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Collarina denticulata Harmelin n. sp., Marseille, Frioul Islands, paratype MNHN-IB-2014-1917.

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ABSTRACT

The genus *Collarina* Jullien, 1886 (Cribrilinidae Hincks, 1879) has until now been known from the Atlantic-Mediterranean region as just two species, *C. balzaci* (Audouin, 1826), synonym of *Collarina cribrosa* Jullien, 1886, type species of the genus, considered to be widely distributed from the northern British Isles to the SE Mediterranean, and *C. fayalensis* Harmelin, 1978 from the Macaronesian Isles. Abundant material collected in the Mediterranean and the NE Atlantic, coupled with examination of museum specimens, allowed better definition of the species-specific morphological features in this genus and some generic traits (ooecium formation, avicularia with nested cystids). Besides the redescription of *C. balzaci* and *C. fayalensis*, this study led to the description of four new species: *C. denticulata* Harmelin, n. sp., recorded only in the Mediterranean, *C. gautieri* Harmelin, n. sp., present in both the NE Atlantic and the Mediterranean, *C. macaronensis* Harmelin, n. sp., from Madeira, Azores and

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disturbance
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new species.

MOTS CLÉS
Biogéographie,
habitat,
bryozoaires,
chélostomes,
Cribrilinidae,
bioindicateurs de
perturbation,
espèces nouvelles.

Galicia, and *C. speluncola* Harmelin, n. sp., from the Mediterranean and the Gulf of Cadiz. A seventh morphotype (*Collarina* sp., from the Mediterranean, seemingly close to *C. speluncola* Harmelin, n. sp., has been left unnamed pending the availability of more abundant material. It was proven that *C. balzaci*: 1) has often been confused with *C. gautieri* Harmelin, n. sp.; 2) is exclusively epiphytic (mainly on *Posidonia oceanica* (L.) Delile, 1813 and brown seaweeds), with life-cycle adapted to ephemeral hosts; 3) is widely distributed in the Mediterranean, but also present in the Canaries on seaweeds, and has probably been overlooked in similar habitats in other warm-temperate NE Atlantic localities; and 4) is able to proliferate dramatically on *Posidonia* leaves in association with diatoms under unusual environmental conditions (Gulf of Gabes, chemical disturbance). All *Collarina* species live in coastal areas, mostly at shallow depth, in shaded microhabitats: plants (*C. balzaci*), dark cave walls (*C. speluncola* Harmelin, n. sp.) and small hard substrates, e.g. shells, pebbles, and anthropogenic debris (all other species).

RÉSUMÉ

Diversité insoupçonnée du genre Collarina Jullien, 1886 (Bryozoa, Cheilostatimida) dans la région Atlantique NE-Méditerranée : nouvelles espèces et réévaluation de C. balzaci (Audouin, 1826) et C. fayalensis Harmelin, 1978.

Le genre *Collarina* Jullien, 1886 (Cribrilinidae Hincks, 1879) n'était connu de la région atlantico-méditerranéenne que par deux espèces, *C. balzaci* (Audouin, 1826), synonyme de *Collarina cribrilosa* Jullien, 1886, espèce type du genre, considérée comme largement distribuée depuis le nord des îles britanniques jusqu'au SE de la Méditerranée, et *C. fayalensis* Harmelin, 1978 des îles macaronésiennes. Un abondant matériel collecté en Méditerranée et en Atlantique NE, couplé avec l'examen de spécimens de muséums, a permis une meilleure discrimination des espèces par leurs caractères morphologiques et la caractérisation de certains traits génériques (formation de l'ooécium, aviculaires avec cystides emboîtés). En plus de la redescription de *C. balzaci* et de *C. fayalensis*, cette étude a conduit à la description de quatre nouvelles espèces : *C. denticulata* Harmelin, n. sp., seulement récoltée en Méditerranée, *C. gautieri* Harmelin, n. sp., présente à la fois en Atlantique NE et en Méditerranée, *C. macaronensis* Harmelin, n. sp., de Madère, des Açores et de Galice, *C. speluncola* Harmelin, n. sp., de Méditerranée et du golfe de Cadix. Le statut spécifique d'un septième morphotype, *Collarina* sp., de Méditerranée, apparemment proche de *C. speluncola* Harmelin, n. sp., n'a pas été précisé dans l'attente d'un matériel plus abondant. Il a été établi que *C. balzaci*: 1) a été souvent confondue avec *C. gautieri* Harmelin, n. sp.; 2) est exclusivement épiphyte (principalement sur *Posidonia oceanica* (L.) Delile, 1813 et des algues brunes) avec un cycle de vie adapté à ces substrats éphémères; 3) est largement distribuée en Méditerranée mais aussi présente aux Canaries sur des algues, un habitat où sa présence dans d'autres sites tempérés chauds de l'Atlantique NE est probable; et 4) est capable de proliférer de manière spectaculaire sur les feuilles de posidonies en association avec des diatomées dans des conditions environnementales inhabituelles (golfe de Gabès, perturbations chimiques). Toutes les espèces de *Collarina* vivent en zone côtière, principalement à faible profondeur dans des microhabitats ombragés : plantes (*C. balzaci*), parois de grotte obscure (*C. speluncola* Harmelin, n. sp.) et petits substrats durs, e.g. coquilles, cailloux et débris d'origine anthropique (toutes les autres espèces).

INTRODUCTION

Awareness that bryozoan species boundaries must be (re)assessed on the basis of precise morphological features highlighted by scanning electron microscopy (SEM) is now well-established, and has boosted an increasing number of taxonomic revisions during the last decade. This trend is supported by the good congruence between small but constant morphological differences and genetic divergence noted in several taxa (e.g. Dick & Mawatari 2005; Fehlauer-Ale *et al.* 2011). Another impetus to taxonomic reassessment is the increasing availability of material supplied by oceanographic campaigns and sampling surveys by diving. It is thus now widely admitted that our knowledge of the diversity of Bryozoa is still substantially incomplete, even in areas where this group has benefited from a large number of studies over a long time, such as the NE Atlantic-

Mediterranean region. Recent taxonomic revisions have thus resulted in unexpected species splitting (e.g. Harmelin 2006; Reverter-Gil *et al.* 2016; Berning *et al.* 2017).

Many poorly defined early-described taxa are obvious examples of catch-all names such as, among Cribrilinidae Hincks, 1879, *Collarina balzaci* (Audouin, 1826) and *Cribrilina punctata* (Hassall, 1841), which have often been mixed up. The taxonomic status of the genera *Collarina* Jullien, 1886 and *Cribrilina* Gray, 1848, and that of species assigned to them, have been clouded by considerable confusion, which Bishop (1986, 1988, 1994) sought to clarify, including the re-assignment to the genus *Collarina* of a specimen previously chosen as the neotype of *C. punctata*, the type-species of *Cribrilina* Gray, 1848.

Up to now, only three species were included in the genus *Collarina*: *C. balzaci* (Audouin, 1826) (WoRMS 111310) recorded from the Mediterranean and the NE Atlantic, *C. fay-*

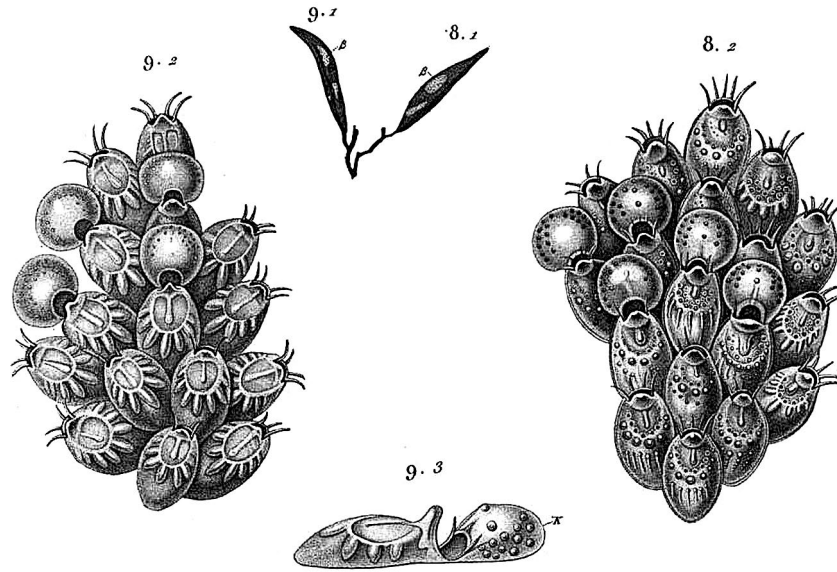


FIG. 1. — Savigny's drawings (1817: pl. 9). *Flustra balzaci* Audouin, 1826, in Savigny's figure 8, and *Flustra jauberti* Audouin, 1826, in Savigny's figure 9.

alensis Harmelin, 1978 (WoRMS 469700) from the Azores and *C. spicata* Winston & Vieira, 2013 (WoRMS 740596) from Brazil (Bock & Gordon 2018). In this paper, the morphological and ecological features of *C. balzaci* are reviewed, clarifying its status as an epiphytic species, *C. fayalensis* is redescribed from new Macaronesian material, and four new species are created: *C. speluncola* Harmelin, n. sp. and *C. denticulata* Harmelin, n. sp. from Mediterranean material, *C. gautieri* Harmelin, n. sp., often erroneously recorded as *C. balzaci*, widely distributed in both the NE Atlantic and the Mediterranean, and *C. macaronensis* Harmelin, n. sp. recorded in the Macaronesian archipelagos and northern Iberian Peninsula. A seventh morphotype, *Collarina* sp., from the Mediterranean, is left unnamed.

MATERIAL AND METHODS

EXAMINED MATERIAL

This study was based first on a large collection of material stored at the Station marine d'Endoume, Marseille (SME) collected by J. G. Harmelin. This material included specimens of several unnamed species and unsorted substrata potentially bearing *Collarina* species, collected by diving and dredging during routine field work or oceanographic expeditions (mainly R/V *Jean Charcot* expeditions ZARCO 1966 and BIAÇORES 1971). Additional material from the Mediterranean and the NE Atlantic was provided by the co-authors and colleagues, and also by historical or more recent specimens kept at the Muséum national d'Histoire naturelle, Paris (MNHN), the Natural History Museum, London (NHMUK) and the Museo de Historia Natural, University of Santiago de Compostela (MHNUSC). Data on the studied material are given in the section 'Material examined' of each species.

Type material was deposited in the MNHN. Most other specimens are kept at the MNHN, the NHMUK and the MHNUSC.

MORPHOLOGICAL ANALYSIS

Most specimens were preserved dry. They were examined with stereomicroscopes and photographed with scanning electron microscopes (SEM) after gold-palladium coating (Hitachi S-570: SME) or without coating, using the backscattered electron (BSD) mode under variable pressure (Quanta 200 FEI, XTE 325/D8395: UB; LEO 1455VP SEM: NHMUK; FEI Inspect S50: University of Vienna).

Measurements were carried out with an eyepiece micrometer and from scales of SEM photos. All measurements are given in microns (μm). Data on costae number do not include the apertural bar.

The terminology of morphologic features follows the Glossary of Special Terms provided by the website Neogene Bryozoa of Britain (www.neogenebryozoans.myspecies.info/glossary – accessed on 27.VII.2018) and Larwood (1962), particularly for the distinction between a large and a small pseudopore or lumen-pore: pelma (plural: pelmata) and pelmatidium (plural: pelmatidia).

ABBREVIATIONS

Measured features

LZo	autozooid length;
WZo	autozooid width;
LOr	orifice length;
WOR	orifice width;
WORov	orifice width in ovicelled zooids;
LOv	ovicell length;
WOv	ovicell width.

Institutions

MHNUSC	Museo de Historia Natural, University of Santiago de Compostela;
MNHN	Muséum national d'Histoire naturelle, Paris;
MZB	Museu de Ciències Naturals de Barcelona, Barcelona;
NHMUK	Natural History Museum, London (formerly British Museum for Natural History, BMNH).

RESULTS

Family CRIBRILINIDAE Hincks, 1879

Genus *Collarina* Jullien, 1886

TYPE SPECIES. — *Collarina cribrrosa* Jullien, 1886.

Collarina balzaci (Audouin, 1826) (Figs 1-4; 7A; 18A; 19; Tables 1-3)

Flustra balzaci Audouin, 1826: 239.

Unnamed drawings – Savigny 1817: pl. 9, figs 8.1, 8.2.

Not *Lepralia cribrrosa* Heller, 1867:109, pl. 2, fig. 6.

Lepralia cribrrosa – Waters 1879: 36, pl. 9, fig. 4.

Collarina cribrrosa Jullien 1886: 607. — Gautier 1958a: 54; 1958b: 198.

Cribrilina punctata – Hincks 1886: 266, pl. 9, fig. 9.

Cribrilina cribrrosa – Calvet 1902: 16. — Gautier 1952: 10.

Puellina gattyae var. *balearica* Barroso, 1919: 340, figs 1-5.

Cribrilina balzaci – Waters 1923: 561, pl. 18, fig. 8 (in part).

Collarina balzaci – Gautier 1962: 107 (in part). — Prenant & Bobin 1966: 602 (in part), fig. 209. — Harmelin 1973: 676; 1978a: pl. 1, fig. 7 (in part). — Hayward 1974: 399, table 3 (in part). — Aristegui 1984: 229, fig. 49c; pl. 11, fig. 4-5. — Zabala 1986: 359, fig. 110. — Zabala & Maluquer 1988: 105, fig. 204. — Bishop 1988: 749, figs 1-6; 1994: 242 (in part). — Koçak *et al.* 2002: 237. — Moissette *et al.* 2007: 206, fig. 8b. — Moissette 2013: 192, fig. 13.6b. — Chimenz Gusso *et al.* 2014: 154 (part), figs 74a-b. — Lepoint *et al.* 2014: 59, 61. — Harmelin *et al.* 2016: 423 (list).

Collarina species B – Bishop 1986: fig. B.

?*Flustra jauberti* – Audouin 1826: 239 (unnamed drawings, Savigny 1817: pl. IX, figs 9.1, 9.2).

Not *Collarina balzaci* – Harmelin 1978a: 189, fig. 8. — Bishop 1994: 242 (in part), figs 66-68. — Reverter *et al.* 1995: 125. — Fernández-Pulpeiro *et al.* 1996: 110. — Rosso 1996: 60. — Hayward & Ryland 1998: 318 (in part), fig. 112 a-b. — Hayward & McKinney 2002: 36, figs 16a-c. — De Blauwe 2006: 126 (list); 2009: 270, figs 282-283; 2019: in press. — Souto *et al.* 2010: 1418 (list). — Chimenz Gusso *et al.* 2014: figs 74c-d. — WoRMS image <http://www.marinespecies.org/aphia.php?p=image&tid=110891&pic=23688> (accessed on 26.IV.2018).

Not *Cribrilina balzaci* – Waters 1899: 9, figs 31-32. — Norman 1903: 98, pl. 9, fig. 6); 1909: 292.

TYPE LOCALITY. — Levant coast, eastern Mediterranean.

MATERIAL EXAMINED. — On *Posidonia* leaves. France. Marseille, Gulf of Prado (depth unknown), 22.I.1951, coll. by Y. V. Gautier, 1 colony, MNHN. — Marseille, Planier Islet, 43°11'54"N, 5°13'43"E, 7 m, 11.VI.2017, coll. by JGH, several colonies (Fig. 3), MNHN, NHMUK. — Port-Cros Island, Croix headland, 18 m, 18.V.1967, St. JGH-67.12., 1 colony, MNHN. — Port-Cros Island, Tuf, 13 m, 8.II.1977, coll. by C. Eugène, several colonies including specimen BMNH 1987.1.4.1 illustrated by Bishop (1988, figs 3-6). — Spain. Catalonia, L'Estartit, Medes Islands, 42°2'43.05"N, 3°13'14.39"E, 8 m, VI.2017, coll. by TM-MZ,

1 colony (SEM stub TM-643), MZB. — Balearic Islands, Mallorca, Punta Galinda, 18 m, 39°33'56"N, 2°20'36.5"E, VIII.2017, coll. by TM-MZ, 5 colonies, MZB. — Tunisia. Kerkennah Islands, Ouled Ezzedine, c. 34°39'04"N, 11°06'31"E, 2-3 m, 26-27.VI.2018, coll. by JGH, hundreds of colonies, MNHN, NHMUK.

On algae. Lebanon. N Lebanon El Heri (Beaulieu), 1-5 m, coll. by G. Bitar, 3.VI.2000: 1 coated colony (SEM stub JGH-276: Fig. 2); MNHN-IB-2014-189: 2 colonies kept dry; MNHN-IB-2014-221: 3 colonies in alcohol. — Spain. Balearic Islands, Cabrera, Cap Llebeig, 39°9'45.19"N, 2°54'48.3"E, 5 m, coll. by TM-MZ, 1 colony on *Cystoseira balearica*, MZB. — France. Corsica, Scandola, Cala di l'Oru, 42°22'18"N, 8°32'42"E, 18 m, 31.VIII.2018, 2 small colonies on *Cystoseira montagnei*, coll. by JGH, MNHN.

On unidentified macrophyte. France. NW Mediterranean, Saint-Raphael, NHMUK (SEM photos: MSJ): NHMUK.1975.7.18.20. — Italy. Rapallo, NHMUK.1911.10.1.704. — Adriatic. NHMUK.1899.5.1.437. — NHMUK.1899.5.1.718. — Greece. Mediterranean, Chios, NHMUK.1987.1.22.1: E.

ADDITIONAL RECORDS. — France, Marseille, Jarre Island, Plateau des Chèvres, 12 m, 4.II.1977, coll. by C. Eugène, 1 colony on *Posidonia*. — Marseille, Frioul archipelago, Tiboulen Pomègues, 12 m, 17.VI.1977, coll. by C. Eugène, 1 colony on *Posidonia*. — Spain, Canaries Is., 2 small colonies on *Cystoseira* sp., coll. by J. Aristegui (Fig. 4).

DIAGNOSIS. — Colonies generally small, early mature; autozooids with broad gymnocyst and small costate shield with short costae relatively flat except for a peripheral bump bearing a large pelma; adventitious avicularia directed laterally perpendicular to the zooid axis, with broad semicircular opesia and short rostrum with slightly serrated edges; apertural bar in the form of a thick triangular mucro with a rounded tip bearing two pelmatidia on the proximal side; orifice poster with a straight proximal edge and two small lateral notches; 3-4 oral spines; ovicell cleithral, oecium kenozooidal; ancestrula with 5 or 6 spines.

DESCRIPTION

Colony encrusting, pluriserial, unilaminar, generally small (50-100 zooids) but occasionally larger in certain environmental conditions (see below), early maturing, with rounded outline (Fig. 2A). Autozooids subhexagonal, longer than broad with proximal part triangular; gymnocyst forming a broad, convex border, particularly extended proximally, clearly visible in frontal view except distal to the orifice; costate shield oval to round, relatively flat except for a peripheral crown of low bumps marking the summit of the ascending basal part of each costa; 5-8 (mostly 6) short costae with a smooth surface, a large pelma on the top of each basal bump, 3-4 rounded intercostal lacunae including that between the steep basal portions of costae (Figs 2C; 3B, E; 4A). Thick apertural bar, roughly triangular, bulging, with 2 pairs of pseudopores on the proximal side of the bar: small pelmatidia near the apex of the mucro, and large pelmata near the base (Figs 2C; 3C, D; 4B, C; 7A). Autozooidal orifice semicircular, wider than long, proximal edge straight with low lateral notches, anter forming a distinct frame ending proximally with slightly angular condyles, broader in ovicelled zooids (Figs 2B; 3C, D; 7A). Oral spines 3-4 with swollen base in non-ovicelled zooids, possibly more numerous in certain conditions (see below), 2 inwardly arched in ovicelled zooids (Figs 2C; 3D; 4C). Adventitious avicularia paired, single or both missing in the same colony, directed laterally on both sides of the apertural bar, subpedunculate with

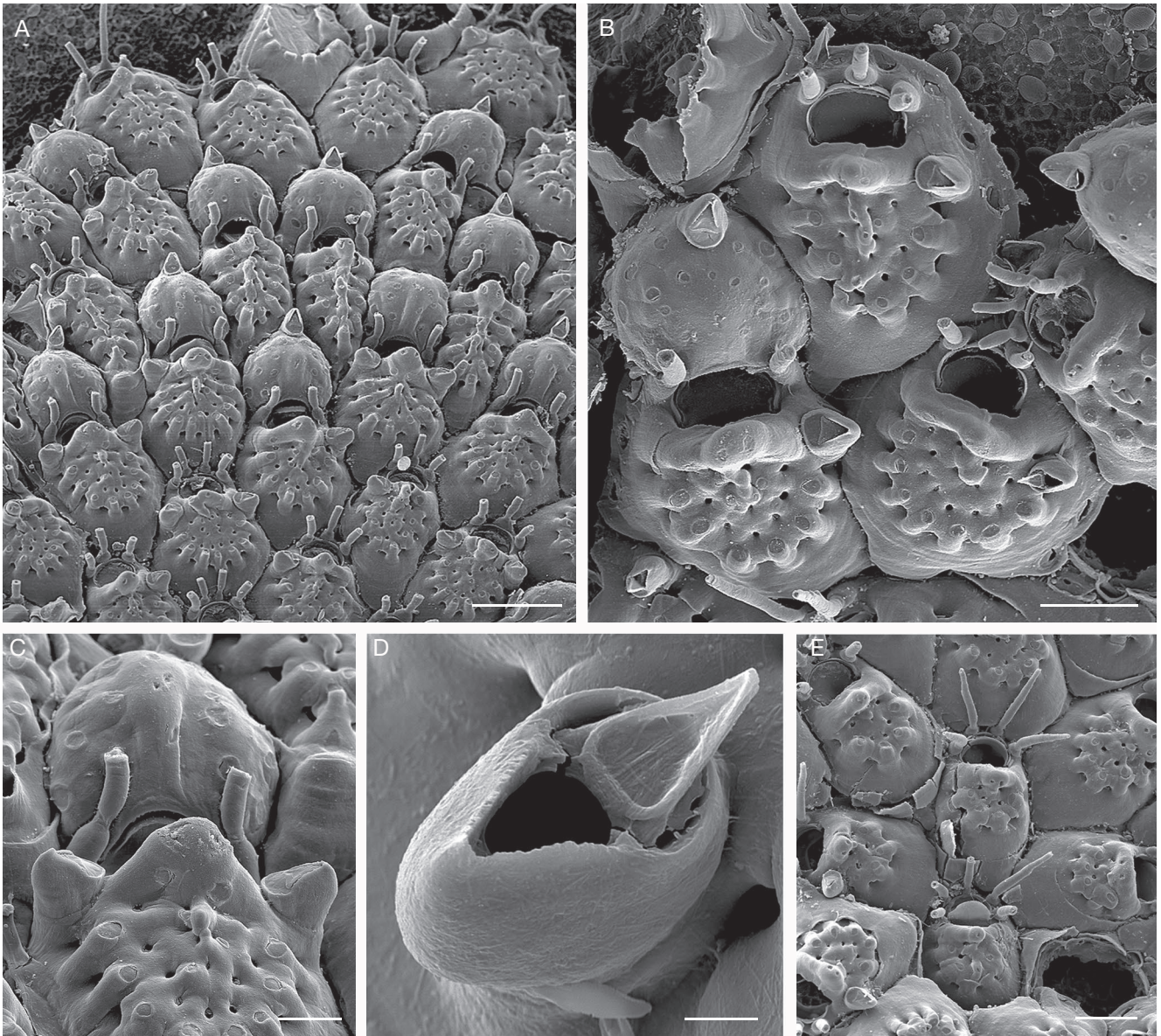


FIG. 2. — *Collarina balzaci* (Audouin, 1826), SE Mediterranean: **A**, part of colony with many ovicells; **B**, ovicelled and non-ovicelled zooids at the edge of a colony; **C**, oblique view of an ovicelled zooid with the spinocyst edge, the apertural bar with paired adventitious avicularia and curved spines; **D**, subpedunculate avicularium with slightly serrated edges of rostrum and raised mandible; **E**, ancestrula with five spines, and zone of astogenetic change. Origin: Lebanon, El Heri, on brown seaweed. Scale bars: A, 200 μ m; B, E, 100 μ m; C, 50 μ m; D, 10 μ m.

rounded proximal area, short triangular rostrum with strong condyles and slightly serrated edges, mandible in the shape of an equilateral triangle, and broad semicircular proximal opesia (Figs 2D; 3F; 4D, E). Ovicell cleithral, prominent, globose, terminal at the edge of the colony, oocidium formed by distal kenozooid, frequently bearing a distally-directed avicularium on the distal edge, ectoocidium with slightly bumpy surface dotted with numerous pelmata (Figs 2B, C; 3B; 4C). Ancestrula cribrimorph with a 4-5 irregularly swollen costae and 5 or 6 oral spines (Figs 2E; 3G; 4F).

