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Erect bifoliate species of *Microporella* (Bryozoa, Cheilostomata), fossil and modern

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Abstract. *Microporella* Hincks, 1877 is one of the most diverse genera of cheilostome bryozoans, containing more than 150 named species. Distributed globally since the early Miocene, the majority of species of *Microporella* have sheet-like colonies encrusting hard and/or ephemeral substrates, while a limited number of species have erect bifoliate colonies starting from an encrusting base. Herein, the four nominal species of erect bifoliate *Microporella* (*M. bifoliata*, *M. hastigera*, *M. hyadesi* and *M. ordo*) are revised, and one new Pliocene (*M. tanyae* sp. nov.) and three new Recent species (*M. ordoides* sp. nov., *M. lingulata* sp. nov. and *M. modesta* sp. nov.) are formally described. Furthermore, the lectotype and paralectotypes were designated for *M. bifoliata* and *M. hastigera*. An additional Recent species, *Microporella* sp. 1, is also described and illustrated but left in open nomenclature owing to the absence of ovicells in the single available fragment. Although the molecular phylogeny of *Microporella* has yet to be resolved, the diversity of character states present among the erect bifoliate species described here suggests that this colony growth-form is not monophyletic but has evolved on multiple occasions.

Keywords. Taxonomy, new species, colony growth-form, Recent, Neogene.

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Introduction

Microporella Hincks, 1877 is one of the most speciose genera of all cheilostome bryozoans, with more than 150 species described to date, both living and fossil (Taylor & Mawatari 2005). The distinctive zooidal morphology of this genus makes it relatively easy to recognize, but species determination is far more challenging as differences between congeneric species can be very subtle (e.g., Suwa & Mawatari 1998; Harmelin *et al.* 2011). Furthermore, adequate descriptions and illustrations are available for only

a small proportion of the nominal species. In all species of *Microporella*, autozooids have a porous frontal shield and a semielliptical orifice beneath which there is an ascopore opening into the ascus. The ascopore varies in shape from circular to elliptical, reniform or crescentic according to species. One avicularium, or less often a pair of avicularia, is normally present proximolaterally or laterally of the autozooidal orifice. Avicularian mandibles in living species may be short, or long and setose.

The great majority of species of *Microporella* have multiserial, single-layered colonies that encrust a variety of substrates, including shells, rocks, algae and seagrasses. Erect vincularian colonies with branches of circular cross-section are unknown in *Microporella*, although a genus with an almost identical zooidal morphology – *Diporula* Hincks, 1879 – does possess this colony growth-form. However, erect bifoliate colonies, with branches or fronds formed of two layers of zooids back-to-back, characterize four previously described species of *Microporella*: *M. bifoliata* Ulrich & Bassler, 1904 from the Miocene of the USA; *M. hastigera* (Busk, 1884), a Recent North Atlantic species; *M. hyadesi* (Jullien, 1888), a Recent subantarctic species; and *M. ordo* Brown, 1952, originally described from the Pleistocene of New Zealand but since found living there today. As part of a broad survey of *Microporella* (see Taylor & Mawatari 2005), one fossil and three Recent undescribed bifoliate species of *Microporella* were discovered in existing collections at the Natural History Museum in London, UK (NHMUK) and the National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA): *M. tanyae* sp. nov. from Pliocene deposits in Virginia (USA), *M. ordoides* sp. nov. and *M. lingulata* sp. nov. collected in New Zealand waters, and *M. modesta* sp. nov. from the Mediterranean off Algeria. An additional, fourth living species was recently collected during a cruise southwest of the South Island of New Zealand off Puysegur Point. Although there is enough to morphologically distinguish this species from all other bifoliate congeners, it is left in open nomenclature owing to the availability of a single, non-ovicellate specimen.

The aim of the current paper is to revise the four established bifoliate species of *Microporella*, and describe and illustrate the four new species plus the additional species left in open nomenclature.

Material and methods

This study is based on both fossil and recent material housed in museum collections as well as newly collected specimens.

Scanning electron microscopy (SEM) was conducted on uncoated specimens using LEO VP-1455 and JEOL IT500 microscopes operated at low-vacuum and back-scattered electron mode at the Natural History Museum, London, and an Hitachi TM4000plus Tabletop at the Natural History Museum, Oslo. JoAnn Sanner provided SEM micrographs of the syntypes of *Microporella bifoliata* Ulrich & Bassler, 1904 (USNM 68592).

Morphometric measurements were taken from SEM images using the image processing program ImageJ (available from <https://imagej.nih.gov/>). Abbreviations for the measurements are:

- AvL = avicularium length
- AvW = avicularium width
- OL = orifice length
- OW = orifice width
- OvL = ovicell/ooecium length
- OvW = ovicell/ooecium width
- ZL = autozooid length
- ZW = autozooid width

Type material of the new species and illustrated specimens are housed at the following institutions: Natural History Museum, London; National Institute of Water and Atmospheric Research, Wellington, New Zealand. The voucher specimen BLEED 151 is stored at the Natural History Museum, University of Oslo.

Repositories

NHMUK = Natural History Museum London, UK
NHM-UIO = Natural History Museum, University of Oslo, Oslo, Norway
NIWA = National Institute of Water and Atmospheric Research, Wellington, New Zealand
USNM = Smithsonian Institution, National Museum of Natural History, Washington, USA

Results

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

Microporella bifoliata Ulrich & Bassler, 1904
Fig. 1; Table 1

Microporella? bifoliata Ulrich & Bassler, 1904: 417, pl. 103, figs 6–8.

Microporella? bifoliata – Canu & Bassler 1923: 121, pl. 20, figs 7–11.

Material examined

Lectotype (designated here)

USA • Syntype of *Microporella bifoliata* Ulrich & Bassler, 1904; Maryland, Cordova; Miocene; Choptank Formation; USNM 68592A (Fig. 1A–B).

Paralectotype (designated here)

USA • Syntype of *Microporella bifoliata* Ulrich & Bassler, 1904; Maryland, Cordova; Miocene; Choptank Formation; USNM 68592B (Fig. 1C–D).

Other material

USA • 4 specimens, syntypes of *Microporella bifoliata* Ulrich & Bassler, 1904; Maryland, Cordova; Miocene; Choptank Formation; USNM 68592C to 68592F.

Description

COLONY. Erect with bifoliate fronds up to several cm wide, curved; colony base and interzooidal communication not observed.

AUTOZOIDS. Distinct, separated by narrow grooves, rectangular, longer than wide (mean L/W = 1.76). Frontal shield flat; marginal areolae typically numbering about 16 (12–18), variable in size (15–40 µm), funnel-shaped, sometimes subdivided internally; reduced number of non-marginal pseudopores, placed more centrally on the frontal shield, irregularly spaced.

PRIMARY ORIFICE. Terminal, semielliptical, widest medially, hingeline slightly concave, without teeth or condyles; oral spines lacking; no peristome.

ASCOPE FIELD. A narrow, raised area of gymnocystal calcification beneath level of adjacent frontal shield but at approximately same level as orifice, located very close to its hingeline; elliptical, ca $35 \times 50 \mu\text{m}$, distal margin with projecting, semielliptical tongue leaving a crescent-shaped opening, ca $10 \times 30 \mu\text{m}$, with radial spines.

AVICULARIUM. Single, located at the same level of ascopore, oriented laterally; crossbar complete; opesia semielliptical; rostrum subtriangular, the distal end a little rounded, not channelled.

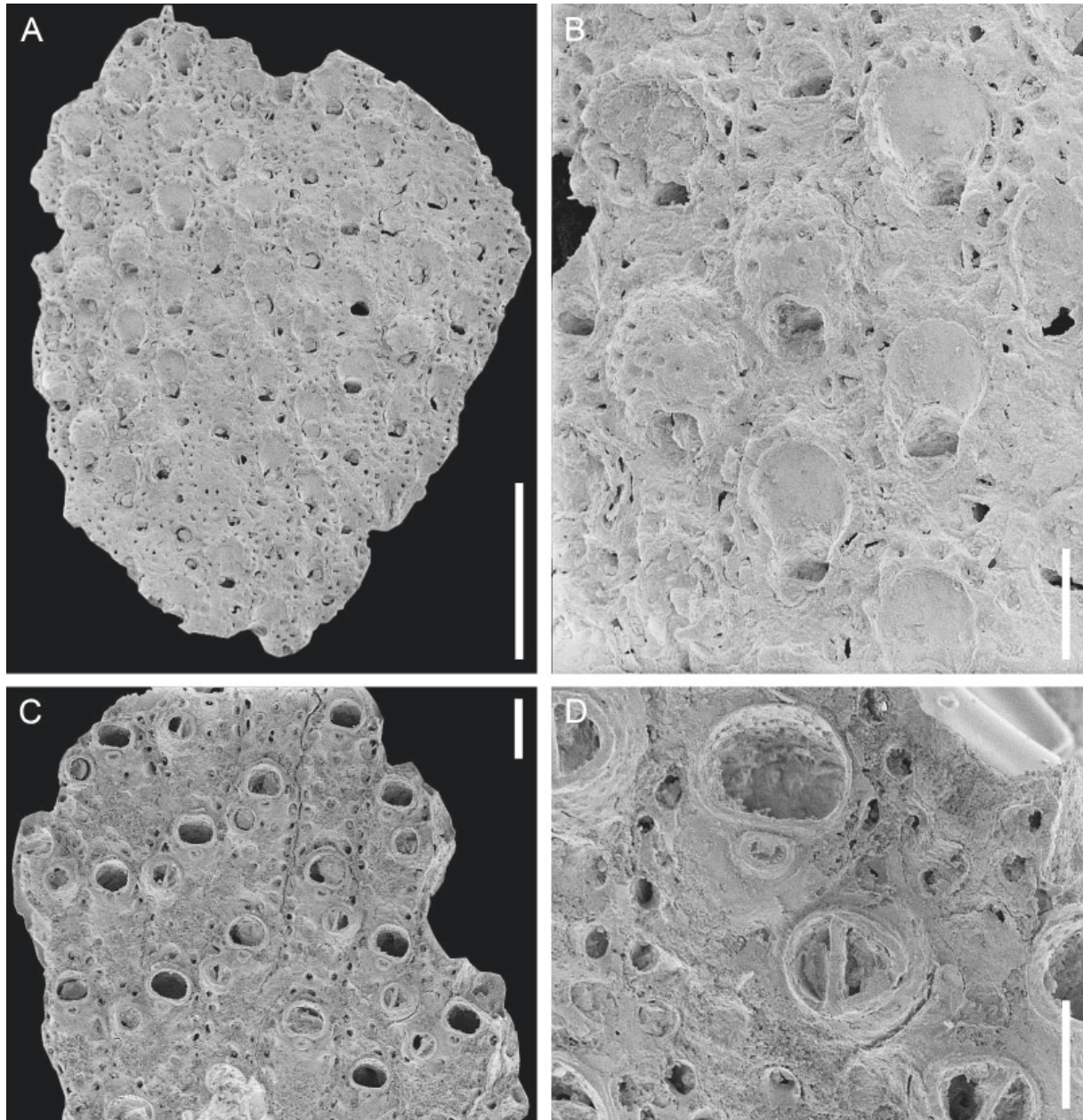


Fig. 1. *Microporella bifoliata* Ulrich & Bassler, 1904, Miocene, Choptank Formation, Maryland, USA. **A–B.** Lectotype USNM 68592A. **A.** General view of the branch fragment. **B.** Group of zooids, mostly ovicellate. **C–D.** Paralectotype USNM 68592B. **C.** Group of autozooids. **D.** Close-up of an autozooid. Scale bars: A = 1 mm; B–C = 200 μm ; D = 100 μm .

Table 1. Measurements in μm of *Microporella bifoliata* Ulrich & Bassler, 1904, Miocene, Choptank Formation, Maryland, USA; lectotype USNM 68592A, paralectotype USNM 68592B.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	16, 2	509	± 73	385	662
ZW	16, 2	290	± 27	245	330
OL	10, 2	91	± 4	85	98
OW	10, 2	114	± 9	102	126
AvL	16, 2	104	± 12	78	122
AvW	16, 2	86	± 14	62	116
OvL	8, 1	243	± 12	231	261
OvW	8, 1	273	± 27	238	312

OVICELL. Prominent, circular in outline, not personate and not obscuring orifice; calcification similar to frontal shield; pseudopores variable in number, scattered over entire surface, variably spaced.

Remarks

This extinct species was described from the Miocene (Choptank Formation 12.6–14.4 Ma; Andrews 1988) of Maryland (Fig. 1).

The form of the mandible is not known in this fossil species, but the fact that the avicularia have closed distal ends without channels may suggest that mandibles were not setose and had a shape identical to that of the rostrum.

Microporella tanyae sp. nov.

