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Cribrilinid bryozoans from Pleistocene Mediterranean deep-waters, with the description of new species

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Abstract.—Cribrilinid bryozoans originating from Pleistocene deep-water sediments from two localities near Messina (Sicily, Italy)—Capo Milazzo (Gelasian) and Scoppo (Calabrian)—were examined. Five cribrilinid species were found, three in each locality and time interval, with only one species shared. Three species, *Cribrilaria profunda* n. sp., *Glabrilaria transversocarinata* n. sp., and *Figularia spectabilis* n. sp., are new to science. Of the two remaining species, *Figularia figularis* was already known from local fossil associations, whereas *Glabrilaria pedunculata*, a present-day Mediterranean species, is recorded for the first time as a fossil. New combinations are suggested for two species previously assigned to *Puellina*, *Cribrilaria saldanhai* (Harmelin, 2001) n. comb. and *Cribrilaria mikelae* (Harmelin, 2006) n. comb. The diagnosis of the genus *Figularia* was amended to include an erect growth morphology in addition to the encrusting form, and the occurrence of oecia formed by the distal kenozooid. Following a literature revision of all species currently assigned to *Figularia*, the new combinations *Vitrimurella capitifera* (Canu and Bassler, 1929) n. comb. and *Hayamiellina quaylei* (Powell, 1967a) n. comb. are suggested, and problematic species are listed and briefly discussed.

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Introduction

Cribrilinidae Hincks, 1879 is an extremely large family of cheilostome bryozoans including 127 genera and more than 700 living and fossil species to date, accounting for ~3% of total bryozoan diversity (Bock, 2020). First appearing ca. 100 Ma, in the Cenomanian, Cribrilinidae underwent a peak of diversification during the Santonian, greatly contributing to the radiation of cheilostomes in the Late Cretaceous (Cheetham, 1971; Jablonski et al., 1997 and references therein). This family is one of the most species-rich in the present-day Mediterranean (Rosso and Di Martino, 2016), as well as in other regions of the world (e.g., Gordon et al., 2019). Cribrilinids exhibit a typical and distinctive costate frontal shield, but also high morphological variability, including different types of heteromorphs (avicularia, kenozooids, articulated and non-articulated spines, etc.) and ovicell structures. A future subdivision of Cribrilinidae into several families or subfamilies is very likely. A more accurate definition of certain genera will, however, require a thorough re-examination of the original material, particularly

of the numerous Cretaceous representatives (e.g., Taylor and McKinney, 2006; Rosso et al., 2018), as well as phylogenetic analyses. Genus and species identification are often based on subtle morphological characters, such as those associated with the zooidal orifice and the suboral bar (e.g., Harmelin, 1970, 1978, 2001, 2006; Bishop and Househam, 1987), which require scanning electron microscopy (SEM), still lacking in the descriptions of numerous taxa. In fossil material, identification of taxa is also jeopardized by taphonomic filters, with abrasion, corrosion, partial dissolution and recrystallization obliterating fine diagnostic characters. This is particularly true for species introduced in old publications, normally including only brief descriptions and often lacking proper illustrations. Descriptions and revisions of fossil cribrilinids based on detailed illustrations are scarce in the modern literature, especially for specific stratigraphic intervals (Berning, 2006; Taylor and McKinney, 2006; Di Martino and Rosso, 2015). In this context, this paper aims to: (1) document cribrilinid associations from Pleistocene deep-water habitats of southern Italy; (2) illustrate fossil representatives of some established species; (3) describe three new species; (4) amend the diagnosis of the genus *Figularia* Jullien, 1886, and provide a comparative morphological analysis of species currently assigned to this genus; and (5) propose new

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combinations for two species of *Puellina* and two species of *Figularia*.

Geological setting

North-eastern Sicily is part of the north Sicily Chain, which, in this sector, includes the Kabilo–Calabride crystalline basement (Paleozoic rocks of different metamorphic grade) and its sedimentary cover (i.e., discontinuous upper Miocene sediments unconformably covered by Plio–Pleistocene deposits; Barrier, 1987). The Plio–Pleistocene succession starts with lower Pliocene deep-water whitish foraminiferal marls, marly limestones, and coarser sediments including breccias, overlaid with middle Pliocene to middle Pleistocene sediments, usually in thin discontinuous, often laterally heteropic bodies. Those bodies can be grouped in: (1) a middle Pliocene–middle Pleistocene “Bathyal Facies Association” (PP), and (2) a middle Pleistocene “Circalittoral–Infralittoral Facies Association” (mP) (Barrier, 1987; Barrier et al., 1987a; Vertino, 2003). PP includes carbonate-dominated and siliciclastic-dominated facies. The former facies mainly consist of coral-rich rudstones, with the frame-building deep-water scleractinians *Madrepora oculata* Linnaeus, 1758, *Desmophyllum pertusum* (Linnaeus, 1758), and *D. dianthus* (Esper, 1794), interfingering with calcarenites and carbonate sands containing scattered isidid octocorals, and locally truncated by erosional surfaces and overlaid with debris-flow deposits. The siliciclastic-dominated facies are mainly characterized by marly and silty clays, sometimes embedding coral rudstone boulders that are often encrusted by corals, bivalves, serpulids, and bryozoans (Barrier, 1986, 1987; Barrier et al., 1996). Facies mP includes the “upper gravels and sands” with fossils of infralittoral–upper circalittoral origin and, locally, large blocks encrusted by circalittoral organisms, and Gilbert-type delta deposits regionally known as the “Messina Formation.” The succession is erosively capped by Upper Pleistocene fluvio-marine terraces.

At Capo Milazzo, the so-called “yellow calcareous marl” crops out along the south-western and the north-eastern coast. The sandy-silty sediments unconformably lie on erosive surfaces of the pre-Messinian basement (Paleozoic metamorphites to upper Miocene shallow-water deposits), constituting discontinuous sedimentary bodies filling small depressions (Fois, 1990). Sediment deposition, previously dated as late Pliocene, occurred during the MPI5 and MPI6 zones, largely overlapping with the Gelasian Stage of Rio et al. (1994), and now considered as the basal part of the Pleistocene (Gibbard et al., 2010; Violanti, 2012). Deposition in epibathyal environments is indicated by both macrofaunal associations, including brachiopods, corals, serpulids, and, occasionally, mollusks (e.g., Gaetani and Saccà, 1984; Langer, 1989), as well as microfaunas, including foraminiferans and ostracodes (e.g., Violanti, 1988; Sciuto, 2014a, b). Bryozoans are common, but hardly detectable in the field owing to the small size of their colonies and/or colony fragments. Bryozoan assemblages are very diverse, including up to 60 species, some exclusively found in these deposits (Rosso, 2002a, b, 2005; Rosso and Braga, 2013; Rosso and Di Martino, 2015; Rosso and Sciuto, 2019).

Scoppo is located immediately west of the city of Messina, in the Messina Strait area, where Pleistocene bathyal sediments discontinuously occur (Barrier, 1984; Barrier et al., 1987a;

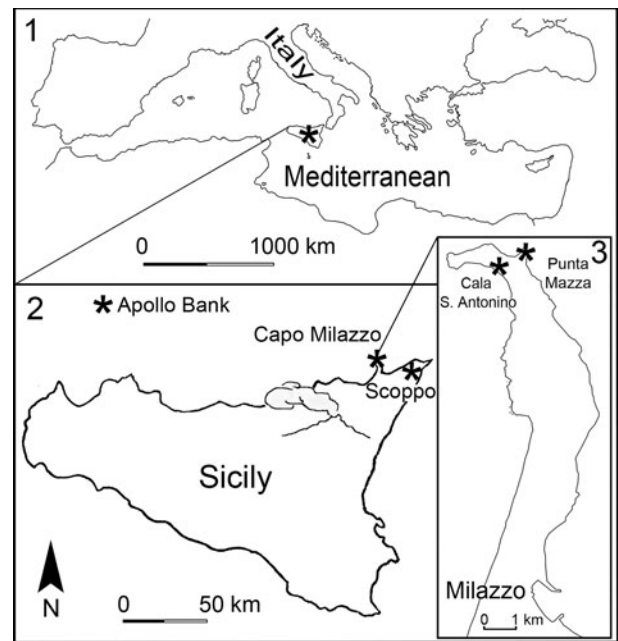


Figure 1. Location of (1) Sicily in the Mediterranean Sea and (2) the study area in northeastern Sicily with sampling localities (Capo Milazzo, Scoppo, and the Apollo Bank, see asterisks); (3) shows Cala Sant’Antonino and Punta Mazza sections at Capo Milazzo. Modified from Rosso and Sciuto (2019).

Vertino, 2003). At Scoppo, these sediments unconformably lie on Messinian brecciated evaporitic limestone. They consist of basal rudstones rich in fragments of cold-water corals (i.e., *M. oculata*, *D. pertusum*, and *D. dianthus*) that are overlain by poorly cemented white marls with sparse corals and plates of the cirriped *Scillaelepas* Seguenza, 1876. These macrofossils, and ostracodes, point to deposition in bathyal environments (Vertino et al., 2013; Sciuto, 2016) in the MNN19b–19c biozones (A. Baldanza, personal communication, 2015), corresponding to the early Calabrian (=Santernian).

Materials and methods

Studied material originates from deep-water sediments cropping out in two different localities near Messina in north-eastern Sicily: Capo Milazzo Peninsula (two outcrops: Cala Sant’Antonino and Punta Mazza) and Scoppo (Fig. 1; see Geological setting for details). Additional material used for comparison derives from a present-day submarine sample collected at the Apollo Bank off Ustica Island in the Tyrrhenian Sea (Fig. 1).

At Capo Milazzo, cribrilnid bryozoans were found in “sample 1 (1999)” collected near the top of the layers exposed at Cala Sant’Antonino West; “sample 17 (2000)” and “sample 2015” collected in the central part of Cala Sant’Antonino outcrop; and “sample 4” and “sample 5” collected in biogenic layers near the base of Punta Mazza section, corresponding to “sample 12” and “sample 11” of Sciuto (2014b), respectively. Further information on these samples can be found in Sciuto (2014b) and Rosso and Sciuto (2019). At Scoppo, cribrilnids were found in a test sample associated with a *Scillaelepas*-rich layer, and in the sample “Scoppo 24 top” coming from unce-

At the Apollo Bank, coarse sediments associated with the kelp *Laminaria rodriguezii* Bornet, 1888 were collected at about 60 m depth. Living and dead bryozoan associations were characterized by high species richness, but delivered only one colony (now fragmented) of *Figularia figularis* (Johnston, 1847) (Di Geronimo et al., 1990).

Sediment was routinely treated (washed, sieved, and dried) at the Paleocological Laboratory of the University of Catania. All bryozoans were picked from residues larger than 0.5 mm. After preliminary identification under a stereomicroscope, selected uncoated specimens were mounted for scanning electron microscopy (SEM) using a TESCAN VEGA 2 LMU in backscattered-electron/low-vacuum mode at the Microscopical Laboratory of the University of Catania. For the attribution of the specimens to the genera *Cribrilaria* Canu and Bassler, 1929 and *Glabrilaria* Bishop and Househam, 1987, we followed the diagnoses in Rosso et al. (2018) summarized herein: *Cribrilaria* has totally calcified non-pseudoporous oecia produced by the distal autozoid or kenozoid, interzoidal avicularia of variable size and shape, usually five (4–8) oral spines, and relatively large uncalcified windows of pore-chambers; *Glabrilaria* has non-pseudoporous oecia that are exclusively produced by the distal kenozoid, erect or semi-erect avicularia, 6–7 (rarely five) oral spines, small to moderately sized uncalcified windows of pore-chambers. Measurements were obtained from SEM images using the image processing program ImageJ (Schneider et al., 2012). Measurements were tabulated and provided in micrometers. The complete range is given first, followed by the mean value plus/minus standard deviation and the number of measurements taken. In specimens of *Glabrilaria*, zooidal boundaries were obliterated by recrystallisation with bands of crystals filling the interzoidal grooves. To estimate zooidal size, length was measured from the distal end of the orifice to the mid-point of the crystal band located proximally, while width was measured from mid-point to mid-point of the crystal bands located laterally.

Repositories and institutional abbreviations.—All specimens described and illustrated in this work are part of the Rosso Collection deposited at the Museum of Paleontology of the University of Catania (PMC) under the catalogue numbers reported in the “Systematic paleontology” section. Other abbreviations: MNHN, Muséum national d’Histoire naturelle, Paris; NHMUK, Natural History Museum, London; NMNH, National Museum of Natural History, Smithsonian Institution, Washington DC.

Systematic paleontology

- Phylum Bryozoa Ehrenberg, 1831
- Order Cheilostomatida Busk, 1852
- Suborder Flustrina Smitt, 1868
- Superfamily Cribriloidea Hincks, 1879
- Family Cribrilineidae Hincks, 1879
- Genus *Cribrilaria* Canu and Bassler, 1929

Type species.—*Eschara radiata* Moll, 1803, by original designation.

