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Article

Morphology and palaeobiogeography of *Retelepralia*, a distinctive cheilostome bryozoan new to the fossil record

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With 5 figures

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Abstract: A new species of ascophoran cheilostome bryozoan, *Retelepralia macmonagleae* sp. nov., is described from Malaysian Borneo (Sabah). Dated as Late Oligocene, it is the oldest known and the first recognized fossil species of *Retelepralia*. A second fossil species of this genus, originally described as *Hippodiplosia voigti* David, Mongereau & Pouyet, 1972, occurs in the Miocene of France and Morocco. Synonymy of *H. voigti* with the Recent type species of *Retelepralia*, *Lepralia mosaica* Kirkpatrick, 1888, is tentatively proposed. Included in the Cheiloporinidae, *Retelepralia* is characterized by a lepralioid frontal shield with a distinctive median gymnocystal strip. The presence of two hypostegal coelomic compartments in living zooids is inferred, and the palaeobiogeography of *Retelepralia* is discussed.

Key words: Cenozoic, Ascophora, Cheiloporinidae, palaeobiogeography, morphology

1. Introduction

Modern bryozoan faunas are dominated by ascophoran cheilostomes. This polyphyletic subordinal group is characterized by zooids with calcified frontal shields overlying a sac (ascus) that fills with water to compensate for the lost volume when the tentacle crown is protruded. Ascophorans are the most skeletally complex of all bryozoans and have developed a wide variety of different colony forms. While many ascophoran genera are common, widespread both geographically and stratigraphically, and rich in numbers of species (e.g. *Schizoporella*, *Microporella*, *Metrarabdotos*, *Celleporaria*), others are more restricted in their distribution and diversity. This paper focuses on one of the latter genera, *Retelepralia* Gordon & Arnold, 1998, unusual in having autozooids with a distinctive median strip of non-porous frontal shield separating two areas of pseudoporous frontal shield.

Here we revise *Retelepralia* based on the study of type and new material. We recognize the first fossil examples of the genus, extending its range from the Recent back to the Oligocene, discuss its palaeobiogeography, and interpret the significance of the median strip for soft part anatomy.

2. Material and methods

Material used in this study includes type and new specimens. Specimens of a new species of *Retelepralia* were collected by Laura B. McMonagle (University of Durham) from the eastern part of the Malaysian province of Sabah (NE Borneo) (Fig. 1), during two field seasons in 2006 and 2007 while making systematic

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Fig. 1. Position of the locality of *Retelepralia macmonagleae* sp. nov., the 'Mosque Quarry III' in the Malaysian province of Sabah (NE Borneo).

collections of well-preserved Late Oligocene-Early Miocene corals. Three colonies of *Retelepralia macmonagleae* sp. nov. were subsequently discovered in the laboratory after preliminary cleaning. These encrust the bases of the scleractinian coral *Hydnophora* collected from muddy carbonate deposits exposed in a small quarry, named 'Mosque Quarry III' (N 05º 32.659'; E 118º 11.590'), bordering the Sukau Road, 15 km to the west of Sukau Village (McMonagle et al. 2011). All of these specimens are catalogued and deposited in the Department of Palaeontology, Natural History Museum, London (abbreviated NHML).

In addition, type and other material of *Retelepralia mosaica* (Kirkpatrick, 1888) housed in the zoological reference collections of the NHML has been studied. Through the kindness of Dr P. Moissette (University of Lyon) we have been able to obtain new SEM images of the type material of *Hippodiplosia voigti* David, Mongereau & Pouyet, 1972, which we here transfer to *Retelepralia*.

Before examining specimens of *Retelepralia macmonagleae* sp. nov. using SEM, fossil corals encrusted by this bryozoan were soaked in a dilute solution of the detergent Quaternary-O to remove clay particles, and were subsequently cleaned ultrasonically. Scanning electron microscopy (SEM) was carried out

Fig. 2. Type material of *Retelepralia mosaica* (Kirkpatrick, 1888). NHM 1888.1.25.33: **a**, two zooids, scale bar = 100 µm. **b**, close-up of a zooid, scale bar = 100 µm. **c**, close-up of the orifice, scale bar = 20 µm. **d**, small colony, scale bar = 100 µm. **e**, basal walls of two zooids, scale bar = 100 µm. **f**, close-up of inner frontal wall and median strip, scale bar = 20 µm.