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Figs 2–3; Table 2

Diagnosis

Colony erect, bifoliate; branches broad. Autozooids rhomboidal. Frontal shield granular, sparsely pseudoporous. Orifice transversely D-shaped; hingeline straight, smooth; oral spines lacking. Ascopore elliptical, opening crescentic with projecting tongue and radial spines. Avicularium single, placed level with ascopore, oriented distolaterally; crossbar complete; opesia semielliptical; rostrum channelled. Ovicells not personate.

Etymology

Named after Dr Tanya Knowles who collected the specimens in 2006.

Material examined

Holotype

USA • Virginia, Chuckatuck; 2006; Tanya Knowles leg.; Pliocene; Upper Yorktown Formation; NHMUK PI BZ 8890 (Fig. 3).

Other material

USA • 1 specimen; Virginia, lower York County, Krause Pit; Edgar Campbell Col.; Pliocene; Yorktown Formation; USNM 387373 (Fig. 2).

Description

COLONY. Starting with an encrusting unilaminar and multiseriate base, later becoming erect with bifoliate fronds up to several cm wide; interzooidal communication not observed.

AUTOZOIDS. Distinct, separated by narrow grooves, rhomboidal, longer than wide (mean $L/W = 1.39$). Frontal shield moderately convex, finely and densely granular; marginal areolae typically numbering about 10 (8–12), variable in size (15–60 μm), funnel-shaped, sometimes subdivided internally; up to about eight non-marginal pseudopores, morphologically very similar to areolar pores, generally placed more centrally on the frontal shield at the same level as the avicularium or slightly below, irregularly spaced, sometimes internally subdivided.

PRIMARY ORIFICE. Terminal, transversely D-shaped, widest medially, hingeline straight, smooth, without teeth or condyles; oral spines lacking; no peristome.

ASCOPE FIELD. A narrow, raised area of gymnocystal calcification beneath level of adjacent frontal shield but at approximately same level as orifice, located very close to its hingeline; elliptical, ca 30–

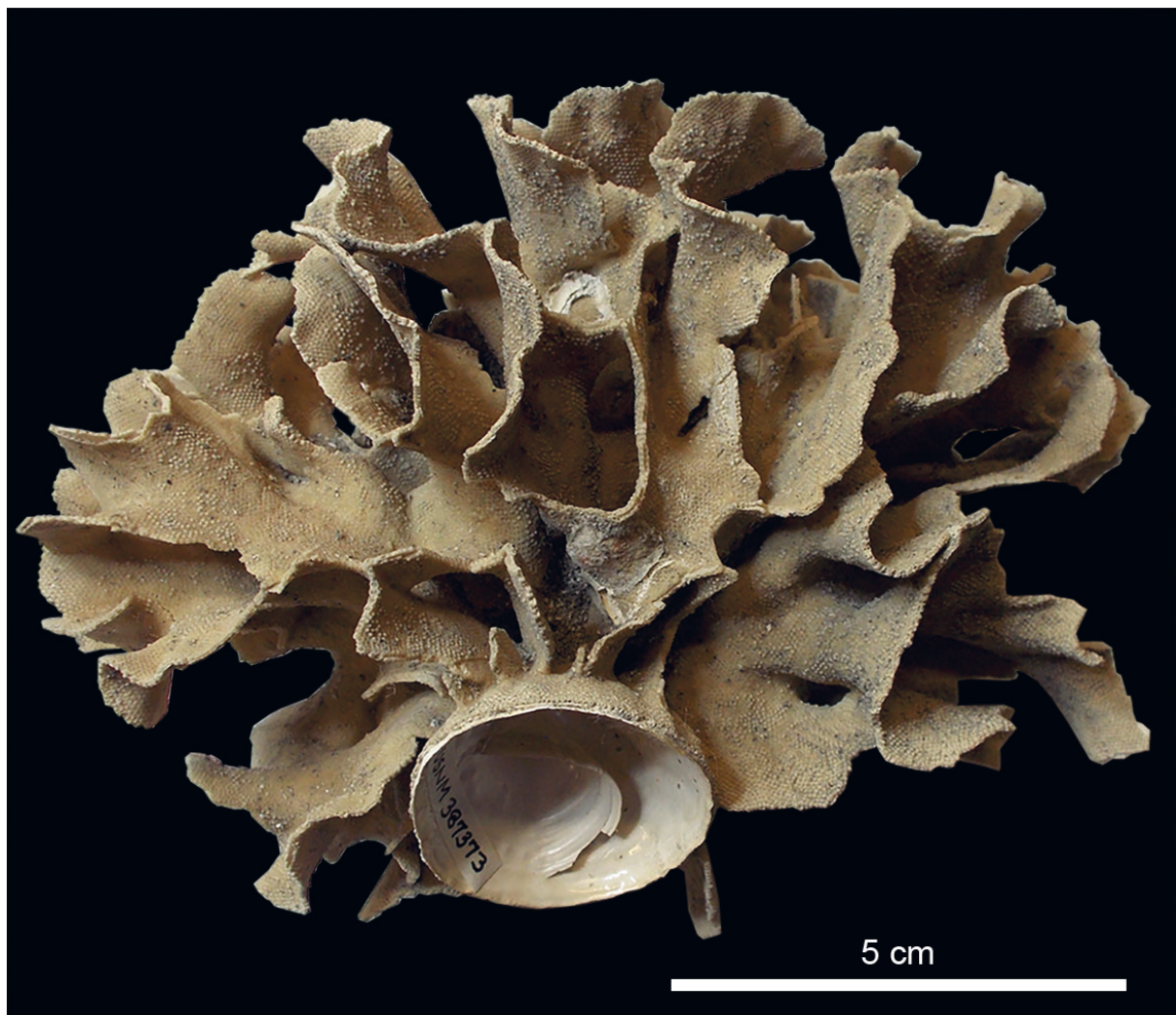


Fig. 2. Colony of *Microporella tanyae* sp. nov. USNM 387373, Pliocene, Yorktown Formation, Krause Pit, lower York County, Virginia, USA (Edgar Campbell Col.).

Table 2. Measurements in μm of *Microporella tanya* sp. nov., Pliocene, Yorktown Formation, Virginia, USA; holotype NHMUK PI BZ 8890.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	16, 1	526	± 53	441	621
ZW	16, 1	378	± 51	307	466
OL	12, 1	115	± 5	106	122
OW	12, 1	142	± 5	137	152
AvL	16, 1	130	± 9	116	147
AvW	16, 1	94	± 6	85	102
OvL	5, 1	250	± 16	235	276
OvW	5, 1	349	± 31	304	389

$35 \times 50\text{--}60 \mu\text{m}$, distal margin with projecting, semielliptical tongue leaving a crescent-shaped opening, ca $5\text{--}10 \times 25\text{--}35 \mu\text{m}$, with radial spines.

AVICULARIUM. Single, located between level of ascopore and lateral corner of rhomboidal autozoooid, oriented laterally to slightly distolaterally; crossbar complete; opesia semielliptical; rostrum subtriangular, channelled.

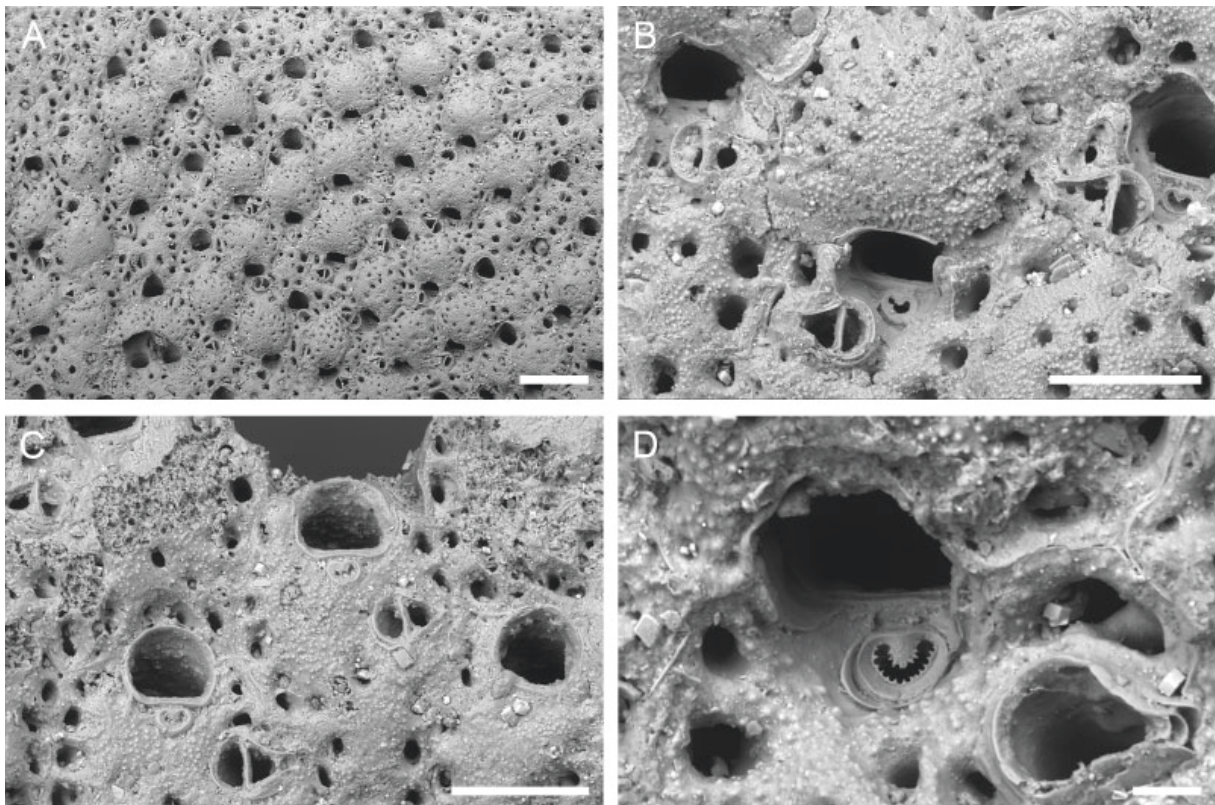


Fig. 3. *Microporella tanya* sp. nov., holotype, NHMUK PI BZ 8890, Pliocene, Yorktown Formation, Virginia, USA. **A.** Group of ovicellate and non-ovicellate zooids. **B.** Close-up of an ovicell. **C.** Close-up of an autozoooid. **D.** Close-up of the ascopore and avicularium with intramural buds. Scale bars: A = $400 \mu\text{m}$; B–C = $200 \mu\text{m}$; C = $200 \mu\text{m}$; D = $40 \mu\text{m}$.

OVICELL. Prominent, circular in outline, not personate and not obscuring orifice; calcification similar to frontal shield, impinging on avicularium of distal autozoid; pseudopores variable in number, confined to marginal areas.

Remarks

This extinct species was found in the Pliocene of Virginia. Although very similar to the Miocene *Microporella bifoliata*, the new Pliocene species shows slightly shorter but wider, and consequently squatter, autozooids with larger orifices, larger avicularia and broader ovicells. Additionally, the rostrum in *M. tanya* sp. nov. narrows distinctly immediately distal to the crossbar, which does not seem to be the case in *M. bifoliata* specimens, and the orifice seems to be more clearly D-shaped with the proximal margin somewhat straighter.

Microporella hastigera (Busk, 1884)

Figs 4–5; Table 3

Flustramorpha hastigera Busk, 1884: 136, text-fig. 40, pl. 21, figs 7, 7a–c.

Diporula hastigera – Waters 1888: 23, pl. 3, figs 28–29. — Jullien & Calvet 1903: 51, pl. 1, fig. 3, pl. 6, fig. 3. — Calvet in Jullien & Calvet 1903: 129. — Calvet 1907: 407.

Microporella hastigera – Calvet 1931: 87. — d’Hondt 1975: 577 (listed).

Material examined

Lectotype (designated here)

AZORES • Unbleached branch fragment figured by Busk (1884: pl. 21, fig. 7a); near Pico Island; [38°38' N, 28°28' W]; depth 450 fms (ca 823 m); HMS Challenger Expedition 1873–1876, St. 75; volcanic mud; NHMUK 1887.12.9.547 (Fig. 4).

Paralectotype (designated here)

AZORES • Bleached branch fragment; same collection data as for lectotype; NHMUK 1887.12.9.549a (Fig. 5).

Description

COLONY. With an encrusting unilaminar and multiseriate base, later becoming erect bilaminar, robust branching (adeoniform); branches narrow, 2–3 mm wide with usually 4–5 but up to eight linear series of alternating zooids on each side; interzooidal communication via multiporous septula.

AUTOZOIDS. Rhomboidal to hexagonal, longer than wide (mean L/W = 1.21). Frontal shield relatively flat to moderately convex, entirely covered by distinct nodules of varying shape with 30–35 pseudopores (diameter 5–15 µm) intercalated between them, plus 5–10 round marginal areolar pores, larger than frontal pores (diameter 20–45 µm); except for a single areolar pore distal to avicularium rostrum, area between proximal margin of the orifice and ascopore field and directly proximally to avicularium rostrum usually devoid of pores.