Cribrilaria profunda new species

Figures 2, 3; Table 1

1988 *Puellina (Cribrilaria) scripta*; Harmelin and Aristegui, p. 526, figs. 18–19, 24.

1993 *Puellina scripta*; Harmelin and d’Hondt, fig. 5.

Holotype.—PMC. B27.10.10.2019a. Capo Milazzo Peninsula: Cala Sant’Antonino center, sample 2015: one small fragment including ovicellate zooids and interzoidal avicularia.

Paratypes.—PMC. B27.10.10.2019b. Additional specimens from Capo Milazzo Peninsula: Cala Sant’Antonino West, sample 1 (1999: surface): one specimen; Cala Sant’Antonino center, sample 17 (2000): three specimens; sample 2015: 12 specimens in addition to the holotype. PMC. B27.10.10.2019c. Scoppo: sample 24 top: two specimens.

Diagnosis.—Colonies encrusting, multiserial. Autozooids nearly flat, oval to irregularly polygonal. Basal pore-chambers present. Gymnocyst visible along the zooidal margins. Frontal shield consisting of 14–25 costae with 4–11 intercostal pores/lacunae. Suboral bar formed by the first pair of widest costae with blunt median prominence and proximal pore. Orifice transversely D-shaped with five (occasionally 6–7) oral spines, four in ovicellate zooids. Interzoidal avicularia with elongate, triangular or parallel-sided, raised rostrum, crossbar lacking. Ovicell hyperstomial, presumably cleithral. Ooecium formed by distal autozoid, with a longitudinal median carina. Kenozooids rare.

Occurrence.—*Cribrilaria profunda* n. sp. is presently known from the early Pleistocene deep-water deposits of southern Italy (Gelasian of Capo Milazzo Peninsula and early Calabrian of Scoppo, Messina), in the Recent Ibero-Moroccan Gulf (223–990 m depth), the Gibraltar Strait (580 m depth) (Harmelin and Aristegui, 1988), and in the Alboran Sea (205 m) (Harmelin and d’Hondt, 1992, 1993).

Description.—Colonies encrusting, multiserial, unilaminar, the largest observed fragment including a dozen zooids. Zooids large and nearly flat, slightly longer than wide (L/W = 1.15; Scoppo; 1.29: Milazzo), oval to rhomboidal or rarely irregularly polygonal in shape, wider in their proximal half; zooidal boundaries marked by shallow grooves (Figs. 2.1, 2.4, 2.7, 3.1, 3.6). Gymnocyst exposed all along the zooidal margins, usually wider laterally to the orifice and at triple zooid junctions (Figs. 2.1, 3.1, 3.2). Interzoidal communication through basal pore-chambers with windows (~70 × 20 μm), visible only in some zooids at colony periphery (Fig. 3.5). Frontal shield flat (Figs. 2.1, 2.7–2.9, 3.1, 3.2), consisting of 14–25 wedge-shaped costae (including suboral), narrowing and tapering towards the center of the zooid (maximum basal width 32–65 μm), converging toward a median point or along a median longitudinal, transverse, or trifurcate midline. Costae connected by several intercostal

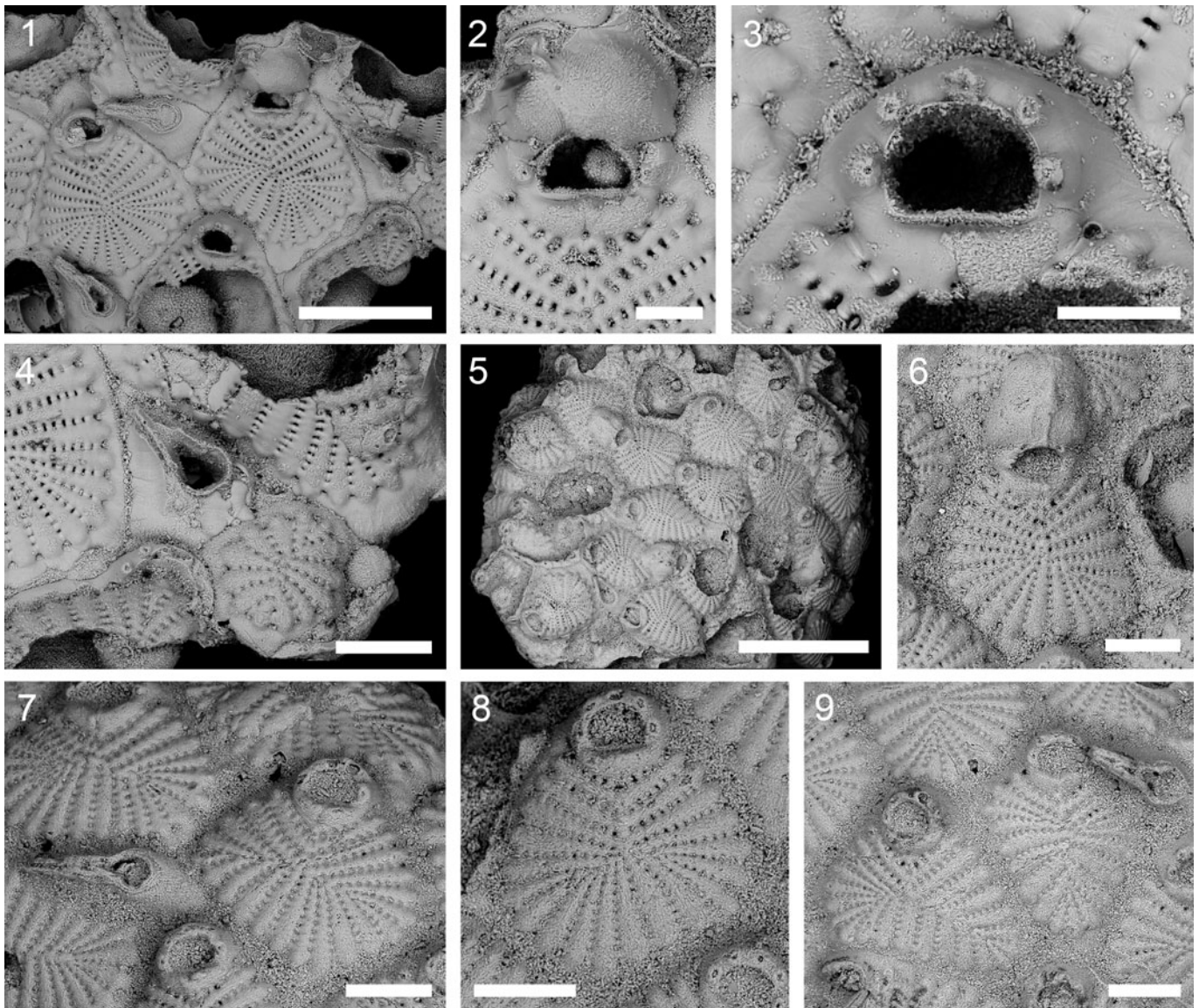


Figure 2. *Cribrilaria profunda* n. sp., Capo Milazzo, Gelasian. (1–4): PMC. B27.10.10.2019a, holotype with slightly recrystallized zooids, Cala Sant’Antonino center, sample 2015: (1) group of autozooids, some ovicellate, and interzooidal avicularia (oecium shows no median carina); (2) distal part of an ovicellate zooid with four spine bases situated laterally to the orifice, the suboral bar, and intercostal lacunae; (3) close-up of autozooidal orifice with five spine bases; (4) close-up of an avicularium and a kenozooid. (5–9) PMC. B27.10.10.2019b, same details as the holotype; one of the largest paratype specimens: (5) general view (note different zooidal shapes); (6) ovicellate zooid tilted to show the median carina of the oecium; (7) autozooids and an avicularium; (8) an autozooid with recrystallized hidden margins; (9) autozooids of different shapes. Scale bars: (1) 500 μ m; (2, 3) 100 μ m; (4, 6–9) 200 μ m; (5) 1 mm.

bridges leaving 4–11, regularly spaced, subrectangular lacunae, 8–16 μ m long; peripheral pores the largest. Intercostal pores reduced to 4–5 proximally to the first suboral pair of costae (Fig. 2.2). These are shorter and larger than the other pairs, and merge along the zooidal midline leaving a suture with a median pore, and often forming a more or less elevated prominence distally, adjacent to the pore (Figs. 2.2, 3.3, 3.4). Orifice transversely D-shaped, outlined by a raised rim. Orifice bearing five (occasionally up to 7) equally spaced, articulated oral spines (Figs. 2.3, 3.3, 3.4), four persisting in ovicellate zooids (Fig. 2.2). Interzooidal avicularia common, directed laterally or rarely distolaterally, with a variably shaped (often triangular) cystid and an elongate triangular to almost parallel-sided rostrum, raised above or positioned

between the costate shield of adjacent autozooids, no crossbar (Figs. 2.1, 2.4, 2.7, 2.9, 3.5, 3.6). Ovicell hyperstomial, presumably cleithral. Oecium formed by the distal autozooid. Ectooecium smooth, with a longitudinal median elevated carina (Figs. 2.1, 2.2, 2.6, 3.6). A single kenozooid with costate frontal shield numbering 13 costae was observed (Fig. 2.4). Ancestrula not seen.

Etymology.—From the Latin *profundus*, alluding to its deep-water distribution.

Remarks.—Specimens from Capo Milazzo and Scoppo are very similar in general appearance, including the occurrence of some irregularly polygonal autozooids with a somewhat trifurcate

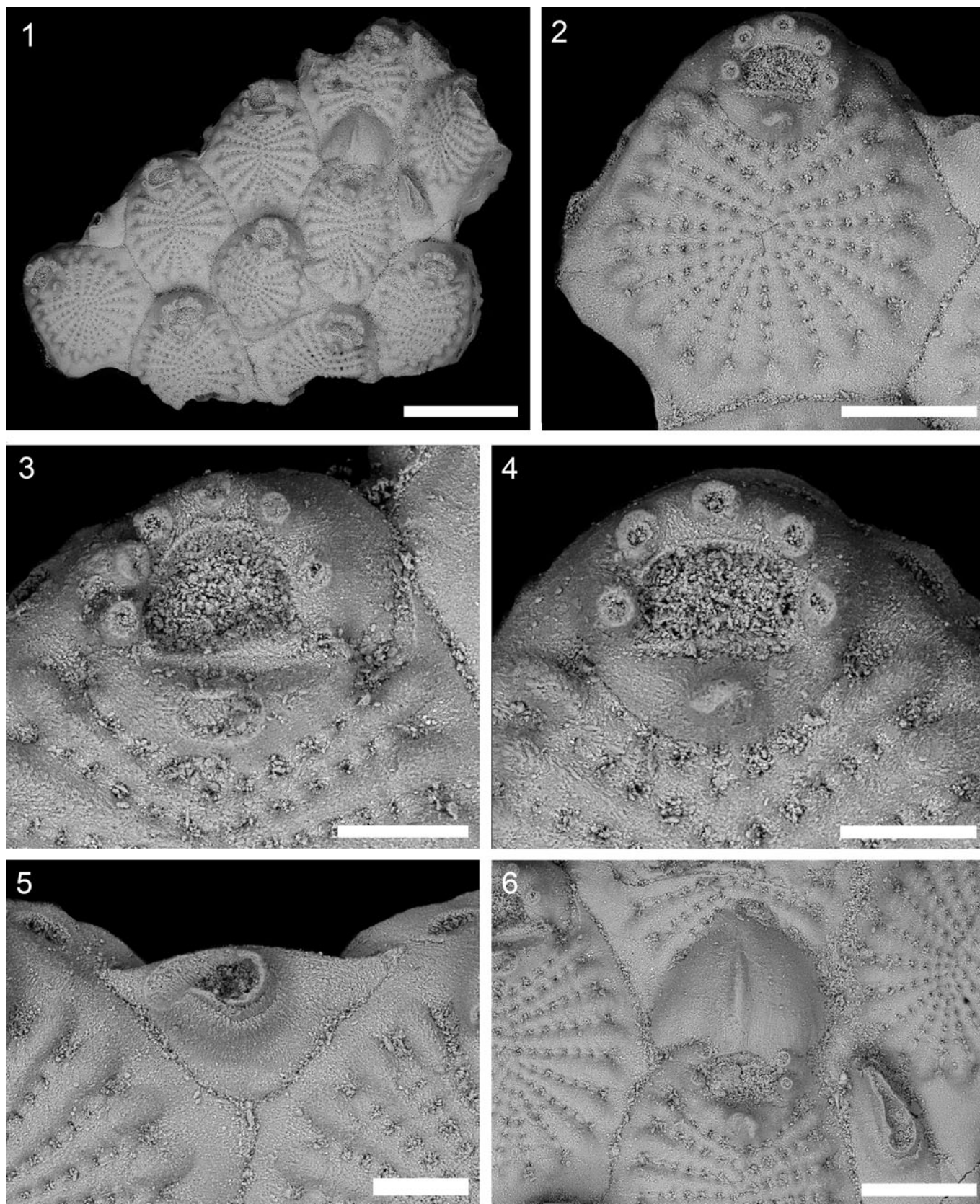


Figure 3. *Cribrilaria profunda* n. sp., Scoppo, sample 24 top, early Calabrian, MNN19b-19c biozones, PMC. B27.10.10.2019c, paratype. (1) The largest fragment; (2) general view of an autozoid; (3) close-up of an orifice with unusual L/W ratio and seven oral spine bases; (4) orifice with five oral spine bases; (5) colony margin showing basal pore-chambers and interzoooidal avicularium; (6) ovicellate zoid, avicularium, and oecium showing longitudinal carina. Scale bars: (1) 500 μ m; (2, 6) 200 μ m; (3–5) 100 μ m.

