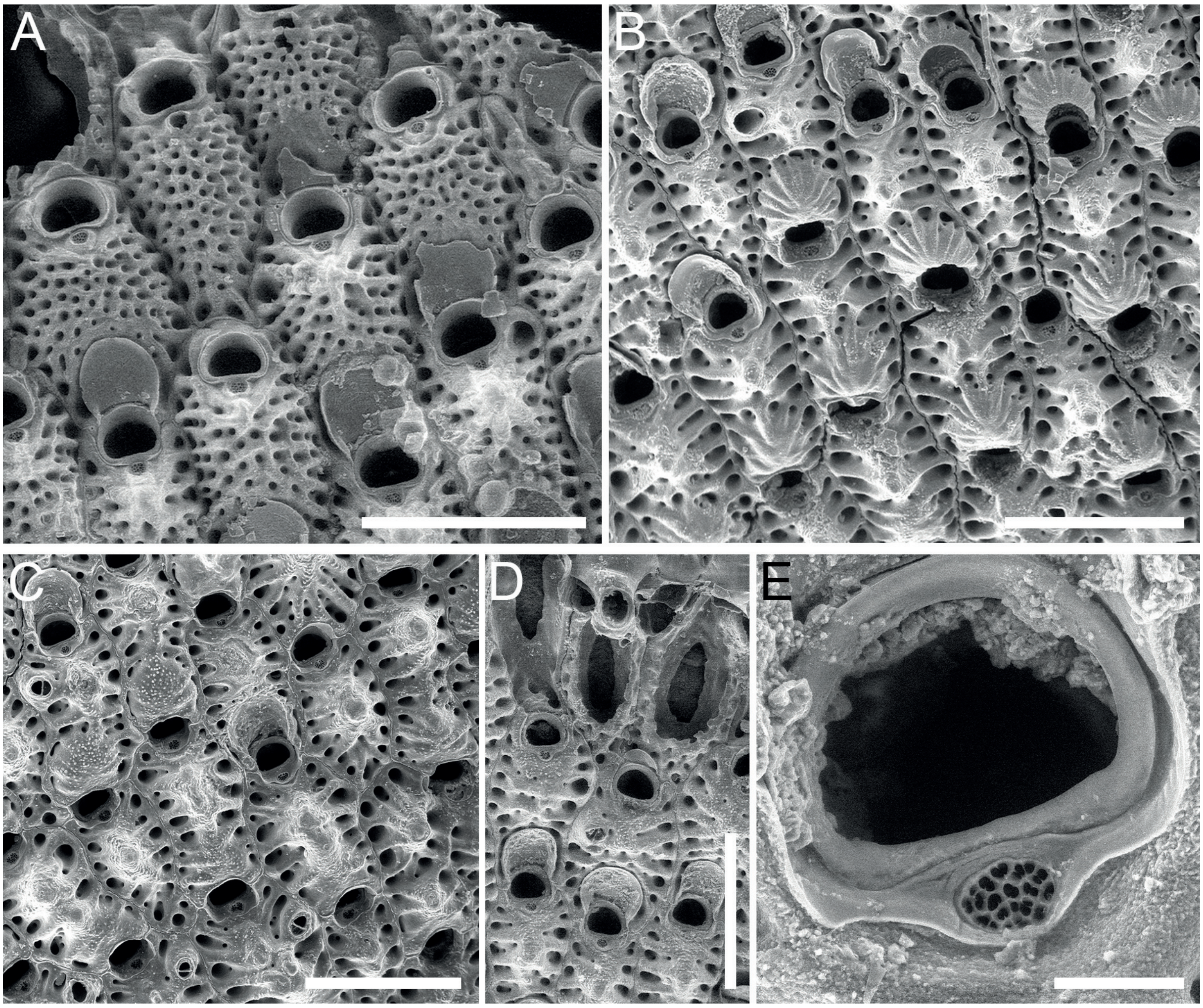

Fig. 8. *Microporella neocribroides* Dick & Ross, 1988 (SBMNH 704692), Stengel Beach, California, USA. **A**. Group of autozooids lacking avicularia and showing two distolateral oral spines. **B**. Group of zooids lacking avicularia, with ovicells in various stages of development. **C**. Group of zooids, mostly ovicellate, and some with avicularia. **D**. Group of zooids, some in formation, at colony growing edge. **E**. Close-up of the orifice and reticulate ascopore. Scale bars: A–D = 500 µm; E = 50 µm.

Avicularium single but often absent, AvL = 54–72 µm (54±8 µm, N = 17), AvW = 30–52 µm (40±6 µm, N = 17), mean AvL/AvW = 1.35; located at zooidal mid-length, always proximal to ascopore, on either left or right side of zooid; crossbar complete; rostrum rounded-triangular, directed laterally or slightly distolaterally, rostrum tip only slightly raised (Fig. 8C). Mandible not observed.

Ovicell prominent, round (Fig. 8B–C); OvL = 198–269 µm (224±15 µm, N = 20), OvW = 242–354 µm (298±29 µm, N = 20), mean OvL/OvW = 0.75; continuous with frontal shield of next distal zooid, sometimes obscuring distal margin of maternal orifice; calcification finely granular, smoother than that of the frontal shield, sometimes with marked ribs when developing, imperforate except for peripheral row of elliptical marginal areolae, 5–34 µm in maximum dimension.

Ancestrula not observed.

Remarks

Our material conforms very well to the original description of *Microporella neocribroides* Dick & Ross, 1988, from Alaska, sharing all the main diagnostic characters, including zooid size, the cribrate ascopore close to the orifice, the smooth proximal margin of the orifice, condyles slight or lacking, two oral spines (though absent in most zooids), the imperforate ovicell, and the shape, location and direction of the avicularium, which is often lacking. Dick & Ross (1988) observed that the calcification of the frontal shield and ovicell becomes thicker and rugose with age, which we likewise observed in the Californian colonies.