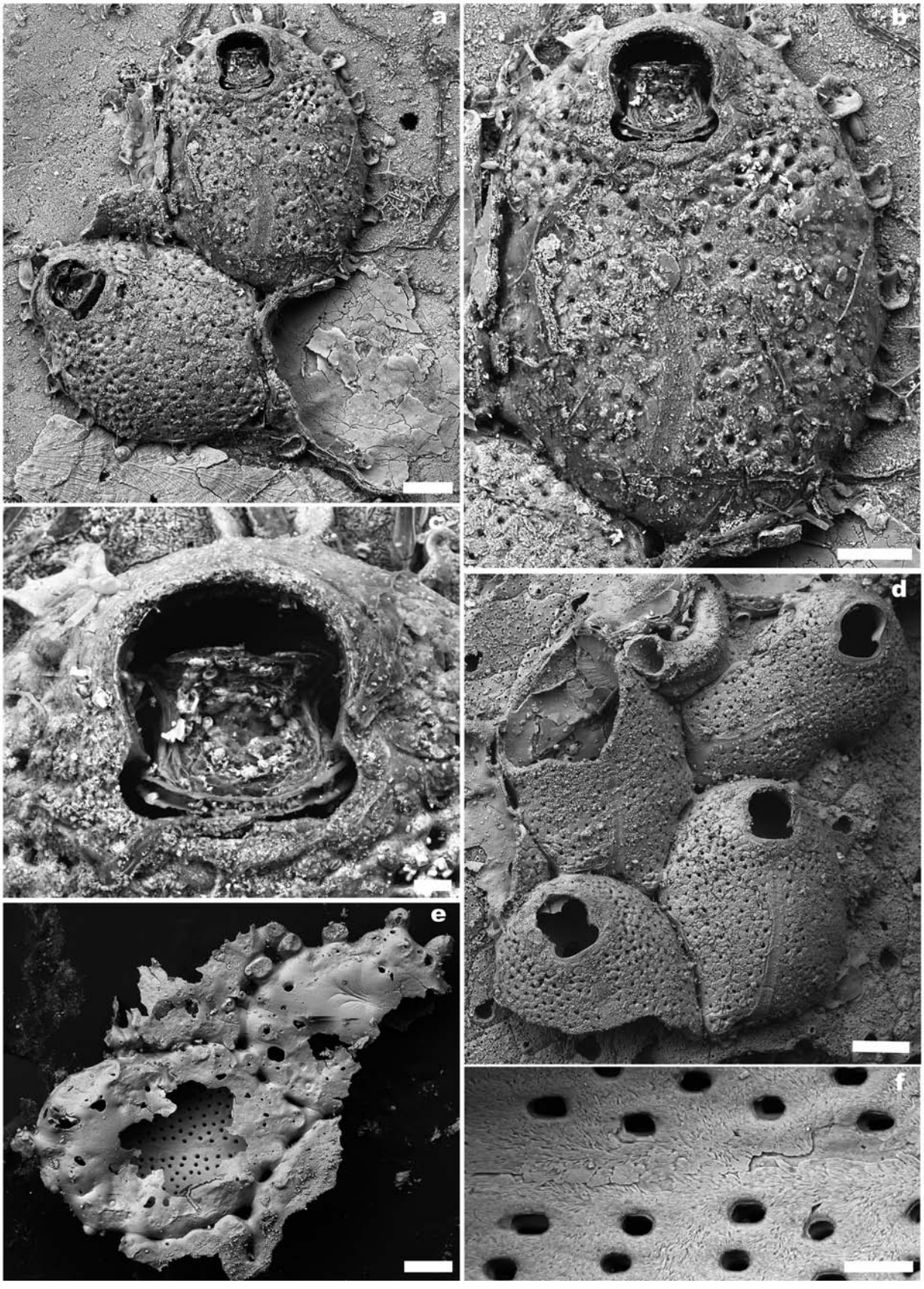

Fig. 2.