Table 1. Measurements (in μm) of *Cribrilaria profunda* n. sp. Abbreviations: L: length; W: width.

Species	<i>Cribrilaria profunda</i> n. sp.	
	Capo Milazzo	Scoppo
Number of costae	17–25; 21 ± 2 (N = 14)	14–19; 17 ± 1 (N = 12)
Zooid length	422–750; 640 ± 85 (N = 14)	491–711; 622 ± 64 (N = 12)
Zooid width	271–676; 495 ± 108 (N = 14)	447–735; 522 ± 85 (N = 12)
L/W	1.29	1.19
Proximal gymnocyst length	60–189; 96 ± 32 (N = 14)	70–246; 112 ± 50 (N = 10)
Costate shield length	299–640; 407 ± 79 (N = 14)	294–442; 358 ± 45 (N = 12)
Costate shield width	300–584; 450 ± 71 (N = 14)	364–586; 423 ± 61 (N = 12)
Orifice length	92–97; 95 ± 4 (N = 2)	73–95; 81 ± 8 (N = 8)
Orifice width	130–144; 137 ± 10 (N = 2)	115–134; 126 ± 7 (N = 8)
Number of articulated oral spines	5 (4 if ovicellate)	5–7 (4 if ovicellate)
Ooecium length	225–285; 261 ± 27 (N = 4)	235–253; 244 ± 24 (N = 2)
Ooecium width	252–303; 271 ± 24 (N = 4)	286–320; 303 ± 24 (N = 2)
Ovicellate orifice length	81–94; 86 ± 7 (N = 3)	93
Ovicellate orifice width	138–148; 142 ± 5 (N = 3)	128
Interzooidal avicularium rostrum length	225–333; 263 ± 35 (N = 12)	135–180; 158 ± 32 (N = 2)
Interzooidal avicularium rostrum width	70–149; 109 ± 20 (N = 12)	57–64; 61 ± 5 (N = 2)
Interzooidal avicularium cystid length	261–396; 336 ± 69 (N = 3)	273–323; 304 ± 27 (N = 3)
Interzooidal avicularium cystid width	236–406; 295 ± 95 (N = 3)	154–386; 238 ± 129 (N = 3)
Kenozooid length	346	Not observed
Kenozooid width	339	Not observed

suture in the costate shield. Measurements also largely overlap, although Capo Milazzo material shows more variability. Yet, some specimens from Scoppo show a slightly convex costate shield with fewer costae, a more raised suboral prominence, and more (occasionally 6–7) oral spine bases. Variability in the number of oral spines within the same species is known in other cribrilinids, such as *Cribrilaria pseudoradiata* Harmelin and Aristegui, 1988. Specimens reported as *Cribrilaria scripta* (Reuss, 1848) by Harmelin and Aristegui (1988) and Harmelin and d'Hondt (1993) share their characters with the Capo Milazzo material and are here considered conspecific (see below).

Cribrilaria profunda n. sp. is very similar to the Recent *C. saginata* Winston, 2005 from off Bahia Honda (Cuba) (Winston, 2005) and the Bahama Bank (Rosso et al., 2018). However, *C. saginata* differs in having a distinctly more extensive proximal gymnocyst, a shorter and squatter orifice (orifice length/orifice width 0.42–0.55 in *C. saginata* vs. 0.64–0.69 in *C. profunda* n. sp.), five constant oral spines, and carinated suboral costae. Hincks (1884), and later Neviani (1900), also suggested conspecificity between *C. saginata*, as *C. radiata* (Moll, 1803) from Florida, and the middle Miocene (Langhian) *Lepralia elegantissima* Seguenza, 1880 from southern Calabria (Italy), which is, however, extremely unlikely owing to the great geographic and temporal distance between the two populations. In addition, the only illustration available for *L. elegantissima* (Seguenza, 1880, pl. 8, fig. 11) is a drawing showing a very distinctive morphology for this species, with ovoidal zooids having a wide and prominent frontal median keel, and seemingly 3–5 suboral tubercles alternating with lacunae.

Cribrilaria scripta and *C. radiata*, although similar in appearance to *C. profunda* n. sp., have smaller zooidal dimensions and larger interzooidal avicularia, and four oral spines occur in most zooids in the latter species (Harmelin, 1970; Bishop and Househam, 1987). Recent specimens of *C. scripta* sensu Harmelin and Aristegui (1988) from deep waters of the Ibero-Moroccan Bay and Gibraltar Strait, are here attributed to *C. profunda* n. sp. based on the

measurements, the presence of generally five oral spines, and presence of a robust and smooth pair of suboral costae forming a median prominence.

In addition, specimens from the early Messinian of Carboneras (SE Spain) identified by J.-G. Harmelin as *Puellina (Cribrilaria) scripta* and mentioned in Barrier et al. (1992), without description or illustrations, might belong to *C. profunda* n. sp.

The Recent *Cribrilaria pseudoradiata* from the upper bathyal Atlanto-Mediterranean region is also similar to *C. profunda* n. sp., but has smaller dimensions and lacks interzooidal avicularia.

Cribrilaria profunda n. sp. could possibly correspond to *Lepralia planicosta* Seguenza, 1880, a cribrimorph species reported from Plio-Pleistocene sediments of the Messina Strait area. Seguenza (1880) distinguished his species from *C. scripta*, adducing that autozooids were irregularly shaped, with a flat costate shield consisting of several costae, as in *C. profunda* n. sp. Unfortunately, *Lepralia planicosta*, supposedly corresponding to *Lepralia scripta* sensu Manzoni (1875) from the early Pliocene of Castrocaro, was not figured and the type material was lost in 1908 during the Messina earthquake. We refrain from selecting our material as the neotype of *L. planicosta* because the original description of this species seems insufficient to ensure their conspecificity, and the type localities, although geographically close, are not exactly the same, and neither are the geologic horizons. Seguenza (1880) abstained from illustrating his new species and referred to drawings of *L. scripta* sensu Manzoni (1875, figs. 25, 25a). Manzoni's specimens, held in the collection of the Museo di Storia Naturale, Geologia e Paleontologia of Florence, should be located and examined before selecting a neotype for this species.

Genus *Glabrilaria* Bishop and Househam, 1987

Type species.—*Puellina pedunculata* Gautier, 1956, by original designation.

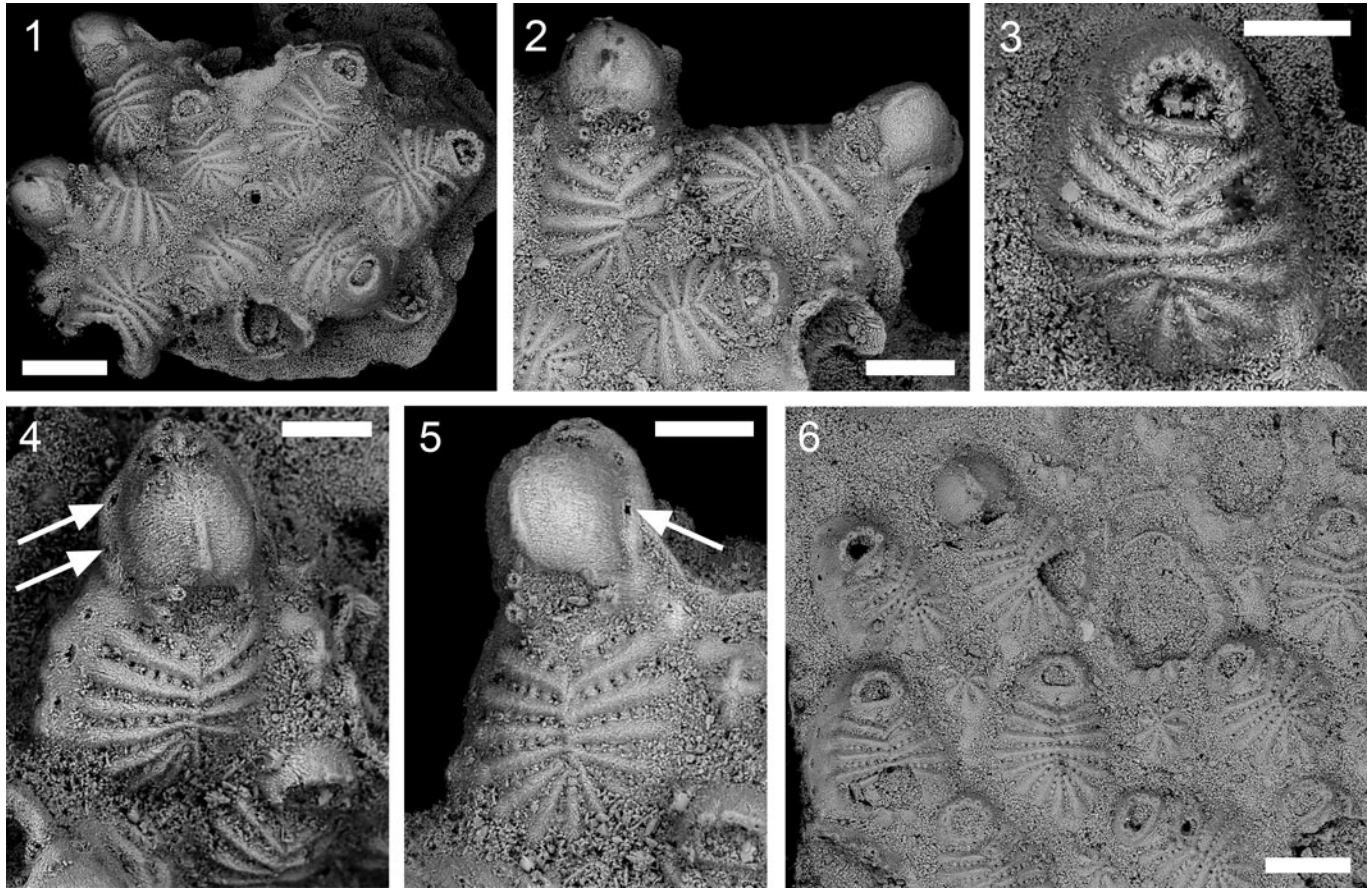


Figure 4. *Glabrilaria* cf. *G. pedunculata* Gautier, 1956, Capo Milazzo, Gelasian, Rosso Collection collective code PMC I. Pl. B.81a. (1–5) Cala Sant’Antonino center, sample 2015: (1) small fertile colony, with autozooids radiating from an apparent central ancestrula, seemingly regenerated as a miniature autozooid; (2) close-up of the three zooids on the top left of (1); note the carinate oecia; (3) frontal view of autozooid with the transversely D-shaped orifice, seven oral spines, and a recrystallized suboral area; (4, 5) inclined views of an ovicellate zooid with four oral spines and oecium formed by the distal kenozooid with small costal shield; arrows indicate the basal pore chambers potentially producing the avicularia lateral to the ovicell; (6) Cala Sant’Antonino center, sample 17 (2000), part of a large worn colony on a bioclast; abundant kenozooids with eight costae are seen between autozooids. Scale bars: (1, 2, 6) 200 μ m; (3–5) 100 μ m.

Glabrilaria cf. *G. pedunculata* (Gautier, 1956)
Figure 4; Table 2

cf. 1966 *Colletosia pedunculata*; Prenant and Bobin, p. 596,
fig. 207 III.

cf. 1970 *Cribrilaria pedunculata*; Harmelin, p. 93, fig. lg, h,
pl. 2, fig. 6.

cf. 1956 *Puellina pedunculata* Gautier, p. 203, fig. 20.

Table 2. Measurements (in μ m) of *Glabrilaria* cf. *G. pedunculata* Gautier, 1956 and *Glabrilaria transversocarinata* n. sp. L: length; W: width.