Distribution and ecology

The species has been described as amphi-Pacific, with a northern boreal distribution (Dick *et al.* 2005). It has been previously reported from Katalla and Kodiak, Alaska, USA (Dick & Ross 1988); Ketchikan, Alaska (Dick *et al.* 2005); and Muroran, Hokkaido, Japan (Suwa & Mawatari 1998). The southernmost record is from Mill Creek, California (this study).

Microporella setiformis O'Donoghue & O'Donoghue, 1923
Fig. 9, Table 2

Microporella setiformis O'Donoghue & O'Donoghue, 1923: 174, pl. 3 fig. 21.

Microporella setiformis – Osburn 1952: 385, pl. 44 fig. 8. — Soule *et al.* 1995: 150, pl. 53 figs a–d. — Dick *et al.* 2005: 3752, fig. 18c–d.

Material examined

USA • 1 living colony of 30 zooids, none ovicellate, on rock; California, Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776a • 1 colony of 20 zooids, none ovicellate, on rock; California, Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776b • 1 colony of 60 zooids, 18 ovicellate, on rock; California, Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776c • 1 colony of 30 zooids, none ovicellate, on rock; California, Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776d • 1 colony of 40 zooids, none ovicellate, on rock; California Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776e • 1 colony of 60 zooids, 13 ovicellate, on rock; California, Black Sand Beach; 40°24′50.5074″ N, 124°23′48.1056″ W; 9 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704776f.

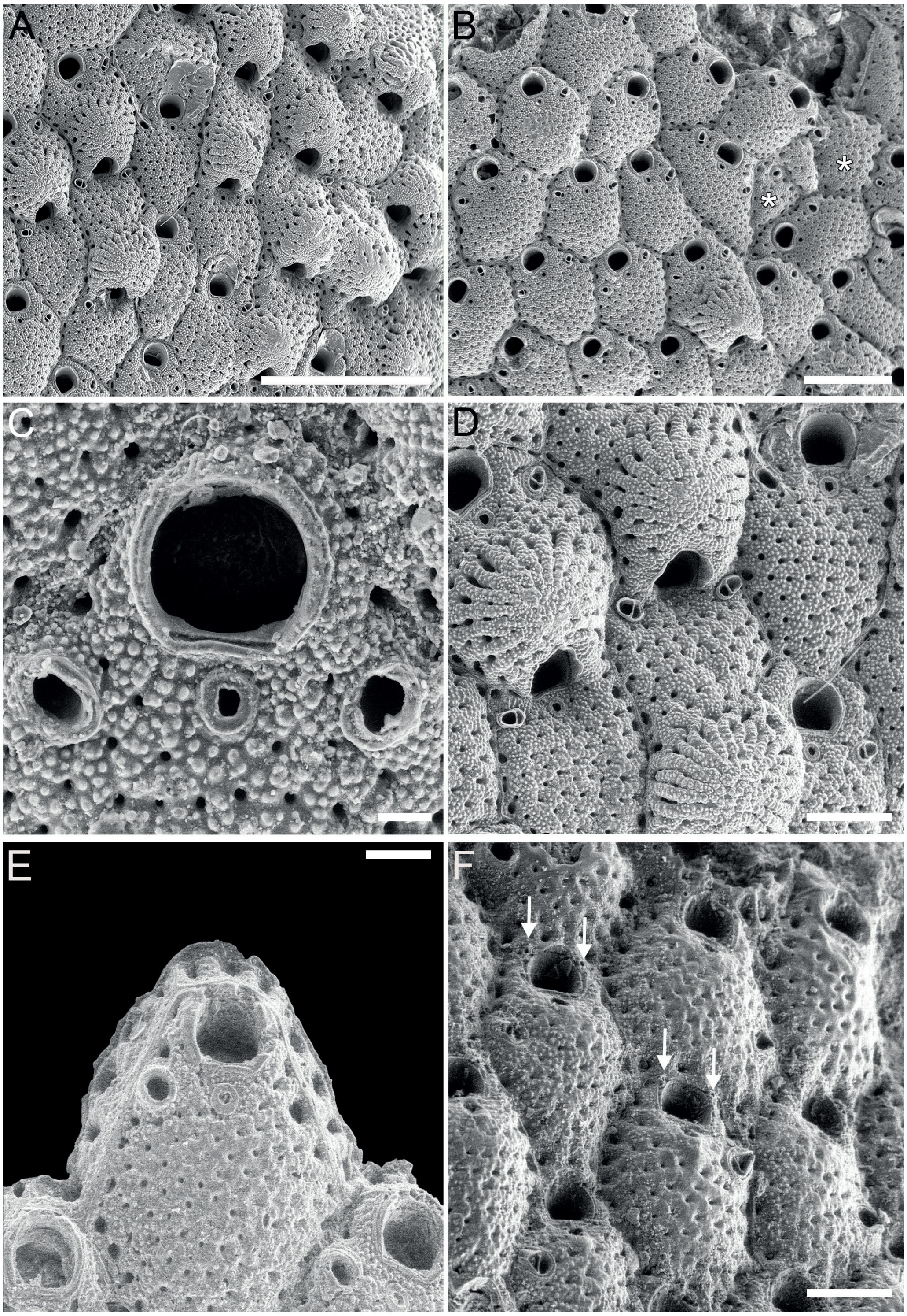

Fig. 9. *Microporella setiformis* O'Donoghue & O'Donoghue, 1923 (SBMNH 704776), Black Sand Beach, Lost Coast, California, USA. **A**. Group of zooids, some ovicellate. **B**. Autozooids and kenozooids (white asterisks) at colony growing edge. **C**. Close-up of orifice, showing low condyles, ascopore, and avicularia with crossbar missing. **D**. Close-up of ovicellate zooids with avicularia showing complete crossbar. **E**. Close-up of marginal zooid showing exposed pore chamber windows. **F**. Group of autozooids with two oral spines, some indicated with arrows. Scale bars: A = 1 mm; B = 500 µm; C = 50 µm; D, F = 250 µm; E = 150 µm.

