Unexpected diversity of the genus Collarina Jullien, 1886 (Bryozoa, Cheilostomatida) in the NE Atlantic-Mediterranean region: new species and reappraisal of C. balzaci (Audouin, 1826) and C. fayalensis Harmelin, 1978

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Unexpected diversity of the genus *Collarina* Jullien, 1886 (Bryozoa, Cheilostomatida) in the NE Atlantic-Mediterranean region: new species and reappraisal of *C. balzaci* (Audouin, 1826) and *C. fayalensis* Harmelin, 1978

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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...
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-
The genus *Collarina* in the NE Atlantic-Mediterranean region

*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**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>LZo</td>
<td>autozooid length;</td>
</tr>
<tr>
<td>WZo</td>
<td>autozooid width;</td>
</tr>
<tr>
<td>LOr</td>
<td>orifice length;</td>
</tr>
<tr>
<td>WOr</td>
<td>orifice width;</td>
</tr>
<tr>
<td>WOrOv</td>
<td>orifice width in ovicelled zooids;</td>
</tr>
<tr>
<td>LOv</td>
<td>ovicell length;</td>
</tr>
<tr>
<td>WOv</td>
<td>ovicell width.</td>
</tr>
</tbody>
</table>

**Institutions**

- **MHNUSC** Museo de Historia Natural, University of Santiago de Compostela;
- **MNHN** Muséum national d'Histoire naturelle, Paris;
- **MZH** 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 cribrosa 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 cribrosa Heller, 1867:109, pl. 2, fig. 6.

Lepralia cribrosa — Waters 1879: 36, pl. 9, fig. 4.


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


Puellina gattya var. balzarica Barroso, 1919: 340, figs 1-5.

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


Collarina species B — Bishop 1986: fig. B.


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), 22.1.1951, coll. by Y. V. Gauthier, 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.III.1977, coll. by C. Eugène, several colonies including specimen BMNH 1987.1.4.1 illustrated by Bishop (1988, figs 3-6). — Spain. Catalonia, L Estarrit, Medes Islands, 42°24’35.05”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°30’36.5”E, VIII.2017, coll. by TM-MZ, 5 colonies, MZB. — Tunisia. Kerkennah Islands, Ouled Eziedine, e 34°39’04”N, 11°06’31”E, 2-3 m, 26-27.VI.2018, coll. by JGH, hundreds of colonies, NHMUK, 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, NHMUK.


Additional records. — France, Marseilles, 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 gymnocoel 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 oepesia and short rostrum with slightly serrated edges; apertural bar in the form of a thick triangular mucro with a rounded tip bearing two pelmatida on the proximal side; orifice poster with a straight proximal edge and two small lateral notches; 3-4 oral spines; ovicell cleithral, ooeicum 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; gymnocoel 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 costa (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 pelma near the base (Figs 2C; 3C; D; 4B; C; 7A). Autozooidal orifice semicircular, wider than long, proximal edge straight with low lateral notches, anterior 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, subedunculate with
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, ooecium formed by distal kenozooid, frequently bearing a distally-directed avicularium on the distal edge, ectooecium with slightly bumpy surface dotted with numerous pelmata (Figs 2B, C; 3B; 4C). Ances-
trula 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 ooecium; 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 µm; B, G, 100 µm; C-E, 50 µm; F, 25 µm.
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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

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**Fig. 4.** — *Collarina balzaci* (Audouin, 1826), NE Atlantic; A, non-ovicelled autozooid; 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 ovice; E, avicularium, rostrum with serrated edges; F, ancestrula with six spines. Origin: Canaries, on *Cystoseira* sp. Scale bars: A-C, 100 µm; F, 50 µm; D, 20 µm; E, 5 µm.
TABLE 1. — Measurements of Collarina Jailien, 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; L佐, W佐, length and width of non ovicelled autozooid; LO, WO, of orifice of non ovicelled zooid; LOv, WOv, of orifice of ovicell. Other abbreviations: Atl., Atlantic ocean; Kerk., Kerkennah Islands; Med., Mediterranean.