Species Locality	<i>Glabrilaria</i> cf. <i>G. pedunculata</i> (Gautier, 1956) Capo Milazzo	<i>Glabrilaria transversocarinata</i> n. sp. Scoppo
Number of costae	13–17; 15 \pm 1 (N = 11)	14–16; 15 \pm 1 (N = 10)
Zooid length	252–425; 337 \pm 67 (N = 10)	407–457; 436 \pm 23 (N = 5)
Zooid width	211–323; 263 \pm 37 (N = 10)	271–337; 302 \pm 27 (N = 5)
L/W	1.28	1.44
Proximal gymnocyst length	narrow and sloping	narrow and sloping, proximal tip
Costate shield length	166–257; 201 \pm 28 (N = 10)	227–268; 250 \pm 19 (N = 5)
Costate shield width	192–277; 238 \pm 31 (N = 10)	244–264; 254 \pm 9 (N = 5)
Orifice length	46–56; 50 \pm 3 (N = 7)	45–70; 59 \pm 9 (N = 4)
Orifice width	69–79; 74 \pm 4 (N = 7)	63–99; 83 \pm 12 (N = 4)
Number of articulated oral spines	7 (4 on ovicellate ones)	6 (4 on ovicellate ones)
Ooecium length	134–148; 139 \pm 8 (N = 3)	139–165; 151 \pm 11 (N = 4)
Ooecium width	159–185; 170 \pm 13 (N = 3)	153–240; 194 \pm 19 (N = 4)
Ooecium length with kenozooid	197	186–213; 200 \pm 19 (N = 2)
Ooecium width with kenozooid	195	199–265; 232 \pm 47 (N = 2)
Ovicellate orifice length	44–47; 46 \pm 2 (N = 2)	60
Ovicellate orifice width	80–86; 83 \pm 4 (N = 2)	74
Kenozooid length	108–173; 119 \pm 28 (N = 4)	92
Kenozooid width	94–144; 103 \pm 24 (N = 4)	78

- cf. 1987 *Puellina (Glabrilaria) pedunculata*; Bishop and Househam, figs. 95–97, tab. 13.
- cf. 1988 *Puellina (Glabrilaria) pedunculata*; Harmelin, p. 31, figs. 9–11.
- cf. 2013a *Puellina (Glabrilaria) pedunculata*; Rosso et al., tab. 17.1.
- cf. 2015 *Puellina (Glabrilaria) pedunculata*; Sanfilippo et al., tab. 2, fig. 5f.
- cf. 2019a *Glabrilaria pedunculata*; Rosso et al., fig. 5e, f.

Holotype.—MNHN-IB-2008-10384, Grand Conclu de Riou (Golfe de Marseille), Mediterranean, Recent.

Occurrence.—*Glabrilaria pedunculata* is an endemic Mediterranean species, widespread throughout the basin, from the Gulf of Lion to the Aegean Sea. Its presence in the Atlantic is restricted to areas swept by Mediterranean outflow water (Harmelin and d'Hondt, 1992). It has been reported from: (1) shallow-water submarine caves in the Provençal area (Harmelin, 1969, 1970, 1988, 2003), in the Ionian sea (Rosso et al., 2013a, b; Sanfilippo et al., 2015) and Aegean sea (Crete: Harmelin, 1988; Lesvos: Rosso et al., 2019a); (2) cryptic microhabitats from shallow waters (Harmelin, 2003), mid-shelf coralligenous cliffs, and outer shelf “Coralligène de Plateau,” at 100–140 m depth off Lybia and near Santorini (Harmelin, 1988); and (3) at bathyal depths, ~700 m in the Sicily Strait (Harmelin, 1979, 1988), ~280 m in the southern Adriatic Sea (D’Onghia et al., 2015), and ~500 m at Leuca, northeastern Ionian Sea (Mastrototaro et al., 2010), usually associated with cold-water coral habitats. Specimens from the Gelasian of Sicily represent the first fossil record for this species, suggesting its persistence, at least in deep-water settings, in the Mediterranean since the early Pleistocene.

Description.—Colony encrusting, multiserial, unilaminar (Fig. 4.1, 4.6), the largest specimen including at least 50 zooids. Zooids oval, longer than wide ($L/W = 1.28$), convex, outlined by furrows filled by incipient re-crystallization (Fig. 4). Interzooidal communication through basal pore-chambers, more than 10 visible only in some marginal zooids, with longitudinally elongate windows $\sim 10 \times 20 \mu\text{m}$ (Fig. 4.4). Gymnocyst narrow, steeply sloping. Costate frontal shield oval and extensive, formed by 13–17 (including suboral) wedge-shaped, prominent costae, 27–45 μm wide at the base, converging towards the midline and forming a slightly raised carina (Fig. 4.4, 4.5). Costae joined by regularly spaced intercostal bridges leaving 6–7 slit-like intercostal pores, $\sim 7\text{--}8 \mu\text{m}$ long (Fig. 4.5). Only four intercostal spaces occur proximally to the suboral pair of costae, which are flat and merge at the midline forming a triangular shelf, possibly leaving a single round pore (Fig. 4.3, 4.6). Orifice transversely D-shaped (Fig. 4.1, 4.3, 4.6), marked by a raised rim, provided with 6–7 closely spaced, articulated oral spines (Fig. 4.1, 4.3), four persisting in ovicellate zooids (Fig. 4.2, 4.5). Ovicells hyperstomial, presumably cleithral. Ooecium formed by distal kenozooid, with frontally visible small costate shield consisting of three costae (Fig. 4.4); ectooecium smooth, with elevated longitudinal carina (Fig. 4.2, 4.4, 4.5). Avicularia not observed. Abundant small kenozooids recorded in larger colonies, interspersed between

autozooids, seemingly polygonal, with boundaries obliterated by recrystallisation, with extensive gymnocyst and costate frontal shield of 6–8 costae (Fig. 4.6). The only ancestrula found seemingly regenerated as a miniature autozooid (Fig. 4.1).

Materials.—Rosso-Collection, collective code: PMC I. Pl. B.81a: Capo Milazzo Peninsula: Cala Sant’Antonino center: sample 2015: three specimens; sample 17 (2000): one specimen; Punta Mazza: sample 4: two specimens; sample 5: one specimen.

Remarks.—The available specimens are worn and recrystallized, preventing recognition of some diagnostic characters. However, the morphology and morphometrics of autozooids, ooecia, and kenozooids are closely reminiscent of *Glabrilaria pedunculata* Gautier, 1956, although with a few small differences. The present-day Mediterranean species invariably shows six oral spines and two median pores in the triangular shelf distal to the suboral costae (Bishop and Househam, 1987, fig. 97; Harmelin, 1988, fig. 17a, c; Rosso et al., 2019a, fig. 5e, f). However, both the variability in the number of oral spines and the presence/absence of median pores are considered to be in the range of intraspecific variability in cribrilinids (e.g., *C. pseudoradiata* Harmelin and Aristegui, 1988 and *G. orientalis* Harmelin, 1988). The long-stalked (=pedunculate) avicularia, originating from basal pore chambers in both autozooids and kenozooids, which are typical of *G. pedunculata*, were not observed in our fossil specimens. This is likely a taphonomic bias, because such avicularia can be easily detached even in living colonies, as observed in *Glabrilaria hirsuta* Rosso in Rosso et al., 2018 from the Bahama Bank. In our fossil specimens, zooidal boundaries are mostly covered by neomorphic calcite crystals that prevent the detection of the basal pore chambers from which the pedunculate avicularia are budded. However, in Figure 4.4 and 4.5 (see arrows) the pores potentially producing the avicularia lateral to the ovicell are visible.

Seven oral spines were described in *Glabrilaria corbula* Bishop and Househam, 1987 and *Glabrilaria orientalis lusitanica* Harmelin, 1988, two closely related extant species reported from the Atlanto-Mediterranean region and the Gibraltar Strait area, respectively. However, the former species shows an ooecium that is formed by a distal kenozooid which is not distinguishable in frontal view, has 4–6 costae-like ridges arranged in a radial pattern, a flatter autozooidal shield with somewhat carinate costae that are sometimes with a pelma, and two large pores in the suboral shelf (Bishop and Househam, 1987; Harmelin, 1988), while the latter species lacks midline pores in the suboral shelf (Harmelin, 1988). *Glabrilaria orientalis lusitanica* also has semi-erect interzooidal avicularia (Harmelin, 1988) backed against the ooecium. Six to seven oral spines also occur in *Glabrilaria africana* (Hayward and Cook, 1983), but this species has numerous variably sized pores in the suboral shelf in addition to semi-erect avicularia associated with the ooecium and squeezed between autozooids.

Glabrilaria transversocarinata new species
Figure 5; Table 2

Holotype.—PMC. B28.10.10.2019a: colony consisting of ~20 autozooids, some ovicellate. Scoppo, sample 24 top, early Calabrian, MNN19b-19c biozones.

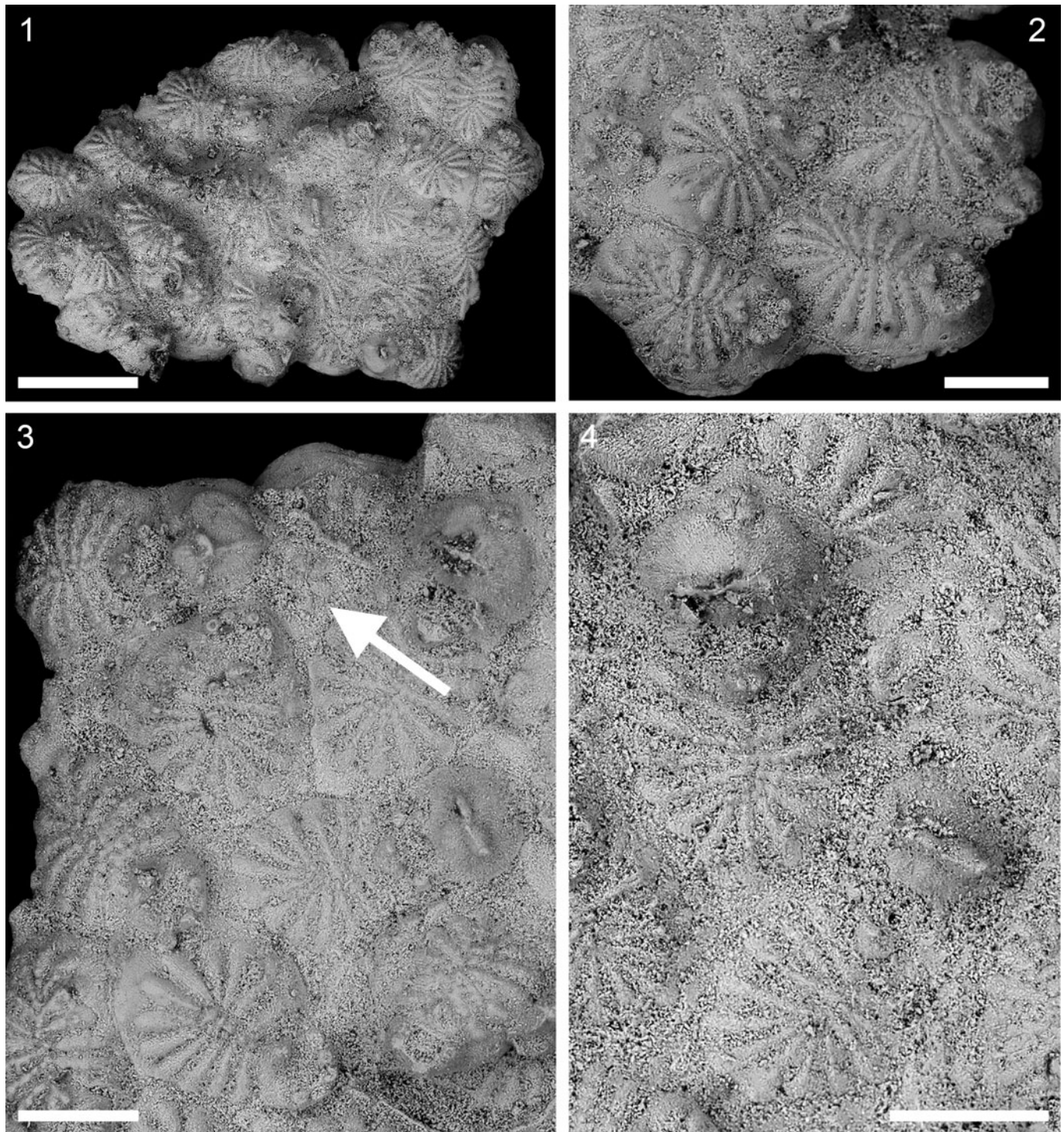


Figure 5. *Glabrilaria transversocarinata* n. sp., Scoppo, sample 24 top, early Calabrian, MNN19b-19c biozones, PMC. B28.10.10.2019a, holotype. (1) The largest specimen consisting of partly superimposed colony layers; (2) group of zooids at the colony margin showing intercostal spaces; (3) cluster of ovicellate and non-ovicellate zooids; arrow indicates a small kenozooid with five costae (note the elevated bases of oral spines and the transversely oriented crest located in the middle of the oecium and the possible persistence of four oral spines); (4) two ovicellate zooids (note the prominent bifid suboral mucro and flat shield composed of somewhat tuberculate costae). Scale bars: (1) 500 μm ; (2–4) 200 μm .

Paratype.—PMC. B28.10.10.2019b: small colony fragment including seven autozooids, two ovicellate. Scoppo: sample 24 top, early Calabrian, MNN19b-19c biozones.

Diagnosis.—Colony encrusting, multiserial. Autozooids convex. Gymnocystr narrow. Frontal shield consisting of 12–14 prominent

and tuberculate costae with 3–7 intercostal spaces. Suboral pair of costae forming a bifid mucro. Orifice transversely D-shaped with six oral spines, four persisting in ovicellate zooids. Ovicells subimmersed. Oecium formed by distal kenozooid, surface smooth, with transverse rib. Avicularia not observed. Kenozooids rare.