PRIMARY ORIFICE. Transversely D-shaped with a straight, distinctly crenulated hingeline; in each corner a short, blunt denticle directed distally; distolateral orificial rim with numerous low rounded and irregularly distributed denticles of variable size; operculum smooth but with a broad and slightly bent transverse depression in the centre; three or four distal oral spines (diameter 15–20 µm); no peristome.

ASCOPE FIELD. Outlined by a low rim and a narrow, raised band of gymnocystal calcification, located at ca 65 µm from hingeline of the orifice, slightly displaced to the side by the avicularium and often

obliquely aligned; gymnocystal field elliptical, ca $50\text{--}60 \times 70\text{--}80 \mu\text{m}$; distal margin with median, subrectangular, projecting tongue leaving a C-shaped opening, ca $10 \times 50 \mu\text{m}$, delimited by finely spinose margins.

AVICULARIUM. Single, placed in close proximity of and lateral or proximolateral to ascopore; rostrum directed distolaterally, broadly triangular with an open funnelled tip and thin raised lateral margins,

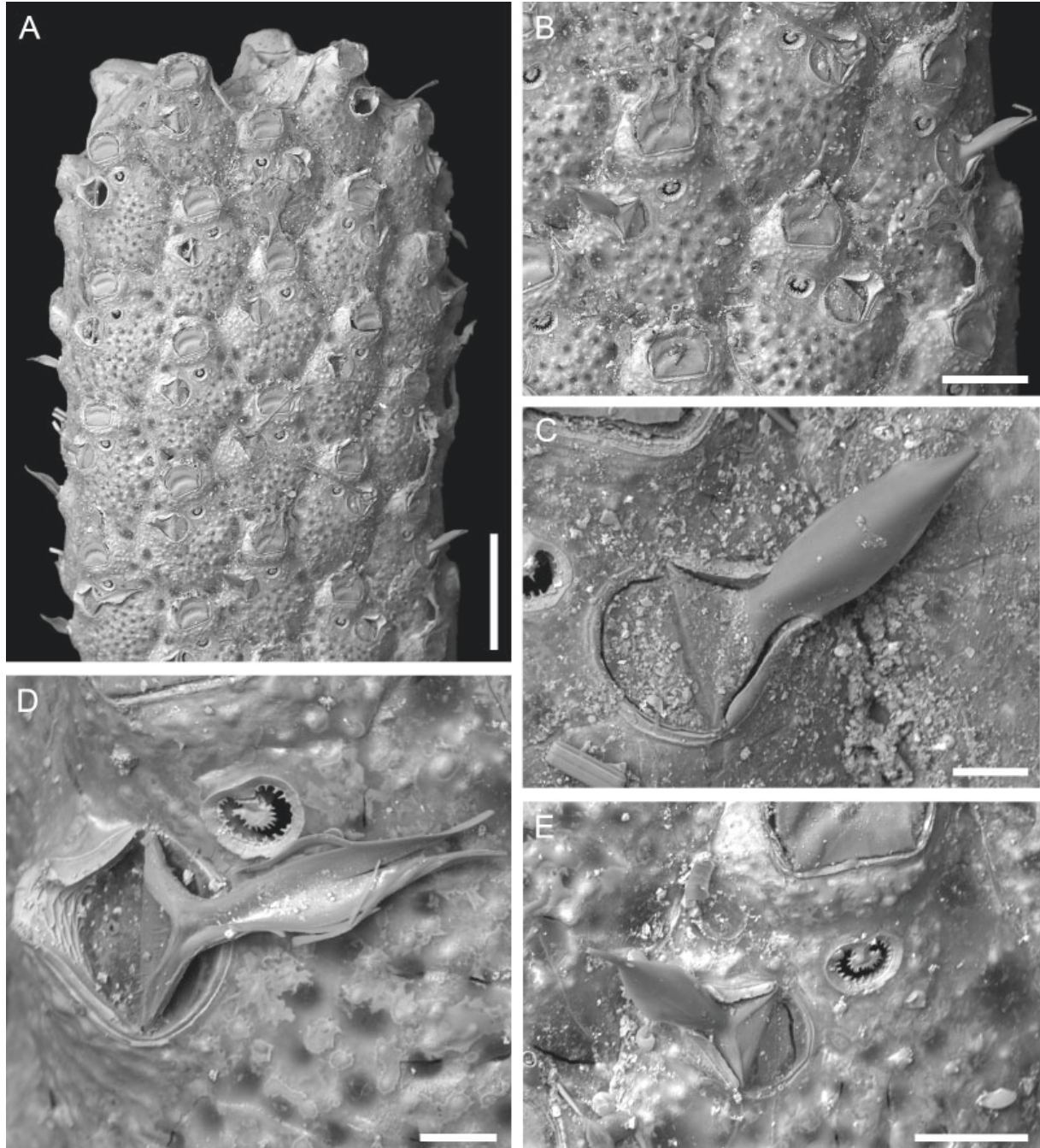


Fig. 4. *Microporella hastigera* (Busk, 1884), lectotype, NHMUK 1887.12.9.547 (unbleached), Recent, Challenger Expedition, St. 75. **A.** Group of zooids at the branch tip. **B.** Close-up of autozooids. **C–E.** Close-ups of the ascopore and adventitious avicularium with the lanceolate mandible either closed (C, E) or open (D). Scale bars: A = $500 \mu\text{m}$; B = $200 \mu\text{m}$; C–D = $50 \mu\text{m}$; E = $100 \mu\text{m}$.

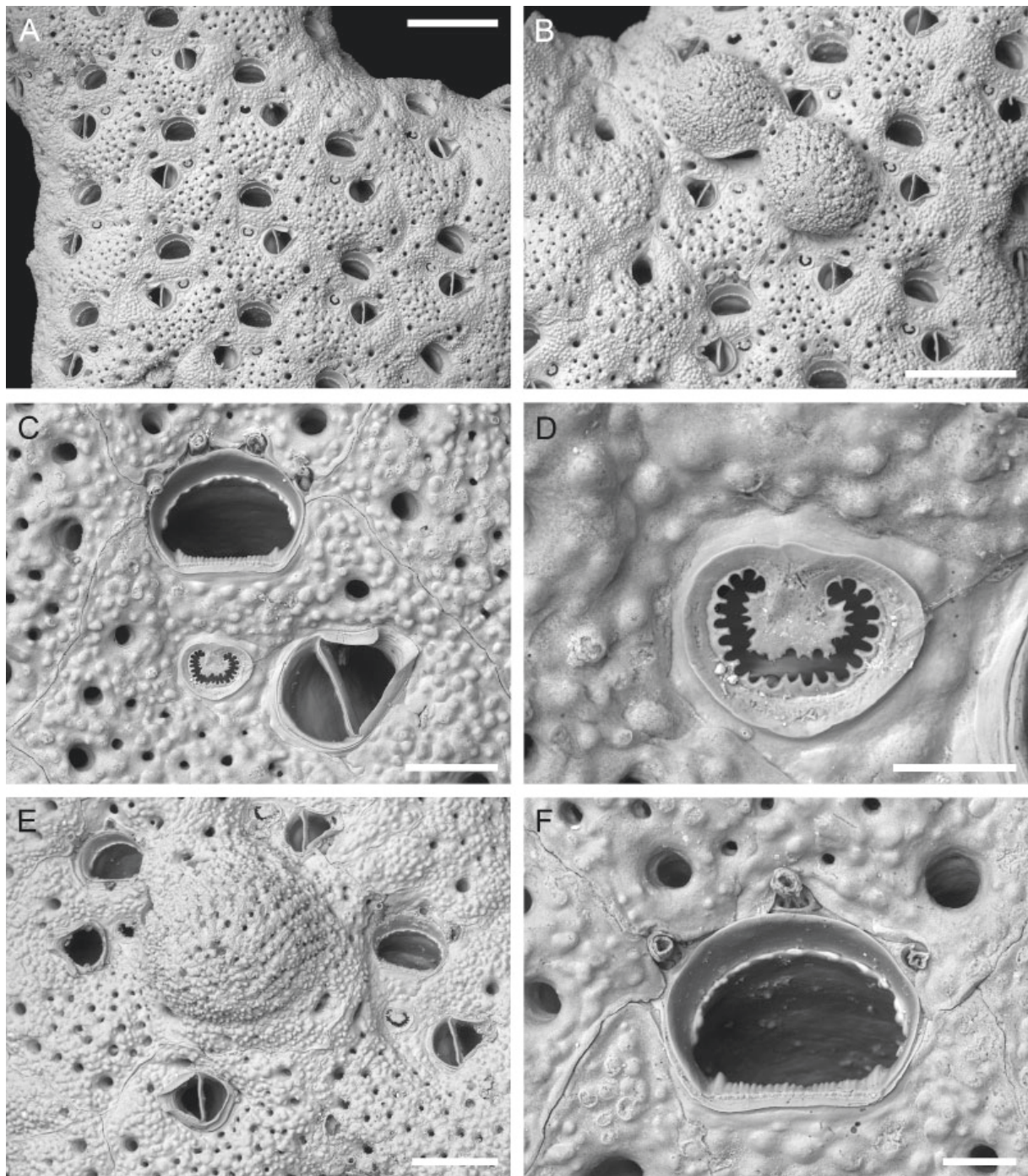


Fig. 5. *Microporella hastigera* (Busk, 1884), paralectotype, NHMUK 1887.12.9.549a (bleached), Recent, Challenger Expedition, St. 75. **A.** Group of zooids at branch bifurcation. **B.** Close-up of two ovicellate zooids with coalescent ovicells. **C.** Close-up of an orifice with four oral spine bases distally, ascopore and avicularium. **D.** Close-up of the ascopore. **E.** Ovicellate zooid with sealed orifice. **F.** Close-up of an orifice with three oral spine bases distally. Scale bars: A–B = 400 μm ; C = 100 μm ; D = 40 μm ; E = 200 μm ; F = 50 μm .

Table 3. Measurements in μm of *Microporella hastigera* (Busk, 1884), Recent, Challenger Expedition, St. 75; lectotype NHMUK 1887.12.9.547 and paralectotype NHMUK 1887.12.9.549a.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	25, 2	604	± 51	541	703
ZW	25, 2	497	± 48	400	572
OL	15, 2	129	± 7	115	138
OW	15, 2	165	± 8	145	175
AvL	25, 2	156	± 11	127	176
AvW	25, 2	132	± 6	124	145
OvL	3, 1	399	± 13	388	413
OvW	3, 1	436	± 32	414	473

slightly acute to frontal plane; mandible lanceolate, significantly exceeding length of rostrum, ca 230 μm long, abruptly decreasing in width between crossbar and rostrum and slightly widening distal to rostrum before thinning again, the distal third or quarter very narrow and downcurved; proximal and distal opesia semicircular, divided by a straight and thin but deep crossbar.

OVICELLS. Globular, entirely obscuring the orifice; surface densely nodular and with numerous pseudopores seemingly aligned in radial rows, the proximolateral margins joining the proximolateral orifice corners, opening arched above proximal orifice margin, often equipped with a slightly projecting lip.

Remarks

This species was originally recorded from off western and northern Pico Island (Azores, central Atlantic) from depths between 80 and 820 m. During the French *Biaçores* expedition it was also reported from around the islands of Flores (105–170 m), Graciosa (190–406 m), São Jorge (245 m), Terceira (90–220 m) and São Miguel (61–550 m), as well as the Formigas Islets south of São Miguel (190–220 m) (d'Hondt 1975). Previous records of this species, especially those pre-dating the advent of scanning electron microscopy (e.g., Calvet (1931) from Cape Verde Islands at 52 m depth), need to be revised.

Microporella hyadesi (Jullien, 1888)

Fig. 6; Table 4

Fenestrulina hyadesi Jullien, 1888: 44, pl. 4, fig. 7 (given as *Fenestrula* in text but *Fenestrulina* on plate and caption).

Microporella hyadesi – López-Gappa 1975: 435, pl. 1, fig. 1, pl. 2, fig. 3. — López-Gappa & Lichtschein 1990: 26, pl. 8, fig. 3. — Hayward & Ryland 1990: 1282, fig. 10a. — Moyano 2000: table 1.

non *Microporella hyadesi* – Brown 1952: 254, figs 186–187.

Material examined

FALKLAND ISLANDS • 1 specimen; depth 74–75 m; 24 Mar. 1927; Discovery Expedition, St. WS 84; Recent; NHMUK 1990.10.22.14 (Fig. 6A–D) • 1 specimen; depth 166 m; 20 Jul. 1928; Discovery Expedition, St. WS 249; Recent; NHMUK 1990.10.10.25 (Fig. 6E–F) • 1 specimen; west end of Magellan Strait; depth 66 m; 16 Mar. 1934; Discovery Expedition, St. 1321; Recent; NHMUK 1990.10.31.12 (Fig. 6G).