Description

Colony encrusting, multiserial, unilaminar, forming subcircular patches, typically encrusting rocks of various sizes; pore chamber windows visible at the colony growing edge (Fig. 9E), circular to elliptical, three on distal margin and 4–5 on each distolateral vertical wall.

Autozooids rounded hexagonal or irregularly polygonal, ZL = 377–540 µm (470±48 µm, N = 20), ZW = 272–439 µm (348±45 µm, N = 20), mean L/W = 1.30; boundaries marked by grooves between slightly raised vertical walls. Frontal shield flat to slightly convex, finely granular, with 52–89 circular pseudopores (D = 5–12 µm) and 10–12 circular to elliptical, marginal areolae per side, clearly distinguishable from pseudopores by their larger size (D = 10–22 µm) (Fig. 9A–B).

Primary orifice transversely D-shaped, OL = 114–139 µm (124±8 µm, N = 10), OW = 120–148 µm (133±8 µm, N = 10), mean OL/OW = 0.93, mean ZL/OL = 3.80; outlined by rim of smooth gymnocyst; hinge-line straight, smooth, with two low, trapezoidal condyles at corners (Fig. 9C). Two oral spines observed in some zooids, later obscured by secondary calcification or ovicell (Fig. 9F).

Ascopore unusually small, circular (18–25 µm in diameter), with smooth margin, covering plate lacking (Fig. 9C); at same level as adjacent frontal shield, 2–3 ascopore widths from orifice, outlined by rim of gymnocystal calcification independent from that encircling orifice.

Avicularia small, single or paired, AvL = 40–51 µm (46±4 µm, N = 7), AvW = 21–30 µm (25±3 µm, N = 7), mean AvL/AvW = 1.85; located distally at same level as ascopore (Fig. 9C); crossbar complete (Fig. 9D); rostrum rounded-triangular, directed laterally or slightly distolaterally, rostrum tip only slightly raised. Mandible not observed.

Ovicell prominent, round, wider than long (Fig. 9A, D); OvL = 194–281 µm (242±33 µm, N = 6), OvW = 305–363 µm (332±21 µm, N = 7), mean OvL/OvW = 0.73; continuous with frontal shield of next distal zooid, obscuring distal margin of maternal orifice; calcification finely granular like that of frontal shield but with marked ribs; perforated by small pseudopores, 5–14 µm in maximum dimension.

Aberrant kenozooids smaller than autozooids or nearly as large, lacking opening such as orifice and ascopore but equipped with avicularium (Fig. 9B, see asterisks).

Ancestrula not observed.

Remarks

Our material fits the description of *Microporella setiformis*, a species originally described from British Columbia, Canada (O'Donoghue & O'Donoghue 1923).

Distribution and ecology

Microporella setiformis has been recorded from intertidal waters to over 100 m depth. The species ranges from Ketchikan, Alaska (Dick *et al.* 2005) southward Channel Islands in southern California (Soule *et al.* 1995).

Microporella umbonata (Hincks, 1883)
Fig. 10, Table 2

Microporella ciliata form *umbonata* Hincks, 1883: 444, pl. 17 fig. 1.

Material examined

USA • 1 colony of 30 zooids, two ovicellate, on rock; California, Greenwood; 39°7′45.0582″ N, 123°43′9.192″ W; 22 Jun. 2020; I.A. Chowdhury and H. Lee leg.; SBMNH 704779 • 1 colony of 40 zooids, six ovicellate, on rock; California, Palmer′s Point, Trinidad; 41°7′51.6″ N, 124°9′49.32″ W; 9 Dec. 2019; I.A. Chowdhury and H. Lee leg.; NHMO H1940.

Description

Colony encrusting, multiserial, unilaminar, forming subcircular patches, typically inhabiting rocks of various sizes; three distal pore chamber windows evident in zooids at colony growing edge.

Autozooids hexagonal, rectangular or irregularly polygonal, ZL = 574–859 µm (689±78 µm, N = 11), ZW = 411–616 µm (522±66 µm, N = 13), mean L/W = 1.32; boundaries marked by grooves. Frontal shield convex centrally due to umbonate process; smaller umbo on each side lateral to orifice; smooth to finely granular, with numerous (38–55) circular pseudopores, D = 7–14 µm; marginal areolae distinguishable from pseudopores because elliptical and slightly larger (ca 20 µm) (Fig. 10A).

Primary orifice transversely D-shaped, OL = 104–131 µm (117±8 µm, N = 13), OW = 142–169 µm (155±9 µm, N = 13), mean OL/OW = 0.75, mean ZL/OL = 5.89; hinge-line smooth, with minute triangular condyles at some distance from corners, slightly concave between condyles (Fig. 10A–B); oral spines absent.