REMARKS

The species *Flustra balzaci* was created by Audouin (1826) without description for a specimen figured by Savigny (1817:

pl. 9, fig. 8.1-2), collected during sampling surveys along the Levant coast (SE Mediterranean) during Napoleon Bonaparte's expedition to Egypt. Unfortunately, the whole collection of bryozoans gathered during this expedition has disappeared (d'Hondt 2006). The confused history of this species and of the genus *Collarina* Jullien has been detailed and clarified by Bishop (1988, 1994). In short, after Audouin (1826), Waters (1899) was the first to use the name *balzaci* for a specimen from Madeira placed in the genus *Cribrilina*, considered herein to belong to a new *Collarina* species (*C. macaronensis* Harmelin, n. sp., see below). Later, Gautier (1962) introduced the combination *Collarina balzaci*. The taxon *Collarina balzaci* was stabilized by Bishop (1988) with the designation of a neotype from Naples selected among specimens of Waters'

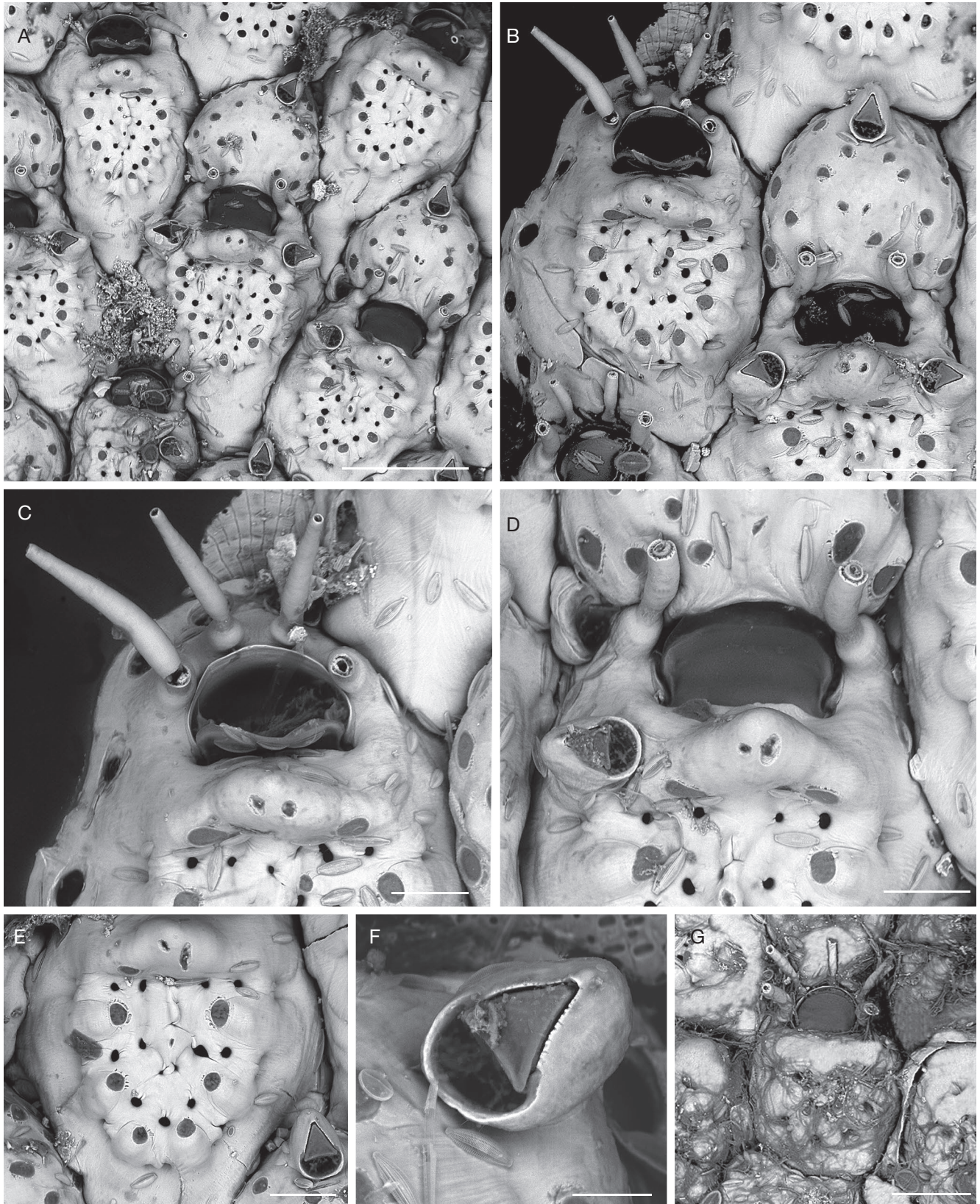


FIG. 3. — *Collarina balzaci* (Audouin, 1826), NW Mediterranean: **A, B**, ovicelled and non-ovicelled zooids, note the abundance of large pseudopores (pelmata) on both the spinocyst and the oecium; **C**, distal portion of a non-ovicelled zooid with no adventitious avicularia; **D**, distal portion of an ovicelled zooid, note the broader orifice, the shape of the apertural bar and the position of the adventitious avicularium; **E**, structure of the costate shield and the peripheral gymnocyst; **F**, adventitious avicularium with rostrum finely serrated, slightly hooked tip, and broad, rounded opesia; **G**, ancestrula with five spines, partly covered by filamentous microphyte. Origin: Marseille, Planier Islet, on *Posidonia* leaf. Scale bars: A, 200 μ m; B, G, 100 μ m; C-E, 50 μ m; F, 25 μ m.

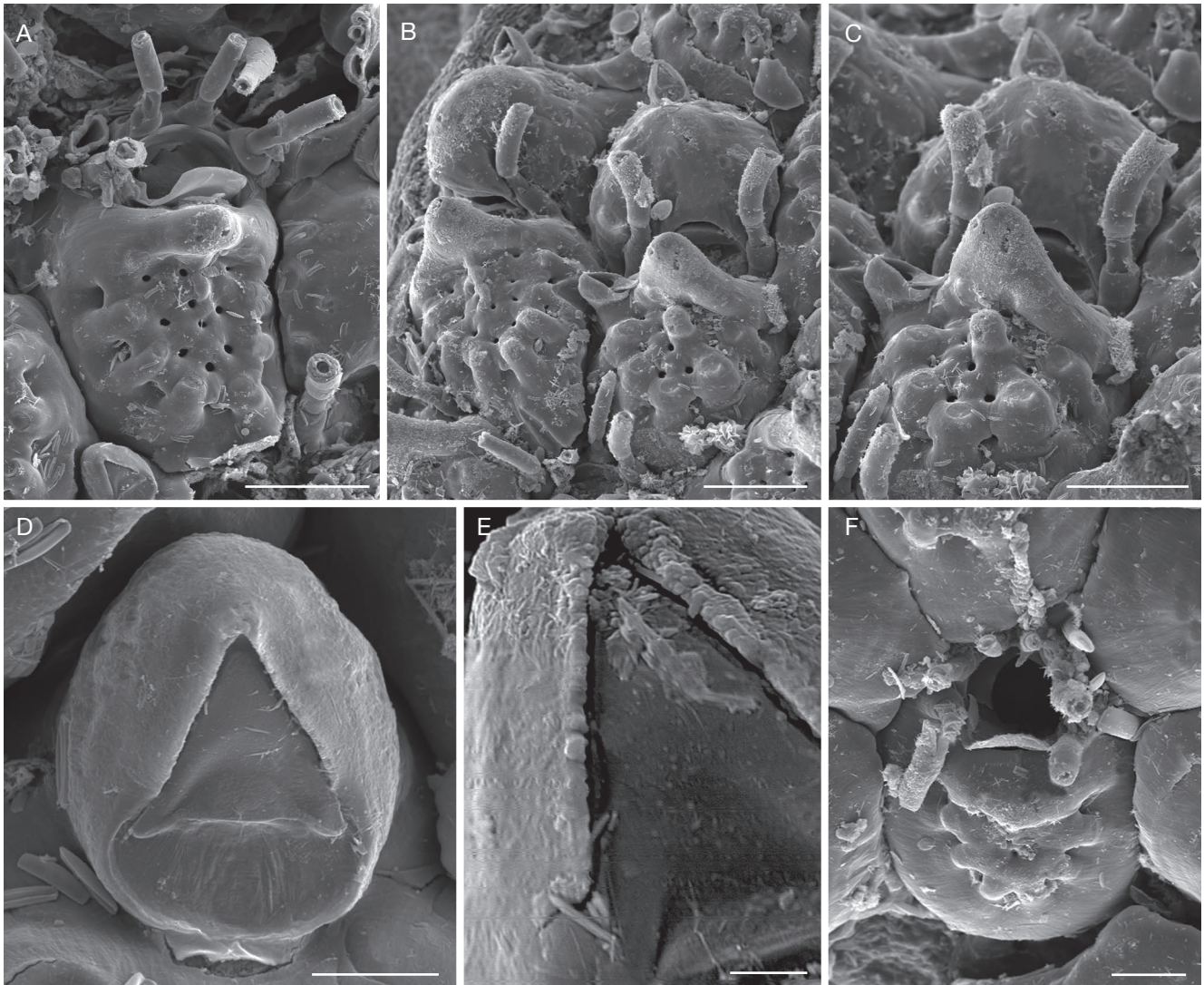


FIG. 4. — *Collarina balzaci* (Audouin, 1826), NE Atlantic: **A**, non-ovicelled autozoid; **B**, two ovicelled zooids; **C**, ovicelled zooid, closer view of the spinocyst, the apertural bar and the articulated spines with long joints; **D**, avicularium adventitious to an ovicell; **E**, avicularium, rostrum with serrated edges; **F**, ancestrula with six spines. Origin: Canaries, on *Cystoseira* sp. Scale bars: A-C, 100 μ m; F, 50 μ m; D, 20 μ m; E, 5 μ m.

collection (Waters 1879). Despite this, however, the species name *C. balzaci* was often attributed inappropriately with the assumption of high morphological plasticity. All specimens ascribed here to *C. balzaci* display the features stated above, including avicularia with broad semicircular opesia and rostrum with serrated edges (Figs 2D; 3F; 4E). This material is mostly Mediterranean, including the neotype (Bishop 1988: figs 1-2) and specimens from Lebanon (MNHN-IB-2014-189, MNHN-IB-2014-221; Fig. 2), but also includes Atlantic colonies from the Canaries collected by J. Aristegui during his thesis work (Fig. 4). The Lebanese material can be a valuable alternative to the neotype because of its geographical origin, similar to that of the specimen illustrated by Savigny (1817). Interestingly enough, he figured on the same plate (herewith Fig. 1) and on the same seaweed as *Flustra balzaci* another species with close features (pl. 9, fig. 9.1-2), which was named *Flustra jaubertii* by Audouin (1826). This species

has been almost completely ignored, however, despite its clear cribrimorph features that might also be attributed to a *Collarina* species with well-calcified zooids (e.g. raised triangular suboral umbo with median extension, small spinocyst with bases of costae protruding widely on the gymnocyst, four oral spines). To our knowledge, this species was cited only by Waters (1879) who synonymized it doubtfully with *Lepralia gattyae* Landsborough, 1852, and by d'Hondt (2006) who synonymized it with *Cribrilaria radiata* (Moll, 1803).

CASE OF THE TUNISIAN MATERIAL FROM KERKENNAH ISLANDS

The recent finding by one of us (JGH, June 2018) of an extremely abundant population of *C. balzaci* epiphytic on *Posidonia* leaves at Kerkennah Islands (north of Gabes Gulf) revealed particular colonial and zooidal features. The collection consisted of some leaves taken at random from spots of

TABLE 1. — Measurements of *Collarina* Jullien, 1886 species: *C. balzaci* (Audouin, 1826); *C. speluncola* Harmelin, n. sp.; *C. denticulata* Harmelin, n. sp.; *C. gautieri* Harmelin, n. sp.; *C. macaronensis* Harmelin, n. sp.; *C. fayalensis* Harmelin, 1978. Abbreviations: **X**, mean; **SD**, standard deviation; **N**, number of measurements and range; **LZo**, **WZo**, length and width of non ovicelled autozoid; **LOr**, **WOR**, of orifice of non ovicelled zoid; **Lov**, **WOv**, orifice of ovicell. Other abbreviations: **Atl.**, Atlantic ocean; **Kerk.**, Kerkennah Islands; **Med.**, Mediterranean.

	<i>C. balzaci</i>				<i>C. gautieri</i>		<i>C. fayalensis</i>	<i>C. macaronensis</i>	<i>Collarina</i> sp.
	–	Kerk.	<i>C. speluncola</i>	<i>C. denticulata</i>	Med.	Atl.			
LZo X	373	548	502	609	439	404	446	403	553
SD (N)	44.0 (13)	46.0 (22)	46.4 (12)	50.8 (22)	45.3 (24)	43.7 (20)	50.0 (36)	33.2 (18)	49.9 (26)
Range	328-473	460-650	435-580	535-695	335-535	330-514	340-560	340-450	485-640
WZo X	233	328	335	411	309	264	293	295	375
SD (N)	15.1 (13)	63 (22)	39.8 (12)	39.2 (22)	32.4 (24)	38.5 (20)	31.5 (36)	18.3 (18)	48.3 (26)
Range	197-256	265-540	240-380	340-485	256-360	209-309	265-410	260-320	290-485
LOr X	65	–	102	121	59	58	97	88	110
SD (N)	3.1 (9)		5.3 (12)	9.4 (41)	7.3 (7)	4.5 (5)	9.4 (24)	8.6 (34)	8.0 (26)
Range	61-71		97-110	110-140	48-68	53-63	80-112	70-110	92-120
WOR X	102	–	123	122	112	98	89	98	149
SD (N)	2.2 (9)		7.9 (12)	8.2 (41)	5.7 (7)	2.9 (5)	7.6 (24)	7.1 (34)	15.7 (26)
Range	100-106		110-135	100-135	105-120	96-103	75-105	85-110	130-180
LOv X	200	221	228	264	215	211	214	223	234
SD (N)	11.5 (9)	19.9 (15)	10.5 (12)	22.2 (21)	27.7 (18)	20.9 (16)	18.0 (28)	17.1 (11)	13.2 (8)
Range	185-215	180-245	210-245	230-315	180-265	179-259	180-255	135-255	220-245
WOv X	203	222	246	286	233	123	213	238	264
SD (N)	10.1 (9)	12.3 (15)	9.6 (12)	16.8 (21)	16.4 (18)		12.9 (28)	10.6 (11)	25.2 (8)
Range	190-213	195-235	230-265	255-315	200-270		195-240	220-255	245-308

a fragmented *Posidonia* bed at shallow depth (2-3 m at high tide). All collected leaves were heavily colonized by *C. balzaci* (e.g. 89 colonies of various sizes counted on a 64 cm long leaf, predominantly on the shaded side). In contrast, other bryozoan species usually common on *Posidonia* leaves (e.g. Harmelin 1973; Lepoint *et al.* 2014) were rare or absent. Only three other species were present in the sample, with small and scarce colonies: *Patinella radiata* (Audouin, 1826), *Electra posidoniae* Gautier, 1954, and *Microporella* sp. Preliminary investigations indicated that this population of *C. balzaci* presented other obvious peculiarities: large size of some colonies (> 150 zoo-ids), autozooids also clearly larger, with more numerous oral spines, and “dirty” surfaces owing to adherent powdery deposits (Fig. 19). A preliminary assessment indicated that the average length and width of non-ovicelled zooids were respectively 44% and 38% greater than the average values measured in the reference collection (Table 1, LZo: 537 µm vs 373 µm, WZo: 322 µm vs 233 µm), and the commonest number of oral spines was 5 instead of 3-4, and could reach 6 or 7 in some colonies. Moreover, SEM examination of two colonies showed that zooids were densely covered with diatom frustules (Fig. 19) despite ultrasonic cleaning. These atypical features are most likely related to particular local environmental conditions (see below).

GEOGRAPHIC AND HABITAT DISTRIBUTION

Collarina balzaci is present throughout the Mediterranean basin including the Adriatic. It is not endemic to the Mediterranean as noted by Koçak *et al.* (2002), but is also present in the near Atlantic. The only Atlantic material that has been correctly assigned to *C. balzaci* are the specimens from the

Canaries recorded by Arístegui (1984: pl. 11, fig. 4-5). On the other hand, all other NE Atlantic specimens ascribed to *C. balzaci* that have been examined belong to two *Collarina* species described here: *C. macaronensis* Harmelin, n. sp. and *C. gautieri* Harmelin, n. sp. (see below).

As confirmed by the present reexamination of the morphological features of *C. balzaci*, all specimens that can be assigned to this species are epiphytic. In most cases, in the Mediterranean, they are associated to leaves of the seagrass *Posidonia oceanica* (L.) Delile (Fig. 16A). This condition was implicit in the redescription of *C. balzaci* by Bishop (1988) based on two epiphytic Mediterranean specimens: the neotype, from Naples, “on seaweed at slight depth” (Waters 1879), and a specimen from Port-Cros Island on a *Posidonia* leaf (BMNH 1987.1.4.1, JGH leg.). It is worthwhile noting that the specimens collected at shallow depth in Lebanon (Fig. 2, MNHN-IB-2014-189, MNHN-IB-2014-221; Harmelin *et al.* 2016), where *Posidonia* beds are absent (Pergent *et al.* 2012), encrusted seaweeds such as the specimen illustrated by Savigny (1817). As noted by Bishop (1988: 753), among the material from Chios ascribed to *C. balzaci* by Hayward (1974), a specimen epiphytic on red algae was correctly identified while another encrusting a stone was “a different, apparently unnamed *Collarina* species”, an assertion verified here (see below, *Collarina* sp.). On the other hand, *C. balzaci* was not present in samples of *Posidonia* leaves from Chios studied by Hayward (1975). On *Posidonia* leaves, *C. balzaci* is a characteristic component of an epiphytic assemblage including *Electra posidoniae* Gautier, 1954, *Fenestulina joannae* (Calvet, 1902) and *Puellina gattyae* (Landsborough, 1852) (Gautier 1962; Harmelin 1973; Eugène 1978; Fresi *et al.* 1982; Bal-

duzzi *et al.* 1983; Koçak *et al.* 2002; Di Martino & Taylor 2014; Lepoint *et al.* 2014). This assemblage associated with *Posidonia* leaves was already present in the early Pleistocene at Rhodes (Moissette *et al.* 2007, 2016; Moissette 2013). The small size of colonies with early sexual maturity (i.e., budding of ovicells soon after ancestrular settlement) and light calcification of walls are distinctive adaptations to life on *Posidonia* leaves, a substrate with major constraints (small size, pliability, life duration generally < 1 year) (Di Martino & Taylor 2014; Lepoint *et al.* 2014). In contrast, *C. balzaci* does not encrust the rhizomes of *P. oceanica*, which provide encrusters with a more rigid, perennial and shaded habitat. The occurrence of *C. balzaci* on other seagrasses than *Posidonia* leaves appears to be infrequent, at least in regions where it is present, but this potentiality should be better documented. It was recorded on another seagrass, *Cymodocea nodosa* (Ucria) Ascherson, in northern Croatia (*vide* sketch and photos by S. Bacrun, pers. com. to JGH, Nov. 2014). Its occurrence on seaweeds is attested first by Savigny's drawings (1817: pl. 9, fig. 8) showing a specimen from the Levant coast (eastern Mediterranean) apparently encrusting pseudo-leaves of the brown seaweed *Sargassum* sp. Further records of *C. balzaci* on *Sargassum* in Sicily (Gautier 1958a) and the Canary Islands (Aristegui 1984) are worth noting. Other indications of the occurrence of *C. balzaci* on shallow-water seaweeds include a specimen on *Cystoseira balearica* Sauvageau at Cabrera Island (TM-MZ), and two colonies on *Cystoseira montagnei* J. Agarth (= *C. spinosa* Sauvageau) at Scandola, Corsica (JGH.) which suggest that *C. balzaci* is frequent in this habitat (very small sample collected by chance). Some published records are not substantiated by figures or specimens in collections, for example on brown (Gautier 1962), red (Hayward 1974) and green algae (Gautier 1958b). Its occurrence on *Udotea petiolata* (synonym of *Flabellia petiolata* (Turra) Nizamuddin) noted by Gautier (1958b) was not confirmed by a recent study on bryozoans from the coralligenous of Port-Cros Island (Harmelin 2017) in which assemblages on this alga were analysed. Mediterranean records of *C. balzaci* in non-epiphytic/epialgal conditions, such as on stones, shells, panels and other small substrates (e.g. Gautier 1962; Hayward 1974; Pisano & Boyer 1985; Rosso 1996) most likely correspond to other *Collarina* species (i.e., *C. denticulata* Harmelin, n. sp., *C. gautieri* Harmelin, n. sp. or *Collarina* sp.). In conclusion, pending a thorough revision of material from the whole Atlantic-Mediterranean region combining morphological and molecular criteria, we consider that *C. balzaci* is exclusively epiphytic/epialgal, and a better investigation of its occurrence on seaweeds in the NE Atlantic should provide a more realistic view of its distribution.

Collarina fayalensis Harmelin, 1978
(Figs 5; 7B; 15B; 17D; 18F; Tables 1-3)

Collarina fayalensis Harmelin, 1978a: 190, fig. 9. — Aristegui 1984 (in part): 230, pl. 11, fig. 7 (not fig. 6).

