



## Bryodiversity in the tropics: taxonomy of *Microporella* species (Bryozoa, Cheilostomata) with personate maternal zooids from Indian Ocean, Red Sea and southeast Mediterranean

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### Abstract

The particularly speciose cheilostomate genus *Microporella* includes taxa whose maternal zooids and associated ovicells present a personate structure, i.e. a particularly developed peristome. Six species of *Microporella* with personate ovicells are analysed from material sampled in the Indian Ocean, Red Sea and southeast Mediterranean. Consideration of highly diagnostic tiny morphological characters displayed by the primary orifice and the avicularium has made it possible to distinguish three new species, *M. browni* n. sp., *M. maldiviensis* n. sp. and *M. collaroides* n. sp., and to better characterise the other species. Among the latter, two species named by Audouin (1826) from Savigny's drawings (1817), *M. coronata* and *M. genisii*, are redescribed and neotypes are selected. Additionally, a new species of the *M. coronata* species group, *Microporella hastingsae* n. sp., is proposed following examination of a museum specimen recorded as *M. ciliata* var. *coronata* (Hastings 1927). The species dealt with in this study revealed remarkably different patterns of geographic distribution, possibly showing different potential for natural and/or anthropogenic dispersal. The bryozoan assemblages sampled along the coast of Lebanon include four of the six studied species, at least three of them presumably non-indigenous including *M. harmeri* Hayward, which displays a remarkably wide distribution from the Indian Ocean to the West Pacific and the East Atlantic (Canary Islands).

**Key words:** bryozoans, biodiversity, Ascophora, Microporellidae, ovicell, new species, biogeography, alien species

### Introduction

Present-day knowledge of marine biodiversity is very incomplete for most higher taxa even in areas that have long been the focus of a considerable scientific effort, such as the European seas (Bouchet 2006). The gap between the presumed actual number of extant species and that of already described ones is particularly wide in tropical regions, which harbour hot-spots of biodiversity (Gray 2001; Bouchet 2006). Shipping and the opening of artificial corridors between basins are the most influential anthropogenic factors affecting the biogeographical ranges of an increasing number of marine species. The opening of the Suez Canal to maritime traffic in 1869 was the start of a new era for the southeastern Mediterranean, leading to an exceptionally extensive colonization of the Levant basin by tropical species that have taken advantage of the warming of the sea (Steinitz 1967; Powell 1969; Galil 2000; Zenetos *et al.* 2005; Por 2009; Bitar 2010).

The known 'bryodiversity' (i.e. the diversity of bryozoans) represents a relatively modest part, approximately 2.6% of the general marine biodiversity, if one considers that about 6,000 living species have been recorded. How-

ever, several thousand species remain unknown (Gordon *et al.* 2009). It is something of a cliché to say that the species-level taxonomy of *Microporella* Hincks, 1877 is puzzling. This genus is one of the most diverse among bryozoans (about 100 species; Taylor & Mawatari 2005) and many inadequate species diagnoses need to be re-assessed using more reliable diagnostic characters and well-preserved material. Recent advances in the taxonomy of *Microporella* have revealed a considerable range of species-specific morphological characters in this genus (e.g. Gordon 1984, 1989; Dick & Ross 1988; Hayward & Ryland 1990; Soule *et al.* 1995; Suwa & Mawatari 1998; Suwa *et al.* 1998; Soule *et al.* 2003; Taylor & Mawatari 2005; Kuklinski & Taylor 2008). The use of SEM has led to species splitting based on a wide array of tiny morphological features of both non-mineralized parts (e.g. avicularium mandibles) and skeletal ones (e.g. microstructures of the primary orifice) that were revealed to be highly diagnostic. These characters were not at all or poorly accessible with optical microscopy and thus were seldom considered in early descriptions. This implies a need for re-description of old taxa, at best from deposited types when available, or after designation of lectotypes from the author's collection or neotypes or topotypes from the assumed type locality. This was the case for the type species of *Microporella*, *M. ciliata* (Pallas), formerly considered to be cosmopolitan and morphologically variable, which was recently re-described by Kuklinsky and Taylor (2008) after choosing arbitrarily a neotype from material obtained off Naples, Italy. A reconsideration of the taxonomic status of the so-called cosmopolitan or widely distributed species is an urgent task for the purpose of both better evaluating the world's biodiversity and characterising habitats that could be at risk (Soule & Soule 2002).

A comparative study of specimens from the Indian Ocean to the southeastern Mediterranean, based on thorough examination of their morphological attributes, has provided a basis for re-assessing the diversity of *Microporella* species having in common ovicells with a 'personate' structure (from Latin *personatus*, masked). This term was introduced by George Busk for *Lepralia personata* Busk, 1854, a *Microporella* from the Falkland Islands in which the ovicell has "the lower lip very much produced and projecting" (Busk 1854, p. 74; see also Hayward & Ryland 1990). Although such a collar forming a peristome is produced by the maternal (i.e. fertile, egg-producing) zooid and not by the ovicell, both the maternal zooid contribution and the ovicell can be termed personate.

In *Microporella*, the double-walled ooecium (protective hood of the ovicell) is formed by the zooid distal to the maternal (which produces the embryos). It consists of a fully calcified entoecium bearing 'pseudopores' (basically small blind pits) and a membranous ectoecium, with a very narrow coelomic cavity in between. The pustulose surface of the entoecium is visible in non-cleaned colonies, and it continues to the zooidal frontal wall, whereas the ooecial cavity is confluent with the zooidal hypostegal coelom. According to Osburn (1952), Hayward and Ryland (1999) and Tilbrook (2006), the ovicell opening is closed by the operculum of the maternal zooid (cleithral type). However, in dry colonies ovicells are open with the operculum in a lower position, closing the primary orifice of the maternal zooid (Ostrovsky 2009).

Six *Microporella* species with personate ovicells are examined here, including three new species: *M. browni* n. sp., *M. maldiviensis* n. sp. and *M. collaroides* n. sp. Two other species, *M. coronata* and *M. genisii*, named by Audouin (1826) from illustrations by Savigny (1817), are redescribed with a selection of neotypes. Morphological discrepancies between *M. coronata* and specimens from the Suez Canal assigned to this species by Hastings (1927) enable us to propose a fourth new species, *M. hastingsae* n. sp. Better characterisation of the sixth species, *M. harmeri* Hayward, 1988, shows that it has a particularly wide geographic distribution and forms a species group with closely allied species from the Pacific Ocean. This study highlights the importance of alien species in the marine assemblages from southeastern Mediterranean coasts, which are particularly susceptible to species introductions by shipping and propagule transfer via the Suez Canal.

## Material and methods

The southeastern Mediterranean material including *Microporella* species was collected by scuba by Drs G. Bitar, H. Zibrowius and J.G. Harmelin at ten localities (3–43 m) distributed along the whole coast of Lebanon, mainly from 1999 to 2003, as part of the Lebanese-French cooperation program CEDRE. Specimens from south Sinai were collected at Ras Mohammed on artifacts from the 'Yolanda' wreck and those from Tadjoura (Gulf of Aden) on corals by J.G. Harmelin in 1983 and 1969 respectively.

The material from Safaga Bay, northern Red Sea, was taken from sediment samples and additionally collected by scuba diving by picking up dead mollusc shells and coral rubble at four stations (2–42 m) in 1987 and 1992.

Collecting was done as part of the study of Safaga Bay undertaken by the Department of Palaeontology, University of Vienna. The material from Jeddah, on the east coast of the Red Sea, was collected by Dr A. Antonius on corals. The material from South Africa (Sodwana Bay) was collected in 1993 by Dr B. Riegl using scuba. *Microporella* colonies from the Maldive Islands were collected in 1983 at three localities (5–35 m) within the North Male Atoll by Dr F.F. Steininger, and in 2008 by A. Azeez A. Hakeem, R. Tomasetti, M. Rifshan, I. Nimad and A.N. Ostrovsky, all using scuba. The material from Oman was collected in 2009 at two localities (8–11 m) by Drs M. Claereboudt and A.N. Ostrovsky using scuba.

Scanning electron microscopy (SEM) was carried out on specimens cleaned in a 7.5% solution of sodium hypochlorite, rinsed, air-dried and coated with gold, using a Hitachi S 570 (Marseille), Jeol JSM-6400 and FEI Inspect S50 (Vienna). Specimens from museum collections were scanned at the Natural History Museum, London (NHM) and the U.S. Natural History Museum, Washington (USNM).

Specimens from Lebanon, south Sinai and Tadjoura (Gulf of Aden) have been lodged at the MNHN, Paris and the Senckenberg Museum, Frankfurt am Main. All the specimens from Safaga Bay and Jeddah (Red Sea), Oman, Maldives and South Africa are currently kept at the Department of Palaeontology, Geozentrum, University of Vienna (DPUV). The final destination of this collection will be the Senckenberg Museum.

In the following descriptions of species, encrusting colonies are qualified as large, medium or small when they are larger than 16 mm, 4–16 mm or smaller than 4 mm, respectively. These values are meaningful only in the context of *Microporella* taxonomy. Measurements of different zooid parts were made using a stereomicroscope with a micrometric eyepiece at the highest magnification possible and alternatively from SEM photos.

For the authorship of *M. coronata* and *M. genisii*, we have deliberately associated Savigny with Audouin (1826), as the latter did not give any description in his text of the species he named from Savigny's very informative drawings, which, in the absence of deposited types, are the only source of morphological information on these species. The publication date of Savigny's plates including bryozoans is not precisely stated; the date chosen here (1817) is that cited by d'Hondt (2002). The pagination of Audouin's descriptions of *M. coronata* and *M. genisii* given below pertains to the second edition of his work (Audouin 1828).

## Systematic account

### *Microporella browni* n. sp.

(Figs 1A–G, 2A–E, Table 1)

**Material examined.** *Holotype*: 2010-0001-0001 DPUV, on *Haliotis mariae* shell. South Oman, Salalah, near Mirbat, Kelp Bay, right side, 9 m, 16 January 2009. *Paratypes*: 2010-0001-0002 DPUV, 2010-0001-0003 DPUV, 2010-0001-0004 DPUV, 2010-0001-0005 DPUV, 2010-0001-0006 DPUV, 2010-0001-0007 DPUV, 2010-0001-0008 DPUV, on the same *Haliotis mariae* shell as the holotype. South Oman, Salalah, near Mirbat, Kelp Bay, right side, 9 m, 16 January 2009. Mounted on SEM stub: 2010-0001-0009 DPUV, 2010-0001-0010 DPUV, taken from bivalve shells. South Oman, Salalah, near Mirbat, Kelp Bay, right side, 9 m, 16 January 2009. *Other material examined*: *M. browni* n. sp. — Lebanon: Beirut, airport pier, 3–11 m, 2 colonies on serpulid tube, 25 September 2002; 4 colonies on shells, 16 July 2003. Indian Ocean: (1) Gulf of Aden, Tadjoura (1146'45 N, 4254'37" E), 20 m, 11 colonies beneath planar coral *Pachyseris*, October 1969; (2) South Oman, Salalah, near Mirbat, Kelp Bay, left side, 11 m, 5 colonies on bivalve shells, 23 January 2009; (3) Maldive Islands, North Male Atoll, Vabbinfaru Is., House Reef, 5–19 m, 4 colonies on bivalve shells, 12–13 January 2008; (4) Maldive Islands, North Male Atoll, Helengeli Is., March 1983, 4 colonies on bivalve shells, coll. F.F. Steininger. *M. orientalis* Harmer, 1957 — SEM photos of the holotype, NHM n 1986.2.1.2 (23.K1/2136) (courtesy of P.D. Taylor and S.F. Mawatari).

**Etymology.** Named in honour of the bryozoologist and geologist David A. Brown (1916–2009).

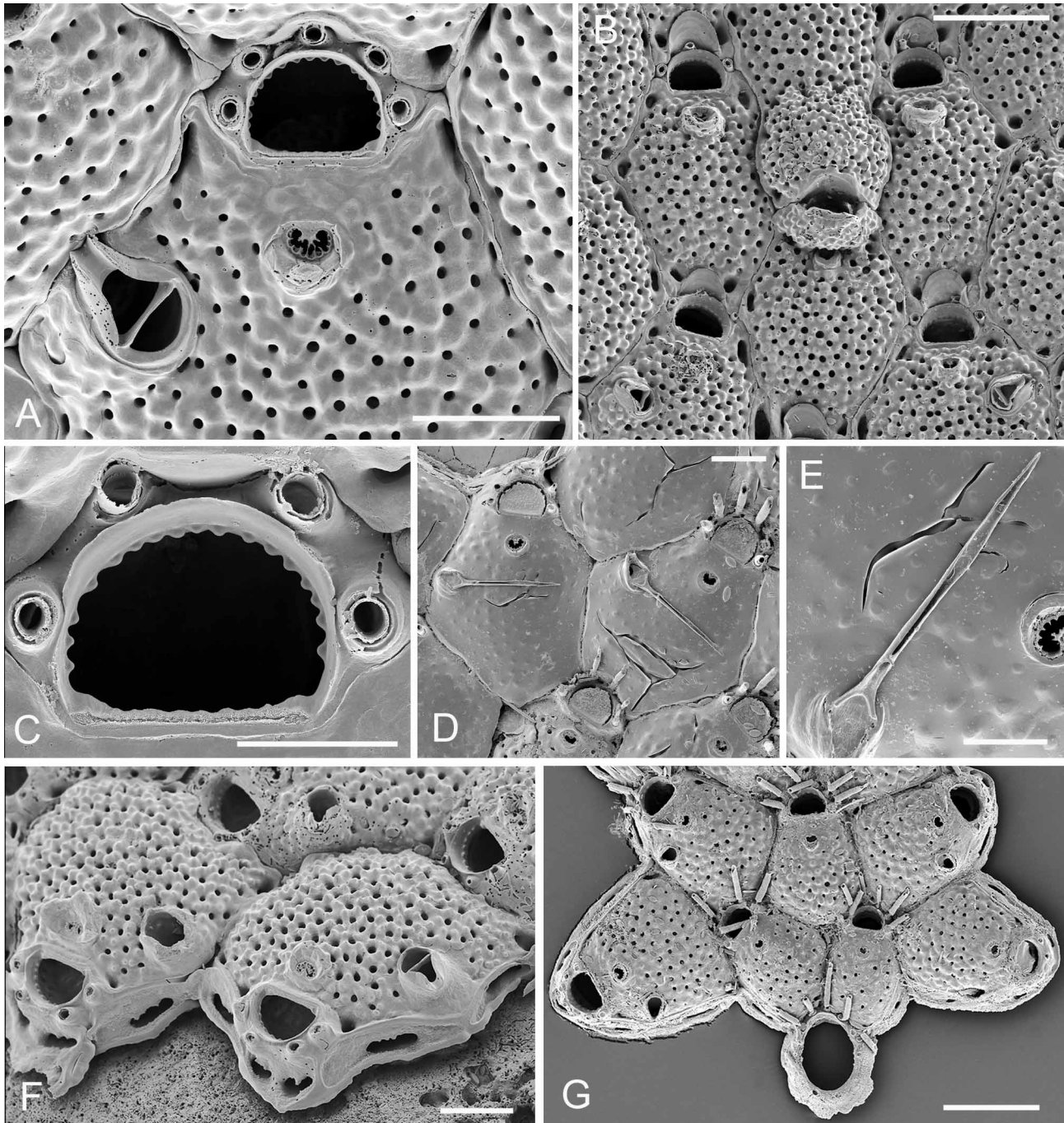
**Description.** Colony encrusting, unilaminar, small or medium-sized. Autozooids approximately pentagonal, hexagonal or oval, longer than broad (mean L/W = 1.32 in Lebanon, 1.28 in Oman and 1.35 in Maldives). Frontal shield moderately convex, entirely covered with small rounded nodes and small pseudopores intercalated between them (93–98 pores in Lebanon, 58–85 in Tadjoura, 70–95 in Oman, 31–51 in Maldives); areolae slit-like, oval or round, often poorly visible. Primary orifice wider than long, anter rounded, serrated with 11–19 denticles, these triangular with rounded summit, proximal border (poster) with an irregular, slightly corrugated edge between two low

shoulder-shaped condyles at each corner, sometimes missing. Oral spines 4–5 in most cases, occasionally 3, 6 or 7, thin, often detached, sometimes particularly long (up to 600  $\mu\text{m}$ ) and curved outwardly in well-preserved zooids. Ascopore proximal to orifice at a distance equal to orifice length or shorter, surrounded by a rim, often more raised proximally, lumen C-shaped with median process relatively large, rounded, rectangular or triangular, both spinous, sometimes with anastomosed denticles forming bars. Avicularium normally single, on the right or left, proximolateral to ascopore, rostrum directed distolaterally, truncated with tapered tip, a little longer than the maximum width of the membranous proximal area, crossbar complete and robust, mandible setiform, thin, moderately long (0.5–0.8 Az L), with lower side gutter-shaped (when dry), bearing at a distance corresponding to rostrum tip 2 pointed lateral processes curved basally. Ovicells with no visible oral spines, personate, i.e. with tall, arched, granular collar, distally adjacent to ascopore, raised over orifice and distally joined to smooth, arched rim on proximal edge of oecium to form a complete peristome. Entoecium globose, broader than long, coarsely granular, evenly ‘perforated’ with many ‘pseudopores’ a little smaller than those of frontal wall. Secondary orifice transversally oval and narrower than primary orifice. Ancestrula tatiform with 10 or 11 spines, with narrow cryptocyst, budding two distolateral autozooids. In youngest periancestrular zooids, denticles of primary orifice are poorly prominent, resembling small rounded knobs, spine number generally 6 or 7, up to 8 (in one zooid).