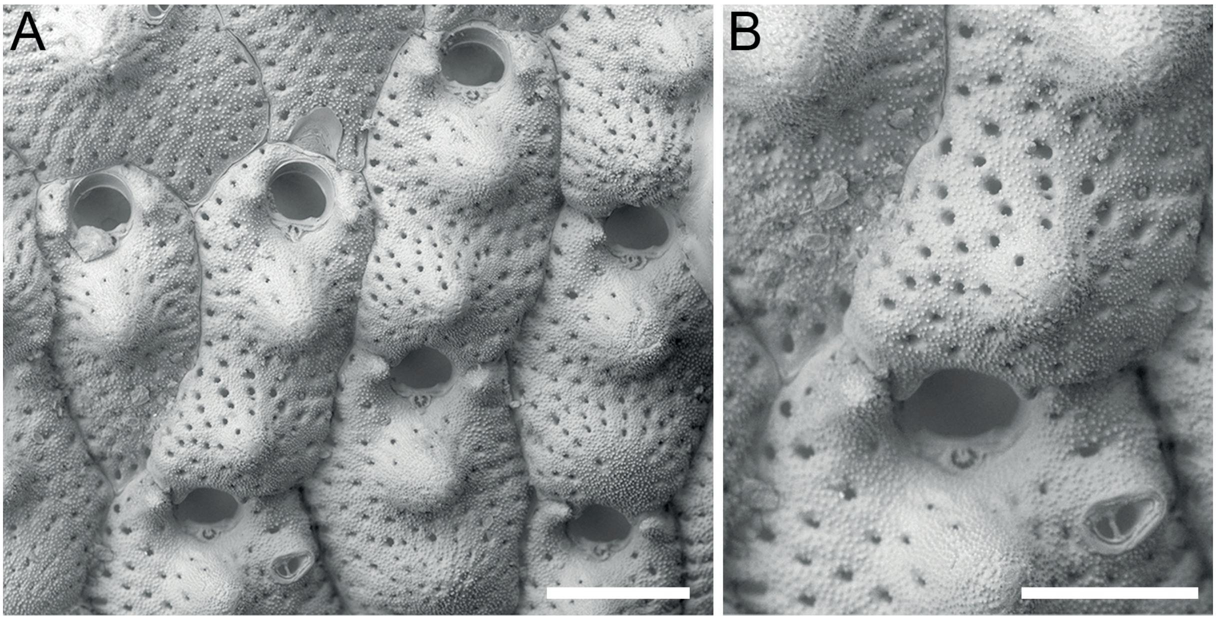

Fig. 10. *Microporella umbonata* (Hincks, 1883) (NHMO H1940), Palmer's Point, Trinidad, California, USA. **A**. Group of ovicellate and non-ovicellate zooids, one zooid with avicularium. **B**. Distal part of autozooid showing umbonate ovicell, small adventitious avicularium, C-shaped ascopore with projecting tongue and denticulate margin, and concave proximal margin of orifice with triangular condyles. Scale bars: A = 500 µm; B = 200 µm.

Ascopore small, depressed relative to adjacent frontal shield, unusually close to orifice, much less than ascopore width from proximal margin, outlined by rim of gymnocystal calcification continuous with the one encircling the orifice; ascopore opening 35–38 µm in diameter, transversely C-shaped, with distal projection and outer margin radially denticulate (Fig. 10B).

Avicularium mostly absent, sometimes single, AvL = 88–94 µm (91±4 µm, N = 2), AvW = 37–51 µm (44±10 µm, N = 2), mean AvL/AvW = 2.10; located laterally in distal half of zooid, proximolateral to ascopore, more or less lateral to frontal umbo; crossbar complete; rostrum triangular, truncated, directed distolaterally, rostrum tip only slightly raised (Fig. 9B). Mandible not observed.

Ovicell globose, wider than long, OvL = 208–257 µm (233±34 µm, N = 2), OvW = 372–384 µm (378±9 µm, N = 2), mean OvL/OvW = 0.63; continuous with frontal shield of next distal zooid, obscuring distal margin of maternal orifice; calcification finely granular, completely and evenly covered with minute, circular pseudopores, 6–13 µm in maximum dimension (Fig. 10A–B).

Ancestrula not observed.

Remarks

Microporella umbonata can be distinguished from *M. umboniformis* Soule, Soule & Chaney, 1995 (Fig. 11) by several consistent morphological differences. *Microporella umbonata* consistently lacks oral spines (Figs 10A, 12A), while *M. umboniformis* has 5–6 robust spines observed in both mature zooids at the colony centre and young zooids at the colony margin (Fig. 11A–B, E–F). *Microporella umbonata* consistently display a small umbo on each side lateral to the orifice (Figs 10A, 12A). In *M. umboniformis*, the development of two lateral umbones may occur exclusively in ovicellate zooids, resulting from the thickening of the proximalmost pair of oral spines as illustrated by Soule *et al.* (1995: pl. 54a). However, it's noteworthy that we did not observe this particular feature in the holotype, where the two proximalmost pair of spines in ovicellate zooids where simply retained in their original state (Fig. 11G–H). This observation suggests the possibility that the figured specimen in Soule *et al.* (1995: pl. 54a) might not be the holotype. Additionally, the adventitious avicularium in *M. umbonata* is either single or frequently absent (Figs 10A–B, 12A–B). On the other hand, *M. umboniformis* consistently exhibits avicularia, which are more commonly single, though they also frequently occur in pairs (Fig. 11A–B, E). The ascopore in *M. umbonata* is unusually close to the proximal margin of the orifice, sometimes in direct contact, and enclosed by the same smooth gymnocystal calcification rim surrounding the orifice (Figs 10B, 12B–C), while in *M. umboniformis* it is clearly separated from the proximal margin of the orifice at a distance of about one ascopore width (Fig. 11C–D).

Soule *et al.* (1995: 21) delineate key characteristics to differentiate between the two species, emphasizing the presence of a "frontal wall with large pores" in *M. umbonata* and a "frontal wall with small pores" in *M. umboniformis*. Our specimens (Fig. 10) and the specimen of *M. umbonata* from Departure Bay, Canada (Fig. 12), used for comparative analysis, show no discernible difference in pseudopore size [D = 7–14 µm (9.75±2.1 µm, N = 20) and D = 6–14 µm (9.3±2.2 µm, N = 20) in *M. umbonata* from California and Canada, respectively] when contrasted with the holotype of *M. umboniformis* [D = 7–15 µm (9.8±2.1 µm, N = 20)]. Notably, it is in the holotype of *M. umboniformis* that we observed larger pseudopores in some zooids (see Fig. 11E–F), seemingly attributable to the absence of the external layer of calcification. The sole difference is in their arrangement of pseudopores, which form radiating lines in our specimens and the specimen from Departure Bay, consistent with Hincks' (1883) description, as opposed to the scattered distribution observed in *M. umboniformis*.