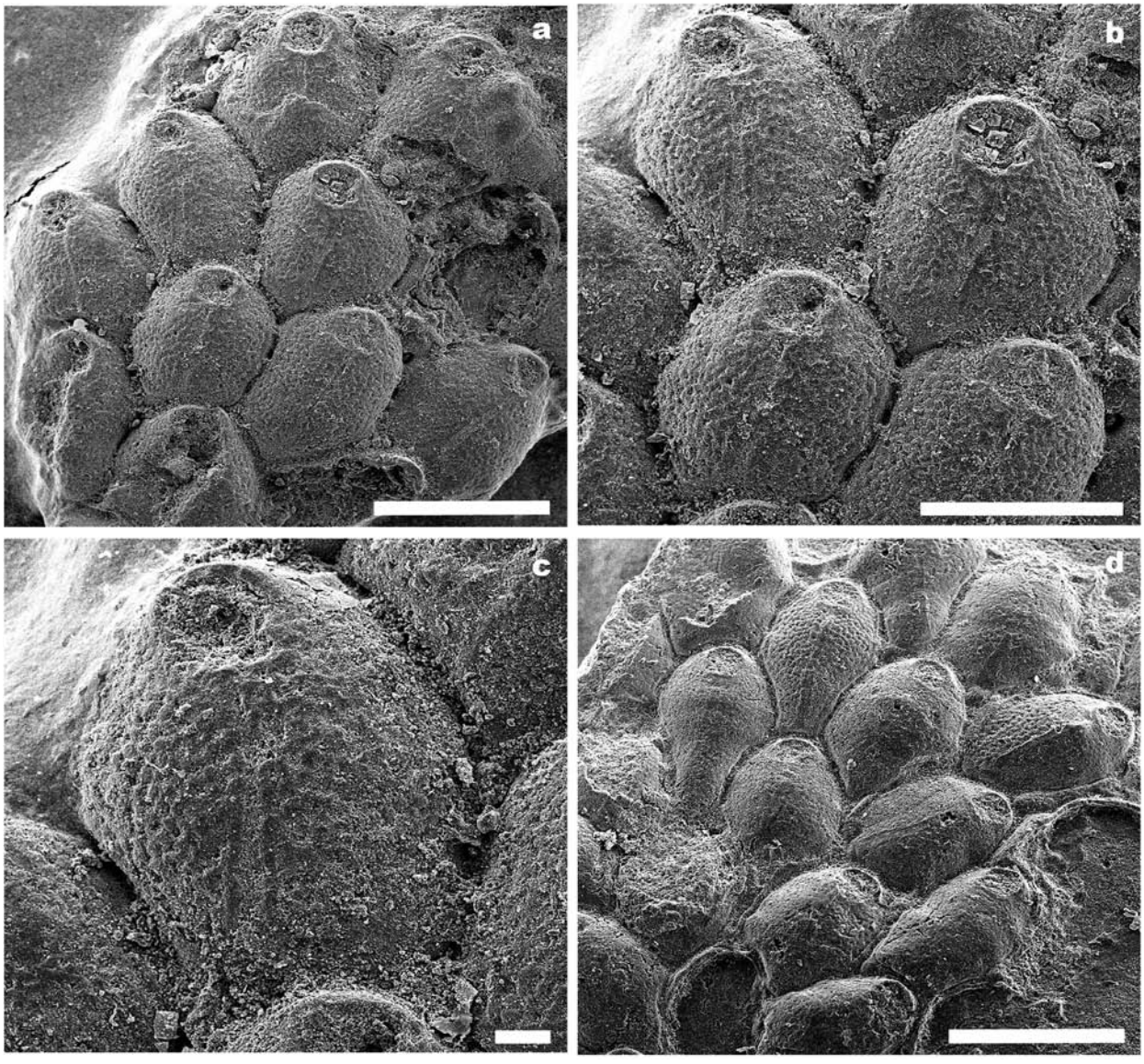

Fig. 3. Type material of *Hippodiplosia voigti* David, Mongereau & Pouyet, 1972, here provisionally synonymized with *Retelepralia mosaica* (Kirkpatrick, 1888). **a**, **d**, FSL 116241 and 491916; several zooids of two different colonies, scale bar = 500 µm. **b**, close-up of four zooids, scale bar = 500 µm. **c**, close-up of a zooid, scale bar = 100 µm.

on uncoated specimens using a low-vacuum scanning electron microscope (LEO VP-1455) at the NHML. Morphometric determinations were made using a stereomicroscope or alternatively from SEM images.

