

***Omanipora pilleri* nov. gen. nov. spec., a new lepraliomorph bryozoan (Cheilostomata) from Oman**

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(With 3 figures and 1 table)

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Abstract

Bryozoans from around the Arabian Peninsula are only poorly known. Here we describe a new cheilostome taxon, *Omanipora pilleri* nov. gen. nov. spec., from the western Indian Ocean, south of the town of Duqm (eastern central Oman). Starting from an encrusting base the colonies grow erect, producing either branching and anastomosing bilaminar fronds or robust radial branches by means of frontal budding, while some specimens even exhibit an intracolony morphological gradient from one branch type to the other. The variability in colony morphology presumably reflects growth under different hydrodynamic conditions.

Based on superficially similar orificial, ooecial, avicularian and frontal wall structures the new taxon is tentatively placed within the Celleporidae JOHNSTON. Some of the characters that justify the introduction of a new genus are: communication of the ooecial coelomic cavity with the maternal zooid proceeds via several distal communication pores, which is a feature that has not been observed before; ovicell closure is of the cleithral type; and the orifices are dimorphic in fertile (egg-producing) and non-fertile zooids.

Keywords: Bryozoa, Indian Ocean, new species, new genus, ovicells.

Zusammenfassung

Die Bryozoen der Arabischen Halbinsel sind immer noch sehr unzureichend bekannt. In der vorliegenden Arbeit wird ein neues Taxon cheilostomer Bryozoen aus dem westlichen Indischen Ozean beschrieben, das an der Ostküste des zentralen Oman (südlich des Ortes Duqm) vorkommt:

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Omanipora pilleri nov. gen., nov. spec. Ausgehend von einer inkrustierenden Basis produzieren die Kolonien eine dreidimensionale Struktur von mehreren Zentimetern Durchmesser und meist rundlich-ellipsoidem Umfang. Die zum Teil anastomosierenden Äste sind entweder bilaminarverzweigt oder, durch frontale Knospung, massiv und rundlich gebaut. Innerhalb einiger Kolonien ist sogar ein morphologischer Gradient von einem zum anderen Ast-Typ zu beobachten. Diese Variabilität in der Morphologie der Kolonien wird auf den Wuchs unter unterschiedlichen hydrodynamischen Bedingungen zurückgeführt.

Aufgrund von ähnlichen Strukturen des Orifiziums, des Ooeciums, der Avikularien und der Frontalwand wird das neue Taxon vorläufig in die Familie Celleporidae JOHNSTON gestellt. Einige der Merkmale, welche die Einführung einer neuen Gattung rechtfertigen, sind: die Kommunikation der ooecialen Körperhöhle mit dem Mutterzooid verläuft über mehrere distale Kommunikationsporen, was bislang noch in keiner anderen Art beobachtet wurde; der Verschluss der Ovizelle ist vom cleithralen Typ; die Orifizien fertiler und nicht-fertiler Zooide sind dimorph.

Schlüsselwörter: Bryozoa, Indischer Ozean, neue Art, neue Gattung, Ovizellen.

Introduction

Despite a number of works from the Persian Gulf (SOULE & SOULE 1985), the Gulf of Aden (AMUI 2005; AMUI & KASELOWSKY 2006), and particularly the Red Sea (e.g. AUDOUIN 1826; WATERS 1909; HASTINGS 1927; BALAVOINE 1959; POWELL 1967; REDIER 1970; DUMONT 1981; D'HONDT 1988), knowledge of the bryozoan fauna around the Arabian Peninsula is still extremely limited. Addressing questions concerning biodiversity, biogeography and ecology is hampered by the fact that most studies predate the use of scanning electron microscopy (SEM), which is crucial for species determination, and that the type specimens of the most comprehensive historical work on the region (AUDOUIN 1826) are lost (D'HONDT 2006). The reliability and value of species checklists (e.g. POWELL 1969; SCHOLZ 2000) and works that do not comprise taxonomic studies (e.g. SOULE & SOULE 1985) are therefore questionable. It is certain, however, that the number of known species in this region (ca 340, OSTROVSKY & CÁCERES-CHAMIZO unpubl. data) is highly underestimated.