**TABLE 1.** Morphometrics (in  $\mu\text{m}$ ) of specimens of *M. browni* n. sp. from Lebanon, Tadjoura, Oman and Maldives. Length (L) and width (W) of autozooid (Az), ovicell (Ov), primary orifice (Or) and avicularium mandible (Md). Mean standard deviation, range and number of measurements (in brackets).

	Lebanon	Tadjoura	Oman	Maldives
AzL	509.2 $\pm$ 46.2	510.9 $\pm$ 62.7	468.9 $\pm$ 40.9	413.0 $\pm$ 42.7
-	415–605 (19)	390–615 (18)	410–550 (55)	340–520 (33)
AzW	383.6 $\pm$ 45.4	363.4 $\pm$ 50.7	367.5 $\pm$ 39.7	307.3 $\pm$ 39.9
-	320–510 (19)	300–485 (19)	300–470 (55)	230–380 (33)
OvL	211.5 $\pm$ 14.2	221.2 $\pm$ 19.3	170.0 $\pm$ 30.2	194.7 $\pm$ 15.9
-	185–230 (17)	195–250 (12)	140–210 (15)	170–230 (17)
OvW	249.4 $\pm$ 17.1	248.8 $\pm$ 20.1	256.0 $\pm$ 25.3	230.0 $\pm$ 10.6
-	220–290 (17)	220–280 (12)	230–300 (15)	220–260 (17)
OrL	78.1 $\pm$ 4.9	81.0 $\pm$ 4.3	71.9 $\pm$ 7.7	73.7 $\pm$ 6.8
-	70–85 (21)	72–90 (18)	60–90 (55)	60–85 (33)
OrW	108.8 $\pm$ 8.5	117.1 $\pm$ 4.4	96.5 $\pm$ 12.0	93.3 $\pm$ 9.6
-	80–108 (17)	110–125 (18)	80–130 (55)	80–110 (33)
MdL	218.6 $\pm$ 21.2	170.7 $\pm$ 12.4	199.4 $\pm$ 38.8	245.7 $\pm$ 7.9
-	185–240 (7)	150–190 (7)	150–277 (8)	240–260 (7)

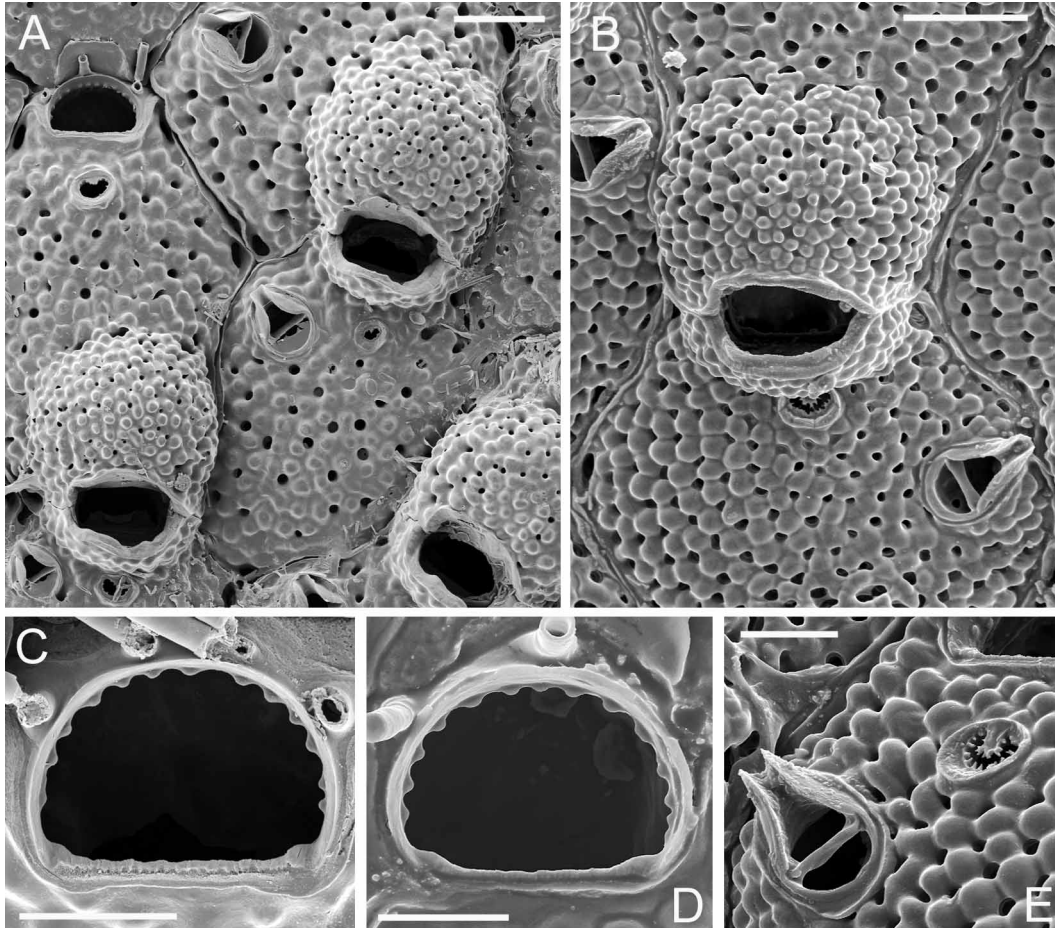
**Remarks.** All specimens of *M. browni* n. sp. from Lebanon, Tadjoura, Oman and Maldives are remarkably similar in features of the primary orifice, particularly the shape and distribution of the denticles on the distolateral edge, and the proximal edge slightly corrugated between low condyles. These condyles can be poorly or not prominent in the colonies from Oman and Maldives. The number of denticles observed in SEM photos indicates that this parameter may range differently according to locality: 12–16 in Lebanon (Beirut), 10–16 in the Gulf of Aden (Tadjoura), 13–18 in south Oman, 10–13 in the Maldives. For the whole suite of specimens, 13 is the modal number of denticles, which represents only 26% of the distribution. However, the tiny morphological traits of the orifice can be considered as highly diagnostic for this personate *Microporella* species. Zooids of *M. browni* n. sp. typically bear a single avicularium, lacking in some zooids including periancestrular ones. However, paired avicularia can be exceptionally present, as observed in two non-ovicellate (i.e. not associated with distal oecium) zooids from two different colonies of the Tadjoura material. The colonies from Tadjoura also differ in their zooidal dimensions, which are larger than those of specimens from the other localities. These two particular features in the Tadjoura material may correspond to a local geographical morphotype. The southeastern Mediterranean specimens are similar in all morphological features to those collected in the Indian Ocean.



**FIGURE 1.** *M. browni* n. sp., specimens from Oman, Indian Ocean (A-C: paratype 2010-0001-0009 DPUV; F: paratype 2010-0001-0009 DPUV). A: Distal half of a cleaned non-ovicellate zooid with five oral spines. B: Part of colony with a personate maternal zooid and ovicell and four zooids with initial stage of ovicell formation, two with a single avicularium and two without. C: Primary orifice with 4 oral spines, distal denticles, corrugated proximal edge and low condyles at the corners. D: uncleaned zooids with 5 or 6 oral spines, avicularium and setiform mandible folded over the frontal wall. E: gutter-shaped lower face of mandible bearing pointed processes near its basis. F: growing margin of a colony showing basal pore chambers. G: ancestrula and peri-ancestrular zooids. Scale bars: A, D, F = 100 µm; B, G = 200 µm; C, E = 50 µm.

*Microporella browni* n. sp. strongly resembles *M. orientalis* Harmer, 1957, originally described from Indonesia and commented on by Tilbrook (2006) after examining the holotype (NHM 1986.2.1.2) and studying one specimen from the Solomon Islands. According to Tilbrook (2006), *M. orientalis* is clearly characterized by orifices with a denticulate distal border and personate ovicells, i.e. with a raised proximal collar fused to the proximal edge of the entoecium. These features also characterise our specimens. However, comparison with unpublished SEM images of Harmer's holotype (made by S.F. Mawatari) show clear differences in the mandible shape, which is seti-

form, thin, moderately long and pointed in *M. browni* **n. sp.**, while it is short, more robust and hooked in *M. orientalis*. Specimens with personate ovicells from the area of Cochin (India) ascribed to *M. orientalis* by Menon and Nandini Menon (2006, fig. 90) bear the same type of short and robust mandible. These authors also mentioned specimens ascribed to *M. ciliata* having orifices denticulated distolaterally. This identification is obviously not correct, but cannot be interpreted given the lack of SEM illustrations. *Microporella browni* **n. sp.** and *M. orientalis* also differ in the shape of the proximal edge of the zooidal orifice. The primary orifice of *M. orientalis* illustrated by Tilbrook (2006, pl. 45B) presents a proximal edge that is smooth and without condyles, while in our material it is normally uneven and presents a pair of low shoulder-shaped condyles.



**FIGURE 2.** *M. browni* **n. sp.**, specimens from Maldive Islands, Indian Ocean (A, C) and Beirut, SE Mediterranean (B, D, E) displaying the same morphological features. A–B: zooids with ovicells; C–D: primary orifice; E: rimmed ascopore and avicularium. Scale bars: A–B = 100  $\mu$ m; C–E = 50  $\mu$ m.

The figures of *M. monilifera* Liu & Liu, 2003 (see also Liu *et al.* 2001) show that this species from the South China Sea is similar to *Microporella browni* **n. sp.** in several features, indicating a very close relationship. Both have ascopores bordered by a circular rim, single adventitious avicularia with similar shape, size, orientation and placement and, particularly, the primary orifices of non-ovicellate zooids are very similar in having a beaded distolateral border with similarly shaped denticles and a proximal edge presenting low condyles at the corners. In *M. monilifera*, however, the condyles are barely prominent and the proximal edge is smoother, the number of oral spines is only 3 vs 4–5 in *M. browni* **n. sp.**, the ovicell is not described as personate and the figured one (Liu *et al.* 2003, pl. II, fig. 3) has only lateral flaps that are abutted to the oocidium differently than the raised collar of *M. browni* **n. sp.** Other differences are presented by the oocidium, which shows a flat, non-porous medioproximal area in *M. monilifera* while it is porous and edged by a proximal rim in *M. browni* **n. sp.**, and by the ancestrula which is encircled with 18 spines in *M. monilifera* vs 10 or 11 in *M. browni* **n. sp.** Another difference is the mandible, described as "elongate triangular, without a horn at either side and with a flagelloid distal portion" (Liu *et al.* 2001, p. 814).

*Microporella browni* n. sp. also strongly resembles *M. maldiviensis* n. sp., with which it shares the same type of personate ovicell, a single avicularium lateroproximal to the ascopore and orifices with the anter bearing denticles and poster slightly corrugated between two shoulder-shaped condyles. However, *M. browni* n. sp. differs from *M. maldiviensis* n. sp. in having denticles more prominent and the avicularium mandibles with a longer projection and not hooked at the tip.

The geographical distribution of *M. browni* n. sp. currently includes the Indian Ocean, with localities in the Oman Sea, the Gulf of Aden and Maldive Islands, and the Eastern Mediterranean.

### *Microporella collaroides* n. sp.

(Fig. 3A–F, Table 2)

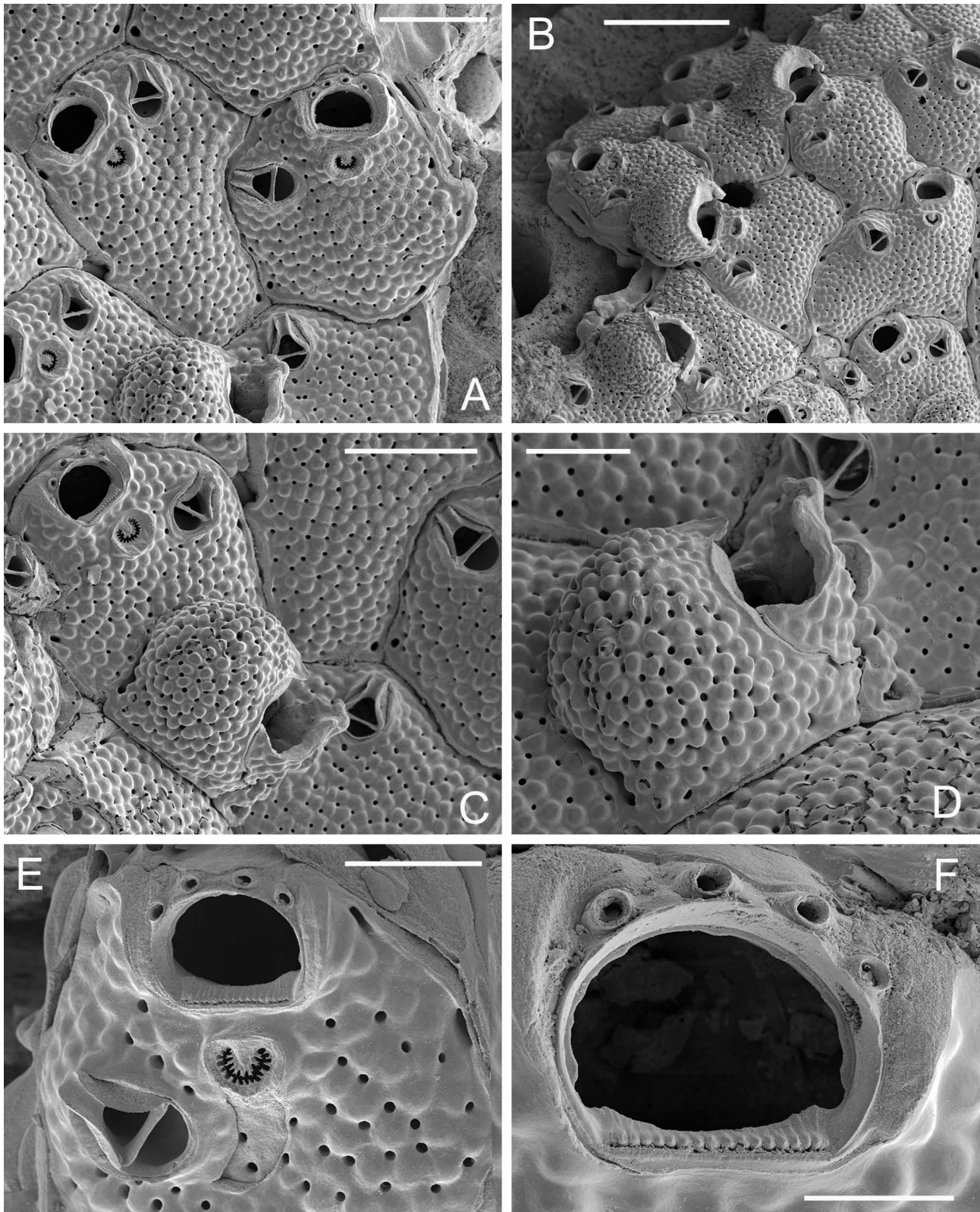
**Material examined.** *Holotype*: 2010-0003-0001 DPUV; on the coral *Leptastrea* sp., Jeddah, Red Sea, coll. A. Antonius. *Paratype*: 2010-0003-0002 DPUV, mounted on SEM stub, on the coral *Leptastrea* sp., Jeddah, Red Sea, coll. A. Antonius. *Other material examined*: Red Sea, Safaga Bay, station B3/2, sand between coral patches, 4 m, 2 colony fragments, 16 July 87; Safaga Bay, south to Ras Abu Soma, 20 m, one colony on coral piece, September 1992.