Table 4. Measurements in μm of *Microporella hyadesi* (Jullien, 1888), Recent, Discovery Expedition; NHMUK 1990.10.22.14, NHMUK 1990.10.31.12.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	22, 2	741	± 84	662	972
ZW	22, 2	443	± 45	359	506
OL	22, 2	110	± 4	102	119
OW	22, 2	190	± 13	167	225
AvL	22, 2	114	± 8	100	127
AvW	22, 2	101	± 11	86	125
OvL	22, 2	465	± 38	394	543
OvW	22, 2	472	± 29	426	527

Description

COLONY. Erect, bifoliate, broad branches fused at edges to form a boxwork colony; growing edge intermediate between a smooth and a stepped edge; interzooidal communication not observed.

AUTOZOIDS. Rounded rectangular to hexagonal, longer than wide (mean L/W = 1.67), distinct with interzooidal boundaries marked by thin band of slightly raised calcification on either side of a narrow groove. Frontal shield flat to very slightly convex, pustulose; marginal areolar pores numbering about 10, elongate near growing edge, becoming smaller, equidimensional and almost indistinguishable from pseudopores, except for those at the proximolateral corners of the zooid which remain larger (diameter 20–40 μm); pseudopores numerous (about 50), small (diameter 5–15 μm), irregularly scattered among pustules.

ORIFICE. Transversely D-shaped, significantly wider than long, hingeline with about 20 equal-sized teeth; oral spines lacking.

ASCOPE FIELD. A narrow band of gymnocystal calcification, positioned at approximately same level as orifice but slightly depressed relative to the adjacent frontal shield, located ca 50–60 μm from the orifice hingeline, separated from it by non-porous pustulose cryptocyst; circular to transversely elliptical (diameter 50–60 \times 60–70 μm), opening C-shaped, 5–10 \times 35–40 μm , with tiny radial denticles, and a circular tongue projecting from distal edge.

AVICULARIUM. Single, moderately large, present in the majority of autozooids, sometimes lacking in smaller zooids, especially immediately following row bifurcations; positioned level with the ascopore, oriented distolaterally, usually at about 60° to the long axis of the autozooid; crossbar calcified; opesia semielliptical; rostrum short, broadly subtriangular with concave sides, the distal end rounded, distinct channel present. Mandible in dried material narrow, short (ca 50–65 μm) and pointed triangular.

OVICELLS. Very large, sometimes covering frontal shield of distal zooid as far as ascopore, bulbous, usually a little longer than wide, personate or semi-personate with variably-developed lobes extending proximally of orifice, calcification fabric similar to frontal shield but with finer pustulation, smoothly continuous with frontal shield of distal zooid; small pores scattered over entire surface, denser close to lateral and distal margins; secondary orifice of personate ovicellate zooids of reduced length, typically boat-shaped, the distal edge concave, the proximal edge convex.

Remarks

This species has been recorded from the subantarctic, Cape Horn and Tierra del Fuego. Records from the Indian Ocean (Thornely 1912) and New Zealand (Brown 1952; Powell 1967) are probably misidentifications, the latter possibly *M. ordo* (see Di Martino *et al.* 2017: fig. 6). It is very common

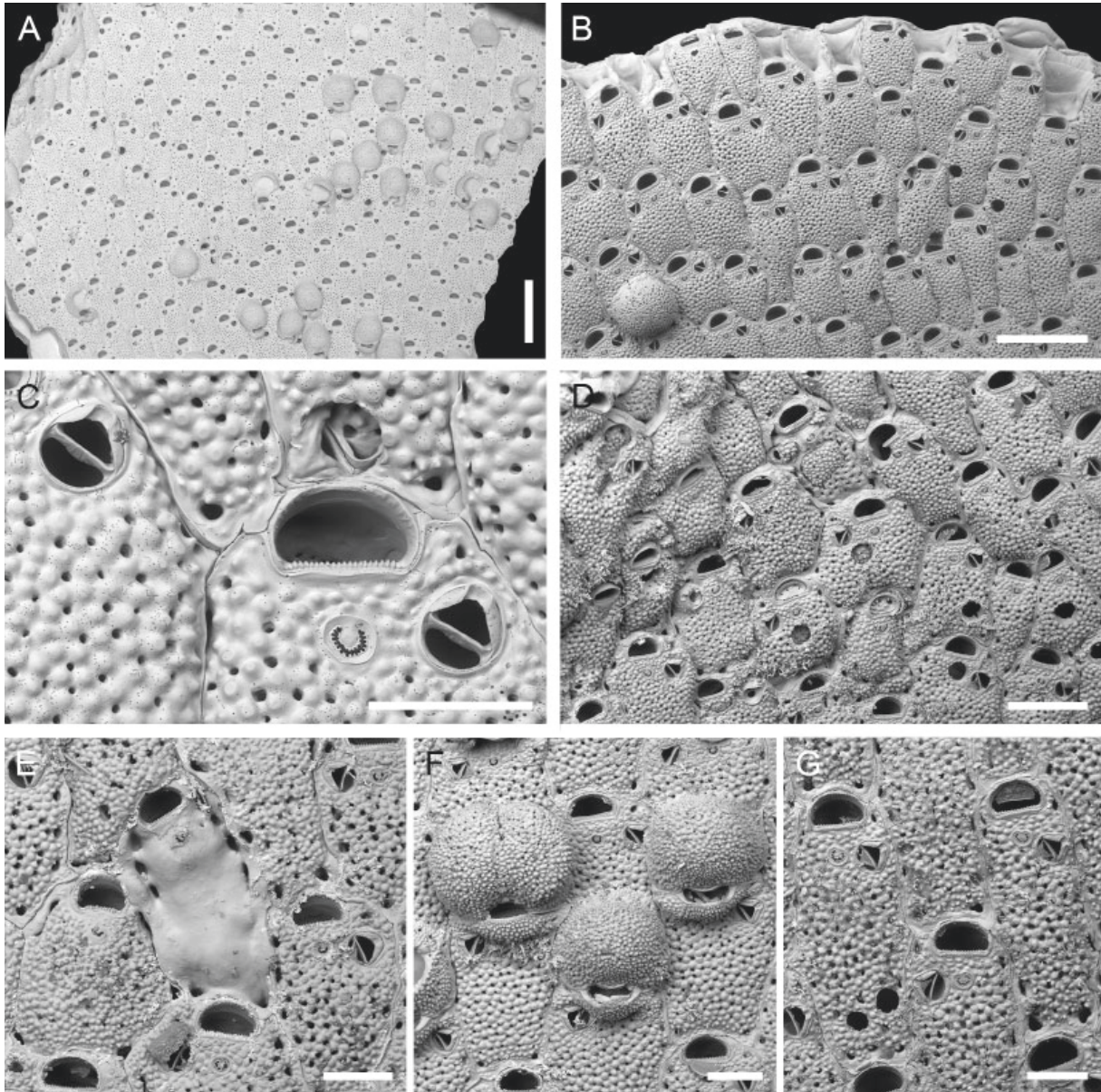


Fig. 6. *Microporella hyadesi* (Jullien, 1888), Recent, Discovery Expedition. **A–D.** NHMUK 1990.10.22.14. **A.** General view of a branch fragment. **B.** Group of zooids, one ovicellate, at the growing edge of the branch. Note the growing edge intermediate between a smooth and a stepped edge. **C.** Close-up of the orifice, ascopore and adventitious avicularia. Note also the borehole patched by an avicularium (top centre). **D.** Group of zooids showing several repaired boreholes and sealed orifices. **E–F.** NHMUK 1990.10.10.25. **E.** Aberrant autozooid with smooth, non-pseudoporous frontal shield. **F.** Close-up of three ovicellate zooids, the ovicell on the left showing teratology. **G.** NHMUK 1990.10.31.12, autozooids with adventitious avicularia preserving triangular mandibles. Scale bars: A–B = 1 mm; C, E–G = 200 μ m; D = 400 μ m.

in material from several widely dispersed Discovery Stations from depths of 49 to 341 m in the South Atlantic around Cape Horn, the Falkland Islands, Burdwood Bank, the southern Patagonian Shelf, Shag Rocks and South Georgia (Hayward & Ryland 1990). Many of the colonies show extensive circular boreholes, about 0.12 mm in diameter, which penetrate autozooidal frontal shields and ovicells (Fig. 6C–D). Similar boreholes were interpreted by Wilson & Taylor (2006) as evidence of boring predation. Often the boring is repaired by a plug of calcification secreted from the underside, or by an adventitious avicularium (Fig. 6C). Bored zooids may possess an additional orificial rim with a new hingeline within the original orifice, representing intramural budding, or have a sealed orifice (Fig. 6D). Teratology was observed in both autozooids (Fig. 6E) and ovicells (Fig. 6F).

***Microporella ordo* Brown, 1952**

Fig. 7; Table 5

Microporella ordo Brown, 1952: 257, figs 189–193.

Microporella ordo – Powell 1967: 291, text-fig. 54.

Material examined

Holotype

NEW ZEALAND • Wanganui, Castlecliff; NZGS Loc. 4013; late Pleistocene; Castlecliffian Horizon CU3 (ca 0.55 myr); NHMUK D36809 (figured in Di Martino *et al.* 2017: fig. 5).

Additional material (figured)

NEW ZEALAND • Fragment from large colony, bleached; Spirits Bay; Recent; NIWA 144880 (Fig. 7A–C) • Fractured section; Recent; NIWA 144881 (Fig. 7D) • Fragment 2, unbleached; Spirits Bay; Recent; NIWA 144882 (Fig. 7E–F).

Additional material (not figured)

NEW ZEALAND • 1 specimen; [33.9655° S, 171.7723° E]; depth 92–96 m; St. TAN1105/42; Recent; NIWA 73196 • 2 specimens; [37.5947° S, 178.8660° E]; depth 56–58 m; St. TAN1108/239; Recent; NIWA 75495, 75499 • 1 specimen; [34.3780° S, 172.7100° E]; depth 48 m; St. KAH9901/45; Recent; NIWA 99099 • 1 specimen; [34.3782° S, 173.0265° E]; depth 64–65 m; St. TAN0906/170; Recent; NIWA 56945 • 1 specimen; [34.3813° S, 172.6618° E]; depth 54 m; St. KAH9901/69; Recent; NIWA 99072 • 1 specimen; [34.3690° S, 172.8250° E]; depth 55 m; St. KAH9901/25; Recent; NIWA 114233 • 1 specimen; [34.3600° S, 172.6968° E]; depth 46 m; St. KAH9901/31; Recent; NIWA 128424.

Description

COLONY. Erect, bifoliate, the largest about 110 × 75 mm, with broad branches fused at edges to form a boxwork colony; interzooidal communication via multiporous septula, elliptical, 55 µm long by 45 µm wide, with at least 12 circular pores ca 4 µm in diameter, placed in the basal lateral walls on distolateral corners of autozooids.

AUTOZOIDS. Distinct with interzooidal boundaries marked by narrow grooves, rounded rectangular to hexagonal, longer than wide (mean L/W = 1.63). Frontal shield flat to very slightly convex, pustulose, the pustules about 20–30 µm in diameter; marginal areolae numbering about 10, elongate near growing edge (25–45 µm long by 15–20 µm wide), becoming indistinguishable from frontal pores in older zooids; non-marginal pseudopores moderately large (diameter 8–18 µm), numbering about 20–30, arranged semi-regularly.

Table 5. Measurements in μm of *Microporella ordo* Brown, 1952, Recent, Spirits Bay, New Zealand; NIWA 144880, 144882.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 2	517	± 31	457	557
ZW	20, 2	318	± 36	234	378
OL	20, 2	96	± 5	84	104
OW	20, 2	151	± 7	130	160
AvL	20, 2	86	± 7	72	107
AvW	20, 2	80	± 6	71	91
OvL	9, 1	406	± 26	362	446
OvW	9, 1	390	± 13	374	404

ORIFICE. Semielliptical, significantly wider than long, hingeline straight to weakly concave, with about 15 teeth, equal in size except for slightly longer outer one or two pairs; oral spines lacking; folded back transverse vertical wall of distal zooid forming a slightly elevated crescent secondary rim above the distal margin of the primary orifice; operculum smooth.

ASCOPE FIELD. As a raised area of gymnocystal calcification at approximately same level as orifice but beneath level of adjacent frontal shield, located moderately close to orifice hingeline, about 60–70 μm below, separated from it by non-porous pustulose cryptocyst; reniform to transversely elliptical, 45 \times 60 μm , opening heart-shaped, 25 \times 40 μm , covered by filigree sieve plate, a narrow, bifurcated tongue usually projecting from the distal edge.

AVICULARIUM. Single, moderately large, present in the majority of autozooids, positioned level with or slightly distally of and almost abutting the ascopore, oriented distolaterally to almost laterally; crossbar complete; opesia semielliptical; rostrum short, teat-shaped, the distal end rounded, distinct channel present. Mandible in dried material with short (ca 90–110 μm) pointed seta, narrow throughout, hooked on underside, lying across or a little proximal of ascopore when open.