Here we describe a new lepraliomorph bryozoan taxon from the east coast of Oman (Fig. 1) that is characterised by forming variable colony morphology in response to micro-environmental conditions, and that has a hitherto unknown type of ooecium formation.

Material and methods

Numerous colonies were collected on a beach to the north of the deserted village Shuwayr (south of the town of Duqm, eastern central Oman; 19°32'49.25''N 57°41'50.30''E) by M. REUTER (University of Graz, Austria) in February 2006 (Fig. 1).

Branch fragments from different parts of two colonies were bleached and treated in an ultrasonic bath for a few seconds in order to remove organic tissue and adhering sediment.

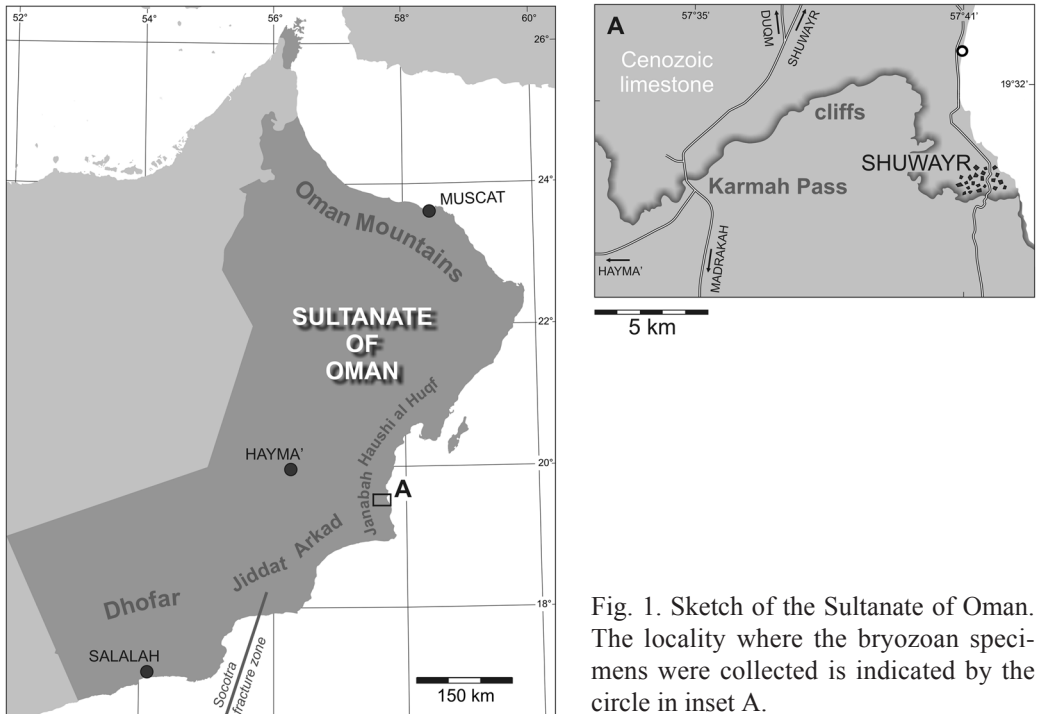


Fig. 1. Sketch of the Sultanate of Oman. The locality where the bryozoan specimens were collected is indicated by the circle in inset A.

They were then sputter-coated with gold and digitally photographed on a Jeol JSM-6400 scanning electron microscope at University of Vienna. Measurements of skeletal characters were taken from these images using the software ImageJ. Owing to the regular budding pattern in bilaminar fronds, zoecium length and width were measured in zooids from these colony regions only, whereas measurements of all other characters were also taken from frontally budded zooids.