3. Taxonomy

Cheiloporinidae Bassler, 1936
Retelepralia Gordon & Arnold, 1998

Type species: *Lepralia mosaica* Kirkpatrick, 1888

Description: Colony encrusting, multiserial, unilaminar, small in size. Autozooids oval or rounded polygonal, longer than broad, contiguous or connected by multiple tubules (> 10 per zooid). Frontal shield convex, finely granular, evenly covered by small round pseudopores except for a median strip of smooth calcification continuous with the proximal rim of the orifice. Primary orifice bell-shaped, longer than wide, a pair of small, sharp lateral condyles directed downwards and separating a rounded anter from a smaller poster with a straight or barely convex proximal edge; oral spines lacking. Ovicell hyperstomial, globular, surface granular without pores. No avicularia.

Retelepralia mosaica (Kirkpatrick, 1888)
(Figs. 2a-f, 3a-d)

(Synonyms: *Lepralia mosaica*, Kirkpatrick, 1888: 79, pl. 8, fig. 6; *Hippodiplosia voigti,* David, Mongereau & Pouyet, 1972: 57, pl. 3, figs 3-8; *Hippopodina mosaica*, Hayward, 1988: 319, fig. 6a, b)

Material: Natural History Museum, London, NHML 1888.1.25.33 and 1934.10.6.20, Recent, Mauritius (on shells, corals and ?algae), depth unknown. Université de Lyon FSL 116241 and 491916, originally determined as *Hippodiplosia voigti* David, Mongereau & Pouyet, 1972, Miocene, Burdigalian, Mus, Gard, France.

Description: Colony encrusting, unilaminar, with zooids arranged quincuncially or pluriserially, small-sized. Autozooids approximately oval, 0.69-0.98 mm long and 0.54-0.75 mm wide, linked by 10-15 short tubules (mean L = 62.5 μm) forming prolongations of basal pore chambers. Frontal shield convex, granular, densely and evenly covered by round pseudopores, except for a median narrow ridge (mean W = 20 μm) of smooth calcification continuous with the proximal rim of the orifice. Primary orifice bell-shaped, longer than wide (mean L = 0.18 mm, mean W = 0.15 mm), having a pair of stout condyles separating a rounded anter from a broad poster with a nearly straight or slight convex proximal edge. Operculum with marginal sclerites. No oral spines. Ovicell hyperstomial, subglobose, surface granular and imperforate, lateral margins and opening edge bordered by a thin gymnocystal strip. Ancestrula not observed. No avicularia.

Remarks: Type material of this species is poor and lacks ovicells. Further specimens were collected and described from northeastern Australia and the Norfolk Ridge by Gordon & Arnold (1998) who gave a much more detailed morphological description. Examination of fossil material of *Hippodiplosia voigti* David, Mongereau & Pouyet, 1972 demonstrates that this species has tubular processes and seems to be conspecific with *R. mosaica*, although zooids are sometimes more polygonal instead of oval in shape, a difference interpreted as due to intraspecific variation. However, more material is required to test this proposed synonymy. In view of the wide geographical and time separation of the French/Moroccan Miocene and Indopacific Recent populations, there are grounds for suggesting that they may represent cryptic species.

Distribution: Miocene of France (Rhône Basin, Burdigalian) (David, Mongereau & Pouyet 1972) and Morocco (Melilla Basin, Messinian) (El Hajjaji 1992); Recent of Mauritius, northeastern Australia and the Norfolk Ridge.

Retelepralia macmonagleae sp. nov.
(Figs. 4a-g)

Material: Holotype: Natural History Museum, London, NHML BZ 5839: Paratypes: NHML BZ 5840, BZ 5841

Etymology: Named after Laura B. McMonagle, collector of the specimens.

Description: Colony encrusting, multiserial, unilaminar, small-sized. Autozooids rounded approximately hexagonal, longer than broad (L = 0.47-0.70 mm, W = 0.36-0.57 mm, mean L/W = 1.34), contiguous, seemingly without connecting tubules. Frontal shield convex, finely granular, evenly covered by small round pseudopores except for a median narrow ridge (mean W = 20 μm) of smooth calcification continuous with the proximal rim of the orifice. Primary orifice bell-shaped, longer than wide (L = 0.13-0.18 mm, W = 0.10-0.15mm) with a pair of small lateral condyles directed downwards separating a rounded anter from a smaller poster with a straight proximal edge; oral spines lacking. Ovicell hyperstomial, globular, wider than long (mean L = 0.17 mm, W = 0.21 mm), surface granular without pores. Ancestrula not observed. No avicularia.