OVICELLS. Very large, often covering frontal shield of distal zooid as far as ascopore, bulbous, subcircular or a little longer than wide, non-personate; calcification similar to frontal shield but with finer pustules, continuous with frontal shield of distal zooid; small pseudopores distributed across entire surface, more closely spaced compared to those on the frontal shield, radially aligned near margins; orifice of ovicellate zooids hidden in frontal view.

Remarks

The description given above and measurements in Table 5 are based on Recent examples of this species which show the morphology of the species better than the type and other fossil material. Although very similar to *Microporella hyadesi* in its general appearance, *M. ordo* is easily distinguished by its heart-shaped ascopore with filigree sieve plate and narrow bifurcated tongue, in addition to the non-personate ovicells.

The present-day range of the species extends from NW of the Three Kings Islands at Middlesex Bank to Ranfurly Banks off East Cape, New Zealand (33.9–37.6° S; depth 46–96 m).

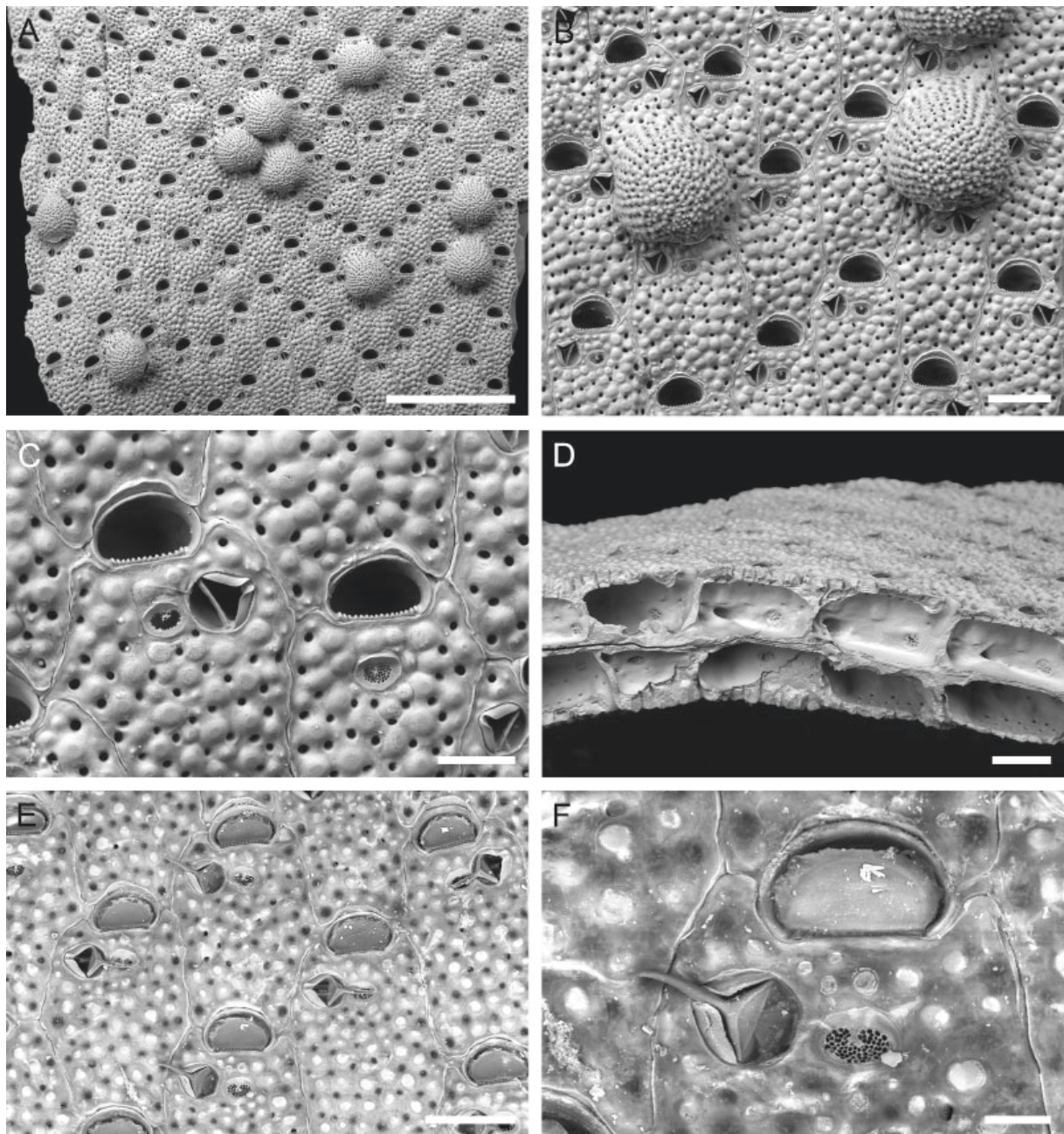


Fig. 7. *Microporella ordo* Brown, 1952, Recent, Spirits Bay, New Zealand. **A–C.** NIWA 144880. **A.** General view of a branch fragment. **B.** Group of ovicellate and non-ovicellate zooids. **C.** Close-up of two autozooids, that on the right with preserved filigree sieve plate. **D.** NIWA 144881, transversal view of the bifoliate branch showing multiporous septula. **E–F.** NIWA 144882. **E.** Group of unbleached autozooids showing opercula and thin, pointed avicularian mandibles. **F.** Close-up of the ascopore and the avicularian mandible. Scale bars: A = 1 mm; B, D–E = 200 μ m; C = 100 μ m; F = 50 μ m.

Microporella ordoides sp. nov.

urn:lsid:zoobank.org:act:D2F60F45-FFFC-4BA0-9682-FD7CE56CBC64

Fig. 8; Table 6

Diagnosis

Colony erect, bifoliate; branches narrow. Autozooids rhomboidal. Frontal shield pustulose, pseudoporous. Orifice semielliptical; hingeline with equal-sized teeth, the outermost smaller; oral spines lacking. Ascopore subcircular, opening horseshoe-shaped covered by a filigree sieve plate and a narrow tongue projecting from the distal edge. Avicularium single, placed level with ascopore, oriented distolaterally; crossbar complete; opesia semielliptical; rostrum channeled. Ovicells personate or semipersonate.

Etymology

Referring to its similarity with *Microporella ordo* Brown, 1952.

Material examined

Holotype

NEW ZEALAND • Bleached specimen; SE of Campbell Island on the Campbell Plateau; [52°56.4' S, 169°23' E]; [159 m]; NZOI St. D35; Recent; NIWA 144883 (Fig. 8A–D).

Paratypes (unbleached specimens)

NEW ZEALAND • 1 specimen; SE of Campbell Island on the Campbell Plateau; [53.2333° S, 171.8000° E]; [435 m]; St. F145; Recent; NIWA 119893 (Fig. 8E–F) • 1 specimen; SE of Campbell Island on the Campbell Plateau; [53.0917° S, 170.2167° E]; [380 m]; St. F143; Recent; NIWA 144885 (not figured).

Description

COLONY. Erect, bifoliate; the longest colony observed about 54 mm with the broadest frond about 15 mm, consisting of more than 30 linear series of alternating zooids; growing edge stepped; interzooidal communications not observed.

AUTOZOIDS. Distinct with interzooidal boundaries marked by narrow grooves, often bordered by salient vertical walls, rhomboidal, longer than wide (mean L/W = 1.30). Frontal shield convex, pustulose, the pustules about 20 µm in diameter; marginal areolae usually 6 or fewer, elongate, elliptical to drop-shaped, larger at corners of zooids (25–35 µm long by 15 µm wide); non-marginal pseudopores variable in size (diameter 3–15 µm), numbering over 50, arranged semi-regularly.

ORIFICE. Semielliptical, significantly wider than long, hingeline straight or somewhat convex, with about 17 teeth, equal-sized apart from the outermost few which are smaller; oral spines lacking; folded back transverse vertical wall of distal zooid forming a crescent above the distal part of the primary orifice.

ASCOPE FIELD. As a raised area of gymnocystal calcification at approximately same level as orifice but beneath level of adjacent frontal shield, located moderately close to orifice hingeline, about 60–70 µm below, separated from it by non-porous cryptocyst with smaller than average pustules; subcircular, 45–60 µm in diameter, opening horseshoe-shaped, 10–15 × 30–35 µm, covered by filigree sieve plate, a narrow, straight tongue usually projecting from the distal edge.

AVICULARIUM. Single, moderately large, present in the majority of autozooids; positioned level with or slightly proximally of ascopore, oriented distolaterally; crossbar complete; opesia semielliptical; rostrum short, teat-shaped, the distal end rounded, distinct channel present. Mandible 160–180 µm long, narrow and pointed.

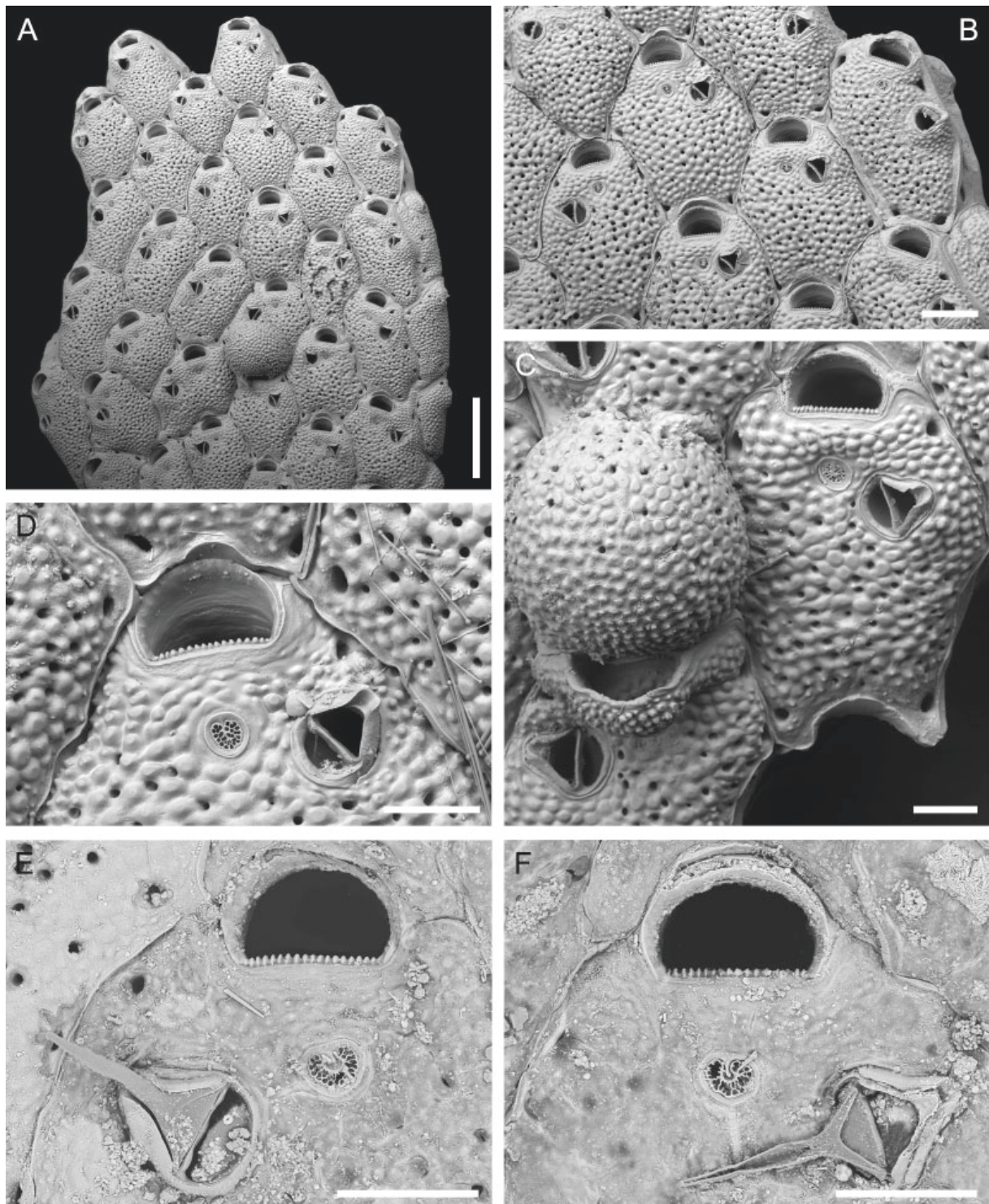


Fig. 8. *Microporella ordoides* sp. nov. **A–D.** Holotype NIWA 144883, Recent, New Zealand. **A.** Group of zooids at the branch tip. **B.** Close-up of autozooids. **C.** Close-up of the orifice, ascopore and adventitious avicularium. **D.** Close-up of an autozooid and ovicell. **E–F.** Paratype NIWA 119893 (unbleached), Recent, New Zealand. Two avicularia with closed and open mandible, respectively. Scale bars: A = 500 μm ; B = 200 μm ; C–D = 100 μm ; E–F = 150 μm .