Occurrence.—Only known from the early Calabrian of Scoppo, Messina.

Description.—Colony encrusting, multiserial, unilaminar, but including superimposed lobes (Fig. 5.1), the largest observed fragment consisting of ~20 zooids. Zooids oval, longer than wide ($L/W = 1.44$), convex, the outline hidden by incipient recrystallization (Fig. 5.4). Interzooidal communication through basal pore-chambers visible in some peripheral zooids, with slightly longitudinally elongate windows ~ $21 \times 18 \mu\text{m}$ (Fig. 5.2). Gymnocyst very narrow, except for proximal and, occasionally, lateral extensions wedged between neighboring zooids (Fig. 5.2, 5.3). Frontal shield oval and extensive, formed by 14–16 (including suboral) wedge-shaped, prominent, tuberculate costae, 26–47 μm wide at the base, converging towards the midline (Fig. 5.2–5.4). Costae joined by intercostal bridges apparently leaving 6–7 intercostal pores (Fig. 5.2), seemingly reduced to 3–4 proximally to the suboral pair of costae. These are shorter and more robust than the other costae and raised at the midline, forming a bifid mucro (Fig. 5.2, 5.3). Orifice transversely D-shaped, provided with six closely spaced, articulated oral spines (Fig. 5.2), four persisting in ovicellate zooids (Fig. 5.3, 5.4). Ovicells subimmersed. Ooecium formed by the distal kenozooid, with frontally visible costate (4–5 costae) shield and distal band of gymnocyst (Fig. 5.3, 5.4); ooecium with prominent, transverse, straight to slightly arched rib possibly with protruding spikes (lost) (Fig. 5.3, 5.4); an additional thinner and lower longitudinal carina was observed in a single ooecium (Fig. 5.3). Avicularia not observed. Only one kenozooid was observed. It was small, polygonal, with a relatively narrow gymnocyst and costate frontal shield of five radial costae (Fig. 5.3). Ancestrula not observed.

Etymology.—From the Latin *transversus*, meaning transversely placed, and *carina* alluding to the typical median crest of the ooecium.

Remarks.—The co-occurrence of a prominent transverse ridge on the ooecium and a bifid suboral mucro is distinctive of this species. Ooecia with a transverse ridge are known in a few species only. One is the extant *Glabilaria hirsuta* Rosso et al., 2018 from the Bahama Bank, in which the ridge is, however, very arched to subtriangular and equipped with prominent spine-like processes (Rosso et al., 2018). Furthermore, in *G. hirsuta*, the number of oral spines (six, four persisting in ovicellate zooids) occasionally increases to seven, the costae have more obvious spine-like processes at the periphery of the frontal shield, the suboral costae form a transverse spiny crest proximal to the orifice, and kenozooids arranged in rows or clusters are very common (Rosso et al., 2018). In the extant *Glabilaria cristata* (Harmelin, 1978) from the Hyères and Meteor banks south of the Azores, the ooecial ridge is extremely protruding and situated more proximally towards the orifice, contributing to form a sort of spiny collar around the orifice together with the second pair of suboral costae. These costae bear cockscomb-like spines that are still present but smaller than those on the other pairs

(Harmelin, 1978). Oral spines are invariably seven in this species.

Occasionally, transverse ornamentation has been reported in the ooecia of other cribrilinid genera. A succession of ribs adds to a longitudinal carina in *Puellina cassidainsis* Harmelin, 1984 from the 3PP submarine cave in the Mediterranean French coast (see Harmelin, 1984, fig. 7b). A cruciform pattern can develop in the ooecia of *Cribrilaria macaronensis* (Harmelin, 2006), and transverse ridges or wrinkles in *Cribrilaria atlantis* (Harmelin, 2006), both species previously assigned to *Puellina* (see Harmelin, 2006, fig. 1).

Measurements of *Glabilaria transversocarinata* n. sp. generally overlap with those of *G. cf. G. pedunculata* from Capo Milazzo (Table 2), but tend towards the higher values, sometimes exceeding the upper limit. The only exception is the size of the kenozooid, which seems to be smaller, although only based on a single measurement. However, morphological differences, including the number of oral spines, shape of costae, suboral lacuna and ooecia, and the rarity of kenozooids, distinguish the two species.

The two colony fragments available are detached from the substratum, a common feature for bryozoan specimens found in the Capo Milazzo “yellow marl.” This may indicate either that the substratum was organic or that selective aragonitic dissolution took place during/before fossilization.

Genus *Figularia* Jullien, 1886

Type species.—*Lepralia figularis* Johnston, 1847, by original designation.

Amended diagnosis.—Colony commonly encrusting, but erect, fan-shaped, or developing erect lobes in some species. Autozooids with variably developed gymnocyst, usually wider proximally; costate shield formed by few to numerous (up to 30) costae, each bearing a pelma (circular to drop-shaped or transversely elongated) varying in size and position. Orifice with well-developed poster and condyles, dimorphic and typically larger in ovicellate zooids. Oral spines absent. Avicularia, when present, vicarious, elongate, and often spatulate, with complete crossbar. Ovicells hyperstomial or subimmersed, cleithral. Ooecium formed by the distal autozooid or kenozooid (sometimes in the same colony), bilobate, consisting of two very large, modified costae, arched and meeting in the midline to form a suture and/or carina; each costa with a wide fenestra. Interzooidal communication via mural pore chambers in the transverse walls and multiporous septula in the lateral walls. Ancestrula only observed in the type species, wider than autozooids, subcircular, with narrow gymnocyst encircling an extensive opesia with differentiated orifice; no spines.

Remarks.—The finding of a new species having morphological skeletal features fitting into the genus *Figularia* Jullien, 1886, but characterized by erect colony form and a very distinctive and large ooecium formed by a distal kenozooid, led to the examination of species currently placed in this genus (Tables 3, 4).

Table 3. List of species currently belonging to the genus *Figularia* with description of the main skeletal morphological characters. These species conform to the diagnosis of the genus. Abbreviations: Dim Or, Dimorphic orifice; Distr, Stratigraphic distribution; E, Eocene; M, Miocene; N, number; O, Oligocene; Orig, Origin; P, Pliocene; Pl, Pleistocene; R, Recent; ZL: autozooidal length; ZW: autozooidal width; Transv. = transversal; Longit. = longitudinal; Or. = orifice. Symbols in the column Orig: *oecium formed by the distal autozoid; § oecium formed by the distal kenozooid; ? uncertain. In the columns Suture and Dim Or the asterisk indicates the occurrence of the feature. Information is mostly compiled from the original descriptions.

Species	Distr	Costate shield	N of costae	Intercostal pores	Pelmata	Oecium			Dim Or	Vicarious avicularia	Additional notes
						Orig	Fenestrae	Suture			
<i>Figularia arnouldi</i> Buge, 1956	P	Extensive	12	numerous	1	*§	Transv. triangular	*carina		Spathulate with bar	Oecium also formed by vicarius avicularium.
<i>F. carinata</i> (Waters, 1887)	R	2/3 ZL; <1/2 ZW	10–12	fissure	1 (slit-like)	*	Transv. drop-shaped to elliptical	*	*	Spathulate with bar	Fenestrae undulate, slit-like in Gordon (1984). Possibly two different species.
<i>F. clithridiata</i> (Waters, 1887)	R	1/2 ZL; 1/2 ZW	7–10	?	1 (oval)	§	Transv. drop-shaped			Duckfoot-shaped	Oecium with peripheral semicircle of pelma seemingly belonging to the distal kenozooid.
<i>F. dimorpha</i> Figuerola et al., 2018	R	2/3 ZL; 1/2 ZW	16	numerous	1	*	Transv. oval to pear-shaped	*carina	*	Ogival with bar	
<i>F. figuraris</i> (Johnston, 1847)	?M–R	2/3 ZL; 4/5 ZW	9–13	~5	1 (circular)	*§	Transv. drop-shaped to irregularly oval	*		Spathulate with bar	Specimens in Souto et al. (2014) possibly different species.
<i>F. fissa</i> (Hincks, 1880)	R	1/3 ZL; 1/2 ZW	8–10	1 (triangular)	1 (circular)	*	Transv. crescentic	*		Spoon-like with bar	Likely a species complex (see Harmer, 1926, figs 20–23 and Ryland and Hayward, 1992).
<i>F. fissurata</i> Canu and Bassler, 1929	R	1/2 ZL; 2/3 ZW	3–12	fissure	1 (circular)	*	Transv. crescentic	*	*	Spoon-like with bar	
<i>F. haueri</i> (Reuss, 1848)	M	Extensive	14–18	numerous	Not mentioned or visible in fig.	*	Not mentioned or visible in fig.	*carina		Absent	Seemingly only differing from <i>F. figuraris</i> by some morphometrics (see Berning, 2006)
<i>F. hilli</i> (Osburn, 1950)	R	3/4 ZL; 4/5 ZW	5–7	1–2 (slit-like)	1 (drop-shaped)	*	Transv. oval	*	*	Absent	Oecium including a pair of proximo-lateral costae.
<i>F. japonica</i> Silén, 1941	R	3/4 ZL; 4/5 ZW	11–13	1–3 (circular)	1 (drop-shaped)	*	2 pairs, transv. triangular	*	*	Duckfoot-shaped with bar	7–10 costae in Yang et al., 2018.
<i>F. mernae</i> Uttley and Bullivant, 1972	R	2/3 ZL; 1/2 ZW	12–18	1 (slit-like)	1 (circular)	*	Longit. drop-shaped	*	*	Lanceolate with bar	
<i>F. pelmatifera</i> Gordon, 1984	R	3/4 ZL; 3/4 ZW	24–30	fissure + 1–2 (elliptical)	1 (elliptical)	*	Longit. drop-shaped	*	*	Not observed	
<i>F. philomela</i> (Busk, 1884)	R	Extensive	14–16	numerous	Not mentioned or visible in figs.	*	Diagonal elliptical to transv. drop-shaped	*carina		Spathulate	Plastic colony morphology including an encrusting phase (var. <i>adnata</i>) and bilaminar erect parts.
<i>F. rhodanica</i> Li, 1990	M	Extensive	14–20	2	Not mentioned or visible in fig.	*	Not mentioned or visible in fig.	*carina		Spoon-like with bar	
<i>F. speciosa</i> (Hincks, 1881)	R	4/5 ZL; 3/4 ZW	12–18	3 (slit-like)	1 (slit-like)	*	Longit. slit-like	*carina	*	Absent	
<i>F. spectabilis</i> n. sp.	Pl	3/4 ZL; 3/4 ZW	8–13	3–4? (subcircular)	1 (drop-shaped)	§	Large quadrangular	*	*	Slightly spathulate	Colony erect, flabelliform, very large oecium.
<i>F. tenuicosta</i> (MacGillivray, 1895)	M, ?R	2/3 ZL; >1/2 ZW	19–20	1 (slit-like)	1 (slit-like)	*	Longit. drop-shaped	*	*	Duckfoot-shaped	
<i>F. triangula</i> Powell, 1967b	R	2/3 ZL; <1/3 ZW	12–14	1 (slit-like)	Absent	?	Transv. slit-like	*		Not observed	

Table 4. List of doubtful species currently attributed to the genus *Figularia*. New combinations are suggested for two species, while attribution of the remaining species awaits examination of the type material. Abbreviations: Dim Or, Dimorphic orifice; Distr, Stratigraphic distribution; M, Miocene; N, number; Orig, Origin. P, Pliocene; Pl, Pleistocene; R, Recent; ZL: autozooidal length; ZW: autozooidal width. Symbols in the column Orig: *oecium formed by the distal autozoid; § oecium formed by the distal kenozooid; ? uncertain. In the columns Suture and Dim Or the asterisk indicates the occurrence of the feature. Information is mostly compiled from the original descriptions. Measurements provided in μm . Additional information from Duvergier (1924), Buge (1957), Grischenko et al. (2004), Winston et al. (2014), NMNH 1, and NMNH 2.