Systematic account

“Grade” Lepraliomorpha GORDON, 1989

Superfamily Celleporoidea JOHNSTON, 1838

Family Celleporidae JOHNSTON, 1838

Remarks: The cryptocystal frontal shield and the absence of a ring scar show clearly that this new taxon is a lepraliomorph. However, it does not readily fit in any of the existing families. General orificial morphology, the presence of dimorphic avicularia, and an ovicell with a calcified pseudoporous ectooecium are shared with certain taxa of both

the Celleporidae and the Bitectiporidae MACGILLIVRAY, 1895. Yet the new taxon differs from these families in having two (to rarely three) rows of lateral areolar pores, dimorphic orifices in ovicellate zooids (but see below), and kenozooidal oecia that are budded from the maternal zooid and communicate with it via numerous distal communication pores. Also, the mode of growth of the new taxon, a combination of bilaminar fronds and massive branches formed by means of frontal budding, seems to be unique: whereas excessive and coordinated frontal budding seldom occurs in the Bitectiporidae, bilaminar fronds are very rarely formed in the Celleporidae (e.g. *Buffonellaria antoniettae* BERNING & KUKLINSKI, 2008).

The type of ovicell closure and oecium formation varies within and among bitectiporid and celleporid taxa. While the ovicells in most species in the bitectiporid genus *Schizomavella* CANU & BASSLER, 1917 are not closed by the operculum, several species do, in fact, show this feature and dimorphic orifices may also be present (pers. comm. O. REVERTER-GIL 2010). Anatomical research revealed that cleithral ovicells are characteristic of the genus *Hippoporina* NEVIANI, 1895 (Bitectiporidae) as well (OSTROVSKY unpubl. data, see also HAYWARD & RYLAND 1999: 196).

Similarly, the latest diagnosis of the family Celleporidae (BERNING & KUKLINSKI 2008) states that the ovicell is not closed by the operculum whereas the Indo-Pacific species hitherto assigned to the celleporid genus *Turbicellepora* RYLAND, 1963 [e.g. “*Turbicellepora*” *redoutei* (AUDOUIN, 1826) and “*T.*” *ovioris* TILBROOK, 2006] have ovicells that are of the (sub)cleithral type.

Thus, the value of this character for family-level systematics is rather uncertain, especially if we consider that in some species the ovicell opening is closed by the operculum during embryonic incubation, whereas the operculum is lowered to the level of the primary orifice when the ovicell is empty. When the operculum is down, the entrance to the brood chamber is either opened or closed by the thin-walled, uncalcified oecial vesicle, which is an evagination of the maternal zooid’s distal wall. This ovicell type is termed subcleithral (OSTROVSKY 2008a, 2009). Thus, at least in some cases, cleithral ovicells are, in fact, subcleithral, and the exact type of ovicell closure can be ascertained only when living reproducing colonies are observed.

The new taxon is special regarding the formation of the oecium, as it is a kenozooid that is produced by the maternal zooid and communicates with it via numerous pores. In contrast, the oecium is considered to be formed by the zooid distal to the maternal one in the Bitectiporidae and also in some celleporid taxa (e.g. *Buffonellaria* Canu & Bassler, 1927). In other Celleporidae (e.g. *Turbicellepora* s. str.) the oecial kenozooid is produced by the maternal zooid but communicates with it only via a single pore. However, communication between maternal zooid and oecial coelom does take place via several pores in “*T.*” *redoutei* (OSTROVSKY, CÁCERES-CHAMIZO & BERNING unpubl. data), and presumably in other Indo-Pacific “*Turbicellepora*” as well, again suggesting a closer relationship with the new taxon.

There is, therefore, clearly a need to revise several taxa in the Bitectiporidae and Celleporidae, and, as a consequence, to emend the diagnoses of both families, which is beyond the scope of the present paper. Despite lacking information on some important characters of the new taxon presented here, such as the ancestrula and early astogeny, owing to its general morphological similarity to Indo-Pacific species that are at present assigned to the genus *Turbicellepora*, we have, nevertheless, decided to tentatively place *Omanipora* nov. gen. in the Celleporidae.

Genus *Omanipora* nov. gen.

