THE TERTIARY BRYOZOAN FAMILY PROSTOMARIIDAE – MORPHOLOGY AND RELATIONSHIPS

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Abstract

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The relationships of the Tertiary Victorian bryozoan genus *Prostomaria* and family Prostomariidae are considered based on SEM examination of well-preserved material. It is concluded that the family is monotypic, the sole included species being *Prostomaria gibbericollis*. Recent species attributed to *Prostomaria* are not related and a new genus and family of Schizoporelloidea (*Mawatarius*, Mawatariidae) are established for a New Zealand species previously attributed to *Prostomaria*. The most likely affinities of the Prostomariidae are with the recent family Urceoliporidae and a new superfamily, Urceoliporoidea, is erected to accommodate these two families.

Introduction

The monotypic bryozoan genus *Prostomaria* and family Prostomariidae were established simultaneously by MacGillivray (1895) on the basis of fossil specimens from Victoria. The possible affinities of the genus are intriguing, but the refining of taxonomic relationships has been hampered by a lack, in *Prostomaria*, of such helpful characters as avicularia and ovicells. These have never been seen in the many specimens available for examination (P.E. Bock, pers. comm). Until recently, the family has remained monotypic and is still poorly understood.

Examination of internal and external skeletal structures by scanning electron microscopy of both well-preserved *Prostomaria gibbericollis* and other possibly related genera has provided a better basis for a statement on the taxonomic affinities of the Prostomariidae. The purpose of this paper is to redescribe *Prostomaria gibbericollis*, comment on its likely relationships with other genera, and introduce new supraspecific taxa based on these relationships.

Prostomaria MacGillivray

Prostomaria MacGillivray, 1895: 105.

Type species. Prostomaria gibbericollis MacGillivray.

Prostomaria gibbericollis MacGillivray

Prostomaria gibbericollis MacGillivray, 1895; 105, pl. 3, fig. 28.

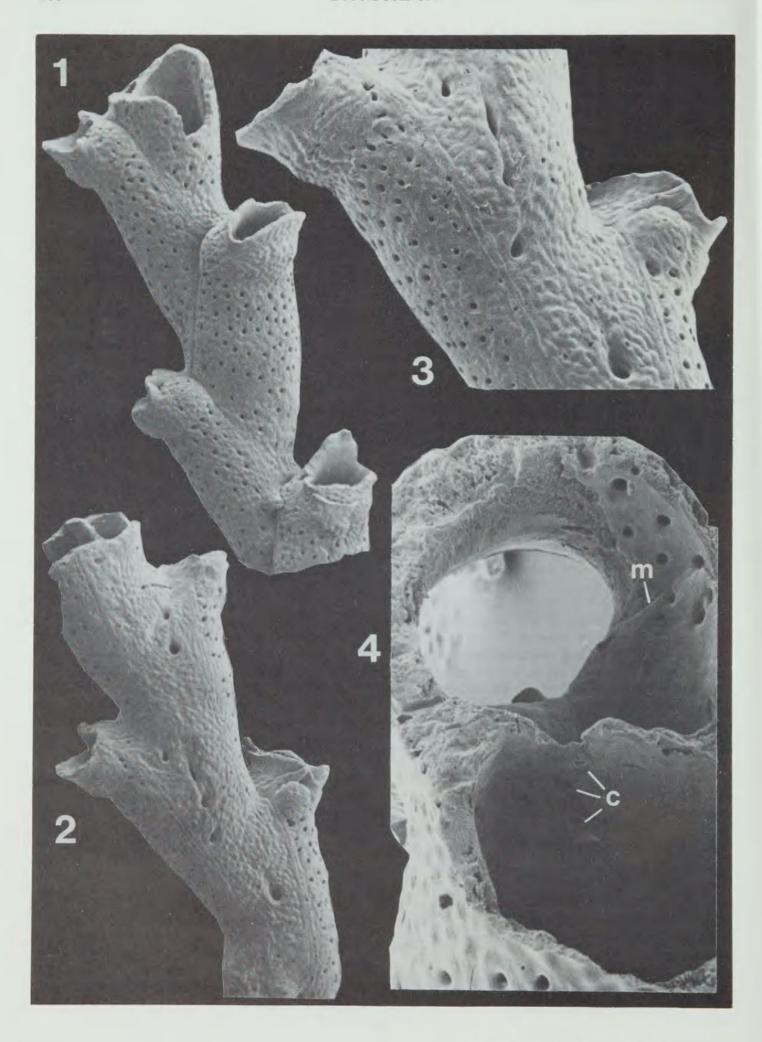
Material examined. Several colony fragments, from "Schnapper Point, Fossil Beach", Victoria, Bal-

combian (Lower Miocene), sent courtesy of P.E. Bock, Museum of Victoria, N.Z. Oceanographic Institute No. Z6720.