**Etymology.** In reference to the ‘personate’ collar, surrounding the zooidal orifice in the maternal zooid, and adjacent to the oecium.

**Description.** Colony small, unilaminar. Autozooids pentagonal or oval, longer than broad (mean L/W = 1.35). Frontal shield poorly convex, ornamented with rounded grains, perforated by 52–86 pseudopores and 5–7 small, elongated or oval marginal pores. Primary orifice broader than long, D-shaped, distal edge with very narrow ‘wavy shelf’ and incidental very low and small ‘denticles’. Proximal edge with 13–19 low oval bars and a pair of low or pointed shoulder-shaped condyles at each corner, seen in the most of the zooids. Furrows between bars often extending to condyles. Oral spines thin, 4 or 5, more rarely 6 in number. Ascopore proximal to orifice by a distance about the half of the orifice length, round or oval, slightly compressed distally with prominent median process round, and 19–24 short and sharp denticles leaving a narrow C-shaped lumen free. It is surrounded by a prominent rim slightly more raised proximally. Avicularium single, sometimes missing, lateral or proximolateral to ascopore, orientated distolaterally or laterally; opesia moderate-sized; rostrum short, with narrow truncated tip. Ovicells with no visible oral spines, personate, i.e. with tall, arched, granular collar, distally adjacent to ascopore, raised over orifice and distally joined to smooth, arched rim on proximal edge of oecium to form a complete peristome. In the paratype, ovicells with either fully or partially developed and even missing proximal collar were co-occurring. Entooecium globose, broader than long, coarsely granular, evenly ‘perforated’ with many ‘pseudopores’ of same size as those of frontal wall.

**TABLE 2.** Morphometrics (in  $\mu\text{m}$ ) of specimens of *M. collaroides* n. sp. from Safaga Bay and Jeddah. Length (L) and width (W) of autozooid (Az), ovicell (Ov) and primary orifice (Or). Mean standard deviation, range and number of measurements (in brackets).

	Safaga	Jeddah	Safaga + Jeddah
AzL	484.5 $\pm$ 40.1	465 $\pm$ 59.9	471.9 $\pm$ 53.8
-	430–540 (11)	330–550 (20)	330–550 (31)
AzW	359.1 $\pm$ 36.5	402.5 $\pm$ 39.1	387.1 $\pm$ 43.1
-	300–410 (11)	350–480 (20)	300–480 (31)
OvL	--	211.8 $\pm$ 12.5	211.8 $\pm$ 12.5
-	--	200–240 (11)	200–240 (11)
OvW	--	262.7 $\pm$ 11.0	262.7 $\pm$ 11.0
-	--	250–280 (11)	250–280 (11)
OrL	75.5 $\pm$ 6.5	78.3 $\pm$ 4.4	77.3 $\pm$ 5.3
-	70–85 (11)	70–85 (20)	70–85 (31)
OrW	98.2 $\pm$ 6.0	103 $\pm$ 5.9	101.3 $\pm$ 6.3
-	90–110 (11)	95–120 (20)	90–120 (31)



**FIGURE 3.** *M. collaroides* n. sp., paratype specimen 2010-0003-0002 DPUV from Jeddah, Red Sea. A: part of the colony with non-ovicellate zooids and personate ovicell (below). B: part of the same colony with ovicells without personate structure. C: distal zooid with oecium and personate maternal zooid with typical peristomial collar. D: latero-distal view of a maternal zooid showing the secondary orifice formed by the peristomial collar and entoecium with 'pseudopores'. E: distal half of a non-ovicellate autozooid with primary orifice, ascopore and avicularium. F: primary orifice with wavy distal edge, broad proximal edge bordered with oval bars and lateral condyles. Scale bars: A, C = 200 µm; B = 400 µm; D, E = 100 µm; F = 50 µm.



**Remarks.** This species recalls *M. maldiviensis* n. sp. in possessing personate ovicells, unpaired avicularia and also the ‘wavy’ relief of the orifice anter. In the latter species it is irregularly ‘denticulate’ with ‘denticles’ very low and rounded, whereas the orifice anter incidentally show tiny low ‘denticles’ in the former. The proximal orifice edge has a similar outline in these species too, but it is provided with well-developed parallel bars in *M. collaroides* n. sp., and smooth and slightly corrugated in *M. maldiviensis* n. sp.

### *Microporella coronata* (Audouin & Savigny, 1826)

(Figs 4A–E, 5, Table 3)

*Flustra coronata* Audouin, 1826, p. 67 (1828); Savigny, 1817, pl. 9, fig. 6.

*Flustra umbracula* Audouin, 1826, p. 67 (1828); Savigny, 1817, pl. 9, fig. 7.

*Microporella coronata*: Balavoine 1959, p. 274, pl. 3, fig. 7–8; d’Hondt 2006, p. 44; ?Norman 1909, p. 297, pl. 39, fig. 4; ?Gautier 1962, p. 173; ?Zabala 1986, p. 513–514, fig. 180.

*Microporella ciliata* var. *coronata*: ?Hastings 1930, p. 727.

*Microporella umbracula*: Harmer 1957, p. 964; ?Di Geronimo *et al.* 1998, p. 250 (Tab. 1); ? Koçak *et al.* 2002, p. 236 (Tab. 1); ? Morri *et al.* 1999, p. 733 (Tab. 1); ?Nicoletti *et al.* 1995, p. 398 (Tab. 1).

Not *Microporella coronata*: Waters 1909, p. 142, pl. 12, figs 6–9 (= *Microporella* n. sp., see below); Osburn 1952, p. 386 (= *Microporelloides coronula* Soule, Chaney & Morris, 2003).

Not *Microporella ciliata* var. *coronata*: Hastings 1927, p. 340, figs 83–84 (= *Microporella* n. sp., see below).

Not *Microporella umbracula*: Balavoine 1959, p. 274, pl. 5, fig. 3 (= *Predanophora longiuscula*).

Not *Microporella umbracula*: Winston 1982, p. 150, fig. 83; Winston 1986, p. 21, fig. 49; Winston & Håkansson 1986, p. 29, figs 68–69; Aristegui 1984, p. 331, fig. 68a,b, pl. 25, figs 3–4 (= *Microporella* n. sp., see below).

**Material examined.** *Neotype*: 2010-0004-0001 DPUV; part of an uncleaned colony comprising ca. 26 zooids with 4 ovicells. Lebanon, Kafar Abida, overhang, 7–8 m, 30 May 2000. *Other material examined*: Lebanon: (1) Tripoli, Ramkine Island, cave wall, 5–7 m, 14 July 2003; (2) Anfey, pebbles, 14 m, 26 October 1999; (3) Chak El Hatab, cave wall, 12 m, 21 September 2002; (4) Kafar Abida, overhangs, on scleractinians (*Phyllangia*, *Polycyathus*), 9 m, 6 August 1995; (5) Kafar Abida, overhangs, 7–8 m, 30 May 2000; (6) Tyre (Sour), pebbles, 14 m, 26 October 1999. Balavoine Collection: Red Sea, Gulf of Suez, MNHN n 7758, Al Sayad Stn XI, labelled *Microporella coronata* (Audouin, 1826); MNHN n 7808, Al Sayad Stn X, labelled *Microporella umbracula*; MNHN n 7803, Al Sayad Stn X, labelled *Microporella umbracula*.

**Description.** Colony small, unilaminar. Autozooids hexagonal or less frequently quadrangular, longer than broad. Frontal shield moderately convex, evenly covered with rounded nodules and 50–60 small frontal pseudopores; 1–3 marginal larger pores occasionally visible. Ascopore relatively close to proximal edge of orifice, i.e. at a distance about half orifice length, crescentic, with rounded median process and C-shaped lumen, both spurred with small spines, and surrounded by low rim with bulge developing proximally. Primary orifice broader than long, with smooth, rounded distal edge and proximal edge slightly concave, smooth, with low step-shaped condyles at corners. Oral spines 7 in most cases (59%), less frequently 6 (22%), rarely 8 (2%). Avicularia paired in most zooids, sometimes single, particularly in periancestrular zooids, placed symmetrically on both sides of zooid at level of ascopore or a little more distally, directed distally or distolaterally with a small angle; rostrum small, truncated, cross-bar complete; proximal area rounded, moderately broad; mandible setoid, slender, as long as zooid length or a little shorter, with lower side gutter-shaped and bearing a pair of triangular pointed processes corresponding to the rostrum tip. Ovicell prominent, rounded, slightly broader than long ( $L/W = 0.85$  in average), nodular and ‘pseudoporous’ like the frontal shield; proximal edge of ectoecium calcified, forming a thick visor overhanging proximal, smooth edge of entoecium; a raised peristomial collar including ascopore fused laterally to oecium proximal corners and presenting two lateral flaps that can join in midline when particularly developed, forming bridge over orifice, or can be reduced to a lower prominence; 2 oral spines occasionally visible against junction between visor and collar. Ancestrula tatiform, oval, with proximal gymnocyst moderately developed, the large oval opesia bordered with 10 spines (5 distal, 2 median, 3 proximal); cryptocyst narrow, developed both proximally and distally. Two autozooids distally budded by ancestrula, the smaller with 8 spines, the larger with 7 spines, both with single avicularium placed proximolateral to ascopore.

**TABLE 3.** Morphometrics (in  $\mu\text{m}$ ) of specimens of *M. coronata* from two localities of Lebanon (Chak El Hatab and Tripoli). Length (L) and width (W) of autozooid (Az), ovicell (Ov), primary orifice (Or) and avicularium mandible (MdL). Mean standard deviation, range and number of measurements (in brackets).

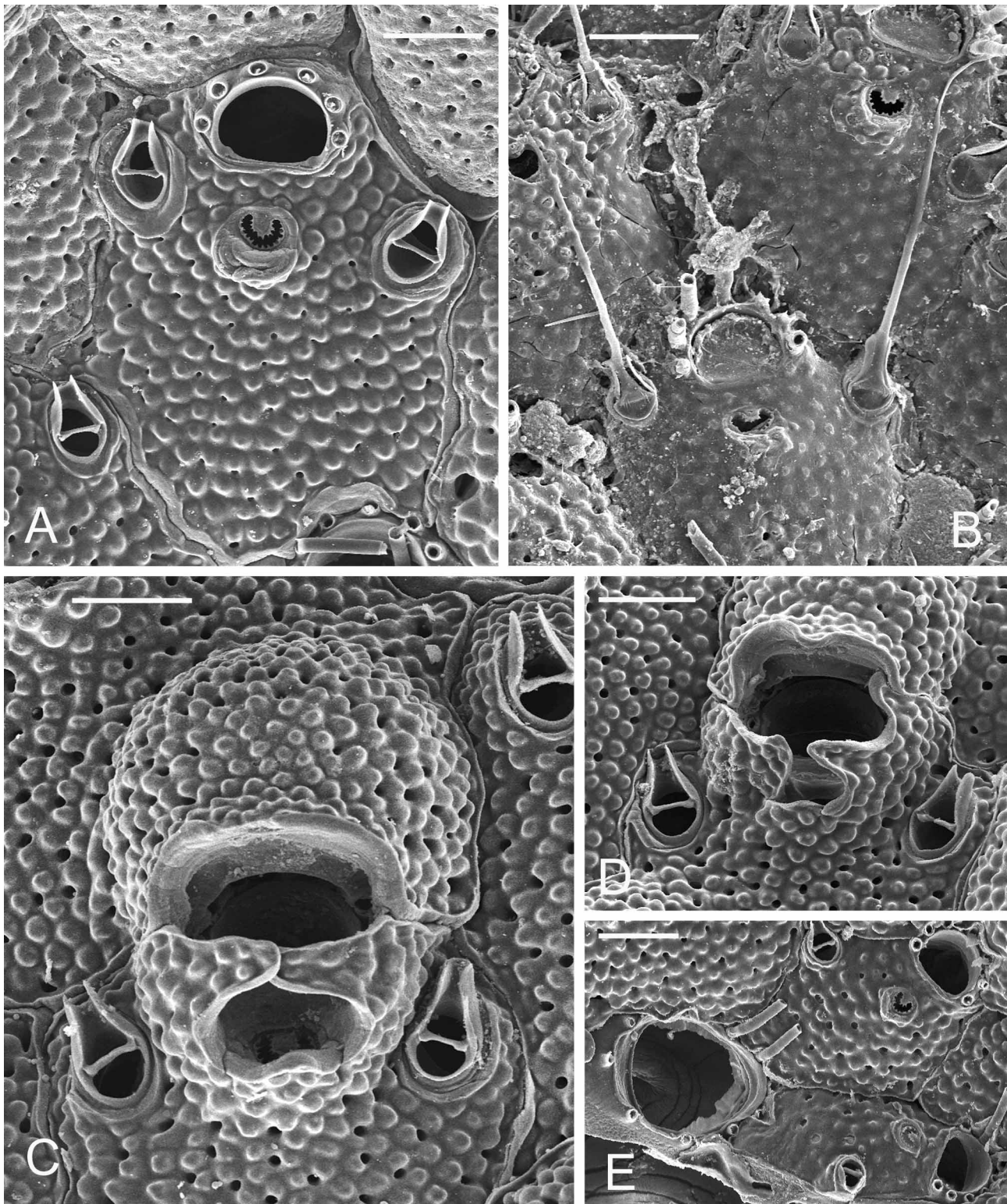
AzL:	582.1 $\pm$ 67.2, 460–730 (17)
AzW:	403.5 $\pm$ 60.5, 315–535 (17)
OvL:	256.4 $\pm$ 20.3, 220–290 (11)
OvW:	303.5 $\pm$ 17.3, 280–340 (11)
OrL:	97.7 $\pm$ 10.5, 85–112 (11)
OrW:	126.2 $\pm$ 11.1, 110–140 (11)
MdL:	403.7 $\pm$ 54.0, 315–510 (15)

**Remarks.** Savigny's drawings of two specimens from the Red Sea, one without ovicells (Savigny 1817, plate 9, fig. 6.1-2) and the other with many ovicells (Savigny 1817, plate 9, fig. 7.1-4), undoubtedly show the same species (Fig. 5). Audouin (1826), however, gave two different species names to these specimens, *coronata* and *umbracula* for Savigny's figures 6 and 7 respectively. As stated by d'Hondt (2006), the name *coronata*, cited before *umbracula* in Audouin's text, has priority and must be used. The specific name *umbracula* has often been preferred to *coronata* (e.g. Harmer, 1957) because of the illustration of ovicells. The non-ovicellate zooids of both specimens illustrated by Savigny clearly show zooids with six oral spines and paired avicularia with long setoid mandibles while the ovicellate zooids present the same avicularia and personate ovicells. The occurrence in this species of a particular peristomial structure in maternal zooids was noticed by Busk (1854, p. 74) when describing *Lepralia personata*: "The form of the ovicell in *F. (L.) umbracula* ... is very similar apparently to that of *L. personata* ...". Personate ovicells with a collar presenting lateral flaps that can fuse into a bridge is also a typical feature of *M. pontifica* Osburn, 1952, redescribed by Soule *et al.* (2003). This particular structure can occasionally be found in British and Dutch specimens attributed to *M. ciliata* by Hayward and Ryland (1999, fig. 136D) and De Blauwe (2009, p. 384, Foto 414). It also characterizes a Canarian species, *M. cooki*, described by Aristegui (1984) in his unpublished thesis, which differs from *M. coronata* in having a personate collar that does not surround the ascopore and avicularia that are generally single and in a more proximal position.

In the present collection, specimens of *M. coronata* were recorded at six localities along the coast of Lebanon, from the north (Tripoli) to the south (Tyre). The ascription of these Lebanese specimens to *M. coronata* is based on the occurrence of paired avicularia with long setoid mandibles directed distally and placed in the distal quarter of the autozooid, orifices with 6–7 spines, smooth distal and proximal borders, and personate ovicells with lateral flaps that can fuse into a bridge over the orifice and the ascopore.