Diagnosis: Colony rising from an encrusting base forming ramifying bilaminar fronds and/or massive branches by means of extensive frontal budding. Frontal wall lepralimorph, imperforate except for two or three rows of lateral areolar pores. Orifice dimorphic (fertile vs. non-fertile zooids), with condyles and sinus, no spines. Ovicells cleithral, ooecium consisting of a thickly calcified ectooecium with pseudopores, and a thinly calcified complete entoecium; formed by the maternal zooid and communicating with it via several disto-frontal communication pores. Avicularia adventitious, dimorphic; a small avicularium usually situated close to the orifice, and larger spatulate ones irregularly dispersed on the surface.

Etymology: Named after the type location, Oman, and the porous skeleton of its type species; gender feminine.

Type species: *Omanipora pilleri* nov. spec.

Remarks: The unique characters of *Omanipora*, distinguishing it from all other celleporid taxa, are the presence of up to three rows of areolar pores in autozooids, the presence of dimorphic orifices, and the communication of the ooecium with the cavity of the maternal zooid via several distal areolar pores. In *Turbicellepora* s. str. ooecial morphology and communication (although via a single pore only) are similar but the ovicell is not closed by the operculum (non-cleithral type), and the obligatory single or double avicularium associated with the orifice is not strictly present in *Omanipora*. The most closely related taxa seem to be the Indo-Pacific species that were hitherto assigned to *Turbicellepora* (e.g. "*T.*" *redoutei*), in which the ovicells are also of the (sub-)cleithral type, and in which communication between maternal zooid and ooecial coelom takes place via several pores as well. TILBROOK (2006: 280) already remarked that it may be more appropriate to accommodate the Indo-Pacific species in another genus. However, a comprehensive study of these taxa, and their relationship with *Omanipora*, is beyond the scope of this paper.

***Omanipora pilleri* nov. spec.**
(Figs 2-3)

Material: The specimens are kept at the Biology Centre (Collection “Invertebrata except Insecta”) of the Upper Austrian State Museum, Linz (LI).

Holotype: LI 2010/156, a semi-erect colony of about 5.8 cm in length, collected on a beach south of Duqm, central Oman (19°32'49.25''N 57°41'50.30''E). Five small fragments of the holotype were mounted on stubs for SEM photography and are kept together with the type.

Paratypes: LI 2010/157, a semi-erect colony of about 4 cm in length, composed entirely of closely spaced bilaminar fronds (one small fragment of LI 2010/157 was mounted on a stub for SEM photography and is kept together with the type). LI 2010/181, a fragment of a semi-erect colony of about 8 cm in length with irregular, anastomosing branches. LI 2010/182, a small colony of 3.5 cm length with widely spaced bilaminar fronds. All paratypes from the same location as holotype

