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New and poorly described bryozoans from the Catalano-Balearic area (NW Mediterranean)

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Abstract. Over the last ten years, we compiled a collection of bryozoans from the Catalano-Balearic Sea (NW Mediterranean), resulting in the description of nine new species or subspecies: *Cribrilaria pseudoradiata balearica* subsp. nov., *Cribrilaria setiformis alata* subsp. nov., *Glabrilaria corbula cyranosa* subsp. nov., *Schizomavella (Schizomavella) harmelini* sp. nov., *Palmiskenea diazi* sp. nov., *Cellepora ballesterosi* sp. nov., *Cellepora gilii* sp. nov., *Cellepora* sp., *Rhynchozoon garraboui* sp. nov., *Rhynchozoon trifolium* sp. nov. We also completed the description of two poorly described species, viz., *Rhynchozoon quadrispinatum* Zabala & Maluquer, 1988 and *Rhynchozoon pseudodigitatum* Zabala & Maluquer, 1988; and amended the description of *Mollia circumcincta* (Heller, 1867) and *Rhynchozoon neapolitanum* Gautier, 1962 to add features that were not included in the original descriptions. This study confirms that even in an area where the fauna is well known, our knowledge remains incomplete, and emphasizes the need for reassessment of regional or local fauna.

Keywords. Redescription, amended description, Western Mediterranean, new species, cheilostomata, *Cellepora*, *Rhynchozoon*, *Schizomavella*.

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Introduction

Even if the Mediterranean bryozoan fauna is one of the most studied overall, there are strong suggestions that our knowledge of Mediterranean bryozoan diversity is still incomplete. Between the two check-lists compiled by Rosso (2003) and Rosso & Di Martino (2016) and the recent update (Rosso & Di Martino 2023), the number of reported bryozoans species in the Mediterranean has increased from 475 to 558 (19%). Thus, in addition to new records, the number of species keeps increasing each time there is a review of a previously studied genus. The expansion of scanning electron microscopy (SEM) as a regular tool of study has shown that under the umbrella of most of the species known by the bryozoologists of the 19th and 20th centuries, reputed to have large geographical expanses, there is housed a plethora of very similar species with much more local distributions. The latest revisions, already including molecular

taxonomy, are also increasing our knowledge on bryozoan diversity (Baptista *et al.* 2022, 2024; Gauff *et al.* 2023). In this context, a complete re-assessment of the local faunas, particularly those that remained at rest during the last decades, was urgently needed.

The Catalano-Balearic area of the Western Mediterranean has been object of a large number of surveys (Barroso 1915, 1918, 1919a, 1919b, 1920, 1922, 1923, 1929, 1935, 1948; Calvet 1927; Silén 1946; Gautier 1957, 1962; Prenant & Bobin 1966; Zabala 1986, 1993; Maluquer 1985; Zabala & Maluquer 1988; López de la Cuadra & García-Gómez 2001; Reverter-Gil *et al.* 2009; Souto *et al.* 2010a, 2010b; Madurell *et al.* 2013), but revision works, as well as the results of new collection efforts, and the recent expansion of non-indigenous bryozoa (Reverter-Gil & Souto 2023) require an update of the known species for this area. During the last years, we tackled the challenge of building an updated check-list of the Bryozoan fauna of the Catalano-Balearic Sea. At present, the list of only the bryozoans with a carbonated skeleton (order Ctenostomatida Busk, 1852 has been excluded) comprises 286 species and varieties (<https://briozous.eu/index.php>). During these tasks of revision, some specimens emerged that deserve an accurate description either because they were already known but poorly described species, or because they seem to represent new species or new varieties (= subspecies) of well described species.

In the present study, the results of that revision, including the description of six new species, three subspecies, and the clarification of four taxa are presented.

Material and methods

Unless otherwise stated, all type and sample specimens revised are part of the MZ-TM collection, which is deposited in the Briozous de la Mediterrània collection (<https://www.bioexplora.cat/WIKICOLLECTA/index.php/ca/briozous>), and held at the Museu de Ciències Naturals de Barcelona (MCNB-MZB). All samples were collected in the Catalano-Balearic area; most shallow samples were collected by scuba diving whereas samples from the shelf were collected during the Indemares surveys (https://www.Indemares.es/proyecto/campanas_oceanograficas) by dredge or submersible. Additional material from the following museums have been also revised: American Museum of Natural History (AMNH), Smithsonian National Museum of Natural History (NMNH; formerly United States National Museum, USNM), the Natural History Museum, London (NHMUK) and the Muséum national d'Histoire naturelle, Paris (MNHN).

Pictures were performed by Scanning Electron Microscopy (SEM) on uncoated specimens, using a Quanta 200 FEI, XTE 325/D8395 from the Centres Científics i Tecnològics de la Universitat de Barcelona (CCiTUB) in backscattered-electron/low-vacuum mode. Abbie Herdman provided SEM pictures of *Schizomavella hastiformis* Hayward & Ryland, 1978 (NHMUK1977.5.2.1) and *Rhynchozoon bispinosum* (Johnston, 1847) (NHMUK2009.10.12.5, NHMUK2010.1.7.3). SEM pictures of *Palmicellaria aviculifera* (Canu & Bassler, 1928) (USNM RB 7565-1) were made available by JoAnn Sanner. Priscilla Bourguignon made SEM pictures of *Rhynchozoon bispinosum* from Gautier collection (MHNH-IB-2008-10999 and MHNH-IB-2008-11001). Óscar Reverter-Gil and Javier Souto provided SEM pictures from *Schizomavella hastata* (Hincks, 1862) and *Rhynchozoon bispinosum* respectively.

All measurements were taken with ImageJ® software and are given in µm. Avicularia measurements for all species and ratios on the frontal shield measurements for cribrilid species (*Cribrilaria* Canu & Bassler, 1929 and *Glabrilaria* Bishop & Househam, 1987) are made according to Harmelin & Aristegui (1988) (Fig. 1).

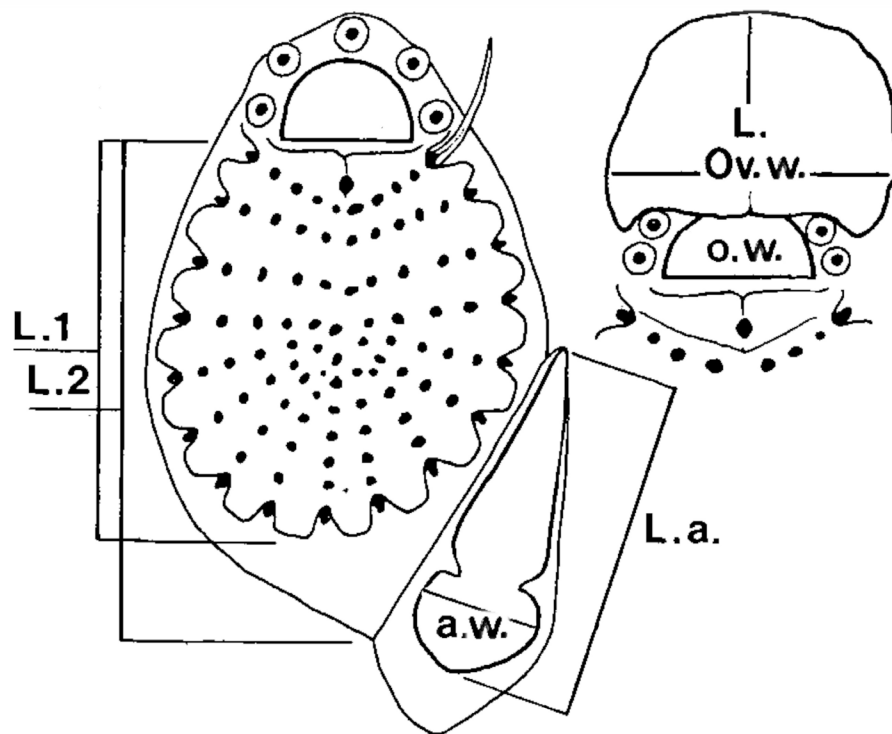


Fig. 1. Zooidal measurement procedure. Abbreviations: a.w. = avicularian width; L.a. = avicularian length; L.1 = length of frontal shield; L.2 = L.1 + proximal gymnocyst; Ov. L. = ovicell length; Ov.w. = ovicell width; o.w. = primary orifice width (modified from Harmelin & Aristegui 1988).

Results

Order Cheilostomatida Busk, 1852
 Suborder Flustrina Smitt, 1868
 Superfamily Microporoidea Gray, 1848
 Family Microporidae Gray, 1848
 Genus *Mollia* Lamouroux, 1816

Mollia circumcincta (Heller, 1867)

Fig. 2

Membranipora circumcincta Heller, 1867: 96, pl. 6 fig. 5.

Mollia circumcincta – Gautier 1962: 61. — Zabala & Maluquer 1988: 91, pl. 2 figs c–d. — Hayward & McKinney 2002: 241, fig. 13d–h. — Chimenz Gusso *et al.* 2014: 105–106, fig. 42a–f. — Pica *et al.* 2022: 383, fig. 11a–d.

Material examined

MEDITERRANEAN CROATIA • 1 ovicellate colony; Channel between Sv. Ivan Island and Pelago Island; 45.042222° N, 13.601944° E; depth 40–41 m; 8 Jun. 1992; dredge, sand bottom; F.K. McKinney leg.; AMNH-B920Acc63274 (Fig. 2A).

MEDITERRANEAN SPAIN • 1 ovicellate colony; Medes Islands; 42.04502° N, 3.22554° E; depth 27 m; 20 Jul. 2013; *Puerulus*; scuba dive, M348, R12, stub 490; MZB 2015-8296 (Fig. 2B) • 1 ovicellate colony; Pollença Bay, Mallorca Island; 39.95735° N, 3.2139° E; depth 40 m; CARBAL, scuba dive, M701, stub 823; MZB 2025-6310.

Amended description

Overall characteristics have been described by Hayward & McKinney (2002: 34, fig. 13d–h). We here give an amended description of the ovicell as: independent ovicell; hemispherical or trapezoidal with rounded corners; ectooecium smooth, forming a calcified rim well developed laterally (sometimes also developed proximally); entoecium forming a central granular area with commonly a large round pore in the most distal corner, and two elongated pores or opesiules in each lateral corner (Fig. 2A); occasional presence of two spines in the growing margin (Fig. 2B).

Remarks

Mollia circumcincta is a pretty species first described by Heller (1867) and redescribed by Hayward & McKinney (2002) with specimens from the Adriatic. The description of the ovicell from Hayward & McKinney (2002) was poor, describing it as “Ovicell hemispherical, partially immersed, with a crenulate vertical wall bordering a vitreous, nodular cryptocystal frontal surface”. However, looking carefully at Hayward & McKinney (2002: fig. 13d, g), it is apparent that the ovicell has a smooth ectooecial rim, a characteristic distal round pore and two lateral opesiules. The presence of these characters was confirmed with the re-examination of the specimen AMNH-B920Acc63274 used by Hayward & McKinney (2002) for the description of *M. circumcincta* (Fig. 2A). These characters were already spotted by Chimenz Gusso *et al.* (2014) that described the presence of the ooecium (“zooidal disto-lateral wall not continuous with the proximal margin of the ovicella”) and mentioned the entoecium (referred as the granular front wall of the ovicell) is perforated by two proximo-lateral pores, pointing that in some cases only one distal pore, in others there are both the proximal-lateral pores and the distal pore. The presence of ectooecium was also observed recently by Pica *et al.* (2022), for the Adriatic and North Ionian specimens, describing the ovicell as having an extremely reduced ectooecium, restricted to the proximolateral edges of the ooecium, although they do not mention the existence or absence of pores. In contrast, Souto *et al.* (2010b) when trying to tell the differences between *M. multijuncta* (Waters, 1879) and *M. circumcincta* stated that the ovicell is lacking an ectooecium and has a continuous entoecium, without the mention

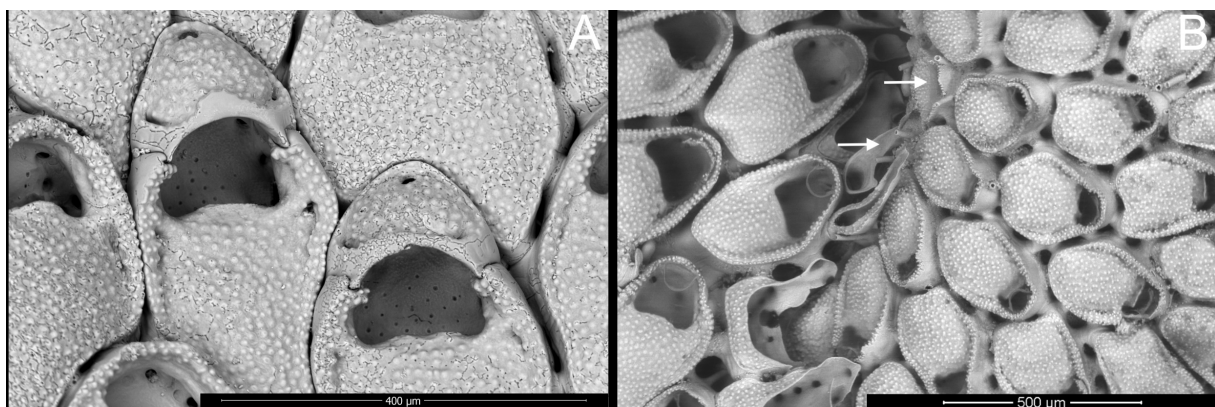


Fig. 2. *Mollia circumcincta* (Heller, 1867). **A.** Ovicells. Notice the presence of a distal round pore, two lateral opesiules and a smooth ectooecial rim only laterally developed (F.K. McKinney leg.; AMNH-B920Acc63274). **B.** When two competing species of *Mollia* (*M. multijuncta* (Waters, 1879) on the left of the image and *M. circumcincta* on the right) meet, the marginal autozooids of *M. circumcincta* can develop two small spines (white arrows) (MZB 2015-8296).

of pores or opesiules. Therefore, to avoid further misunderstandings, we amend in this account the description of the ovicell for *M. circumcincta*

These characters help to discriminate *M. circumcincta* among the four *Mollia* described from the Atlanto-Mediterranean area (Souto *et al.* 2010b). *Mollia patellaria* (Moll, 1803) is the most distinct with a globose and smooth ovicell, and rounded zooids that are linked to the contiguous zooids by a sole connecting tube. *Mollia multijuncta* and *M. cristinae* Souto, Reverter-Gil & Fernández-Pulpeiro, 2010 share with *M. circumcincta* the characteristic of several tubes connecting a single zooid and the presence of two opesiules in the ovicell; nevertheless, the former ones have a crescentic ovicell, much wider than long, an ectooecial rim wide and smooth and lack the distal pore, which is characteristic of *M. circumcincta*.

In addition, *M. circumcincta* occasionally presents two spines in the growing margin (Fig. 2B). To our knowledge the presence of spines in the genus *Mollia* has not been mentioned by any previous author, except for their presence in the first two or three astogenetic generations (Hayward & McKinney 2002).

Superfamily Cribrilinoidea Hincks, 1879

Family Cribrilinidae Hincks, 1879

Genus *Cribrilaria* Canu & Bassler, 1929

Cribrilaria pseudoradiata (Harmelin & Aristegui, 1988)

***Cribrilaria pseudoradiata balearica* subsp. nov.**

[urn:lsid:zoobank.org:act:8CBD61EF-582B-4710-BB4C-51564AD466B4](https://zoobank.org/act:8CBD61EF-582B-4710-BB4C-51564AD466B4)

Fig. 3; Table 1

Differential diagnosis

Colony encrusting, cribrimorph. Autozooids variable in size (the length of the smallest almost half that of the largest). Proximal gymnocyst of autozooid narrow (more than the other subspecies); perycyst relatively large. Frontal shield oval or flattened, with 11–19 (most commonly 16) costae. Five to six spines in non-ovicellate zooids, four spines in ovicellate zooids. Oral spines with basal apophyses. Ovicell of type A (Bishop & Househam 1987), often displaced and bent to one side; as long as wide, with a median suture, non-punctate, without apparent tubercles. No avicularia. Kenozooids rare.

Etymology

Referring to the Balearic Islands, the geographic origin of the material.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Menorca Channel; 40.09533° N, 3.655° E; depth 170 m; 9 Apr. 2011; Indemares 4; JAGO dive; stn 103, M632, R401, stub 9181; MZB 2025-6311 (Fig. 3A–B, measurements).

Paratypes

MEDITERRANEAN SPAIN • 1 ovicellate colony; Menorca Channel; 40.019317° N, 3.157317° E; depth 117 m; 29 Jun. 2012; Indemares 6; Rauschert sledge; stn 32, stub 554; MZB 2016-3782 (Fig. 3C–D, measurements) • 1 ovicellate colony; Menorca Channel; 40.036383° N, 3.163301° E; depth 130 m; 3 Apr. 2011; Indemares 4, JAGO dive, stn 41, M623; MZB 2025-6312 • 2 ovicellate colonies; Menorca Channel; 40.997665° N, 3.120167° E; depth 240 m; 2 Apr. 2011; Indemares 4, JAGO dive, stn 24, M657, stub 9184; MZB 2025-6313.

Description

Colony encrusting, unilaminar, small to medium size (ca 100 zooids) (Fig. 3A). Autozooids longer than wider, variable in size (the larger ones almost twice as long as the smaller ones). Autozooidal gymnocyst more visible laterally than proximally, except when they produce finger-like extensions between adjacent proximal zooids (Fig. 3B). Frontal shield oval, flat or slightly convex, with 11–19 (most commonly 16) costae (Fig. 3B). Costa narrow, ornamented with one or two spiniform denticles on the internal and external periphery, with a proximally adjacent pelmatidium. Intercostal spaces with three to six pores, variable in form but mainly quadrangular to rounded, and generally smaller in proximal costae; without denticles. First (distalmost) pair of intercostal spaces with two or three large pores on each side, the first or the second being particularly enlarged; and the inner ones sometimes merged into one single pore (Fig. 3C). Distal setiform papillae reaching or exceeding the lateral margin of the autozooid (Fig. 3B). Orifice D-shaped (semicircular), wider than long; 1.1–1.2 times wider in the ovicellate zooids; proximal margin straight and smooth (Fig. 3C). Mostly five but sometimes six (ca 15%) oral spines in non-ovicellate zooids, four spines in ovicellate zooids (Fig. 3B). Spines with small processes at the base of

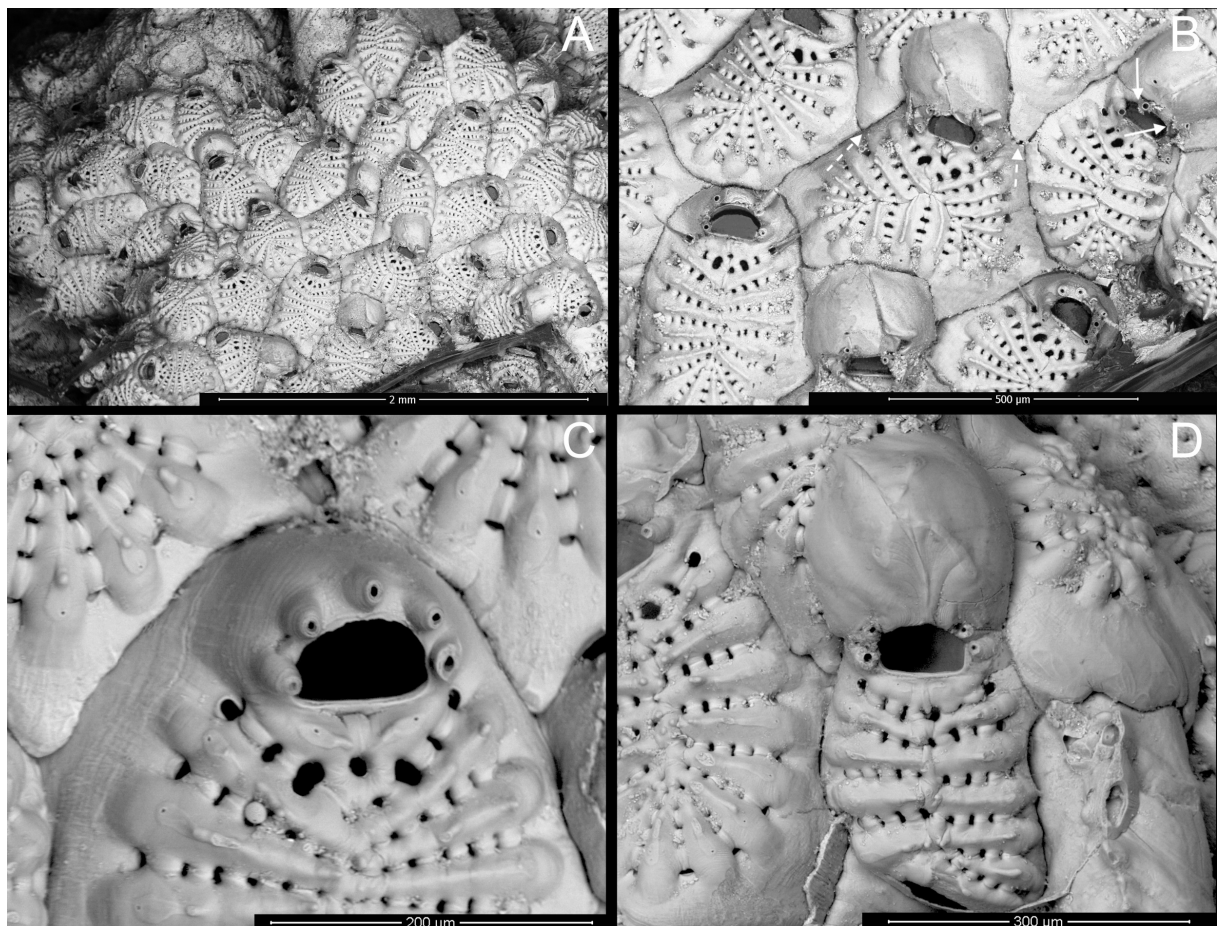


Fig. 3. *Cribrilaria pseudoradiata balearica* subsp. nov. **A.** Ovicellated colony view (holotype MZB 2025-6311). **B.** Non-ovicellated and ovicellated autozooids, notice that the non-ovicellated zooids exhibit a variable number of spines (five or six); white arrows point to small processes at the base of the spine; dashed arrows point to gymnocyst extensions (holotype MZB 2025-6311). **C.** Primary orifice and suboral bar without lacunae and distalmost intercoastal space showing the characteristic uneven pores (paratype MZB 2016-3782). **D.** Ovicell type A, lacking lateral tubercles and kenozooid (top right) (paratype MZB 2016-3782).

Table 1. Measurements (in μm) of *Criblaria pseudoradiata balearica* subsp. nov. (holotype MZB 2025-6311 and paratype MZB 2016-3782). *C. pseudoradiata pseudoradiata* (Harmelin & Aristegui, 1988) and *C. pseudoradiata canariensis* (Harmelin & Aristegui, 1988); measurements from Harmelin & Aristegui (1988). Abbreviations: Max = maximum; Min = minimum; N = number of measurements; SD = standard deviation.