Distribution. Balcombian (Lower Miocene), Victoria, Australia. Schnapper Point is the type locality of the Balcombian (Brown, 1958: 30).

Description. Colony erect, probably of articulated segments since there is no evidence of bifurcation, each segment attaining at least 6-7 mm in length and comprising up to about 8 zooids. Zooids about 1.32-1.60 × 0.53-0.64 mm, back to back and alternating, but facing more towards one side (Figs 1, 2). Frontal wall granular-tubercular, and regularly and evenly perforated with numerous small pores, except for an abfrontal area which is marked off by a line in the calcification; roughly down the middle of the abfrontal face are larger, scattered, areolar pores (Figs 2, 3). Primary orifice (Fig. 4) sunken, transversely elliptical, lacking a sinus or condyles, surrounded by a high, transversely set peristome of which both the proximal and distal rims project from the branch. Avicularia and ovicells absent.

Discussion. When MacGillivray (1895) established the monotypic genus Prostomaria, he underscored its uniqueness by placing it in its own family, Prostomariidae, commenting "its nearest allies [are] the Tubucellariidae". Harmer (1957) compared Prostomaria gibbericollis to a new species that he was describing – Lagenipora cylindrica (Lageniporidae) [sic]. Gordon (1985), commenting on MacGillivray's opinion, compared Prostomaria (not having seen specimens,



however) with Margaretta Gray (formerly Tubucellaria d'Orbigny) and Porina d'Orbigny (Porinidae). Thus three separate families have been suggested as being related to Prostomaria.

Each of these supposed relationships can be ruled out. *Margaretta* (a jointed genus of Margarettidae) has an erect colony and a primary orifice similar to that of *Prostomaria*. It differs substantially in having internodes with as many as ten longitudinal series of zooids (depending on the species), an ascopore, and peristomial brood chambers; internodes lack frontal and abfrontal surfaces.

Harmer's (1957) Lagenipora cylindrica is not a Lagenipora Hincks (Celleporidae) but appears rather to belong to Lagenicella Cheetham and Sandberg, 1964 (Teuchoporidae). It has little in common with *Prostomaria*, being entirely encrusting and possessing ovicells.

Similarly, the Porinidae are quite unrelated, with: bilamellar branches (in the type species of *Porina*), or cylindrical branches (in *Haswellina* Livingstone) in which zooids open on both (or all) sides, a peristomial spiramen (superficially resembling an ascopore), and peristomial ovicells.

A recent study by Gordon (1988) of the families Bifaxariidae and Urceoliporidae suggests additional, more likely, candidates for close relationship with Prostomaria, especially the genera Aberrodomus Gordon and Urceolipora MacGillivray. Aberrodomus looks, superficially, quite like Prostomaria. In both genera the zooids alternate back to back, are regularly and evenly perforated, and have similar orifices and peristomes. There are significant differences, however. Aberrodomus is non-articulated (assuming Prostomaria was articulated in life) and produces lateral branches. The species of Aberrodomus also produce avicularia and ovicells. Importantly, the well-preserved specimens of P. gibbericollis that I have examined clearly lack the separate internal zooidal chamber seen in Aberrodomus candidus Gordon for example.