Soule *et al.* (1995) synonymized Osburn's records of *M. umbonata* with their newly described species *M. umboniformis*, but it remains unclear whether they re-examined Osburn's specimens. In their

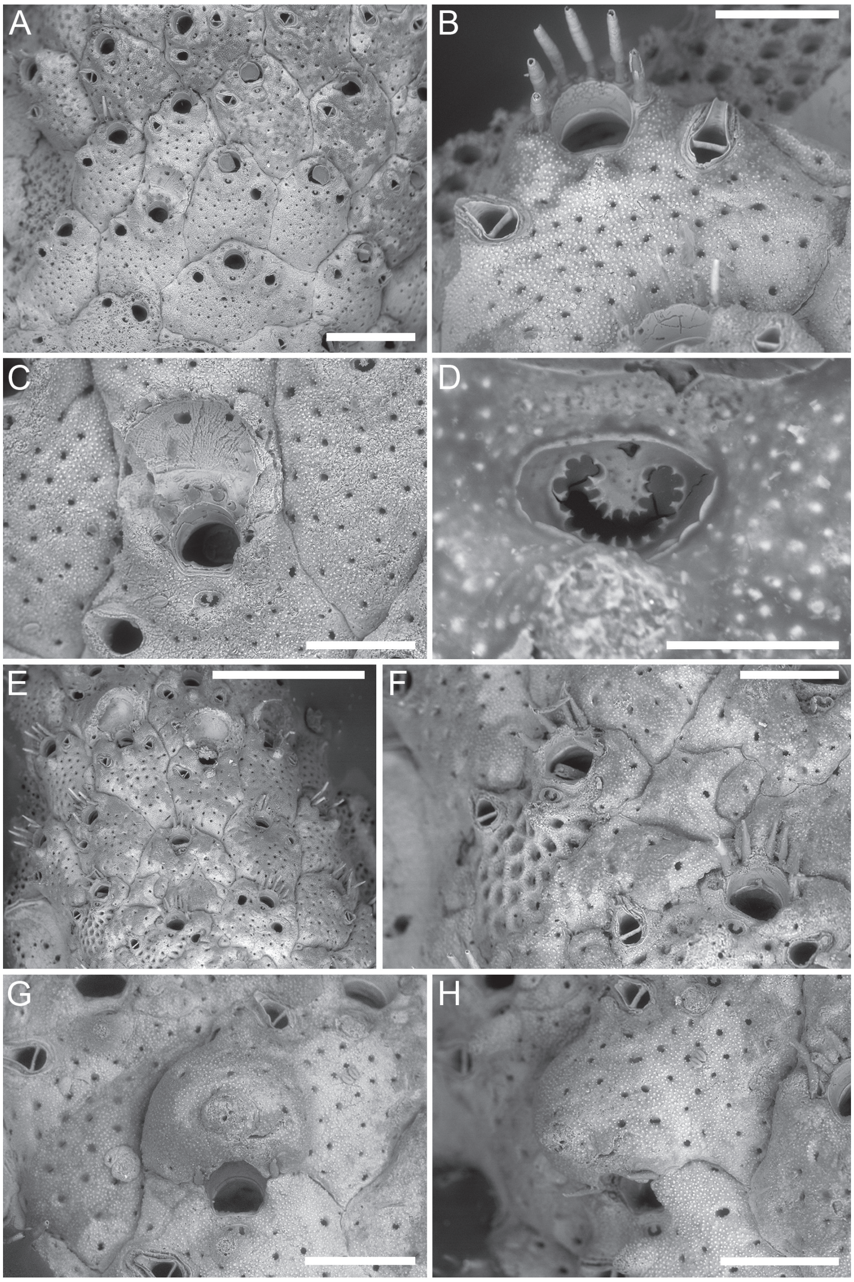

Fig. 11. *Microporella umboniformis* Soule, Soule & Chaney, 1995, holotype (SBMNH 671678) (previously AHF 213), Velero BS 1064, off Santa Barbara Island (33°30′1.00008″ N, 119°2′20.00004″ W), depth 49 m, California, USA. **A**. Group of zooids showing single or paired adventitious avicularia and five to six oral spines. Note the consistent absence of umbones lateral to orifice. **B**. Close-up of a zooid at colony margin showing six robust spines, paired avicularia and a short, pointed umbo proximal to ascopore. **C**. Close-up of orifice showing two small condyles at some distance from corners and proximal margin slightly concave between condyles as in *M. umbonata*. **D**. Close-up of C-shaped ascopore with denticulations. **E**. Group of zooids with some at the bottom showing larger pseudopores, likely due to the absence of the external layer of calcification, and some others with extensive secondary calcification. **F**. Close-up of one of the zooids in (E) showing larger pseudopores likely due to the lack of external frontal calcification. **G–H**. Close-ups of the same ovicell in frontal and lateral view, respectively. Note that the two proximalmost spines are retained. Scale bars: A = 500 µm; B–C = 200 µm; D = 50 µm; E = 1 mm; F–H = 250 µm.

paragraph on distribution, they referred to Osburn's records as "probably the new species", a statement that introduced some uncertainties. Nevertheless, Osburn (1952: 378) described "4 to 6 small oral spines which are evanescent" but he did not illustrate them (see Osburn 1952: pl. 44 fig. 4), suggesting the possibility that he might have been dealing with both species.

The shape and size of ovicell in *M. umbonata* vary among zooids, even within the same colony (Fig. 10A), likely influenced by the extent of secondary calcification.

Distribution and ecology

Microporella umbonata has been recorded along the eastern Pacific coast, with previous records from the Queen Charlotte Islands, British Columbia, Canada (Hincks 1883). Osburn's records of *M. umbonata*, though uncertain, originated from San Pedro Island, Santa Cruz Island and Dillon Beach in California, and Puget Sound, Washington, USA, from the intertidal zone down to a depth of 102 m (Osburn 1952; Soule *et al.* 1995). Colonies from this study were found in Greenwood and Palmer's Point, Trinidad, California, USA, both encrusting rocks.