Considering that the collection illustrated by Savigny (1817) was most likely lost (d'Hondt 2006) and that both *coronata* and *umbracula* species names have been improperly attributed in many cases, leading to wrong information concerning geographic and stratigraphic distribution, a neotype of *M. coronata* has been chosen from the present Lebanese collection. The choice of a Lebanese specimen for neotype designation, despite the asserted Red Sea origin of the specimens illustrated by Savigny (see Audouin 1828, p. 67) is justified by good morphological congruence and the existence of faunal exchanges between the two basins (see below).

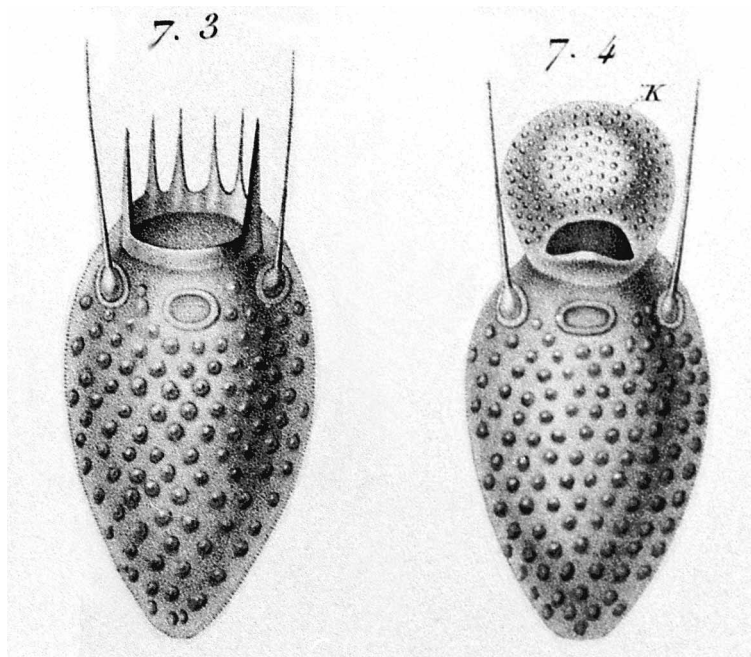
*Microporella coronata* was listed several times as *M. umbracula* in faunal inventories from warm regions of the Mediterranean (Turkey: Nicoletti *et al.* 1995; Ionian Sea: Di Geronimo *et al.* 1998; Milos Is.: Morri *et al.* 1999; Cyprus: Koçak *et al.* 2002). According to Hastings (1927), Waters (MS) had also recorded *M. coronata* from the Mediterranean. However, although this is very probable, the distribution of *M. coronata* or of another species with paired avicularia in the eastern Mediterranean cannot be ascertained from these records without comment or figures. Similarly, the fossil records of *M. coronata* from Miocene to Pleistocene assemblages around the Mediterranean (e.g. Rosso 1987; Moissette 1988) are not easy to interpret and may correspond to other species (Berning 2006), such as that recorded by Hastings (1927) (see below). Zabala (1986, pp. 513–514, fig. 180) recorded *M. coronata* from the western Mediterranean but without personal collected material or a precise Mediterranean reference. His description and figure (copied from Osburn 1952, pl. 45, fig. 1, Bay of California) indicate 5–6 oral spines, paired avicularia with long setoid mandibles directed distolaterally and non-personate ovicells with a few 'pores' identical to the pseudopores of the zooidal frontal shield.



**FIGURE 4.** *M. coronata*, specimens from Lebanon, SE Mediterranean. A: cleaned non-ovicellate zooid with 6 oral spines, paired avicularia and ascopore edged with a proximal bulge. B: uncleaned non-ovicellate zooid with long setiform mandibles. C: maternal zooid with peristomial collar including the ascopore and joined lateral flaps, and ovicell with vizor (proximal part of ectooecium) and nodular, pseudoporous wall (entooecium). D: secondary orifice of a maternal zooid with un-fused lateral flaps. E: ancestrula (to the left) with 10 spines. Scale bars: A–E = 100  $\mu$ m.

*Microporella coronata* was recorded from Madeira by Norman (1909, p. 297) and *M. umbracula* from the Canary Isles by Aristegui (1984, p. 331). Norman's description and illustration of *M. coronata* depict a species with six oral spines and paired avicularia with long setoid mandibles directed distally. These characters may correspond

to Audouin's species, but curiously the proximal area of the avicularia was illustrated as having the same pointed shape as the rostrum. Also the ovicell presents no lateral flaps. Canu and Bassler (1928, p. 112, pl. 34, fig. 5), without justification that the Madeiran material differed from *M. coronata*, erected a new species, *M. normani*. Paradoxically they illustrated it with a Pliocene specimen from Panama bearing single avicularia. This species group also includes species from Florida and Jamaica (Winston 1982, 1986; Winston & Håkansson 1986) recorded as *M. umbracula*, which have non-personate ovicells, a smaller number of oral spines and zooids commonly with a single avicularium. *Microporella lunifera* (Haswell), redescribed by Hayward and Ryland (1995) from the Great Barrier Reef, may belong to the same species group having paired avicularia with long, setiform mandibles, placed distally and directed distolaterally, and non-personate ovicells. The record of *M. coronata* from Marmar (Red Sea, south of Jeddah) by Gautier (1962) is disputable as the description without illustration mentions 5–6 oral spines with a dark base and does not indicate a peristome associated with the ovicell. In Balavoine's collection from the Gulf of Suez, specimen MNHN n 7803 labelled *Microporella umbracula* is *M. harmeri*. Another specimen labelled *Microporella umbracula* in the same collection (MNHN n 7808, Al Sayad Stn X, 28–62 m), recorded as *Microporella umbracula* and figured by Balavoine (1959, p. 274, pl. 5, fig. 3), is not a *Microporella* but *Predanophora longiuscula* (Harmer, 1957).



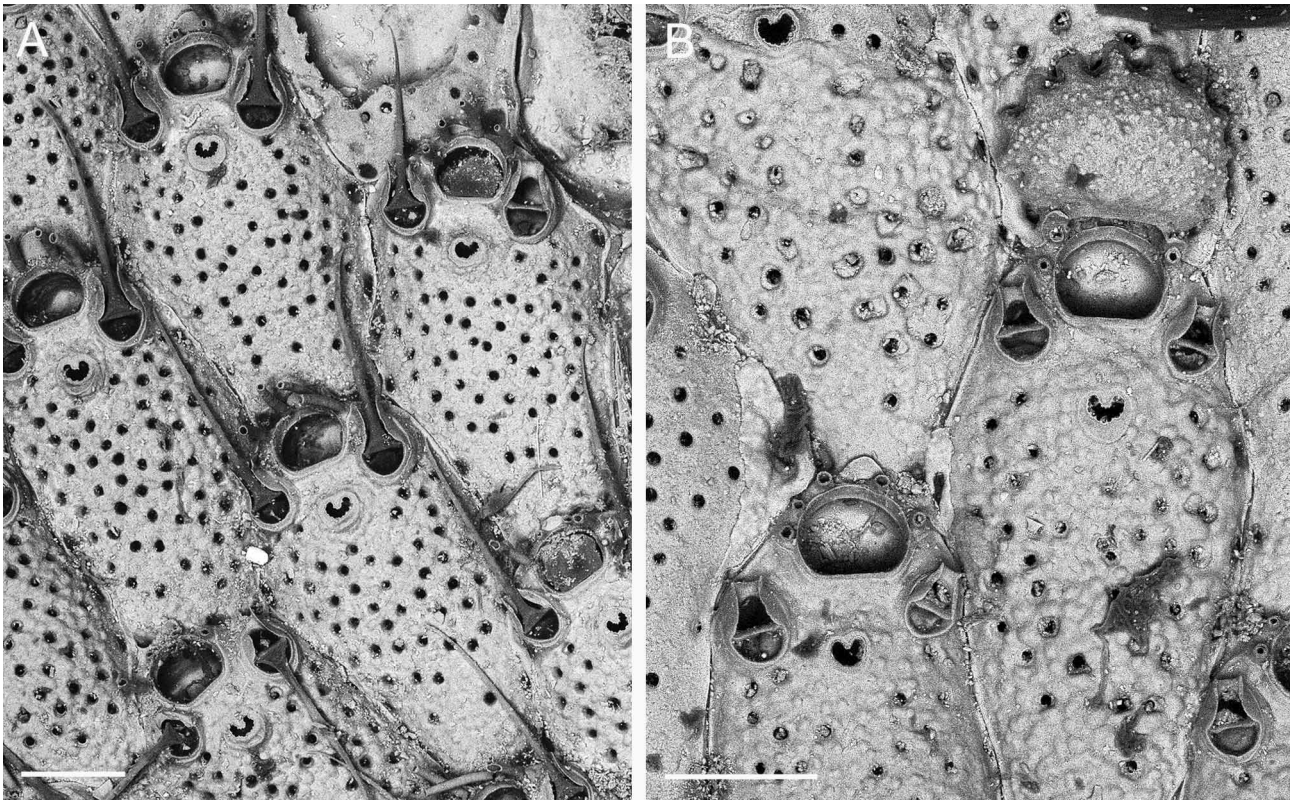
**FIGURE 5.** Savigny's drawings of *M. coronata*. Left: non-ovicellate zooid (Savigny 1817, pl. 9, fig. 7.3); right: zooid with personate ovicell (Savigny 1817, pl. 9, fig. 7.4), named *Flustra umbracula* by Audouin (1826)

The Albatross collections of bryozoans from the Philippine Archipelago (Canu & Bassler 1929), kept at the USNM, Washington, include an uncleaned specimen (Albatross Stn 5141) labelled *Microporella* that resembles *M. coronata*. SEM photos of this specimen show paired avicularia with robust setiform mandibles, six oral spines, a crescentic, spinous ascopore with rounded median process placed close to the proximal border of the orifice and encircled by a broad plate-shaped rim with a smooth surface and the edges raised distally. This *Microporella*, in which the ovicells are incompletely developed, differs from *M. coronata* at least in having not step-shaped condyles at the corners of the primary orifice.

Specimens collected in the Suez Canal near its Red Sea entrance (Km. 157), identified by Hastings (1927) as *M. ciliata* var. *coronata*, clearly belong to another species despite the occurrence of paired distal avicularia with setoid mandibles. SEM photos (courtesy of M. Spencer Jones and J. Scholz) of these specimens (Fig. 6), in the Natural History Museum, London (n 1926.9.6.238), show that they differ from *M. coronata* in the following characters: four oral spines in most cases (range 3–6) in non-ovicellate zooids, two (sometimes three) remaining free at the proximal corners of the ovicells; a primary orifice with smooth edges but without step-like condyles; a frontal shield with large pseudopores; paired avicularia with truncate rostra and proximal area clearly broader than in *M.*

*coronata*, with robust setoid mandibles; and ovicells with finely nodular calcified entoecium without ‘pseudopores’, encircled by 9–14 notches corresponding to marginal pores. The peculiarity of the ovicells with large marginal pores in these specimens was already noticed by Berning (2006, p. 104). The same combination of typical features occurs in a specimen from Suez docks figured by Waters (1909, pl. 12, figs 6–7) and recorded as *M. coronata*: four oral spines in non-ovicellate zooids, absence of personate collar, paired avicularia with robust mandibles, ovicell with indented border and a pair of oral spines at the proximal corners. The same type of ovicell was present in a specimen from the Gulf of Suez (MNHN 7758, Al Sayad Stn XI) recorded as *Microporella coronata* by Balavoine (1959, p. 274, pl. 3, figs 7–8). Similarly, specimens from the Canary Islands ascribed to *M. umbracula* by Aristegui (1984, pp. 331–332, figs 68a–b, pl. 25, figs 3–4) are also characterized by 4–6 oral spines in non-ovicellate zooids and ovicells without personate structure and ‘pseudopores’ and encircled by particularly large marginal pores.

The particular features of these specimens justify their placement in a new species within the *M. coronata* species group. We propose to name it *Microporella hastingsae* n. sp., in honour of Anna B. Hastings, with specimen NHM n 1926.9.6.238 as holotype.



**FIGURE 6.** *M. hastingsae* n. sp., specimen Natural History Museum, London n° 1926.9.6.238, from the Suez Canal. A: non-ovicellate zooids with two avicularia. B: zooids with complete ovicell without personate collar (to the right) and young forming oocidium. Note large marginal pores surrounding entoecium (photos courtesy M. Spencer Jones and J. Scholz).

### *Microporella genisii* (Audouin & Savigny, 1826)

(Fig. 7A–F, Table 4)

*Flustra? genisii* Audouin, 1826, p. 67 (1828); Savigny, 1817, pl. 9, fig. 5.1–2.

*Microporella ciliata*: d'Hondt 2006, p. 42.

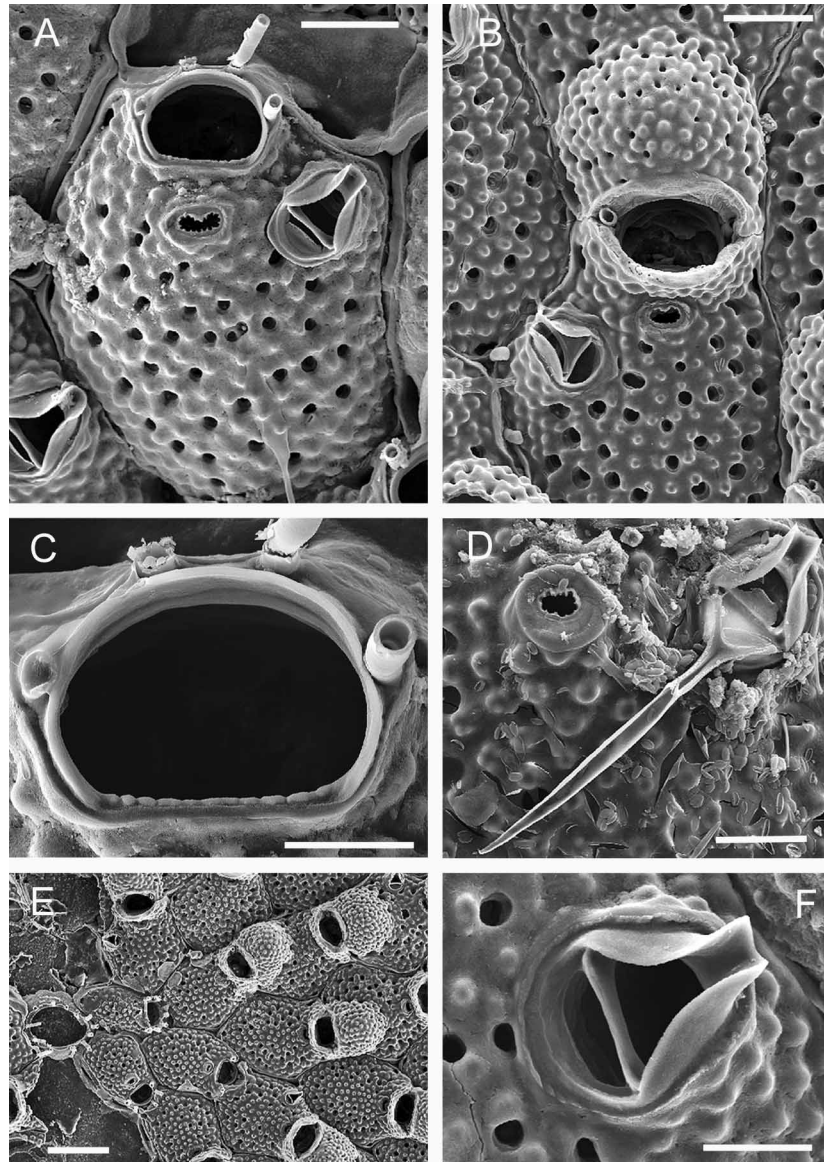
*Microporella intermedia* Aristegui, 1984, p. 321, fig. 67a–c, pl. 24, figs 1–3.

*Microporella orientalis*: ?Tilbrook *et al.* 2001, p. 87, figs 19 C–D; ?Sternhell *et al.* 2002, p. 229, fig. 4b.

Not *M. intermedia* Livingstone, 1929; Gordon 1984, p. 102, pl. 38 C–D.