	<i>Criblaria pseudoradiata balearica</i> subsp. nov.					<i>C. pseudoradiata pseudoradiata</i>		<i>C. pseudoradiata canariensis</i>	
	N	Mean	SD	Min	Max	Mean	Range	Mean	Range
Autozoid length	31	476	47.7	399	569	–	–	–	–
Autozoid width	36	351	63.04	244	555	–	–	–	–
Frontal shield length (L1)	29	321	37.3	257	390	316	240–415	337	265–378
Frontal shield length + proximal gymnocyst (L2)	29	383	49.1	314	496	388	290–485	391	306–522
Ratio L1/L2	29	0.8	–	0.8	0.9	0.8	0.6–1.0	0.8	0.6–0.9
Orifice length	12	52	6.8	43	68	–	–	–	–
Orifice width (non–ovicellated)	29	86	7.3	70	98	83	75–90	76	69–89
Aperture width (ovicellated)	16	92	4.1	86	98	91	80–97	88	83–94
Ovicell length	18	190	21.3	145	229	184	150–220	201	178–222
Ovicell width	18	221	17.3	197	260	187	160–230	208	180–228
Costae number	34	15	1.6	12	19	15	12–19	14	12–16
Spines number	27	5.6	0.4	5	6	5.0	–	6.0	–

the spine articulation. Suboral bar triangular, domed, lacking lacunae (or with a small one in the central suture), bearing two small lateral umbones, with pematidia (Fig. 3C). Fourteen to 17 pore-chambers present on the autozooids. Ovicell type A, resting on a distal autozoid, often displaced and bent to one side; as long as wide with a median suture, sometimes with a central ridge but lacking lateral tubercles; cleithral (Fig. 3B, D). Avicularia not observed. Cribrimorph kenozooids very rare (Fig. 3D). Ancestrula not observed.

Ecology and distribution

At present, *C. pseudoradiata balearica* subsp. nov. is only known from the platform/shelf edge of the Menorca Channel (Balearic Islands), from 72 to 292 m depth, on detritic bottoms, deep coralligenous and cold-water coral communities.

Remarks

The material that we describe as a new subspecies fits perfectly within the description of *Criblaria pseudoradiata*. The problem appears when assigning it to one of the two subspecies, supposedly allopatric, that these authors defined: *C. pseudoradiata pseudoradiata* (Harmelin & Aristegui, 1988), distributed in the Mediterranean, or *C. pseudoradiata canariensis* (Harmelin & Aristegui, 1988), characteristically found in the Canary Islands. After Harmelin & Aristegui (1988): “the two subspecies are quite similar, except for the shape of the frontal shield which is flatter and ornamented with peripheral tubercles in the Canarian population, and above all for the number of oral spines: five in *C. pseudoradiata pseudoradiata*, six in *C. pseudoradiata canariensis*. This character is constant throughout the available material. Although these subspecies show a great similarity in zooid size, slight

differences are also noticeable in certain morphometric characters, especially in orifice width, which is larger in the Mediterranean form, and in the extent of the autozooidal gymnocyst [see ratio L1/L2 in Table 1], which is a little greater in the Canarian colonies. The two subspecies are found in the same type of habitat: small detrital substrates from sandy bottoms of the lower circalittoral zone or the upper bathyal”.

The shape found in the Menorca Channel presents mixed characters of the two subspecies, for the number of spines (mainly five but six spines in 15% of the cases), as for the measurements that show intermediate values between those of the two variants (Table 1). The frontal shield is sometimes clearly flat, others oval and convex, and always ornamented with peripheral spiniform denticles. The gymnocyst seems slightly less developed than in the other two subspecies already described, but sometimes more developed laterally in some zooids (Fig. 3B).

The number of costae, despite being framed within the extremes defined for the two previous subspecies, seems to be greater (16 on average). The most discriminant metric character is the ovicell width, wider in the *balearica* shape (see Table 1). The ovicell has the characteristic continuous suture, often with a central ridge, without developing the lateral tubercles noted in the *canariensis* form. The mixed characters found in the form found in the Menorca Channel can be viewed in two ways (but ultimately both have the same meaning): that the differentiation of the two subspecies makes sense, or that the new form is the proof of the clinal nature of the variability in this species. The second interpretation has a geographical flaw; thus, whilst Menorca is situated in the middle of the western Mediterranean, Harmelin & Aristegui (1988) found the characteristically Mediterranean form *C. pseudoradiata pseudoradiata* up to the westernmost borders of this sea, and even on the Atlantic side of the Gibraltar Strait and on Atlantic seamounts (i.e., Josephine Seamount, see Harmelin & Aristegui 1988: fig. 17). Records from the Alboran Sea and Alboran platform could provide further insight; however, the accounts from this area (Harmelin & d’Hondt 1992; Templado *et al.* 2006; Ramalho *et al.* 2022) do not discriminate between subspecies.

Cribrilaria setiformis (Harmelin & Aristegui, 1988)

Cribrilaria setiformis alata subsp. nov.

[urn:lsid:zoobank.org:act:AF566D42-5C16-453C-934B-09D055C123C5](https://zoobank.org/urn:lsid:zoobank.org:act:AF566D42-5C16-453C-934B-09D055C123C5)

Fig. 4; Table 2

Differential diagnosis

Colony encrusting, cribrimorph. Gymnocyst well developed laterally and proximally. Frontal shield with raised laminar spiny ridges. Five spines in non-ovicellate zooids, four spines in ovicellate zooids; with basal apophyses. Avicularia with a very long and narrow rostrum placed at the outer edge of an extensive, almost quadrate, gymnocyst; rostrum serrated. Ovicell of category A, with 1–2 pairs of acute tubercles. Costate kenozooids of variable size, frequent.

Etymology

The term ‘*alata*’ refers to the winged shape formed by the spiny ridges, that protrude slightly from the frontal, like wings.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Menorca Channel; 40.85403° N, 3.542017° E; depth 74 m; 10 Apr. 2011; Indemares 4; JAGO dive, stn 100, M625, stub 709; MZB 2025-6314 (Fig. 4A, measurements).

Paratypes

MEDITERRANEAN SPAIN • 1 ovicellate colony; same collection data as for holotype; MZB 2025-6315 • 1 ovicellate colony; Cap de Formentor, Menorca Channel; 40.060051° N, 3.1574767° E; depth 82 m; 29 Jun. 2012; Indemares 6; trawling, stn 39, M659, stub 9185; MZB 2025-6316 (measurements) • 1 ovicellate colony; same data as for preceding; stub 852, MZB 2025-6317 (Fig. 4D, measurements). • 1 ovicellate colony; Menorca Channel; 40.800650° N, 3.153333° E; depth 137–190 m; 7 Apr. 2011; Indemares 4; JAGO dive, stn 90, M392; MZB 2014-1460 (Fig. 4B–C).

Description

Colony encrusting, unilaminar, of medium size (up to 100 zooids). Autozooids longer than wide. Autozooidal gymnocyst of variable extension, generally wider laterally than proximally. Frontal shield oval, flat or slightly convex, with 9–15 costae. Bases of the costae steeply raised with a tall and rounded tubercle. Costal ridge rising as 3–5 spiniform processes (Fig. 4A–B) which, when fully developed, fuse in a wing-shaped, longitudinal crest, occupying almost the entire length of costa, and decreasing gradually from the highest point at the periphery to the centre of the shield (Fig. 4A); provided with a proximally adjacent pematidium. Intercostal spaces with 3–5 reniform pores, partially filled by 1–2 acute denticles adjacent to intercostal suture. Distal setiform papillae surpassing largely the border of the autozoid (Fig. 4B). Orifice D-shaped (semicircular), wider than long, 1.2–1.4 times wider in ovicellate zooids; proximal margin straight and smooth. Five oral articulated spines, four in ovicellate zooids; provided with inwardly directed, basal apophyses. Basis of the spines (below the joint), stout, forming half a crown around the distal edge of the orifice. Suboral bar triangular and narrow, domed, with a small round lacuna in the central suture, flanked laterally by two tall, slender and sometimes acute umbones; with minute pematidium at each side of median suture (Fig. 4A). Each autozoid with 9 to 14 small circular pore-chambers (4–5 on avicularia).

Ovicell dependent on distal autozoid (type A), slightly bent to one side; as long as wide, with a median suture flanked by 1–2 acute tubercles on each side, which sometimes evolve as short ridges converging to the centre (Fig. 4A). Avicularia with a very long and narrow rostrum placed at the outer edge of an extensive, almost quadrate, gymnocyst; infrequent, located mainly on the peripheric margins of the colony and directed outwards, but also present in interzooidal grooves. Rostrum with parallel, serrated sides, truncated and curved downward at the distal end. Mandible very long and acute (almost setiform), clearly exceeding the distal tip of the palate (Fig. 4C). Kenozooids frequent, up to the size of autozooids, with cribrimorph frontal shield of 8–9 costae in radiating pattern (Fig. 4C). Ancestrula tatiform, with 11 marginal spines, and filled with a cribrimorph shield (Fig. 4D).

Ecology and distribution

Despite a large sampling effort all along the Catalan coast, *C. setiformis alata* subsp. nov. has been collected only from a few localities off the Balearic Islands. It has been found on the platform/shelf edge of the Menorca Channel, from 74 to 137 m depth, lying on detritic and deep coralligenous communities and sharing the same substrates with other cribrilininid species as *Glabrilaria corbula cyranosa* subsp. nov., *Puellina setosa* (Waters, 1899), *Cribrilaria innominata* (Couch, 1844), *Cribrilaria pseudoradiata balearica* subsp. nov. and *Cribrilaria radiata* (Moll, 1803); it was also collected once in a dark cave of the Cabrera Archipelago, at a depth of 35 m.

Remarks

Harmelin & Aristegui (1988) described *Cribrilaria setiformis* as a polytypic species with a Canarian variety (*C. setiformis* subsp. *setiformis*) which diverges by constant microanatomical characters from the Mediterranean morphotype (*C. setiformis* subsp. *romana*). Almost all the morphologic characters of the specimens described here are consistent with the common characters shared by the two subspecies

depicted in the description of *Cribrilaria setiformis*. Indeed, the form of avicularia, the number of spines, the suboral bar, the shape of ovicells, intercostal pores, kenozooids and ancestrula agree with the accurate details provided by these authors. Nevertheless, some constant differences exist which support the creation of a new subspecies.

The more striking difference concerns the shape of the frontal shield, and namely the ornamentation of the costae that, when fully developed, appear as blade or wing-shaped converging ridges; in contrast, costae of the previously known varieties are poorly ornamented by a sole row of peripheral tubercles. Other differential characters are the development of the basis of spines which form a stout half-crown in *C. setiformis alata* subsp. nov. and the presence of apophyses on the basis of oral spines (detail not mentioned in the original description). Finally, other differences are of metric nature (Table 2): even if the number of costae is similar, the frontal shield is smaller in *C. setiformis alata* than in the other two varieties; the dimorphism in the width of the aperture seems a bit higher and the size of avicularia

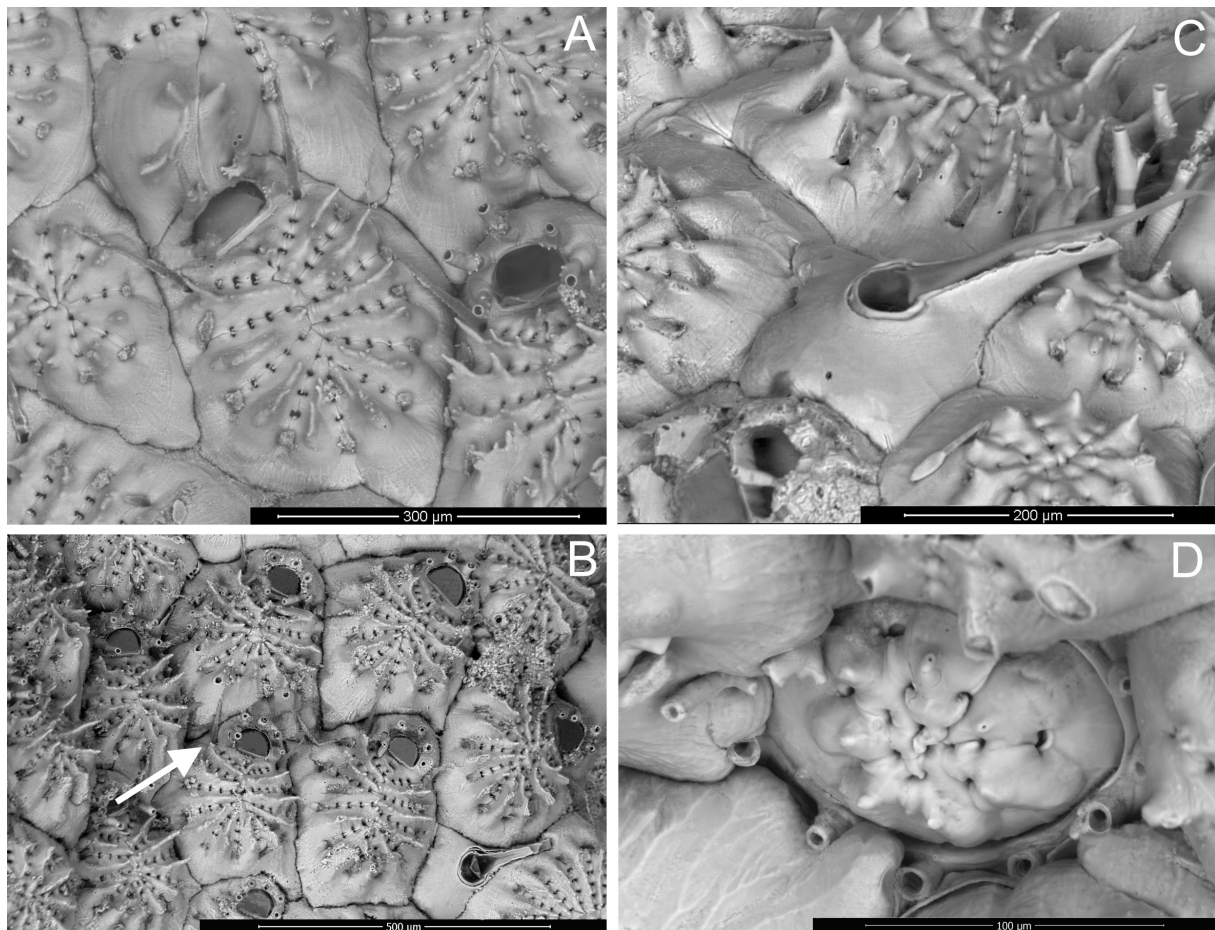


Fig. 4. *Cribrilaria setiformis alata* subsp. nov. **A.** Ovicellate and non-ovicellate autozooids. Notice the spiniform ridges on the ovicell, the basal apophyses on the basis of oral spines and the small lacuna on the center of the suboral bar (holotype MZB 2025-6314). **B.** Non-ovicellate autozooids showing the characteristic winged costal crests and the extension of the suboral papillae (white arrow) (paratype MZB 2014-1460). **C.** Avicularium showing the characteristic, almost quadrate gymnocyst, the truncated rostrum provided with serrated margins and the long mandible clearly exceeding the limit of the palate (paratype MZB 2014-1460). **D.** Ancestrula tatiform with 11 spines and filled with a cribrimorph shield (paratype MZB 2025-6317).

Table 2. Measurements (in μm) of *Cribrilaria setiformis alata* subsp. nov. (holotype MZB 2025-6314, and paratypes MZB 2025-6316, MZB 2025-6317), *C. setiformis setiformis* (Harmelin & Aristegui, 1988) and *C. setiformis romana* (Harmelin & Aristegui, 1988); measurements from Harmelin & Aristegui (1988). Abbreviations: Max = maximum; Min = minimum; N = number of measurements; SD = standard deviation.

	<i>Cribrilaria setiformis alata</i> subsp. nov.					<i>C. setiformis setiformis</i>		<i>C. setiformis romana</i>	
	N	Mean	SD	Min	Max	Mean	Range	Mean	Range
Autozoid length	62	365	50.9	209	480	–	–	–	–
Autozoid width	72	244	46.2	115	376	–	–	–	–
Frontal shield length (L1)	20	213	28.2	159	257	298	225–370	247	220–280
Frontal shield length + proximal gymnocyst (L2)	20	300	34.1	231	355	348	265–430	339	290–400
Ratio L1/L2	18	0.7	0.1	0.6	0.8	0.9	0.7–0.9	0.7	0.7–0.8
Orifice length	23	47	3.9	41	56	–	–	–	–
Orifice width (non-ovicellate)	21	73	8.4	60	91	66	60–75	82	75–90
Orifice width (ovicellate)	7	89	4.7	85	97	79	75–85	87	85–90
Avicularia length	12	312	32.2	259	362	334	225–430	392	330–485
Avicularia width	12	164	29.2	119	232	–	–	–	–
Ovicell length	8	179	6.6	168	187	187	165–200	171	150–205
Ovicell width	8	180	3.8	173	184	189	160–220	196	160–230
Costae number	32	13.4	0.8	12	15	13	11–16	14	12v17

is clearly smaller in *C. setiformis alata* subsp. nov. than in *C. setiformis setiformis* and *C. setiformis romana*. As a whole, this new subspecies approaches more the Canarian than the Mediterranean variety.

Cribrilaria setiformis alata subsp. nov. shows morphological similarities with two other species of *Cribrilaria* sharing similar geographic ranges: *C. hincksi* (Friedl, 1917), and *C. cassidainsis* Harmelin, 1984. The three species exhibit similar avicularia, with a long, narrow rostrum placed at the outer edge of a well-developed gymnocyst and share five oral spines in non-ovicellate zooids, which can be provided with basal apophyses. However, the wing-shaped expansions which ornate the costate shield of *C. setiformis alata* allow for an easy distinction of this subspecies. Furthermore, the Mediterranean specimens of *C. cassidainsis* have only two spines in ovicellate zooids, and they lack the median lacuna of the suboral bar and the avicularian rostrum is smooth. On the other hand, the rostrum of the avicularium of *C. hincksi* is also serrated but it typically rests on the frontal shield of the neighbour distal autozoid; furthermore, the ovicell lacks the paired tubercles that ornate the ovicell of *C. setiformis* and the umbones of the suboral bar are placed proximally (no level) to the suboral lacuna.

The singular shape of the frontal shield makes this subspecies near to *Glabrilaria cristata* (Harmelin, 1978), but in most other characters they differ strongly: *G. cristata* has seven oral spines in non-ovicellate zooids, has less costae in the frontal shield and shows the typical adventitious, pedunculate avicularia from *Glabrilaria* species.

Genus *Glabrilaria* Bishop & Househam, 1987
Glabrilaria corbula (Bishop & Househam, 1987)

Glabrilaria corbula cyranosa subsp. nov.

[urn:lsid:zoobank.org:act:218A1C31-42AE-4BD4-9109-871DB3B91ABB](https://zoobank.org/act:218A1C31-42AE-4BD4-9109-871DB3B91ABB)

Fig. 5; Table 3

Differential diagnosis

Colony encrusting, cribrimorph. Frontal shield round or oval and flat with 12–16 costae. Suboral bar triangular with one or two suboral lacunae. Aperture semicircular, proximal margin straight, with seven or eight long spines forming a high dense arch, ovicellate zooids with four spines. Avicularia small, typically pedunculated, rostrum serrated. Ovicell of type C with a prominent central ridge, with a down-curved tip, giving the whole a nose-like look.

Etymology

The term ‘*cyranosa*’ refers to the nose-like look given by the prominent central ridge in the ovicell.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Menorca Channel; 40.076° N, 3.637867° E; depth 292 m; 7 Apr. 2011; Indemares 4; JAGO dive, stn 70, M621, stub 9114; MZB 2016-3589 (Fig. 5B–D, measurements).

Paratype

MEDITERRANEAN SPAIN • 1 ovicellate colony; Menorca Channel; 40.09533° N, 3.655° E; depth 170 m; 9 Apr. 2011; Indemares 4; JAGO dive, stn 103, M632, stub 9181; MZB 2025-6318 (Fig. 5A).

Description

Colony encrusting, unilaminar. Autozooids round or oval, longer than wide. Gymnocyst of variable development, with lateral and proximal extensions between neighbouring zooids. Frontal shield oval and flat, moderately calcified, with 12–16 costae. Bases of the costae wide, slightly raised with a small tubercle and frequently with pematidium. Costal ridge flat, neatly fused without spiniform processes nor median thickening (Fig. 5A–B). Inter-costal spaces with 5–8 rectangular or reniform pores, partially filled by 1–2 acute denticles adjacent to intercostal suture, generally larger in first costae, and becoming smaller in proximal costae. Orifice D-shaped (semi-circular), slightly wider than long, wider in ovicellate zooids; proximal margin straight and smooth (Fig. 5B). Seven or eight oral articulated spines, four in ovicellate zooids; without basal apophyses (Fig. 5B–C). Basis of the spines (below the joint), stout, forming an arch around the distal edge of the orifice. Suboral bar triangular; with one or two rectangular lacunae in the central suture, as large as intercostal pores, sometimes with median denticle; with minute pematidium at each side in median position; without tubercles. Marginal autozooids with few circular pore-chambers (3–4). Ovicell type C (Bishop & Househam 1987), very large, longer than wide, smooth surface, with pematidia (in a more or less radiating pattern), and a nose-like central protuberance (Fig. 5A–C). Avicularia characteristically pedunculated, triangular, small, infrequent, located mainly on peripheric margins of the colony but also present in interzooidal grooves, directed outwards. Rostrum long and narrow, serrated, with tip curved upwards at the distal end (Fig. 5B, D). Avicellarium sub-conical and erect, with one pore at each side. Kenozooids and ancestrula not observed.

Ecology and distribution

Collected only from a few localities off the Balearic Islands, on the shelf edge of the Menorca Channel, from 170 to 292 m depth, on detritic bottoms. Found mixed with a plethora of other cribrimorph species like *Glabrilaria orientalis lusitanica* (Harmelin, 1988), *Glabrilaria pedunculata* (Gautier, 1956), *Cribrilaria innominata* (Couch, 1844), *Cribrilaria radiata* (Moll, 1803), and *Cribrilaria pseudoradiata balearica* subsp. nov.