Remarks: *Retelepralia macmonagleae* sp. nov. differs from *R. mosaica* (Kirkpatrick, 1888) in the smaller size of the zooids: L = 0.47-0.70 mm, W = 0.36-0.57 mm in *R. macmonagleae* vs. L = 0.77-0.92 mm, W = 0.57-0.72 mm in *R. mosaica*. This difference in zooid size does not seem to be ecophenotypic, even though the size of cheilostome zooids can be determined by temperature, with size inversely proportional to the temperature at which the zooid was budded (see Okamura et al. 2011) and smaller zooids therefore characterising warmer waters. Australasian material of *R. mosaica* was taken at 71 m depth from a bottom of biogenic rubble or soft-sediment seafloor. Specimens of *R. macmonagleae* were associated with the scleractinian coral *Hydnophora*. This coral genus is nowadays encountered across a wide depth range, from 0 to 368 m, and a wide temperature range, from 22.1 to 28.9 °C (Wells 1986).

An important difference between the two species is the lack of tubular processes in *R. macmonagleae*. Gordon & Arnold (1998) considered these short tubular processes linking the quincuncially arranged zooids to be a generic character. The lack of tubular processes in *R. macmonagleae* allows tubular processes to be reinterpreted as a specific rather than a generic character. Hincks (1885) showed that separation of zooids in other cheilostomes is not necessarily a generic character as it occurs in species belonging to several different genera. A good example is seen in the genus *Cauloramphus* in which tubules are lacking in the majority of species but are present in *C. disjunctus* Canu & Bassler, 1929 and *C. amphidisjunctus* Dick, Mawatari, Sanner & Grischenko, 2011 (Dick et al. 2011).

Distribution: Late Oligocene of the eastern part of the Malaysian province of Sabah, NE Borneo (Fig. 1).

4. Palaeobiogeography

So far, the bryozoan genus *Retelepralia* has been found in five different geographical regions, either as a fossil or living. The geologically oldest report of *Retelepralia* is from Malaysian Borneo, dated as Late Oligocene using biostratigraphical (nannofossil and larger benthic foraminifera data) and isotopic methods (Sr isotopes) (McMonagle et al. 2011). Subsequently,