Species	Distr	Costate shield	N of costae	Intercostal pores	Pelmata	Ooecium			Dim Or	Vicarious avicularia	New combination	Additional notes
						Orig	Fenestrae	Suture				
<i>Figularia ampla</i> Canu and Bassler, 1928	R	2/3 ZL; 1/3 ZW	10	fissure	none	*	Absent	*carina		Not mentioned		Frontal shield densely pseudoporous
<i>F. capitifera</i> Canu and Bassler, 1929	R	Vestigial, suboral	2+2		1 (elliptical)	*	Single, central			Spathulate	<i>Vitrimurella capitifera</i>	Frontal shield and ooecium with massive pseudopores
<i>F. contraria</i> Lagaaij, 1963	R	2/3 ZL; 1/2 ZW	8–11	2	1 (circular)	§	Two pairs of small membranous areas	*carina	*	Not observed		Ovicell subimmersed. Ooecium with a pair of small oval membranous areas centrally. Two more membranous areas are situated on the ectooecium laterally
<i>F. ? crassicostulata</i> Canu and Bassler, 1920	E	Extensive	16–20	3–6	Not mentioned or visible in fig.	*	Transv. crescentic			Spathulate, ?no bar		
<i>F. duvergieri</i> Bassler, 1936	M	2/3 ZL; = ZW	14–16	4–6	Not mentioned or visible in fig.	*	Absent/not visible	*		Elliptical with bar		Orifice with finely denticulate anter.
<i>F. echinoides</i> Brown, 1952	O	Extensive	22–24	numerous	2–3 spine-like		Ovicells not observed/Absent			Spathulate, no bar		
<i>F. jucunda</i> Canu and Bassler, 1929	R	2/3 ZL; 3/5 ZW	8–9	1 (triangular)	1 (circular)	§	Pseudopores and/or pelmatidia	*carina	*	Not observed		Ooecium with pseudopores and/or pelmatidia
<i>F. kenley</i> Brown, 1958	M	1/2 ZL; 4/5 ZW	14–16	1 (slit-like)	Visible/present only on suboral costae?	?	2 large	*carina		Not observed		Erect bilaminar; pelma only on suboral costae
<i>F. peltata</i> (Reuss, 1874)	M	Extensive	15–18	numerous	Absent/not visible	*	Absent			Not mentioned		Flat ooecium
<i>F. planicostulata</i> Canu and Lecointre, 1928	M	Extensive	17	several, large	Absent/not visible	?	Absent/not visible		*	Spathulate		Smooth ooecium.
<i>F. pulcherrima</i> Tilbrook et al., 2001	R	1/2 ZL; 1/2 ZW	9–10	3–5	1 (circular)	§	2 drop-shaped, basal lateral + 2 slit-like, median	*		Not observed		Ooecium with central costate area. cf. <i>F. tahitiensis</i> .
<i>F. quaylei</i> Powell, 1967a	R	Extensive	10–12	fissure	2 (circular)	*	4–7			Not observed	<i>Hayamiellina quaylei</i>	Costate ooecium
<i>F. rugosa</i> (Maplestone, 1901)	M				Absent/not visible	?			*	Lanceolate no bar		Costate ooecium
<i>F. ryukuensis</i> Kataoka, 1961	Pl	Extensive	8–10	1 (slit-like)	Absent/not visible	*	Pseudopores			Not mentioned		Pseudoporous ooecium with ill-defined keel
<i>F. tahitiensis</i> (Waters, 1923)	R	2/3 ZL; 1/2 ZW	11	numerous	1 (circular)	§	2 drop-shaped, basal lateral + 2 slit-like, median	*		Not figured		Ooecium with central costate area. cf. <i>F. pulcherrima</i> .



Figure 6. *Figularia figularis* (Johnston, 1847), Southern Tyrrhenian Sea, Rosso collection PMC. I. Pl. B.71.b, Apollo Bank sample. (1) Small fragment consisting of five autozooids, two ovicellate, and a vicarious avicularium; left oecium is formed by the distal autozooid, right by the distal kenozooid with frontally visible costal shield; (2) close-up of the oecium formed by the distal autozooid. Scale bars: (1) 500 μm ; (2) 200 μm .

Figularia was introduced by Jullien (1886, p. 608) who designated *Lepralia figularis* Johnston, 1847, an Atlanto-Mediterranean extant species, as the type species of the genus, and included an additional fossil species *Lepralia elegantissima* based on the unique drawing available (Seguenza, 1880, p. 83, pl. 8, fig. 11). This latter species, depicted with oral spine bases, is more likely to be a species of *Cribrilaria* (see also Remarks on *Cribrilaria profunda* n. sp.). Oral spines are absent in the type species *F. figularis* (see Soule et al., 1995, fig. 45C), as well as in all living and fossil specimens found to date (e.g., Figs. 6, 7). The absence of oral spines has also been reported almost consistently in the diagnosis of the genus, with only a few exceptions (e.g., Gordon, 1984). Further diagnostic characters include a complete crossbar in the vicarious avicularia, and the presence of large, symmetrical ectooecial fenestrae and a median carina in the oecium (see Soule et al., 1995; Hayward and Ryland, 1998; Kukliński and Barnes, 2009; Yang et al., 2018).

The erect colony-form has never been mentioned in the generic diagnosis before. However, Busk (1884, p. 132) described *Figularia philomela* as “free; erect or decumbent (hemescharan).” Subsequently, Hayward and Cook (1979, p. 76) found a bilaminar fragment of *F. philomela* interpreted as part of an erect foliaceous colony possibly arising from an encrusting phase (var. *adnata* of Busk, 1884). Gordon (1989, p. 15, 16) recorded the occasional occurrence of an erect bilamellar lobe, arising from the adjacent encrusting zooids, in a colony of *Figularia mernae* Uttley and Bullivant, 1972 from

Puysegur Bank, off the South Island of New Zealand. The fan-shaped colonies of the newly discovered *Figularia* species from Capo Milazzo, although often fragmentary (Fig. 8), show a configuration comparable to that observed in *F. mernae*, with basal zooids elongated and arranged in back-to-back adjacent pairs (Fig. 8.1, 8.2, 8.6). The lack of a costate frontal shield, with no obvious evidence of breakage, in several proximal/basal zooids, suggests that simplified polymorphs, reminiscent of those in *Corbulipora* MacGillivray, 1895 (see Bock and Cook, 2001) may occur. However, the raising of the erect fan-shaped portions from an encrusting phase is doubtful until encrusting colonies, or at least isolated encrusting zooids, are found.

The oecium in *Figularia* is generally described as bivalved/bifenestrate (Ostrovsky, 2013). In *F. figularis*, the prominent bilobate oecium is formed by the distal autozooid, with two costae meeting in the midline leaving a suture and/or forming a slightly raised carina; each costa bearing a large, irregularly shaped and transversely elongate fenestra (membranous area in non-cleaned specimens). The colony fragment of *F. figularis* from the Apollo Bank (Tyrrhenian Sea, Mediterranean) shows that oecia formed by the distal kenozooid can co-occur in the same colony in this species (Fig. 6). Though uncommonly reported, and here recorded in *F. figularis* for the first time, the co-occurrence of oecia produced by the distal autozooid and kenozooid is known in other cribriliniids, such as *Cribrilaria punctata* (Hassall, 1841), “*Puellina*” *harmeri* Ristedt, 1985 (see also discussion in Rosso et al., 2018), *Cribrilaria innominata* (Couch, 1844) (see Chimenz Gusso et al., 2014),

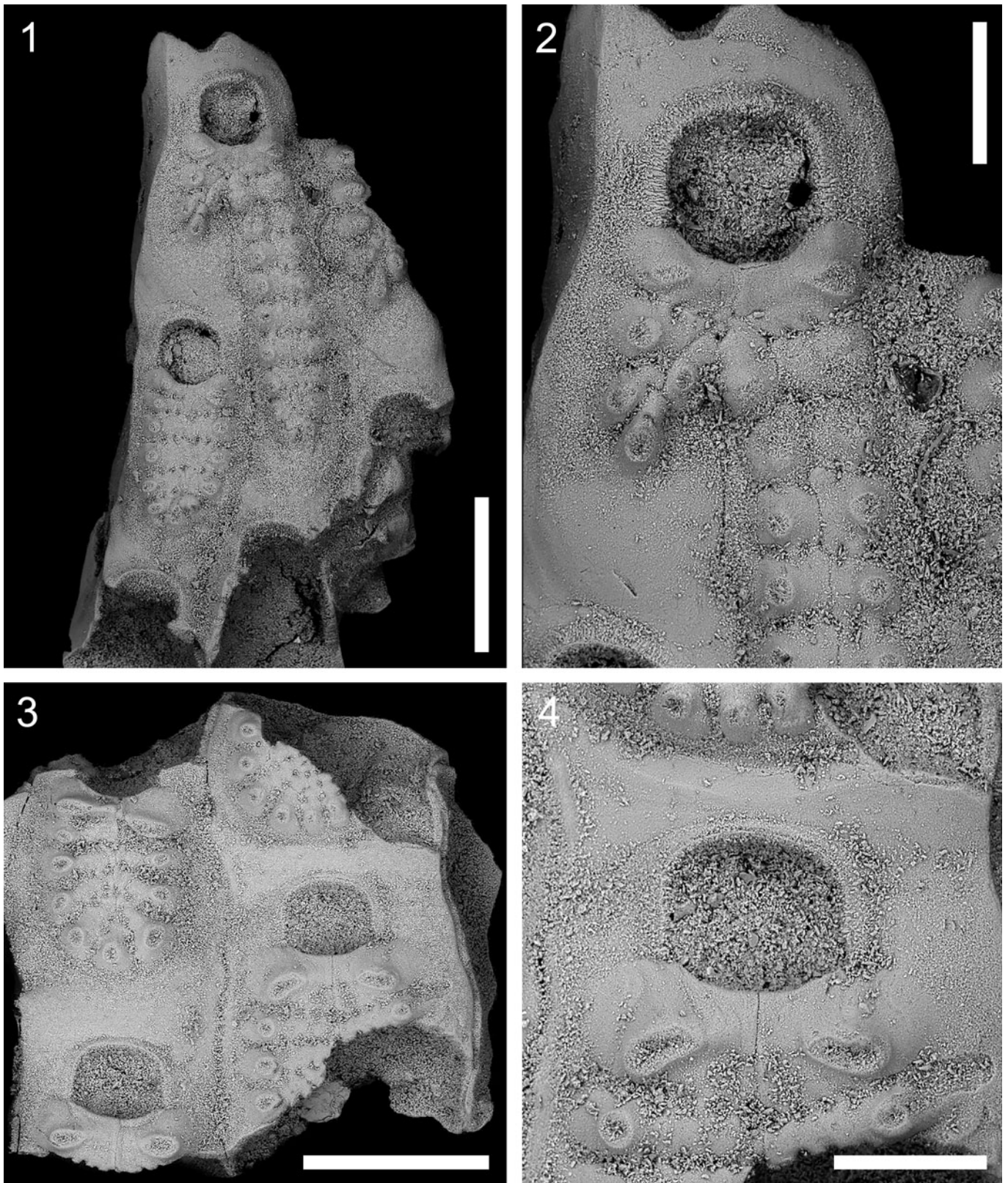


Figure 7. *Figularia figularis* (Johnston, 1847), Scoppo, sample 24 top, early Calabrian, MNN19b-19c biozones, Rosso collection PMC I. Pl. B.71.c. (1) Fragment with few autozooids (note the teratologic autozooid); (2) close-up of the distal half of the teratologic autozooid shown in (1); (3) fragment with four, incomplete autozooids; (4) close-up of the orifice. Scale bars: (1, 3) 500 μm ; (2, 4) 200 μm .