<table>
<thead>
<tr>
<th>C. balzaci</th>
<th>C. speluncola</th>
<th>C. denticulata</th>
<th>C. gautieri</th>
<th>C. fayalensis</th>
<th>C. macaronensis</th>
<th>Collarina sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOv X</td>
<td>373</td>
<td>548</td>
<td>502</td>
<td>609</td>
<td>439</td>
<td>404</td>
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<tr>
<td>SD (N)</td>
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<td>46.0 (22)</td>
<td>46.4 (12)</td>
<td>50.8 (22)</td>
<td>45.3 (24)</td>
<td>43.7 (20)</td>
</tr>
<tr>
<td>WOv X</td>
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<td>328</td>
<td>335</td>
<td>411</td>
<td>309</td>
<td>264</td>
</tr>
<tr>
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<td>63 (22)</td>
<td>39.8 (12)</td>
<td>39.2 (22)</td>
<td>32.4 (24)</td>
<td>38.5 (20)</td>
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<tr>
<td>LOr X</td>
<td>65</td>
<td>–</td>
<td>102</td>
<td>121</td>
<td>59</td>
<td>58</td>
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<tr>
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<td>53-63</td>
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<tr>
<td>WOr X</td>
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<td>–</td>
<td>123</td>
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<td>98</td>
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<td>–</td>
<td>7.9 (12)</td>
<td>8.2 (11)</td>
<td>5.7 (7)</td>
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<tr>
<td>Range</td>
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<td>100-135</td>
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<td>96-103</td>
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<td>LOv X</td>
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<td>221</td>
<td>228</td>
<td>264</td>
<td>215</td>
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<tr>
<td>SD (N)</td>
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<td>19.9 (15)</td>
<td>10.5 (12)</td>
<td>22.2 (21)</td>
<td>27.7 (18)</td>
<td>20.9 (16)</td>
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<td>WOv X</td>
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<td>223</td>
<td>246</td>
<td>286</td>
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</tr>
<tr>
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<td>12.3 (15)</td>
<td>9.6 (12)</td>
<td>16.8 (21)</td>
<td>16.4 (18)</td>
<td>12.9 (28)</td>
</tr>
</tbody>
</table>

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; Lepton ef 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 zooids), 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, L佐; 537 μm vs 373 μm, W佐; 322 μm vs 235 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 ef 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 Aristegui (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, Fenestrulina joannae (Calvet, 1902) and Puelenia gattyae (Landsborough, 1852) (Gautier 1962; Harmelin 1973; Eugène 1978; Frei et al. 1982; Bal-
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**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, RV *Jean-Charcot*, BIAÇORES 1971 St. P11, 38°31’12”N, 28°42’27”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.


**Diagnosis.** — Colonies small to large; autozooids longer than broad, with very extensive gymnocoyst 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 gymnocoyst; apertural bar poorly prominent and pierced by large pellma; orifice less than broad with proximal edge slightly concave, 2-5 thin oral spines; adventitious avicularia paired, directed disto-laterally; ooccium ke-nozoidal 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. Gymnocoyst occupying the largest part of the frontal surface, moderately convex, punctured by several large gymnocoyst pseudopores at the zoid 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%); ooccium kenozoidal, formed at the colony edge, with surface pierced by about 12-15 medium-
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,

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**Fig. 5.** — Collarina fayalensis Harmelin, 1978: A-G, 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’ Biaçores 1971, P.43 (D); Faial, ’Jean Charcot’ Biaçores 1971, P.11 (E). Scale bars: A, 200 µm; B-D, 100 µm; F, 50 µm; G, 25 µm.
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, Elbou, 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’Estari, Medes Islands, 42°14’53.102”N, 03°75’52.183”E, 9 m, 07.V.2015, coll. by TM-MZ, 1 colony on *Pinnola* 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, aceleithral, with a distinctive sclerite sealing the ooeial vesicle, ooeum 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 (pelmatidia) opening at the summit of a conical protuberance, occasionally alternating with a small pelma (Figs 6E, F). 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 pelmatidia at the tip and a pair of large pelmates 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 overlapping 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 as long as wide on average (Table 1); in ovicelled zooids, 2 in ovicelled zooids; basal part thick and conical, whip part thin and long (Fig. 6C, D).

The genus *Collarina* in the NE Atlantic-Mediterranean region
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 ooeia 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 pelmatidia and the poorly developed gymnocyost; 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 µm; C-E, G, 100 µm; F, 50 µm.
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**Ovicell** slightly prominent, endozooidal, acleithral, ooecial vesicle protected by a pseudo-operculum, i.e., a thick chitinous sclerite (Fig. 15D), ooecium formed by distal autozooid or, more rarely, by a distal kenozooid, broader than long (Figs 15D; 16E; Table 1), ectooecium with numerous pseudopores and relief variably pronounced according to calcification level. Ancestrula cribriomorph, 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 ofovicells with the formation of the ooecium by a distal autozooid. 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.

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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 µm (orifices), 50 µm (avicularia).
**Collarina gautieri** Harmelin, n. sp.

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


NE Atlantic, North Sea

*Lepalia 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 & Prent 1951: 13. — Hayward & 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.