TYPE MATERIAL. — **Holotype and paratypes.** Azores, Faial Is., Castelo Branco, R/V *Jean-Charcot*, BIAÇORES 1971 St. P.11, 38°31'12"N,

28°42'7"W, 5-7 m, 12.X.1971, H. Zibrowius leg., 12 small colonies on pebble together with colonies of *C. macaronensis* Harmelin, n. sp. (recorded as *C. balzaci*: Harmelin 1978a), MNHN-IB-2008-7909.

OTHER MATERIAL EXAMINED. — **Azores archipelago.** Formigas Is., R/V *Jean-Charcot*, BIAÇORES 1971 St. P. 43, 37°16'14"N, 24°46'54"W, 15 m, 7.XI.1971, H. Zibrowius leg., 1 small colony on pebble, MNHN. — São Miguel Is., Ilhéu de Vila Franca do Campo, Azores Bio-Oceanographic Survey 1979, ABOS St. AC-79.6, 37°42'20"N, 25°26'33"W, 15 m, 24.VII.1979, coll. by JGH, c. 30 colonies on 7 pebbles, 5 colonies on broken *Pinna* shell, MNHN, NHMUK. — São Miguel Is., Ponta da Galera, ABOS St. AC-79.7, 37°42'25"N, 25°30'32"W, 14 m, 24.VII.1979, coll. by JGH, 3 colonies on 2 small pebbles in submarine cave; 3 colonies on *Pinna* shell, MNHN, NHMUK. — São Miguel Is., Capelas, ABOS St. AC-79.9, 37°50'37"N, 35°41'19"W, 15 m, 25.VII.1979, coll. by JGH, 6 colonies on 1 pebble, MNHN. — São Jorge Is., Ponta da Rosais, ABOS St. AC-79. 29, 38°45'06"N, 28°18'59"W, 20-22 m, 6.VIII.1979, coll. by H. Zibrowius, 1 colony on pebble, MNHN. — Graciosa Is., Ilhéu da Praia, ABOS St. AC-33, 39°03'36"N, 27°57'11"W, 20 m, 8.VIII.1979, coll. by JGH, 1 ovicelled colony on pebble from a tunnel, MNHN.

DIAGNOSIS. — Colonies small to large; autozooids longer than broad, with very extensive gymnocyst and minute costate shield, formed by 2-5 very short costae with smooth surface and a large marginal pelma; presence of large pseudopores on the gymnocyst; apertural bar poorly prominent and pierced by large pelmata; orifice longer than broad with proximal edge slightly concave, 2-5 thin oral spines; adventitious avicularia paired, directed disto-laterally; oecium kenozooidal bearing a distal avicularium; ancestrula with 5 or 6 spines.

DESCRIPTION

Colony encrusting, pluriserial, unilaminar, small- to large-sized (> 1000 autozooids). Autozooids longer than broad, roughly pentagonal with shorter distal side bearing the oral spines. Gymnocyst occupying the largest part of the frontal surface, moderately convex, punctured by several large gymnocystal pseudopores at the zooid margin or occasionally nearer to the costate shield (Fig. 5B, D, E). Costate shield very small, with only 3-4 costae in most cases (range 2-5), with smooth surface and poorly demarcated basal, ascending part, the latter bearing a large pelma and generally with a second smaller pore near the centre of the shield; intercostal lacunae generally limited to a single, very small one per pair, centrally located and a much larger, semi-rectangular "basal intercostal space" with a tiny median slot (Fig. 5G). Apertural bar low, with a slightly prominent centre, pierced by four pseudopores, two medium-sized on either side of the midline and two larger lateral pores, close to and below the base of the avicularia (Figs 5B, C, F; 7B). Adventitious avicularia paired in most cases (> 95%), directed laterally with a slight distal angle (Figs 5A, B, D, F; 14C), nested cystids occasionally present (Fig. 17D). Orifice longer than broad (Table 1), proximal edge slightly concave and often irregularly indented, with a small knob at each corner; condyles small (Figs 5B, F; 7B). Oral spines with relatively narrow base, 2-5 in non-ovicelled zooids, 3 in majority (75%), 2 relatively thin in ovicelled zooids (Fig. 5C). Ovicell present in large colonies, less frequently in medium-sized ones, bearing a distal avicularium in most cases (> 80%); oecium kenozooidal, formed at the colony edge, with surface pierced by about 12-15 medium-

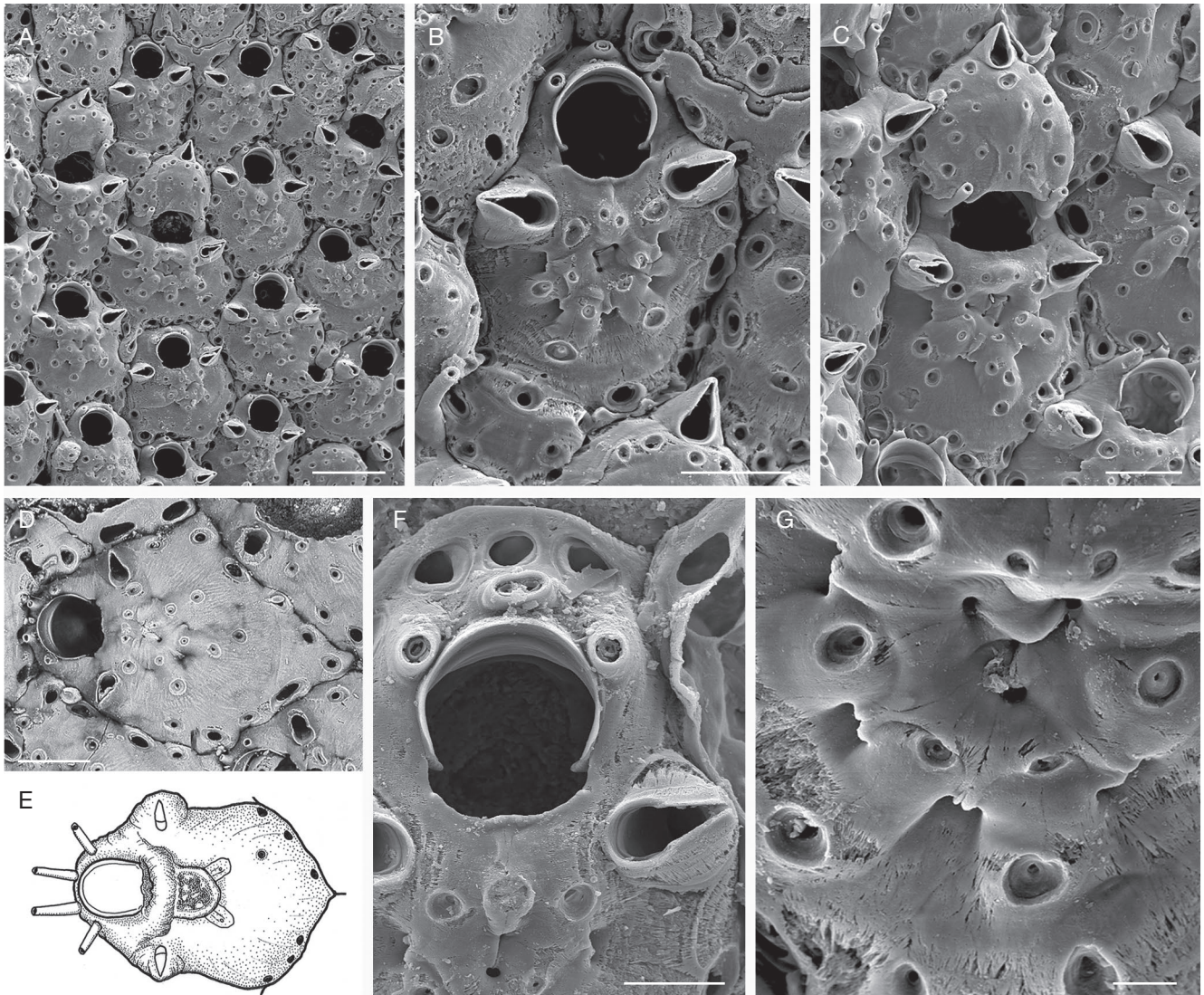


Fig. 5. — *Collarina fayalensis* Harmelin, 1978: **A-C**, non-ovicelled and ovicelled autozooids showing the structure and limited extent of the costate shield, orifice dimorphism, small spines and relatively narrow avicularia; **D**, non-ovicelled zooid, for marginal pores; **E**, drawing from Harmelin (1978: fig. 9); **F**, distal part of a non-ovicelled zooid from a colony edge; **G**, proximal half of costate shield, note the distribution of pelmata and the shape of the basal intercostal spaces. Origin: Azores - São Miguel, Vila Franca Is., 15 m (A-C, F, G); Formigas Is., 15 m, 'Jean Charcot' Białoçores 1971, P.43 (D); Faial, 'Jean Charcot' Białoçores 1971, P.11 (E). Scale bars: A, 200 µm; B-D, 100 µm, F, 50 µm; G, 25 µm.

sized pseudopores, orifice about 40% larger on average than that of a non-ovicelled zooid, a distal avicularium in most cases (Figs 5C; 15B). Ancestrula similar to older zooids but smaller, 3 very small costae, 6 spines, orifice longer than broad.

DISTINCTIVE FEATURES

Collarina fayalensis is easily identified by the minute size of the costate shield, formed by 2-4 very short costae, which contrasts with the huge development of the gymnocyst. The greater number of costae (4-6) noted by Harmelin (1978a) included the pair forming the apertural bar. The latter is typically poorly prominent and pierced by large pelmata. The presence of large pseudopores on the gymnocyst is also a peculiar feature, shared with *C. macaronensis* Harmelin, n. sp., in which these marginal pseudopores are less numerous. The Azorean material examined here, much more abundant than

the one (small colonies on a single pebble) of the type-series (Harmelin 1978a, herewith Fig. 5E), showed that this species can develop large colonies and provided information on the ovicell and the habitat. Ovicells were not frequent, present only in relatively large colonies. This feature may indicate that *C. fayalensis* is not able to develop fertile colonies on ephemeral substrates, in contrast to *C. balzaci*.

HABITAT AND GEOGRAPHICAL DISTRIBUTION

Most sampled specimens, including the types, encrusted pebbles and cobbles at shallow depth (Fig. 18F). On the other hand, few colonies were found on empty shells of *Pinna rudis* Linnaeus, 1758 from the same sites which, otherwise, were colonized by many other bryozoans. Therefore, pebbles can be considered the typical habitat of *C. fayalensis*. These pebbles and cobbles were of volcanic origin, with a smooth surface,

small- to medium-sized (up to 15 cm, but sample constraints may have limited this maximum size), and densely colonized on all faces by various species of bryozoans and secondarily by serpulids. This type of colonization, equally distributed all around the subspherical substrates, indicates that the sampling sites were washed by active water circulation limiting sedimentation. The most frequent bryozoans in the assemblage including *C. fayalensis* were *Microporella* sp., *Schizoporella* sp., *Chorizopora brongniartii* (Audouin, 1826) and *Disporella* sp. All examined specimens of *C. fayalensis* came from various localities of five Azores isles: Faial, São Miguel, Formigas, São Jorge, Graciosa. This species has also been recorded in the Canary Islands by Aristegui (1984), but his figures indicate that *C. fayalensis* co-occurs with *C. macaronensis* Harmelin, n. sp. in the Canary Islands (see below).

Collarina denticulata Harmelin, n. sp.
(Figs 6; 7C; 15D; 16E; 18C; Tables 1-3)

[urn:lsid:zoobank.org:act:2D62C756-80CF-4745-B5E3-6FC6EE64264D](https://doi.org/10.22005/zoobank.org/act:2D62C756-80CF-4745-B5E3-6FC6EE64264D)

TYPE LOCALITY. — France, Marseille, Frioul Is.

TYPE MATERIAL. — **Holotype.** France, Marseille, Frioul Is., quarantine port, 43°16'36"N, 5°18'18"E, 12 m, 26.II.1990, coll. by JGH, ovicelled colony on asbestos tile, [MNHN-IB-2014-1916](#).

Paratypes. France, Marseille, Frioul Is., quarantine port, same origin and substrate as the holotype, 3 colonies + coated colony, [MNHN-IB-2014-1917](#). — Marseille, Ratonneau Is., Croix headland, 43°17'12"N, 5°19'24"E, 5 m, 25.X.1978, coll. by JGH, 3 large colonies on underside of cobble, [MNHN-IB-2014-1918](#). — Port-Cros, Bagaud Is., 43°00'56"N, 6°21'37"E, 7 m, IX.1985, coll. by JGH, 5 colonies on plastic debris, [MNHN-IB-2014-1919](#).

OTHER MATERIAL EXAMINED. — **France.** Gulf of Fos, Renaire, 43°22'00"N, 5°00'27"E, 10 m, 25.VII.1994, coll. by JGH, 8 large colonies on biogenic flat stone, MNHN. — Côte Bleue, La Vesse, 43°20'29"N, 5°15'43"E, 6 m, 03.VII.1999, coll. by JGH, 3 colonies on *Haliotis* shell, MNHN. — Marseille, Frioul Is., quarantine port, 43°16'36"N, 5°18'18"E, 4 m, 28.I.1971, coll. by JGH, 5 colonies detached from glass debris + 3 colonies on tile, MNHN, NHMUK. — Marseille, Frioul Is., quarantine port, same origin and substrate as holotype and paratypes 3, 7 colonies, MNHN. — Marseille, Calanques Coast, Sormiou, Capellan, 43°12'20"N, 5°25'35"E, 18 m, 23.IV.1998, coll. by JGH, 2 colonies on pebble and plastic debris, MNHN. — Marseille, Calanques Coast, Sormiou, Figuier Cave, 43°12'26"N, 5°12'26"E, 19 m, VII.2000, coll. by JGH, 2 colonies on experimental substrate (one year colonization), MNHN. — Cassis, Trémies, 43°11'60"N, 5°30'44"E, 15 m, VII.1987, coll. by JGH, 2 colonies on pebble, MNHN. — Cassis, Port-Miou, 43°12'11"N, 5°30'53"E, 18 m, 23.II.1971, coll. by JGH, 17 colonies on underside of pottery, JGH-St. 71.3, MNHN. — Cassis, 43°12'22"N, 5°30'44"E, 18 m, 20.VIII.1975, 2 colonies on clay-pigeon target, JGH-St.75.2, MNHN. — Port-Cros, Bagaud Is., same site as paratype 2, 7 m, VII.1985, coll. by JGH, 1 colony on pebble + 1 coated colony, MNHN, NHMUK. — Corsica, Île-Rousse Is., 42°38'42"N, 8°56'04"E, 5 m, 09.IV.1978, 1 colony on a pebble together with *Collarina* sp., MNHN. — Corsica, Scandola, Imbutu, 42°22'26"N, 8°33'06"E, 6 m, 24.VIII.2018, coll. by JGH, 5 colonies on small pebbles, MNHN, NHMUK. — Corsica, Stareso, 42°34'49"N, 8°43'28"E, 7 m, 26.VIII.2018, coll. by JGH, 4 colonies on small pebbles together with *Collarina* sp., MNHN. — Corsica, Scandola, Elpa Nera, 42°24'21"N, 8°36'30"E, 7 m, 27.VIII.2018,

coll. by JGH, 5 colonies on pebbles in *Posidonia* bed, MNHN, NHMUK. — Corsica, Scandola, Gargallo, 42°21'58"N, 8°32'26"E, 7 m, 27.VIII.2018, coll. by JGH, 25 colonies on small pebbles together with *Collarina* sp., MNHN. — Corsica, Scandola, Elbu, 42°22'19"N, 8°33'21"E, 10 m, 30.VIII.2018, coll. by JGH, 4 colonies on pebbles in a cave, together with *C. gautieri* Harmelin, n. sp., MNHN. — Corsica, Scandola, Cala di l'Oru, 22 m, 31.VIII.2018, coll. by JGH, 2 colonies on stones together with *C. gautieri* Harmelin, n. sp., MNHN.

Spain. Catalonia, L'Estartit, Medes Islands, 42°14'53.102"N, 03°7'52.183"E, 9 m, 07.V.2015, coll. by TM-MZ, 1 colony on *Pinna nobilis* Linnaeus, 1758, MZB.

ETYMOLOGY. — From Latin *denticulatus*: with denticles, in reference to the denticulate proximal edge of the orifice.

DIAGNOSIS. — Colonies eventually large-sized; autozooids with narrow marginal gymnocyst and moderately convex costate shield formed by 8-14 costae thickened when fusing at the midline; orifice as long as broad, with proximal edge convex and fringed with denticles; 3-4 oral spines; adventitious avicularia paired in most cases, with rostrum acute, directed laterally; ovicells endozooidal, acleithral, with a distinctive sclerite sealing the oocelial vesicle, oocidium formed by a distal autozooid, occasionally by a distal kenozooid; ancestrula with 6 spines (occasionally 5).

DESCRIPTION

Colony encrusting, unilaminar, multiserial, irregularly shaped, reaching large size (> 1000 autozooids). Autozooids roughly hexagonal with a rounded distal end, but appearing oval owing the shape of the costal shield. Gymnocyst narrow, little visible except at the zooid proximal corners. Costate shield relatively flat, oval to circular made up of 8-14 costae (predominantly 9, Table 2), their fusion in the midline forming a thickening that joins the apertural bar in highly calcified colonies (Fig. 6A, B). Costae irregularly broad, with smooth surface; a large, funnel-shaped pelma at the base of each costa and, nearer to the shield centre, 1-2 smaller pseudopores (pelmaticidia) opening at the summit of a conical protuberance, occasionally alternating with a small pelma (Figs 6E, F; 7C). Intercostal lacunae rather small, generally transversally compressed and partially occluded by 1-2 small, blunt denticles rising from the inner edge (Fig. 6B, F). Apertural bar forming a thick, variably raised, triangular bulge with 2-3 pelmaticidia at the tip and a pair of large pelmata on the proximo-lateral sides (Figs 6C, D; 7C). Adventitious avicularia always present, occurring on both sides of the apertural bar in most cases (88%), or single, directed laterally, relatively narrow, with acute, triangular mandible (Figs 6C, D; 7C), occasionally presenting nested cystids (Fig. 6G, see below). Orifice of non-ovicelled zooids as long as wide on average (Table 1); anter (distal frame of primary orifice) semicircular, with proximal ends forming smooth-edged, poorly prominent condyles; proximal edge (poster) convex and denticulate, with 5-7 small denticles and a thick knob overhanging the condyles at each corner (Figs 6C, D; 7C). Ovicelled orifice clearly broader, with proximal edge less convex, bearing 7-12 denticles (Figs 6B; 15D). Oral spines 3 (> 70%) or 4 in non-ovicelled zooids, 2 in ovicelled zooids; basal part thick and conical, whip part thin and long (Fig. 6C, D).

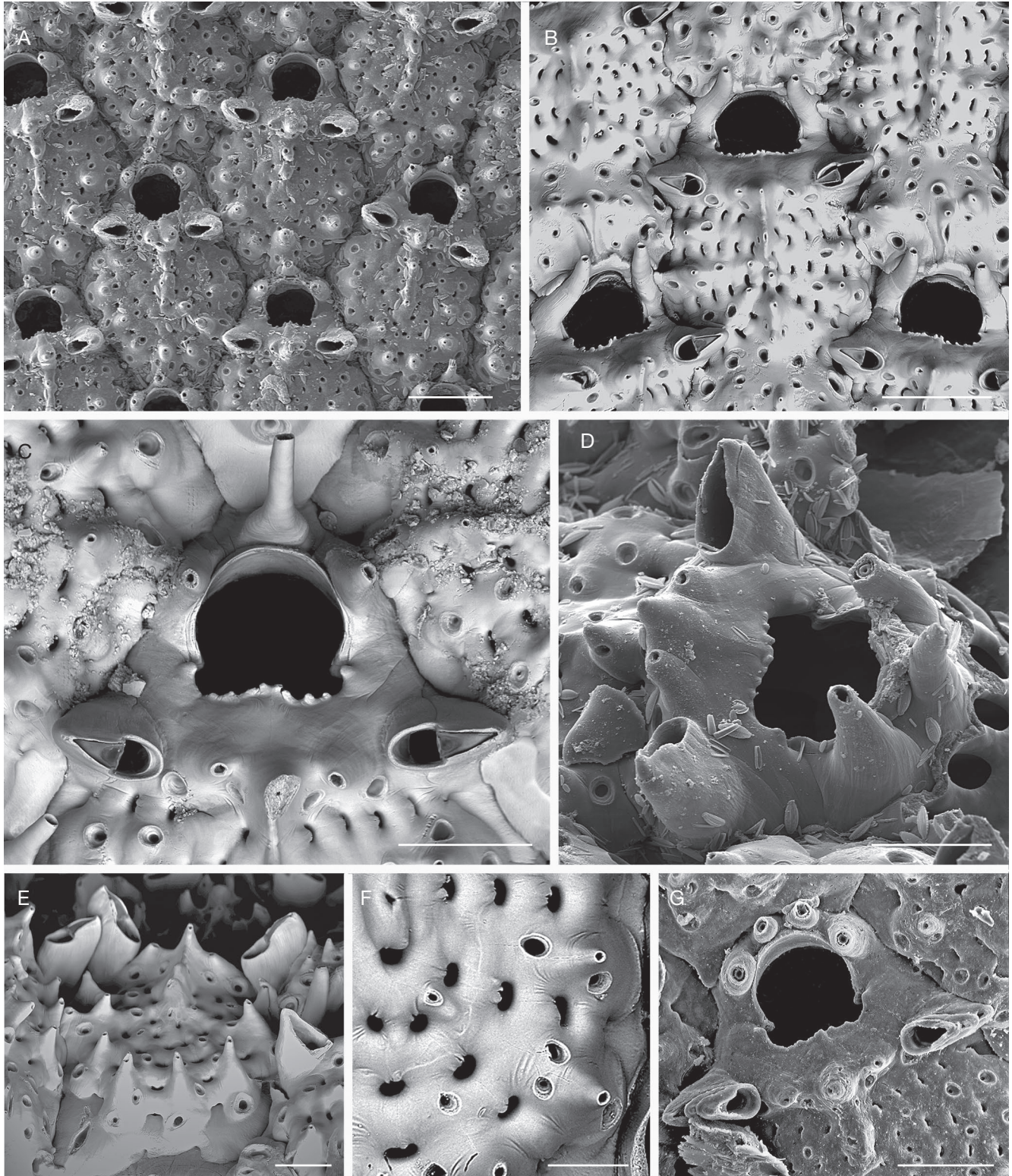


FIG. 6. — *Collarina denticulata* Harmelin, n. sp.: **A**, non-ovicelled autozooids with paired avicularia, three spines and large costate shield with prominent medial crest running into the apertural bar; **B**, ovicelled zooids, note the shape of the orifices and the poorly prominent oecia built by the autozooid distal to the maternal zooid; **C**, distal part of a non-ovicelled zooid showing the particular shape of the orifice, the spines with conical base and the paired avicularia with narrow rostrum; **D**, oblique view of the distal part of a non-ovicelled zooid showing the apertural bar, the sub-pedunculate avicularia and the spine bases; **E**, oblique view of the proximal part of an autozooid showing the pedunculate marginal pematidia and the poorly developed gymnocyst; **F**, lateral portion of the costate shield with oblong intercostal lacunae; **G**, autozooid with adventitious avicularia with nested cystids. Origin: A, D, paratype MNHN-IB-2014-1917, Marseille, Frioul; B, C, E, F, Medes Is. on *Pinna* shell; G, Port-Cros, Bagaud Is., on stone. Scale bars: A, B, 200 μ m; C-E, G, 100 μ m; F, 50 μ m.