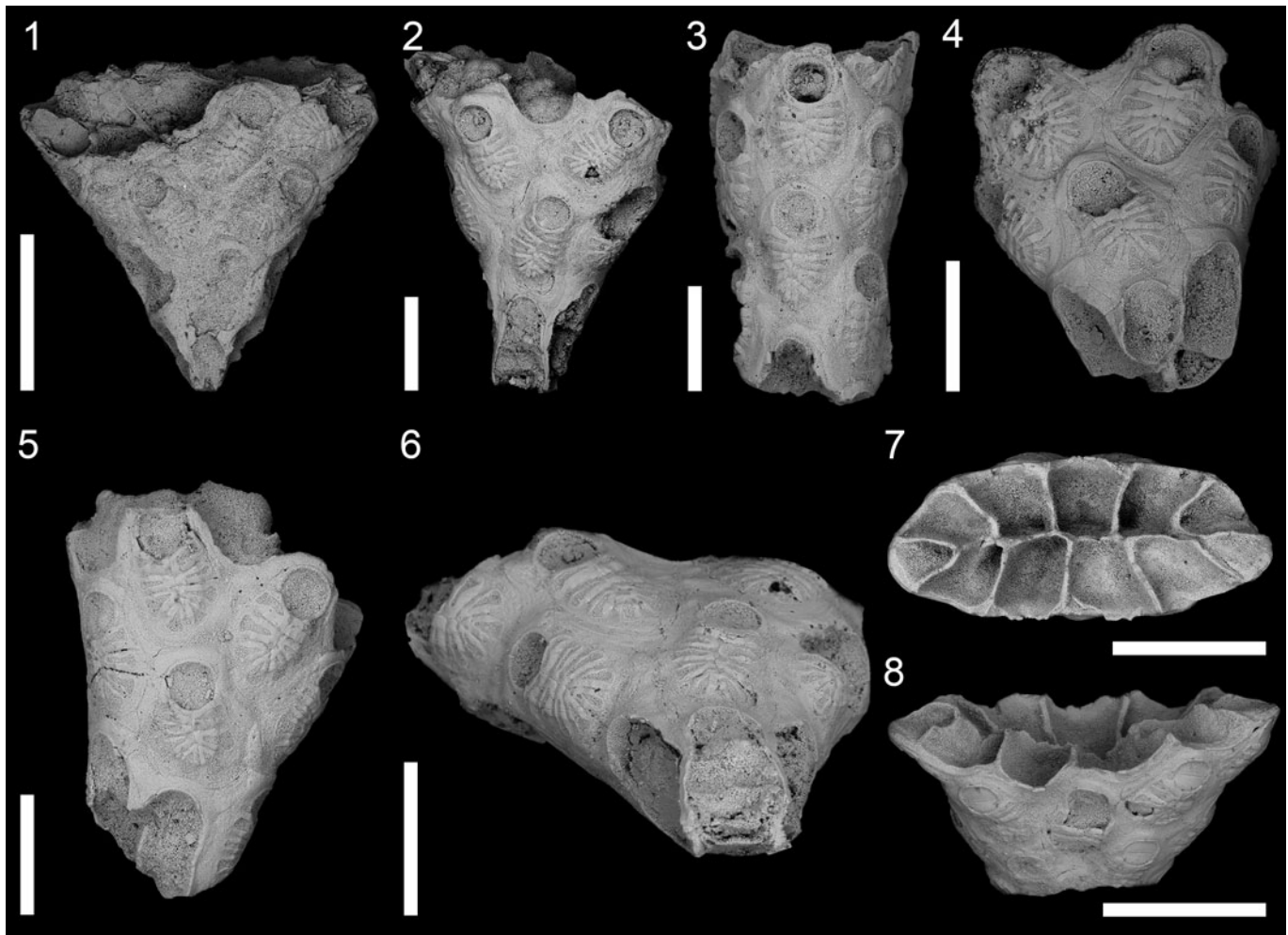


Figure 8. *Figularia spectabilis* n. sp., Capo Milazzo, sample Cala Sant'Antonino center, 2015, Gelasian, PMC. B22. 5.4.2015.b, paratypes, colony morphology. (1, 2) Lateral view of two fan-shaped colony fragments with thin cylindrical proximal base; (3) side view of a narrow ribbon-like fragment; (4, 5) inclined proximal view and lateral view of fan-shaped colony fragments with slightly diverging sides; (6) proximal view of a fan-shaped colony fragment; (7, 8) inclined distal and top view of a fan-shaped colony fragment. Scale bars: (1, 7, 8) 1 mm; (2–6) 500 μ m.

Puellina saldanhai Harmelin, 2001, and *Puellina mikelae* Harmelin, 2006. Following Rosso et al. (2018), the latter two species are here allocated to the genus *Cribrilaria*: *Cribrilaria saldanhai* (Harmelin, 2001) n. comb. and *Cribrilaria mikelae* (Harmelin, 2006) n. comb. Both ovicell variants sometimes may appear within the same colony (e.g., in *C. punctata* and “*P.*” *harmeri*) indicating a developmental plasticity of this character (reviewed in Ostrovsky, 2013). A similar plasticity in ovicell formation is only known in some Calloporidae (Ostrovsky and Schäfer, 2003; Ostrovsky et al., 2009; Ostrovsky, 2013) that are presumed ancestors of cribrilinids.

The kenozooid producing the oecium in *F. figularis* shows a crescent-shaped shield of short radial costae, each with a single pelma as in the autozooids, but also with a single intercostal pore (Fig. 6). The same structure is also evident in the fossil species from Capo Milazzo (Fig. 9). Ovicells with oecia formed by the distal kenozooid also occur in other species currently assigned to this genus, based on examination of available SEM images and, to a lesser extent, drawings (see Table 3).

Ostrovsky (2013, fig. 1.28A) illustrated sectioned decalcified ovicells of *F. figularis* in which most of the brood cavity

is situated in the proximal part of the distal zooid predominantly below the colony surface, thus corresponding to endozooidal type. Whether this position of the brood cavity was an effect of decalcification of the skeleton (and, thus, sagging of the originally raised oecium) during preparation for sectioning is currently not clear, but this contradicts most descriptions showing hyperstomial ovicells in this species (see references above). Still, a degree of the brood cavity immersion may vary, and, for example, both hyperstomial and subimmersed ovicells are known within the genus *Figularia*, and hyperstomial, subimmersed, and endozooidal ovicells are described in the different species of *Puellina* (Ostrovsky, 2013). Subimmersed ovicells were present in Recent colonies of *F. figularis* from the Mediterranean (A. Ostrovsky, personal observations).

Ostrovsky and Taylor (2005) noted the occurrence of species of *Figularia*—*F. clithridiata* (Waters, 1887), *F. tahitiensis* Waters, 1923, and *F. pulcherrima* Tilbrook, Hayward and Gordon, 2001—having costate oecia (see also Ostrovsky, 2002). Winston et al. (2014) remarked that the occurrence of costate oecia in *F. pulcherrima* possibly suggests a better allocation of this species in a distinct genus. Inclusion of costae in the



Figure 9. *Figularia spectabilis* n. sp., Capo Milazzo, sample Cala Sant'Antonino center, 2015, Gelasian, PMC. B22. 5.4.2015.a, holotype, oecium. (1) Colony fragment with unique ovicellate zooid and vicarious avicularium; (2) close-up of the ovicellate zooid with oecium formed by the distal kenozooid. Scale bars: (1) 500 µm; (2) 200 µm.

construction of the oecium has also been observed in *Figularia hilli* (Osburn, 1950), with two small costae similar to those of the frontal shield added proximally to the larger oecial halves (see Table 3).

Yang et al. (2018), while including pseudoporous oecia in the diagnosis of *Figularia*, also suggested the examination of species with multiple ectoecial pseudopores in order to determine if they are genuinely congeneric. These species are here re-assigned to different genera (see also below and Table 4).

Suboral costae often differ from the other pairs. In the type species of *Figularia*, suboral costae merge, forming a smooth, wide shelf facing the orifice, most evident in ovicellate zooids (Fig. 6). Wide suboral costae associated with ovicellate zooids were also observed in *F. rhodanica* Li, 1990. In *F. pelmatifera* Gordon, 1984 the suboral pair of costae develops into two lateral, divergent, spinose processes (see Gordon, 1984, pl. 19, fig. E).

A certain variability occurs in the presence/absence of palmata in the frontal shield, and in their position along the costal length. Sometimes this variability was noted (e.g., Gordon, 1984). Nevertheless, all *Figularia* species lacking palmata (i.e., not included in formal descriptions and/or undetectable in available images) are fossil, except “*F. philomela* var. *adnata*” (Busk, 1884), suggesting that their absence may be a preservation artefact.

The ancestrula is generally not mentioned in species descriptions to our knowledge. In the amended diagnosis, we include characters of the ancestrula for the first time, based on the ancestrula found in a colony of *F. figularis* from the Mediterranean illustrated in Rosso et al. (2019b, fig. 5C). The large size of both autozooids and ancestrula (0.65 × 0.67 mm) and the absence of spines are rare and remarkable among cribrilinids, which usually have small, tatiform ancestrulae, and this may have implications on the systematics/phylogeny of this genus within the family Cribrilinidae. However, observation of

ancestrulae in additional species is needed to confirm whether this morphology is constant among congeners, which has been proven not to be the case in other cheilostome genera, such as e.g., *Escharina* Milne Edwards, 1836 (see Berning et al., 2008).

Several species previously assigned to *Figularia* were recently displaced in different genera of the families Cribrilinidae and Calloporidae (e.g., *Vitrimurella*, *Reginella* Jullien, 1886, *Inferusia* Kukliński and Barnes, 2009, *Valdemunitella* Canu, 1900; see Bock and Gordon, 2020), and *Jullienula* Bassler, 1953 (Yang et al., 2018). Here, we suggest further displacements: both *Figularia? ampla* Canu and Bassler, 1928, only tentatively included in *Figularia* when first described, and *Emballotheca? capitifera*, Canu and Bassler, 1929, subsequently referred to his new genus *Calyptotheca* by Harmer (1957) and to *Figularia* by Di Martino and Taylor (2018), fit better in *Vitrimurella*, owing to the pseudoporous zooidal gymnocyst and oecia, and the extremely reduced costate shield. *Figularia ryukyuensis* Kataoka, 1961 and *F. jucunda* Canu and Bassler, 1929 also need to be revised, pending examination of the type material. These species have pseudoporous oecia formed by the distal kenozooid without a visible frontal part. *Figularia divergieri* Bassler, 1936 has an unusual denticulate proximal orifice margin, and lacks costal palmata and fenestrae in the oecium. A detailed revision based on SEM images is needed to confirm generic allocation for these problematic species (Table 4). This issue has been partially addressed by López Gappa et al. (in press).

Figularia figularis (Johnston, 1847)
 Figures 6, 7; Table 5

1847 *Lepralia figularis* Johnston, p. 314.

1966 *Figularia figularis*; Prenant and Bobin, p. 604, fig. 2010 I–IV, VI.

Table 5. Measurements (in μm) of *Figularia figularis* and *Figularia spectabilis* n. sp. *Refers to an aberrant zooid (see text for further explanation). L: length; W: width.

Species Locality	<i>Figularia figularis</i> (Johnston, 1847) Scoppo	<i>Figularia spectabilis</i> n. sp. Capo Milazzo
Number of costae	10–20; 14 ± 5 (N = 3)*	7–14; 10 ± 2 (N = 18)
Zooid length	858	588–1057; 759 ± 135 (N = 16)
Zooid width	402	319–525; 442 ± 55 (N = 16)
L/W	2.13	1.72
Proximal gymnocyst length	41–111; 86 ± 31 (N = 4)*	60–210; 114 ± 47 (N = 14)
Costate shield length	455–457; 456 ± 1 (N = 2)	294–582; 388 ± 93 (N = 14)
Costate shield width	307–396; 352 ± 63 (N = 2)	306–543; 378 ± 65 (N = 14)
Orifice length	202–228; 213 ± 12 (N = 4)	176–292; 236 ± 32 (N = 18)
Orifice width	202–244; 225 ± 21 (N = 4)	179–295; 233 ± 31 (N = 18)
Number of articulated oral spines	absent	absent
Ooecium length	not observed	702
Ooecium width	not observed	730
Ovicellate orifice length	not observed	297
Ovicellate orifice width	not observed	323
Interzooidal avicularium length	not observed	473–642; 566 ± 86 (N = 3)
Interzooidal avicularium width	not observed	273–337; 298 ± 34 (N = 3)

1998 *Figularia figularis*; Hayward and Ryland, p. 338, fig. 120, cum syn.

2002 *Figularia figularis*; Hayward and McKinney, p. 38, fig. 16 D–E.

2006 *Figularia figularis*; Berning, 2006, p. 49, pl. 3, figs. 7, 10, cum syn.

2014 *Figularia figularis*; Chimenz Gusso et al., p. 167, fig. 84a–c.

Holotype.—NHMUK 1847.9.16.39, English Channel, Recent.

Occurrence.—*Figularia figularis* is widely distributed in the Atlanto-Mediterranean area since the middle Miocene (Moissette et al., 1993; Berning, 2006). This species has been commonly reported from shelf habitats, mostly from the deep shelf, often associated with deep coralligenous facies (Di Geronimo et al., 1990; Ballesteros, 2006), and at the shelf break in both the Mediterranean (110–145 m; see Harmelin and d’Hondt, 1992) and the eastern Atlantic as far north as the British Isles (Hayward and Ryland, 1998).

Materials.—Rosso collection PMC. I. H. B.71.b, Apollo Bank sample: two specimens, Recent; Rosso-Collection PMC I. Pl. B.71.c, Scoppo: sample 24 top: two specimens, early Calabrian, MNN19b-19c biozones.

Remarks.—Two fossil fragments were found, each consisting of a few zooids (Fig. 7). Zooidal morphological characters allow a reliable identification, even in the absence of ovicells and avicularia. Morphometrics fall within the ranges reported for this species. Inferred teratology in an autozooid resulted in a double-bifurcated frontal shield (Fig. 7.1, 7.2). This unusual feature also occurs in the type specimen of *F. tenuicosta* MacGillivray, 1895 from the middle Miocene of Victoria, Australia (Bock, 2020). Although *F. figularis* exhibits a certain range of morphological variability, some historical records, mostly beyond its confirmed geographical range, proved to be different species (e.g., Brown, 1952). The conspecificity of the colony found on a rock at

Armação de Pêra in Portugal (Souto et al., 2014) needs to be verified. This colony has an unusual triangular ooecial fenestra with narrow horizontal part and could represent a different species.

Figularia spectabilis new species Figures 8–11, Table 4

Holotype.—PMC. B22. 5.4.2015.a: bilaminar fragment including some autozooids and the only observed ovicell. Cala Sant’Antonino, sample Cala Sant’Antonino center, 2015, Gelasian.

Paratypes.—PMC. B22. 5.4.2015.b: additional 39 fragments from the same sample as the holotype, including several fan-shaped colony portions. One fragment from sample 17 (2000), Cala Sant’Antonino center.