Remarks

Glabrilaria corbula cyranosa subsp. nov. closely resembles the Atlantic, nominal material of *G. corbula* (Bishop & Househam, 1987) but differs in some key characters significantly enough to differentiate it as a new subspecies. In *G. corbula cyranosa* the number of costae is higher (12–16) and the number of spines

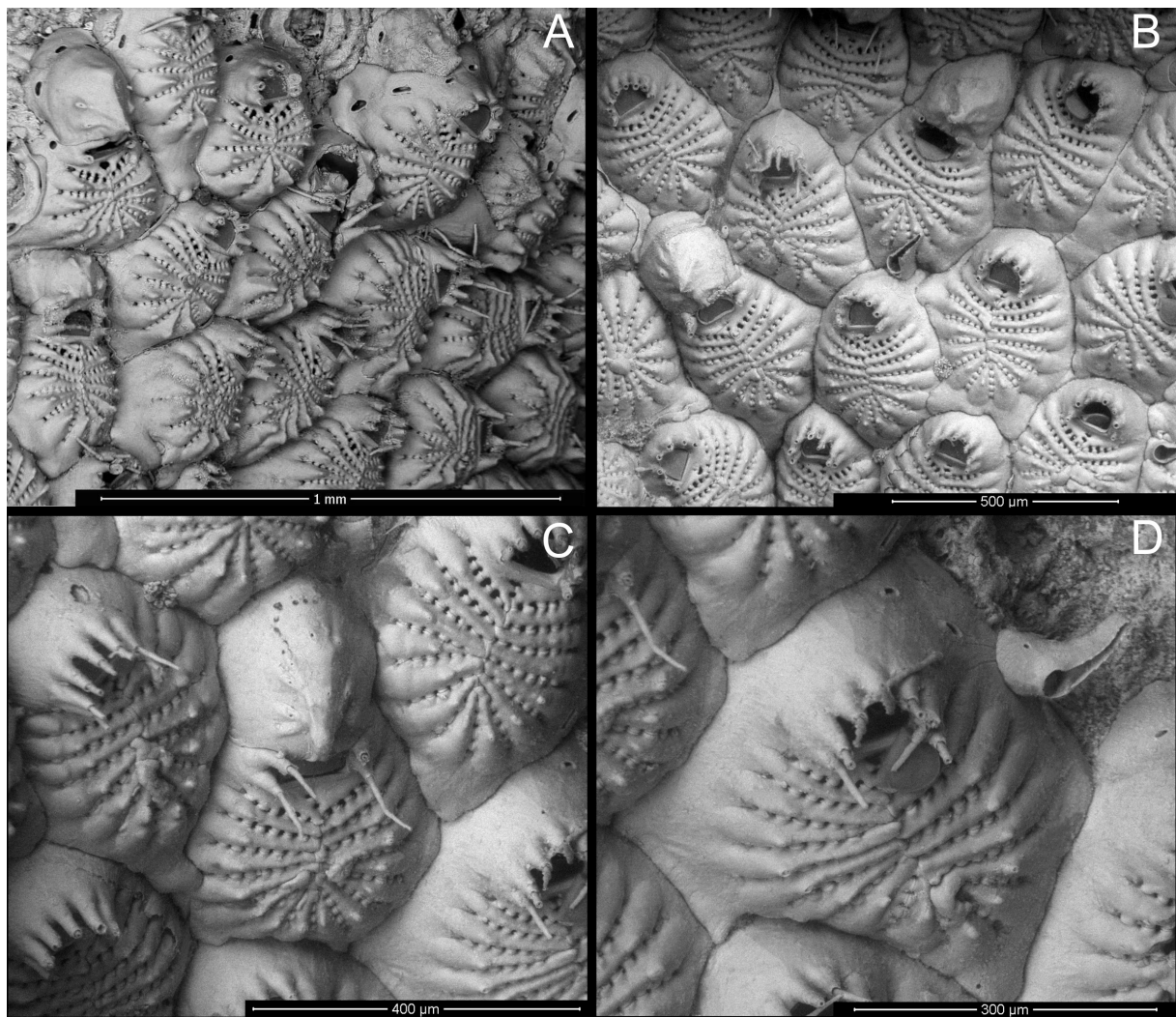


Fig. 5. *Glabrilaria corbula cyranosa* subsp. nov. **A.** Colony view (paratype MZB 2025-6318). **B.** Non-ovicellate and ovicellate autozooids: notice the flat frontal shield, the stout arch formed by the basis of oral spines around the distal edge; some non-ovicellate autozooids exhibit eight spines (holotype MZB 2016-3589). **C.** Ovicell with the characteristic nose-like central protuberance (holotype MZB 2016-3589). **D.** Pedunculated avicularium growing from a marginal pore of an autozooid. Notice that it is much longer than high (holotype MZB 2016-3589).

Table 3. Measurements (in μm) of *Glabrilaria corbula cyranosa* subsp. nov., holotype MZB 2016-3589. Measurements for *G. corbula* (Bishop & Househam, 1987) in different depths and localities from Harmelin & Aristegui (1988). Abbreviations: Max = maximum; Min = minimum; N = number of measurements; SD = standard deviation.

	N	<i>Glabrilaria corbula cyranosa</i> subsp. nov.				<i>G. corbula</i> Superficial Mediterranean			<i>G. corbula</i> Upper bathyal Mediterranean			<i>G. corbula</i> Ibero-Maroccan Bay			<i>G. corbula</i> (Bishop & Househam, 1987)		
		Mean	SD	Max	Min	Mean	Range	Mean	Mean	Range	Mean	Mean	Range	Mean	Range	Mean	Range
Autozooid length	19	395	39.6	461	309	–	–	–	–	–	–	–	–	–	–	–	–
Autozooid width	30	292	53.8	475	205	–	–	–	–	–	–	–	–	–	–	–	–
Frontal shield length (L1)	7	247	10.2	255	229	226	180–280	242	195–270	248	220–300	232	198–270				
Frontal shield length + proximal gymnocyst (L2)	7	299	20.3	320	266	275	230–380	302	235–365	300	255–365	304	245v450				
Ratio L1/L2	7	0.8	0.05	0.9	0.8	0.8	0.7–0.9	0.8	0.7–0.9	0.8	0.7–0.9	0.8	0.6v0.8				
Orifice length	2	50	5.7	54	46	–	–	–	–	–	–	60	–69				
Orifice width (non-ovicellate)	26	73	7.6	93	58	67	58–75	68	62–75	67	60–70	66	57–80				
Orifice width (ovicellate)	7	85	7.8	97	76	79	65–90	85	78–90	82	75–90	80	69–89				
Avicularia length	7	107	10.9	119	92	–	–	–	–	–	–	149	–				
Ovicell length	8	215	10.9	228	199	177	170–215	172	160–195	169	160–195	161	145–182				
Ovicell width	8	183	15.3	204	159	–	–	–	–	–	–	198	182–222				
Costae number	24	14.9	0.7	16	14	12.8	10–15	12.5	11–16	12.8	10–14	–	–				
Pores number	53	6.8	0.8	8	5	–	–	–	–	–	–	–	–				
Spines number	21	7.3	0.5	8	7	–	–	–	–	–	–	–	–				

is variable (7–8), whereas in *G. corbula* the number of costae is 9–14 (usually 10–12) and the number of spines is always seven. The avicularial rostrum of *G. corbula cyranosa* is finely serrated whereas the avicularium of *G. corbula* has a completely smooth rostral border. Finally, the most conspicuous difference is the shape of ovicells: in *G. corbula* the ovicell is as wide or slightly wider than long and has 4–6 low ridges in a more or less radiating pattern whereas in *G. corbula cyranosa* the ovicell is clearly longer than wide, lacks lateral ridges, and develops a large median ridge provided with a pointed protuberance, curving down like a long nose (Fig. 5C).

Glabrilaria corbula cyranosa subsp. nov. differs from *G. orientalis lusitanica* (Harmelin, 1988) in several significant characters. Even if the number of spines is also (but always) seven, *G. orientalis lusitanica* has a smooth, imperforate suboral bar and two kinds of dimorphic avicularia: the long pedunculated type, scattered among the autozooids and much higher than long, and a sessile adventitious avicularium (often a pair) placed at each side of an ovicell of type B (with an associate distal kenozooid).

Glabrilaria pedunculata, another similar Mediterranean species of *Glabrilaria*, has a more elongate and bulging frontal shield provided with 10–14 costae and displays a lower number of spines (six). Furthermore, the pedunculate avicularia have a much elongate basis so that it is much higher than long, whereas in *G. corbula cyranosa* subsp. nov. the avicularium is always much longer than high. Finally, the ovicell can be of type B (with an associated distal kenozooid), whereas in *G. corbula cyranosa* is always of type C.

At first glance, one might think of *G. corbula cyranosa* subsp. nov. as the Mediterranean variety of *G. corbula*, as it occurs with other pairs of recently distinguished species (i.e., *Crassimarginatella matildae* Pica & Berning, 2022 vs *Crassimarginatella crassimarginata* (Hincks, 1880) or *Schizomavella* (*Schizomavella*) *biancae* Pica & Berning, 2022 vs *Schizomavella* (*Schizomavella*) *discoidea* (Busk, 1859) (Pica *et al.* 2022); or as a clinal trend of variation from the Atlantic to the Mediterranean as has been signalized for *Cribrilaria setiformis setiformis* vs *Cribrilaria setiformis romana* (Harmelin & Aristegui 1988) or for *Cribrilaria pseudoradiata canariensis* vs *C. pseudoradiata pseudoradiata* (Harmelin & Aristegui 1988) (with the addition of a new variety in this paper; see above). Nevertheless, although a long list of previous signalizations of *G. corbula* in the Mediterranean exists (Harmelin & Aristegui 1988), these specimens show intermediate metric characteristics between those of the Atlantic type and the *cyranosa* variety described here (Table 3) and none shows the differential characters depicted above.

Superfamily Smittinoidea Levinsen, 1909

Family Bitectiporidae MacGillivray, 1895

Genus *Schizomavella* Canu & Bassler, 1917

Subgenus *Schizomavella* (*Schizomavella*) Canu & Bassler, 1917

***Schizomavella* (*Schizomavella*) *harmelini* sp. nov.**

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Figs 6A–E, 7A; Table 4

Schizomavella hastata – Gautier 1962: 149. – Zabala 1986: 471, fig. 160, pl. 13a–b. — Zabala & Maluquer 1988: 132, fig. 305, pl. 17e–f. — López de la Cuadra 1991: pl. 26 fig. f. — Novosel 2007: 64, fig. 28a, d.

? *Schizomavella linearis hastiformis* morphotype – Reverter-Gil *et al.* 2015: fig. 11c–e, table 9.

Non *Schizomavella hastiformis* – Hayward & Ryland 1978: 152, fig. 5c–d.

Non *Schizomavella hastata* – Hayward & Thorpe 1995: 668, pl. III. — Hayward & Ryland 1999: 284, figs 129, 130a–b.

Differential diagnosis

Primary orifice rounded or trapezoidal, slightly wider than long, its greatest width across the distal quarter; sinus shallow and large, occupying almost half of the proximal border; condyles smooth and narrow, almost flat or gently dropping to the edges of the sinus. Orifice surrounded by an even rim, describing two pronounced notches in the proximolateral corners. Three (sometimes two or four) long, stout, hollow oral spines. A single suboral avicularium on a large, conical, tuberculate or spinose umbo, upright directed (= orthogonal to the zooidal plane), proximo-lateral to the sinus, finely serrated on the borders (SEM). Ovicell acleithral with spinose processes developed by secondary calcification leaving a porous ectooecial surface, longer than wide, with up to 40 tear-shaped uneven pseudopores grouped at the two lateral margins. Ancestrula tatiform with eight spines.

Etymology

Named in honour of Prof. Jean-Georges Harmelin, the most prominent bryozoologist of the last half century contributing to the knowledge of Mediterranean species.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Pta Salines, Montgri; 42.06119° N, 3.21475° E; depth 28 m; 12 Jun. 2015; scuba dive, M433, R147; Mikel Zabala leg.; MZB 2015-8350 (Fig. 6A–D, measurements).

Paratypes

MEDITERRANEAN SPAIN • 1 ovicellate colony; La Vaca, Medes Islands; 42.0482° N, 3.226° E; depth 20 m; 10 Jul. 2019; scuba dive, M583, stub 662; Mikel Zabala leg.; MZB 2025-6320 (Fig. 6E) • 1 ovicellate colony; Pollença Bay, Mallorca Island; 39.95735° N, 3.2139° E; depth 40 m; CARBAL; scuba dive, M701, stub 848; MZB 2025-6321 (measurements) • 16 ovicellate colonies; same data as for preceding; MZB 2025-6322.

Other material

MEDITERRANEAN CORSICA • 3 ovicellate colonies; Sec a Giraglia, Cap Corse; 43.02784° N, 9.40314° E; depth 17 m; 14 Jun. 2018; scuba dive; M539, R256; Mikel Zabala leg.; MZB 2025-6325.

MEDITERRANEAN SPAIN • 5 ovicellate colonies; Colonia de Sant Jordi, Mallorca Island; 39.30843° N, 2.90877° E; depth 35 m; 17 Jul. 1985; scuba dive; M702; Mikel Zabala leg.; MZB 2025-6323 • 5 ovicellate colonies; Roca Retja, Medes Islands; 42.0424° N, 3.22963° E; depth 54 m; 4 Sep. 2018; scuba dive; M543, R265; Mikel Zabala leg.; MZB 2025-6324 • 2 colonies; Cap de Creus; 42.36° N, 3.3269444° E; depth 139 m; 23 Sep. 2009; Indemares 1; Draga Rauschert, stn 12, M357; MZB 2014-1525 • 1 colony; same data as for preceding; MZB 2015-8265.

Description

Colony encrusting, unilaminar, yellow-orange when alive; initially growing in regular radial series but soon developing as irregular, spiky crusts (Fig. 6A). Autozooids rectangular to polygonal, often wider than long, separated by fine, raised sutures. Frontal shield extremely nodular, with large rounded pores (especially large at the areolar borders); completely dominated by a strong, suboral umbo that is variable in length but on average almost as long as the autozooid; the rugosity of this umbo is variable but often covered by spiny, sometimes bi-forked processes (Fig. 6B).

Primary orifice rounded to faintly trapezoidal, slightly wider than long with its greatest width across the distal quarter; sinus shallow and wide, occupying almost more than two thirds of the proximal margin; condyles smooth, dropping to the edges of the sinus (Fig. 6C). Orifice surrounded by a fine, smooth

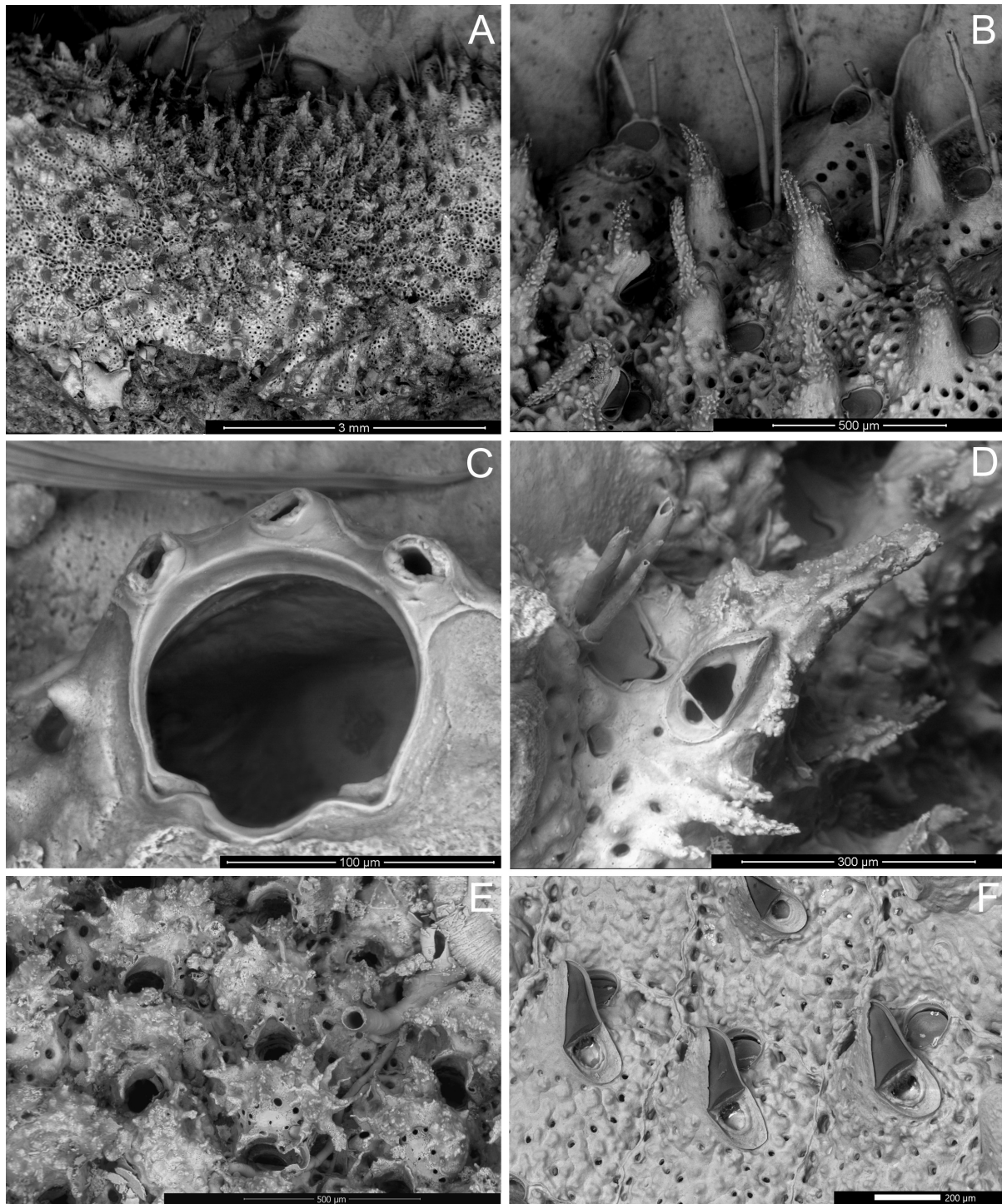


Fig. 6. A–E. *Schizomavella (Schizomavella) harmelini* sp. nov. A. Hirsute shape of a unbroken colony (holotype MCNB-MZB 2015-8350). B. Autozooidal frontal shield with spiny umbos (holotype MCNB-MZB 2015-8350). C. Primary orifice with shallow sinus and smooth condyles (holotype MCNB-MZB 2015-8350). D. Avicularia leaning on the middle section of a raised umbo; notice the serrated margins of rostrum (holotype MZB 2015-8350). E. Ovicells enveloped by a nodular ooecial cover formed by spiniform processes (paratype, MZB 2025-6320). F. *S. (S.) hastiformis* Hayward & Ryland, 1978. Avicularia placed at the basis of raised umbos (holotype, NHMUK1977.5.2.1, Bay of Biscay, 46.8750° N, 5.133333° W).

rim, more developed around the sinus. Two to four (usually three) long, stout, deciduous oral spines, the bases still visible at the proximal margin of the ovicells. A large monomorphic avicularium, resting on a raised umbo (in fact avicellarium) placed laterally to the sinus and directed upright; with a wide opesia surrounded by a large smooth rim and a slender crossbar, lacking columella; palate triangular with finely serrated margins (Fig. 6D).

Ovicell acleithral, recumbent on succeeding zooid, almost as long as wide, enveloped by a coarsely nodular ooecial cover provided with several spiniform processes and sometimes a tall conical umbo, leaving a porous ectooecial area with characteristic shape (Fig. 6E). It is perforated with up to 40 asymmetrical circular to tear-shaped pores concentrated at latero-distal margins and leaving an almost imperforate central area where two keels converge from the latero-distal margins of the orifice to the center of the ovicell (Fig. 7A).

Ecology and distribution

We have collected *Schizomavella* (*Schizomavella*) *harmelini* sp. nov. 35 times in up to 17 different localities from Cap de Creus (North) to Columbretes Islands (South) and the Balearic Islands (East). Depths ranged from 10 to 150 m, lacking a clear modal value. It has been collected primarily from

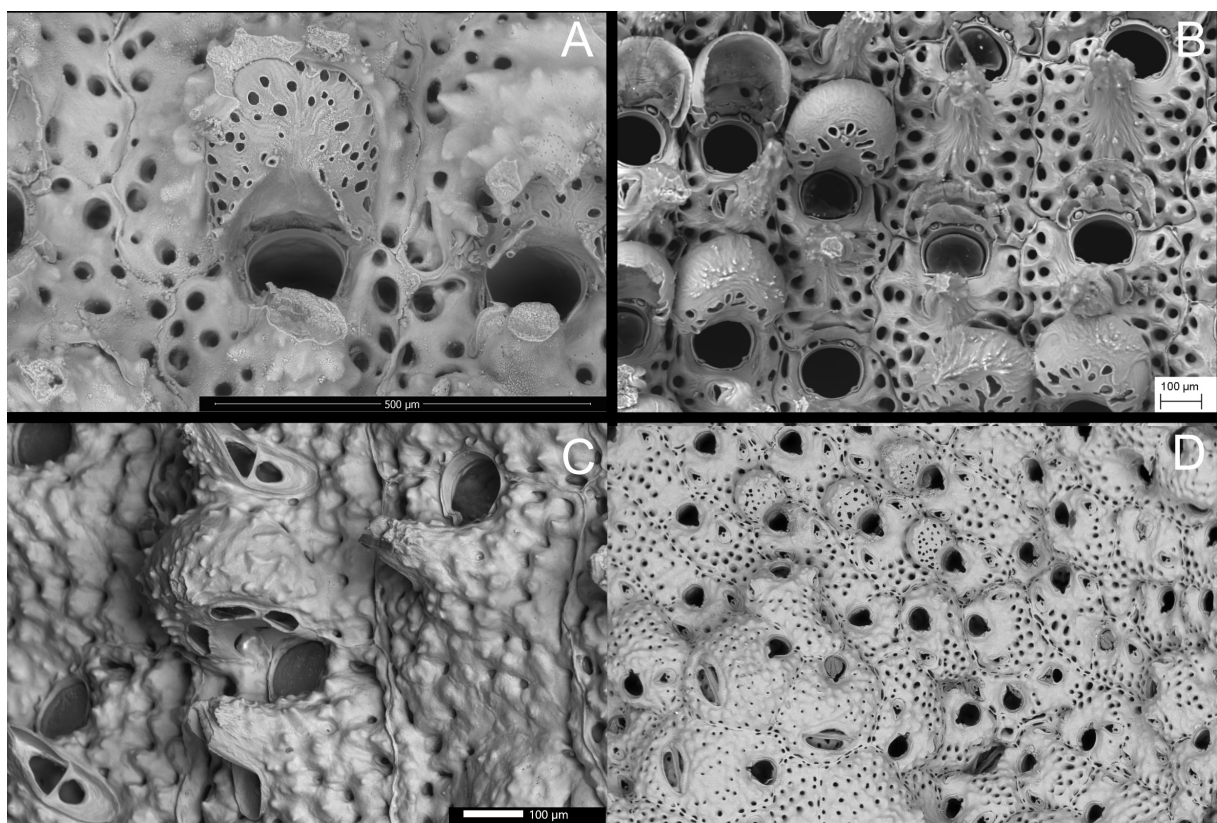


Fig. 7. Comparative view of ovicells from the four discussed species. **A.** *Schizomavella* (*Schizomavella*) *harmelini* sp. nov. The ectooecial punctured area when the spinous secondary cover has been removed; notice the numerous tear-shaped pores and the two converging keels (paratype MZB 2025-6321). **B.** *S. (S.) hastata* (Hincks, 1862) (Óscar Reverter-Gil coll, Atlantic Spain). **C.** *S. (S.) hastiformis* Hayward & Ryland, 1978, holotype NHMUK1977.5.2.1, Bay of Biscay, 46.8750° N, 5.133333° W. **D.** *S. (S.) linearis* f. *typica* (Hassall, 1841). Notice the orifice shape, much longer than wide, the narrow deep sinus and the dimorphic avicularia (MZB 2025-6339).