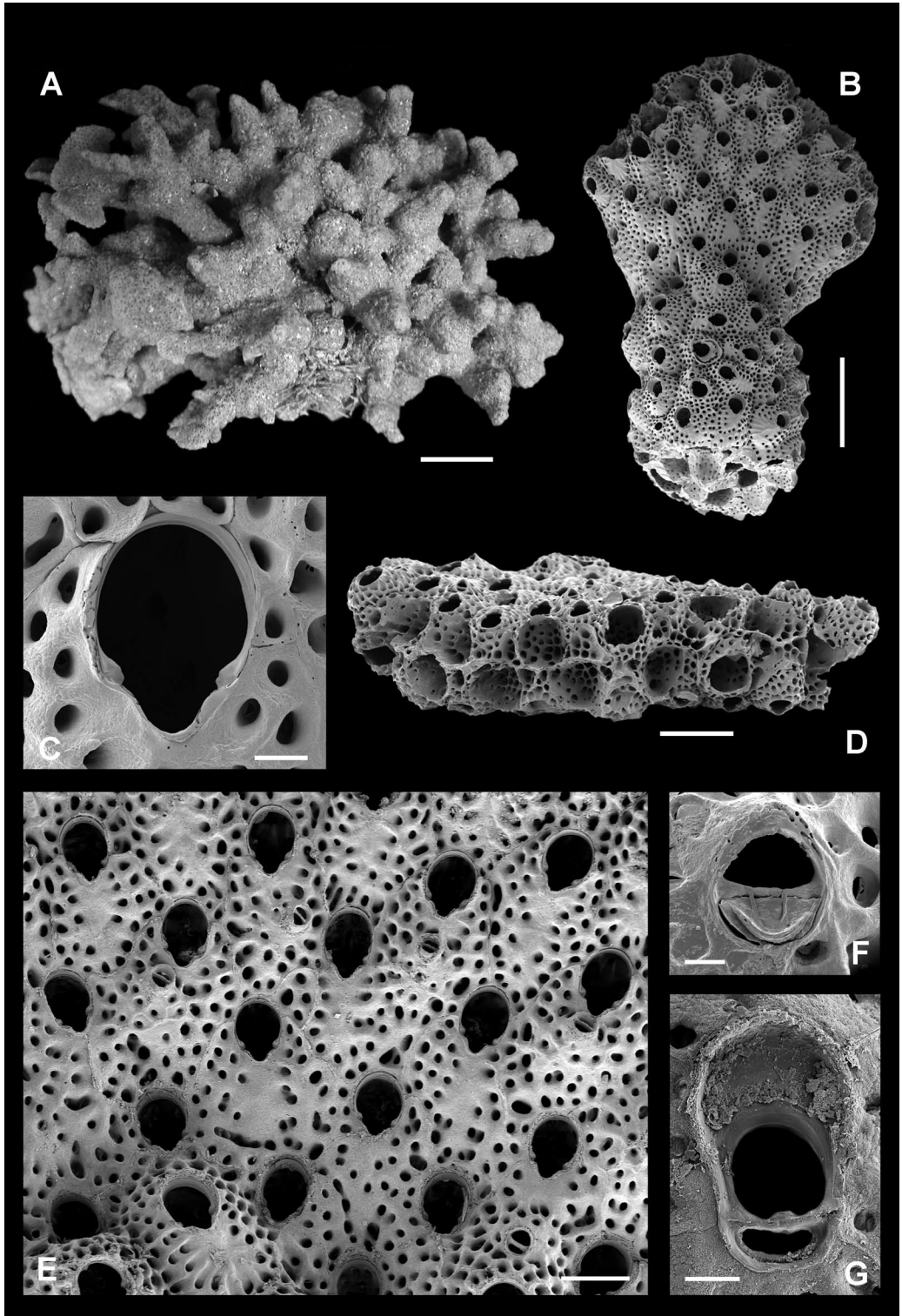
Sixteen additional, mostly abraded colonies from the same location (LI 2010/183).

Etymology: The new species is named in honour of Werner E. PILLER for his contributions to (actuo)palaeontology.

Description: Colony initially encrusting, later semi-erect, polymorphic, producing (a) short, stout, tapering and irregularly anastomosing branches by means of frontal budding, and/or (b) bilaminar branching fronds that increase in thickness by frontal budding to produce short compact and anastomosing plates, occasionally within the same colony (Figs 2A, B, D); colonies roughly spheroidal in shape overall, and reaching several cm in diameter.

Zooids in bilaminar branches elongate-oval (Fig. 2E), frontally budded zooids shorter and broader (Fig. 3B), separated by indistinct sutures. Vertical and basal zooidal walls with numerous uniporous septula (Fig. 2D). Frontal wall slightly convex (frontally bud-