**Mediterranean**


**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 Pinnula nobilis shell, 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. — 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,
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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**, kenozoidal ooecium 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 µm; **B-D**, **F**, **H**, 100 µm; **E**, **G**, 50 µm.
apertural bar with raised, massive umbo bearing 2 apical pelmatidia, composed of 7-12 costae bordered by a collar of large, prominent autozooids with narrow marginal gymnocyst, costate shield com-
diagnosis

Etymology


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

Description

Colony encrusting, pluriserial, unilaminar, small- to medium-sized (< 500 zooids) (Figs 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 or more 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, ooeicum hyperstomial, subpherical, formed by distal kenozooid at the colony border (Figs 9E; 10E; 16A-D); ectooecium with uneven surface owing to numerous large pelmata and pedunculate pelmatidia; an avicularium on the middle of the distal edge, distally directed, present in most cases (> 80%). Ancestrula cribriiform with 5 spines, costate shield oval with 6-8 costae and gymnocyst clearly broader than long (Table 1), resembling a collar of large, prominent pelmata at the top of the steep base of each costa, pelmatidia often at the tip of a conical pillar; orifice with small I/W ratio; apertural bar with raised, massive umbo bearing 2 apical pelmatidia 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, ooeicum ken- nozooidal, ectooecium bumpy, punctured with many pseudopores with prominent edge, the smaller at the tip of conical processes; ancestrula with 5 spines.

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 Mediterranean specimens.
The genus *Collarina* in the NE Atlantic-Mediterranean region

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 Ismail 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-
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 Vigo) to 88 m on detritic-biogenic bottom (site features unknown, coll. by Fernández-Pulpeiro & Reverter leg., 1 colony on pebble, MNHN-IB-2014-1927; coated ovicelled colony for SEM examination).


**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, 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)
The genus *Collarina* in the NE Atlantic-Mediterranean region

**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 pelmata also present on the gymnocyct; 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 µm; B, C, 200 µm; D, H 100 µm; F, G, 50 µm.
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 pellets, 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), nestled 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 alechitral (Fig. 15C); ooeicum formed by a distal kenozooid at the colony growing edge or by a distal daughter autozooid (Figs 12A-C; 15C, É), slightly broader than long, ectooecium with relatively smooth surface, punctured with a dozen medium-sized pseudopores. Ancestrula cribiform, 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, almost always paired, rostrum with slightly hooked tip (Figs 8B; 12B, D, H; 15C), nestled 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 alechitral (Fig. 15C); ooeicum formed by a distal kenozooid at the colony growing edge or by a distal daughter autozooid (Figs 12A-C; 15C, É), slightly broader than long, ectooecium with relatively smooth surface, punctured with a dozen medium-sized pseudopores. Ancestrula cribiform, with small spinocyst and 6 spines.

**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.

**Paratypes.** Same data as the holotype. MNHN-IB-2014-1913; 5 alive + 3 dead colonies, on wall fragment. — MNHN-IB-2014-1914: 12 colonies, on wall fragment. — MNHN-IB-2014-1915: 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 Baleira. 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 *speluncula* 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,
The genus *Collarina* in the NE Atlantic-Mediterranean region

**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 μm), 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 μm); 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

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**Figure 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 ooeicum and a well developed gymnocyst; **D**, ovicelled zooid with twin ooeicells, 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 μm; **C, D**, 100 μm; **B, E**, 50 μm.
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, ooecium 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 avicula (i.e., aviculae with two buds). 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. Ancestra 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 that 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).

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 Haplopora 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 seepage. 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 (Bouy-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).

C. speluncola Harmelin, n. sp. is distributed around the orifice 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 that 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).

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”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 rough 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 peltma laterally at the base of the proximal side (Fig. 14C). Adventitious avicula...
The genus *Collarina* in the NE Atlantic-Mediterranean region

**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 oovicell 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

**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 µm; B, 100 µm; C, 50 µm.
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. speluncula* Harmelin, n. sp. are distinct species or two conspecific ectotypes 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 (pelmatidia) 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, ooecium formation involving distal daughter zooids, the latter being, according to species, kenozooids or both kenozooids and autozooids in the same colony; ectooecium 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 ooecia, absent in autozooidal ooecia. Ancestrula cribiform with small costate shield and spines around the edge of the orificial area.