**Material examined.** *Neotype*: 2010-0005-0001 DPUV; large colony (ca 10 x 11 mm) including many ovicells, from South Sinai, Ras Mohammed, ‘Yolanda’ wreck, 18 m, 15 May 1983. Additional material examined: Lebanon:

(1) Tripoli, Ramkine Island, 12 m, one colony on pottery debris, 22 October 1999; (2) Batroun, “Phoenician wall, 9 m, two colonies on serpulid tubes, 16 October 1999; (3) Jonnieh Bay, Aquamarina, 20–30 m, two colonies on stone, 10 July 2003; (4) Beirut, Harf el Kalb, 34 m, one colony on *Spondylus* shell, 21 October 1999; (5) Tyre (Sour), El Kasmieh, 36–42 m, two colonies on shell, 25 October 1999. Red Sea: (1) South Sinai, Ras Mohammed, ‘Yolanda’ wreck, 18 m, 10 colonies on aluminium plates, 15 May 1983; (2) Safaga Bay, transect B2, depth 42 m, one colony on *Cymodocea* sp.; (3) Safaga Bay, west part of Safaga Is., transect A5, 1–2 m, 6 colonies on *Cymodocea* sp., September 1992.



**FIGURE 7.** *M. genisii*, specimens from Ras Mohammed, Red Sea. A: cleaned non-ovicellate zooid with relatively large pseudopores and small nodules, ascopore with poorly developed median process, avicularium and orifice with 4 spines. B: maternal zooid with entoecium with small ‘pseudopores’ and personate peristomial collar leaving apparent a pair of oral spines at the junction with the vizor of the ovicell. C: primary orifice with smooth distal edge and proximal edge sculptured with low beads. D: avicularium in open position showing the gutter-shaped lower side of mandible and pointed processes; note the nearly round ascopore. E: young colony with ancestrula and peri-ancestrular zooids including early-formed ovicells. F: calcified part of avicularium. Scale bars: A, B = 100  $\mu$ m; C, D, F = 50  $\mu$ m; E = 200  $\mu$ m.

**Description.** Colony small or medium-sized, unilaminar. Autozooids relatively small, mainly hexagonal or oval, longer than broad (in average, L/W = 1.3–1.4); frontal shield coarsely granular, perforated with 18–30 irregularly scattered pseudopores; marginal elongate areolae occasionally visible. Ascopore separated from proximal border of orifice by a distance shorter than orifice length, oval or slightly compressed distally; median process not very prominent in most cases or even absent, with 8–15 short denticles leaving a wide lumen; surrounded by a

thick, prominent rim, frequently with a proximal bulge (particularly in Lebanese colonies and in Red Sea colonies collected on sea-grasses). Primary orifice wider than long; distolateral edge (anter) smooth; proximal border straight and crenulate with 8–16 low, flat or rounded beads, and without condyles at the corners. Oral spines slender, 4 in most cases, sometimes 3 or 5 (6 in zone of astogenetic change). Avicularium single, on right or left, sometimes missing, lateral or proximolateral to ascopore, orientated distolaterally or laterally; opesia moderate-sized; rostrum short, with narrow truncated tip; mandible elongated, lanceolate, shorter than autozooid width, gutter-shaped on lower side when dry, bearing 2 pointed lateral processes curved basally, which lean against rostrum tip. Ovicells often numerous and appearing early among post-ancestrular zooids (Fig. 7E), oecium double-walled with membranous ectooecium visible in non-cleaned colonies; entoecium thickly calcified, globular, granular, perforated with tiny ‘pseudopores’, which may be filled in with calcification; proximal edge bordered by smooth rim. Maternal zooids with personate peristome formed by arched collar rising vertically close to ascopore and sometimes hiding it partially, fused side by side with proximal rim of oecium; 1–2 oral spines often visible at corners where oecium and proximal collar meet. In some colonies from Safaga Bay, Red Sea, ovicells with either fully or partially developed or even missing proximal collar were co-occurring. Ancestrula tatiform with 11 or 12 spines and narrow cryptocyst, budding 2 distal autozooids.

**TABLE 4.** Morphometrics (in  $\mu\text{m}$ ) of specimens of *M. genisii* from Lebanon (5 localities), Ras Mohammed and Safaga Bay. Length (L) and width (W) of autozooid (Az), ovicell (Ov), primary orifice (Or) and avicularium mandible (Md). Mean standard deviation, range and number of measurements (in brackets).

	Lebanon	S Sinai	Safaga
AzL	383.5 $\pm$ 31.6	475.8 $\pm$ 33.9	436.7 $\pm$ 25.3
-	320–440 (23)	440–530 (18)	380–490 (27)
AzW	280.0 $\pm$ 34.7	372.6 $\pm$ 51.9	309.6 $\pm$ 28.2
-	245–400 (23)	295–485 (18)	250–380 (27)
OvL	186.3 $\pm$ 12.5	182.2 $\pm$ 9.5	192.2 $\pm$ 11.4
-	170–205 (17)	170–200 (16)	170–220 (38)
OvW	225.0 $\pm$ 21.6	210.9 $\pm$ 12.7	217.1 $\pm$ 11.4
-	195–265 (17)	180–230 (16)	200–250 (38)
OrL	58.8 $\pm$ 4.4	70.6 $\pm$ 2.7	61.3 $\pm$ 3.0
-	50–65 (17)	65–72 (7)	60–70 (15)
OrW	91.1 $\pm$ 7.8	111.5 $\pm$ 5.3	94.3 $\pm$ 5.6
-	80–108 (17)	105–120 (14)	90–105 (15)
MdL	155.8 $\pm$ 13.2	181.8 $\pm$ 17.7	200.4 $\pm$ 10.7
-	145–180 (6)	160–220 (16)	190–220 (13)

**Remarks.** The beautiful Savigny drawing (pl. 9, fig. 5.2) of the Red Sea *Microporella* species named *Flustra? Genisii* by Audouin (1826) clearly shows personate ovicells, three to five oral spines, a single avicularium placed proximolaterally to ascopore and at a variable distance to it, directed distolaterally with long and narrow mandible, persistent and well visible; a round or oval ascopore, sometimes with median distal process and peripheral ring; conspicuous frontal nodules (or pseudopores?), round ovicell, slightly broader than long, maternal zooid with a personate collar adjacent to ascopore, vertical and relatively narrow, not completely fused with the oecium rim but leaving a narrow suture. The close agreement in most respects between *Flustra? Genisii* and the *Microporella* specimens described here from Lebanon and the Red Sea argues for considering the former as a valid *Microporella* species and for referring the latter to it. A neotype has thus been selected among the Red Sea material. The only differences concern the crenulation of the proximal edge of the orifice and the paired spines at the proximal corners of the oecium, which are missing in Savigny’s drawing. However, these tiny morphological characters were not observable with the optical means available in the early 19<sup>th</sup> century.

*Flustra? Genisii* was synonymized by Harmer (1957) with *Microporella ciliata* (Pallas, 1766), the type species of *Microporella*, without comment. This opinion was already expressed by Hastings (1927, p. 242) and followed by d’Hondt (2006) in his review of the bryozoan species illustrated by Savigny. *Microporella* species with a single

avicularium proximalateral to the ascopore and having a setiform mandible have often been ascribed to *M. ciliata*, to which a cosmopolitan distribution was often wrongly attributed. Recently, a neotype of *M. ciliata* was chosen by Kuklinsky and Taylor (2008) among specimens collected at Naples. The features of *M. ciliata*, now fixed by this neotype designation, differ from those shown by specimens of *M. ciliata* commonly present in the Mediterranean and Adriatic (e.g. Gautier 1962; Hayward & McKinney 2002) or in British waters (e.g. Hayward & Ryland 1999). It also clearly differs from *M. genisii*, particularly in having orifices with the proximal edge finely serrated between distinct condyles and bordered by 1–4 oral spines.

The Sinai and Safaga Bay specimens of *M. genisii* differ from the Lebanese specimens in having a larger cystid size (mean AzL and AzW are respectively 24% and 33% larger in Sinai, and 14% and 11% larger in Safaga Bay) and a higher frequency of occurrence of one or two spines at the proximal corners of the ovicell. The other features, such as the number of spines, the ornamentation of the proximal side of the orifice, the avicularium, the personate ovicell and the ancestrula, are similar.

Aristegui (1984) described in his unpublished thesis a new species of *Microporella* from Tenerife, Canary Islands — *M. intermedia* **sp. nov.** — that he considered intermediate between *M. ciliata* and *M. orientalis* (Harmer, 1957). This species name is a junior primary homonym of *M. intermedia* Livinstone, 1929, from New Zealand, which clearly differs (cf. Gordon 1984) from the Canarian species in many characters. Thus, according to the Principle of Priority, *M. intermedia* Aristegui, 1984 is invalid. We consider that this Canarian species is conspecific with *M. genisii* from Lebanon, South Sinai and Safaga Bay redescribed here. The identity of the specimens from the Canaries with the Lebanese and Red Sea specimens is attested by the following characters: four oral spines, one or two remaining visible in the ovicell corners; ascopore circular, oval or reniform, surrounded by a bulging ring; avicularia single, located below the ascopore, orientated distolaterally with an angle < 45, sometimes missing (cf. Aristegui 1984: pl. 24-2), with a narrow-lanceolate, gutter-shaped mandible moderately long, bearing two lateral processes on the lower side (Aristegui 1984: fig. 67-c); ovicells personate (Aristegui 1984, fig. 67a, pl. 24-1–2), ancestrula tatiform with 11 spines and narrow cryptocyst. Aristegui did not notice any crenulation of the proximal edge of the primary orifice. However, this apparent difference between the Lebanese and Red Sea specimens may not be real as these beads are low and not easily visible.

It is likely that *M. genisii* has been confused with other personate *Microporella* species with a single avicularium, particularly *M. orientalis* Harmer, 1957. The species growing on artificial substrata at Eilat (Red Sea, Gulf of Aqaba) recorded as *M. orientalis* by Sternhell *et al.* (2002) presents the general aspect of *M. genisii* based on the following characters: appearance of the cryptocystal walls; shape and position of the single avicularium; and shape and proportions of personate collar and ovicell, including a pair of spines visible at the proximal corners of each ovicell. Unfortunately, the number of oral spines of non-ovicellate zooids and the ornamentation of the proximal border of the orifice are not visible in the SEM photo of this specimen. Also, both photos and description of specimens from Vanuatu Islands ascribed to *M. orientalis* by Tilbrook *et al.* (2001) strongly suggest that they belong to *M. genisii*.

The description of *M. epihalimeda* Tilbrook, 2006 from the Solomon Islands indicates that it is closely related to *M. genisii*. Both species have 3–4 spines, similarly shaped avicularia and maternal zooids, a tatiform ancestrula with 11 spines and a primary orifice without condyles. In *M. epihalimeda* the primary orifice is described as smooth but the SEM illustration (Tilbrook 2006, pl. 46D) shows a rather uneven proximal edge, resembling that of *M. genisii* although less rippled. Another similarity is the oral spines seen at the proximal corners of the personate ovicells — although “none visible in ovicellate zooids” is mentioned in Tilbrook’s description (p. 213). The only apparent difference is that the setiform avicularian mandible has a length equal to zooidal width and no basal processes in *M. epihalimeda*.

### ***Microporella harmeri* Hayward, 1988**

(Figs 8A–F, 9A–D, 10A–F, 11A–D, Table 5)

*Microporella harmeri* Hayward, 1988, p. 324, pl. 10e; Scholz *et al.* 2001, p. 222, fig. 5c; ?Gordon *et al.* 2007, p. 51, fig. 3c.

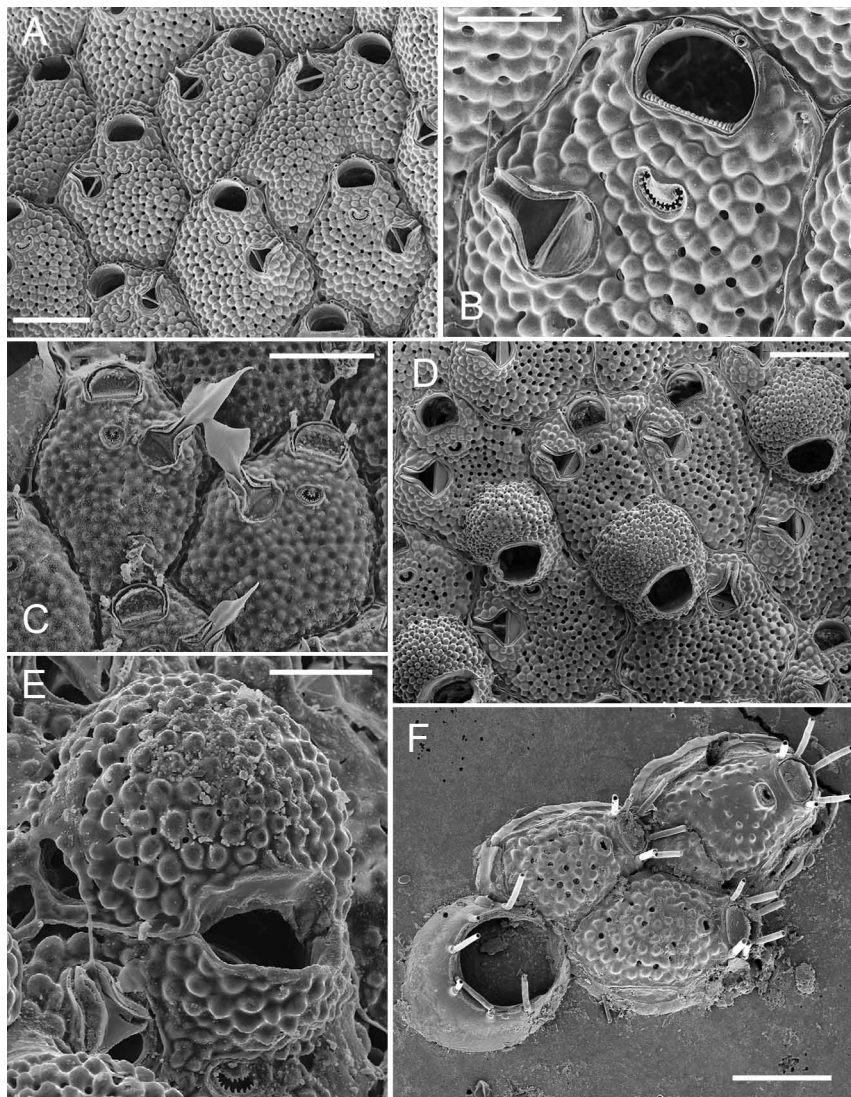
*Microporella orientalis* var. Harmer, 1957, p. 963, pl. 62, fig. 30; ?d’Hondt 1988, p. 194.

*Microporella orientalis*: Aristegui 1984, p. 329, figs 67d–f, pl. 24, figs 7–8, pl. 25, figs 1–2; ?Zabala & Maluquer 1988, p. 140, fig. 338; Ryland & Hayward 1992, p. 279, figs 25e–f.

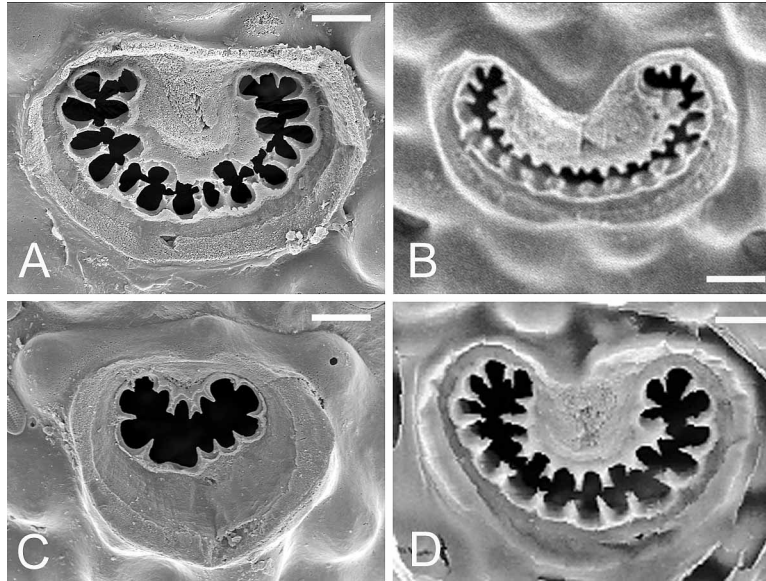
*Microporella ciliata* var. *personata*: Thornely, 1905, p. 112.