Table 6. Measurements in μm of *Microporella ordoides* sp. nov., Recent, NZOI St. D35, New Zealand; holotype NIWA 144883.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	15, 1	631	± 58	522	729
ZW	15, 1	487	± 55	401	594
OL	15, 1	99	± 6	89	109
OW	15, 1	158	± 7	142	169
AvL	15, 1	127	± 12	99	141
AvW	15, 1	106	± 10	78	120
OvL	1, 1	367	–	–	–
OvW	1, 1	448	–	–	–

OVICELLS. Large, bulbous, subglobular or a little longer than wide, personate or semipersonate, proximal arms forming bridge above ascopore; calcification of similar fabric to frontal calcification, continuous with frontal shield of distal zooid; pores small, sparse, mostly located near margins; partly formed ovicells common; orifice of ovicellate zooids hidden in frontal view; secondary orifice of personate ovicells boat-shaped with convex proximal and concave distal edge.

Remarks

This new species is extremely similar to *Microporella ordo* but differs in a sufficiently large number of characters to justify recognition as a separate species. Colonies of *M. ordoides* sp. nov. have narrow branches, contrasting with the broad fronds of *M. ordo*, and the growing edge is stepped rather than smooth. Differences in zooidal morphology include the greater number of pseudopores in the frontal shield of *M. ordoides* sp. nov., smaller outer teeth on the hingeline of the orifice, a horseshoe-shaped ascopore opening, personate or semi-personate ovicells containing fewer pores, and avicularia tending to be located more proximally than in *M. ordo*. Specimens of *M. ordoides* sp. nov. were collected off Campbell Island (New Zealand) on the Campbell Plateau at a depth of 159–435 m.

Microporella lingulata sp. nov.

[urn:lsid:zoobank.org:act:A74444C9-3AA5-4A19-B08D-245169244E6A](https://doi.org/10.3897/zoobank.org/urn:lsid:zoobank.org:act:A74444C9-3AA5-4A19-B08D-245169244E6A)

Figs 9–10; Table 7

Diagnosis

Colony bifoliate, tongue-shaped. Ancestrula ascophoran with associated avicularium. Autozooids rounded quadrate. Frontal shield pustulose and pseudoporous; pustules flat-topped, pseudopores sometimes coalescent. Orifice transversely D-shaped; hingeline smooth; oral spines lacking. Ascopore reniform, opening crescentic, covered by a plate pierced by pores arranged in rows. Avicularium single, at level with ascopore, oriented laterally or slightly distolaterally; crossbar complete; rostrum subtriangular, not channeled. Ovicells not personate.

Etymology

From the Latin ‘*lingulata*’, meaning tongue-shaped and referring to the shape of the colonies.

Material examined

Holotype

NEW ZEALAND • Unbleached specimen; Foveaux Strait; [46°55.0' S, 168°24.0 E]; [53 m]; NZOI St. B263; Recent; NIWA 144886 (Fig. 9).

Paratypes

NEW ZEALAND • 1 specimen; same collection data as for holotype; NIWA 144887 (Fig. 10A–B) • 1 specimen; same collection data as for holotype; NIWA 144888 (Fig. 10C–D) • 1 specimen; same collection data as for holotype; NIWA 144889 (Fig. 10E–F).

Additional material (not figured)

NEW ZEALAND • 2 specimens; same collection data as for holotype; NIWA 144890, 144891.

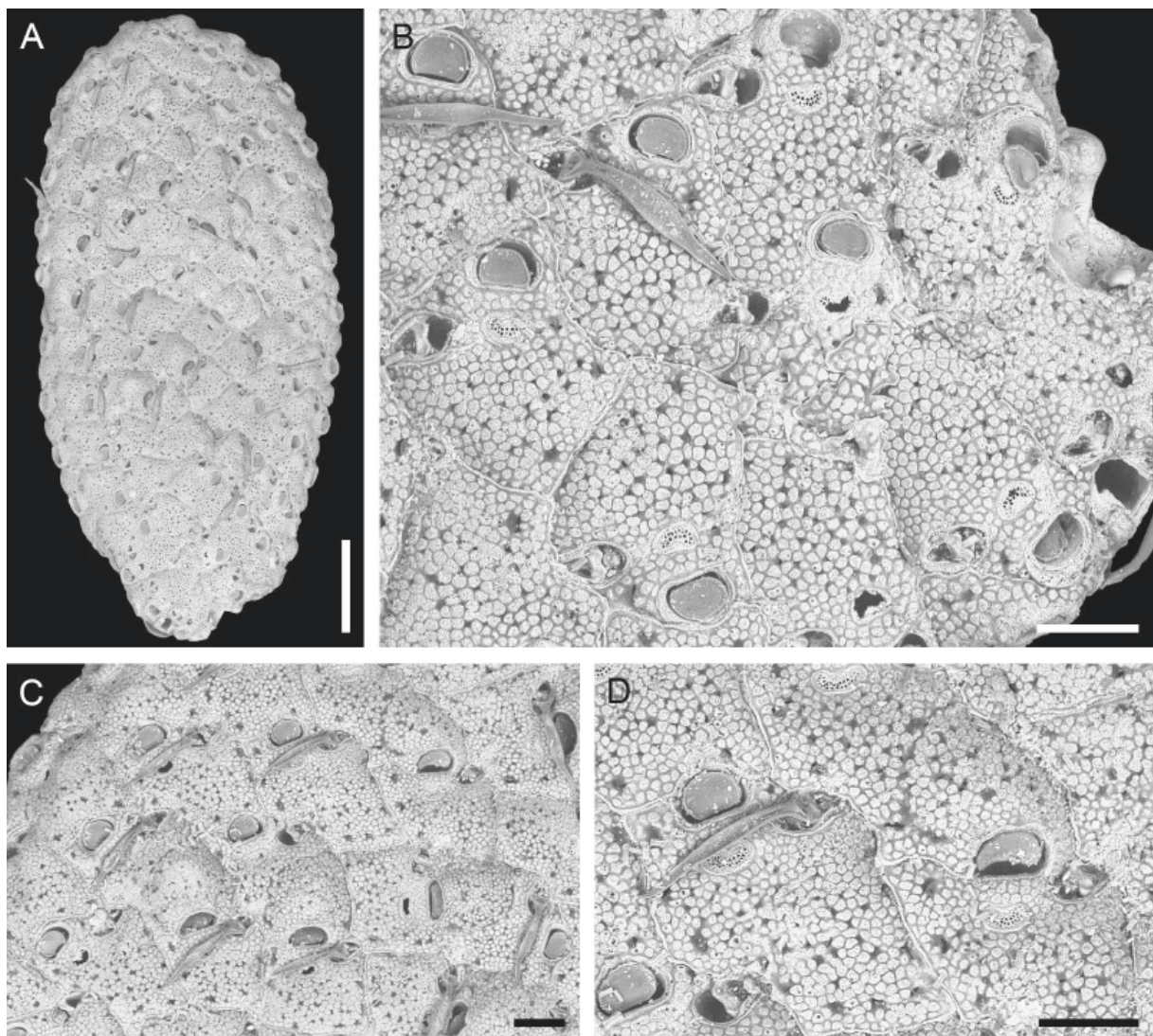


Fig. 9. *Microporella lingulata* sp. nov., holotype, NIWA 144886 (unbleached), Recent, Foveaux Strait, New Zealand. **A.** General view of the tongue-shaped colony. **B.** Apparent ancestrula and periancestrular zooids. **C.** Group of ovicellate and non-ovicellate zooids. Some avicularia show the long, lanceolate mandibles. **D.** Close-up of an autozooid, having the avicularian mandible open, and an ovicellate zooid (right). Scale bars: A = 1 mm; B–D = 200 μ m.

Description

COLONY. Erect, bifoliate, comprising a single, non-bifurcating branch, tongue-shaped, 4–6 mm long by 3–4 mm wide (0.5–1 mm at the tip), proximal end rounded, distal end truncate forming growing edge; basally unattached; interzooidal communications not observed. Apparent ancestrula ascophoran in morphology (damaged in scanned examples), about $300 \times 185 \mu\text{m}$, with an associated avicularium; located on one side of branch close to but not at proximal extremity of colony, oriented proximally. New buds at distal growing edge oriented obliquely to colony axis, facing distolaterally to the left on the left

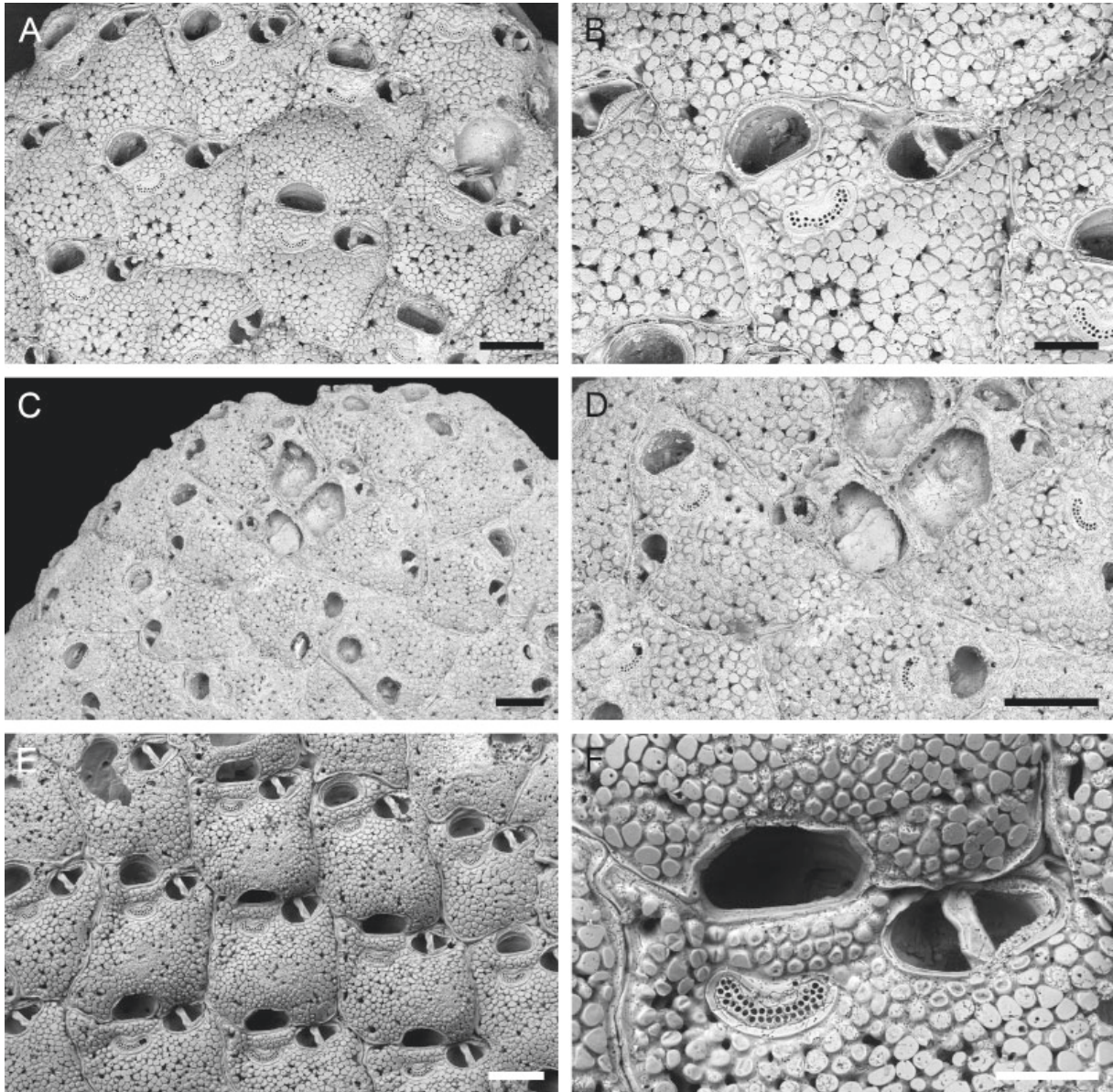


Fig. 10. *Microporella lingulata* sp. nov., paratypes, Recent, Foveaux strait, New Zealand. **A–B.** NIWA 144887. **A.** Group of ovicellate and non-ovicellate zooids. **B.** Close-up of an autozooid showing the reniform, cribrate ascopore. **C–D.** NIWA 144888. **C.** General view of the branch proximal tip including the ancestrular area. **D.** Close-up of damaged ancestrula and periancestrular zooids. **E–F.** NIWA 144889. **E.** Ovicellate zooids. **F.** Close-up of orifice, ascopore and avicularium in an ovicellate zooid. Scale bars: A, C–E = 200 μm ; B, F = 100 μm .