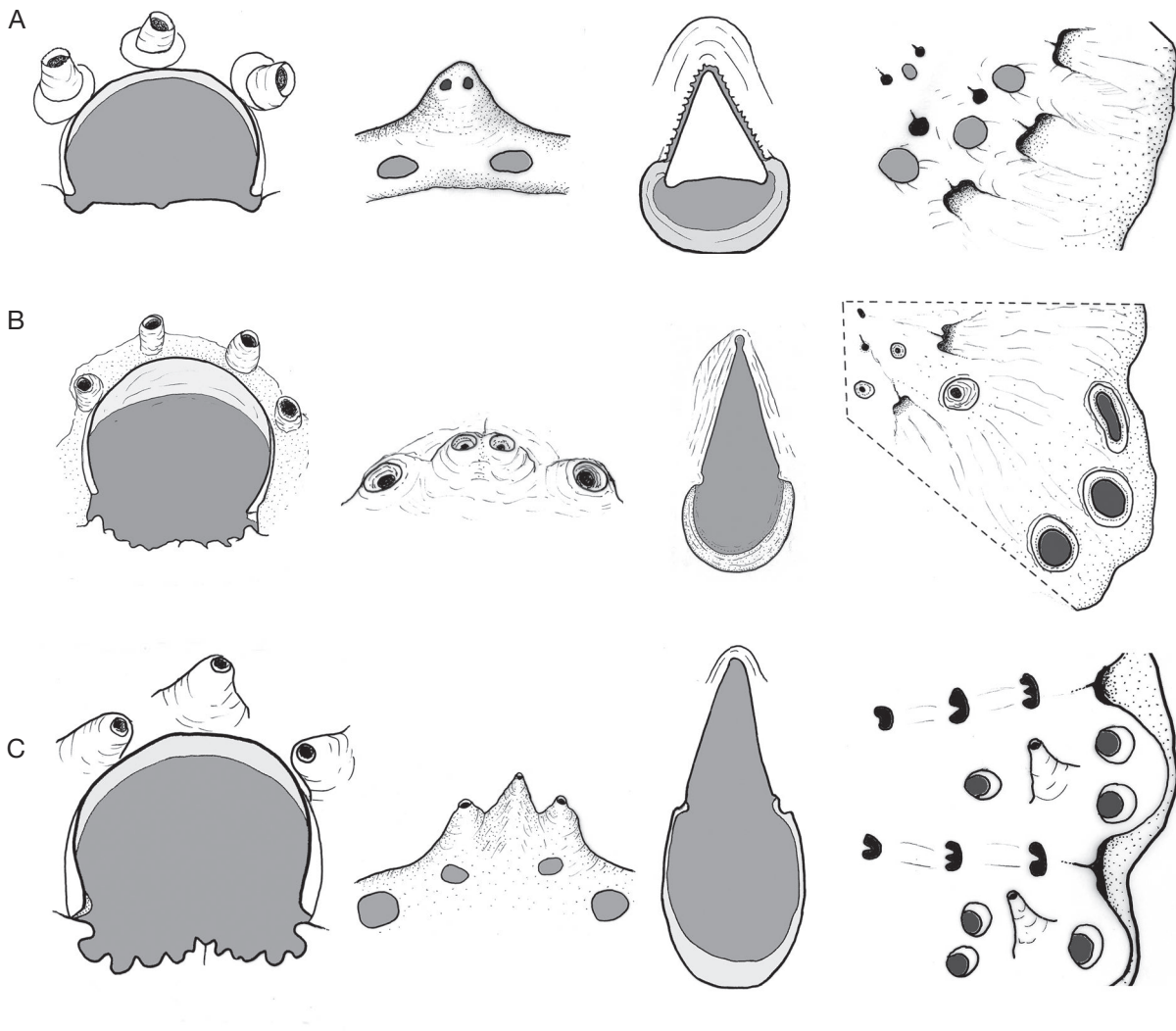


FIG. 7. — Outlines of orifice, apertural bar, avicularium and portion of costate shield and gymnocyst: **A**, *Collarina balzaci* (Audouin, 1826); **B**, *C. fayalensis* Harmelin, 1978, **C**, *C. denticulata* Harmelin, n. sp. Scale bar: 100 μ m (orifices), 50 μ m (avicularia).

Ovicell slightly prominent, endozooidal, acleithral, oocial vesicle protected by a pseudo-operculum, i.e., a thick chitinous sclerite (Fig. 15D), oocium formed by distal autozoid or, more rarely, by a distal kenozooid, broader than long (Figs 15D; 16E; Table 1), ectoocium with numerous pseudopores and relief variably pronounced according to calcification level. Ancestrula cribrimorph, orifice length a little less than one third the total length, predominantly 6 spines.

REMARKS

Collarina denticulata Harmelin, n. sp. is easily distinguished from the other *Collarina* species in having orifices with proximal edge clearly convex and serrate. Another obvious feature is the endozooidal nature of ovicells with the formation of the oocium by a distal autozoid. These particular features, never noted in previous descriptions of specimens assignable

to *Collarina*, make the differences with the other *Collarina* species indisputable.

HABITAT AND GEOGRAPHICAL DISTRIBUTION

The habitat range of *C. denticulata* Harmelin, n. sp. appears to be limited to the nearshore zone, at shallow depth (< 25 m), in sites little affected by sedimentation, on undersides of rigid substrates, either natural (e.g. cobbles, empty shells) or artificial (e.g. pottery, plastic debris) (Fig. 18C). In five sites from Corsica (5–22 m, list above), colonies of *C. denticulata* Harmelin, n. sp. occurred on pebbles with *Collarina* sp. or *C. gautieri* Harmelin, n. sp. All examined specimens of *C. denticulata* Harmelin, n. sp. were collected in the NW Mediterranean (Provence, Catalonia, Corsica). It seems probable that this species is endemic to this region. It is unlikely to have been completely overlooked elsewhere, considering its distinctive morphology and its easily accessible habitat.

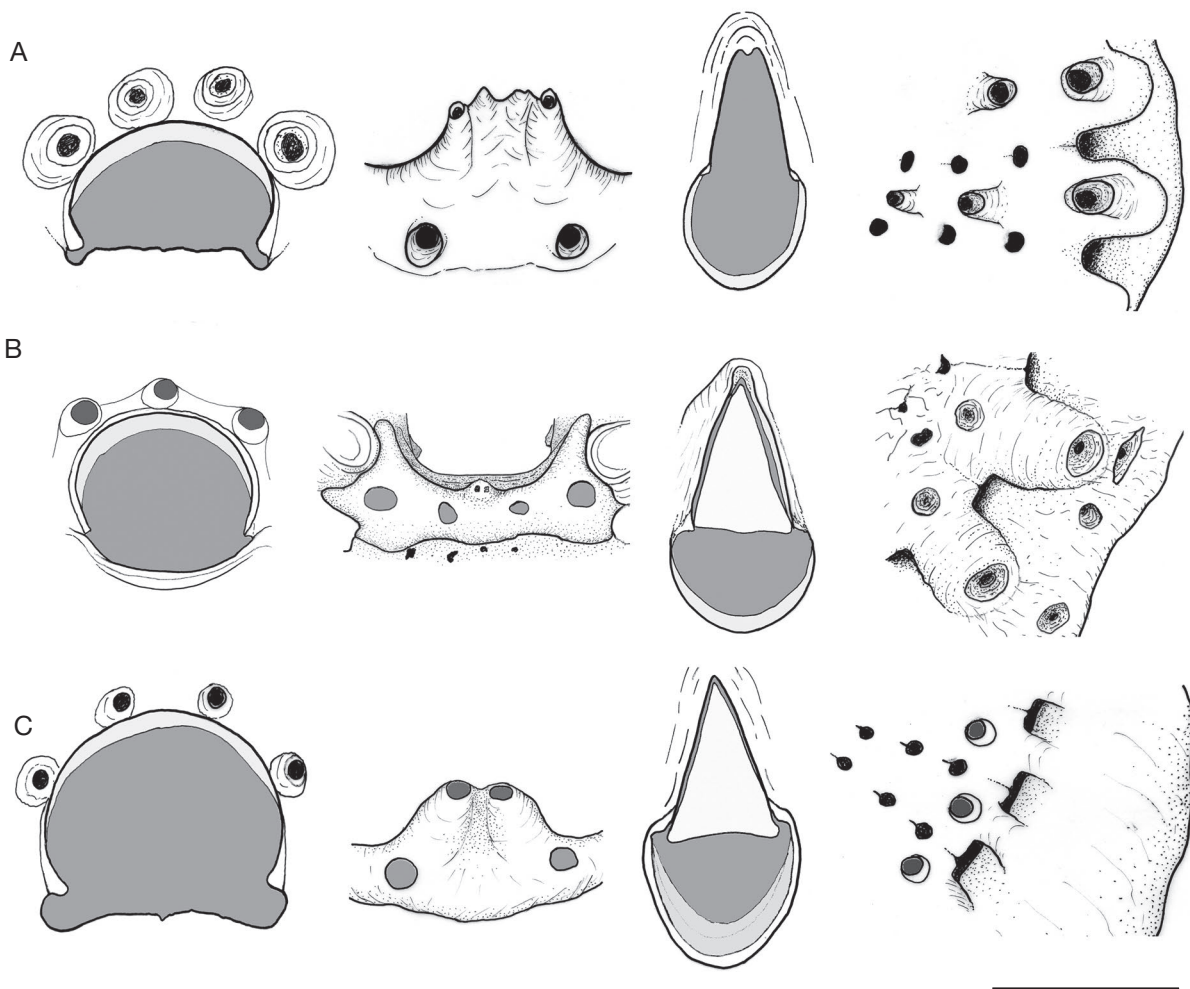


FIG. 8. — Outlines of orifice, apertural bar, avicularium and portion of costate shield and gymnocyst: **A**, *Collarina gautieri* Harmelin, n. sp.; **B**, *C. macaronensis* Harmelin, n. sp.; **C**, *C. speluncola* Harmelin, n. sp. Scale bar: 100 µm (orifices), 50 µm (avicularia).

Collarina gautieri Harmelin, n. sp.

(Figs 8A; 9; 10; 11; 16A-D; 17B; 18D; Tables 1-3)

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NE Atlantic, North Sea

Lepralia punctata – Busk 1854: 79-80 in part, pl. 96, fig. 3.

Cribrilina punctata var. a – Hincks 1880: 191, pl. 26, fig. 4.

Cribrilina punctata – Waters 1923: 563, figs 3, 7. — Echalier & Prenant 1951: 13. — Ryland & Stebbing 1971: 68, fig. 2b (top-right figure on p. 66; figures 1 and 2 are reversed relative to the legends on this page). — Hayward & Ryland 1979: 56, fig. 13. — Álvarez 1987: 44, pl. 9c-d.

Species A – Bishop 1986: fig. A.

Collarina balzaci – Bishop 1994: 242 (in part), figs 66-68. — Reverter *et al.* 1995: 125. — Reverter & Fernández 1996: 1248. — Hayward & Ryland 1998: 318 (in part), fig. 112a-b. — De Blauwe 2006: 126 (list); 2009: 270, figs 282-283; 2019: in press. — Souto *et al.* 2010:

1418 (list). — WoRMS image <http://www.marinespecies.org/aphia.php?p=image&tid=110891&cpic=23688> (accessed on 26.IV.2018).

Mediterranean

Cribrilina punctata – Calvet 1906: 398. — Prenant & Bobin 1966: 581 (in part). — Harmelin 1976: 227, 233, 236; 1977: 145; 1978b: 139. — Zabala 1986: 366, fig. 114.

?*Collarina punctata* – Gautier 1962: 108.

Collarina balzaci – Hayward & McKinney 2002: 37 (in part), figs 16a-c. — Chimenz Gusso *et al.* 2014: 154 (in part), figs 74c-d.

TYPE LOCALITY. — France, Marseille, Veyron.

TYPE MATERIAL. — **Holotype**. France, Marseille, Veyron, 43°12'44.2"N, 5°15'14.8"E, 23 m, 23.IX.1983, coll. by JGH, ovicelled colony of about 200 zooids, on fragmented empty *Pinna nobilis* shell, [MNHN-IB-2014-1920](https://doi.org/10.26025/MNHN-IB-2014-1920).

Paratypes. France. 6 colonies including JGH stub 75, same origin as the holotype, on other shell fragments, [MNHN-IB-2014-1921](https://doi.org/10.26025/MNHN-IB-2014-1921). — Marseille, Morgiou Cape, 43°12'04.41"N, 5°27'08.22"E, 40 m, 20.I.1986, coll. by JGH, 3 colonies on empty *Spatangus* test,

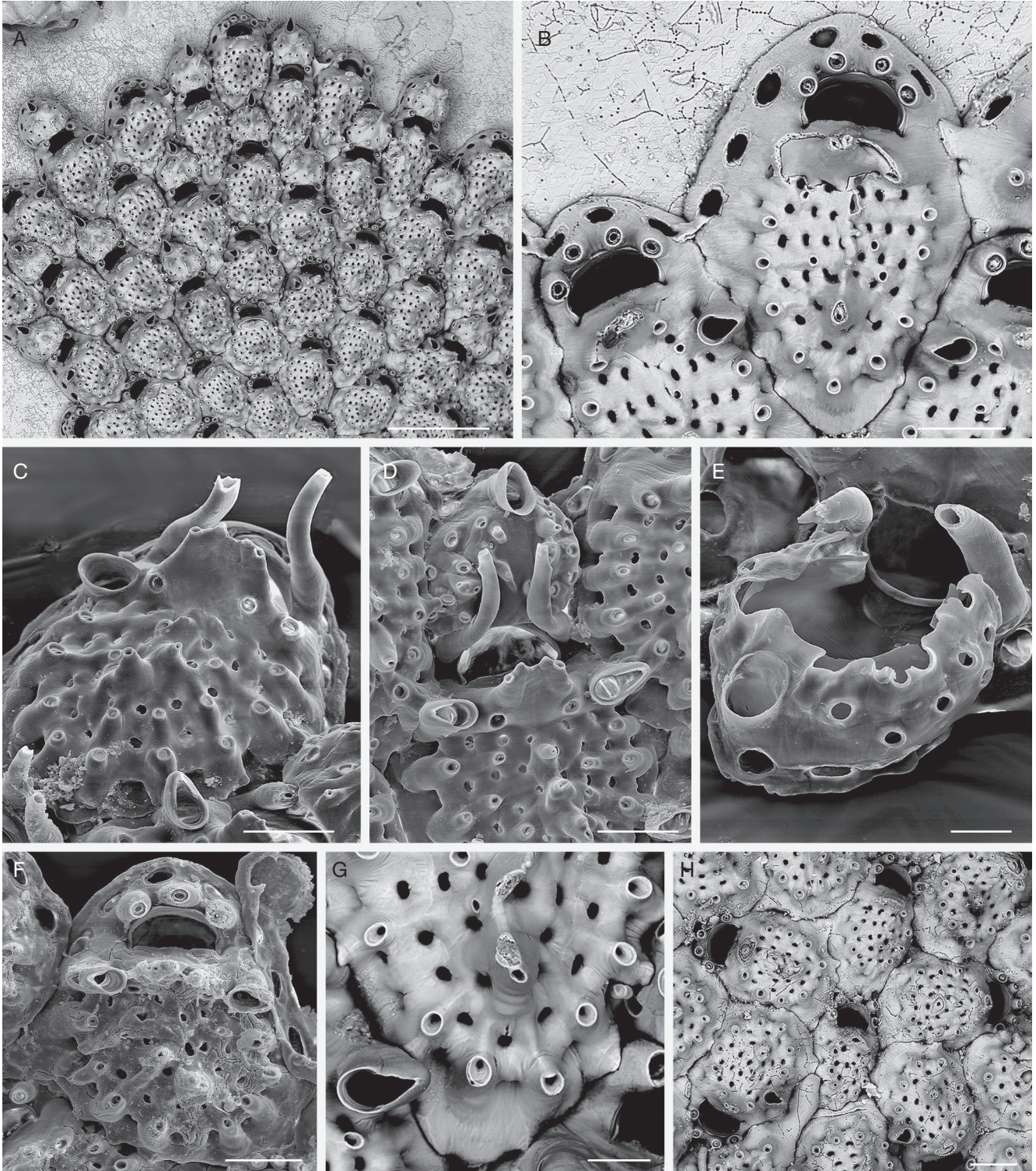


FIG. 9. — *Collarina gautieri* Harmelin, n. sp., NW Mediterranean: **A**, general view of a colony; note the frequency of ovicells; **B**, two non-ovicelled autozooids at the colony edge; **C**, oblique view of a non-ovicelled zooid showing the shape of the apertural bar and the structure of the costate shield; **D**, ovicelled zooid with typically curved spines, 2 lateral and 1 apical avicularia; **E**, kenozooidal ooeonium in formation; **F**, strongly calcified non-ovicelled zooid; **G**, proximal half of the costate shield showing the poorly developed gymnocyst, the large marginal pelmata and the intercostal lacunae; **H**, ancestrula and the zone of astogenetic change. Origin: A, B, G, H, paratype MNHN-IB-2014-1923, Port-Cros Is. on *Pinna* shell; C, D, E, F, paratype MNHN-IB-2014-1920, Marseille, Veyron. Scale bars: A, 500 μ m; B-D, F, H, 100 μ m; E, G, 50 μ m.

MNHN-IB-2014-1922. — Port-Cros Island, La Palud, 43°00'52"N, 6°23'26"E, 30 m, VI.1995, coll. by JGH, 1 colony on empty *Pinna* shell, SEM photos (TM-MZ), **MNHN-IB-2014-1923.**

OTHER MATERIAL EXAMINED. — **Mediterranean. France.** Marseille, Grand-Conglue Island, 43°10'33"N, 5°24'09"E, 62 m, 13.IX.1972, coll. by JGH, 6 colonies on pottery and glass fragments, MNHN. — Same origin as paratype 3, 1 detached colony. — Cassis, 20 m, 12.III.1971, 43°12'22"N, 5°30'44"E, coll. by JGH, 1 ovicelled colony on clay-pigeon target, MNHN. — Corsica, Bonifacio, R/V *Travailleur* 1881, Dr. 24, 55-77 m, on shell: 1 colony labelled *Cribrilina punctata*, Calvet coll. (Calvet 1906), **MNHN-IB-2008-2814.** — Corsica, Scandola, Elbu, 42°22'19"N, 8°33'21"E, 10 m, 30.VIII.2018, coll. by JGH coll., 2 colonies on small stones in cave, together with *C. denticulata* Harmelin, n. sp., MNHN, NHMUK. — Corsica, Scandola, Cala di l'Oru, 42°22'18"N, 8°32'42"E, 22 m, coll. by JGH, 2 colonies on stones, together with *C. denticulata*, MNHN. — **Spain.** Catalonia, Cap de Creus, 42°20'1.14"N, 3°17'10.09"E, 40 m, 17.VII.2017, on stone (STUB 9121), coll. by TM-MZ, 1 colony, MZB. — Balearic Islands, Menorca Channel, 60-80 m, VIII.2011, 39°51'01.5408"N, 03°30'22.2948"E, on stone, INDEMARES-coll. by TM-MZ, 1 colony, MZB. — Catalonia, Medes Islands, 42°03'00.1332"N, 03°13'29.2512"E, 40 m, coll. by TM-MZ, one colony on stone, MZB. — **Italy.** Naples, NHMUK 1911.10.1.684, SEM photos (MSJ).

NE Atlantic. France. Brittany, Roscoff, Taureau, G. Echaliere dredging (depth unknown), 2.IX.1950, 2 colonies on *Pecten* shell, **MNHN-IB-2014-446.** — W Brittany, R/V *Jean-Charcot*, 1968, DR01, 48°01'N, 05°44'W, 130 m, 3.XII.1968, B. Métiévier leg. (= Bishop 1994, fig. 66), 1 colony on *Chlamys* shell, **MNHN-IB-2008-13269.** — Brittany, Roscoff, J.-L. d'Hondt leg., 1 colony on shell, **MNHN-IB-2008-6553.** — France, NHMUK 1911.10.1.686: Britain?, A. M. Norman leg., SEM photos (MSJ). — **North Sea.** Westhinderbank 2005, SEM photos (courtesy of H. De Blauwe). — **United Kingdom.** Raasay Sound, Scotland, SEM photos (JDB) (= fig. A in Bishop 1986 & fig. 67 in Bishop 1994), NHMUK 1973.4.6.1. — English Channel, Plymouth, off Stoke Point, 20-21 m, coll. by JDB, several colonies on bivalve shells and settled in culture tanks, NHMUK. — **Spain.** Galicia, Ria de Ferrol, 43°27'09"N, 08°18'51"W, 12 m, 13.IX.1989, dredging D-10 Reverter & Fernández (1996, as *C. balzaci*), colony on shell, MHNUSC-Bry-126. — Galicia, Ria de Ferrol, 43°28'15"N, 08°15'30"W, 15 m, 13.IX.1989, dredging D-18 Reverter & Fernández (1996, as *C. balzaci*), colony on shell MHNUSC-Bry-113. — Galicia, Malpica, 43°28'41"N, 08°58'15"W, depth unknown, 23.XI.2002, colony on echinoid test, SEM photos (courtesy of O. Reverter), MHNUSC-Bry-583. — Galicia, Cies Is., 42°12'41.38"N, 08°54'20.37"W, 12 m, 23.VIII.2012, on shell, SEM photos (courtesy of O. Reverter), MHNUSC-Bry-614. — Galicia, Ría de Vigo, several localities, 23-38 m, 1986, on shells, MHNUSC-Bry-34. — Galicia, Ría de Pontevedra, MHNUSC-Bry-78j. — **Portugal.** S Portugal, Armação de Pêra Bay, 37°0'59.256"N, 08°11'25.367"W, 21 m, colony on calcareous algae and SEM photos MHNUSC-Bry-660. — S Portugal, Armação de Pêra Bay, 37°0'59.256"N, 08°11'25.367"W, 21 m, colony on calcareous algae and SEM photos, MHNUSC-Bry-661.

ADDITIONAL RECORDS. — France, Brittany, off Roscoff, 90 m, 1 colony on *Glycymeris* shell, L. Cabioch dredging (JGH leg.). — Brittany, Pléneuf-Val-André, SEM photos (courtesy of H. De Blauwe).

ETYMOLOGY. — Dedicated to the late Dr Y. V. Gautier, who contributed greatly to knowledge of the Mediterranean bryozoans.

DIAGNOSIS. — Colonies small- to medium-sized, early mature; autozooids with narrow marginal gymnocyst, costate shield composed of 7-12 costae bordered by a collar of large, prominent pelmata, one at the top of the steep base of each costa, pematidia often at the tip of a conical pillar; orifice with small L/W ratio; apertural bar with raised, massive umbo bearing 2 apical pematidia

and 2 large basal pelmata; 3-5 oral spines; adventitious avicularia paired or single, directed laterally; ovicell frequent, associated with a pair of thick oral spines typically arched inwardly, oecium kenozooidal, ectooecium bumpy, punctured with many pseudopores with prominent edge, the smaller at the tip of conical processes; ancestrula with 5 spines.