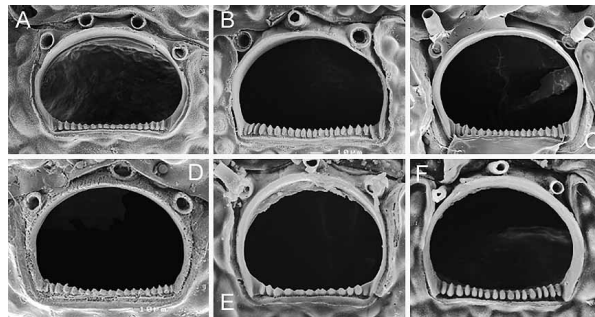
**Material examined.** Lebanon: Selaata, 3–8 m, on cave wall, 18–23 October 1999. Red Sea: (1) South Sinai, Ras Mohammed, ‘Yolanda’ wreck, 18 m, on aluminium sheet, 15 May 1983; (2) Safaga Bay, south to Ras Abu Soma, depth 1–20 m, 3 colonies on coral pieces, September 1992; Safaga Bay, west part of Safaga Island, transect A5, 1–2 m, one colony on *Cymodocea* sp., September 1992; Safaga Bay, station A 1-2/2, 10 m, sand, one fragment, 27 April 1986; Safaga Bay, transect B2, 42 m, one fragment on bivalve shell, date unknown. Indian Ocean: (1) south Oman, Salalah, near Mirbat, Kelp Bay, right side, depth 9 m, 5 colonies on bivalve shells and coral pieces, 16 January 2009; (2) south Oman, Salalah, near Mirbat, depth 8 m, one colony on bivalve shell, 18 January 2009; (3) Maldive Islands, North Male Atoll, Helengeli Is., March 1983, one colony on bivalve shell, coll. F.F. Steininger; (4) South Africa, Sodwana Bay, 2 Mile Reef, 1993, one colony on coral, coll. B. Riegl. *Other material examined:* (1) Balavoine Collection, MNHN n 7803, one colony labelled as *Microporella umbracula* (Audouin, 1826), Gulf of Suez, Al Sayad station X. (2) Specimen of *Microporella ciliata* var. *personata* from Ceylon, Thornely Collection, NHM n 1999.7.19.18, SEM photos (courtesy M. Spencer Jones). (3) Specimen of *M. harmeri* from Mauritius, Hayward collection, NHM n 1987.1.18.23, SEM photos (courtesy P.J. Hayward). (4) Specimens attributed to *M. orientalis* from Heron Island, Stn 25, Ryland & Hayward collection, NHM n 1996.2.23.92, SEM photos (courtesy P.D. Taylor).



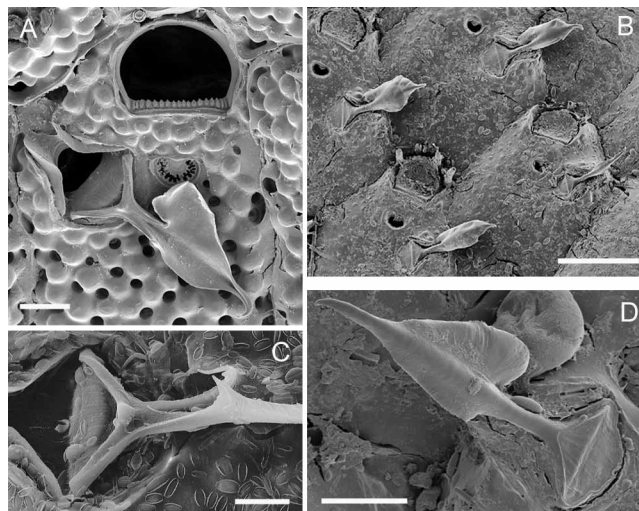
**FIGURE 8.** *M. harmeri*, specimens from Red Sea, Safaga Bay (A, B) and Ras Mohammed (C), Indian Ocean, Oman (D, F) and SE Mediterranean, Selaata (E). A: part of colony with non-ovicellate zooids. B: Distal half of a cleaned non-ovicellate zooid. C: uncleaned non-ovicellate zooids with asymmetrical lanceolate mandibles. D: part of colony with ovicells. E: detail of a cleaned maternal zooid with ovicell showing the entooecium and the personate peristomial collar. F: ancestrula and peri-ancestrular zooids. Scale bars: A, C, D, F = 200  $\mu$ m; B, E = 100  $\mu$ m.



**FIGURE 9.** *M. harmeri*, ascopore: variability of shape. A: S Africa, Indian Ocean. B: Safaga Bay, Red Sea. C: Oman, Indian Ocean. D: Ras Mohammed, Red Sea. Scale bars A-D = 10  $\mu$ m.



**FIGURE 10.** *M. harmeri*, primary orifice in specimens from different localities. Red Sea: Safaga Bay (A) and Ras Mohammed (F); Indian Ocean: S Africa (B), Oman (C) and Maldives (D); SE Mediterranean: Lebanon (E).



**FIGURE 11.** *M. harmeri*, mandible of avicularium. A: channelled rostrum and mandible folded over the frontal shield; S Africa, Indian Ocean. B: zooids with mandibles in resting position; note the more or less curled lanceolate wings; Oman, Indian Ocean. C: detail of an opened mandible showing the articulation, the stalk and the basal hook which clamps the mandible to the rostrum tip; Ras Mohammed, Red Sea. D: mandible in resting position, with a typical asymmetrical lanceolate shape; Oman, Indian Ocean. Scale bars: A, D = 50  $\mu$ m; B = 200  $\mu$ m; C = 25  $\mu$ m.

**Description.** Colony small or medium-sized, unilaminar. Autozooids quadrangular, hexagonal or oval, longer than broad (mean L/W = 1.2 in Lebanon, 1.3 in Safaga Bay, 1.3–1.4 in Oman); frontal shield weakly convex, ornamented with rounded grains, perforated by numerous pseudopores (45–90) and 5–9 larger, elongated or oval marginal pores. Ascopore placed at distance from orifice, proximal border equivalent to orifice length or a little smaller, crescentic, median process rounded, either well-developed and broad or small, leaving C-shaped lumen partially filled with sharp denticles, sometimes ramified and fusing in transverse bars, surrounded by low rim. Primary orifice broader than long, with distal edge smooth and proximal edge serrated with 11–20 (11–15 in Selaata, 11–17 in Oman, 16–20 in South Africa) sharp, triangular or conical denticles that are often slightly shorter in middle part of edge. Oral spines thin, vanishing in older ontogeny, 3 in most cases, occasionally 2 or 5. Avicularium single on left or right side, exceptionally paired (1 example in a South African colony), directed distolaterally, located slightly proximal to ascopore, but sometimes in a distal position; opesia notably broad (width of crossbar equal to or a little smaller than width of orifice proximal edge), crossbar complete and robust; rostrum short, channelled, with parallel sides or slightly flared at tip; mandible lanceolate with asymmetrical leaf-like projection, internal side broader than external one; two pointed lateral processes curved basally, leaning against rostrum tip. Double-walled oecium with membranous ectoecium and calcified entoecium; latter globular, slightly broader than long, granular, bearing ‘pseudopores’ that are distinctly smaller than those of frontal shield, scarcer on proximal third of oecium; proximal edge forming slightly arched smooth rim; proximal part of ovicell personate, as a raised, granular collar distally adjacent to ascopore, overhanging orifice and fusing with proximal rim of entoecium; this proximal collar sometimes only partially developed or totally absent (2 cases in a South African colony). Ancestrula tatiform with narrow and smooth cryptocyst, bordered by 11 spines.

**TABLE 5.** Morphometrics (in  $\mu\text{m}$ ) of specimens of *M. harmeri* from SE Mediterranean, Red Sea and Indian Ocean. Length (L) and width (W) of autozoid (Az), ovicell (Ov), primary orifice (Or) and avicularium mandible (Md). Mean standard deviation, range and number of measurements (in brackets).

	Lebanon	S Sinai	Safaga	Oman	Maldives	S Africa
AzL	479.4 $\pm$ 35.6	594.5 $\pm$ 44.9	509.1 $\pm$ 44.7	562.3 $\pm$ 34.8	687.2 $\pm$ 59.7	522 $\pm$ 43.6
-	440–540 (16)	535–660 (10)	410–620 (65)	470–630 (26)	600–800 (18)	440–600 (20)
AzW	401.8 $\pm$ 55.5	506.5 $\pm$ 66.1	406 $\pm$ 49.5	417.3 $\pm$ 36.0	496.1 $\pm$ 46.0	409.5 $\pm$ 48.2
-	300–485 (16)	435–630 (10)	310–550 (65)	350–480 (26)	410–580 (18)	290–500 (20)
OvL	255.1 $\pm$ 25.0	292.5 $\pm$ 31.4	-	228.4 $\pm$ 19.2	179.4 $\pm$ 14.8	-
-	205–300 (12)	245–340 (10)	-	180–260 (19)	160–200 (16)	-
OvW	291.5 $\pm$ 20.4	345.0 $\pm$ 19.7	-	278.9 $\pm$ 38.3	224.4 $\pm$ 8.9	-
-	240–320 (12)	315–365 (10)	-	220–320 (19)	210–240 (16)	-
OrL	74.7 $\pm$ 3.3	-	80.6 $\pm$ 6.5	88.3 $\pm$ 4.0	84.4 $\pm$ 6.8	89.5 $\pm$ 4.8
-	70–80 (6)	-	72–90 (55)	80–95 (26)	70–90 (18)	80–100 (20)
OrW	109.4 $\pm$ 7.0	123.4 $\pm$ 4.7	106.7 $\pm$ 7.6	107.9 $\pm$ 7.1	110.3 $\pm$ 8.1	120 $\pm$ 6.5
-	100–115 (9)	117–128 (5)	90–120 (55)	90–120 (26)	100–120 (18)	110–135 (20)
MdL	188.8 $\pm$ 25.6	273.1 $\pm$ 30.0	245 $\pm$ 16	258.7 $\pm$ 17.2	260.3 $\pm$ 16.6	266 $\pm$ 30.6
-	145–240 (17)	216–316 (9)	210–260 (8)	240–300 (26)	230–290 (15)	210–300 (10)

**Remarks.** *Microporella harmeri* was introduced by Hayward (1988) for specimens from Mauritius characterized in particular by three ephemeral spines, a primary orifice with finely crenulate proximal border, maternal zooids with a peristome formed by a prominent proximal lip, and unpaired avicularia with a large opesia and a lanceolate mandible with broad, asymmetric, lateral flaps. This very particular mandible shape was noticed first by Harmer (1957, p. 504) in specimens from the Indian Ocean recorded as *M. orientalis* var., synonymized with *M. harmeri* by Hayward (1988). *Microporella orientalis* var. was recorded from Eilat by d’Hondt (1988) without comment or illustration. When recording *Microporella ciliata* var. *personata*, Busk from the Gulf of Manaar, Ceylon, Thornely (1905, p. 112) specified that "The avicularia on the Ceylon specimens have wing-like membranous extensions of the sides of the mandibles". This record was included by Harmer (1957) in the synonymy of *Microporella*

*orientalis* var. SEM photos of one of these Ceylon specimens in the NHM (courtesy of M. Spencer Jones) allowed confirmation of its identity with *M. harmeri* based on the typical personate ovicells, avicularia with particularly broad opesia and the proximal edge of the orifices having pointed teeth.

Specimens from the Indian Ocean (south Oman, Maldives, South Africa), Red Sea (Ras Mohammed, Safaga Bay) and southeastern Mediterranean (Lebanon) are ascribed to *M. harmeri* with a good level of confidence. All of the specimens found on artificial substrata (Ras Mohammed) or on bivalve shells and coral rubble (remainder of material) present orifices with a finely denticulate proximal edge, three thin ephemeral spines, personate ovicells with a raised peristome and single avicularia with large opesia and leaf-like mandibles with asymmetric lobes. Although the number of teeth on the proximal edge of the orifice can vary among these specimens, their shape is remarkably constant (Fig. 10) and is similar to that observed in specimens studied by Hayward (1988) and Thornely (1905). The shape of the leaf-like mandibles is also very constant among Red Sea and Indian Ocean specimens (Figs 8C, 11) and similar to that of mandibles illustrated by Harmer (1957, pl. 62, fig. 30, Kei Isl., Indonesia), Hayward (1988, pl. 10e, Mauritius) and Scholz *et al.* (2001, fig. 5c, Socotra). The only differences are observed among Lebanese colonies, which have mandibles with narrower wings and smaller frontal and marginal pores. In all our specimens, the lower face of the mandible presents pointed lateral processes on both sides of the proximal end of the rachis, which inserts in the channelled rostrum. However, when the broadest side of the mandible is particularly developed with a proximal lobe, the process corresponding to it on the back side is generally much less developed (South Africa) or even missing (Oman). Examination of numerous dry mandibles in the Oman and South African material showed that there is only one mandible type, but curling of their wings when drying often results in a narrow 'setiform' shape. This result contrasts with the dimorphism observed in colonies of *M. harmeri* by Shirakawa (1999, *vide* Taylor & Mawatari 2005). The shape and development of the ascopore are relatively variable within colonies and between localities (Fig. 9). The median process was particularly developed and broad in specimens from Safaga Bay and South Africa. The presence in specimens from Bangladesh of orifices with a denticulate proximal rim, 3-4 oral spines and unpaired avicularia, among other characters, allowed Gordon *et al.* (2007) to assign them to *M. harmeri*. However, this attribution may be questionable in the absence of data on the mandible type and because the avicularian opesia appears to be smaller than in *M. harmeri*, such as in *M. ventricosa* Canu & Bassler, 1929 (see below).

*Microporella harmeri* also occurs in the Eastern Atlantic. This is evidenced by the precise illustrations and description of specimens from the Canary Islands attributed to *M. orientalis* by Aristegui (1984). These specimens have all typical features of *M. harmeri* including those associated with the ovicell (personate structure), the orifice (spines, denticulation) and the avicularium, particularly the broad opesia and the mandible with asymmetric lateral flaps and pointed processes on the lower face.

A specimen from the Gulf of Suez labelled as *Microporella umbracula* in the Balavoine Collection (MNHN n° 7803) is a *Microporella* species with personate maternal zooids and single avicularia with a broad lanceolate mandible. These features may correspond to *M. harmeri*.

The type of denticulate proximal edge and the shape of avicularium rostrum and mandible of specimens from Heron Island, Great Barrier Reef, attributed by Ryland and Hayward (1992) to *M. orientalis* suggested that they belong to *M. harmeri*. This was subsequently confirmed by checking unpublished SEM photos (courtesy of P.D. Taylor) of these specimens kept in the Natural History Museum, London (n° 1996.2.23.92).

Zabala and Maluquer (1988, p. 140, fig. 338) included in their key to the Mediterranean species of *Microporella* one that they ascribed to *M. orientalis* and characterized by personate ovicells ("expansions of the ovicell surrounding the aperture, often forming a tube rising above the orifice or curving towards the ascopore") and single avicularia having "mandible setiform, with a pair of hook-shaped processes, situated halfway along its length". Curiously, although their description was copied from Hayward (1974, p. 381), who gave no illustration of a single specimen from Chios ascribed to *M. orientalis*, Zabala and Maluquer illustrated their key with a drawing showing orifices with denticulate proximal edge, avicularia with particularly wide opesia and, in contradiction with their description, a mandible bearing two almost symmetrical lateral flaps. This Mediterranean (?) species, noted by Zabala and Maluquer (1988) as rare but without indication of origin, differs from that described by Hayward (1974); it is not *M. orientalis* and could belong to the *M. harmeri* species group.

*Microporella harmeri* has many features in common with *Microporelloides* (*Patorporella*) *hawaiiensis* Soule, Chaney & Morris, 2003, particularly three spines, marginal areolae, denticulate proximal edge of orifice, personate maternal zooids with porous oocelia, and similarly shaped ascopore and avicularia. However, lanceolate mandibles

were not noted in *M. hawaiiensis* by Soule *et al.* (2003) and the ascopore is clearly distant from the personate collar instead of being adjacent to it as in *M. harmeri*. Another similar species is *Microporelloides (Microporelloides) lepueana* Soule, Chaney & Morris, 2004, but it sometimes has paired frontal avicularia. These two Pacific species obviously constitute a species group with *M. harmeri*. Considering the geographical distribution of the latter (Atlantic Ocean, Red Sea, Indian Ocean), it might be possible that several cryptic species remain to be identified.