I believe the relationships of *Prostomaria* and the Prostomariidae are with the Urceoliporidae. The Urceoliporidae (comprising *Urceolipora* and *Reciprocus* Gordon) have the following important features in common with *Prosto-*

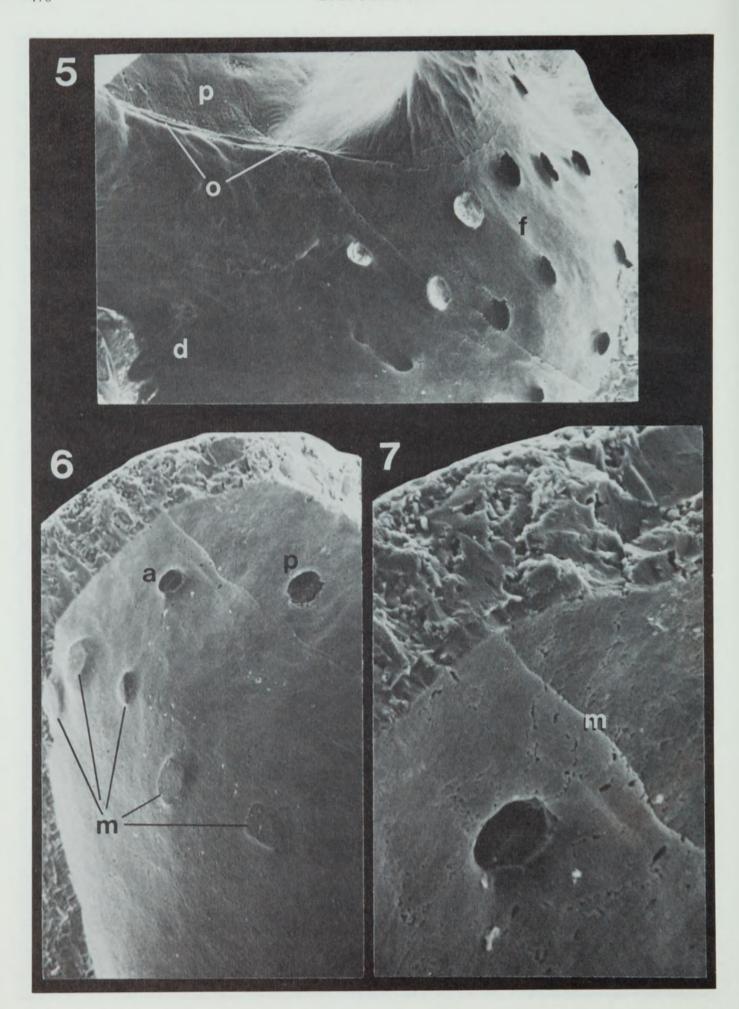
maria - biserial segments of back-to-back zooids which incline to one side so that each segment has an oral face and an aboral face; no oral spines or avicularia, and no internal ultrastructure (e.g., planar spherulitic) (Figs 5–7) indicating an umbonuloid frontal wall (see Gordon, 1988). Urceolipora, particularly, is reminiscent of Prostomaria because its two species (U. nana MacGillivray and U. lucida Busk) have a longitudinal ridge on one side of the frontal wall dividing the cryptocyst into two fields – a large one which includes most of the frontal wall and a lateral one which includes some of the areolar pores by which the zooidal body cavity communicates with the outer hypostegal coelom. This is exactly the case in Prostomaria (except that a line replaces the ridge), which argues for a close relationship between the two genera.

I conclude that the Prostomariidae and Urceoliporidae are related, but separate, families. *Prostomaria* has a frontal wall which is evenly perforated all over (except in the lateral field) whereas the pseudopores of *Urceolipora* (lacking in *Reciprocus*) are confined to a cluster adjacent to the orifice (see Gordon, 1988, figs 76, 77). Further, the orifice of *Prostomaria* lacks a sinus, there is a peristome, and ovicells have not been seen. [Ovicells are lacking in *Reciprocus* also but there are recognisable fertile orifices.]

I have earlier suggested (Gordon, 1988) that the Urceoliporidae might be accommodated in the cryptocystidean superfamily Schizoporelloidea, although "somewhat on the fringe". With the association of the Prostomariidae with the Urceoliporidae it now seems appropriate to unite these two families into a new superfamily Urceoliporoidea. The outstanding and distinctive features of this superfamily are summarised below in a formal diagnosis.

Prostomaria and the Prostomariidae are presently strictly monotypic and known only from the Tertiary of Victoria. Two Recent species have been described but it is now clear that they are unrelated to Prostomaria. D'Hondt and Schopf (1984) described Prostomaria cyclostomata from about 4800 m depth north-west of Bermuda. Like Prostomaria gibbericollis, it is erect and biserial with zooids alternating back to back. However the frontal wall is imperforate

Figures 1–4. Prostomaria gibbericollis, Schnapper Point, Victoria. Figs 1 and 2, frontal and abfrontal sides, respectively, of parts of branch segments (× 40). Fig. 3, part of fig. 2 enlarged, showing a series of areolar pores in the imperforate field of zooidal walls on the abfrontal side of a branch segment (× 72). Fig. 4, internal view of parts of two zooids showing a primary orifice, connections between adjacent dorsal walls (c), and a line marking the attachment of the ascus membrane (m) in life (× 175).