Table 4. Measurements (in μm) of *Schizomavella* (*Schizomavella*) *harmelini* sp. nov., holotype MCNB-MZB 2015-8350 and paratype MZB 2025-6321. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	26	459	42.9	396	544
Autozoid width	35	357	46.2	299	461
Orifice length	24	113	6.5	105	128
Orifice width	29	124	13.2	104	158
Sinus length	3	22	1.0	21	23
Sinus width	4	55	2.0	53	57
Avicularia length	14	142	24.1	110	187
Avicularia width	19	72	8.1	57	82
Umbo height	13	417	55.5	317	496
Ovicell length	27	293	42.4	227	377
Ovicell width	34	302	39.6	222	372
Spines number	11	2.3	0.4	2	3

coralligenous communities ($n = 12$) but also from semidark caves ($n = 7$), dark caves ($n = 3$), maerl beds ($n = 3$), detritic bottoms ($n = 2$), sciaphilic algae ($n = 4$), photophilic algae ($n = 1$) and also encrusting experimental panels ($n = 3$); we never collected this species from *Posidonia* beds or harbors. If older Mediterranean reports of “*Schizomavella hastata*” (Hincks, 1862) and modern Mediterranean references of “*Schizomavella linearis f. hastiformis*” Hayward & Ryland, 1978 represent *S. (S.) harmelini*, this species is known throughout the central and western Mediterranean from the Adriatic Sea (Hvar Island) to the Strait of Gibraltar (La Atunara). If *S. (S.) hastiformis* from the Bay of Biscay (Hayward & Ryland 1978) proves to be an originally different species, its distribution range seems limited to the Eastern Atlantic coasts, and its presence in the Mediterranean appears unlikely.

Remarks

Schizomavella (*Schizomavella*) *harmelini* sp. nov. is, in fact, a well-known species to Mediterranean bryozoologists who used to report it as “*Schizomavella hastata*” (Waters 1879; Gautier 1962; Harmelin 1976; Zabala 1986; Zabala & Maluquer 1988; López de la Cuadra 1991).

Schizomavella (*S.*) *harmelini* sp. nov. vs *Schizomavella* (*S.*) *hastata* (Hincks, 1862)

However, after the true identity of *S. (S.) hastata* (Hincks, 1862) was clarified by Hayward & Thorpe (1995), it became clear that most (if not all) of the Mediterranean material previously assigned to “*S. hastata*” corresponds to another species.

Schizomavella (*S.*) *hastata* differs from *S. (S.) harmelini* sp. nov. in the primary orifice form. The former has no true sinus but a gentle concavity occupying the entire proximal margin between two very small condyles (Fig. 7B); in contrast, the primary orifice of *S. (S.) harmelini* shows a shallow but conspicuous sinus occupying no more than half the proximal margin, and is framed by two large and flat condyles (Fig. 6C). As suggested by Reverter-Gil *et al.* (2015): “... all ancient records of “*Schizomavella hastata*” in the Mediterranean needed a whole reassessment with reference to their original material to ascertain its true distribution.”.

***Schizomavella* (S.) *harmelini* sp. nov. vs *Schizomavella hastiformis* Hayward & Ryland, 1978**

Hayward & Ryland (1978) described a new species of *Schizomavella* from the Atlantic coasts of the Bay of Biscay that they named *S. hastiformis* after its similarity to *S. hastata*. They based the distinction between the two species in the orifice shape and sinus. Afterwards, Hayward & Thorpe (1995) reassigned *S. hastiformis* to *Schizomavella linearis* arguing a strong similarity in the form of the orifice; thus, they simply created a new morphotype: *S. linearis* f. *hastiformis* (see Hayward & Ryland 1999). By assuming the identity with the morphotype of Hayward & Ryland and following their same criterion, most recent bryozoologists assigned the material pertaining to “*Schizomavella hastata*” from previous Mediterranean authors to *S. (S.) linearis* f. *hastiformis* (Chimenz Gusso *et al.* 2014; Reverter-Gil *et al.* 2015; Rosso *et al.* 2016). Nevertheless, the identity between the Atlantic *S. hastiformis* and the material named “*Schizomavella hastata*” by earlier Mediterranean bryozoologists or *S. (S.) linearis* f. *hastiformis* by modern authors was unclear; actually, we can show that it was incorrect. Indeed, the ovicell of *S. hastiformis* (Fig. 7C) is very different from the ovicell we described here, as it exhibits a short (wider than long) ectoocelial porous area with few (3–4) and very large, irregular pores. Unfortunately, Reverter-Gil *et al.* (2015) did not provide descriptive details or illustrate the ovicell of their Mediterranean specimens of *S. (S.) linearis* f. *hastiformis*; nevertheless, the biometric details they provide agree completely with those of the ovicell of *S. (S.) harmelini* sp. nov. (Reverter-Gil *et al.* 2015: table 8). Besides the ovicell, other characters help to discriminate between both species. The suboral umbo of *S. (S.) harmelini* is long (it greatly exceeds the tip of the avicularium resting on it) and extremely acute; in contrast, the suboral umbo of *S. hastiformis* is stout, blunt, and only slightly exceeds the tip of the avicularium (Fig. 6F). Both species have a rough frontal wall, but while it is simply nodular in *S. hastiformis* (Fig. 7C), in *S. (S.) harmelini* it appears deeply spiky (Fig. 6B, D).

***Schizomavella hastiformis* Hayward & Ryland, 1978 vs *Schizomavella linearis* (Hassall, 1841)**

On the other hand, we disagree with the decision of Hayward & Thorpe (1995), which most modern authors follow (Hayward & Ryland 1998; Reverter-Gil *et al.* 2015) to arrange the *S. hastiformis* as a morphotype of *S. (S.) linearis*. In Hayward and Thorpe’s opinion (1995: 672): “Comparison of the type material of *S. hastiformis* with a wide selection of specimens of *S. linearis* demonstrates that they are the same species, and accordingly *S. hastiformis* Hayward and Ryland may be put into the synonymy of *S. linearis* (Hassall)”. In support of this decision, they state that: “The polymorphism of the avicularia seen in *S. linearis* may be expressed within a single colony, and is perhaps responsible for much of the taxonomic confusion surrounding this species. Paired avicularia may be equal or unequal in size: single avicularia may be small, or may have successively larger cystids through several astogenetic generations, and eventually assume the ‘*hastata*-like’ morphology, with the cystid prolonged apically as a stout spike”.

It seems even more surprising that after hard work demonstrating the usefulness of the smallest apertural details for clear discrimination among the species of *Schizomavella* (see Reverter-Gil & Fernández-Pulpeiro 1996, 1997), Reverter-Gil *et al.* (2015) consider the orifices of their Mediterranean *S. (S.) linearis* f. *hastiformis* (probably *S. (S.) harmelini* sp. nov.) a mere variety of the orifices of *S. (S.) linearis*. In fact, the orifice of *S. (S.) linearis* f. *typica* is longer than wide (even if barely), with a proximal margin much shorter than the distal margin, and with two proximo-lateral notches and a narrow (less than one-third of the proximal margin) and deep sinus (ratio width/length sinus ca 1.5) that made it almost drop-shaped (Fig. 7D). In contrast, the orifices of both “*S. hastiformis*” and *S. (S.) harmelini* are always wider than long (even if vaguely), with a proximal margin almost as wide as the distal one; the sinus is much larger (about half of the proximal margin) and shallower (ratio width/length sinus ca 3). Furthermore, as noted by Gautier (1962), the similarities of “*S. hastata*” (= *S. (S.) harmelini*) with *S. (S.) linearis* are only apparent: not only is the orifice very different, but the operculum is also of a different kind, i.e., it is distally demarcated by a wide sclerite and it has two muscular insertion points.

In our opinion, the characters that best define *S. (S.) linearis* are the dimorphic avicularia, both the crescentic single avicularium and the small, usually paired avicularia placed at both sides of the orifice. Both types of avicularia never lack in the actual forms of *S. linearis*, i.e., *S. (S.) linearis* f. *profunda* Harmelin & d'Hondt, 1992, *S. (S.) linearis* f. *cruciformis* (Norman, 1862), or *S. (S.) linearis* f. *pseudolinearis* Reverter-Gil *et al.*, 2015. In contrast, neither the crescentic single avicularium nor the small paired avicularia have ever been found in *S. hastiformis* nor in the Mediterranean material previously assigned to “*S. hastata*” or later to *S. (S.) linearis* f. *hastiformis*. Furthermore, the large monomorphic avicularium nested in the stout umbo is a constant character that clearly discriminates both *S. hastiformis* and *S. (S.) harmelini* sp. nov. from all varieties of *S. (S.) linearis*.

In summary, we advocate for the recognition of *S. hastiformis* Hayward & Ryland, 1978 as a distinct species that needs to be restored as *S. (S.) hastiformis* Hayward & Ryland, 1978.

Schizomavella (S.) harmelini sp. nov. is close to a fourth species, *S. (S.) gautieri* Reverter-Gil & Fernández-Pulpeiro, 1997, a rarely reported Mediterranean species that also presents a stout umbo housing an upright directed avicularium. However, *S. (S.) gautieri* has an almost quadrate orifice provided with only two spines and framed by an upraised rim forming a peristome. Furthermore, the avicularian palate has rounded tips and lacks serrated margins. Finally, the ovicellar secondary thickening produces a conical umbo, but never shows the nodular processes of *S. (S.) harmelini*; in addition, the porous ectooecial area is much shorter, triangular in shape and has a smaller number of pores.

Superfamily Lepralielloidea Vigneaux, 1949
Family Bryocryptellidae Vigneaux, 1949
Genus *Palmiskenea* Bishop & Hayward, 1989

***Palmiskenea diazi* sp. nov.**

[urn:lsid:zoobank.org:act:388D2894-5F99-434D-9327-06218C81DEB6](https://zoobank.org/act:388D2894-5F99-434D-9327-06218C81DEB6)

Fig. 8A–E; Table 5

Palmicellaria aff. *aviculifera* – Gautier 1962: 201, fig. 18. — Harmelin 1969: 297, fig. 5, 2–3. — Zabala 1986: 410, fig. 136, pl. 6d–f. — Zabala & Maluquer 1988: 118, figs 250–251, pl. 9e.

Palmiskenea gautieri (part.) – Madurell *et al.* 2013: 125, fig. 1a.

Differential diagnosis

Colony encrusting, unilaminar, growing in a ribbon-like mode, zooids hexagonal, large, provided with a tricuspidate peristome logging 3–5 oval avicularia. Frontal shield finely granulose, with big marginal pores. Ovicellate zooids with an almost cylindrical, slender peristome. Ovicell sub-globose, smooth with many (more than 20) small, scattered, round pores.

Etymology

This species is named after Dr David Díaz, friend and colleague, in recognition of his significant contribution to the collection of this and other species of bryozoans.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Roca Retja, Medes Islands; 42.042396° N, 3.229628° E; depth 54 m; 4 Sep. 2018; *Puerulus*; scuba dive, M543, R269, stub 9149; MZB 2025-6326 (Fig. 8A, D, measurements).

Paratypes

MEDITERRANEAN SPAIN • 3 ovicellate colonies; Pedra de Deu, Medes Islands; 42.050127° N, 3.224673° E; depth 42 m; 4 Sep. 2019; *Puerulus*; scuba dive, M586, stub 9191; MZB 2025-6327 (Fig. 8B, measurements) • 1 ovicellate colony; same data as for holotype; stub 9134; MZB 2025-6328 (Fig. 8C, measurements) • 2 dead colonies; Cap Formentor, Menorca Channel; 40.020402° N, 3.15742° E; depth 82 m; 29 Jun. 2012; Indemares; Rauschert sled, stn 39, M659; MZB 2025-6329 • 1 live colony; Illa Messina, Cap de Creus; 42.2881351° N, 3.3106734° E; depth 50 m; 13 Jul. 2022; scuba diving, M682; Mikel Zabala leg.; MZB 2025-6330.

Description

Colony encrusting, unilaminar, growing in a ribbon-like mode (Fig. 8A), with lobes composed of 4–10 zooids per series, grey-brownish when alive. Zooids hexagonal, large (630–800 µm long; 490–630 µm wide) (Fig. 8B). Frontal shield convex, strongly calcified, finely granulose (at SEM), imperforate except for a row of 14–17 big marginal pores (Fig. 8B). Primary orifice hidden by the peristome, orbicular, slightly longer than wide (240–265 µm long, 235–255 µm wide); proximal margin concave, with inconspicuous condyles and lacking lyrula (Fig. 8C). Peristome in the non-ovicellate autozooids stout, with three umbos, one medio-proximal and two in lateral position, each provided with a small avicularium, placed at the basis of the internal side of the umbo, orthogonal to the plane of the orifice (Fig. 8B); rostrum widely oval, with a complete cross-bar and the disto-lateral margin rimed by a ‘crown’ of denticles (Fig. 8D). Peristome of ovicellate zooids raised as a fine cylindrical tube; provided with 3–5 avicularia of the same shape and size, lodged within secondary orifice, on prominent cystids (Fig. 8D). Ovicell sub-globose (disto-proximally compressed), not closed by autozooids operculum (acleithral), opening to the peristome; surface smooth with up to 30 small, uniformly scattered, round pores (Fig. 8D). Ancestrula unknown.

Ecology and distribution

Palmiskenea diazi sp. nov. is a sciaphilic species dwelling in two different habitats. The shallower samples (27–53 m) came from undersides of hard substrates like small rocks accumulated at the base of coralligenous cliffs. On two occasions these small rocks were collected at the floor of dark caves. The second habitat is represented by the undersides of calcareous algae on deep coralligenous outcrops, where Harmelin (1968) collected the species between 100–128 m deep. This is the same habitat where the submersible JAGO collected this species in the Menorca Channel, between 80 and 130 m deep. It was also collected by JAGO on detritic bottoms near the Cap de Creus Canyon at a depth of 106 m.

At present, the geographical range of *Palmiskenea diazi* sp. nov. seems to expand all around the Mediterranean. Harmelin (1968) found it in the Eastern Mediterranean (Santorini), and also in Port-Cros and the Marseille region. Gautier reported *Palmicellaria* aff. *aviculifera* in Alboran; however, we do not know whether it was the encrusting form (*diazi*) or the erect form (*gautieri*), the latter has been found in the area by other authors (Ramalho *et al.* 2020, 2022). In our collections, most specimens came from the northern part of the Catalan coast (Cap of Creus and Costa Brava area, i.e., Medes Islands, Montgrí and Cap Begur) but it is also present in the Balearic Islands. Despite a deep sampling effort, we failed to find it in the Columbretes Islands area.

Remarks

Palmiskenea diazi sp. nov. is not totally new to Mediterranean bryozoologists. Gautier described (and unusually illustrated) an intriguing species from the coasts of Marseille, Hyères and Alboran under the name *Palmicellaria* aff. *aviculifera* Canu & Bassler, 1928 (Gautier 1962: 202, fig.18) because of the extreme similarity with the western Atlantic species “*Palmicellaria*” *aviculifera* described by Canu & Bassler from the Gulf of Mexico (Canu & Bassler 1928) whose type species (labeled “Albatross

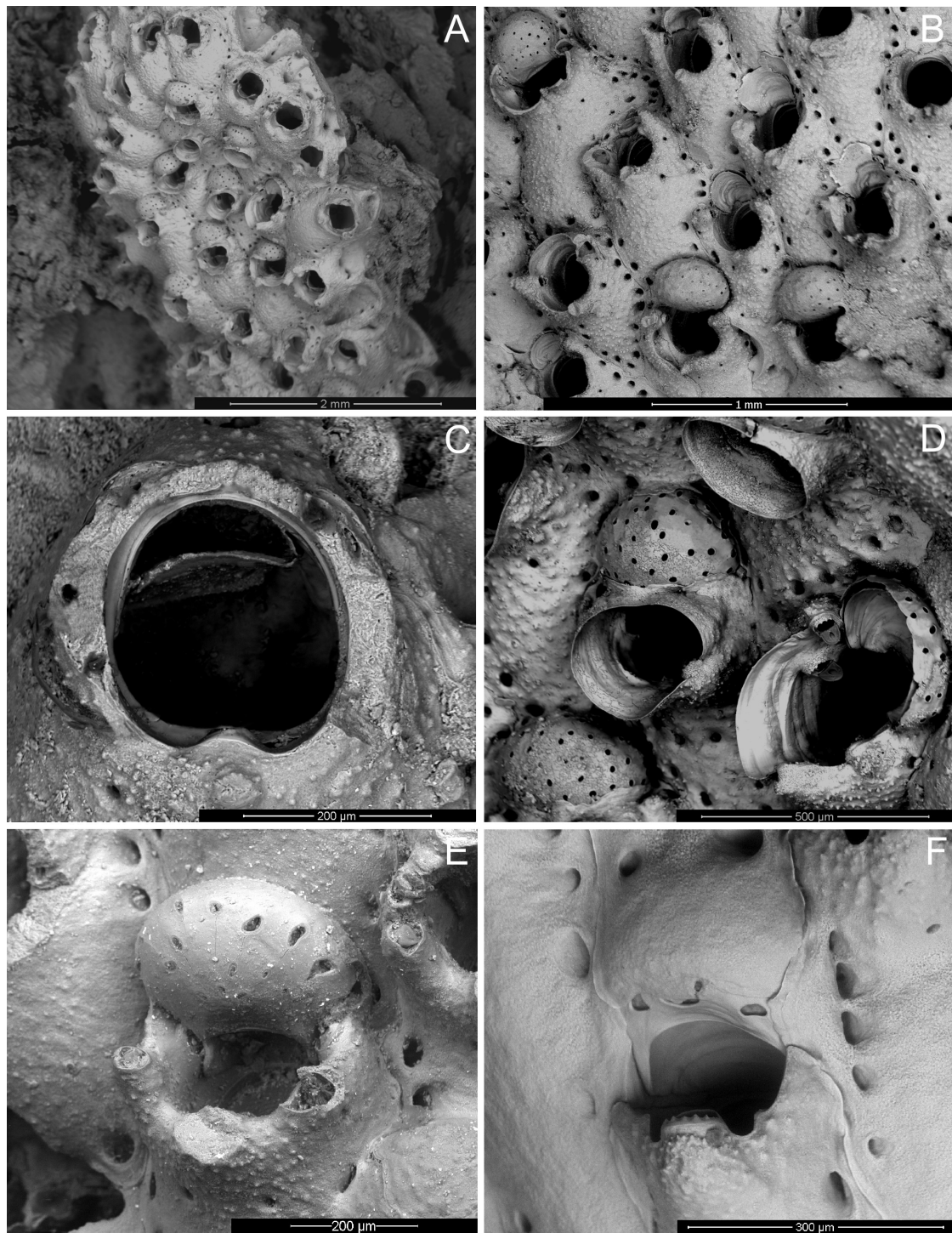


Fig. 8. A–E. *Palmiskenea diazi* sp. nov. A. Colony view (holotype MZB 2025-6326). B. Ovicellated and non-ovicellated zooids (paratype MZB 2025-6327). C. Primary orifice (paratype MZB 2025-6328). D. Cylindrical peristome of ovicellate zooids; notice the numerous ovicellar pores and the adventitious avicularia on the inner margins of peristome (holotype MZB 2025-6326). E. *Palmicellaria aviculifera* (Canu & Bassler, 1928), ovicellate zooid with low peristome and rough rim (lectotype USNM RB 7565, Bahama Islands; 23°34'30" N, 76°34'00" W). F. *Palmiskenea gautieri* Madurell, Zabala, Gili & Dominguez, 2013, ovicellate autozooids; notice the presence of two sole pores (holotype MZB 2013-0072, Cap de Creus, Mediterranean).

Table 5. Measurements (in μm) of *Palmiskeneia diazi* sp. nov., holotype MZB 2025-6326, and paratypes MZB 2025-6328, MZB 2025-6327. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	23	855	119.0	630	1087
Autozoid width	23	551	107.4	362	927
Primary orifice length	3	257	14.0	241	267
Primary orifice width	3	245	9.2	235	253
Secondary orifice length	22	302	28.2	251	364
Secondary orifice width	23	285	26.9	239	348
Ovicellate peristome width	4	257	16.5	238	278
Avicularia length	10	66	7.7	53	78
Avicularia width	22	56	7.4	43	72
Ovicell length	19	228	32.8	185	318
Ovicell width	15	350	29.6	308	409
Ovicell pores number	13	26.8	5.0	21	37

st. D 2650 Bahamas-Cuba 32-3-7-59”) he was able to examine. More recently, bryozoologists who have collected this species in the Western Mediterranean (i.e., Harmelin 1969; Zabala 1986; Zabala & Maluquer 1988) kept the same name without addressing the discussion of its precise status.

To our knowledge, the true “*Palmicellaria*” *aviculifera*, Canu & Bassler (1928) has never been reported again. We could not physically access the type specimen but could compare the SEM images of the type material deposited at the Smithsonian National Museum of Natural History (USNM) (Fig. 8E). They share the same colonial shape, most autozooidal and apertural characters, and also avicularia and ovicell shape. Despite the similarities, Gautier already showed his reservations when observing the differences in zooid size (larger in the Mediterranean species) and in the number of peristomial umbones (generally three in the Mediterranean form, five in *P. aviculifera*).

In addition to the differences noted by Gautier (1962), more substantial discrepancies appear that concern the form of ovicellate zooids. The peristome of the new species, which in non-ovicellate zooids appears as somewhat open at the proximal edge and tricuspidate by three stout umbones, in ovicellate zooids develops as an almost tubular, finely edged cylinder (Fig. 8D). In contrast, the ovicellate zooids of *P. aviculifera* exhibit a low peristome outlined by a rough rim (Fig. 8E). Furthermore, the ovicell seems to have very few and larger pores in *P. aviculifera*, while it has a higher number of minute pores (up to 30) in the Mediterranean specimens. It should be noted that the type material, whose SEM pictures we have examined, corresponds to dead, heavily eroded specimens, which seem to have been buried in sediments. Erosion could explain the low profile of the peristome in the type specimen of *P. aviculifera*; also, burial could contribute to fill up the pores of ovicells. But in this case the remaining pores should be smaller than those of the Mediterranean form, not the contrary; this suggests that the differences observed both in the shape of the peristome and the number of pores of ovicells are not an artefact due to the different age and/or conservation status of each material.

Gautier (1962) probably made the same mistake that we later repeated (Madurell *et al.* 2013), mixing in his description two different species: the one we now call in his honor *Palmiskeneia gautieri* Madurell, Zabala, Domínguez-Carrió & Gili, 2013 (Madurell *et al.* 2013) and the other we describe here as

P. diazi sp. nov. Indeed, this author describes the shape of the colony as mainly erect, vinculariform and only rarely encrusting (membraniporiform). We also assumed that in this species the colonies originated as an encrusting sheet, developing afterwards as erect bilaminar or vinculariform, branching forms. We now know that *P. gautieri* always has erect, vinculariform colonies while *P. diazi* always exhibits encrusting colonies. Besides the zoarial shape, the remarkable similarity of the autozooids of both species disappears when we look at the ovicellate zooids: *P. gautieri* exhibits an almost completely smooth ovicell, with only two rounded, symmetrical pores located near the proximal margin (Fig. 8F) and the peristome maintains the stout umbo and rough edges of non-ovicellate zooids; in contrast, ovicellate zooids of *P. diazi* have a finely tubular peristome and a homogeneously perforated ovicell with more than 20 scattered small pores.

Some Mediterranean records of *Palmiskeneia skenei* (Ellis & Solander, 1786) could correspond to *P. diazi* sp. nov. In fact, *P. skenei* is an Atlantic species whose presence in the Mediterranean must be confirmed. In particular, the records from Harmelin must be taken with prudence as he reported both species at the same habitats (Harmelin 1976: 25). Both species share many of the discriminative characters provided, i.e., the orifice, peristome and avicularia. However, *P. skenei* develops bilaminar erect colonies; furthermore, its zooids are smaller and the ovicells have a greater number of large pores of irregular shape.