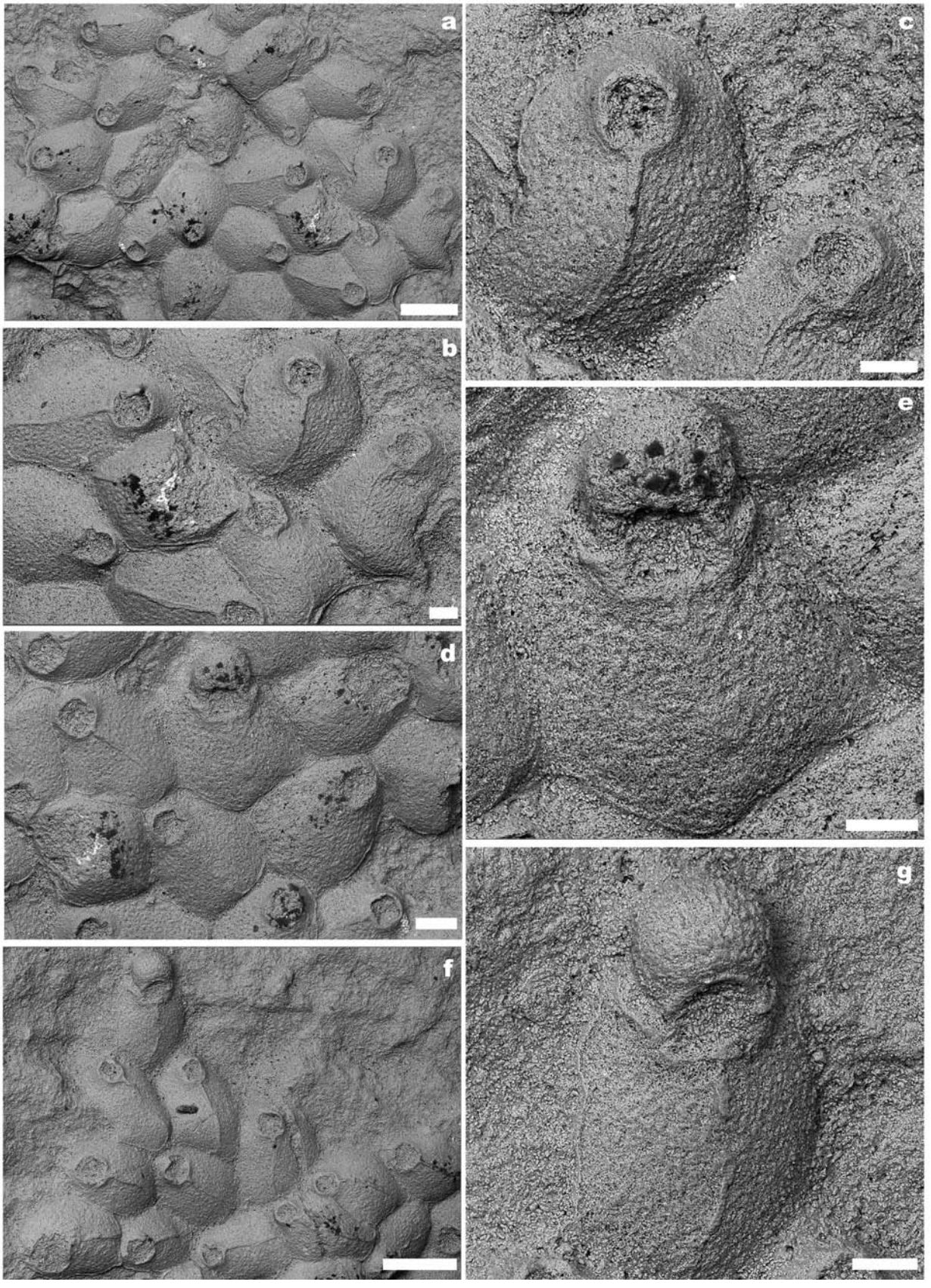

Fig. 4.

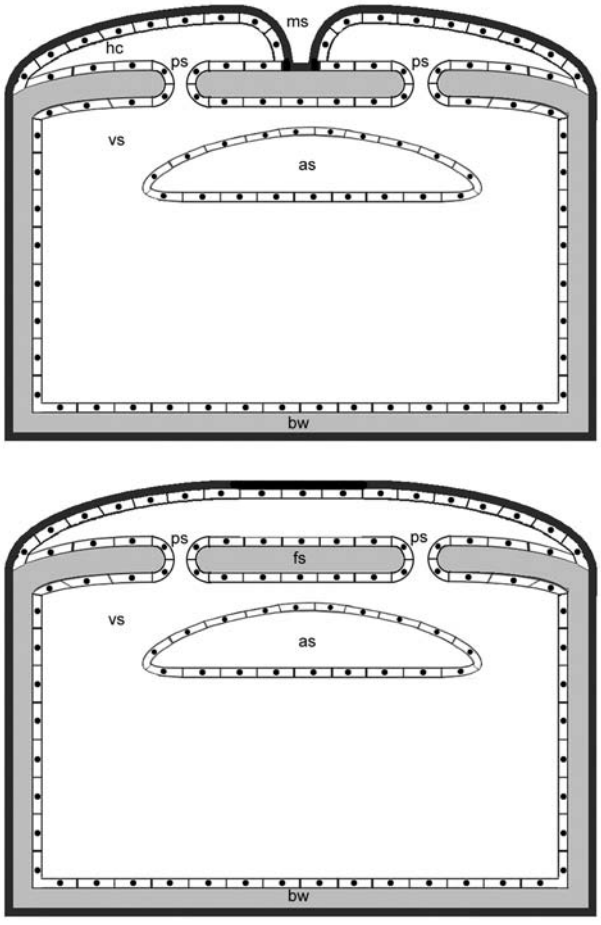

Fig. 5. a, inferred soft tissue distribution in the frontal shield of *Retelepralia* as seen in a diagrammatic transverse vertical section of a single zooid. **b**, comparative diagram showing soft tissue distribution in a typical lepralioid ascophoran bryozoan. Note the twin hypostegal coelomic compartments inferred for *Retelepralia*, one each side of the median strip of gymnocyst. Abbreviations: **ms**, median strip; **hc**, hypostegal coelom; **ps**, pseudopore; **vs**, visceral coelom, **as**, ascus; **bw**, basal wall.