(apart from the marginal areolae), and there is no division of the cryptocyst into fields nor are there frontal or abfrontal faces. Ovicells were not seen but d'Hondt and Schopf reported a "scar" on the proximal border of the zooidal orifice indicating a possible suboral avicularium. D'Hondt and Schopf's (1984) P. cyclostomata certainly represents a new genus, possibly a new family, and, judging from the external morphology, the possibility exists that it could be umbonuloid. The ultrastructure of the inner surface of the frontal wall needs to be examined.

A second Recent species, Prostomaria inexpectabilis, was described by Gordon (1985) from about 1170 m on pumice gravel north of Raoul Island, Kermadec Ridge. It resembles Prostomaria in being erect, with perforated walls and sunken orifices, but differs significantly in being uniserial, with a somewhat sinusoid orifice and peristomial ovicells. The colony is also nonsegmented and branching. The affinities of this species are obscure. It is reminiscent of Vix (Vicidae) (Gordon, 1988) but that genus is quadriserial, has avicularia, and is non-ovicellate. Prostomaria inexpectabilis clearly represents a new, presently monotypic, genus. I name this genus Mawatarius in recognition of the contribution, over many decades, of Dr Shizuo Mawatari to knowledge of the Bryozoa. A new family of Schizoporelloidea, Mawatariidae, is established to accommodate it. [The species name, inexpectabilis, was coined as a hybrid, connoting "unexpected and spectacular".]

Ureoliporoidea Bassler, 1936 n. superfam.

Diagnosis. Colony erect, biserial, segmented, basally rooted. Zooids cryptocystidean, arranged back to back, each connecting with three others dorsally; orientated such that segments tend to have an oral face and an aboral face. Orifice variable, with or without a sinus. Frontal wall with scattered pseudopores or these limited in distribution or lacking. No oral spines. No avicularia. Ovicells present or lacking.

Included families. Urceoliporidae Bassler, 1936; Prostomariidae MacGillivray, 1895.

Urceoliporidae Bassler, 1936

Diagnosis. Zooids frontally imperforate or with only a cluster of pores near the orifice; orifice with a shallow or distinct sinus and oral processes; no peristome. Ovicells prominent and recumbent, or absent and zooids with dimorphic orifices.

Included genera. Urceolipora MacGillivray, 1881; Reciprocus Gordon, 1988.

Prostomariidae MacGillivray, 1895

Diagnosis. Zooids with an evenly perforated frontal wall; orifice lacking a sinus; peristome well developed. Ovicells lacking, orifices monomorphic.

Included genus. Prostomaria MacGillivray, 1895

Schizoporelloidea Jullien, 1883

Diagnosis. See Gordon (1984).

Mawatariidae n. fam.

Diagnosis. Colony erect, uniserial, branching, non-segmented, the zooids facing mainly on one aspect. Frontal wall cryptocystidean, with scattered pores. Primary orifice sunken, with shallow sinus; secondary (peristomial) orifice with pseudosinus. No oral spines. No avicularia. Ovicell peristomial. Ancestrula resembling later zooids, anchored by a chitinous portion.

Included genus. Mawatarius n. gen.

Mawatarius n. gen.

Type species. Prostomaria inexpectabilis Gordon, 1985.

Diagnosis. With characters of the family.

Acknowledgements

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Figures 5–7. Prostomaria gibbericollis, Schnapper Point, Victoria. Fig. 5, enlargement of part of fig. 4, showing an interior view of parts of the peristome (p), distal rim of primary orifice (o), frontal wall (f) and dorsal wall (d) (\times 374). Fig. 6, interior of zooidal wall, showing a pseudopore (p), areolar pore (a), and attachment scars of parietal muscles (m) (\times 380). Fig. 7, enlargement of part of fig. 6, showing the areolar pore, and the attachment scar of the ascus membrane (m) with no difference in skeletal ultrastructure either side (\times 902).

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