DESCRIPTION

Colony encrusting, pluriserial, unilaminar, small- to medium-sized (< 500 zooids) (Fig. 9A). Autozooids more or less oval in outline. Gymnocyst narrow, little visible in frontal view, except for a short triangular proximal part (Figs 9B, G; 10B, C, E). Costate shield subcircular to oval, with uneven surface (Fig. 9C, F); 7-12 costae, most frequently 9 (46%), with ascending base clearly defined, bearing a large, peripherally positioned pelma with a slightly prominent edge and funnel-shaped, i.e., with a large outer opening and a small inner pore; a smaller pelma, occasionally missing, in a more central position on the shield (Figs 7G; 8C, E). Intercostal lacunae relatively large, in most cases 3 more or less rectangular (Mediterranean) or 2 rounded (Atlantic) between adjacent costae (Figs 9; 10). Apertural bar with a fairly high (particularly in ovicelled zooids), proximo-distally flattened umbo with proximal side slightly concave and large paired pelmata placed laterally at the base, tip often irregularly shaped but typically with two short pointed processes each with a sub-terminal lateral pelmatidium (Figs 8A; 9C, D; 10B, C). Sub-pedunculate avicularium inserted laterally to the apertural bar, paired or single, occasionally absent, directed laterally, tilted proximally at a shallow angle; proximal opesia large, rounded, with a narrow rim of cryptocyst; rostrum with a triangular mandible (Figs 8A; 9B, D); nested cystids occasionally present (Fig. 17B). Orifice of non-ovicelled zooids broader than long (Table 1), poster straight with small lateral notches, anter semi-circular with each proximal end forming a slightly prominent triangular condyle (Figs 8A; 9B; 10E); orifice of ovicelled zooids clearly broader. Oral spines 3-5 in non-ovicelled zooids, in majority 4 (Mediterranean: > 70%, Atlantic: > 80%); in ovicelled zooids, two robust spines with basal parts particularly thick and long, typically bent toward the ovicell midline, and upper parts still relatively thick and curving back away from the ovicell midline (Figs 9D, E; 10B, C). Ovicells frequent, apparently cleithral, oecium hyperstomial, subspherical, formed by distal kenozooid at the colony border (Figs 9E; 10E; 16A-D); ectooecium with uneven surface owing to numerous large pelmata and pedunculate pematidia; an avicularium on the middle of the distal edge, distally directed, present in most cases (> 80%). Ancestrula cribrimorph with 5 spines, costate shield oval with 6-8 costae and gymnocyst clearly broader than in zooids of the zone of astogenetic repetition (Figs 9H; 10D, F).

REMARKS

There are no marked morphological differences between Atlantic and Mediterranean specimens of *C. gautieri* Harmelin, n. sp. The only apparent divergence concerns the shape of intercostal lacunae that tends to be quadrangular in the

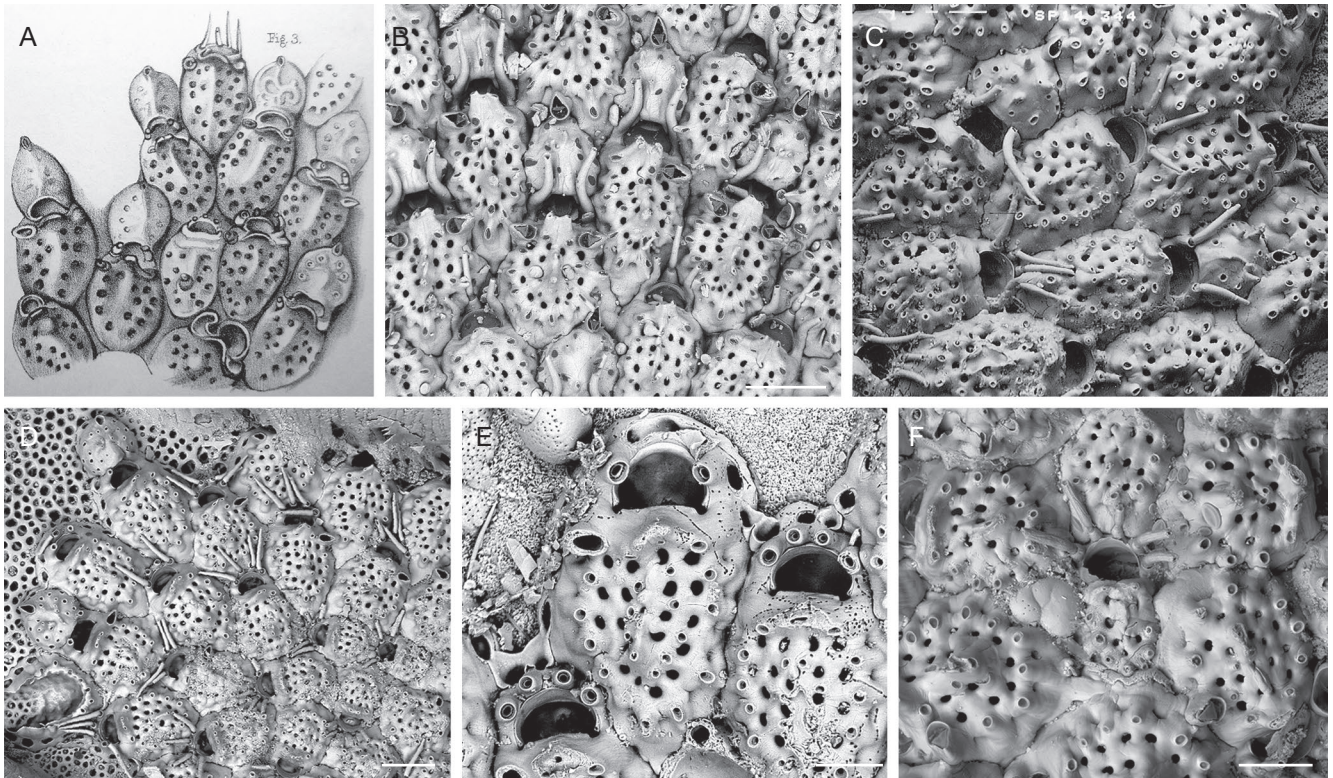


FIG. 10. — *Collarina gautieri* Harmelin, n. sp., NE Atlantic: **A**, *Lepralia punctata* Hassall, 1841: Busk 1854, pl. 96, fig. 3; **B**, **C**, ovicelled and non-ovicelled autozooids, note the typically curved spines associated with ovicells, the orientation of the avicularia and the respective extent of costate shield and gymnocyst; **D**, part of a young colony including the ancestrula (right) and the colony edge with 2 ovicelled zooids (left); **E**, non-ovicelled zooid (right) and fertile zooid with an early stage of the oocyst formation (middle), note the typical shape of the orifices and the structure of the costate shield with large marginal palmata; **F**, ancestrula. Origin: B, Devon, coll. by JDB; C, NHMUK 1973.4.6.1, Raasay Sound, Scotland: Species A, Bishop (1986); D, Galicia, Malpica; E, Galicia, Ferrol; F, Algarve, coll. by JS. Scale bars: B, D, 200 μ m; E, F, 100 μ m.

Mediterranean and more rounded in the Atlantic, and their number, generally higher in the Mediterranean (three vs two). Throughout the Mediterranean and the NE Atlantic, specimens of this species were recorded either as *Cribrilina punctata* or *Collarina balzaci*. The taxonomic status of the latter was stabilized by Bishop (1988) with the designation of a neotype from the Mediterranean material examined by Waters (1879). At the same time, the confused background of records as *C. punctata* of the present species in the British Isles (Busk 1854; Hincks 1880; Waters 1923; Ryland & Stebbing 1971; Hayward & Ryland 1979) was clarified by Bishop (1986, 1988, 1994). The species attribution of this northern material, however, was not clearly defined and the opinion of Bishop (1994) that it may belong to *C. balzaci* despite some morphological variations predominated afterwards. Examination of material or SEM photos corresponding to records of *C. balzaci* in the NE Atlantic (Bishop 1994; Reverter *et al.* 1995; Reverter & Fernández 1996; Hayward & Ryland 1998; De Blauwe 2006, 2009, 2018; Souto *et al.* 2010) showed that these specimens presented all discriminant characters of *C. gautieri* Harmelin, n. sp. In the Mediterranean, the record of *Collarina punctata* at Marseille by Gautier (1962) was based on a few colonies encrusting shells and tests of echinoids in the 50 m depth zone, a habitat typical of *C. gautieri* Harmelin, n. sp., and on a specimen from Bonifacio (R/V *Travailleur* expedition)

identified by Calvet (1906) as *Cribrilina punctata*. Examination of the latter, kept at the MNHN, confirmed conspecificity with the types of *C. gautieri* Harmelin, n. sp. The choice of Gautier (1962) to ascribe his material to the genus *Collarina* was appropriate and rather innovative, but did not involve Hassall's species, particularly since he formerly considered that *C. punctata* was absent from the Mediterranean (Gautier 1953), a statement also sustained by Bishop (1988, 1994) and Rosso & Di Martino (2016). This is also confirmed by the absence of Mediterranean specimens of true *C. punctata* in the material examined for this study. All Mediterranean specimens formerly recorded as *C. punctata* (e.g. Harmelin 1976; Zabala 1986) are, therefore, obvious misidentifications of *Collarina* and belong to *C. gautieri* Harmelin, n. sp., or to another *Collarina* species described here. Similarly, it is likely that the record without illustration of *Cribrilina punctata* from Tunisia (Ben Ismaïl *et al.* 2007) corresponds to a *Collarina* species. Morphological features visible on several published SEM photos of Mediterranean specimens ascribed to *C. balzaci* are undoubtedly typical of *C. gautieri* Harmelin, n. sp., and this similarity is confirmed by their habitat: 1) specimen from northern Adriatic (Hayward & McKinney 2002, Fig. 16A-C), collected on sandy bottom at 30-40 m depth (site features supplied by L. Becniker, AMNH, pers. com., 24.X.2017); and 2) specimen from Palmorola Is., Tyr-

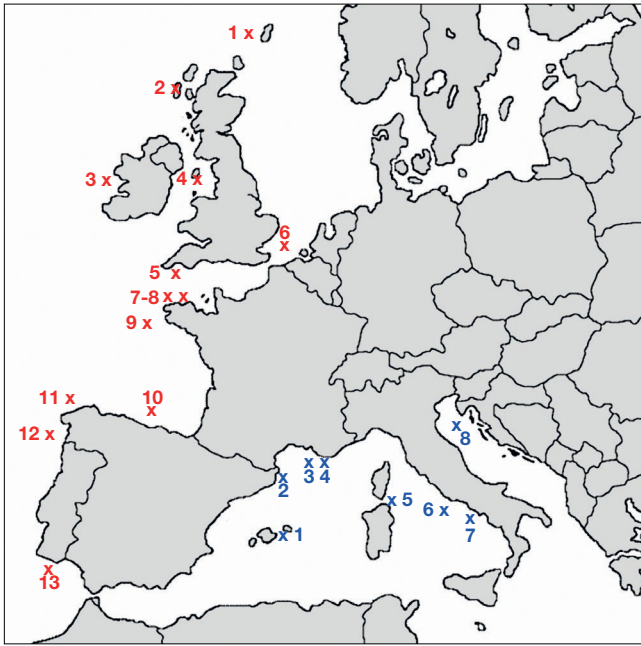


FIG. 11. — Geographical distribution of *Collarina gautieri* Harmelin, n. sp. in the NE Atlantic and the Mediterranean. Origin of records: **Red**, Atlantic; **1-5**, Bishop (1994); **6**, De Blauwe (2006); **7-8**, MNHN; **9**, De Blauwe (2019); **10**, Álvarez (1987); **11-12**, Reverter collection; **13**, Souto *et al.* (2010); **Blue**, Mediterranean; **1-2**, this paper, coll. by TM-MZ; **3-4**, this paper, coll. by JGH; **5**, MNHN collection, Calvet (1906); **6**, Chimenz Gusso *et al.* (2014); **7**, NHMUK 1911.10.1.684; **8**, Hayward & McKinney (2002).

rhenian Sea, Italy (Chimenz Gusso *et al.* 2014: fig. 74c-d), collected at 88 m on detritic-biogenic bottom (site features supplied by C. Gusso, pers. com., 29.X.2017).

HABITAT AND GEOGRAPHICAL DISTRIBUTION

Unlike *C. balzaci*, all specimens of *C. gautieri* Harmelin, n. sp. collected in the NE Atlantic and the Mediterranean were not epiphytic but occupied the same alternative type of habitat, i.e., small substrates, mainly shells, on coarse sandy bottom (Fig. 18D). The depth range of these samples was broad in the Atlantic, from the intertidal zone (Ria de Ferrol: Reverter & Fernández 1996) to 130 m (W Brittany: specimen MNHN-IB-2008-13269). The “Faciès à *Cribrilina punctata*” recorded by Prenant (1927) on stones in hollows of the upper intertidal zone at Roscoff (Brittany) may correspond to a particular abundance of *C. gautieri* Harmelin, n. sp. An experiment of small-scale cultivation of a different shell-encrusting species in Plymouth at the laboratory of the Marine Biological Association revealed an unexpected spontaneous settlement of *C. gautieri* Harmelin, n. sp. with the development of circular colonies. The very high proportion of ovicelled zooids in these colonies suggests that this species has large adaptive capacities to colonize opportunistically available substrata in the Atlantic coastal zone. In the Mediterranean, the habitat niche of this species is narrower as shown by the collected material, in any case found on shells, stones or pottery fragments in contact with coarse soft bottom, at depth ranging from 10 m to 88 m. The geographical distribution

of *C. gautieri* Harmelin, n. sp. covers both the NE Atlantic and the Mediterranean. In the Atlantic, it is widely distributed from the Faeroes and the Shetlands (Bishop 1994) to the southern coasts of the Iberian Peninsula. In the Mediterranean, its range is seemingly more limited, perhaps owing to sampling bias induced by less-extensive habitat in this sea (see below) (Fig. 11).

Collarina macaronensis Harmelin, n. sp.
(Figs 8B; 12; 15C; E; 17A, C; 18E; Tables 1-3)

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Cribrilina balzaci – Waters 1899: 9, figs 31-32. — Norman 1903: 98, pl. 9, fig. 6; 1909: 292.

Collarina balzaci – Harmelin 1978a (in part): 189, fig. 8 (not pl. I, fig. 7).

Cribrilina punctata – Fernández Pulpeiro & Rodríguez Babio 1980: 136, fig. 2. — Álvarez 1988: 348, fig. 3B-D.

Collarina fayalensis – Aristegui 1984 (in part): 230, fig. 49b, pl. 11, fig. 6 (not fig. 7).

TYPE LOCALITY. — Portugal, Madeira, Porto Santo, Baixo Is.

TYPE MATERIAL. — **Holotype**. Portugal, Madeira, Porto Santo, Baixo Is., R/V *Jean-Charcot*, ZARCO 1966 St. 23, 33°0'32"N, 16°23'13"W, 5-8 m, dark tunnel, 1 large ovicelled colony (> 1000 zooids) on a pebble, MNHN-IB-2014-1924.

Paratypes. Same origin as the holotype: MNHN-IB-2014-1925: 2 colonies together with the holotype. — MNHN-IB-2014-1926: 4 colonies on 2 pebbles. — MNHN-IB-2014-1927: coated ovicelled colony for SEM examination.

OTHER MATERIAL EXAMINED. — **Azores**, Faial, Castelo Branco, R/V *Jean-Charcot*, BIAÇORES 1971 St. P.11, 38°31'12"N, 28°42'7"W, 5-7 m, 12.X.1971, coll. by H. Zibrowius, MNHN-IB-2008-7909: 2 colonies on pebble together with holotype and paratypes of *C. fayalensis*. — Galicia, Sisargas Is., 43°21'22"N, 8°50'17"W, depth unknown, coll. by Fernández-Pulpeiro & Reverter leg., 1 colony (SEM photos), MHNUSC-Bry-662. — Material from NHMUK collections, SEM photos (MSJ): NHMUK 1899.7.1.1344 (*Collarina balzaci*), Madeira, J. Y. Johnson leg., ovicelled colony; NHMUK 1899.7.1.2419 (*Collarina* sp.), Madeira, J. Y. Johnson leg., ovicelled colony; NHMUK 1899.7.1.2105 (*Collarina* sp.), Madeira, J. Y. Johnson leg., ovicelled colony. 3d; NHMUK 1911.10.1.705 (*Collarina balzaci*), Madeira, ovicelled colony.

ETYMOLOGY. — From Macaronesia, biogeographical area including the Canary Islands, Madeira and the Azores where this species was recorded.

DIAGNOSIS. — Colonies medium- to large-sized; autozooids with broad marginal gymnocyst, costate shield with a lower central area, predominantly composed of 6-7 costae with smooth surface and long basal part; apertural bar moderately raised, forming an arch; proximal edge of orifice smooth and slightly concave; 3-4 oral spines; paired adventitious avicularia with marked disto-lateral orientation; oecium formed by distal kenozooid or autozooid; ancestrula with 6 spines.

DESCRIPTION

Colony encrusting, pluriserial, unilaminar, reaching large size (> 1000 zooids) (Fig. 18E). Zooids subpentagonal with distal

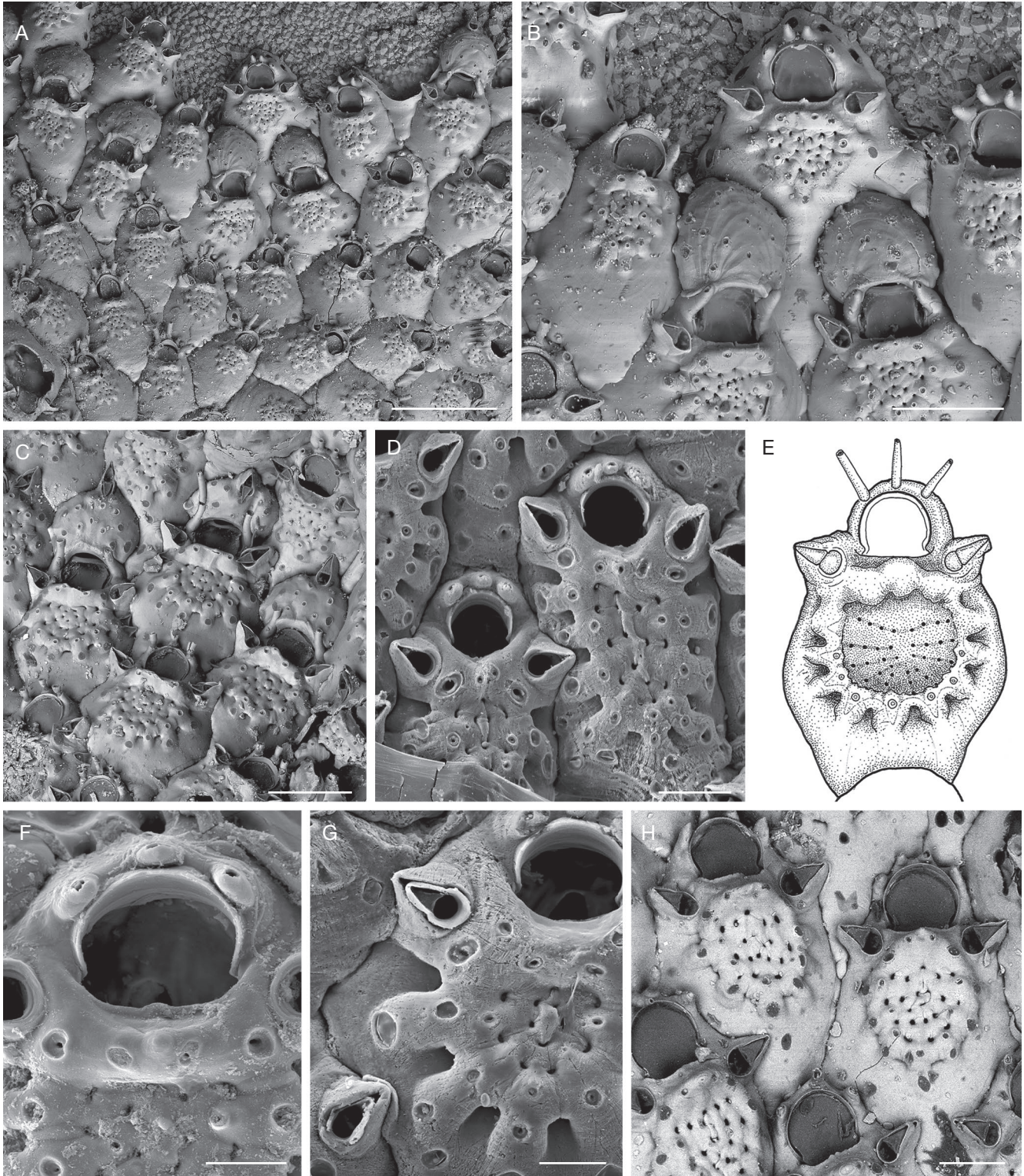


FIG. 12. — *Collarina macaronensis* Harmelin, n. sp.: **A, B**, colony edge, general view and detail with ovicelled and non-ovicelled zooids; **C**, oblique view: structure of costate shield, apertural bar, paired and apical avicularia; **D, G**, non-ovicelled zooids with typical traits: concave orifice poster, avicularia directed disto-laterally, costate shield with lower central part and digitate margin, large palmata also present on the gymnocyst; **E**, *Collarina balzaci* (Audouin, 1826): Harmelin (1978a, fig. 8), Azores, Faial; **F**, distal part of non-ovicelled zooid with typical orifice, apertural bar with large and small pseudopores, and 3 spines; **H**, specimen from a continental area. Origin: A, B, NHMUK 1899.7.1.2105, Madeira, J.Y. Johnson leg.; C, NHMUK 1911.10.1.705, Madeira; D, F, G, MNHN-IB-2014-1927, Madeira, Baixo Is.; H, Galicia, Sisargas Is. Scale bars: A, 400 μ m; B, C, 200 μ m; D, H 100 μ m; F, G, 50 μ m.

edge rounded. Gymnocyst visible in frontal view, of variable width laterally, clearly much wider in the proximal part, with some gymnocystal pseudopores (Fig. 8B; 12C, H). Costate shield with central part lower than the periphery, composed of 4–9 (6–7: > 60%) short and thick costae, with each ascending basal part forming a clearly distinct lobe, prominent on the gymnocyst and bearing a large pelma, a second, smaller pelma in inner position, before the central, lower part of the shield. Intercostal lacunae 2–3 between adjacent costae, small, irregularly slot-shaped (Fig. 12D–H). Apertural bar arched below the orifice, with a moderately raised tip, a pair of medium-sized pseudopores on both sides of the tip and two larger lateral pelmata, near the base of the avicularia (Figs 8B; 12F, G; 15C). Adventitious avicularia typically directed laterodistally, almost always paired, rostrum with slightly hooked tip (Figs 8B; 12B, D, H; 15C), nested cystids relatively frequent (Fig. 17A, C). Orifice wider than long, dimorphic, broader in ovicelled zooids; proximal edge slightly or noticeably concave; condyles triangular, moderately prominent (Figs 8B; 12D, F, G). Spines thin, with small conical base, 3 in most cases or 4, 2 arched in ovicelled zooids (Fig. 12B, D, F). Ovicell prominent, seemingly acleithral (Fig. 15C); oecium formed by a distal kenozooid at the colony growing edge or by a distal daughter autozooid (Figs 12A–C; 15C, E), slightly broader than long, ectoecium with relatively smooth surface, punctured with a dozen medium-sized pseudopores. Ancestrula cribri-morph, with small spinocyst and 6 spines.