The generic status of this species seems even more controversial. Canu & Bassler (1928) chose for the Bermudean species the genus *Palmicellaria* which has an umbonuloid frontal shield and sinuate orifices. *Palmiskeneia* was introduced by Bishop & Hayward (1989) with the type species *Millepora skenei*, for species formerly referred to *Palmicellaria* but with umbonuloid frontal shield, an orifice provided of convex or straight proximal border and blunt lateral condyles. In our species condyles are non-existent or indistinct; but this fact should not represent a hard obstacle as subsequently Hayward & Ryland (1999) described the condyles of the type species, *P. skenei*, as small and rounded. The colony growth raises another problem, as the type and most other species of *Palmiskeneia* have erect colonies while the new species has strictly encrusting colonial growth.

Superfamily Celleporoidea Johnston, 1838

Family Celleporidae Johnston, 1838

Genus *Cellepora* Linnaeus, 1767

***Cellepora ballesterosi* sp. nov.**

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Fig. 9; Table 6

Differential diagnosis

Primary orifice almost perfectly circular with two inconspicuous condyles, surrounded by a low, cylindrical peristome, lacking columnar avicularium. Single oral avicularium on the margin of peristome, flat or in acute angle with the orifice, small and narrow (avicularium length < 100 µm, avicularium width < 60 µm). Ovicell sub-spherical on the margin of peristome, smooth, with one central pore.

Etymology

This species is dedicated to Prof. Enric Ballesteros, friend and colleague who helped us to collect bryozoans by scuba diving.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Pota de Llop, Medes Islands; 42.0493° N, 3.225° E; depth 8 m; 27 Sep. 2019; *Puerulus*; M770, stub 743; MZB 2025-6331 (Fig. 9A–F, measurements).

Paratype

MEDITERRANEAN SPAIN • 1 non-ovicellate colony; Punta de la Vaca, Medes Islands; 42.0482° N, 9.403° E; depth 20 m; 10 Jul. 2020; M567, stub 671; MZB 2025-6332.

Other material

MEDITERRANEAN CORSICA • 1 non-ovicellate colony; Sec a Giraglia, Capu Corsu; 43.02784° N, 3.226° E; depth 17 m; 14 Jun. 2020; T-MEDNET; M539, stub 656, R252; MZB 2025-6334.

MEDITERRANEAN SPAIN • 1 non-ovicellate colony; Pota de Llop, Medes Islands; 42.04938° N, 3.225° E; depth 8 m; 14 Mar. 2014; scuba dive, M388, R87, stub 9115; Mikel Zabala leg.; MZB 2016-3595.

Description

Colony encrusting, celoporiform, slightly domed, of medium size (Fig. 9A). Recumbent autozooids at colony margin oval, convex, separated by distinct grooves (Fig. 9B); inner autozooids erect, disordered, as long as wide. Frontal shield smooth, only visible as a narrow band around the orifice, with 8–10 round marginal pores (Fig. 9C). Primary orifice round, the perfect circularity only broken by two fine, elongated condyles, framing an inconspicuous proximal margin of the orifice (Fig. 9D). No oral spines. Peristome cylindrical, variable in height, symmetrically developed all around, never hiding completely the orifice (Fig. 9C). An adventitious oral avicularium on the margin of most peristomes; cystid low, no columnar, on the right or left; outline oval, acute to frontal plane; small (Table 6), with a complete crossbar but lacking columella; rostrum acute and distally hooked (Fig. 9E). No vicarious avicularia. Ovicell prominent, sub-spherical, smooth with 1–2 central pores, opening to the peristome (Fig. 9F). Kenozooids like small autozooids with an elongate or rounded, central orifice scattered among the autozooids (Fig. 9C). Ancestrula not observed.

Ecology and distribution

Found in littoral waters from five to 20 m depth, on broken *Mytilus* Linnaeus, 1758 shells and holds of sciaphilic algae (genus *Flabellia*); also found in *Posidonia* meadows and coralligenous bottoms. To present, *Cellepora ballesterosi* sp. nov. has been found at two different localities: Medes Islands and Sec of Giraglia (Capu Corsu, Corsica).

Remarks

Cellepora ballesterosi sp. nov. is similar to all the other Mediterranean species of genus *Cellepora*, but differs from all of them by the absence of a raised umbone supporting the avicularia. On the contrary, the single peristomial avicularium is almost wedged in the margin of peristomes, almost flat or in an acute angle with the plane (never orthogonal) only projecting a hooked tip over it; this avicularium is also smaller (length < 100 µm) and narrower (avg. width < 50 µm) than those of other species of *Cellepora* (Tables 6–8). Furthermore, the peristome of *C. ballesterosi* approaches a cylinder, variable in height but almost symmetrical, lacking the lateral expansions of different heights that characterize the other species.

Cellepora ballesterosi sp. nov. can be superficially confounded with some Mediterranean species of genus *Turbicellepora* Ryland, 1963. However, it lacks the vicarious avicularia and the punctured ovicells characteristic of this genus.

Cellepora gilii sp. nov.

[urn:lsid:zoobank.org:act:8678CBFB-CE68-4F50-AD59-42AD799E0805](https://zoobank.org/urn:lsid:zoobank.org:act:8678CBFB-CE68-4F50-AD59-42AD799E0805)

Fig. 10; Table 7

Differential diagnosis

Colony forming stout, multilaminar cylinders around erect substrata. Peristome extremely developed as asymmetrical plate laplets which can merge in a hood over the orifice. Primary orifice wider

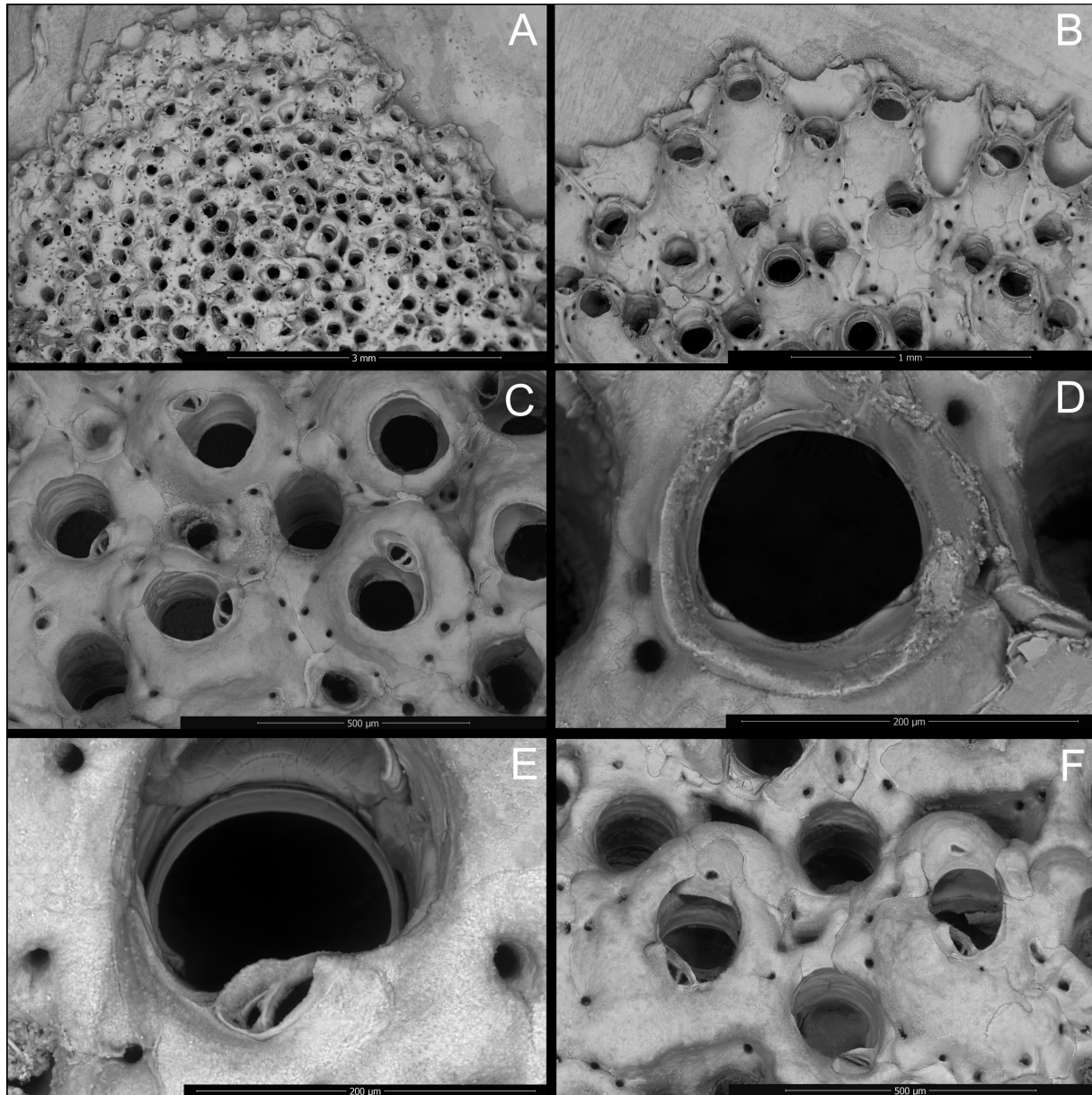


Fig. 9. *Cellepora ballesterosi* sp. nov., holotype MZB 2025-6331. **A.** Colony view. **B.** Marginal autozooids recumbent on the substratum. **C.** Older, erect autozooids lacking columnar avicularia. **D.** Primary orifice with inconspicuous condyles and a symmetrically low peristome. **E.** Suboral avicularium almost wedged in the peristome. **F.** Ovicells; notice the presence of a sole pore.

Table 6. Measurements (in μm) of *Cellepora ballesterosi* sp. nov., holotype MZB 2025-6331. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	8	497	66.6	437	608
Autozoid width	20	372	44.7	282	446
Orifice length	5	124	1.3	123	126
Orifice width	21	133	5.9	123	142
Avicularia length	16	87	9.2	70	103
Avicularia width	13	48	8.2	34	61
Ratio avicularia length/width	12	1.9	0.4	1.4	3.0
Ovicell length	4	183	15.3	162	199
Ovicell width	4	230	32.9	188	264
Pores number	4	1.3	0.5	1	2

than long, poster slightly concave without condyles; hidden by the peristome. Big oral avicularium, raised perpendicular to orifice on a bulged avicularium with two distal pores; rostrum oval, with an acute, hooked tip; crossbar complete, slender and curve; basalmost part of the avicularium developed as two asymmetrical lobes (one longer than the other), forming with the edge of peristome a round pseudospiramen. Smaller avicularia scattered among autozooids. Ovicell sub-spherical with two big pores near the margin; the rim of the peristome extends across the frontal surface of the ovicell, encircling and partially hiding the pores.

Etymology

This species is dedicated to Prof. Josep M^a. Gili, friend and colleague who led the Indemares campaigns on the Menorca Channel where this species was first found.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Menorca Channel; 39.85043° N, 3.50619° E; depth 70 m; 1 Aug. 2011; Indemares; trawling, M353, R33, stub 498; MZB 2015-8324 (Fig. 10A–F, measurements).

Paratype

MEDITERRANEAN SPAIN • 3 ovicellate colonies; same data as for holotype; MZB 2015-8258.

Description

Colony celleporiform, forming stout, multilaminar cylinders around erect substrata (Fig. 10A). Autozooids erect, disordered, globose. Frontal shield smooth, with 6–8 round marginal pores. Primary orifice orbicular or sub-quadrangular, clearly wider than long, almost completely hidden by peristomes; poster almost flat, with inconspicuous condyles and a small concavity (Fig. 10B). No oral spines. Peristome raised, extraordinarily developed as asymmetrical, flat flaps that can merge in a hood hovering over the orifice (Fig. 10C). It develops proximally a bulged avicularian cystid, columnar but not tapered, lodging a big oval avicularium, perpendicular to the orifice; with a rostrum wider than in other species of the genus ($R \text{ length} / \text{width} < 1.5$, Tables 6–8) and an acute, strongly hooked tip; crossbar complete, slender and curve, lacking columella; basalmost margin of the avicularium characteristically developed as two asymmetrical lobes (one longer than the other), forming with the edge of peristome a round

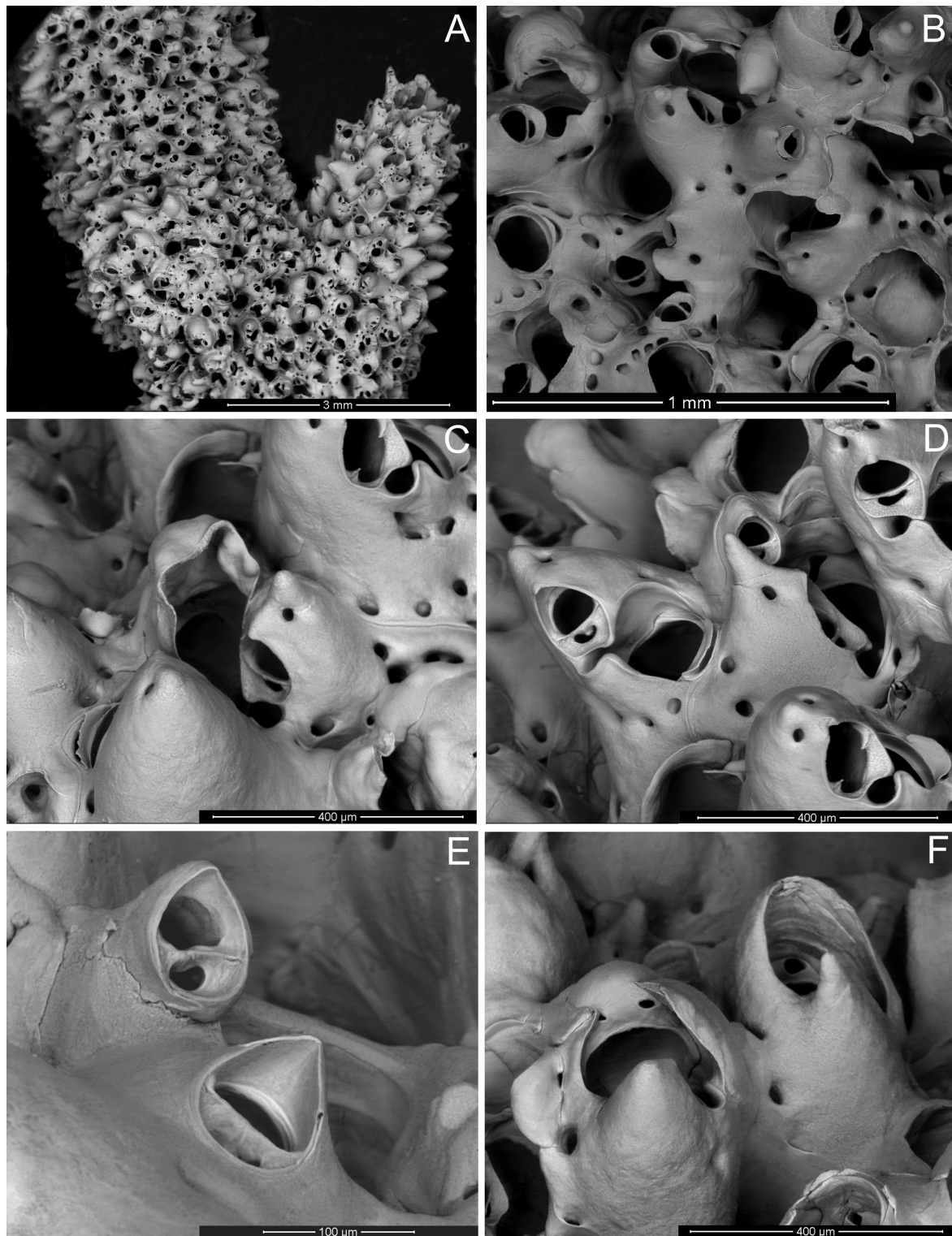


Fig. 10. *Cellepora gilii* sp. nov., holotype MZB 2015-8324. **A.** Erect colony growing on an algal holdfast. **B.** Young autozooids without peristome showing the primary orifices. **C.** Characteristic peristomial development forming a hood over the orifice. **D.** Avicularian columnar cystid showing the uneven marginal expansions and the characteristic pseudosinus. **E.** Avicularia of smaller size lacking marginal expansions and pseudosinus. **F.** Two ovicells; notice the presence of two pores and the deep development of the peristomial rim that encircles totally the ovicell.

Table 7. Measurements (in μm) of *Cellepora gilii* sp. nov., holotype MZB 2015-8324. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid width	15	339	57.4	245	480
Orifice length	3	137	5.3	131	141
Orifice width	3	157	9.5	147	166
Avicularia length	28	123	20.6	78	163
Avicularia width	33	90	17.5	56	119
Ratio avicularia length/width	27	1.4	0.1	1.2	1.7
Ovicell length	11	164	20.2	138	206
Ovicell width	11	228	24.6	203	287
Pores number	5	1.8	0.4	1	2

pseudo-spiramen (Fig. 10D); two big pores on tip of the avicularian cystid. Other avicularia, similar in shape but smaller, appear scattered among the autozooids (Fig. 10E). Ovicell sub-spherical, projecting above the peristome rim, with a wide, highly arched aperture and two irregular pores near the distal edge; the rim of the peristome extends across the frontal surface of the ovicell, encircling and partially hidden the pores (Fig. 10F). Ancestrula unknown.

Ecology and distribution

This species has been found only once, on a coralligenous bottom, 70 m deep, in the Menorca Channel (Balearic Islands).

Remarks

Cellepora gilii sp. nov. shares with the other Mediterranean species of *Cellepora* much of the characteristic attributes of the genus: orifice, peristomes, avicularia and ovicells. In fact, it can be seen as a variety of the common *Cellepora pumicosa* (Pallas, 1766), where the peristomes have reached an extreme development. Nevertheless, the singular colony shape, the primary orifice, more quadrangular, the characteristic form of the peristome, the size and specially the outline of the big avicularium makes this species clearly different from any other species of *Cellepora* previously described.

Cellepora sp.?

Fig. 11; Table 8

? *Cellepora* “*pumicosa*” (sensu Waters 1879) – Gautier 1962: 266, fig. 24.

Non *Cellepora pumicosa* (Pallas, 1766) – Gautier 1962: 265 as auctt (non Linnaeus, 1768)

Differential diagnosis

Colony encrusting, domed or nodular. Autozooids erect, only showing a narrow band of smooth frontal shield around the orifice. Primary orifice vaguely wider than long, orbicular but not perfectly circular. Peristome low, with a raised, acute umbo, frequently developed as a spiky process lodging a single avicularium, perpendicular to orifice; rostrum triangular, acute, narrower than in other species of the genus (R length/width >1.7, Tables 6–8). Ovicell spherical, prominent above the peristomial rim, which extends across its frontal surface.

Material examined

MEDITERRANEAN SPAIN • 1 ovicellate colony; Medes Islands; 42.04953° N, 3.22594° E, depth 20 m; 2 Jul. 2020; T-MEDNET; M598, stub 856; MZB 2025-6335 (Fig. 11A–D, measurements).

Description

Colony encrusting, celleporiform (Fig. 11A). Recumbent autozooids at colony margin oval, convex, separated by distinct grooves; inner autozooids erect, disordered, as long as wide. Frontal shield smooth, only visible as a narrow band all around the orifice, with 4–6 round marginal pores, two of them framing proximo-laterally the orifice. Primary orifice, vaguely wider than long, orbicular but not perfectly circular: the rim of the poster describing a more concave arch than the rim of the anter; no condyles visible (Fig. 11B). No oral spines. Peristome low, with a raised, acute umbo, frequently developed as a spiky process lodging a single avicularium, perpendicular to orifice, oval, narrower than in other species (R length/width > 1.7); with acute, slightly hooked tip; with slender crossbar lacking columella; palate with an extensive foramen; tip of avicularian cystid with two distal pores (Fig. 11C). No vicarious avicularia. Ovicell sub-spherical, prominent, projecting above the peristomial margin, smooth (Fig. 11D), lacking frontal pores (only one ovicell has been observed). Ancestrula unknown.

Ecology and distribution

This species has been found only once, on a coralligenous bottom of the Medes Islands at 20 m depth.

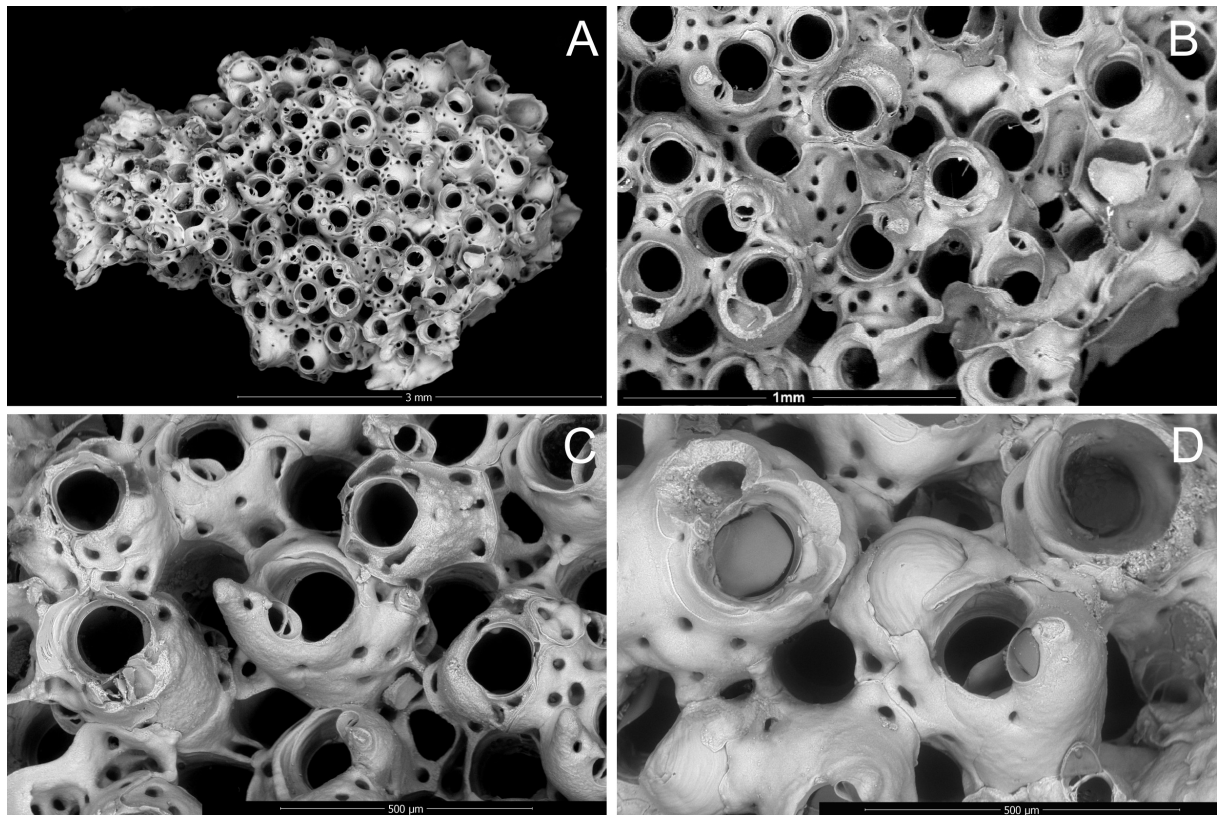


Fig. 11. *Cellepora* sp.?, MZB 2025-6335. **A.** Colony view. **B.** Detail of autozooids with primary orifice. **C.** Erect autozooids with columnar avicularian cystid and low peristomes that enable the vision of primary orifices. **D.** Ovicell in formation.