Assessment of *Microporella* specimens from the Albatross expedition to the Philippine Archipelago (Canu & Bassler 1929), in the USNM, Washington, revealed unexpected taxonomic connections. SEM examination revealed that several specimens ascribed to *M. ciliata* (Canu & Bassler 1929, p. 331, pl. 40, figs 2–4) are conspecific with *M. ventricosa* Canu & Bassler, 1929 (p. 333, pl. 40, fig. 6), whose characters indicate evident similarities with *M. harmeri*. The holotype of *M. ventricosa* (USNM 8109, Albatross Stn 5217) and specimens identified as *M. ciliata* by Canu and Bassler (USNM 8103, 8104, 8105, 8106) display primary orifices with a denticulate proximal edge as in *M. harmeri*, a feature not mentioned by Canu and Bassler, and other characters also observed in *M. harmeri* (e.g. single avicularium, granular frontal wall). However, this set of specimens including *M. ventricosa* differs from *M. harmeri* in having 4–5 strong, not ephemeral oral spines, ascopores surrounded by a cup-like prominent rim and avicularia with a smaller opesia. The average ratio of the width of the avicularian crossbar to the width of the orifice proximal edge calculated on SEM photos is about 0.6 in those Philippine specimens while it reaches 0.8–1 in *M. harmeri*. The ancestrula seen in specimen 8105 has a more developed cryptocyst than in our specimens of *M. harmeri*. Therefore, we consider that *M. ventricosa* differs significantly from *M. harmeri*, but belongs with the latter and with *M. hawaiiensis* and *M. lepueana* in a distinct species complex. It also should be noted that the set of USNM specimens mentioned might belong to more than one species. Personate ovicells seen in 8103 have oral spines in the corners of the personate structure, whereas they are absent in the ovicells of 8106. There is a conspicuous rim around the avicularia in specimens 8103, 8104 and 8105, but not in 8106.

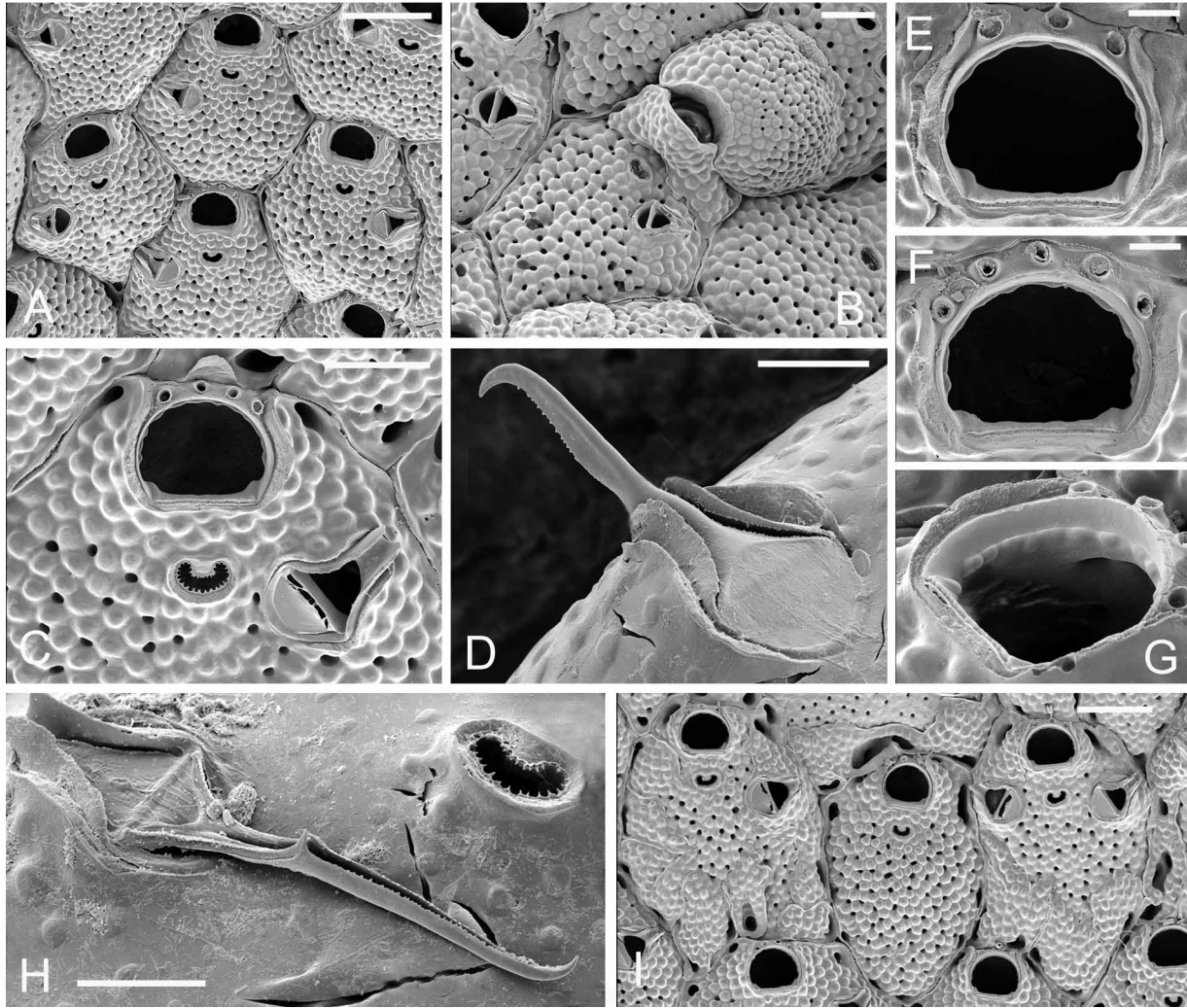
### *Microporella maldiviensis* n. sp.

(Fig. 12A–I, Table 6)

**Material examined.** *Holotype*: 2010-0002-0001 DPUV, on *Pteria penguin*. Maldives Islands, North Male Atoll, Helengeli Island, March 1983, coll. F.F. Steininger. Piece of the holotype mounted on SEM stub. *Paratypes*: 2010-0002-0002 DPUV, on *Pteria penguin*, Maldives Islands, North Male Atoll, Helengeli Island, March 1983, coll. F.F. Steininger. Mounted on SEM stubs: 2010-0002-0003 DPUV, 2010-0002-0004 DPUV, on coral overgrowing bivalve shell, Maldives Islands, North Male Atoll, Helengeli Island, March 1983, coll. F.F. Steininger. 2010-0002-0005 DPUV, on bivalve shell. Maldives Islands, North Male Atoll, Kuda Haa, 04°20'914" N, 073°40'778" E, 8–35 m, 26 January 2008.

**Etymology.** From the Maldives Islands where the species was discovered.

**Description.** Colony encrusting, unilaminar, small or medium-sized. Autozooids oval, penta- or hexagonal, longer than broad (mean L/W 1.40). Frontal shield moderately convex, entirely covered with small rounded nodes and 69–86 pseudopores. Marginal areolae well differentiated, elongated or oval, 7–11 in number. Primary orifice slightly wider than long, anter round, with semicircle of 7–15 irregular, wide and low ‘denticles’ with round summit, wave-shaped in frontal view. Proximal border smooth or slightly corrugated, with shoulder-shaped condyles. Spines 3–4 in most cases, sometimes 5, always in distal position. Ascopore at a distance to proximal edge of orifice, equal to orifice length or a little shorter, oval or round, slightly compressed distally, surrounded by thin rim; lumen large, kidney-shaped with relatively small median process, round, bordered by 24–32 short denticles, sometimes with bifurcated tip. Avicularium single, lateral or proximolateral to ascopore, orientated distolaterally or laterally; opesia relatively large; rostrum short, channelled with nearly parallel sides and narrow truncated tip; crossbar complete, robust; mandible shorter than autozoid width, setiform, narrow, with strong, backwardly curving hooked tip, preceded by finely serrated edges and 2 pointed lateral processes curved basally, which lean against the rostrum tip; avicularia can be occasionally paired in zooids showing traces of repair; a few zooids devoid of avicularia. Ovicells personate, with a tall, arched, granular collar, distally adjacent to ascopore; entoecium granular, bearing ‘pseudopores’ that are distinctly smaller than those of frontal shield. Triangular, oval or irregularly shaped kenozooids with nodular frontal shield and a few marginal pores occasionally present. Older zooids often with irregular patches of ‘secondary calcification’ developing over zooidal margins.



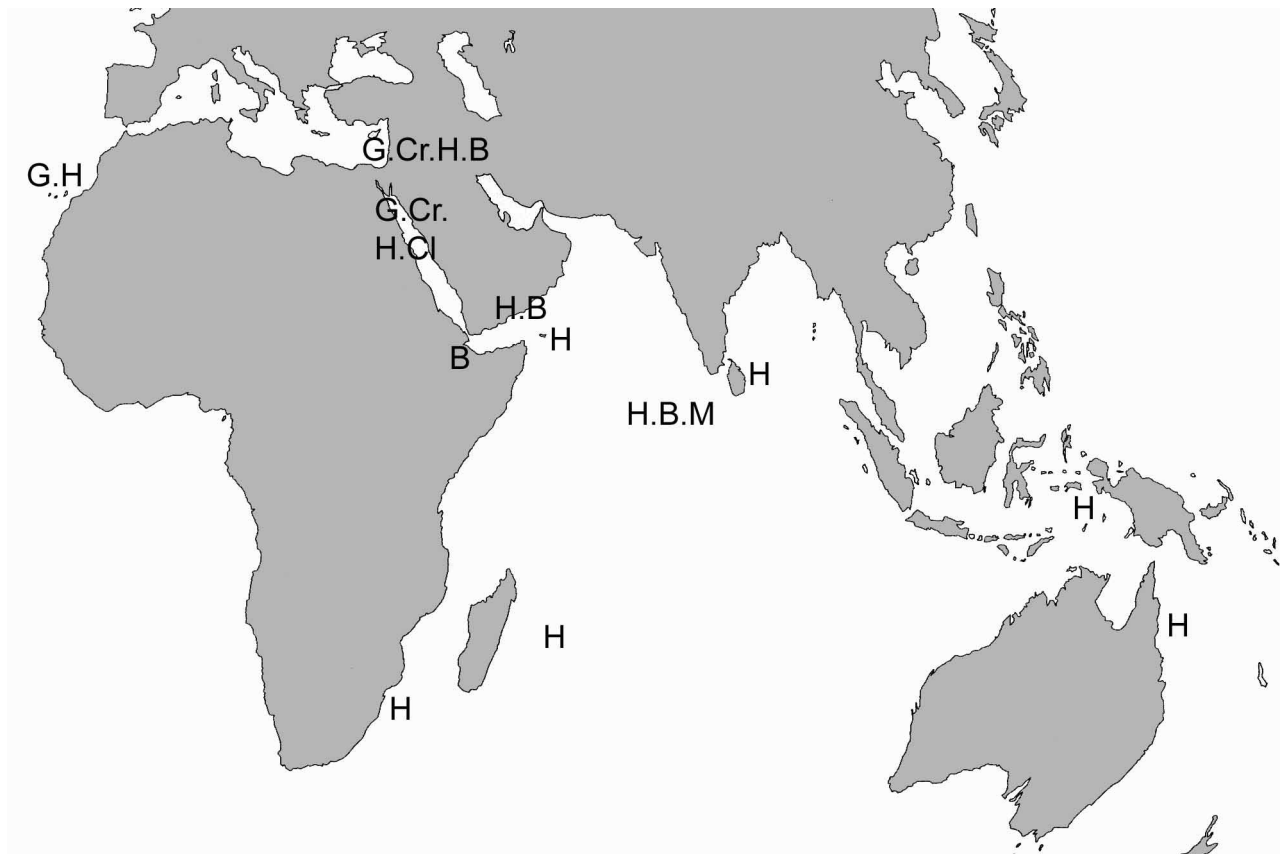
**FIGURE 12.** *M. maldiviensis* n. sp., specimens from Maldive Islands (A, F: paratype 2010-0002-0005 DPUV; B, G: paratype 2010-0002-0004 DPUV; C, E, I: fragment of the holotype 2010-0002-0001 DPUV; D, H: paratype 2010-0002-0003 DPUV). A: non-ovicellate zooids. B: maternal zooid and ovicell with typical personate structure. C: distal half of non-ovicellate zooid with 4 oral spines in distal position. D: avicularium with hooked and finely denticulate mandible resting in the rostrum. E–G: primary orifice with 3 (E), 4 (G) or 5 spines (F), low rounded denticles on the distal edge, shoulder-shaped condyles and slightly corrugated proximal edge. H: avicularium with mandible in open position showing the pointed processes corresponding to the rostrum tip. I: three non-ovicellate zooids with 1, 0 or 2 avicularia respectively, and patches of ‘secondary calcification’. Scale bars: A, I = 200  $\mu$ m; B, C = 100  $\mu$ m; D, H = 50  $\mu$ m; E–G = 30  $\mu$ m.

**TABLE 6.** Morphometrics (in  $\mu$ m) of specimens of *M. maldiviensis* n. sp. from Maldive Islands. Length (L) and width (W) of autozooid (Az), ovicell (Ov), primary orifice (Or) and avicularium mandible (Md). Mean  $\pm$  standard deviation, range and number of measurements (in brackets).

AzL:	659.3 $\pm$ 62.5, 560–760 (30)
AzW:	469.7 $\pm$ 41.4, 390–570 (30)
OrL:	91.2 $\pm$ 4.5, 80–100 (30)
OrW:	109.8 $\pm$ 7.8, 100–125 (30)
OvL:	263.3 $\pm$ 5.8, 260–270 (3)
OvW:	363.3 $\pm$ 20.8, 340–370 (3)
MdL:	257.6 $\pm$ 17.9, 220–300 (25)

**Remarks.** *Microporella maldiviensis* n. sp. recalls *M. browni* n. sp., *M. collaroides* n. sp. and *M. orientalis* in possessing orifices with distal ‘dentition’ (a feature shared with only very few species), personate ovicells and

unpaired avicularia. It differs from these species in the shape and size of the distal denticles, which are less developed than in *M. orientalis* and *M. browni* **n. sp.** and like the ‘denticles’ in *M. collaroides* **n. sp.** in being rather low and forming a wavy shelf rather than a succession of individualized teeth. The condyles, which are similarly developed in both *M. maldiviensis* **n. sp.** and *M. collaroides* **n. sp.** but have a different shape, are more prominent in these species than in *M. browni* **n. sp.** and, moreover, than in *M. orientalis*. The particular shape and size of the avicularian mandible, relatively short with a hooked tip and serrated edges, is another diagnostic character of *M. maldiviensis* **n. sp.**, which clearly distinguishes it from *M. browni* **n. sp.**, while in *M. orientalis* the mandible is also hooked but distinctly shorter. On the other hand, these four species share the same type of personate ovicell and most likely constitute a species complex. Interestingly, the validity of the morphological differences observed between *M. maldiviensis* **n. sp.** and *M. browni* **n. sp.** is reinforced by the finding of both species cohabiting the same locality in the Maldive Islands.



**FIGURE 13.** Geographical distribution of the six studied *Microporella* species with personate ovicells. B: *M. browni* **n. sp.**; Cl: *M. collaroides* **n. sp.**; Cr: *M. coronata*; G: *M. genisii*; H.: *M. harmeri*; M: *M. maldiviensis* **n. sp.**

## Discussion

**Morphological features.** The possibility of detecting small morphological discrepancies between sets of specimens by SEM observations has greatly improved the criteria of species discrimination and led to a boom in the estimation of diversity in many taxa (Soule & Soule 2002). The existence of groups of sibling species distinguished by tiny morphological traits concerns particularly the cheilostome genus *Microporella*, present in all seas, from tropical regions (Liu *et al.* 2001, 2001; Soule *et al.* 2003, 2004; Tilbrook 2006) to boreal, polar and subpolar regions (Aristegui 1984; Hayward & Ryland 1990; Suwa & Mawatari 1998; Shirakawa 1999; Kuklinski & Taylor 2008). Repeated species splitting, particularly among so-called ‘cosmopolitan’ species, has considerably increased the number of described species in this genus, but many of those sibling species remain unnamed. Recently, the type species, *Lepralia ciliata* Pallas, 1766, has been recharacterized, based on a neotype from the Mediterranean (Kuklinski & Taylor 2008). As a result, the biogeographical status of *M. ciliata* has changed from cosmopolitan to Med-

iterranean endemic and most specimens assigned to this species all around the world probably belong to several undescribed species.