Table 7. Measurements in μm of *Microporella lingulata* sp. nov., Recent, Foveaux Strait, New Zealand; paratypes NIWA 144887, 144888, 144889.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 3	563	± 55	421	669
ZW	20, 3	441	± 52	342	570
OL	15, 3	95	± 10	83	115
OW	15, 3	138	± 19	118	180
AvL	20, 3	174	± 10	159	193
AvW	20, 3	108	± 8	96	127
OvL	15, 3	268	± 27	233	318
OvW	15, 3	406	± 36	347	468

side and distolaterally to the right on the right side; zig-zag seam between left- and right-facing zooids approximately parallel to axis but typically displaced from midline.

AUTOZOIDS. Distinct with interzooidal boundaries marked by narrow grooves, usually rounded quadrate, slightly torqued, longer than wide (mean $L/W = 1.28$). Frontal shield convex, pustulose, the pustules conspicuously flat-topped, about $20 \mu\text{m}$ in diameter; marginal areolae numbering about 8, elongate, larger at corners of zooids, ca $20\text{--}35 \mu\text{m}$ long by $10\text{--}15 \mu\text{m}$ wide; non-marginal pseudopores located in grooves between flat-topped pustules, irregularly arranged, variable in number and size (diameter $10\text{--}20 \mu\text{m}$), sometimes coalescent.

ORIFICE. Transversely D-shaped, significantly wider than long, hingeline straight or slightly convex, without teeth or condyles; oral spines lacking; operculum smooth.

ASCOPE FIELD. Bordered by a thick rim of gymnocystal calcification, located moderately close to orifice, about $70 \mu\text{m}$ below, separated from it by non-porous cryptocystal calcification with smaller than average pustules; broad, reniform, $35\text{--}55 \times 100\text{--}110 \mu\text{m}$, opening crescentic, $10\text{--}15 \times 70\text{--}85 \mu\text{m}$, covered by a plate pierced by about $30\text{--}40$ circular pores arranged in two rows, sometimes three rows at the outer ends.

AVICULARIUM. Single, moderately large, present in most autozooids, located on right of autozooids at the left side of colony and on the left of those at the right side; level with or distal of ascopore, oriented laterally or slightly disto-laterally; crossbar deep, distal edge straight, proximal edge scalloped; opesia semielliptical; rostrum short, subtriangular, the distal end rounded and without a channel. Mandible long, ca $315\text{--}450 \mu\text{m}$, lanceolate, pointed, slightly hooked, open examples mostly lying across ascopore. Intramural budding common in avicularia.

OVICELLS. Large, low in profile, not personate; calcification of identical fabric to frontal shield, continuous with frontal shield of distal zooid; pores irregularly scattered over surface; secondary orifice of ovicellate zooids shallower than infertile zooids.

Remarks

The ascopore of this new species is unusually wide compared with congeners, and the flat-topped cryptocystal pustules are another very notable feature. However, it is the peculiar tongue-shape of colonies that provides the easiest way of recognizing *Microporella lingulata* sp. nov. while at the same time posing questions about its mode of life. No substrate of attachment is visible, although it is possible

that a small substrate is present but totally enveloped by later growth. Regardless, it is difficult to understand how adult colonies were supported as there are no indications of rhizoids to root the colonies into a particulate substratum, nor are rhizoids known in any other species of *Microporella*. Functional autozooids were evidently budded at equal rates on both sides of the branch, arguing against the idea that colonies rested horizontally on the sea-bed with one side down against the sediment. The most plausible options are either a vertical orientation with only the rounded proximal end embedded in the sediment, or the entire colony living interstitially within a coarse substratum. According to St. B263 sediment data, the seafloor at the exact locality that yielded the specimens comprises medium and fine sand (62.5 to 500 μm particle size). Given the colonies are not rooted, it is possible that they just sit on the seafloor. The robust avicularian mandibles may have a supportive role, perhaps analogous to that in free-living lunulitiform bryozoans (e.g., Chimonides & Cook 1981).

Microporella modesta sp. nov.

[urn:lsid:zoobank.org:act:18FA46FC-2D1B-4464-B5EC-34A6D51D9DAF](https://zoobank.org/act:18FA46FC-2D1B-4464-B5EC-34A6D51D9DAF)

Fig. 11; Table 8

Diagnosis

Colony erect, bifoliate; branches narrow. Autozooids rhomboidal. Frontal shield pustulose and pseudoporous; pustules densely-packed. Orifice transversely D-shaped, over twice as wide as long; hingeline toothed, a large tooth at each extremity; sometimes a low cowl-like peristome developed distally; three or four oral spines. Ascopore reniform to elliptical, opening crescent-shaped, lined by denticles; ascopore hidden by prominent mucro in frontal view. Avicularium single, located proximally of ascopore, oriented distolaterally; crossbar complete; rostrum channelled. Ovicells not personate.

Etymology

From the Latin ‘*modesta*’, meaning modest, moderate and referring to the ascopore concealed beneath a mucro.

Material examined

Holotype

ALGERIA • Unbleached specimen; Yates Johnson leg.; Recent; NHMUK 1869.10.6.6a (Fig. 11A–C).

Paratypes

ALGERIA • 3 specimens; Same collection data as for holotype; NHMUK 1869.10.6.6b (Fig. 11D–F), 1869.10.6.6c (Fig. 11G), 1869.10.6.6d (Fig. 11H).

Description

COLONY. Erect, bifoliate, branches narrow, strap-like, ca 5 mm wide with up to 15 linear series of alternating zooids on each side; growing edge stepped; interzooidal communications not observed.

AUTOZOIDS. Distinct with interzooidal boundaries marked by a narrow groove between salient vertical walls of adjacent zooids, rhomboidal, longer than wide (mean L/W = 1.33). Frontal shield convex, pustulose, the pustules densely-packed and up to 20 μm in diameter; marginal areolae numbering about 6, not always differentiated from pseudopores, sometimes elongate, ca 30 μm long; pseudopores circular, numbering up to about 50, arranged semi-regularly in grooves between pustules (diameter 10–25 μm).

ORIFICE. Transversely D-shaped, over twice as wide as long, hingeline straight or slightly concave, equipped with a large tooth close to each end and numerous tiny teeth in between; low cowl-like peristome sometimes developed distally around orifice; three or four oral spines (diameter 10–15 μm), a

Table 8. Measurements in μm of *Microporella modesta* sp. nov., Recent, Foveaux Strait, New Zealand; holotype NHMUK 1869.10.6.6a, paratypes NHMUK 1869.10.6.6b, 1869.10.6.6c.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 3	630	± 99	499	803
ZW	20, 3	472	± 103	298	709
OL	20, 3	83	± 16	58	108
OW	20, 3	171	± 23	141	214
AvL	20, 3	100	± 14	73	123
AvW	20, 3	108	± 8	96	127
OvL	20, 3	302	± 47	218	366
OvW	20, 3	359	± 60	281	460

spine just above each proximolateral corner of orifice plus a single distal median spine or spines inwards of the two distolateral corners.

ASCOPE FIELD. As a flared, raised area of gymnocystal calcification, located moderately close to orifice, ca 40 μm below, separated from it by non-porous pustulose cryptocyst field; reniform to transversely elliptical, 25 \times 60 μm , opening crescent-shaped, 5 \times 30 μm , lined by denticles; prominent mucro proximal of ascopore with spine-like or flap-like overhang hiding ascopore in frontal aspect.

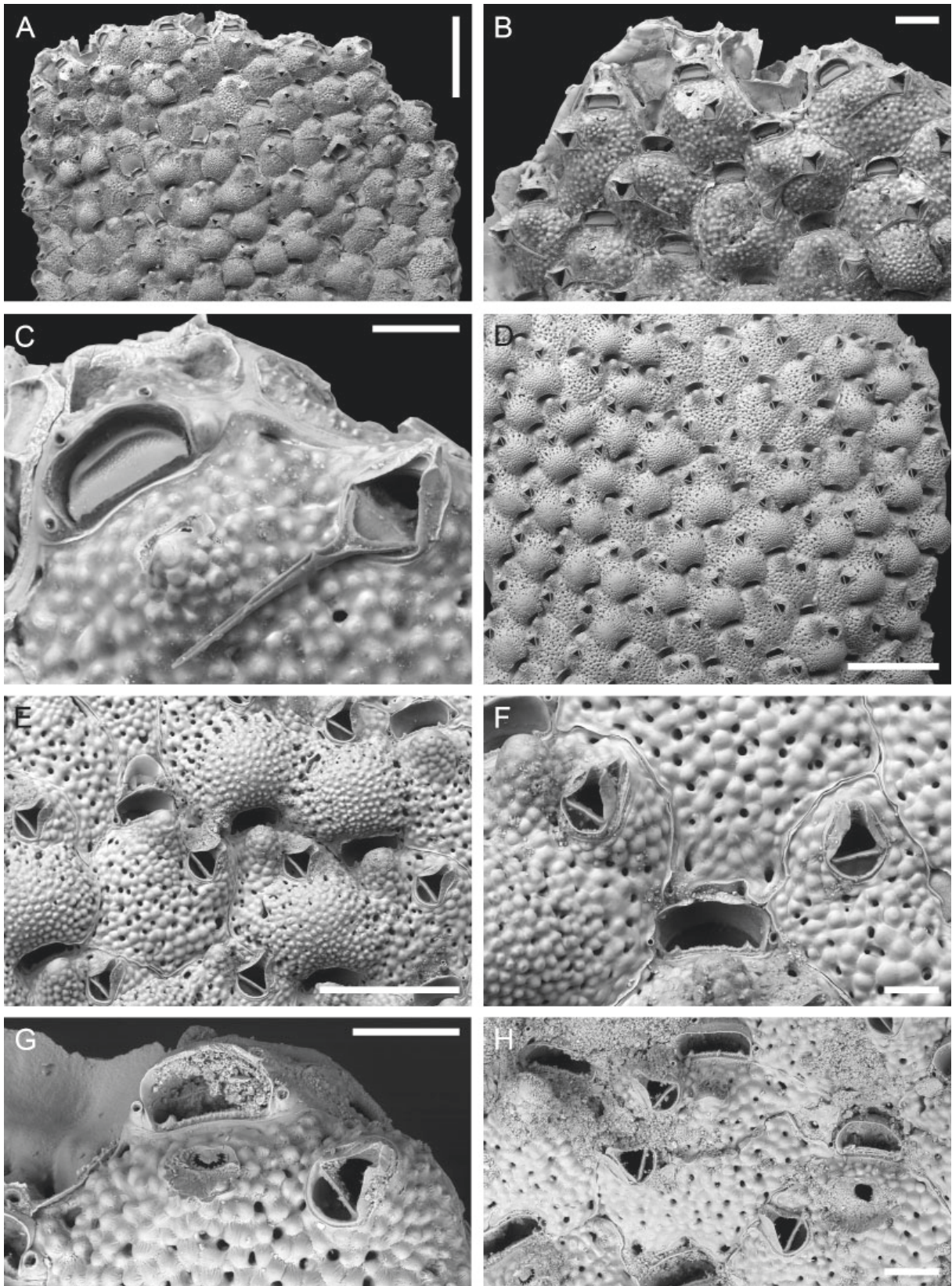
AVICULARIUM. Single, moderately large, present in the majority of autozooids on side closest to branch margin, positioned proximally of ascopore, close to mucro, oriented distolaterally; crossbar complete; opesia semielliptical, shallow; rostrum short, subtriangular, rounded distally and channelled. Mandible long, about 250–320 μm , pointed, toothed, lying proximally of ascopore when open. Intramural budding often observed in avicularia.

OVICELLS. Moderately large, subglobular or rounded quadrate, not personate, proximal arms forming bridge above ascopore; calcification of similar fabric to cryptocyst but pustules smaller and more closely-spaced, continuous with frontal shield of distal zooid; pseudopores small, peripheral only, those near margins aligned in radial rows; orifice of ovicellate zooids partly hidden in frontal view.

Remarks

This is the only bifoliate species of *Microporella* known from the Mediterranean (coast of Algeria). The presence of a mucro projecting over the ascopore enables *M. modesta* sp. nov. to be readily distinguished from its bifoliate congeners described above, as well as the encrusting European species of *Microporella* (i.e., *M. ciliata* (Pallas, 1766), *M. marsupiata* (Busk, 1860), *M. appendiculata* (Heller, 1867)). The

Fig. 11 (opposite page). *Microporella modesta* sp. nov., Recent, Algeria. **A–C.** Holotype NHMUK 1869.10.6.6a (unbleached). **A.** General view of the branch tip. **B.** Group of autozooids at the branch tip. **C.** Close-up of the orifice with four oral spine bases, suboral mucro concealing the ascopore, and avicularium with the long, pointed mandible open. **D–F.** NHMUK 1869.10.6.6b. **D.** Group of zooids, mostly ovicellate. **E.** Close-up of ovicells. **F.** Close-up of an orifice and two avicularia, the one on the left with intramural budding. **G.** NHMUK 1869.10.6.6c, ascopore. **H.** NHMUK 1869.10.6.6d, damaged zooid with two avicularia on the left zooidal margin. Scale bars: A, D = 1 mm; B = 200 μm ; C, F–H = 100 μm ; E = 500 μm .



new species is also unusual in possessing oral spines which are mostly lacking in bifoliate species of *Microporella*, another exception being *M. hastigera*.