Table 8. Measurements (in μm) of *Cellepora* sp.?, MZB 2025-6335. Measurements for *C. adriatica* Hayward & McKinney, 2002 from Hayward & McKinney (2002); for *C. posidoniae* (Hayward, 1975) from Chimenz Gusso *et al.* (2014) and Harmelin *et al.* (2016); for *C. pumicosa* (Pallas, 1766) from MZ-TM leg. (MZB 2016-3636), Mediterranean Spain. Abbreviations: Max = maximum; Min = minimum; N = number of measurements; SD = standard deviation.

	<i>Cellepora</i> sp. ?					<i>C. adriatica</i>				<i>C. posidoniae</i>					<i>C. pumicosa</i>			
	N	Mean	SD	Min	Max	Mean	Min	Max		N	Mean	SD	Min	Max	N	Mean	Min	Max
Autozoid length	15	360	44.3	288	460	468	337	630		5	463	49.8	402	521		–	–	–
Autozoid width	20	286	27.5	233	353	–	–	–		10	366	51.9	298	433	5	440	395	530
Aperture length	29	128	10.0	112	146	148	134	158		9	123	9.2	114	140	6	161	143	183
Aperture width	29	142	10.6	122	166	140	123	156		12	142	6.5	128	153	12	152	138	176
Avicularia length	23	111	18.6	76	144	128	116	137		19	102	13.5	87	134	13	137	112	180
Avicularia width	23	61	12.0	34	79	87	83	94		14	65	10.0	45	76	14	78	61	96
Ratio avicularia length/width	23	1.9	0.3	1.4	2.6	1.5	1.4	1.5		14	1.7	0.4	1.2	2.8	12	1.8	1.5	2.1
Ovicell length	1	166	–	166	166	147	124	192		4	183	33.3	159	230	6	201	186	224
Ovicell width	1	227	–	227	227	222	199	238		4	233	39.0	184	278	6	243	220	296
Pores number	1.0	–	–	0.0	0.0	1.0	–	–		3.0	2.0	0.0	2.0	2.0	5	3.0	3.0	3.0

Remarks

The species we describe here could be “*Cellepora pumicosa*” (sensu Waters), not Pallas, 1766, that Gautier (1962) described in his monographic work on Mediterranean Bryozoans (Gautier 1962: 266). Most morphological details and all the metric parameters fully coincide with his description. As clearly stated by Gautier, this species does not correspond to the true *Cellepora pumicosa* (Pallas, 1766), which has been identified since Hincks (1880), but is coincident with the Water’s type that he examined at the UKNM (79.4.25.65). Sadly, Waters did not figure this species but Gautier exceptionally drew his specimen (Gautier 1962: fig. 24); however, the quality of his drawing is so poor that it is not helpful for the identification.

This *Cellepora* is similar in all respects to *C. pumicosa* but is dimensionally smaller (orifice length <150 µm, Table 8). It is also similar to *Cellepora adriatica* Hayward & McKinney, 2002. Still, the size of the orifice is bigger and the form of the avicularium is wider in the second (R length /width <1.5, Table 8). Biometrically, this species could also correspond to *C. posidoniae* (Hayward, 1975); nevertheless, the latter shows a peristomial pseudosinus at the base of the avicularian cystid and grows exclusively encrusting *Posidonia* leaves as small circular plates. See all comparative measurements in Table 8.

Family Phidoloporidae Gabb & Horn, 1862

Genus *Rhynchozoon* Hincks, 1895

***Rhynchozoon garraboui* sp. nov.**

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Fig. 12; Table 9

Differential diagnosis

Colony encrusting, unilaminar, autozooids recumbent, disordered; frontal shield smooth, with 6–8 round areolae. Primary orifice as wide as long; distal and lateral rim almost round, with 18 denticulations; proximal margin with a V-shaped sinus framed by high, round condyles; 3–5 oral spines, only in young, peripheral autozooids; peristome enclosing the orifice proximally and laterally, with three knobs of similar size, not developing digitate umbones. Suboral avicularium triangular, with a hooked rostrum; frontal avicularia monomorphic, single or rarely twinned, triangular; placed near the aperture and laterally directed.

Etymology

Named in honour of Joaquim Garrabou, friend and colleague who led the sampling campaigns of the T-MEDNET project where this species was first recognized as new.

Material examined

Holotype

MEDITERRANEAN SPAIN • non-ovicellate colony; Medes Islands; 42.0495° N, 3.22137° E; depth 9 m; 10 Dec. 1977; scuba dive, M20, stub 9214; Mikel Zabala leg.; MZB 2025-6336 (Fig. 12A–D, measurements).

Paratype

MEDITERRANEAN SPAIN • 1 non-ovicellate colony; as previous; stub 738; MZB 2025-6337 (measurements).

Description

Colony encrusting, forming small patches of medium size (less than 200 autozooids) (Fig. 12A). Young marginal autozooids hexagonal, slightly longer than wide, separated by conspicuous grooves, boundaries becoming indistinct in later ontogeny. Older autozooids regularly spaced. Frontal wall thick, always smooth and vitreous (Fig. 12B). Primary orifice almost round, as wider than long (Table 9); distal margin rounded, distal and lateral rim denticulate provided with 18 fine denticulations; proximal border with a well-defined V-shaped sinus, framed by two high, round condyles (Fig. 12C); three-five deciduous spines in young peripheral zooids (Fig. 12C). Peristome thick, enclosing the primary orifice laterally and proximally with three knobs of similar size, not developing big, digitate umbone as in other species of *Rhynchozoon* (Fig. 12D). Suboral avicularium single, rare, enclosed by the peristome, lateral to the orifice; rostrum triangular with a hooked tip. Frontal avicularia monomorphic, rarely twined (Fig. 12D), usually rare or even inexistent in large areas of the colony; triangular, small (Table 9) on the plane of the frontal shield, placed near the orifice and laterally or disto-laterally oriented. Ovicell and ancestrula not observed.

Ecology and distribution

The available specimens came from a shallow bottom, 9 m deep, and a more mesophotic one at 35 m of the same locality of Medes Islands (NW Mediterranean). The formers (two colonies) were found in a community of sciaphilic algae mixed with a canopy of the white gorgonian *Eunicella singularis* (Esper, 1791); the latter came from the underside of a stone placed at the foot of a coralligenous wall.

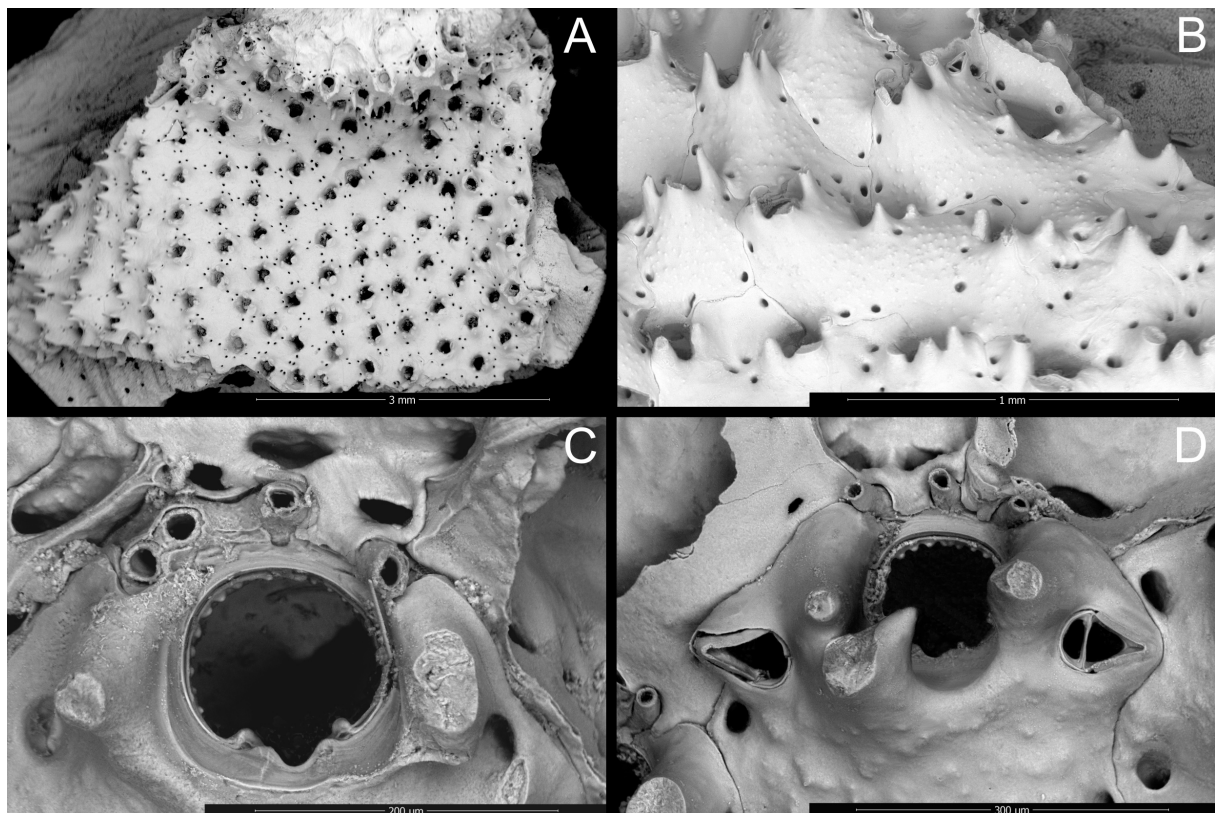


Fig. 12. *Rhynchozoon garraboui* sp. nov., holotype MZB 2025-6336. **A.** Encrusting colony. **B.** Autozooids regularly spaced with smooth and vitreous frontal wall. **C.** Primary orifice denticulated with V-shaped sinus and two round condyles. **D.** Peristome with three knobs of similar size and frontal triangular avicularia (twined).

Table 9. Measurements (in μm) of *Rhynchozoon garraboui* sp. nov., holotype MZB 2025-6336 and paratype MZB 2025-6337. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	5	480	5.5	472	487
Autozoid width	14	395	27.7	363	468
Orifice length	5	108	11.2	98	125
Orifice width	6	117	10.4	104	129
Avicularia length	3	86	7.1	80	94
Avicularia width	3	54	7.0	46	59

Remarks

The shape of the primary orifice separates *Rhynchozoon garraboui* sp. nov. from all previously described species worldwide with a similar number of spines. The primary orifice, with a well-defined V-shaped sinus and 18 distal denticulations, approaches it to *R. bispinosum*; however, in the latter, the orifice is neatly wider than long, the sinus is wider, and the condyles are flatter and reach the corners of the proximal margin. Furthermore, *R. bispinosum* has no more than two spines. Strangely, only three colonies of this species from two samples have been found despite a strong sampling effort comprising more than 750 samples. Sadly, these specimens have no ovicells, and they do not allow for a description of the intraspecific variability. The whole description of this enigmatic species remains incomplete pending of more abundant further material.

Rhynchozoon neapolitanum Gautier, 1962

Fig. 13

Rhynchozoon neapolitanum Gautier, 1962: 243.

Rhynchozoon neapolitanum – Zabala & Maluquer 1988: 149, figs 367–370, pls 21f, 22a. – Hayward & McKinney 2002: 241. – Chimenz Gusso *et al.* 2014: 234, fig. 127a–e.

Material examined

MEDITERRANEAN SPAIN • 1 ovicellate colony; Medes Islands; 42.04636° N, 3.224738° E; depth 17 m; 23 Sep. 2017; M744, stub 9210; MZB 2025-6338 (Fig. 13A).

Amended description

Well described by Hayward & McKinney (2002: 94–95, fig. 43a–e). Ovicells sometimes display quadrate labellum on the proximal border (Fig. 13A). Occasionally, zooids present two spines on the distal margin of the orifice (Fig. 13B).

Remarks

Rhynchozoon neapolitanum is a well-known species, the easier to be identified among the Mediterranean *Rhynchozoon*'s due to the nodular colony form produced by frontal growth. The ability for frontal growth is an unusual trait in the Mediterranean species of this genus and it also allows for an easy observation of the primary orifice, another unusual trait, which exhibits a characteristic round sinus. Gautier's description, exhaustive enough, was improved by that of Hayward & McKinney (2002) which also provided good SEM pictures. Nevertheless, two details must be added in order to avoid further misunderstandings. First, when describing the form of ovicells, Gautier clearly states that it is "...dépourvue de labellum...". Indeed, we have observed that most of the ovicells appear devoid of

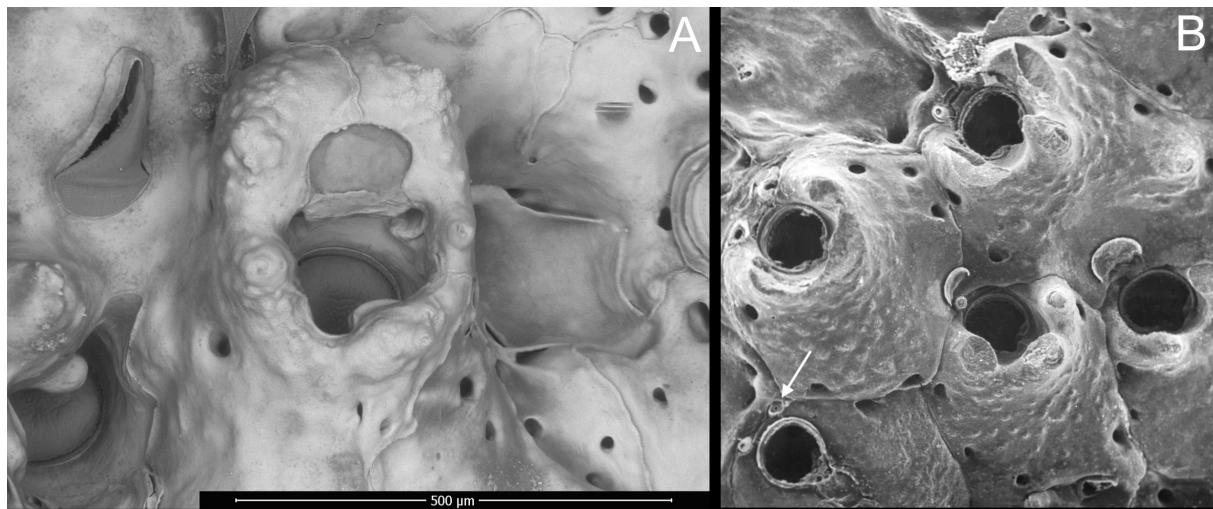


Fig. 13. *Rhynchozoon neapolitanum* Gautier, 1962 **A.** Ovicell with quadrate labellum, MZB 2025-6338, Medes Islands. **B.** Two sprouts of spines on the distal margin of the orifice (white arrow), Cathedral Cave, Mallorca Island; 39.7413° N, 3.46022° E; depth 9 m; M247, M. Zabala 1986.

it; but in some instances, the proximal border shows a clear, quadrate labellum (Fig. 13A). Second, *R. neapolitanum* is described as a species lacking oral spines; however, one specimen of this species where two sprouts of spines clearly emerged on the distal margin of the orifice was collected by Zabala (1986) (Fig. 13B).

***Rhynchozoon pseudodigitatum* Zabala & Maluquer, 1988**

Figs 14, 15A–C; Table 10

Rhynchozoon pseudodigitatum Zabala & Maluquer, 1988: 147–149, figs 384–387, pls 20e–f, 21a.

? *Cellepora digitata* – Waters 1879: 197, pl. xiv fig. 13.

? *Rhynchozoon digitatum* – Gautier 1962: 241.

Rhynchozoon sp I – Hayward 1974: 387, fig. 8a–b.

Rhynchozoon pseudodigitatum – Hayward & McKinney 2002: 96, fig. 43f–h. — Chimenz Gusso *et al.* 2014: 236, fig. 128a–d.

Non *Rhynchozoon bispinosum* (Johnston, 1847) – Gautier 1962: 240 pars (Gautier leg. Le Frioul, N° MHNH-IB-2008-10999). — Zabala & Maluquer 1988 (pars): 147–149, figs 376–379, pl. 20a–d.

Differential diagnosis

Colony encrusting. Frontal shield variable in shape, finely granular in young zooids becoming smooth and vitreous as calcification advances, bordered by a series of up to nine large, round marginal pores. Primary orifice orbicular, wider than long, distal rim with 12–14 denticles; proximal border shallowly concave, lacking a true sinus. Two oral spines in young autozooids. Peristome developed proximally as a stout, cylindrical umbo and two or three lateral smaller umbones. Avicularia of three different types, a large, triangular, deeply hooked, suboral avicularium and two frontal dimorphic avicularia: 1–3 acute avicularia with slender, almost parallel margins, scattered over the frontal shield, and a rare big avicularium mounted on a voluminous cystid, proximally directed.

Material examined

Neotype (designated here)

MEDITERRANEAN SPAIN • ovicellate colony; Pollença Bay, Mallorca Island; 39.95811° N, 3.21422° E; depth 40 m; scuba dive, M703, stub 729; Mikel Zabala leg.; MZB 2025-6341 (Fig. 14E, H, measurements)

Other material

MEDITERRANEAN FRANCE • 1 ovicellate colony; Moyade; depth 29 m; 24 May 1966; J.-G. Harmelin leg. labelled *Rhynchozoon digitatum*; stub 9215; MZB 2025-6364 • 1 non-ovicellate colony; Le Frioul; depth 11 m; 1 Apr., 1966; J.-G. Harmelin leg. labelled *Rhynchozoon digitatum*; stub 9216; MZB 2025-6365 • 1 ovicellate colony; Le Frioul; Gautier leg., Gautier 1962: 240 pars; MHNH-IB-2008-10999.

MEDITERRANEAN GREECE • 1 ovicellate colony; Cape Mastika, Chios; depth 9–36 m; 16 Aug. 1967; P. Hayward leg. labelled *Rhynchozoon* sp I; BMNH 2009.10.15.5 • 12 colonies; Emborios Bay, Chios; depth 1–15 m; Aug. 1967; P. Hayward leg. labelled *Rhynchozoon* sp I.; BMNH 1975.1.12.300 to 1975.1.12.310, BMNH 1975.1.12.408, BMNH 1975.1.12.409.

MEDITERRANEAN SPAIN • 1 colony; same collection data as for neotype; stub 730; MZB 2025-6342 • 1 ovicellate colony; Columbretes Islands; 39.83634° N, 0.68126° E; depth 40 m, M424, stub 495; MZB 2019-0491 (Fig. A, D, F, measurements) • 1 ovicellate colony; Columbretes Islands; 39.89604° N, 0.68274° E; depth 35 m; 19 Aug. 2012; M457; MZB 2017-0686 (Fig. 14C, measurements) • 1 ovicellate colony; Pedra Joaquin, Columbretes Islands; 39.878278° N, 0.630069° E; depth 32 m; 29 Aug. 2015; *Puerulus*; M556; MZB 2025-6348 (Fig. 15A) • 1 colony; Illa Messina, Cap de Creus; 42.28814° N, 3.31062° E; depth 50 m; 13 Jul. 2022; scuba dive, M682, stub 732; Mikel Zabala leg.; MZB 2025-6343 (Fig. 14B, measurements) • 1 ovicellate colony; Colònia de St Jordi, Balearic Islands; 39.31952° N, 2.91005° E; depth 35 m; 13 Jul. 1985; scuba dive, M702, stub 9209; Mikel Zabala leg.; MZB 2025-6344 (Fig. 14G, measurements) • 2 ovicellate colonies; Medes Islands; 42.0482° N, 3.226° E; depth 20 m; 10 Jul. 2019; M583, stub 9194; MZB 2025-6345 • 3 ovicellate colonies; Medes Islands; 42.0495° N, 3.22137° E; depth 9 m; 10 Dec. 1977; M20, stub 739; MZB 2025-6346 (Fig. 15B) • 1 ovicellate colony; Illes Formigues (Costa Brava); 39.89604° N, 3.23734° E; depth 61 m; 8 Jul. 2022; stub 816, M686; MZB 2025-6347 • 2 ovicellate colonies; Menorca Channel; 40.997665° N, 3.120167° E; depth 240 m; Indemares 4; stn 24, JAGO dive, M657; not preserved • 2 ovicellate colonies; Cap de Formentor, Menorca Channel, 40.020402° N, 3.157420° E; depth 82 m; 29 Jun. 2012; Indemares; Rauschert sled, stn 39, M659; not preserved.

Redescription

Colony encrusting, developing moderately large (100–200 zooids), unilaminar (Fig. 14A–B), only rarely nodular (celleporiform) patches. Autozooids highly variable in shape throughout the ontogeny. Young marginal autozooids hexagonal, strongly convex, separated by deep grooves (Fig. 14C). Subsequent zooids become strongly recumbent on the younger series, stacked like roof shingles (Fig. 14B), the borders becoming indistinct as secondary calcification thickens during late ontogeny. Frontal shield also variable in shape, finely granular in young zooids (Fig. 14D) becoming smooth and vitreous as calcification advances; bordered by a series of up to nine large, round marginal pores (Fig. 14C–D). Primary orifice obscured by peristomes, only partially visible in young, marginal autozooids (its complete outline being almost impossible to observe in a sole autozooid); orbicular, slightly wider than long, lateral and distal rim with 12–14 conspicuous, regularly spaced denticles; proximal border shallowly concave, framed by two flat, smooth condyles placed at opposite extremes, lacking a true sinus (Fig. 14E), obscured by peristomial mucrones (Fig. 14D). Two widely spaced oral spines are present only in young marginal autozooids (Fig. 14F). Peristome thick and deep, hiding the primary orifice proximally and laterally, developed proximally as a stout, cylindrical umbo and two or three lateral smaller umbones

(Fig. 14C–D); the large umbo has a acute, granular tip but appears usually broken at the base. Within the peristome, a stout uncinat process on one side and a short-rounded knob on the other form the rounded pseudosinus characteristic of the genus (Fig. 14H).

Avicularia of three different types. In some zooids the stout proximal umbo is replaced by a suboral avicularium, large, triangular and deeply hooked; with a wide mandible (ratio avicularium length/avicularium width ca 1.8), frequently bearing a pair of knobbed processes on each side of the tip; placed in an almost orthogonal plane to the orifice plane and laterally directed (Fig. 14G). Scattered over the frontal shield, one to three small acute avicularia, more or less hooked, widely variable in size but always with long, slender, almost parallel margins (ratio avicularium length/avicularium width >2.5); in steep angle to the frontal plane and preferably distally or disto-laterally directed (Fig. 14H). Occasionally, a large frontal avicularium (avicularium length >200 µm) appears among these frontal avicularia, hardly distinguishable in shape from them, but wider (ratio avicularium length/avicularium width ca 2.3, Table 10) and mounted at a steeper angle on a voluminous cystid; proximally or proximo-laterally directed (Fig. 15A).