Discussion

This paper represents the first comprehensive survey of *Microporella* along the intertidal rocky coast of California, USA. From approximately 240 colonies of *Microporella* examined, our study identified seven species, including three that are new to science, confirming *Microporella* as one of the most species-rich genera in the region. Prior to this investigation, the total number of recent species of *Microporella* reported from the diverse habitats of California stood at 13, namely *M. californica*, *M. catalinensis*, *M. cribrosa*, *M. franklini* (Soule, Chaney & Morris, 2004), *M. infundibulipora*, *M. planata*, *M. sanmiguelensis* (Soule, Chaney & Morris, 2004), *M. santabarbarensis*, *M. setiformis*, *M. umbonata*, *M. umboniformis*, *M. vibraculifera*, and *M. wrigleyi*. Four fossil species are also known from Californian Pleistocene deposits: *M. eustomata* (Gabb & Horn, 1862), *M. gibbera* Canu & Bassler, 1923, *M. heermannii* (Gabb & Horn, 1862), and *M. papulifera* Canu & Bassler, 1923. However, based on the original drawing in Gabb & Horn (1862: fig. 26) and the figure in Canu & Bassler (1923: pl. 36 fig. 13), which show a very large number of oral spine bases but lack evidence of the ascopore, there are doubts whether *M. eustomata* belongs in *Microporella*.

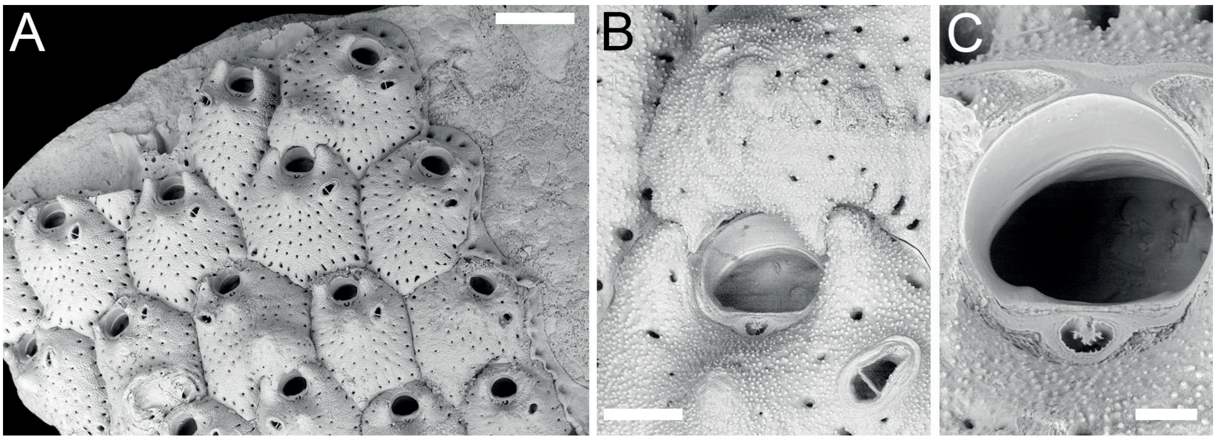

Fig. 12. *Microporella umbonata* Hincks, 1883, (NHMUK 1921.11.17.15), Departure Bay, Vancouver, Canada. **A**. Group of zooids, some with ovicells. **B**. Distal end of zooid, showing ovicell and avicularium. **C**. Close-up showing C-shaped ascopore with projecting tongue and denticulate margin, and concave proximal margin of orifice with triangular condyles. Scale bars: A = 400 µm; B = 100 µm; C = 40 µm.

Our study increases the known diversity of Recent *Microporella* in California's waters to 18 species. We added three new species based on newly sampled intertidal material, *M. dentata* Chowdhury & Di Martino sp. nov., *M. pauciperforata* Chowdhury & Di Martino sp. nov. and *M. rota* Chowdhury & Di Martino sp. nov., and an additional new species following the re-examination of museum specimens originally attributed to *M. cribrosa*, along with a new record for *M. neocribroides*. Originally described from Kodiak Island, Alaska, USA, *M. neocribroides* was previously thought to have a northern boreal distribution (Dick & Ross 1988). However, Suwa & Mawatari (1998) later found it in Hokkaido, Japan and described its range as amphi-Pacific. Our study further extends the known range of distribution of *M. neocribroides* to Sonoma State Beach in California.

The diversity of *Microporella* in California is currently not only high but has also shown periodic increases in connection with new research efforts. This situation is comparable to other regions worldwide. In the Mediterranean, the extant diversity of *Microporella* has increased from eight to 15 species in approximately seven years (Rosso & Di Martino 2016, 2023). In New Zealand, there are currently eight known extant species of *Microporella*, with three having been recently identified (Di Martino *et al.* 2020), while four additional fossil species have been reported from Miocene and Pleistocene deposits (Di Martino *et al.* 2017; Ramsfjell *et al.* 2022). The increase in the number of discovered and described species of *Microporella* can be attributed not only to new investigations of habitats and localities previously overlooked, but also to significant advances in research techniques. The routine use of scanning electron microscopy and growing support from molecular analysis (e.g., Orr *et al.* 2018, 2021, 2022) have played a vital role in deconstructing species complexes, enabling the identification of new species as demonstrated by the reevaluation of previous records of *M. cribrosa* in this study, leading to the attribution of these records to two distinct new species (*M. rota* Chowdhury & Di Martino sp. nov. and *M. similis* Chowdhury & Di Martino sp. nov.). Moreover, *Microporella* has gained recognition as an optimal model system to investigate life history and phenotypic evolution (Di Martino & Liow 2021, 2022), necessitating a robust taxonomic baseline.