***Microporella* sp. 1**

Fig. 12; Table 9

Material examined

NEW ZEALAND • Single infertile fragment; SW of South Island, Puysegur Bank; [46.43° S, 166.08° E]; depth 187 m; Recent; NHM-UIO BLEED 151 (voucher specimen).

Description

COLONY. Erect, bifoliate, branches narrow; fragment available ca 3 mm wide with up to six linear series of alternating zooids on each side; interzooidal communications through multiporous septula visible at colony growing edge.

AUTOZOIDS. Distinct with interzooidal boundaries marked by thin band of slightly raised calcification on either side of a narrow groove, rounded rectangular to hexagonal, longer than wide (mean L/W = 1.31). Frontal shield convex, pustulose, the pustules flat-topped, varying in size; marginal areolae numbering about 10–12, usually elongate (25–40 µm long) especially at zooidal corners, sometimes indistinguishable from frontal pores along lateral sides of the zooids; non-marginal pseudopores about 40–60, small (diameter 10–15 µm), irregularly scattered among pustules, sometimes coalescent.

ORIFICE. Transversely D-shaped, significantly wider than long, hingeline with about 14–18 equal-sized teeth; oral spines lacking. Operculum smooth.

ASCOPE FIELD. As a narrow band of gymnocystal calcification, at approximately same level as orifice but beneath level of adjacent frontal shield, located at ca 55–75 µm from the orifice hingeline, separated from it by non-porous pustulose cryptocyst; circular (diameter 50–60 µm) to transversely elliptical (55 µm long by 80 µm wide), opening C-shaped, 10 × 50 µm, with tiny radial denticles, and a circular tongue projecting from the distal edge.

AVICULARIUM. Usually single, rarely paired, moderately large, present in all autozooids, positioned at level with the ascopore, oriented distolaterally, usually at about 45° to the long axis of the supportive autozooid; crossbar calcified; opesia semielliptical; rostrum short, subtriangular with concave sides, the distal end rounded, distinct channel present. Mandible 150–180 µm long, narrow and pointed. Multiple intramural buds observed in avicularia.

OVICELLS. Not observed.

Remarks

Among all bifoliate congeners, *Microporella* sp. 1 mostly resembles *M. hyadesi*. The two species share a transversely D-shaped orifice with equal-sized teeth in the hingeline, the characters of the ascopore and the appearance of the frontal shield made of flat-topped pustules. Differences include: the shape of the zooids (mean L/W = 1.67 and 1.31, respectively) which are rectangular and flat in *M. hyadesi*, rhomboidal to hexagonal and convex in *Microporella* sp. 1; the avicularium is more laterally oriented and has a wider channel in the rostrum than *M. hyadesi*. The two species also differ in their geographical distributions. The single available fragment of *Microporella* sp. 1 was found at Puysegur Bank, south west of South Island of New Zealand at a depth of 187 m, while *M. hyadesi* is a South Atlantic species found at a depth of 49–341 m (Hayward & Ryland 1990).

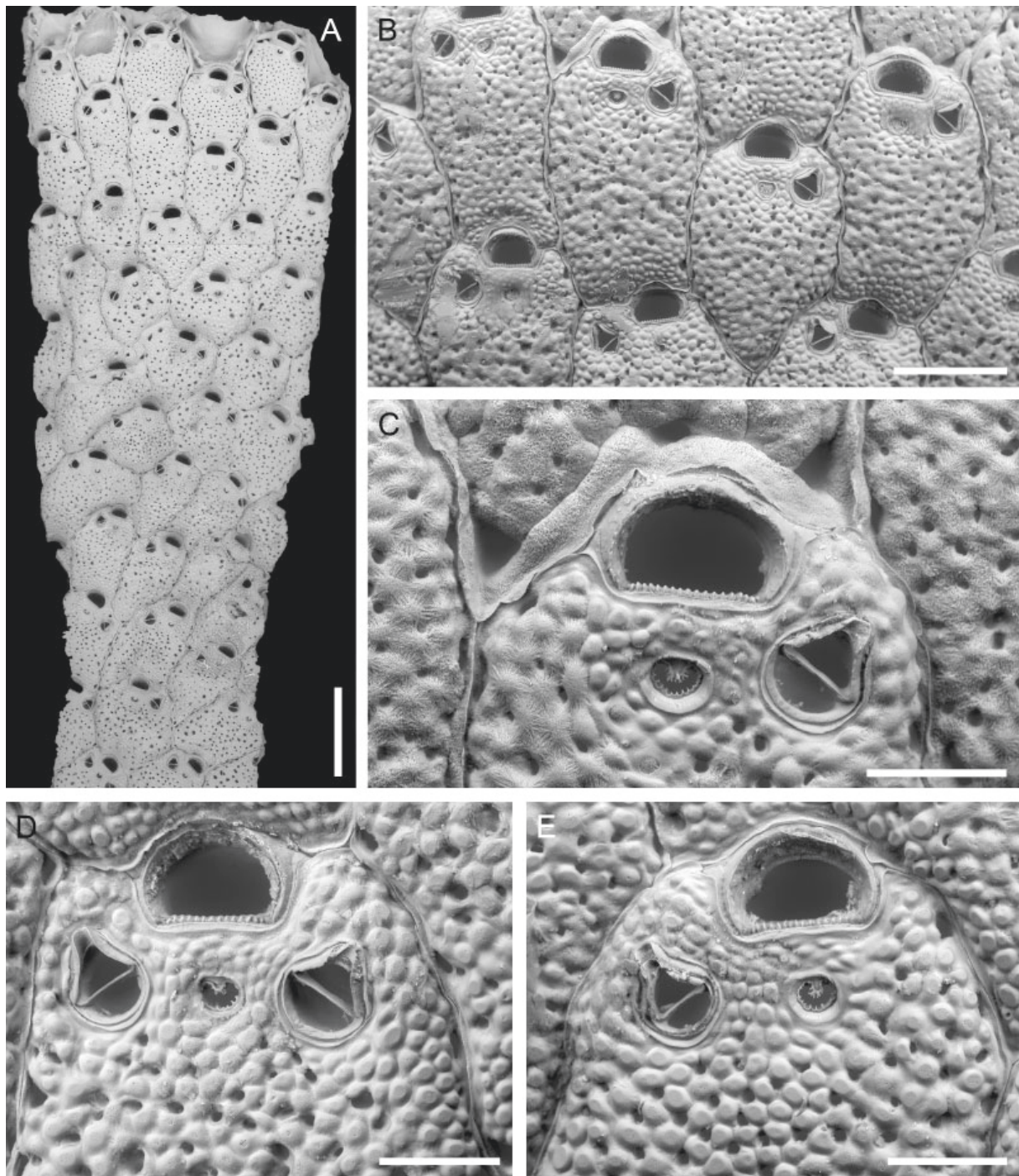


Fig. 12. *Microporella* sp. 1, BLEED 151, Recent, Puysegur Bank. **A.** General view of the branch fragment. **B.** Group of autozooids. **C.** Close-up of orifice, ascopore and avicularium. **D.** Close-up of an autozooid with paired avicularia. **E.** Close-up of an autozooid with avicularium showing intramural budding. Scale bars: A = 1 mm; B = 500 μ m; C–E = 150 μ m.

Table 9. Measurements in μm of *Microporella* sp. 1, Recent, Puysegur Bank, New Zealand; voucher specimen BLEED 151.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 1	736	± 78	599	899
ZW	20, 1	562	± 94	417	776
OL	18, 1	114	± 6	101	125
OW	18, 1	183	± 9	163	200
AvL	20, 1	135	± 11	113	151
AvW	20, 1	107	± 11	81	126

Discussion

Although uncommon, erect bifoliate growth can be inferred to have evolved on several occasions in *Microporella* from ancestral species with encrusting colonies. On the basis of zooidal features, the two fossil bifoliate species described here appear to be closely related, as do four of the seven Recent bifoliate species. The two North American fossil species, the Miocene *M. bifoliata* and the Pliocene *M. tanyae* sp. nov., are very similar yet specifically distinct species, chronologically separated by ca 7



Fig. 13. Geographical distribution of the nine bifoliate species of *Microporella* Hincks, 1877 known to date. Red circles indicate fossil occurrences, while black lozenges indicate living records. 1 = *M. bifoliata*, Miocene, Maryland, USA; 2 = *M. tanyae* sp. nov., Pliocene, Virginia, USA; 3 = *M. hastigera* (Busk, 1884), Recent, Azores, Central Atlantic; 4 = *M. hyadesi* (Jullien, 1888), Recent, Falklands Islands and Magellan Strait, South Atlantic; 5 = *M. ordo* Brown, 1952, Pleistocene (Wanganui Basin) to Recent (Spirits Bay) New Zealand; 6 = *M. ordoides* sp. nov., Recent, Campbell Plateau, New Zealand; 7 = *M. lingulata* sp. nov., Recent, Foveaux Strait, New Zealand; 8 = *M. modesta* sp. nov., Recent, Mediterranean off Algeria; 9 = *M. sp. 1*, Recent, Puysegur Bank, New Zealand.

million years (ca 12 vs 5 million years old, respectively). *Microporella hyadesi*, *M. ordo*, *M. ordoides* sp. nov. and *M. sp. 1* show sufficient similarities to one another and differences from other species of *Microporella* indicating that they may represent a distinct clade, a hypothesis that could be tested when molecular sequence data become available. The other three Recent bifoliate species (*M. hastigera*, *M. lingulata* sp. nov. and *M. modesta* sp. nov.) have little in common, except for being bifoliate, and are probably more closely related to different encrusting species of *Microporella* than they are to other bifoliate species of *Microporella*.

The two exclusively fossil species are both recorded from North American Cenozoic deposits. Four out of the seven living species are distributed in New Zealand waters (*M. ordo*, *M. ordoides*, *M. lingulata*, *M. sp. 1*), *M. hyadesi* and *M. hastigera* were reported from several close localities in the South and Central Atlantic respectively, while *M. modesta* sp. nov. is a Mediterranean species from off Algeria (Fig. 13). Among these, only *M. ordo* was first described from Pleistocene deposits in the Wanganui Basin, New Zealand.

Two other genera of Microporellidae – *Diporula* and *Flustramorpha* Gray, 1872 – comprise *Microporella*-like species having erect colonies with cylindrical and bifoliate branches, respectively. However, colony growth-form alone seems a feeble character to justify the distinction among the three genera. In fact, most erect bilaminar colonies start with a more or less developed encrusting base before growing as erect bilaminar sheets back-to-back. For example, *Microporella tanyae* sp. nov. starts with an extended encrusting base completely wrapping the shelly substrate (see Fig. 2). In addition to the colony growth-form, Hincks (1880: 220) emphasized the different structure of the orifice, semicircular in *Microporella*, horseshoe-shaped in *Diporula*. The shape of the orifice may also be somehow variable. In encrusting species of *Microporella* from Hokkaido (Japan), the shape of the orifice varies from high-arched semicircular to transversely D-shaped, to oval (Suwa & Mawatari 1998).

The diagnosis of the genus *Microporella* given by Hayward & Ryland (1999: 292) includes an imperforate oecium and the presence of conspicuous basal pore-chambers, while in the diagnosis of *Diporula* (Hayward & Ryland 1999: 302) the oecium is perforate and basal pore-chambers are substituted by small multiporous septula. However, pseudopores also occur in the oecium of many encrusting species of *Microporella*, including the type species *Microporella ciliata* (see Kukliński & Taylor 2008: fig. 1c). The presence of small multiporous mural septula in lateral walls has been also observed in erect bifoliate species of *Microporella* (e.g., *Microporella ordo*, Fig. 7D).

Microporella hastigera offers an example of how the boundaries among *Microporella*, *Diporula* and *Flustramorpha* can be indistinct. Busk (1884: 135), who originally described *Microporella hastigera* as *Flustramorpha*, expressed his doubts about the separation of this genus from *Microporella* based solely on colony growth-form, and suggested that *Flustramorpha* may be a subgenus of *Microporella*. Subsequently, *M. hastigera* was placed in *Diporula* and eventually in *Microporella* by Calvet (1931) and d'Hondt (1975), who regarded *Diporula* as a synonym of *Microporella*.

A meaningful phylogenetic analysis of *Microporella* and closely-related genera (i.e., *Diporula* and *Flustramorpha*) currently in progress will be of paramount importance to resolve the phylogenetic relationships of microporellids and offer robust evidence for formal synonymy of these genera.

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