Ovicells usually immersed in the peristomes (Fig. 15B) but exposed ovicells can exist in young zooids (Fig. 15C), slightly wider than long, flattened frontally, with an area of uncovered entoecium framed by two lateral triangular lapels of ectoecium, sometimes developing a wide, quadrate labellum; obscured by calcification in late ontogeny, sometimes with a blunt mucro on top (Fig. 15B). Ancestrula unknown.

Ecology and distribution

We found *R. pseudodigitatum* in 54 samples in almost any habitat sampled between 5 and 72 m deep, excluding harbors, deep coralligenous outcrops, and cold coral habitats: it has been found in habitats with photophilic algae (4), sciaphilic algae (3), *Posidonia* meadows (3), semi-dark caves (2), dark caves (2), coralligenous (9), under blocks (5) maërl (2) and detritic bottoms (1). *Rhynchozoon pseudodigitatum* appears to be the most common among the Mediterranean species of *Rhynchozoon*. In our research, *R. pseudodigitatum* has been found along the entire Catalan coast, around the Balearic and Columbretes Islands and north of Corsica (Cap Corse). As *R. digitatum* and *R. bispinosum* it has been collected near Marseille (Moyade, Frioul) by Harmelin (Harmelin leg.). As *R. pseudodigitatum* it has been cited from Italy (Tuscany, Lazio, Vulcano, Ustica, Lampedusa, Brindisi, Turchia meridionale) by Chimenz Gusso *et al.* (2014), Croatia (Hayward & McKinney 2002), and Lebanon (Harmelin *et al.* 2016). As *Rhynchozoon* sp. I it has been cited from Cape Mastika and Chios Island by Hayward (1974).

Remarks

Variability in shape during ontogenic development is a common characteristic for all species of *Rhynchozoon*, but it appears as the most striking attribute of this species. Only young, marginal zooids allow the primary orifice, the two ephemeral spines and the large suboral avicularia to be visible. With the development of the stout central umbo, the apertural area becomes obscured. The frontal shield, which is finely granulated in young zooids, becomes glassy and vitreous with secondary calcification. The number of frontal avicularia can vary from almost absent to very abundant, allowing for an extremely variable general shape. Ovicells, occasionally fully exposed, are usually deeply immersed in the peristomes; they may occur with and without labellum and sometimes bear a blunt knob on top.

Perhaps due to the great ontogenic variability, or perhaps the way zooids stack like roof tiles, preventing observation of details surrounding the apertures, the genus *Rhynchozoon* has been very poorly described by Mediterranean bryozoologists. Waters (1879) described *Cellepora digitata* together with two other species, *Cellepora verruculata* Smitt, 1873 and *Cellepora lobulata* Waters, 1879, that were later assigned to the genus *Rhynchozoon* (Gautier 1962). After its description by Waters, *R. lobulatum* (Waters, 1879) has only been cited by Gautier (1962) who found only one specimen in Marseille. In Hayward's opinion (see

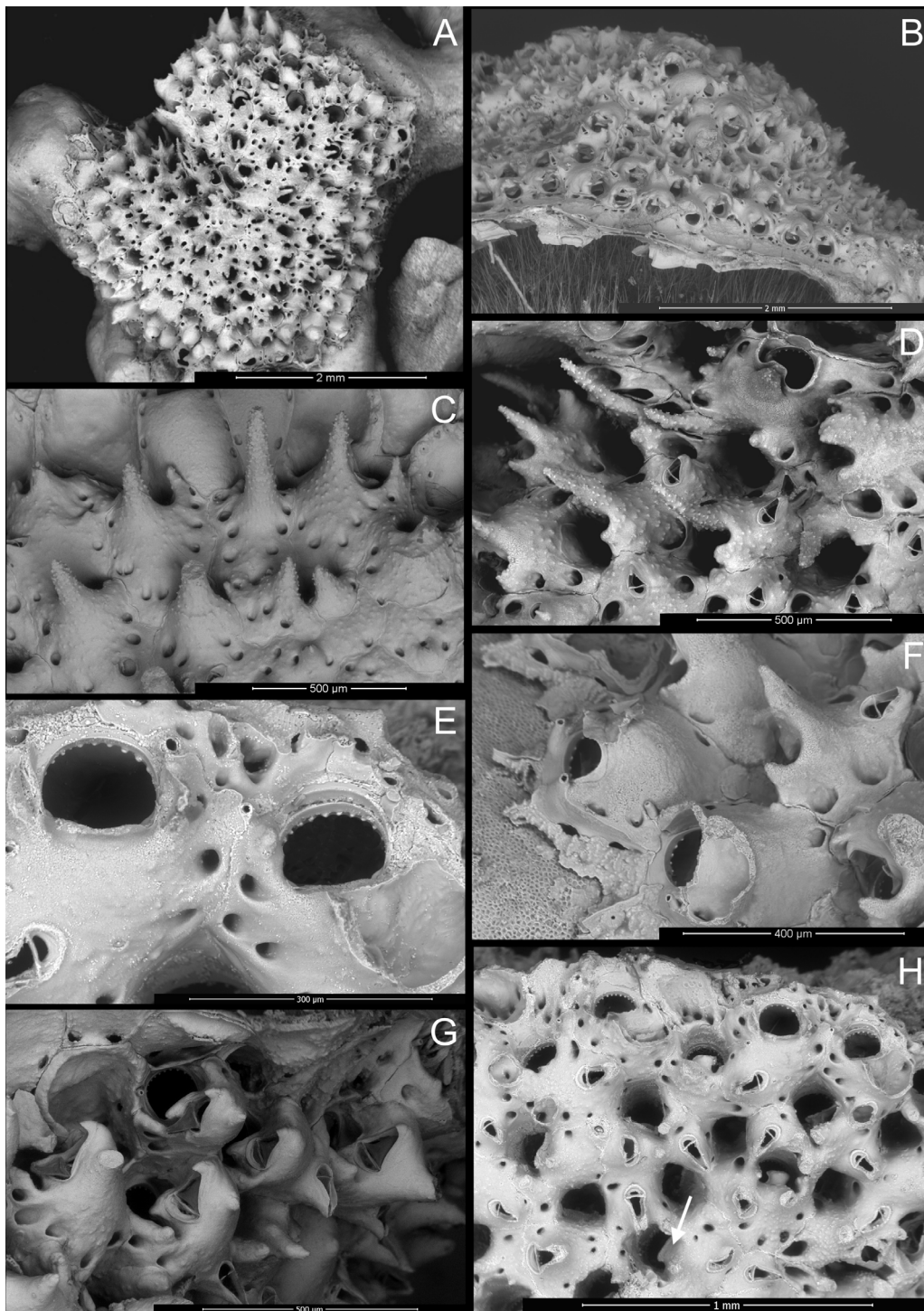


Fig. 14. *Rhynchozoon pseudodigitatum* Zabala & Maluquer, 1988. **A.** Colony view (paratype MZB 2019-0491). **B.** Autozooids in colony margin stacked as the shingles of a roof (paratype MZB 2025-6343). **C.** Young marginal autozooids with smooth surface (paratype MZB 2017-0686). **D.** Young autozooids with rough surface (paratype MZB 2019-0491). **E.** Primary orifice shallowly concave with 12–14 denticles and two flat condyles (neotype MZB 2025-6341). **F.** Orifices of young marginal zooids with 2 deciduous spines (paratype MZB 2019-0491). **G.** Suboral avicularia, triangular and hooked, with a pair of knobbed processes on each side of the tip (paratype MZB 2025-6344). **H.** Slender frontal avicularia; notice the uncinuate process and the pseudosinus (white arrow) (neotype MZB 2025-6341).

Hayward 1974: 387 for discussion), *R. lobulatum* differs little from *R. digitatum* and perhaps represents an aged form of the latter. Gautier (1962) created *Rhynchozoon neapolitanum* for *C. verruculata* (because the name was pre-occupied) and described the two other species more precisely but did not illustrate them. Later, Hayward (1974) described two other species from Chios (Aegean Sea) that he considered different from the former species: *Rhynchozoon* species I and *R. species II*. The latter was subsequently redescribed as *R. revelatus* by Hayward & McKinney (2002), but this species has been identified as a junior synonym of *Dentiporella sardonica* (Waters, 1879) by Souto *et al.* (2010b). The case of *Rhynchozoon* sp. I is here clarified. After examining the original material of *Rhynchozoon* sp. I preserved at the NHMUK, we can confirm that it corresponds to *R. pseudodigitatum*. The main difference with the previous description of *R. pseudodigitatum* consisted in the presence/absence of two deciduous oral spines. After discovering that *R. pseudodigitatum* can also exhibit these spines, the only notable difference between the two species disappears.

Undoubtedly due to the difficulties just mentioned, Waters' description of *C. digitata* is very succinct and does not provide details that could help discriminate it from other species. Furthermore, Waters (1879) mixed a single specimen from Naples with several specimens from Australia, with most details coming from the latter. Since it was evident that these were two different species and it was not feasible to distinguish the Naples specimen among Waters' types, Zabala & Maluquer (1988) described as *Rhynchozoon pseudodigitatum* a new species they assumed must correspond to Waters' "*Cellepora digitata*" and Gautier's *Rhynchozoon digitatum*. However, the description of this new species was still very poor by current standards, and the types still need to be stabilized. We attempt to fill this gap here,

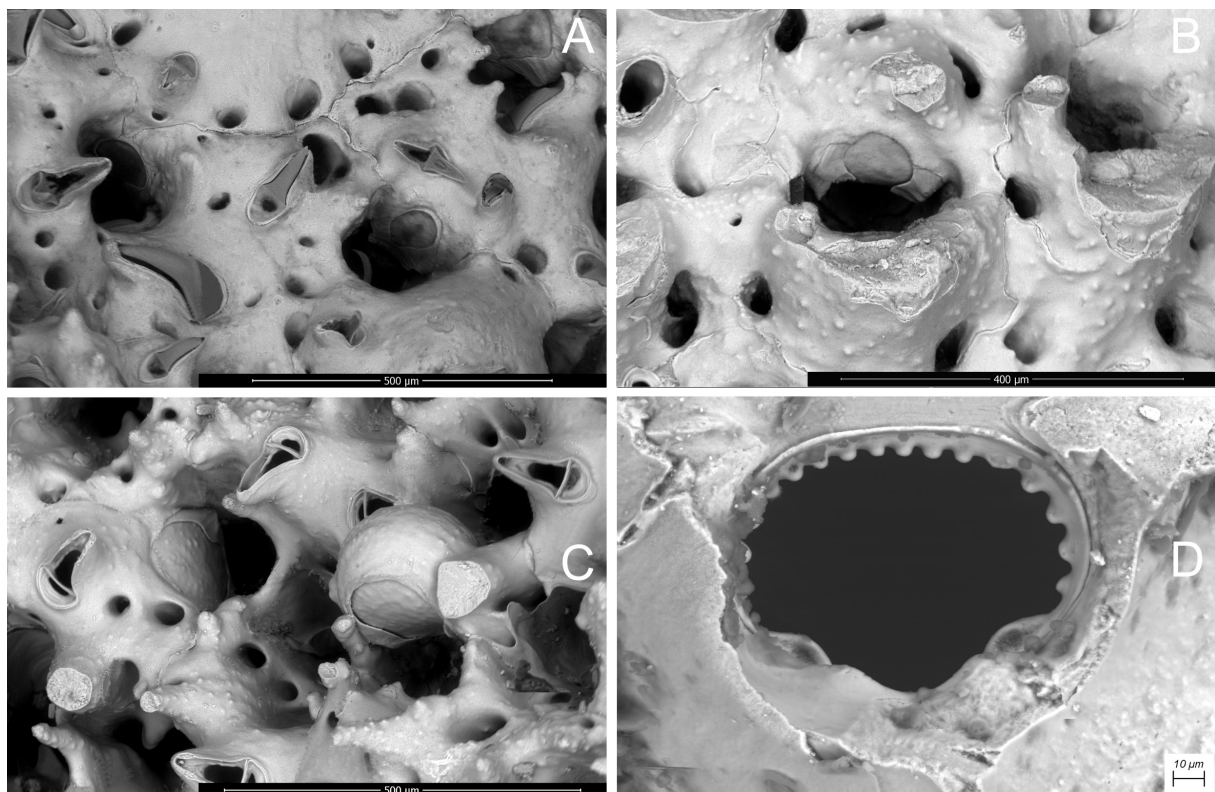


Fig. 15. A–C. *Rhynchozoon pseudodigitatum* Zabala & Maluquer, 1988. **A.** Big frontal avicularia on large avicellarium (MZB 2025-6348). **B.** Immersed ovicell in young, rough autozooids (MZB 2025-6346). **C.** Ovicells with some frontal avicularia (neotype MZB 2025-6341). **D.** *R. bispinosum* (Johnston, 1847), primary orifice from Laxe (Galicia, NW Spain; Javier Souto leg.).

Table 10. Measurements (in μm) of *Rhynchozoon pseudodigitatum* Zabala & Maluquer, 1988, neotype MZB 2025-6341, paratypes MZB 2017-0686, MZB 2025-6343, MZB 2025-6344, MZB 2019-0491. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	33	430	59.5	313	563
Autozoid width	102	321	44.7	243	451
Orifice length	35	104	9.8	82	119
Orifice width	46	129	12.7	106	150
Suboral avicularia length	39	156	25.4	106	206
Suboral avicularia width	33	82	17.3	48	122
Slender frontal avicularia length	233	111	24.1	53	199
Slender frontal avicularia width	216	45	10.9	23	77
Big frontal avicularia length	37	209	41.0	120	298
Big frontal avicularia width	37	95	35.8	49	207
Ovicell length	28	158	19.0	124	197
Ovicell width	31	193	36.6	139	274

and since a type specimen was never deposited, we designate a neotype (in accordance to the Art. 75.3.1 of the International Code of Zoological Nomenclature, ICZN 1999).

Rhynchozoon pseudodigitatum is very similar to the Atlantic species *Rhynchozoon bispinosum*. In the same work where Zabala & Maluquer (1988) described *R. pseudodigitatum* they presented another species that they (wrongly) identified as *R. bispinosum* due to the presence of two spines, when *R. pseudodigitatum* was supposed to completely lack spines. However, the present analysis on new material proved that *R. pseudodigitatum* can develop two deciduous spines in some marginal zooids. The definitive difference lies in the shape of the primary orifice, which presents a conspicuous sinus in *R. bispinosum* (Fig. 15D) but only a slight concavity in *R. pseudodigitatum* (Fig. 14E); unfortunately, this character is barely visible. Other characters, including the presence of two ephemeral spines, the development of a large umbo, the shape of the pseudo-sinus, and the shape of the labial avicularia, can be very similar depending on the ontogenic development. In his description of *C. digitata*, Waters already recognized that at a certain developmental stage, the zooids completely resemble the figures of *Lepralia bispinosa* in Hincks' British Marine Polyzoa (1880: pl. XXX fig. 1). The frontal avicularia of *R. bispinosum* (only one per zooid) are always small and are associated with marginal areolae. Only when the frontal avicularia of *R. pseudodigitatum* are abundant across the entire frontal surface, both the small and slender (1–3 per zooid) (Fig. 14H) and the rarer, larger ones (Fig. 15A), can this character be used to differentiate between the two species.

Rhynchozoon bispinosum has been widely cited in the Mediterranean (Heller 1867; Calvet 1902; Barroso 1915; Gautier 1958, 1962; Harmelin 1976) but since the citations do not include precise definitions of the primary orifices, it remains to be verified whether some or all of these citations actually refer to the species described here, *R. pseudodigitatum*. At minimum, part of the material proceeding from Harmelin's collection (see above for revised specimens) and almost all the material identified by Zabala & Maluquer (1988) as *R. bispinosum* corresponds to *R. pseudodigitatum*.

***Rhynchozoon quadrispinatum* Zabala & Maluquer, 1988**

Fig. 16; Table 11

Rhynchozoon quadrispinatum Zabala & Maluquer, 1988: 147, figs 371–375, pl. 22b–c.

? *Rhynchozoon rosae* Souto, Reverter-Gil & Fernández-Pulpeiro, 2010b: 1432, fig. 12a–d, table 10.

Material examined

Neotype (designated here)

MEDITERRANEAN SPAIN • ovicellate colony; Menorca Channel, 39.48897° N, 3.3403° E; depth 67 m; 31 Jul. 2012; *Puerulus*; scuba dive, M431, R139, stub 594; MZB 2016-3607 (Fig. 16C, measurements).

Other material

MEDITERRANEAN SPAIN • 1 ovicellate colony; Menorca Channel; 40.85403° N, 3.542017° E; depth 74 m; 10 Apr. 2011; Indemares 4; stn 100, JAGO dive, M625, stub 812; MZB 2025-6350 (measurements) • 1 ovicellate colony; same data as for preceding; stub 734; MZB 2025-6351 (Fig. 16F, measurements) • 1 ovicellate colony; same data as for preceding; stub 9187; MZB 2025-6352 • 1 ovicellate colony; same data as for preceding; M624; MZB 2025-6357 (Fig. 16D) • 1 ovicellate colony; Menorca Channel; 40.85403° N, 3.542017° E; depth 82 m; 11 Sep. 2010; Indemares 3; JAGO dive, M652, stub 811; MZB 2025-6353 (Fig. 16A, measurements) • 1 ovicellate colony; Menorca Channel; 39.85043° N, 3.506193° E; depth 70 m; 1 Aug. 2011; Indemares; trawling, M353, stub 610; MZB 2016-3627 (Fig. 16B, E, measurements) • 1 ovicellate colony; same data as for preceding; stub 9106; MZB 2016-3609 (measurements) • 1 ovicellate colony; same data as for preceding; stub 9119; MZB 2019-0503 (measurements) • 1 ovicellate colony; Menorca Channel; 40.837333° N, 3.021° E; depth 80 m; 8 Apr. 2011; Indemares 4; JAGO dive, M622, stub 9188; MZB 2025-6358 • 1 ovicellate colony; same data as for preceding; stub 9190; MZB 2025-6359 • 1 ovicellate colony; Pollença Bay, Mallorca Island; 39.94773° N, 3.26492° E; depth 53 m; CARBAL, scuba dive, M758, stub 740; MZB 2025-6360 • 1 ovicellate colony; same data as for preceding; stub 741; MZB 2025-6360 • 1 ovicellate colony; same data as for preceding; stub 742; MZB 2025-6360 • 1 ovicellate colony; Medes Islands; 42.04782° N, 3.22755° E; depth 63 m; 6 Sep. 2016; *Puerulus*; scuba dive, M474, stub 9176; MZB 2025-6363.

Redescription

Colony encrusting, forming mostly small patches of reduced number of zooids (usually less than 60) (Fig. 16A). Zooids hexagonal or quadrangular, strongly convex, celleporiform. Frontal wall thick, always smooth and vitreous with few, small, round areolae (Fig. 16B). Primary orifice orbicular, slightly wider than long, smaller than in the other species of the genus (orifice length < 100 µm, Table 11); distal and lateral rim with 16 denticles. Proximal border with a shallow U-shaped sinus (Fig. 16C), bordered by a pair of blunt condyles; three to five (mainly four) oral spines (Fig. 16C) slender and fragile in peripheral zooids (Fig. 16B), immersed in the peristome and mainly inconspicuous in older zooids. Peristome well developed enclosing the primary orifice, thickened with a blunt central mucro and 2–3 smaller knobs; with a developed uncinat process that supports the suboral avicularia (Fig. 16D). Suboral avicularium very constant except in peripheral autozooids; rostrum triangular in shape, long and narrow, with a smooth tip slightly hooked, laterally directed (Fig. 16D–F). Frontal avicularium monomorphic, small (< 100 µm), drop-shaped (characteristic), with acute, triangular mandible (Fig. 16F). Ovicell typical of *Rhynchozoon*, short and wide; imperforate, flattened frontally, with a transversely oval area of membranous ectooecium; aperture not closed by the operculum, straight edged (Fig. 16E), sometimes developing a small mucro on top and short labellum. Ancestrula not observed.

Remarks

Rhynchozoon quadrispinatum was described from two samples collected in Jul. 1985, in Pollença Bay and two others from the Cabrera archipelago (Balearic Islands, NW Mediterranean). A brief description,

supported by several illustrations and SEM photographs (Zabala & Maluquer 1998: 147, figs 371–375, pl. 22b–c) but missing the ovicell was included in the *Illustrated Keys of Mediterranean Bryozoans* (Zabala & Maluquer 1988). Since then, we have collected again many ovicellate samples of the species in different areas of the Balearic Islands and Columbretes Archipelago; however, the complete description,

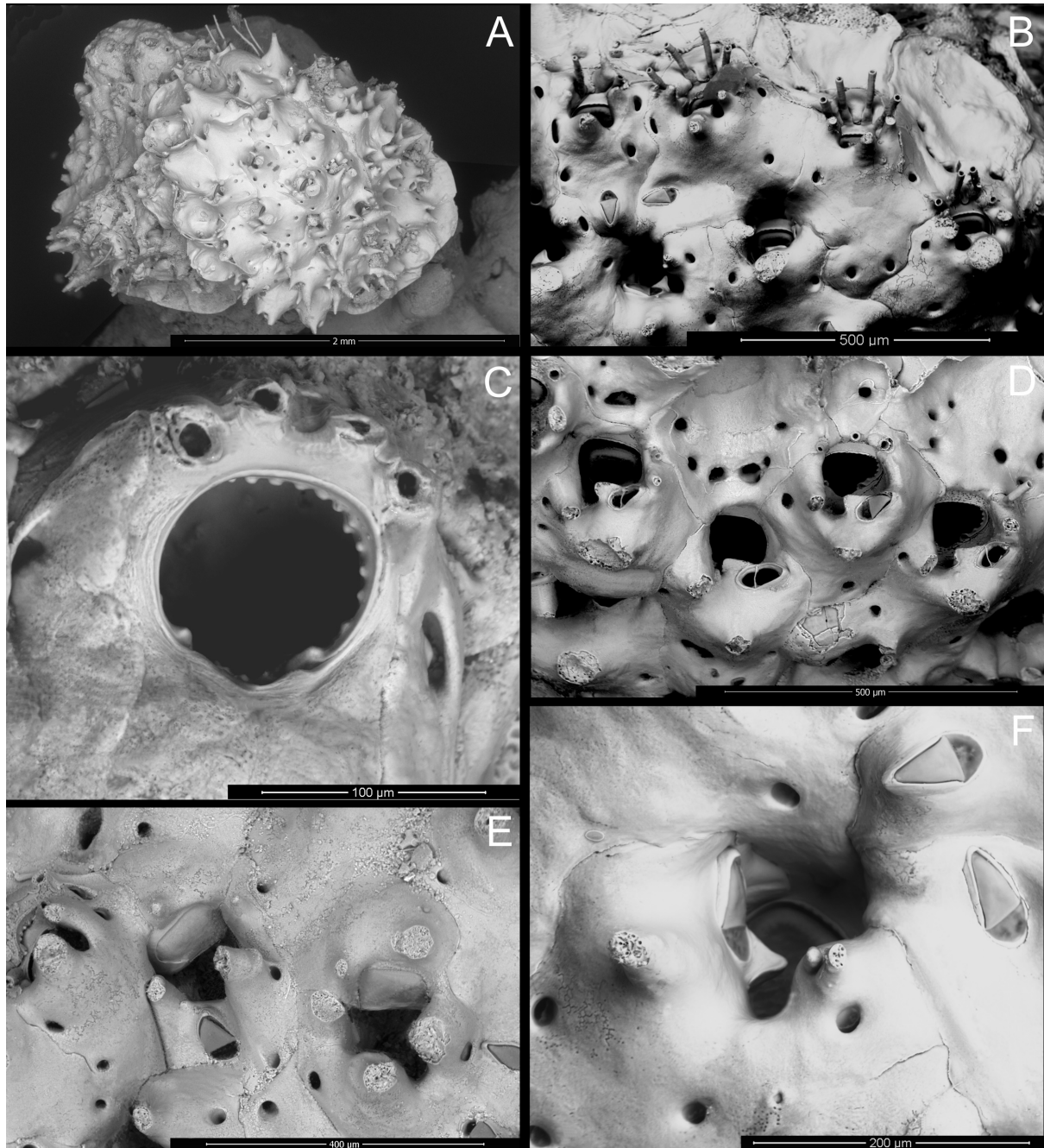


Fig. 16. *Rhynchozoon quadrispinatum* Zabala & Maluquer, 1988. **A.** Encrusting colony forming a small patch over maerl rhodolites (MZB 2025-6353). **B.** Marginal autozooids with spines (MZB 2016-3627). **C.** Primary orifice with 12 denticles, U-shaped sinus, a pair of blunt condyles and 4 spines (neotype MZB 2016-3607). **D.** Secondary orifice showing the big uncinuate process and suboral avicularia (MZB 2025-6357). **E.** Frontal avicularia (top right) and suboral avicularia (down left) (MZB 2016-3627). **F.** Ovicell developing short labellum and small mucros on top (MZB 2025-6351).