REMARKS

Collarina macaronensis Harmelin, n. sp. is closely related to *C. fayalensis* in having orifices with a concave proximal edge, costae with similarly shaped ascending base bearing a large pelma and well-developed gymnocyst. However, in *C. macaronensis* Harmelin, n. sp., the paired adventitious avicularia are more distinctly directed disto-laterally and the costate shield involves more costae. Specimens from Faial, Azores recorded and figured as *Collarina balzaci* by Harmelin (1978a: fig. 8; reproduced here: fig 12E) present these typical characters and belong undoubtedly to *C. macaronensis* Harmelin, n. sp. This Azorean sample consisted in two colonies on a pebble bearing also the type series of *C. fayalensis*. The co-occurrence of these two species on the same small substrate confirms they are not ecomorphs of the same species. The discriminant features of *C. macaronensis* Harmelin, n. sp. are recognizable in part of the figured material from Canary Islands ascribed to *C. fayalensis* by Aristegui (1984: fig. 49b; pl. 11, fig. 6) and also in figures of colonies ascribed to *Cribrilina punctata* by Fernández Pulpeiro & Rodríguez Babio (1980: Galicia, Ria de Vigo) and Álvarez (1988: Basque region). SEM examination of specimens from Sisargas Islands, Galicia (coll. by Fernández Pulpeiro, courtesy of O. Reverter) confirmed the occurrence of *C. macaronensis* Harmelin, n. sp. on the Iberian coast (Fig. 12H).

SEM examination of three specimens kept at the NHMUK, collected by J. Y. Johnson at Madeira and labelled *Collarina balzaci* or *Collarina* sp., has proved that they belong to *C. macaronensis* Harmelin, n. sp. (Fig. 12A, B). As indicated

by Norman (1909) in his introduction the Johnson collection was examined by G. Busk, Waters (1899) and himself. Waters (1899) ascribed this material to *Cribrilina balzaci* and noted thereafter (Waters 1923) that “There are specimens from Madeira, which I took for *balzaci*, which must perhaps be considered a variety”. The figure of the spinocyst edge of a Madeiran specimen named *Cribrilina balzaci* by Norman (1903: pl. 9, fig. 6; same specimen shown here as Fig. 12C) shows costae with basal parts protruding greatly from the gymnocyst, a typical character of *C. macaronensis* Harmelin, n. sp.

Habitat and geographical distribution

In both the Azores and Madeira *C. macaronensis* Harmelin, n. sp. was found on pebbles and cobbles in shaded conditions (Fig. 18E). On the other hand, its absence on rocky walls of dark caves at Madeira despite an extensive sampling survey (JGH, September 2000) suggests that this habitat is unsuitable to this *Collarina* species, in contrast to several *Cribrilina* species which were very abundant (JGH, unpublished data). Small substrates in contact with a flat bottom at shallow depth may be an ecological requirement of this species. It is worth noting that this species was noticed by Norman (1909, as *C. balzaci*) on stones between tide-marks at Madeira. At the present state of knowledge, the geographical range of *C. macaronensis* Harmelin, n. sp. includes the NE Atlantic archipelagoes (Canaries, Madeira, Azores) and the northern coast of the Iberian Peninsula.

Collarina spelunca Harmelin, n. sp.

(Figs 8C; 13; 15A; 17E; 18B; Tables 1–3)

[urn:lsid:zoobank.org:act:9FCF7C95-06C5-4FFF-A4E1-701C4E070962](https://doi.org/10.21203/rs.3.rs-1000000)

TYPE LOCALITY. — France, Marseille, Calanques Coast.

TYPE MATERIAL. — **Holotype.** France, Marseille, Calanques Coast, Conger Cave, dark chamber, 43°12'34"N, 5°27'47"E, 3 m, 2.VI.1987, coll. by JGH, 1 ovicelled colony (c. 160 zooids, circled in red) together with 2 smaller colonies, on fragment of rocky wall, [MNHN-IB-2014-1912](https://doi.org/10.21203/rs.3.rs-1000000).

Paratypes. Same data as the holotype. [MNHN-IB-2014-1913](https://doi.org/10.21203/rs.3.rs-1000000): 5 alive + 3 dead colonies, on wall fragment. — [MNHN-IB-2014-1914](https://doi.org/10.21203/rs.3.rs-1000000): 12 colonies, on wall fragment. — [MNHN-IB-2014-1915](https://doi.org/10.21203/rs.3.rs-1000000): 3 coated colonies (JGH stubs 64 & 72).

OTHER MATERIAL EXAMINED. — Same data as the holotype and paratypes, many colonies, MNHN, NHMUK. — **France.** La Ciotat, Gameau Cave, dark chamber, 43°09'53"N, 5°35'56"E, 2–3 m, VII.1992, coll. by JGH, 5 colonies on fragments of rocky wall; MNHN. — **Monaco.** jetty outer side, 18 m, 18.X.1997, coll. by JGH, 1 colony on pebble from boulder piling, MNHN. — **Atlantic.** Portugal, Sagres, Ponta da Baleeira, Donzelle Cave, 37°00'17"N, 8°55'43"W, 4 m, 8.VII.1986, coll. by JGH, 3 colonies on dead coral in dark chamber, MNHN.

ETYMOLOGY. — From Latin noun *spelunca*: cave. Named for the preference of this species for dark marine caves.

DIAGNOSIS. — Colonies medium- to large-sized. Autozooids with marginal gymnocyst visible frontally, costate shield moderately convex,

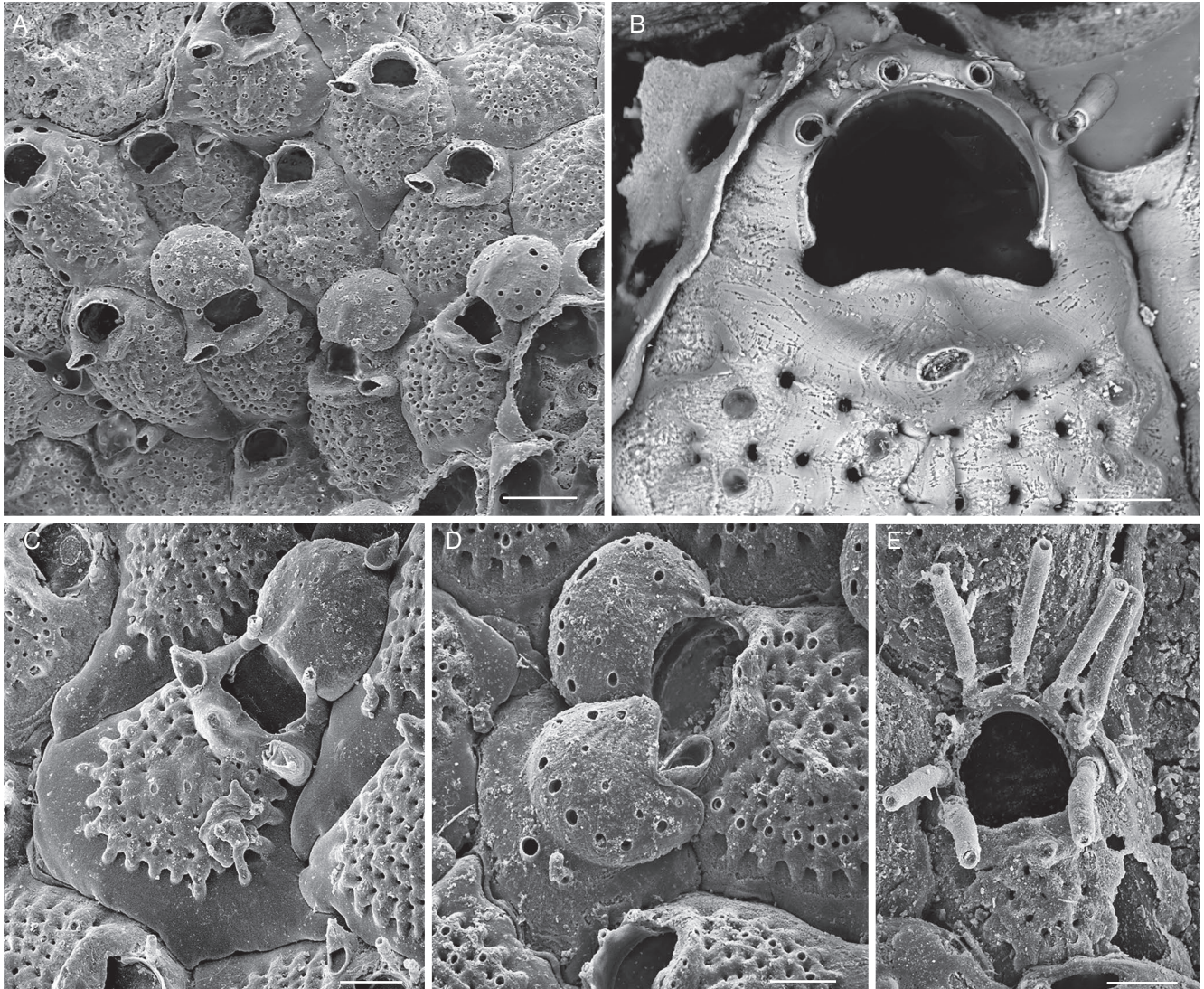


FIG. 13. — *Collarina speluncola* Harmelin, n. sp.: **A**, portion of colony with ovicelled and non-ovicelled autozooids; **B**, distal part of a non-ovicelled autozooid, note the particular shape of the proximal edge of the orifice and the small diameter of the basal part of oral spines; **C**, ovicelled zooid with paired adventitious avicularia, a distal avicularium on the ooecium and a well developed gymnocyst; **D**, ovicelled zooid with twin ovicells, the additional one with a large kenozooid; **E**, ancestrula with height spines (one broken). Origin: paratype MNHN-IB-2014-1915, Marseille, Morgiou, Conger Cave. Scale bars: A, 200 μ m; C, D, 100 μ m; B, E, 50 μ m.

made of numerous costae without protuberances, separated by small lacunae forming several concentric rings; apertural bar moderately raised; orifice with clearly visible condyles delimiting a proximal part (poster) broader than the anter and slightly convex; 3-5 thin oral spines; adventitious avicularia mostly single or paired, directed laterally or slightly disto-laterally; ooecium formed by distal kenozooid, with smooth ectooecium; ancestrula with 8 spines (occasionally 7).

DESCRIPTION

Colonies encrusting, pluriserial, unilaminar, medium- to large-sized (i.e. > 150 zooids) when fully grown, irregularly shaped but often elongated, white in young parts, brownish when older due to exogenous metallic coating. Autozooids longer than wide, surrounded by 7-8 pore-chambers (1 or 2 distal) visible at the growing margin; peripheral gymnocyst generally clearly visible frontally, wider proximally (Fig. 13A, C). Costal shield (spinocyst) weakly convex, smooth, composed

in most zooids of 15-16 costae (14-20) (Fig. 13A). Costae faintly prominent, their layout forming a relatively smooth surface except for a slightly raised bulge corresponding to the midline fusion of costae on the distal half of the costal shield of some zooids (Fig. 13A, C); intercostal lacunae small (5-8 μ m), rounded, 3-4 between adjacent costae; a relatively large pelma (diameter twice that of lacunae) at the base of each costa, its edge slightly prominent and funnel-shaped, i.e., with a rounded external orifice larger than an internal one (12-15 vs 5-8 μ m); a second pelma occasionally present close to the middle line of the shield. Apertural bar forming a thick, roughly triangular bulge, more or less irregularly shaped, often with a slight concavity on the proximal side, a pair of pelmatidia opening upwardly at the tip and a large pelma on each side of the bar, these pseudopores often being hidden by calcification (Figs 8C; 13B). Adventitious avicularia present in

most autozooids (70%), generally single (80%), more rarely paired (20%), inserted at the lateral corners of the apertural bar, directed laterally or slightly laterodistally, with pointed mandible and large, half-oval, proximal area (Figs 8C; 13A), occasionally with nested cystids (Fig. 17E). Autozooidal orifice wider than long (W/L = 1.2; Table 1), with the maximum width below the condyles, i.e., between the two rounded proximal corners of the orifice (Figs 8C; 13B), broader (> 20–25%) in ovicelled zooids (Fig. 13C); condyles thick, with a rounded tip; proximal edge slightly convex in most cases, sometimes indented in the middle by a small notch. Oral spines thin, 3–5 in number, 4 in most cases, inserted on the distal half of the orifice edge, 2 in ovicelled zooids (Fig. 13B, C). Ovicell prominent, globose, seemingly cleithral, oecium formed by distal kenozooid (Figs 13C; 15A), slightly wider than long (W/L = 1.1; Table 1), smooth ectooecium punctuated with 12–16 large pseudopores similar to those of the spinocyst (i.e., pelmata with double orifice); apical adventitious avicularium directed distally, rarely present (on *c.* 3% of ovicells). Occasional occurrence of twin ovicells (Fig. 13D) with the additional one associated to a large kenozooid visible frontally, budded by the maternal zooid from a laterodistal pore-chamber. Ancestrula cribrimorph with costate shield composed of 7–9 costae including the primary apertural bar, occupying slightly over half of the frontal area, 8 spines evenly distributed around the orifice (Fig. 13E).

REMARKS

Collarina speluncola Harmelin, n. sp. differs from the other *Collarina* species of the Atlantic-Mediterranean region first by the general appearance of zooids given by a slightly convex spinocyst made of numerous smooth costae, the shape of the orifice with a broad poster, thin oral spines and ancestrula with 8 spines. The occurrence of twin ovicells, only observed at the type-locality, may be induced by local site peculiarities (see below). These features were constant in colonies from two submarine caves of the Marseille area (including the type-locality) where *C. speluncola* Harmelin, n. sp. forms large aggregations (see below), but also in colonies from Monaco and Sagres (S Portugal). The main difference shown by the Atlantic colonies was the number of spines, in most zooids 3 instead of 4 in the Mediterranean colonies. The apparent similarity between *C. speluncola* Harmelin, n. sp. and *Collarina* sp. awaits further investigation pending more abundant material. Seemingly, there is no indication in the literature of previous records of this species.

Habitat and geographical distribution. Most material of *C. speluncola* Harmelin, n. sp. came from dark caves where this species occupied vertical walls (Fig. 18B). In both Conger Cave (type locality) and Gameau Cave, the local population was very abundant and formed a typical ‘facies’ (Pérès & Picard 1964), i.e., an aggregative concentration of colonies that contrasted with the quasi-absence of other encrusters, except for *Haplopoma cf. graniferum* (Johnston, 1847), which presented the same growth-form. The microenvironment on cave walls densely populated by *C. speluncola* Harmelin, n. sp. was characterized by complete darkness and freshwater seep-

age. In Conger Cave, where seepage was particularly active, salinity of the water body close to the *Collarina* facies was 30.6–32.0 instead of 38.6 outside the cave (measured on June 2nd 1987). In both *C. speluncola* Harmelin, n. sp. and *H. cf. graniferum*, the brown colour of the oldest parts of colonies was due to coating by Fe–Mn oxides, as commonly observed on organic and inorganic substrates from dark habitats as well in the coastal zone as in the deep sea (Allouc & Harmelin 2001). No freshwater seepage was noticed during the sampling survey in the dark caves of Sagres, including Donzelle Cave (Boury-Esnault *et al.* 2001) where a few colonies of *C. speluncola* Harmelin, n. sp. were found in a dark, upper chamber communicating with the main chamber by a narrow corridor, together with *Puellina (Cribrilaria) saldanhai* Harmelin, 2001. The colony from Monaco was not collected in a cave but encrusted the lower face of a pebble found below a jetty boulder, i.e., a discrete cryptic habitat. Freshwater seepage was not observed at this site but light occasional infiltration may occur. However, the habitat of this specimen is similar to that of *Collarina* sp. suggesting that the morphological and molecular relationships between the latter and *C. speluncola* Harmelin, n. sp. should be investigated (see below).

The known geographical range of *C. speluncola* Harmelin, n. sp. is limited, including only three sites in the NW Mediterranean (Marseille area and Monaco) and one in the southern Atlantic coast of the Iberian Peninsula (Sagres).

Collarina sp.
(Fig. 14; Table 1)

?*Collarina balzaci* – Hayward 1974 (in part): 399, table 3.

MATERIAL EXAMINED. — **France.** Corsica, Île-Rousse islets., 42°38'42"N, 8°56'04"E, 5 m, 9.IV.1978, coll. by H. Zibrowius, 8 small colonies on 2 small pebbles (together with 1 colony of *C. denticulata*), MNHN-IB-2014-1928. — Corsica, Calvi, Stareso, 42°34'48"N, 8°43'28.60"E, 3 m, IX.1980, coll. by JGH, 2 small colonies on pebble, MNHN-IB-2014-1929. — Corsica, Stareso, 42°34'49"N, 8°43'28"E, 7 m, 26.VIII.2018, coll. by JGH, 1 colony on small pebble, MNHN. — Corsica, Scandola, Gargallo, 42°21'58"N, 8°32'26"E, 7 m, 27.VIII.2018, coll. by JGH, 2 colonies (one fertile) on small pebbles, together with *C. denticulata*, MNHN. — **Greece.** Chios, P. J. Hayward leg., 1 colony on pebble (Photos MSJ), NHMUK 1975. 1. 12. 419.

DESCRIPTION

Colony encrusting, pluriserial, unilaminar, medium-sized in available material. Autozooids roughly oval with marginal gymnocyst generally poorly visible in frontal view except at proximal edge (Fig. 14A, B). Costate shield moderately convex; costae smooth, 9–11 in most cases, with a large pelma at the top of the ascending base, the latter with a rounded outline, often a smaller pelma in inner position; intercostal lacunae 2–4 between adjacent costae, rounded (Fig. 14B). Apertural bar more or less triangular, with distal side broad, concave, sloping towards the proximal edge of orifice; a pair of pelmatidia near the tip of the bar and a pair of pelmata laterally at the base of the proximal side (Fig. 14C). Adventitious avicu-

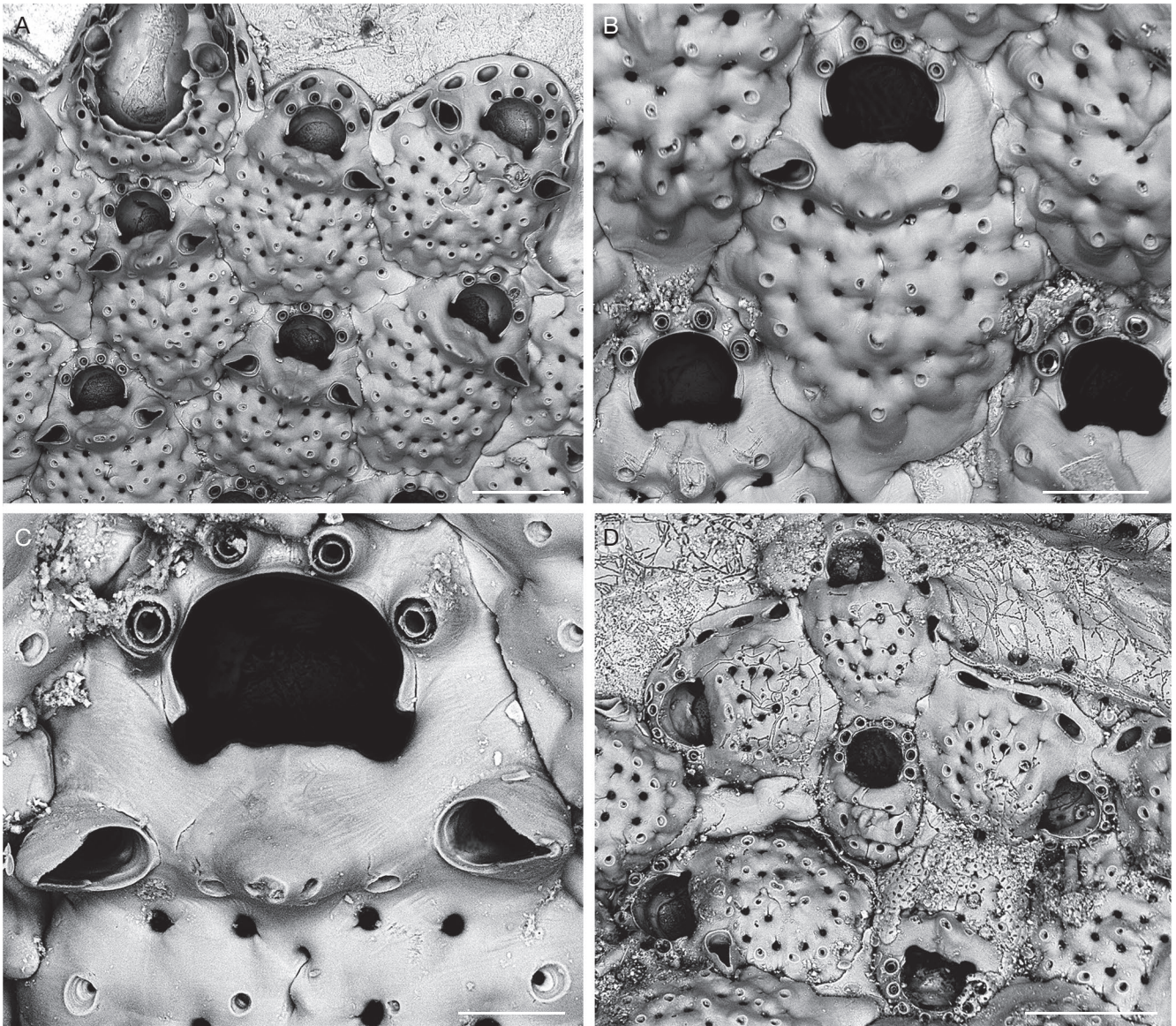


FIG. 14. — *Collarina* sp.: **A**, colony growing edge; **B**, non-ovicelled zooid; **C**, orifice, note the particular shape of the proximal edge (poster) and the structure of the apertural bar with two laterally directed avicularia; **D**, ancestrula and zone of astogenetic change. Origin: MNHN-IB-2014-1928, Corsica, Île-Rousse, 5 m. Scale bars: A, D, 200 μ m; B, 100 μ m; C, 50 μ m.

laría 2 in majority of autozooids, directed laterally, proximal membranous area relatively large and rounded. Autozooidal orifice clearly wider than long, with maximum width at the proximal corners, the latter in the form of broad square indentations; proximal edge straight and somewhat resembling a lyrula (Fig. 14C). Oral spines relatively thin, 3-5 (3-4 in most zooids), 2 in ovicelled zooids. Ooecium with moderate relief, formed by distal kenozooid. Ancestrula cribrimorph with few costae and 7 spines (specimen from Île-Rousse: Fig. 14D) or 9 spines (fertile specimen from Gargallo).