Retelepralia appeared in the Miocene of France (Rhône Basin, Burdigalian; David et al. 1972) and Morocco (Melilla Basin, Messinian; El Hajjaji 1992) in the Mediterranean. Recent specimens were first collected in Mauritius (Kirkpatrick 1888; Hayward 1988), and later in northeastern Australia and along the Norfolk Ridge (Gordon & Arnold 1998). It should be noted that bryozoan faunas in some regions are as yet unknown or have been poorly investigated; therefore, the discontinuous pattern of distribution of *Retelepralia* does not necessarily reflect its total distribution in time or space. However, this genus is not present in the modern Mediterranean Sea, the bryozoan fauna of which has been rather thoroughly studied (e.g. Zabala & Maluquer 1988).

5. Interpretation of soft tissue anatomy

Ascophoran-grade cheilostomes have calcified frontal shields arching over and protecting the membrane that is depressed to raise hydrostatic pressure and cause the tentacle sheath to evert and the tentacle crown to be protruded through the orifice. Four basic kinds of frontal shield exist in ascophorans: spinocystal, gymnocystal, umbonuloid and lepralioid. Spinocystal ascophorans ('cribrimorphs') have frontal shields consisting of spines variably fused. Gymnocystal ascophorans (mostly 'hippothoids') have exterior-walled frontal shields, with a cuticle directly over the calcified layer of the wall. In umbonuloid ascophorans the frontal shield is a non-porous, inside-out structure, the hidden, inward-facing surface having cuticle directly against the calcified layer of the wall while the exposed, outward-facing surface is covered by hypostegal coelom. When umbonuloid frontal shields are viewed from within, a line, the umbonuloid ring scar, is visible at the junction between the shield and the supporting walls. Finally, lepralioid frontal shields are interior walls lacking a cuticular layer and generally perforated all over by pseudopores. The occurrence of pseudopores in the frontal shield and the lack of an umbonuloid ring scar show clearly that *Retelepralia* is a lepralioid ascophoran.

In lepralioid (and umbonuloid) ascophorans the

Fig. 4. *Retelepralia macmonagleae* sp. nov. **a-c**, holotype, NHM BZ 5839; **a**, view of colony, scale bar = 500 μm; **b**, close-up of several zooids, scale bar = 100 μm; **c**, close-up of a zooid, scale bar = 100 μm. **d-g**, paratypes NHM BZ 5840 and BZ 5841; **d**, **f**, several zooid of a colony, including one ovicelled zooid, scale bar = 100 μm (d), scale bar = 500 μm (f); **e**, **g**, close-up of ovicellate zooid, scale bar = 100 μm.

calcified layer of the frontal shield is covered by a hypostegal coelom during life. An inner epithelium overlies the outer surface of the calcified wall, followed by the coelom itself, an outer epithelium and finally the cuticle. Pseudopores in the calcified layer link the visceral coelom beneath the frontal shield with the hypostegal coelom above it. The cuticle is attached around its outer edges to exterior walls, which can be either narrow borders of subhorizontal gymnocyst (particularly in the proximal part of the zooid) or the vertical walls bounding the zooid. Further attachment points for the cuticle occur around the orifice.

The presence of the distinctive median strip in *Retelepralia* implies a modification of the typical lepralioid soft tissue organization (Fig. 5). The median strip lacks pseudopores and also the granulations seen elsewhere on the frontal shield. Both of these features are typical of cryptocystal walls. Instead, the median strip is smoothly calcified and is morphologically and texturally continuous with narrow exposed areas of gymnocyst at the edges of the zooid as well as around the orifice. Therefore, the median strip can be interpreted as an exterior wall; this is implicit in Gordon & Arnold's (1998) description of it as gymnocyst. As the hypostegal coelom does not normally cover the exterior walls in bryozoans, it is possible to infer that the cuticle is attached along the left and right sides of the median strip. The median strip runs the length of the zooid proximally of the orifice, with a continuation visible distal of the orifice in some zooids, suggesting that these cuticular attachments run without break along the axis of the zooid. If so the hypostegal coelom is divided into two components, a left side and a right side, that are not in continuity above the frontal shield (although they are almost certainly continuous via the visceral coelom beneath the frontal shield). We know of no other ascophoran cheilostomes with distinct left and right hypostegal coeloms.

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