Fig. 2. *Omanipora pilleri* nov. gen. et nov. spec. A: Holotype, LI 2010/156; semi-erect colony showing the morphological gradient from thick, anastomosing branches produced by frontal budding at right, to bilaminar fronds prevailing at the far left of the colony; scale bar: 1 cm; B: Fragment of holotype; distal part of a bilaminar frond proximally merging into a cylindrical branch through frontal budding of zooids; scale bar: 1 mm; C: Fragment of holotype; orifice of autozooid; scale bar: 50 µm; D: Fragment of holotype; growth margin of a bilaminar frond; scale bar: 500 µm; E: Fragment of holotype; autozooids at distal margin of bilaminar frond, note the infrequent presence of small avicularia and their variable positions on the frontal shield; scale bar: 200 µm; F: Fragment of holotype; suboral avicularium with the lower surface of the mandible exposed, showing the crescentic ridge to where the muscles attach; scale bar: 30 µm; G: Fragment of paratype, LI 2010/157; spatulate avicularium; scale bar: 50 µm. ▶



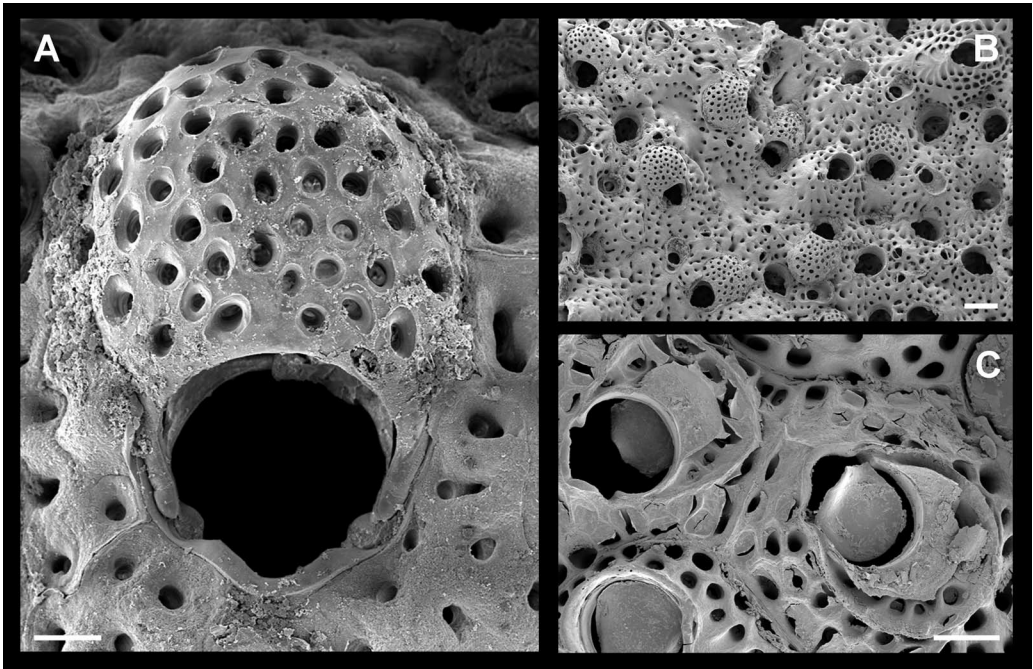


Fig. 3. *Omanipora pilleri* nov. gen. et nov. spec. A: Fragment of paratype, LI 2010/157; ooeonium with the thickly calcified, porous ectooecium exposed; note the shallow sinus and the relatively broad proximal rim of smooth calcification in the dimorphic orifice; scale bar: 50 μm ; B: Fragment of paratype; frontally budded zooids with oecia and spatulate avicularia; scale bar: 200 μm ; C: Fragment of holotype, LI 2010/156; formation of oecia with the cuticle partly preserved – note the thinly calcified entooecium, the presence of numerous areolar pores in the base of the ectooecium through which the coelomic cavity of the ooeonium communicates with the maternal zooid, and the bend in the proximal operculum that rests on the primary orifice at lower right; scale bar: 100 μm .

ded zoecia are distinctly more convex), centre imperforate with two to three lateral rows of areolar pores, the extensions of which encroach upon the entire frontal area during later ontogeny as terminal growth of the interareolar ridges proceeds, resulting in the appearance of a completely porous frontal wall. Orifices dimorphic; autozooidal orifice longer than wide with proximolateral edges sloping towards deep, rounded V-shaped sinus comprising more than half of the proximal orifice width, condyles short but distinct, rounded, not quite reaching the edges of the sinus, proximal margin a relatively narrow area of gymnocystal calcification (Fig. 2C); ovicell opening perfectly closed by the operculum, slightly broader than long, sinus distinctly shallower and broader and with less pronounced edges than in non-fertile zooids, gymnocystal calcification of proximal margin also markedly broader (Fig. 3A); the proximal sinusoidal part of the operculum in maternal zooids is distinctly bent upwards relative to the distal part (Fig. 3C).