REMARKS

The available specimens present several morphological features that suggest some relationship with *C. speluncola* Harmelin, n. sp., i.e. the smooth aspect of the costate shield and more

particularly the shape of the orifice with the proximal corners cut by a broad indentation and the same number of thin oral spines. The main features differentiating *Collarina* sp. from *C. speluncola* Harmelin, n. sp. are the more pronounced lateral indentations of the orifice, the more raised and straighter proximal edge of the orifice, autozooids with narrower lateral gymnocyst, costate shield with fewer costae and lacunae, and ovicell with ectooecium less smooth. The number of spines of the ancestrula was curiously variable in the available material, but close to that of *C. speluncola* Harmelin, n. sp. (seven or nine vs height). Two specimens in poor condition (Monaco, 18.X.1997 and Stareso, 26.VIII.2018) encrusting small pebbles with characters apparently intermediate between *Collarina* sp. and *C. speluncola* Harmelin, n. sp. could not be placed with certainty in either of the two taxa. One specimen on a small

pebble from the Aegean Sea (Chios: NHMUK 1975.1.12.419), ascribed to *C. balzaci* by Hayward (1974), presents the same type of orifice and costate shield. The divergence of this specimen from the typical features of *C. balzaci* had already been noticed by Bishop (1988), who considered that it may be an unnamed species of *Collarina*. The question whether *Collarina* sp. and *C. speluncola* Harmelin, n. sp. are distinct species or two conspecific ecotypes induced by very different habitat conditions remains open pending more abundant further material.

HABITAT AND GEOGRAPHICAL DISTRIBUTION

The specimens from Corsica were found in three shallow-water sites on the west coast (3-7 m), encrusting small pebbles collected among boulders. In these sites, *Collarina* sp. occurred with *C. denticulata* Harmelin, n. sp. on the few sampled pebbles. The specimen from Chios was collected in the same type of habitat. Knowledge of the geographical distribution of *Collarina* sp. is poor; its records include Corsica, Chios and, possibly, Monaco.

DISCUSSION

The extremely brief definition of the genus *Collarina* given by Jullien (1886) is misleading and not informative of the typical features of this taxon (Gautier 1962; Bishop 1988). The main characters of this genus were specified by Bishop (1986, 1988, 1994) when clarifying the confusion related to designation of the type-species of the genus and misidentification with *Cribrilina*. Gautier (1962) was the first to combine the generic name *Collarina* and Audouin's species *balzaci*, but did not give a formal definition of the genus. Definitions given by Prenant & Bobin (1966), Zabala (1986), Zabala & Maluquer (1988) and Hayward & Ryland (1998) were based on material attributed to *C. balzaci*, but also actually or potentially including the form distinguished here as *C. gautieri* Harmelin, n. sp. Considering six species, including four new to science, the present work provides a new approach to the generic peculiarities of this genus together with a better characterisation of the morphological features of each species. A fuller diagnosis of the genus *Collarina* is thus proposed below.

DIAGNOSIS OF THE GENUS *COLLARINA*

Colony encrusting, unilaminar, irregularly shaped and variously sized at mature stage. Frontal shield costate with costae varying notably in number and surface structure among species. Gymnocystal lateral walls variously broad, little or extensively visible in frontal view, sometimes with a few large pseudopores in certain species. Pore-chambers large, numerous, visible in frontal view at the colony edge. Costae punctured with large (pelmata) and small (pelmata) pseudopores, the largest typically forming a peripheral ring, the smallest sometimes raised at the top of a process. Intercostal lacunae circular or quadrangular, varying in size and number. Apertural bar (actually, the first pair of costae) more or less prominent, with specifically shaped umbo and large paired pseudopores and

smaller ones near the tip. Orifice dimorphic, broader in ovicelled zooids, anter semi-circular, with specific height/width ratio and subtriangular proximal condyles; proximal edge of orifice (poster) with specific shape. Adventitious avicularia on autozooids, typically paired but one or both can be missing in some autozooids, inserted at the ends of the apertural bar, directed laterally with varying angle, rostrum triangular, without cross-bar. Oral spines present, jointed on a variably developed conical base, reduced to a pair in ovicelled zooids. Ovicells hyperstomial, oecium formation involving distal daughter zooids, the latter being, according to species, kenozooids or both kenozooids and autozooids in the same colony; ectoecium punctured with large and small pseudopores similar to those of the costal shield; an adventitious inconstant avicularium directed distally on the distal edge of kenozooidal oecia, absent in autozooidal oecia. Ancestrula cribrimorph with small costate shield and spines around the edge of the orificial area.

SPECIFIC FEATURES

Apart from *C. fayalensis*, distinctive because of its much-reduced spinocyst, all *Collarina* specimens recorded in the NE Atlantic-Mediterranean region were, until now, ascribed to *C. balzaci*. Examination of abundant material has proved that the genus *Collarina* is represented in this area by at least six species. The complex skeletal structure of *Collarina* species presents multiple features that can be used for discriminating the species. The most useful morphological traits to consider are the extension and shape of both the costal shield and the gymnocyst, the number and ornamentation (processes, pseudopores) of the apertural bar and costae, the shape of both the anter and the poster of the orifice, the orientation and shape of the adventitious avicularia, the mode of formation of oecia and the surface structure of the ectoecium. The combination of these features allows separation of the species with some confidence. Because of their small size, some species-specific features can only be assessed through SEM examination, for instance the serrated edges of the rostrum of avicularia of *C. balzaci*. A more thorough approach using molecular tools would, however, certainly be useful, particularly in the case of *C. balzaci* and *C. gautieri* Harmelin, n. sp. because of their distribution in both the NE Atlantic and the Mediterranean. The most evident discriminating features of the six *Collarina* species have been grouped together in Table 2 and some of them are shown schematically in Figures 7 and 8.

OVICELLS

The frequency of occurrence of mature autozooids within the zone of astogenetic repetition of colonies varies greatly among *Collarina* species (Table 3A). Two groups, however, can be distinguished: *a*) species with ovicelled zooids moderately frequent (18-25%: *C. speluncola* Harmelin, n. sp., *C. denticulata* Harmelin, n. sp., *C. macaronensis* Harmelin, n. sp., *C. fayalensis*), and *b*) species with clearly more frequent ovicells (48-60%: *C. balzaci*, *C. gautieri* Harmelin, n. sp.). It is worth noting that the four species of group *a* can develop large colonies while in group *b*, *C. balzaci* and *C. gautieri* Harmelin,

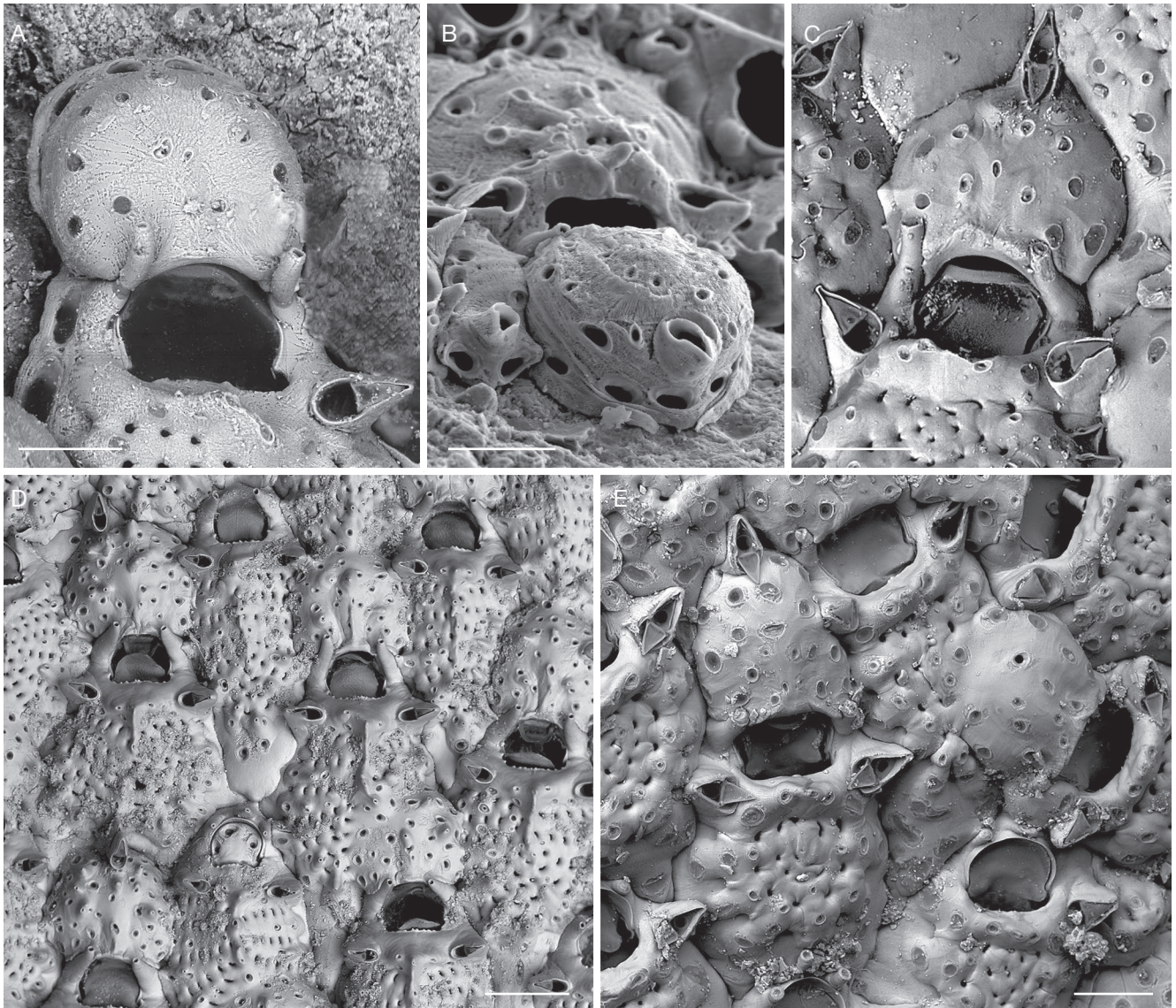


FIG. 15. — Types of oecia in *Collarina* Jullien, 1886 species: **A-C**, kenozooidal oecia with and without distal avicularium (**A**, *C. speluncola* Harmelin, n. sp.; **B**, *C. fayalensis* Harmelin, 1978; **C**, *C. macaronensis* Harmelin, n. sp.); **D**, *C. denticulata* Harmelin, n. sp., colony portion with two kenozooidal oecia (left) and three oecia incorporated in distal autozooid (right); **E**, *C. macaronensis* Harmelin, n. sp., 2 ovicelled zooids with kenozooidal oecium (left) vs oecium incorporated in distal autozooid (right). Origin: A, Marseille, Conger Cave ; B, Azores, Saõ Miguel, Vila Franca Is.; C, E, Madeira, NHMUK 1911.10.1.705; D, Catalonia, Medes Is. Scale bars: A-C, E 100 μ m, D, 200 μ m.

n. sp. present only small colonies with early maturity. These differences are linked to the life-history of the species and their ecology, particularly the attributes of the habitat they occupy (e.g. stability, size, perenniality, food resources, etc.). Thus, *C. balzaci*, epibiont on ephemeral macrophytes, contrasts obviously with the cave-dwelling *C. speluncola* Harmelin, n. sp. in both the habitat features and the size of mature colonies.

As in many cheilostomes (Ostrovsky 2013), brooding *Collarina* colonies ensure protection of embryos by immersion of the incubation cavity within a distal daughter zooid of the maternal autozooid, from which the calcareous ectooecium is built. In the Atlantic-Mediterranean *Collarina* species, this distal zooid can be either exclusively a kenozooid (*C. balzaci*, *C. speluncola* Harmelin, n. sp., *C. gautieri* Harmelin, n. sp., *C. fayalensis*: Figs 15A-C; 16), or either a kenozooid or an

autozooid, both types co-occurring within the same colony (*C. denticulata* Harmelin, n. sp., *C. macaronensis* Harmelin, n. sp.: Fig. 15D, E). These two modes of protection of the incubation chamber were placed in the same category (type 1) by Ostrovsky (2013) while Bishop & Househam (1987) distinguished among *Puellina* species oecia formed by a distal autozooid (category A) from oecia formed by a distal kenozooid (category B) (see also Rosso *et al.* 2018). The early stages of the construction of oecia are visible on the growing edge of colonies. In all cases, budding of the entoecium by the maternal zooid starts before that of the ectooecium by the daughter zooid (Fig. 16A, B). The entoecium appears first as a small, roughly quadrangular basal blade, as observed in *C. balzaci*, *C. denticulata* Harmelin, n. sp. (Fig. 16E) and *C. macaronensis* Harmelin, n. sp. from SEM photos. After-

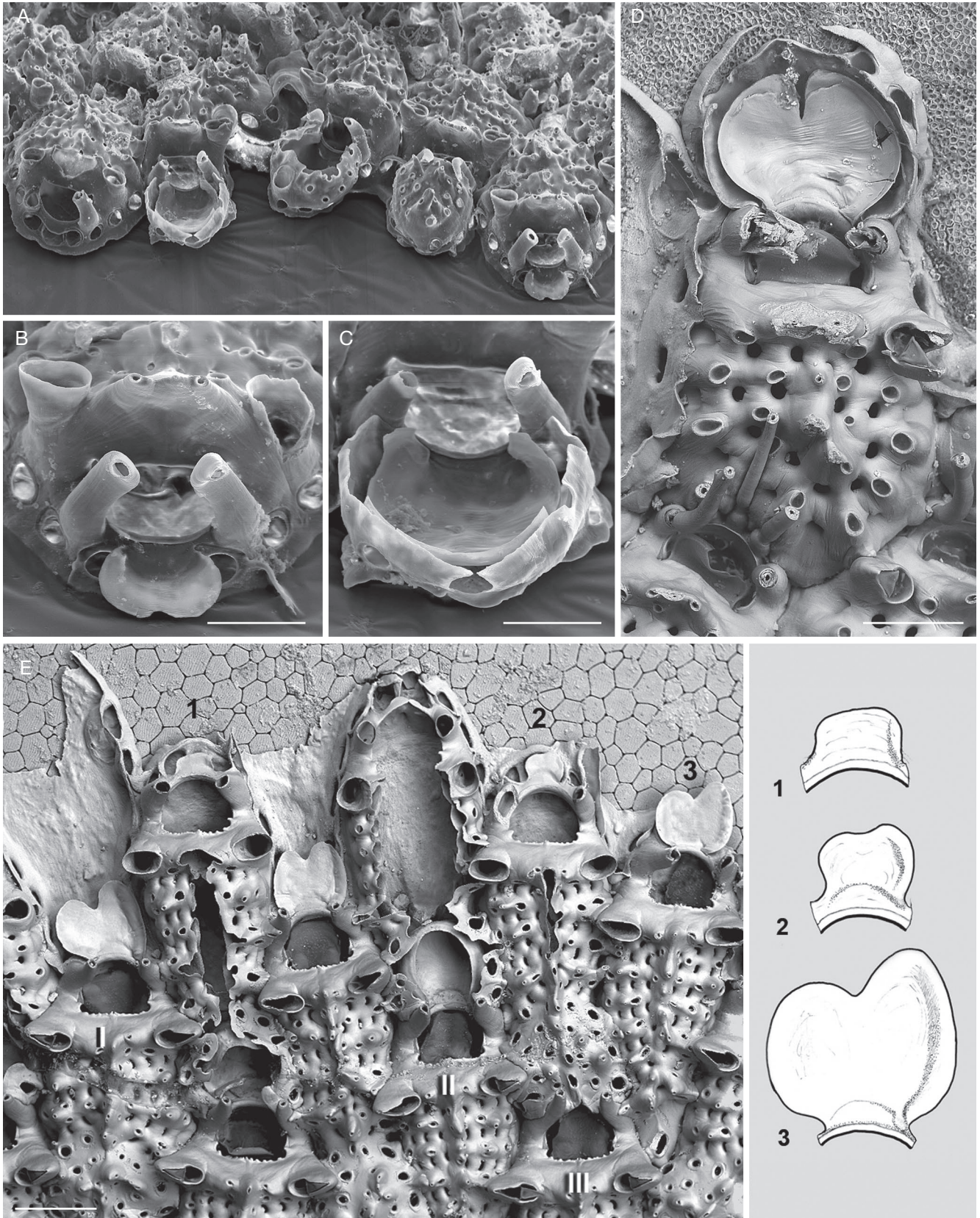


Fig. 16. — Phases of oecium construction involving a daughter zooid (kenozooid or autozooid) of the maternal zooid in *Collarina* Jullien, 1886 species: **A-D**, growth of entooecium with bilobate stages, and its incorporation by distal kenozooid in *C. gautieri* Harmelin, n. sp.; **E**, oecium formed by a distal autozooid in *Collarina denticulata* Harmelin, n. sp., three successive early stages (1, 2, 3: SEM photo + stylized outlines) at the colony edge from single to bilobate blade with unequal lobes, and three older stages (I, II, III) with distal autozooids incorporating progressively the growing entooecium. Origin: A-C, Marseille, Veyron; D, S Portugal, MHNUSC-Bry-661; E, Medes Islands, on *Pinna* shell. Scale bars: B-D 100 μ m; E, 200 μ m.

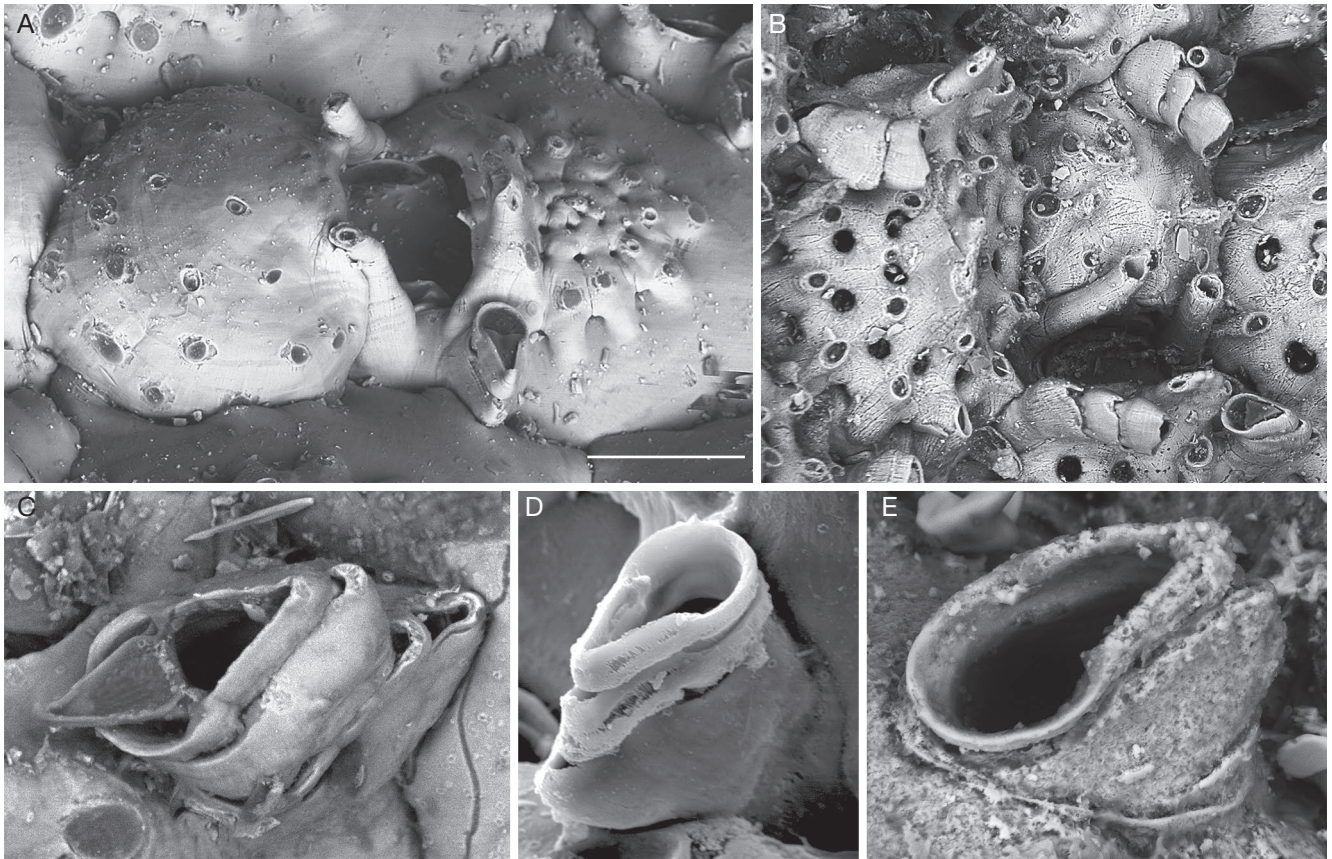


FIG. 17. — Adventitious avicularia with nested cystids in *Collarina* Jullien, 1886 species: **A**, *C. macaronensis* Harmelin, n. sp., ovicelled zooid; **B**, *C. gautieri* Harmelin, n. sp., four piles of nested avicularian cystids adventitious on two autozooids and an oecium; **C**, *C. macaronensis* Harmelin, n. sp.; **D**, *C. fayalensis* Harmelin, 1978; **E**, *C. speluncola* Harmelin, n. sp. Origin: A, Madeira, NHMUK 1899.7.1.2105; B, Galicia, Ria de Ferrol, MHNUSC-Bry-113; C, Galicia, Sisargas Is., MHNUSC-Bry-662; D, Azores, Saó Miguel, Vila Franca; E, Marseille, Conger Cave. Scale bar: A, 100 μ m.

wards, a light concavity appears on the middle of the distal edge of the blade, which increases slightly in size. Later, the basal blade of the entoecium increases notably in size and becomes distinctly bilobate (Fig. 16B, D). Curiously, in *C. denticulata* Harmelin, n. sp., the two lobes are clearly unequal, one being shorter and more rounded (Fig. 16E). This trend was also perceptible in *C. macaronensis* Harmelin, n. sp., but less obviously. It is not clear if the tempo of the incorporation of the entoecium within the daughter zooid is the same in the two types of oecia (kenozooid vs autozooid). In *C. denticulata* Harmelin, n. sp., which presents both types, the fact that the entoecium at the bilobate stage can be both terminal (Fig. 16E: 3, on right) or already incorporated within the initial proximal part of the distal autozooid despite similar size of lobes (Fig. 16E: 2 cases on left) might suggest that the terminal one is involved in the construction of a kenozooidal oecium. In *C. gautieri* Harmelin, n. sp. (Fig. 16B), the early bilobed entoecium is terminal and its incorporation by the basal part of the kenozooid starts at more advanced stages of growth (Fig. 16C, D). It was also evident (Table 3B) that the distal avicularium borne by the oecium, which is present in all six species considered here and one of the most typical features of the genus *Collarina* (see diagnosis above), occurs exclusively on oecia formed by a kenozooid, from

which it is budded. In contrast, it is never present on oecia formed by a distal autozooid (Table 3B). The frequency of occurrence of oecial avicularia is very variable according to species, even among those having exclusively kenozooidal oecia (Table 3). For instance, they are rare in *C. speluncola* Harmelin, n. sp. (< 5% of oecia) but present on all oecia in *C. gautieri* Harmelin, n. sp.