This is the first study investigating *Microporella* from exposed boulder fields in intertidal waters. Among the seven species identified, three (*M. californica*, *M. neocribroides* and *M. rota* Chowdhury & Di Martino sp. nov.) were prevalent and abundant, present at ten sites usually with more than five colonies each (Table 2). Conversely, the remaining four species were less common, with one (*M. dentata* Chowdhury & Di Martino sp. nov.) present at three sites, and the other three (*M. pauciperforata* Chowdhury & Di Martino sp. nov., *M. umbonata*, and *M. setiformis*) restricted to single sites, each with a number of colonies ranging from one to three, except for *M. setiformis* present with 20 colonies. Among the 15 sampling sites, Point Saint George and Pillar Point exhibited the highest abundance of *Microporella*, with 31 and 30 colonies, respectively, representing three species. On the other hand, Trinidad Head South showed the lowest occurrence of *Microporella*, with only one colony of *M. californica* observed. The highest richness, four species, was observed at Greenwood; three species were observed at eight additional sites, while two species each were recorded at two other sites, and four sites had only a single species. There were no distinct patterns regarding the composition of species among sites or any evident distributional trends correlated with latitude, temperature, salinity or tidal ranges (Fig. 1, Tables 1–2).

In this study, most species displayed notable intraspecific variability, likely influenced by environmental factors prevalent in intertidal habitats such as high energy conditions, the exposure to intermittent submersion and emersion coinciding with changes in oxygen and food availability, heat and desiccation stress, as well as grazing and predation. The most variable features we observed were in the morphology of the frontal shield, where an umbo developed to varying degrees proximal to the ascopore and sometimes on the ovicell, and in the number of oral spines. The development of an umbo has been observed in other species of *Microporella* living as epibionts on soft, ephemeral substrates, such as seagrasses and algae (Di Martino & Rosso 2021). Knob-like tubercles are likely to function as bumpers to reduce friction between neighbouring colonies on moving substrates, and a similar protective function has been proposed for the formation of a higher number of long oral spines (Di Martino & Taylor 2014; Reich *et al.* 2015).

Some zooids of certain species also displayed poorly preserved frontal shields possibly due to the high wave action that causes rock substrates to overturn. Some sites such as Mill Creek, Black Sand Beach and False Klamath are exposed to high wave action throughout the year, while most northern sites experience severe winter storms. Abrasion of the colony surface might also be caused by the observed presence of sea-urchins and limpets damaging bryozoans incidentally when grazing on algae.

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References

Blanchette C.A., Miner M.C., Raimondi P.T., Lohse D., Heady K.E. & Broitman B.R. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography* 35 (9): 1593–1607. https://doi.org/10.1111/j.1365-2699.2008.01913.x

Bock P.E. 2023. *The Bryozoa Home Page. Recent and Fossil Bryozoa*. Available from http://bryozoa.net/ [accessed 20 July 2023].

Busk G. 1856. Zoophytology. 1. Polyzoa Cheilostomata. *Quarterly Journal of Microscopical Science* 4: 308–312. https://doi.org/10.1242/jcs.s1-4.16.308

Busk G. 1860. Zoophytology. Catalogue of the Polyzoa collected by J.Y. Johnson, Esq., at Madeira, in the years 1859 and 1860, with descriptions of new species. *Quarterly journal of Microscopical Science* 8: 213–214, 280–285. https://doi.org/10.1242/jcs.s1-8.32.280

Canu F. & Bassler R.S. 1923. North American later Tertiary and Quaternary Bryozoa. *United States National Museum Bulletin* 125: 1–302. https://doi.org/10.5962/bhl.title.159661

Canu F. & Bassler R.S. 1930. The Bryozoa of the Galapagos Islands. *Proceedings of the U.S. National Museum* 76: 1–78. https://doi.org/10.5479/si.00963801.76-2810.1

Dick M.H. & Ross J.R.P. 1988. Intertidal Bryozoa (Cheilostomata) of the Kodiak vicinity, Alaska. *Occasional Paper*, *Center for Pacific Northwest Studies* 28: 1–133.

Dick M.H., Grischenko A.V. & Mawatari S.F. 2005. Intertidal Bryozoa (Cheilostomata) of Ketchikan, Alaska. *Journal of Natural History* 39 (43): 3687–3784. https://doi.org/10.1080/00222930500415195

Di Martino E. & Liow L.H. 2021. Larger offspring associated with lower temperatures across species of Microporella, a widespread colonial invertebrate. *Marine Ecology Progress Series* 662: 1–13. https://doi.org/10.3354/meps13656

Di Martino E. & Liow L.H. 2022. Changing allometric relationships among fossil and Recent populations in two colonial species. *Evolution* 76 (10): 2424–2435. https://doi.org/10.1111/evo.14598

Di Martino E. & Rosso A. 2021. Seek and ye shall find: new species and new records of *Microporella* (Bryozoa, Cheilostomatida) in the Mediterranean. *ZooKeys* 1053: 1–42. https://doi.org/10.3897/zookeys.1053.65324

Di Martino E. & Taylor P.D. 2014. A brief review of seagrass-associated bryozoans, Recent and fossil. *In*: Rosso A., Wyse Jackson P.N. & Porter J.S. (eds) *Bryozoan Studies 2013. Studi Trentini di Scienze Naturali 94*: 79–94.

Di Martino E., Taylor P.D., Gordon D.P. & Liow L.H. 2017. New bryozoan species from the Pleistocene of the Wanganui Basin, North Island, New Zealand. *European Journal of Taxonomy* 345: 1–15. https://doi.org/10.5852/ejt.2017.345

Di Martino E., Taylor P.D. & Portell R.W. 2019. *Anomia*-associated bryozoans from the upper Pliocene (Piacenzian) lower Tamiami Formation of Florida, USA. *Palaeontologia Electronica*: 22.1.11. https://doi.org/10.26879/920

Di Martino E., Taylor P.D. & Gordon D.P. 2020. Erect bifoliate species of *Microporella* (Bryozoa, Cheilostomata), fossil and modern. *European Journal of Taxonomy* 678: 1–31. https://doi.org/10.5852/ejt.2020.678

Gabb W.M. & Horn G.H. 1862. The fossil Polyzoa of the Secondary and Tertiary Formations of North America. *Journal of the Academy of Natural Sciences of Philadelphia* 5: 111–179.