**Specific Features**

Apart from *C. fayalenis*, 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 gymnocystal, 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 ooecia and the surface structure of the ectooecium. 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. speluncula* Harmelin, n. sp., *C. denticulata* Harmelin, n. sp., *C. macaronensis* Harmelin, n. sp., *C. fayalenis*), 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,
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 ooecia formed by a distal autozooid (category A) from ooecia formed by a distal kenozooid (category B) (see also Rosso et al. 2018). The early stages of the construction of ooecia are visible on the growing edge of colonies. In all cases, budding of the entooecium by the maternal zooid starts before that of the ectooecium by the daughter zooid (Fig. 16A, B). The entooecium 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. 15. — Types of ooecia in *Collarina* Jullien, 1886 species: A-C, kenozooidal ooecia 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 ooecia (left) and three ooecia incorporated in distal autozooid (right); E, *C. macaronensis* Harmelin, n. sp., 2 ovicelled zooids with kenozooidal ooecium (left) vs ooecium incorporated in distal autozooid (right). Origin: A, Marseille, Conger Cave; B, Azores, São Miguel, Vila Franca Is.; C, E, Madeira, NHMUK 1911.10.1.705; D, Catalonia, Medes Is. Scale bars: A-C, E 100 µm, D, 200 µm.
Fig. 16. — Phases of ooecium 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, ooecium 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 µm; E, 200 µm.
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 entooecium 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 entooecium within the daughter zooid is the same in the two types of ooecia (kenozooid vs autozooid). In *C. denticulata* Harmelin, n. sp., which presents both types, the fact that the entooecium 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 ooecium. In *C. gautieri* Harmelin, n. sp. (Fig. 16B), the early bilobed entooecium 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 ooecium, 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 ooecia formed by a kenozooid, from which it is budded. In contrast, it is never present on ooecia formed by a distal autozooid (Table 3B). The frequency of occurrence of ooecial avicularia is very variable according to species, even among those having exclusively kenozooidal ooecia (Table 3). For instance, they are rare in *C. speluncola* Harmelin, n. sp. (<5% of ooecia) but present on all ooecia in *C. gautieri* Harmelin, n. sp.

Ovicells also present species-specific differences in the type of closure protecting the ooecial vesicle (Table 3C). Ovicells are cleithral in *C. balzaci* while they are acleithral in *C. denticulata* Harmelin, n. sp. (A. Ostrovsky pers. com., 05.IV.2018). In *C. denticulata* Harmelin, n. sp., as shown by SEM photos of unbleached colonies, the operculum does not close the ooecium opening. This function is performed by a thickening of the ooecial 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
some colonies of *Collarina 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 ooecia were observed in Recent specimens of *Cleiochasmidra portisi* (Neviani, 1895) by Rosso et al. (2015). This anomaly evolves but may differ from the disorderly budding of multiple ovicells (ovicell hyperplasia) sometimes observed in *Schizoporella* and *Fenestrulina* 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 *Collarina 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 cibrillind genus, *Puellina*, in dark caves (*Cribriilaria cremulata* Harmelin = *Puellina venusta* Canu & Bassler, Harmelin 1970: fig. 1k, pl. I13) 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* (Audouin, 1826) from a dark cave (JGH, unpublished). According to Berning (2008), intramural buds would be a process 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 *Glabrilaria biersuta* 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 seafloor in places from which macrophytes are excluded.
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. 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, São Miguel, Vila Franca, 15 m. Scale bars: 1 cm.
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 specification 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 (Páez-Escolá *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.*, 2018) 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 *Collarina speluncola* Harmelin, n. sp. presents some similarity with that of *C. balzaci* though the cryptic micro-habitat 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 assignation 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.

**References**


Au sujet des Bryozoaires, on trouve une multitude de publications sur divers aspects de leur biologie, écologie et systématique. Voici quelques exemples :

1. Au début du XXe siècle, des travaux ont été menés sur la distribution et la diversité des Bryozoaires en Méditerranée. Un exemple significatif est l'étude de la race de Bryozoaires en Méditerranée, y compris les implications écologiques et systématiques. Ces recherches ont été publiées dans la revue *Cahiers de Biologie marine*.

2. Les travaux ont continué dans les années 1980 avec la publication de *Mémoires de l'Institut Océanographique, Monaco* sur l'aire des Cyclostomes en Méditerranée. Ce travail a souligné les liens écologiques et systématiques à travers des études de théorie et de pratique.

3. En 1998, un article intitulé *Bryozoaires de l'Afrique* a été publié dans la revue *Notes in Earth System Sciences*.

4. Au cours des années 2000, les recherches ont été focalisées sur les Echinodermes et les Bryozoaires, y compris l'impact de changements climatiques. Un exemple est le travail publié dans *Biologie Marine* sur les changements climatiques et leur impact sur les populations de Bryozoaires.

5. Les travaux ont également montré l'importance des Bryozoaires dans les écosystèmes, y compris leur rôle dans les chaînes alimentaires et le maintien de la biodiversité. Un article publié dans *Mémoires de l'Institut Océanographique, Monaco* a souligné l'importance des Bryozoaires dans les écosystèmes marins.

6. Enfin, les travaux ont été conduits sur des questions spécifiques, comme l'impact des changements climatiques sur les populations de Bryozoaires. Un exemple est un article publié dans *Biologia* sur les effets des changements climatiques sur les populations de Bryozoaires dans la Méditerranée.

Ces exemples montrent l'importance croissante des recherches sur les Bryozoaires et leur rôle essentiel dans les écosystèmes marins.