Avicularia dimorphic; a single small oval one occurring variably frequent, situated directly suborally or at some distance to the orifice (Figs 2E, 3B), slightly oblique to frontal plane and generally pointing proximally, the distal tip forming the highest elevation on the frontal surface; mandible semicircular to semielliptical, the interior side with a distal crescentic ridge to which the muscles are attached (Fig. 2F); crossbar simple, complete. Larger spatulate avicularia forming during later ontogeny, irregularly dispersed on the colony surface, pointing in various directions (Fig. 3B); rostrum gradually increasing in width distally, lateral edges straight, distal uncalcified area subcircular to subelliptical, proximal area semicircular (Fig. 2G); crossbar complete, with a small central thickening on the distal edge.

Ovicells formed by frontally budded zooids only, in younger zooids prominent, becoming subimmersed owing to frontal calcification during later ontogeny (Fig. 3B), closed by the zooidal operculum. The ooeonium is a kenozooid budded from the maternal zooid, with its coelomic cavity communicating with the zooidal coelom via several areolar pores at the disto-frontal zooidal wall (Fig. 3C). Ooeonium globular but frontally slightly flattened, outline almost circular but with the proximolateral margins reaching towards the proximolateral corners of the zooidal primary orifice, thus longer than wide overall (Fig. 3A); ectooeonium thickly calcified with numerous funnel-shaped pits leading from the rather even surface to subcircular or subelliptical pseudopores; entoeeonium thinly but entirely calcified.

An ancestrula and early astogenetic stages were not observed.

Table 1. Measurements of skeletal characters (in μm). SD: standard deviation, #: number of measurements made.

Character	mean \pm SD	min.-max.	#
Zooecium length	601 \pm 75	508–785	20
Zooecium width	359 \pm 36	306–425	20
Orifice length	195 \pm 10	176–209	20
Orifice width	148 \pm 10	134–167	20
Orifice length in ovicellate zooecia	146 \pm 6	137–153	5
Orifice width in ovicellate zooecia	149 \pm 6	142–159	5
Ooeonium length	327 \pm 22	303–358	13
Ooeonium width	285 \pm 22	258–337	13
Oral avicularium length	92 \pm 11	73–112	20
Oral avicularium width	76 \pm 10	61–97	20
Spatulate avicularium length	211 \pm 22	181–246	8
Spatulate avicularium width	142 \pm 9	134–156	8

Discussion

The colonies were found cast on a rocky beach south of the town of Duqm (north of the deserted village Shuwayr), together with the remains of gastropods, bivalves and sponges. The Miocene limestone cropping out in this part of the coastline provides the hard substratum for shallow-water epilithobionts (M. REUTER pers. comm. 2010; see also REUTER et al. 2008). Accordingly, a fracture zone present at the base of most colonies indicates the former attachment to a stable substratum, e.g. to a rock bottom. As numerous colonies were found on the beach the upper depth limit of this species can be regarded as well above storm wave base. Several colonies were observed to encrust and encase the agglutinated and calcareous tubes of three polychaete species, possibly suggesting a symbiotic relationship between these taxa.

The relatively shallow occurrence of *O. pilleri* is presumably the reason for the rather ellipsoidal primary colony shape, the morphological variability between colonies, and for the presence of an intracolony gradient in morphology. In some of these semi-erect colonies one end (and most of the remaining colony) is composed of thick, short, tapering branches produced by frontal budding, whereas at the other extreme end bilaminar fronds prevail that are thickened by frontal budding only during later stages (Fig. 2B). It is conceivable that both colony shape and the morphological gradient are induced by a strong directional current such as wave action, with the long axis of the colony directed parallel to the current, and with the more robust shorter branches growing towards the incoming waves and the less pressure-resistant bilaminar fronds towards the leeward side.