Of the six species found in our samples, three are new: *M. browni* **n. sp.**, *M. collaroides* **n. sp.** and *M. maldiviensis* **n. sp.** Two other species are old taxa that needed to be redescribed, viz. *M. coronata* (= *M. unbracula*) and *M. genisii*, both named by Audouin (1826) from the beautiful Savigny drawings (Savigny 1817) made during Bonaparte's expedition in Egypt. The first taxon was repeatedly misused while the second has been resurrected. Consequently, in order to fix their status, neotypes have been designated. Comparison of our material of *M. coronata* with other material assigned to this species, including a museum specimen from the Suez Canal (Hastings 1927) and published descriptions of specimens from Suez (Waters 1909) and the Canary Islands (Aristegui 1984), has led to the erection of a new species, *M. hastingsae* **n. sp.** The sixth species, *M. harmeri*, originally well-defined from Mauritian material (Hayward 1988) with unequivocal characters, has in fact a surprisingly wide geographical distribution as revealed by our material and critical examination of data in the literature (see below).

The significance of the various morphological features as diagnostic of *Microporella* species is a fundamental topic of discussion (e.g. Suwa & Mawatari 1998; Taylor & Mawatari 2005). Within a single species, characters may vary at different levels: (1) within colonies, (2) between colonies from the same locality, (3) between sites in the same region, and (4) between regions grouping several sites. The determination of the amount of variability that can be accepted within each species' limits is a tricky problem. The help of molecular tools for identifying the respective roles of environment and genome in the observed morphological differences is hardly conceivable in small unilaminar encrusting colonies, such as those of *Microporella* species. Because of its abundance, our material offers the possibility of appreciating different aspects of the variability of morphological characters within and between species.

Two morphological attributes, the denticulation of the primary orifice and the personate ovicell with a raised peristome, considered to be relatively uncommon among *Microporella* species (Taylor & Mawatari 2005), appear with singular frequency in the six studied species. Undoubtedly, the set of features linked to the orifice, including the associated spines and the peristome in maternal zooids, is of crucial interest for species differentiation. The type of ornamentation of the anter and poster of the primary orifice was found to be particularly stable within species. Only *M. coronata* among the six species shows a primary orifice with both distolateral and proximal edges smooth. In the five other species the poster is ornamented to various degrees and a smooth anter is observed only in *M. genisii* and *M. harmeri* (Table 7). Serration of the proximal border is particularly marked in *M. harmeri* and *M. collaroides* **n. sp.**. In *M. harmeri*, the shape and size of the 'teeth' are non-variable among specimens from the Indian Ocean, Red Sea, Mediterranean and Atlantic localities (Fig. 10). In this species, the pointed denticles always form a nearly straight narrow row, but their number ranges from 11 to 15 in specimens from Lebanon and 16 to 20 in specimens from South Africa. In *M. collaroides* **n. sp.**, all specimens have the poster serrated with oval bars located on the frontal edge of a broad, concave rim. Serration of the poster is typically limited to very low beads in *M. genisii* and to a slightly corrugated edge in *M. browni* **n. sp.** and *M. maldiviensis* **n. sp.**. In the three species with an ornamented anter, the type of denticulation presents a gradation, with (1) numerous, conspicuous denticles in *M. browni* **n. sp.**, (2) fewer, lower denticles in *M. maldiviensis* **n. sp.** and (3) an irregularly wavy rim in *M. collaroides* **n. sp.**. In *M. browni* **n. sp.**, the range in tooth number varies according to locality and the lower scores may be similar to the number of teeth observed in *M. maldiviensis* **n. sp.**. However, the shape of these distal denticles is not the same in these two closely allied species, which are sympatric in the Maldivian Islands. Condyles are not apparent in *M. harmeri* and *M. genisii* and are shoulder-shaped protuberances at both ends of the official proximal rim in the four other species. Although generally stable within species, this character may vary between sites as in *M. browni* **n. sp.**, where condyles can be occasionally poorly projecting or absent in specimens from Oman and Maldives.

Despite showing certain variability within species, the number of oral spines is a good species character when the most frequent value is considered. The smallest modal number was found in *M. harmeri* (three spines) and the highest in *M. coronata* (seven spines) and in both species other values were relatively infrequent. Conversely, in *M. browni* **n. sp.**, the spine number ranged widely from three to seven, four and five spines being the most frequent scores. The oral spines are generally aborted or hidden by the development of the ovicell. In contrast, the persistence of spines at the corners of the ovicells is a typical feature of *M. genisii* and *M. hastingsae* **n. sp.**, also occasionally observed in *M. coronata*. The number and position of oral spines change as the colony grows. In the zone of astogenetic change, zooids have more numerous spines, which are evenly distributed around the whole or most of the anter. In the zone of astogenetic repetition oral spines tend to be less numerous and more distal. This trend is



particularly clear in species with 'adult' zooids bearing a low number of spines, such as *M. harmeri*, but is not apparent in *M. coronata*. In *M. maldiviensis* **n. sp.** oral spines are placed around the distal third of the anter in all zooids seen.

The six species found in our samples have in common the occurrence of a personate peristome in maternal zooids. The shape of this peristome, a raised collar abutted on the ovicell, is very similar in all species except *M. coronata* in which the peristome is formed by alate lateral expansions joined in a bridge. Even within a fertile colony, some ovicells may be devoid of a personate peristome. This was occasionally the case in specimens of *M. harmeri* from South Africa, *M. collaroides* **n. sp.** and *M. genisii*. In *M. coronata*, the degree of completion of the peristomial bridge may be variable among maternal zooids of the same colony, with lateral wings reduced to a low projection in some of them.

In all species examined here except *M. hastingsae* **n. sp.**, the entoecium wall is perforated by 'pseudopores', which are smaller than those of the frontal wall. This feature could argue for their assignment in *Microporelloides* Soule, Chaney & Morris, 2003. Tilbrook (2006) did not accept this genus because of the existence of intermediate forms between species with 'non-perforate' ovicells and those with 'perforate' ovicells.

The aspect of the ascopore may change between and within species according to several variables: the size, general shape of the lumen and its rim, development of the median process, abundance and size of the denticulations, and the extent of development of a marginal rim and/or proximal umbo. In our material, for example, the modest development of the median process and the general oval outline clearly differentiate *M. genisii* from the other species despite some intraspecific variation. The highest degree of within-species variability of the ascopore was observed in *M. harmeri* (Fig. 9), which displays the most diverse geographical distribution in our collection. In the same species, the development of the median process also varies between colonies at the same locality (e.g. at Safaga Bay).

Avicularia offer an assortment of useful characters for discriminating *Microporella* species. In our material, five species bear single avicularia and only *M. coronata* has paired avicularia. As stressed by Taylor and Mawatari (2005), the number of adventitious avicularia borne by *Microporella* autozooids is species-specific but not strictly fixed within colonies. Exceptions to the specific rule were sometimes observed in *M. coronata*, with periancestrular zooids bearing single avicularia. In the other species typically with single avicularia, few zooids bearing paired avicularia were observed in colonies of *M. browni* **n. sp.** (from Tadjoura), *M. harmeri* (from South Africa) and *M. maldiviensis* **n. sp.** (from the Maldives). In all but one species studied (*M. coronata*), avicularia were missing in some zooids. The orientation and location of the avicularia relative to the ascopore or the orifice may show small local variation within colonies, even among adjacent zooids, as in *M. genisii*, bearing close avicularia both directed laterally and distolaterally. The shape and relative size of the rostrum and opesia are stable characters within species, which are easily perceptible with classical optical means in cleaned and uncleaned colonies (e.g. large size of opesia in *M. harmeri*). The type and size of the mandibles were different in the five species in which they were observed (Table 7) but all can be assigned to the lanceolate type according to the classification by Suwa and Mawatari (1998). These authors distinguished three categories of mandibles among *Microporella* species: (i) simple, i.e. without projection beyond the rostrum tip, (ii) with a setiform projection and a basal beak and (iii) with a lanceolate projection and a pair of hooks at the base. Paired basal hooks, which are projections allowing the mandible to rest firmly on the avicularium tip, were observed in the six species studied. When the lanceolate mandibles are narrow and long, the difference with the setiform type (*sensu* Suwa & Mawatari 1998) is not clear-cut and this latter term is widely used in a more general sense. It is even more equivocal when, as noticed by Suwa and Mawatari (1998), drying modifies the shape of broad lanceolate mandibles by curling the edges, giving them a narrower aspect. This was observed in *M. genisii* and particularly in *M. harmeri*. The two types of mandibles observed by Shirakawa (1999, *fide* Taylor & Mawatari 2005) in the latter species may result from this phenomenon. In several species of our collection, the characters based on the mandible constitute a set of diagnostic tools of crucial importance in species characterisation, e.g. in *M. maldiviensis* **n. sp.**, in which the typically setiform mandible is relatively short and has a beak-like tip and finely denticulate edges, and in *M. harmeri* whose mandibles present a spectacular wing-like lateral expansion.

Ancestrulae display a uniform shape and structure in the four species in which this primary stage was observed. All ancestrulae present in our material are tatiform, with a narrow cryptocyst rim, a moderately developed gymnocyst, a crown of 10–12 marginal spines (Table 7) and two daughter autozooids budded distolaterally.

The broad geographical range of the *Microporella* species in our material enables us to assess the between- and within-species variability of the zooidal dimensions, particularly those which are the most reliably measured, i.e. AzL, AzW, OvW and OrW. For these four dimensions the smallest average sizes were observed in colonies of *M. genisii* from Lebanon. The largest average dimensions (in brackets, multiplier of the average value noted in Lebanese specimens of *M. genisii*) were observed in *M. harmeri* from the Maldives for AzL (x 1.8), in *M. harmeri* from south Sinai for AzW (x 1.8), in *M. maldiviensis* from the Maldives for OvW (x 1.7) and in *M. coronata* from Lebanon for OrW (x 1.4). The variability of the zooidal dimensions is also great but disordered within species presenting a broad distributional range. For example, in *M. harmeri* average AzL was 30% larger in the Maldives than in Lebanon whilst, conversely, average OvW was 30% larger in Lebanon than in the Maldives. However, one should be aware that the morphometric characterisation of local populations should be performed from a rigorous sampling procedure and that the present results provide only indications.

**TABLE 7.** Features associated with the orifices of non-ovicellate zooids, the ancestrulae and the avicularia. **Anter** – 0: smooth; 1: wavy relief; 2: low denticles; 3: prominent denticles. **Poster** – 0: smooth; 1: corrugate; 2: low beads; 3: oval bars; 4: pointed denticles. **Condyles** – 0: absent; X: present, shoulder-shaped. **N spines Or**: modal number(s) of oral spines and observed range in brackets. **N spines An**: number of marginal spines in ancestrulae. **Av (N) Type**: single (1) or paired (2); type A: setiform, long and slender; type B: setiform, medium-sized; type C: setiform, short and hooked; type D: lanceolate, narrow; type E: lanceolate, wing-like. **Md L/Ro L**: ratio of mandible length on rostrum length.

	Anter	Poster	Condyles	N spines Or	N spines An	Av (N) Type	Md L/Ro L
<i>M. browni</i>	3	1	X	4, 5 (3–7)	10, 11	(1) B	3.5–4
<i>M. collaroides</i>	1	3	X	4, 5 (4–6)	10	(1) -	-
<i>M. coronata</i>	0	0	X	7 (6–8)	-	(2) A	6–7
<i>M. genisii</i>	0	2	0	4 (3–5)	11, 12	(1) D	2.5–3.5
<i>M. harmeri</i>	0	4	0	3 (2–5)	11	(1) E	2.2–3
<i>M. maldiviensis</i>	2	1	X	3, 4 (3–5)	-	(1) C	2–2.5

**Biogeography.** Based on the present state of knowledge, the geographical distributions of the six *Microporella* species with personate ovicells presents contrasted patterns (Fig. 13). Two of the three new species are known only from limited geographical sectors: the coast of the Arabian peninsula in the Red Sea for *M. collaroides* n. sp., and the North Male Atoll of the Maldives archipelago for *M. maldiviensis* n. sp.. Conversely, *M. harmeri* appears to have a very broad distribution, including several localities in the Indian Ocean, Red Sea, Pacific Ocean (Coral Sea, Indonesia), southeastern Mediterranean and the eastern Atlantic (Canary Islands). However, one should be aware that these contrasting patterns of geographical distribution may only reflect a partial knowledge of the actual situation. This is likely for the new species whose restricted known distribution may be only a matter of sampling failure and of the newness of the identification criteria. The case of *M. harmeri* is different and raises several questions: does the very wide distribution imputed to this taxon really correspond to a single biological species, as suggested by the morphological similarity observed between the various specimens, or is it a species group of sibling species? In the case of a single species, what is the role of the anthropogenic factors in shaping its observed geographical distribution beyond its native range? The intensification of maritime traffic contributes greatly to interprovincial exchanges of propagules, including those of bryozoans (Ryland 1965; Gordon *et al.* 2006; Ryland *et al.* 2009). *Microporella* species are not commonly recorded among fouling communities (e.g. Gordon & Mawatari 1992; Koçak 2007; but see Liu *et al.* 2001). However, their small early-brooding encrusting colonies are potential foulers and privileged candidates for ship-induced dispersal.

Because they are subject to intense international maritime traffic, the Indian seas and the Indo-Malaysian area are a major centre of introduction of exotic biota, which are afterwards dispersed towards other areas (Subba Rao 2005). The Levant basin of the Mediterranean is another particularly interesting area for observing changes in biodiversity owing to the two great anthropic vectors of species dispersal: shipping (via hull fouling and ballast water) and the opening up of natural barriers between marine basins.

The four *Microporella* species recorded at ten Lebanese localities were the only ones found in a large collection of plurispecific samples collected by diving in a relatively wide depth range (3–43 m) at 20 localities along the whole Lebanese coast. The absence of *Microporella* species that are common in the Mediterranean and the Adri-

atic, such as *M. 'ciliata'* (*sensu* Gautier 1962 and Hayward & McKinney 2002) or *M. appendiculata* (Heller) (= *M. pseudomarsupiata* Aristegui), is worth noting. The *Microporella* species recorded in the eastern Mediterranean include *M. ciliata* (Greece: Harmelin 1968[1969]; Turkey: Ünsal 1975), *M. marsupiata* (Turkey: Ünsal & d'Hondt 1979), *M. orientalis* (Chios: Hayward 1974), which was described as having personate ovicells but not illustrated, and *M. umbracula* listed from Cyprus (Koçak *et al.* 2002), Milos (Morri *et al.* 1999) and Turkey (Nicoletti *et al.* 1995) without any description or figure that could ensure identity with *M. coronata*. The stock of *Microporella* species found in Lebanon is thus remarkable as it is composed only of tropical species alien to the Mediterranean, if one admits that the native range of *M. coronata* does not include the Mediterranean. This finding is consistent with increases in the list of alien bryozoan species recorded in the Mediterranean (Zenetos *et al.* 2005).

The Levant basin is the warmest region of the Mediterranean (Abboud-Abi Saad *et al.* 2004) and also the most highly impacted by alien species (e.g. Zibrowius 1991; Zibrowius & Bitar 2003; Galil 2007; Bitar 2010). Most of those alien species have been introduced from the Red Sea and Indo-Pacific Ocean through the Suez Canal (96% of the metazoan alien species recorded along the coasts of Israel: Galil 2007; see also Steinitz 1967). The means of introduction of the benthic 'Lessepsian' or 'Erythrean' species is larval dispersal, with the possible aid of relays ('stepping stones') along the canal, including local working boats, and also by direct shipping (Zibrowius 2002; Galil 2007). However, thousands of large vessels enter the Mediterranean annually through the Gibraltar Strait before converging towards the Levant ports, the Black Sea and the Mediterranean entrance of the Suez Canal. This part of the maritime traffic in the eastern Mediterranean can be an important vector of introduction of ship-borne aliens independently of the Lessepsian route, e.g. from tropical Atlantic regions. The finding of *M. browni* n. sp. near the harbour of Beirut (Lebanon) — the only Mediterranean record of this species which has not yet been recognized in the available Red Sea collections — is a strong indication that this species was introduced there by shipping from tropical waters.

Our study clearly shows the huge amount of revision work that should be done to bring order to the chaos characterizing the current status of most species of *Microporella*, one of the most diverse cheilostomate genera. The major problem here is the availability of the type specimens dispersed throughout collections of various museums. However, such a speciose genus may also be a valuable model in a phylogeographical approach to the 'species groups' of sibling species using molecular tools that could help us to understand different aspects of the species' distribution.

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