Ovicells also present species-specific differences in the type of closure protecting the oecial vesicle (Table 3C). Ovicells are cleithral in *C. balzaci* while they are acleithral in *C. denticulata* Harmelin, n. sp. (A. Ostrovsky pers. com., 5.IV.2018). In *C. denticulata* Harmelin, n. sp., as shown by SEM photos of unbleached colonies, the operculum does not close the oecium opening. This function is performed by a thickening of the oecial vesicle which, according to A. Ostrovsky (pers. com., 05.IV.2018), is an arch-like chitinous sclerite for the muscle attachment resembling a small operculum (Fig. 15D). The same type of structure seems also to be present in *C. macaronensis* Harmelin, n. sp. (Fig. 15C). Investigation using better preserved material and sections would be, however, necessary for defining accurately the structure of ovicell closures of *Collarina* species.

Twin ovicells involving a large additional kenozooid budded from a laterodistal pore-chamber (Fig. 11D) were observed in

TABLE 2. — Characterization of *Collarina* Jullien, 1886 species by contrasting character states. Abbreviations: **C.b.**: *C. balzaci* (Audouin, 1826); **C.s.**: *C. speluncola* Harmelin, n. sp.; **C.d.**: *C. denticulata* Harmelin, n. sp.; **C.g.**: *C. gautieri* Harmelin, n. sp.; **C.m.**: *C. macaronensis* Harmelin, n. sp.; **C.f.**: *C. fayalensis* Harmelin, 1978; **Ov.**, ovicell; **Kz**, distal kenozooid; **Az**, distal autozooid.

Features	C.b.	C.s.	C.d.	C.g.	C.m.	C.f.
Mature colony small	x	–	–	x	–	–
Mature colony large	–	x	x	–	x	x
Gymnocyst narrow	–	–	x	x	–	–
Gymnocyst broad	x	x	–	–	x	x
Spinocyst smooth	x	x	–	–	x	x
Spinocyst rough	–	–	x	x	–	–
Costae N ≤ 6	x	–	–	–	–	x
Costae N > 6	–	x	x	x	x	–
Orifice L/W ratio ≈ 0.5	–	–	–	x	–	–
Orifice L/W ratio ≤ 1, > 0.5	x	x	x	–	x	–
Orifice L/W ratio > 1	–	–	–	–	–	x
Orifice poster straight-convex	x	x	x	x	–	–
Orifice poster concave	–	–	–	–	x	x
Orifice poster smooth	x	x	–	x	x	x
Orifice poster denticulate	–	–	x	–	–	–
Ov. numerous	x	–	–	x	–	–
Ov. less frequent	–	x	x	–	x	x
Ooec.: Kz	x	x	–	x	–	x
Ooec.: Kz + Az	–	–	x	–	x	–

some colonies of *C. speluncola* Harmelin, n. sp. from Conger Cave but not in the material from the other sites. According to A. Ostrovsky (pers. com., 4.IX.2017) this phenomenon may occur occasionally in other species. Apparently similar teratologic twin oecia were observed in Recent specimens of *Cleidochasmidra portisi* (Neviani, 1895) by Rosso *et al.* (2015). This anomaly evokes but may differ from the disorderly budding of multiple ovicells (ovicell hyperplasia) sometimes observed in *Schizoporella* and *Fenestrolina* species. According to Powell *et al.* (1970), who reported this phenomenon from *Schizoporella* in California, ovicell hyperplasia would be an effect of contamination by petroleum hydrocarbons, a hypothesis challenged by Straughan & Lawrence (1975). In the Mediterranean, ovicell hyperplasia was observed in *Schizoporella* colonies living in natural conditions (JGH, unpublished data). The particular hydrologic conditions observed in Conger Cave may have triggered the production of twin ovicells in the local population of *C. speluncola* Harmelin, n. sp.

AVICULARIA

Collarina species show, with variable frequency, the nesting of successive avicularian cystids. This phenomenon was observed in all species except *C. balzaci*: *C. denticulata* Harmelin, n. sp. (Fig. 6G), *C. speluncola* Harmelin, n. sp. (Fig. 17E), *C. gautieri* Harmelin, n. sp. in Galician (Fig. 17B) and Mediterranean specimens, *C. macaronensis* Harmelin, n. sp. (Fig. 17A, C), *C. fayalensis* (Fig. 17D) and *Collarina* sp. The same nesting of avicularia was previously observed in another cribrilininid genus, *Puellina*, in dark caves (*Cribrilaria crenulata* Harmelin = *Puellina venusta* Canu & Bassler, Harmelin 1970: fig. 1k, pl. II3) and on substrata from deep-water (*P. radiata*, *P. venusta*: JGH, unpublished). Similar nesting but concerning orifice frames was also observed in a colony of *Escharina dutertrei*

TABLE 3. — Features of ovicells in the six *Collarina* Jullien, 1886 species (Mediterranean and Atlantic material for *C. gautieri* Harmelin, n. sp.). Frequency data in %: **A**, occurrence frequency of ovicelled autozooids within colonies; **B**, oocium types: frequency of oecia produced by a kenozooid (**Kz**) or a distal autozooid (**Az**), and frequency of oecia bearing a distal avicularium (**Av**); **C**, type of ovicell closure. Origin of data – *C. balzaci* (Audouin, 1826): Turkey, Lebanon, Adriatic, France Planier, 7 colonies, 88 zooids, 53 oecia; *C. speluncola* Harmelin, n. sp.: Morgiou, Conger Cave, 8 colonies including types, 473 zooids, 89 oecia; *C. denticulata* Harmelin, n. sp.: Port-Miou & Renaire, 6 colonies, 342 zooids, 104 oecia (63 Az, 41 Kz); *C. gautieri* Harmelin, n. sp., Mediterranean: Medes, Naples, Bonifacio, Port-Cros, Veyron (holotype), 5 colonies, 173 zooids, 92 oecia; *C. gautieri* Harmelin, n. sp., Atlantic: Plymouth, Brittany (2 sites), Algarve, 9 colonies, 191 zooids, 100 oecia; *C. macaronensis* Harmelin, n. sp.: Madeira (NHMUK 4 colonies + Baixo Is., holotype & paratype), 298 zooids, 67 oecia; *C. fayalensis* Harmelin, 1978: Sao Miguel, I. Villa Franca, 3 colonies, 433 zooids, 72 oecia. Frequency numbers in %. **n.d.**: no data.

<i>Collarina</i> spp.	A. Ovicelled zooids		B. Oocium types		C. Ovicell closure
	Kz	Av	Az	Av	
<i>C. balzaci</i>	60	100 (61)	0	0	cleithral
<i>C. speluncola</i> Harmelin, n. sp.	19	100 (4.4)	0	0	? cleithral
<i>C. denticulata</i> Harmelin, n. sp.	25	39 (21)	61 (0)	0	acleithral
<i>C. gautieri</i> Harmelin, n. sp. – Med.	53	100 (100)	0	0	n.d.
<i>C. gautieri</i> Harmelin, n. sp. – Atl.	52	100 (100)	0	0	n.d.
<i>C. macaronensis</i> Harmelin, n. sp.	24	82 (51)	18 (0)	0	? acleithral
<i>C. fayalensis</i>	18	100 (83)	0	0	n.d.

(Audouin, 1826) from a dark cave (JGH, unpublished). According to Berning (2008), intramural buds would be a processus of regeneration after predation targeted on orifices or avicularia. Similarly, Lidgard *et al.* (2012) interpreted the nested avicularia of *Puellina* illustrated by Harmelin (1970) as the consequence of damage localized on the polymorph. Also, for Rosso *et al.* (2018), the frequent occurrence of intramural regeneration in *Glabilaria hirsuta* Rosso, 2018 may be a clue of predation. In the case of *Collarina*, it is more likely that nested cystids are the outcome of an ageing process affecting some avicularia with decay phases alternating with rebudding of a new cystid from the same pore. It is noticeable that nested avicularia were not observed in *C. balzaci* in normal conditions, i.e., with small, short-lived colonies living on ephemeral macrophytes (cf. below) but they can also occasionally occur in larger colonies from the Kerkennah Islands.

HABITAT (Fig. 18)

At present, *C. balzaci* is the only *Collarina* species known to grow exclusively on seagrasses and algae, with adaptive traits allowing completion of the colony life cycle on flexible, short-lived substrata. All other *Collarina* species live on hard substrata at various shade levels. Among these species, however, *C. speluncola* Harmelin, n. sp. is the only one found on rocky walls of dark caves, forming colony aggregations (facies) in places influenced by light freshwater seepage (see below). The remaining four species (five with *Collarina* sp.) live on the undersides of discrete, small substrata (cobbles, pebbles, shells, pottery or other artificial fragments) on the seabed in places from which macrophytes are excluded.

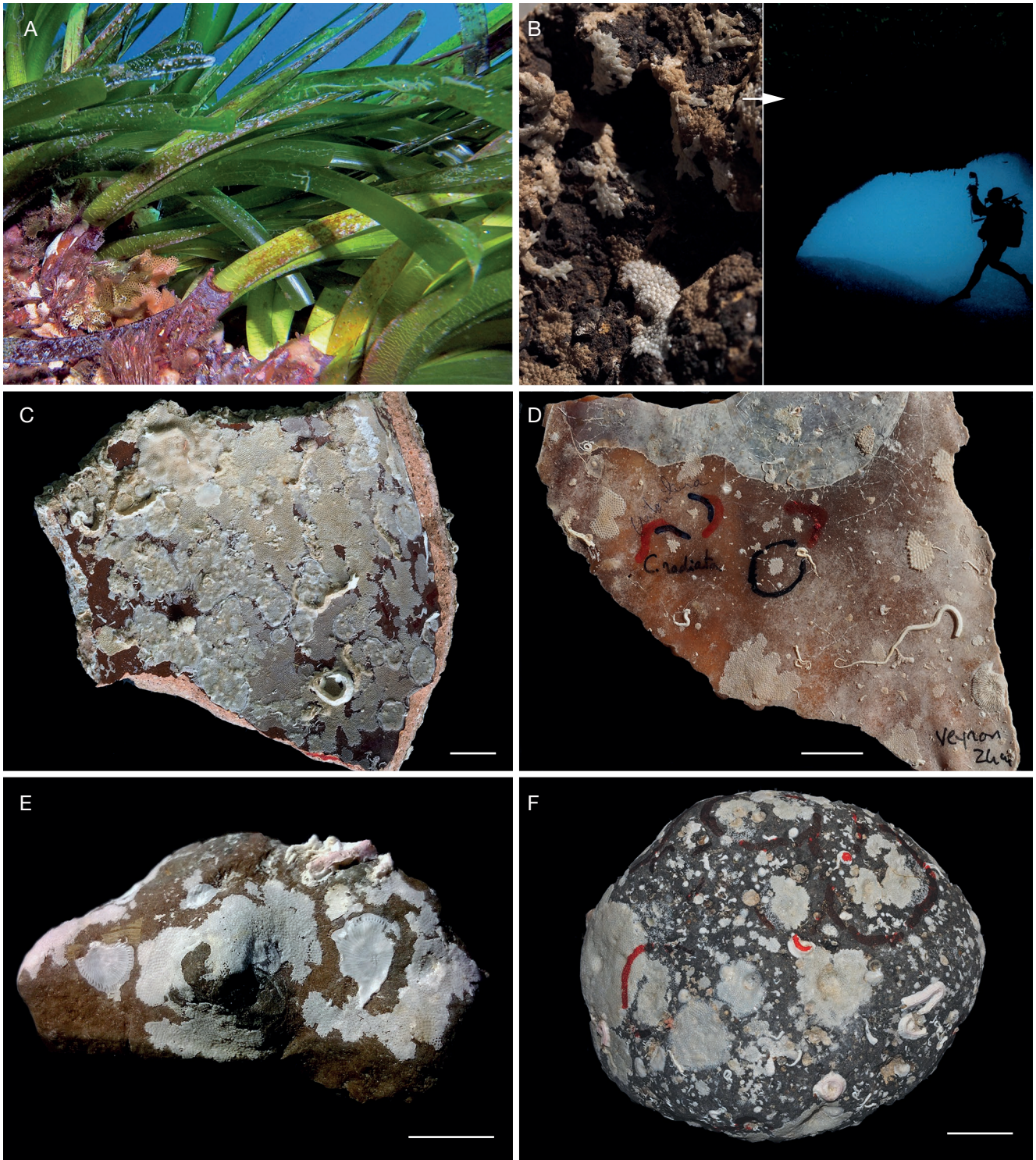


FIG. 18. — Habitats of *Collarina* species: **A**, *C. balzaci* (Audouin, 1826), bundles of *Posidonia* leaves; **B**, *C. speluncola* Harmelin, n. sp., wall of dark submarine cave with freshwater seepage; **C**, *C. denticulata* Harmelin, n. sp., underside of pottery fragment, Cassis, Port-Miou, 18 m; **D**, *C. gautieri* Harmelin, n. sp., underside of *Pinna* shell, paratype MNHN-IB-2014-1921, Veyron, 24 m; **E**, *C. macaronensis* Harmelin, n. sp., underside of pebble, paratype MNHN-IB-2014-1926, Madeira, Porto Santo, Baixo Is.; **F**, *C. fayalensis* Harmelin, 1978, underside of pebble, Azores, Saô Miguel, Vila Franca, 15 m. Scale bars: 1 cm.

With few exceptions, all examined *Collarina* specimens came from nearshore sites, mostly at shallow depth (< 25 m). The species with the broadest depth range was *C. gautieri* Harmelin, n. sp., in both the NE Atlantic (from shore

pools to 130 m off the coasts of Brittany) and the Mediterranean (from 5 to 60-80 m depth). Interestingly, several *Collarina* species can occupy the same microhabitat at the same time, and sometimes even co-occur on the same small

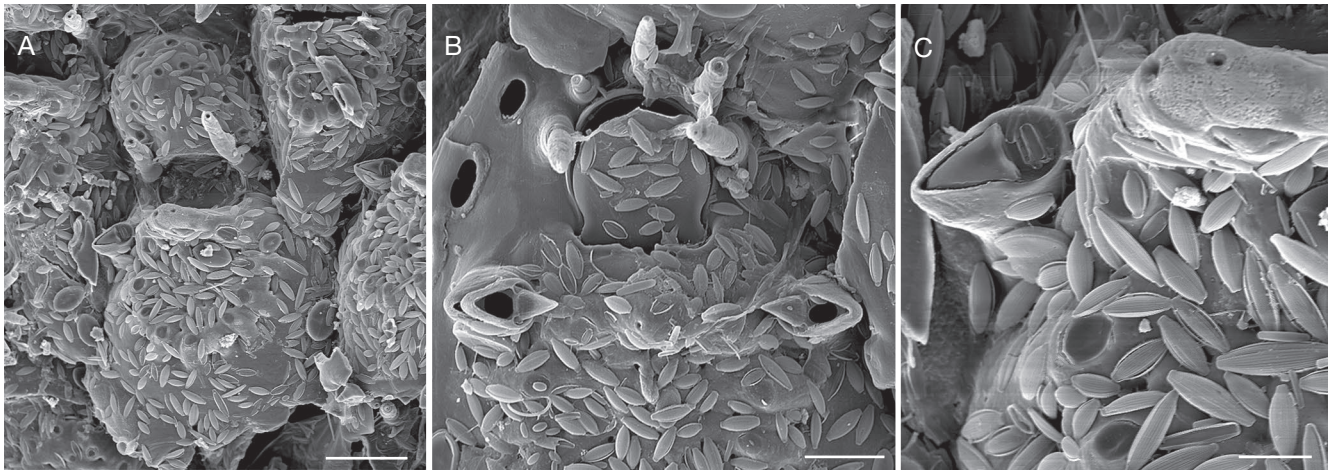


FIG. 19. — *Collarina balzaci* (Audouin, 1826), from Tunisia, Kerkennah Islands, on *Posidonia* leaf (coll. by JGH, June 2018). Ultrasonically cleaned colony covered with diatom frustules: **A**, ovicelled zooid; **B**, distal part of a non-ovicelled zooid, note the left avicularium with nested cystids; **C**, enlarged part of ovicelled zooid with a lateral avicularium and the apertural bar. Scale bars: A, 100 μ m, B, 50 μ m, C, 25 μ m.

pebble (e.g. *C. denticulata* Harmelin, n. sp. with *C. gautieri* Harmelin, n. sp. or *Collarina* sp.). The contrast between the strong habitat differences of *C. speluncola* Harmelin, n. sp. and *Collarina* sp. and their morphological similarities raises the question of their genetic relationships. The alternative between high intraspecific phenotypic plasticity and speciation by habitat specialization and reproductive isolation would be an interesting matter for a molecular approach and transplantation experiments.

EFFECTS OF DISTURBANCE

Among the six *Collarina* species examined here, two of them, *C. balzaci* and *C. speluncola* Harmelin, n. sp., can develop dense local populations with strong dominance over other bryozoans of the same microhabitat when they face environmental conditions involving disturbance. In the case of *C. balzaci*, the population sampled at Kerkennah Is. on *Posidonia* leaves presented both outstanding abundance and large colonies and autozooids, the latter with more numerous oral spines and a cover of diatom frustules (Fig. 19). Although preliminary, these observations strongly suggest that these abnormal features are triggered by particular local environmental conditions. First, this area presents unique oceanographic characteristics with very high sea temperature in summer (27–28°C observed at 2 m depth in June) and large tidal range, exceptional in the Mediterranean, reaching 1 m in the Kerkennah area (Sammari *et al.* 2006; Hattour *et al.* 2010). However, even if positive temperature anomalies can be a stressor for benthic communities (e.g. Bensoussan *et al.* 2010) and bryozoans in particular (Pagès-Escolà *et al.* 2018), the summer thermal regime at Kerkennah is apparently similar to that in Lebanon (Abboud-Abi Saad *et al.* 2004), where *C. balzaci* presents normal features. Second, the sampling site is located at the northern limit of the Gulf of Gabes, which is one of most polluted areas in the Mediterranean due to the phosphate industry (El Zrelli *et al.*, 2015) and is relatively close to Sfax, one of the industrial sites located along the

Gulf of Gabes. Discharge into the sea of phosphogypsum and other wastes leads to heavy-metal contamination, high nutrient inputs, siltation and eutrophication, with severe impacts on marine communities (El Kateb *et al.* 2018), particularly on *P. oceanica* beds (El Zrelli *et al.* 2017). These preliminary observations need to be complemented by more thorough investigations involving different areas from the same region and comparison with reference sites. However, these Tunisian specimens provided unexpected insights concerning the morphological plasticity of *C. balzaci* and its ability to cope with particular environmental conditions and high nutrient levels with a huge increase of abundance. The paradoxical exuberant abundance with increase in size of colonies and zooids (Table 1) of *C. balzaci* on *Posidonia* leaves reveals the surprising compatibility of this species with the particular environment of the northern Gulf of Gabes and its potential to be a bioindicator of environmental disturbance. These preliminary observations open an interesting field of research on the drivers that lead a modest species of an epiphytic community to become highly dominant. Diatoms can be useful bioindicators of pollution (Desrosiers *et al.* 2013). Their abundance on *Posidonia* leaves at Kerkennah Islands may be linked to the excess of nutrient in the water column. Their role in the association with *C. balzaci* is enigmatic; is it a neutral epibiosis implying that the populations of both associates are enhanced independently, or is it a more complex symbiotic relationship? Another explanatory hypothesis for the extraordinary pattern shown by the zooids, colonies and population of *C. balzaci* at Kerkennah is hormesis, i.e., “stimulatory effects caused by low levels of potentially toxic agents” (Stebbing 1982). This term is used chiefly in toxicology for describing a biphasic dose-response with a low dose beneficial effect and a high-dose negative effect (Mattson 2008). *Collarina balzaci* might be a valuable natural model for testing the effects of hormesis on phenotypic plasticity (Calabrese & Mattson 2011) in the wild, e.g. along pollution gradients in the Gulf of Gabes.

The case of *C. speluncola* Harmelin, n. sp. presents some similarity with that of *C. balzaci* though the cryptic microhabitat in which this species proliferates is not impacted by anthropogenic disturbance but by freshwater seepage. It is probable that the occurrence of twin ooecia in colonies from the cave with the most active seepage is an effect of freshwater disturbance. The peak of abundance of *C. speluncola* Harmelin, n. sp. observed in two dark caves with freshwater seepage raises the question of what is the 'normal' habitat of this species. Is this particular environment a fundamental feature of the ecological niche of this species or just a local disturbance triggering a considerable increase of abundance and dominance, such as in the Tunisian population of *C. balzaci*? As discussed above, *C. speluncola* Harmelin, n. sp. appears to be closely related to *Collarina* sp. Better knowledge of the latter from a larger collection of specimens including fertile colonies will provide more precise data on its actual habitat range and possible relationships with *C. speluncola* Harmelin, n. sp.

GEOGRAPHIC DISTRIBUTION

According to current information, three species, *C. balzaci*, *C. gautieri* Harmelin, n. sp. and *C. speluncola* Harmelin, n. sp., occur in both the Mediterranean and the NE Atlantic. Knowledge of the actual range of *C. balzaci* in the latter is incomplete. All previous records of this species in the Atlantic were erroneous, except the one from the Canaries by Arístegui (1984). It is likely that better knowledge of the bryozoan fauna epiphytic on particular algae, such as *Cystoseira* and *Sargassum*, will increase significantly the records of *C. balzaci* in the NE Atlantic. The current taxonomic revision has revealed that *C. gautieri* Harmelin, n. sp. presents the broadest geographic range (Fig. 9). It is widespread in the Mediterranean and, in the Atlantic, it ranges from the Faeroes to southern Iberian coasts, but has not been recorded in the Macaronesian archipelagos. In contrast, two other species exclusively recorded in the NE Atlantic, *C. fayalensis* and *C. macaronensis* Harmelin, n. sp., have distributions centred on the Macaronesian archipelagos, though that of the latter also includes the Galicia coast. The actual geographic range of *C. speluncola* Harmelin, n. sp. in Atlantic and Mediterranean dark caves needs to be better documented together with its possible relationships with *Collarina* sp. The lack of Atlantic records of *C. denticulata* Harmelin, n. sp. may signify a genuine absence considering the distinctive character of its zooidal orifice and its easily accessible habitat; it is therefore conceivable that it is a Mediterranean endemic. To our knowledge (Bock & Gordon 2018, accessed on 10.IX.2018), only one *Collarina* species, *C. spicata* Winston & Vieira, 2013, has been recorded from outside the Atlantic-Mediterranean region. Features of this tiny species from SE Brazil living on sand grains, however, are not typical of *Collarina*: absence of avicularia, apertural bar formed by a pair of flat, very broad costae, proximal pair of spines extremely thick. The assignment of *C. spicata* to the genus *Collarina* may thus be disputable. Therefore, at the present state of knowledge, one may consider that the geographic range of the genus *Collarina* is restricted to the Atlantic-Mediterranean region.

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Author contributions

JGH conceived the study from the basis of a large personal collection of material, made the taxonomic decisions, wrote the paper with the contributions of all co-authors and designed the figures. JDB was very happy to resume correspondence with JGH on *Collarina* after a 30-year interruption, and supplied new British material. MSJ retrieved historical specimens from the NHMUK collections and took SEM photos of them. TM, MZ and JS supplied specimens and SEM photos.

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