Alternatively, the colony morphology could be an adaptation to improve feeding efficiency: a similar colony shape and morphological gradient formed by *Celleporaria tridenticulata* (BUSK, 1881) from Australia was interpreted by MCKINNEY (1990: fig. 12, as *C. tridens*) as such. However, other colonies are wholly consisting of either the thick tapering branches or bilaminar fronds, thus presumably indicating higher and lower energetic conditions, respectively, compared to specimens with an intracolony gradient.

The presence of numerous lateral and basal communication pores in autozooea of *O. pilleri* (Fig. 2D) is reminiscent of the highly porous skeleton of the erect branching *Myriapora truncata* (PALLAS, 1766) from the Mediterranean Sea (see e.g. BERNING 2007). In both species this type of skeleton formation certainly provides a rigid and robust, yet lightweight mode of construction for life in relatively high-energy, rocky shore, subtidal environments.

The new species also shares with *M. truncata* the dimorphic orifices and cleithral ovicells (Fig. 3A). The high degree of integration between the morphology of the maternal zooid and ovicell (i.e. the distinct orifice/operculum shape, and the perfect fit of operculum and ovicell opening) reflects an improved protection of the developing embryo compared to acleithral ovicells, in which the ovicell interior is merely closed by the membranous oocelial vesicle, and non-cleithral ones, in which the ovicell opening is not closed at all.

Nevertheless, the exact type of ovicell closure may be identified only after checking living colonies of *O. pilleri* carrying embryos. In the dried uncleaned colonies studied some ovicells were evidently closed by the maternal operculum. Yet in other ovicellate zoecia the operculum was lowered to the primary orifice (Fig. 3C), thus keeping the option of the subcleithral type open. The bend in the operculum at the level of the sinus, which reflects the angle between the planes of the ovicell opening and the proximal orifice margin, suggests, however, that the operculum mainly functions to close the ovicell. Whenever the operculum is lowered to the primary orifice its proximal part is raised above the level of the sinus, thus leaving a gap open between the proximal margins of the operculum and the orifice (Fig. 3C). We therefore suggest that in *O. pilleri* ovicell closure is of the cleithral type.

More research on living colonies is also needed regarding the exact type of oecium formation. The oecium in *O. pilleri* is a kenozooid that is budded from the disto-frontal wall of the maternal autozooid, while the oecial coelomic cavity communicates with the visceral coelom via several areolar pores that are obviously closed by pore-cell complexes (Fig. 3C). Such kenozooidal oecia are relatively rare among cheilostomes (in fact, the very type of oecium communication present in *O. pilleri* has never been observed before), since in most cases the oecium is not a kenozooid but an outfold of the frontal wall of the distal zooid in a series (OSTROVSKY 2008a-b, 2009; OSTROVSKY et al. 2009). On the other hand, oecia are formed only by the frontally budded zooids, and the distal zooid is missing in this case. Nevertheless, the one or two rows of distal areolar pores are initially also present in basal zooids but are soon disguised by frontal calcification of the distal zooid.

Several taxa within the Celleporidae also produce a distal kenozooidal oecium from frontally budded zooids, e.g. species in the genera *Celleporina* GRAY, 1848, *Galeopsis* JULLIEN & CALVET, 1903, and *Turbicellepora* s. str. However, their oecia communicate with the maternal zooid via a single pore. Numerous communication pores were only detected in the Indo-Pacific species that were tentatively placed in the genus *Turbicellepora* before (e.g. “*T.*” *redoutei*). Future studies to resolve the systematic position of *Omanipora* should therefore include “*T.*” *redoutei* and other related Indo-Pacific species (e.g. “*T.*” *ovioris*).

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