Table 11. Measurements (in μm) of *Rhynchozoon quadrispinatum* Zabala & Maluquer, 1988, neotype MZB 2016-3607, and other material MZB 2025-6350, MZB 2025-6351, MZB 2025-6353, MZB 2016-3609, MZB 2019-0503. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	57	339	43.1	247	439
Autozoid width	89	295	58.4	193	480
Orifice length	23	81	13.0	60	106
Orifice width	39	100	12.3	79	144
Suboral avicularia length	10	71	15.0	35	85
Suboral avicularia width	8	33	3.8	25	38
Avicularia length	68	76	11.6	58	124
Avicularia width	73	35	4.1	24	48
Ovicell length	29	161	21.8	87	217
Ovicell width	34	168	26.7	115	205

biometric study and selection of types remained to be settled. This paper tries to amend this lack and we designate here a neotype since the original material was never deposited (in accordance to the Art. 75.3.1 of the International Code of Zoological Nomenclature, ICZN 1999).

At the time of its description, *R. quadrispinatum* was the only species of *Rhynchozoon* of the Atlanto-Mediterranean region provided with four oral spines and this fact rendered it easily distinguishable from all the other described species of *Rhynchozoon*. In 2010, Souto *et al.* described another species of *Rhynchozoon* provided with four spines from the coasts of the Algarve (South Portugal) as *Rhynchozoon rosae* Souto, Reverter-Gil & Fernández-Pulpeiro, 2010. Even if it is supported by both a good SEM iconography and biometric study, the description of this new species lacks some key characters as the form of the primary orifice, obscured by the suboral avicularium (Souto *et al.* 2010b: fig. 12c–d), the ovicells or the ancestrula.

These authors studied the material of *R. quadrispinatum* (two specimens from Cabrera) and considered that their material showed enough differences to be considered as a different species. We disagree with this opinion, as we consider that the differences between the two species are very vague and probably can be explained by differences in the ontogenetic degree of development of the specimens selected for each description: those from Zabala & Maluquer putting the focus on young, peripheral zooids and those of Souto *et al.* (2010b), coming from central, older and fully developed zooids. Indeed, the main differences between both species seem to lay in the length and thickness of the oral spines and on the development of frontal knobs. In a fully developed colony, the younger peripheral autozooids show four long and slender spines; furthermore, they lack both the stout frontal umbones and the suboral avicularia, allowing for a complete vision of the primary orifice. But the more we move to the centre of the colony, the more the frontal umbones and the suboral avicularium develop to hide the orifice; even if the basis of the spines remain, they are often covered by secondary calcification to appear as an uncinat process; furthermore, they are almost completely obscured by the peristome.

Moreover, the metric data corroborate an almost full coincidence (see Table 11). The other noted divergence was the habitat where these specimens were collected. Original material of *R. quadrispinatum* came from two different environments: a dark cave, 20 m deep and circalittoral sample, 40 m deep, where the red alga *Osmundaria volubilis* (L.) R.E. Norris was the dominant species; in contrast, *Rhynchozoon rosae* was described from maerl bottoms at 19 m depth. In later samplings many other colonies of

R. quadrispinatum have been collected, most of them on maerl bottoms of the Menorca Channel, showing that rhodolits of red coralligenous algae constitute the preferred substratum for this species. Thus, also the habitat divergence seems an artifact, only due to insufficient sampling. In summary, we suspect that *R. rosae* could be a junior synonym of *R. quadrispinatum*; but this assumption needs more material of *Rhynchozoon rosae* to be collected.

***Rhynchozoon trifolium* sp. nov.**

[urn:lsid:zoobank.org:act:D961DAD3-9C8B-49FB-A817-0C48AECE078D](https://zoobank.org/act:D961DAD3-9C8B-49FB-A817-0C48AECE078D)

Fig. 17; Table 12

Differential diagnosis

Colony encrusting, unilaminar, autozooids recumbent, disordered; frontal shield smooth, with 6–8 scattered asymmetrical areolae which appear as bi or tri-lobate because of the presence of small denticulations growing to the center of the pore. Primary orifice wider than long; distal margin sub-quadrate, with 17–19 small denticulations; proximal margin with quadrate condyles but lacking sinus; obscured by a stout, transverse uncinat process. Suboral avicularium triangular, with a hooked rostrum; frontal avicularia monomorphic, usually single, triangular. Ovicell sub-spherical, longer or as long as wide, immersed in the peristome, smooth, with part of the entooecium visible in the frontal area and a mucro on top.

Etymology

Latin adjective, in reference to the trifoliate shape of some of their characteristic areolar pores.

Material examined

Holotype

MEDITERRANEAN SPAIN • ovicellate colony; Medes Islands; 42.04502° N, 3.22554° E; depth 27 m; 20 Jul. 2013; scuba dive, M348, stub 471; Mikel Zabala leg.; MZB 2015-8309 (Fig. 17F).

Paratypes

MEDITERRANEAN SPAIN • 1 non-ovicellate colony; Medes Islands; 42.05201° N, 3.22212° E; depth 36 m; 9 Sep. 2016; scuba dive, M485, stub 9221; Mikel Zabala leg.; MZB 2025-6366 (Fig. 17B, G) • 2 ovicellate colonies; Illa Portaló, Cap de Creus; 42.33367° N, 3.28599° E; depth 40 m; 17 Jul. 2017; scuba dive, M521, R235, stub 646; Mikel Zabala leg.; MZB 2025-6367 (Fig. 17C–E) • 1 ovicellate colony; same data as for preceding; stub 745; MZB 2025-6368 • 1 ovicellate colony; Cap Norfeu, Cap de Creus; 42.23904° N, 3.26588° E; depth 25 m; 28 Jun. 2020; scuba dive, M593, stub 9156; Mikel Zabala leg.; MZB 2025-6369 (Figs 17A, H).

Description

Colony encrusting, forming small patches of medium size (fewer than 200 autozooids) (Fig. 17A). Young marginal autozooids hexagonal or quadrangular, almost as wide as long, strongly convex. Older autozooids erect, disordered, with inconspicuous margins obscured by secondary calcification. Frontal wall thick, always smooth and vitreous. Few (4–6), small, scattered areolae with asymmetrical outlines that are bi- or tri-foliate due to the presence of small denticulations growing toward the center of the pore (Fig. 17B). Primary orifice always obscured by a transverse, stout uncinat process (Fig. 17C); wider than long; distal border sub-quadrate (not rounded), distal and lateral rim denticulate with 17–19 fine denticulations; proximal border lacking sinus, almost flat with two quadrate condyles at each angle (Fig. 17D); two deciduous spines in young peripheral zooids, slender and fragile (Fig. 17C). Peristome well developed all around the primary orifice, with 4–5 knobs of similar size, not developing large, digitate umbones (Fig. 17E). Suboral avicularium lying on the uncinat process, laterally directed,

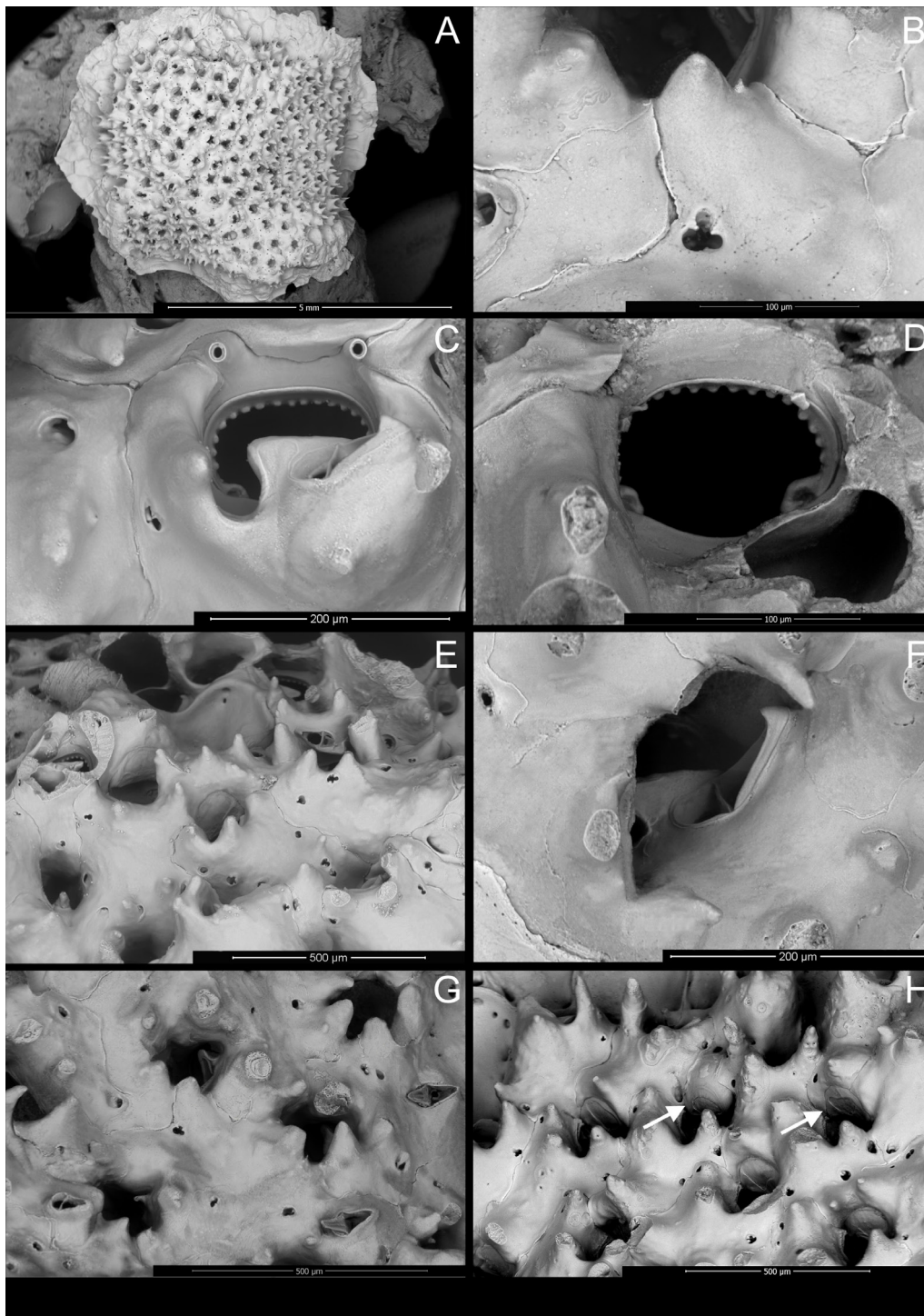


Fig. 17. *Rhynchozoon trifolium* sp. nov. **A.** Colony view (paratype MZB 2025-6369). **B.** Tri-foliate areolae (paratype MZB 2025-6366). **C.** Primary orifice normally obscured by uncinat process (paratype MZB 2025-6367). **D.** Primary orifice sub-quadrata, with two quadrate condyles and with 17–19 fine denticulations (paratype MZB 2025-6368). **E.** Peristome well developed all around the primary orifice, with 4–5 knobs (paratype MZB 2025-6367). **F.** Suboral avicularium laying on the uncinat process, laterally directed, triangular, with a hooked rostrum (holotype MZB 2015-8309). **G.** Rare frontal avicularia (paratype MZB 2025-6366). **H.** Immersed ovicell with uncovered area of entoecium (white arrows) and mucro (paratype MZB 2025-6369).

Table 12. Measurements (in μm) of *Rhynchozoon trifolium* sp. nov., holotype MZB 2015-8309, paratypes MZB 2025-6366, MZB 2025-6367, MZB 2025-6369. Abbreviations: N = number of measurements; SD = standard deviation.

	N	Mean	SD	Minimum	Maximum
Autozoid length	14	373	41.7	311	429
Autozoid width	16	266	20.3	235	314
Orifice length	2	88	4.2	85	91
Orifice width	6	134	5.6	127	141
Suboral avicularia length	7	87	10.7	73	107
Suboral avicularia width	2	34	13.4	24	43
Avicularia length	14	85	9.7	75	104
Avicularia width	14	43	7.7	30	60
Ovicell length	10	200	13.8	173	220
Ovicell width	12	156	15.7	131	190

triangular, with a hooked rostrum (Fig. 17C, F). Frontal avicularia monomorphic, usually single, rare or even inexistent in large areas of the colonies; triangular, on the plane of the frontal shield, variously oriented, mostly near the margins of autozooids (Fig. 17G). Ovicell sub-spherical, immersed in the distal autozooids and peristome, longer or as long as wide (Table 12), smooth, with an uncovered area of entooecium frontally and a mucro on top (Fig. 17E, H). Ancestrula unknown.

Remarks

Rhynchozoon trifolium sp. nov. must have been overlooked by early Mediterranean bryozoologists, perhaps being confused with the repeatedly cited Atlantic species *R. bispinosum*, which is probably absent from the Mediterranean Sea. Indeed, both species share several morphological characters including the number of oral spines (two), the general shape of frontal shield and avicularia, most metrical attributes and the number of denticulations of the distal border of primary orifice. Nevertheless, at least three features clearly distinguish them when studied under SEM. First, the proximal margin of the primary orifice in *R. trifolium* lacks a sinus, showing instead a gentle concavity framed by two strong, quadrate condyles; conversely, in *R. bispinosum*, the proximal margin of primary orifice has a V-shaped sinus and two flatter condyles (Fig. 15D).

Second, and most characteristically, the singular shape of the areolar pores in *R. trifolium* sp. nov. are not round as in *R. bispinosum* (and all other known species of *Rhynchozoon*), but are irregularly bi- or tri-lobate due to the presence of 2–3 small denticulations (this detail, which is clearly visible under SEM, may have been overlooked by bryozoologists working with older stereo microscopes).

Third, the shape of the ovicell in *R. trifolium* sp. nov. is uniquely longer than wide, whereas all other species of *Rhynchozoon* show ovicells that are clearly wider than long; furthermore, it exhibits a pointed mucro on the upper surface that may also be present in other species (e.g., *Rhynchozoon quadrispinatum*) but not in *R. bispinosum*.

The shape of the primary orifice, with its gentle concavity lacking a true sinus, brings *R. trifolium* sp. nov. closer to *R. pseudodigitatum*; they also share two deciduous oral spines. Nevertheless, the latter species has a bigger suboral avicularium, two types of different frontal avicularia, a frontal shield with large, rounded areolae, and peristomes that exhibit a stout, digitate umbo.

Discussion

Despite being one of the most intensively studied marine regions, the Mediterranean Sea continues to reveal new bryozoan species. The steady increase in recorded species from 475 in 2003 to 558 in 2023 (Rosso 2003; Rosso & Di Martino 2016, 2023) highlights the important contribution of numerous generic revisions undertaken during the last 25 years (Berning & Kuklinski 2008; Berning *et al.* 2008; Rosso & Novosel 2010; Souto *et al.* 2012; Vieira *et al.* 2013, 2014; Fehlaue *et al.* 2015; Reverter-Gil *et al.* 2015; Berning *et al.* 2019; Harmelin *et al.* 2019; Madurell *et al.* 2019; Reverter-Gil & Souto 2019; Harmelin 2020; Ramalho *et al.* 2020; Rosso *et al.* 2020a, 2020b; Berning *et al.* 2021; Di Martino & Rosso 2021; Ramalho *et al.* 2022; Ramalho & Caballero-Herrera 2022; Harmelin & Rosso 2023).

Although most of these works agree that the Mediterranean bryozoan fauna remains incompletely known, after accounting for all these revisions, our perspective is somewhat different: the study of more than 750 samples, collected from the shallow and deep waters of the Catalano-Balearic Sea, has rendered difficult to detect problematic specimens that have not yet been correctly described.

Nevertheless, some exceptions remain, and our recent efforts to update the checklist of calcified bryozoans in the Catalano-Balearic area (NW Mediterranean) have led to the discovery and description of nine new species or subspecies, and the clarification of four poorly described taxa.

Setting aside certain genera of Cyclostomatida (such as *Crisia* or *Disporella*) or Ascophorina (i.e., *Reteporella*) that will necessarily need to be addressed by molecular taxonomy (Baptista *et al.* 2002, 2024; Waeschenbach *et al.* 2009; Taylor *et al.* 2015) and have remained outside the scope of this study, our challenge has focused on three genera that have shown special difficulties for three different reasons.

The *Puellina* complex

The previous super-genus “*Puellina*”, now split into the genera *Cribrilaria*, *Glabrilaria*, and *Puellina*, is a highly speciose group, probably involved in a process of recent speciation throughout the Atlanto-Mediterranean region. In this group, a number of subspecies arranged in more or less geographical clines have been identified (Harmelin & Aristegui 1988).

The material from the Menorca Channel yielded three new subspecies within the family Cribriliniidae. The designation of these three new subspecies – *Cribrilaria pseudoradiata balearica* subsp. nov., *Cribrilaria setiformis alata* subsp. nov., and *Glabrilaria corbula cyranosa* subsp. nov. – is based on very fine but consistent morphological differences related to regional endemism and the existence of microevolutionary processes. These findings underscore the need for integrative approaches: incorporating molecular analyses would be essential to understand the evolutionary relationships and biogeographic patterns underlying these taxonomic differences.

The genus *Cellepora*

A very different case is that of the genus *Cellepora*, where perhaps the absence of clear discriminative characters (other than metric ones), within a framework of general structural homogeneity, has hindered the recognition of its true diversity.

In their checklists of Mediterranean bryozoans, Rosso & Di Martino (2016, 2023) listed only three different species of *Cellepora*: *C. adriatica* Hayward & McKinney, 2002; *C. posidoniae* (Hayward, 1975); and *C. pumicosa* (Pallas, 1766). However, the recognition of two new species of *Cellepora*, *C. ballesterosi* sp. nov., *C. gili* sp. nov., and a potentially new species, *Cellepora* sp.?, in such a small area of the Mediterranean Sea as the Catalano-Balearic Sea suggests that the true diversity of the genus *Cellepora* in the Mediterranean has been underestimated and calls for a revision of its status throughout the entire Mediterranean basin.

The genus *Rhynchozoon*

The problems with the genus *Rhynchozoon* are of a different nature and mainly twofold. On the one hand, as occurs with all members of the family Phidoloporidae, the colonies show an astonishing ontogenic variability, to the extent that observation of representatives from only one of the different developmental stages may lead to the creation of different species from a single true species (Madurell *et al.* 2019). On the other hand, the singular arrangement whereby the zooids stack like roof tiles and the development of stout peristomial umbos prevents observation of the most discriminative characters, which are those surrounding the apertures.

Probably due to these obstacles, the genus *Rhynchozoon* has been very poorly described by Mediterranean bryozoologists, and considerable uncertainty has persisted around the exact composition of the Mediterranean fauna. In their latest checklist, Rosso & Di Martino (2023) listed seven known species: *Rhynchozoon bispinosum*; *R. digitatum* (Waters, 1879); *R. larreyi* (Audouin, 1826); *R. neapolitanum* Gautier, 1962; *R. pseudodigitatum* Zabala & Maluquer, 1988; *R. quadrispinatum* Zabala & Maluquer, 1988; and *Rhynchozoon* sp. I sensu Hayward (1974).

However, this work demonstrates that the actual diversity of *Rhynchozoon* in the Mediterranean is far from well established: *R. larreyi* is a well-known species, probably confined to the Eastern Mediterranean basin, and *R. neapolitanum* is a well-known species from the Western and Central basins, but the status of all other species remains controversial.

The *Rhynchozoon bispinosum* enigma

Another enigmatic species, *Rhynchozoon bispinosum*, has been cited in Mediterranean reports, further contributing to the controversial status of Mediterranean species of *Rhynchozoon*. In the absence of details of the primary orifice, both species (*R. bispinosum* and *R. digitatum*) may appear very similar; indeed, in his description of *Cellepora digitata*, Waters already recognized that at a certain stage of development, the zooids completely resemble the figures of *Lepralia bispinosa* in Hincks' *British Marine Polyzoa* (1880: pl. XXX fig. 1).

Rhynchozoon bispinosum has been widely cited from the Mediterranean (Heller 1867; Calvet 1902; Barroso 1915; Gautier 1958, 1962; Harmelin 1976), but since the citations do not include precise definitions of the primary orifices, it remains to be verified whether some or all of these citations actually refer to the species described here, *R. pseudodigitatum*. At minimum, part of the material from Harmelin's collection (see above for revised specimens) and almost all the material identified by Zabala & Maluquer (1988) as *R. bispinosum* (the remainder has been identified as *R. trifolium* sp. nov.) corresponds to *R. pseudodigitatum*.

At present, we suspect that *R. bispinosum* may not actually occur in the Mediterranean.

By improving the long-required redescriptions of *Rhynchozoon pseudodigitatum* and *R. quadrispinatum*, in addition to the designation of neotype specimens, by describing two new species (*R. garraboui* sp. nov. and *R. trifolium* sp. nov.), and by amending the description of *R. neapolitanum*, we expect to have contributed to the clarification of the status of this genus in the Mediterranean. Nevertheless, a satisfactory revision of the genus will require re-examining museum type specimens, assembling much larger collections, and studying material from additional Mediterranean regions..

The description of *Schizomavella* (*Schizomavella*) *harmelini* sp. nov. resolves a long-misidentified species of *Schizomavella*, historically attributed to *S. hastata* (Hincks, 1862). Similarly, the designation of *Palmiskenea diazi* sp. nov. clarifies the true identity from earlier attributions to *Palmicellaria* aff. *aviculifera*. Both cases highlight the need for reevaluating historical records and integrating detailed morphological analysis to refine bryozoan taxonomy.

All these new descriptions and taxonomic clarifications indicate that even in well-explored regions significant gaps in biodiversity knowledge persist. Overall, this work provides new insights into bryozoan biodiversity, biogeography, and taxonomy, and highlights the ongoing need for detailed faunal surveys and taxonomic revisions.

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