Hincks T. 1883. Report on the Polyzoa of the Queen Charlotte Islands. 2. *Annals and Magazine of Natural History Series 5* 11: 442–451. https://doi.org/10.1080/00222938309459178

Kukliński P. & Taylor P.D. 2008. Arctic species of the cheilostome bryozoan *Microporella*, with a redescription of the type species. *Journal of Natural History* 42: 1893–1906. https://doi.org/10.1080/00222930802126904

Mawatari S.F. & Suwa T. 1998. Two new species of Japanese *Microporella* (Bryozoa, Cheilostomatida) in the Döderlein Collection, Musée Zoologique, Strasbourg. *Cahiers de Biologie Marine* 39: 1–7.

O'Donoghue C.H. & O'Donoghue E. 1923. A Preliminary list of Bryozoa (Polyzoa) from the Vancouver Island Region. *Contributions to Canadian Biology and Fisheries New Series* 1: 143–201. https://doi.org/10.1139/f22-010

Orr R.J.S., Waeschenbach A., Enevoldsen E.L.G., Boeve J.P., Haugen M.N., Voje K.L., Porter J.S., Zágoršek K., Smith A.M., Gordon D.P. & Liow L.H. 2018. Bryozoan genera *Fenestrulina* and *Microporella* no longer confamilial; multi-gene phylogeny supports separation. *Zoological Journal of the Linnean Society* 186: 190–199. https://doi.org/10.1093/zoolinnean/zly055

Orr R.J.S., Di Martino E., Gordon D.P., Ramsfjell M.H., Mello H.L., Smith A.M. & Liow L.H. 2021. A broadly resolved molecular phylogeny of New Zealand cheilostome bryozoans as a framework for hypotheses of morphological evolution. *Molecular Phylogenetics and Evolution* 161: e107172. https://doi.org/10.1016/j.ympev.2021.107172

Orr R.J.S., Di Martino E., Ramsfjell M.H., Gordon D.P., Berning B., Chowdhury I., Craig S., Cumming R.L., Figuerola B., Florence W., Harmelin J.-G., Hirose M., Huang D., Jain S.S., Jenkins H.L., Kotenko O.N., Kukliński P., Lee H.E., Madurell T., McCann L., Mello H.L., Obst M., Ostrovsky A.N., Paulay G., Porter J.S., Shunatova N.N., Smith A.M., Souto-Derungs J., Vieira L.M., Voje K.L., Waeschenbach A., Zágoršek K., Warnock R.C.M. & Liow L.H. 2022. Paleozoic origins of cheilostome bryozoans and their parental care inferred by a new genome-skimmed phylogeny. *Science Advances* 8 (13): eabm7452. https://doi.org/10.1126/sciadv.abm7452

Osburn R.C. 1950. Bryozoa of the Pacific Coast of America, part 1, Cheilostomata – Anasca. *Report of the Allan Hancock Pacific Expeditions* 14: 1–269. https://doi.org/10.5962/bhl.title.6542

Osburn R.C. 1952. Bryozoa of the Pacific Coast of America, part 2, Cheilostomata – Ascophora. *Report of the Allan Hancock Pacific Expeditions* 14: 271–611.

Ramsfjell M.H., Taylor P.D. & Di Martino E. 2022. New early Miocene species of the cheilostome bryozoan *Microporella* from the South Island of New Zealand. *Alcheringa* 46: 208–217. https://doi.org/10.1080/03115518.2022.2084564

Reich S., Di Martino E., Todd J.A., Wesselingh F.P. & Renema W. 2015. Indirect paleo-seagrass indicators (IPSIs): A review. *Earth-Science Reviews* 143: 161–186. https://doi.org/10.1016/j.earscirev.2015.01.009

Robertson A. 1908. *The Incrusting Chilostomatous Bryozoa of the West Coast of North America* 4: 253–344.

Rosso A. & Di Martino E. 2016. Bryozoan diversity in the Mediterranean Sea: an update. *Mediterranean Marine Science* 17 (2): 567–607. https://doi.org/10.12681/mms.1706

Rosso A. & Di Martino E. 2023. Capturing the moment: a snapshot of Mediterranean bryozoan diversity in the early 2023. *Mediterranean Marine Science* 24 (2): 426–445. https://doi.org/10.12681/mms.34329

Soule D.F., Soule J.D. & Chaney H.W. 1995. Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel. The Bryozoa. *Irene McCulloch Foundation Monograph Series* 2: 1–344.

Soule D.F., Chaney H.W. & Morris P.A. 2003. New taxa of Microporellidae from the northeastern Pacific Ocean. *Irene McCulloch Foundation Monograph Series* 6: 1–38.

Soule D.F., Chaney H.W. & Morris P.A. 2004. Additional new species of *Microporelloides* from southern California and American Samoa. *Irene McCulloch Foundation Monograph Series* 6A: 1–14.

Suwa T. & Mawatari S.F. 1998. Revision of seven species of *Microporella* (Bryozoa, Cheilostomatida) from Hokkaido, Japan, using new taxonomic characters. *Journal of Natural History* 32 (6): 895–922. https://doi.org/10.1080/00222939800770461

Taylor P.D. & Mawatari S.F. 2005. Preliminary overview of the cheilostome bryozoan *Microporella*. *In*: Moyano G., Hugo I., Cancino, Juan M. & Wyse Jackson, Patrick N. (eds) *Bryozoan Studies 2004*: 329–339. A.A. Balkema Publishers, Leiden / London / New York / Philadelphia / Singapore.

Toonen R.J., Bowen B.W., Iacchei M. & Briggs J.C. 2016. Biogeography, Marine. *Encyclopedia of Evolutionary Biology*: 166–178. https://doi.org/10.1016/B978-0-12-800049-6.00120-7

Wilkinson T., Wiken E., Bezaury-Creel J., Hourigan T., Agardy T., Herrmann H., Janishevski L., Madden C., Morgan L. & Padilla M. 2009. *Marine Ecoregions of North America*. Commision for Environmental Cooperation. Montreal, Canada.

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