Diagnosis.—Colony erect, bilaminar with fan-shaped fronds, the tapering proximal terminations possibly consisting of heteromorphs, likely rising from an encrusting phase. Zooidal frontal shield consisting of flat costae, each with a large, elongate drop-shaped pelma placed on its peripheral half; gymnocyst wider laterally and proximally, narrower distally, with faint striations. Vicarious avicularia elongate, spatulate, with extensive rostral palate and complete crossbar. Ovicell subimmersed, presumably cleithral. Ooecium formed by the distal kenozooid with frontally visible costate part, and consisting of two very large, wing-shaped costae merging in the midline producing a longitudinal suture, with two large fenestrae exposing wide areas of endooecium; the costae of the ooecium-producing kenozooid smaller, forming a distal, crescent-shaped crown, each costa with a small pelma.

Occurrence.—Exclusively known from early Pleistocene (Gelasian) deep-water sediments of Capo Milazzo (NE Sicily, Italy).

Description.—Available colony fragments bilaminar, fan-shaped (the largest ~2 mm long by 3 mm wide); fragments diverging distally at variable angles from a subcylindrical proximal

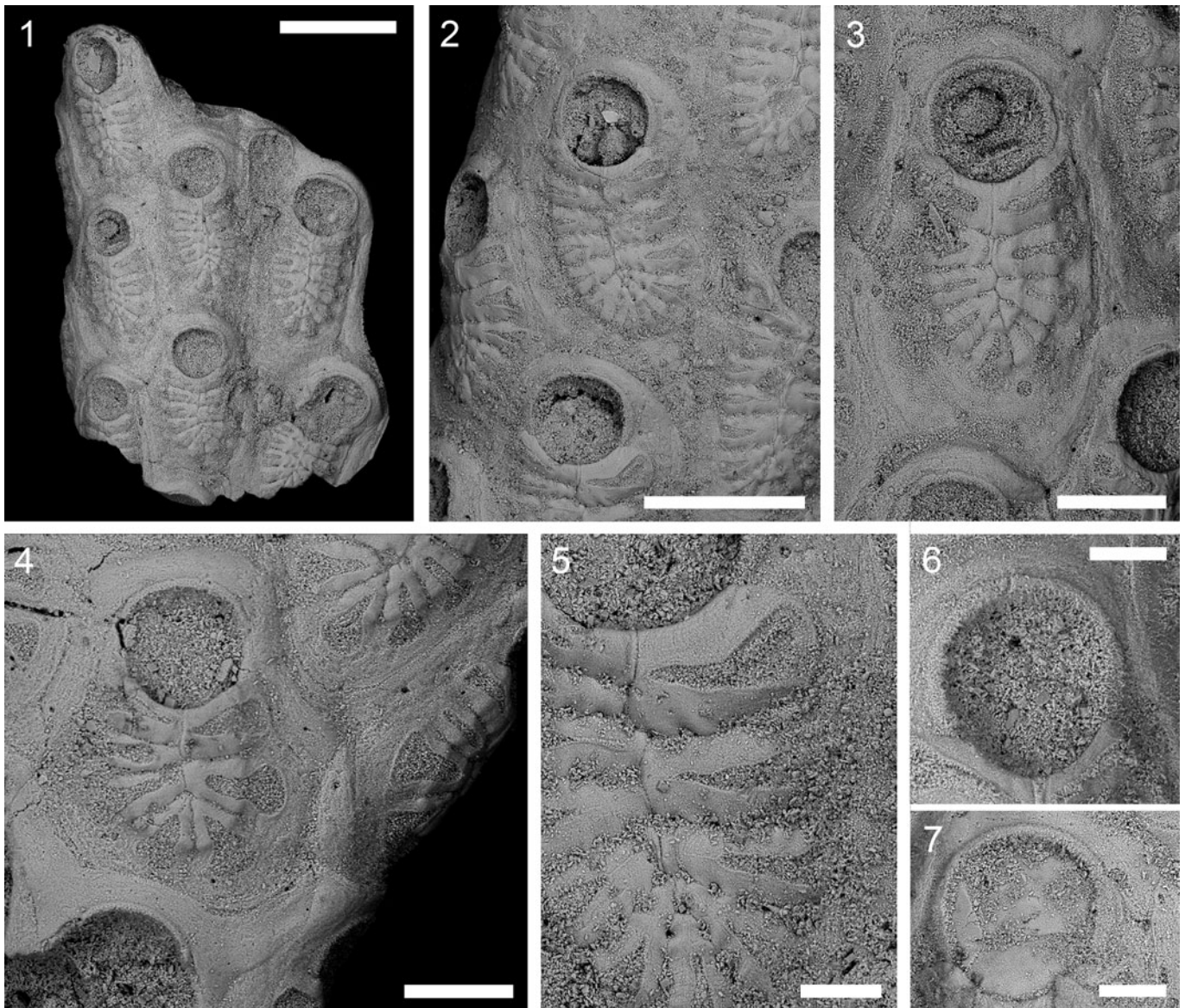


Figure 10. *Figularia spectabilis* n. sp., Capo Milazzo sample Cala Sant'Antonino center, 2015, Gelasian, PMC. B22. 5.4.2015.b, paratypes, autozooids. (1) Fragment of a bilaminar branch with zooids arranged in longitudinal rows and distal vicarious avicularium; (2) group of autozooids; (3) close-up of elongated autozooid with well-defined boundaries and growth lines in the gymnocyst (note the smooth texture of the costae, converging towards the midline, and the elongate pelmata); (4) wider autozooid with large wedge-shaped costae and very large drop-shaped pelmata; (5) close-up of some costae; (6) orifice; (7) orifice with closure plate or calcified operculum. Scale bars: (1, 2) 500 μm ; (3, 4) 200 μm ; (5–7) 100 μm .

portion, consisting of four zooids arranged in back-to-back pairs (Fig. 8.1, 8.2, 8.4–8.8). Other fragments of similar size include only the edges of presumably ribbon-like colonies (Figs. 8.3, 10.1). Putative proximal heteromorphs, possibly arising from an encrusting phase and forming the basal stalk, lacking calcified frontal shield. Zooidal boundaries marked by grooves. Zooids large, about twice as long as wide ($L/W = 1.72$), gently arched distally, wedged proximally. Gymnocyst more extensively exposed proximally and laterally (Figs. 8.2, 8.3, 8.5, 10.1–10.4), locally obliterated by recrystallization (Fig. 10.5). Costate shield extensive ($\sim 75\%$ of the frontal surface), gently convex, formed by 7–14 flat and smooth costae (maximum basal width 72–111 μm), varying from short and subtriangular proximally to long and parallel sided distally; the suboral pair often the largest (Fig. 10.1–10.5). Costae defined by grooves, connected

by an uncertain number of intercostal bridges, presumably 3–4 (Fig. 10.5), with small oval to subcircular intercostal pores in between. A longitudinal suture marking the costal fusion along zooidal midline (Fig. 11.1). Each costa bearing a single, elongate, drop-shaped pelma with the rounded base placed in correspondence with the base of the costa, while the acute vertex extends up to half to two thirds of costal length. Orifice oval to round, slightly longer than wide, concave proximally, gently arched distally, outlined by a rim of calcification (Fig. 10). Oral spines absent. Avicularia vicarious, infrequent, elongate and slightly asymmetrical, varying in size; rostrum long, spatulate, directed distally and slightly inclined, facing frontally (Figs. 9.1, 11); post-mandibular area short, palate wide, crossbar complete (Fig. 11.3). Ovicell subimmersed, presumably cleithral. A single observed oecium formed by

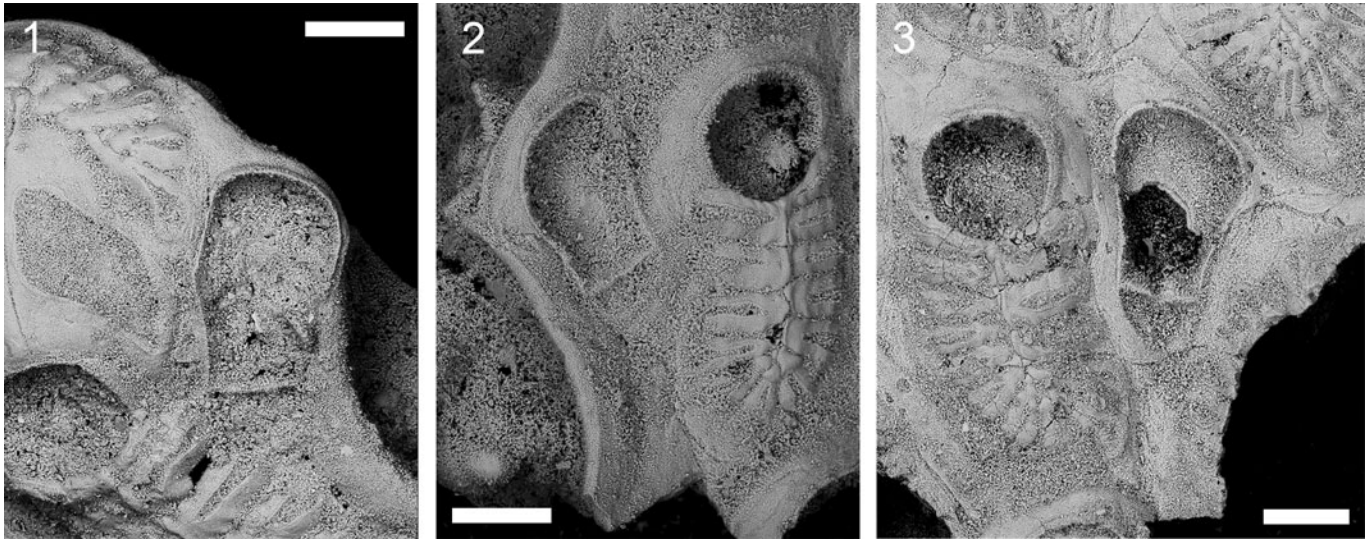


Figure 11. *Figularia spectabilis* n. sp., Capo Milazzo, sample Cala Sant'Antonino center, 2015, Gelasian, vicarious avicularia. (1) Holotype PMC. B22. 5.4.2015.a; (2, 3) paratypes PMC. B22. 5.4.2015.b, same details as the holotype (note the spatulate rostrum and the thin crossbar); (3) view showing the wide rostral palate. Scale bars: 200 μ m.

the distal kenozooid with frontally visible costate shield of 10 costae, longer than wide, wider and slightly more prominent than the ovicellate zooid (Fig. 9). Very large oecium consisting of two flat, wing-shaped costae converging along the midline, the fusion marked by a longitudinal suture, distally with two small tubercle-like prominences. Large rhomboidal fenestra exposing finely granular endooecium. Orifice of the ovicellate zooid slightly larger than those of autozooids, rounded rectangular. Closure plates or calcified opercula sometimes occluding orifices (Fig. 10.7).

Etymology.—From the Latin *spectabilis*, meaning remarkable, exceptional, alluding to the distinctive architecture of the colony and oecium.

Remarks.—The morphology of the colony, zooids and oecium distinguish *Figularia spectabilis* n. sp. from congeners. The flabellate to short, ribbon-like morphology of the colony, with putative heteromorphs placed basally, may suggest the occurrence of basal rhizoids for fixation to the substratum. Alternatively, the connection to an encrusting portion may develop through “sites of articulation” as in *Bryobaculum carinatum* Rosso, 2002a, occurring in the same sediment.

Discussion

Five species of cribrilininid bryozoans, three of which are new to science, namely *Cribrilaria profunda* n. sp., *Glabilaria* cf. *G. pedunculata*, *G. transversocarinata* n. sp., *Figularia figularis*, and *F. spectabilis* n. sp., were found in Pleistocene deep-water sediments from north-eastern Sicily.

Figularia figularis was already recorded from the area by Seguenza (1880) and Neviani (1900), while *C. profunda* n. sp. was possibly recorded as *Lepralia planicosta* (see Remarks above), while the remaining three species, including *G. cf. G. pedunculata*, represent new records.

Cribrilininids are generally rare in Plio-Pleistocene associations from deep-water environments in Sicily and Calabria, as well as in their enclaves in shallow waters, such as past submarine cave habitats, from which a single species, *Cribrilaria venusta* (Canu and Bassler, 1925), and undetermined cribrilininid taxa were previously reported (Di Geronimo et al., 1997, 2005; Rosso, 2005; Rosso et al., 2015). Thus, this study raises the total number of cribrilininids from these paleoenvironments to six species in three genera. Shallower shelf paleoenvironments from the same regions, mostly Pleistocene but as old as Miocene, yielded seven species of cribrilininids: *Cribrilaria radiata* (Moll, 1803), *C. hincksi* (Friedl, 1917), *C. innominata* (Couch, 1844), *Puelina gattyae* (Landsborough, 1852), *Distansescharella seguenzai* Cipolla, 1921, *Gephyrotes moissettei* Di Martino and Rosso, 2015, and “*Cribrilina punctata*” (Hassall, 1841), the latter species probably being a *Collarina* (Barrier et al., 1987b; Harmelin et al., 1989; Di Geronimo et al., 1994; Rosso and Sanfilippo, 2005; Di Martino and Rosso, 2015). As for other taxa authored by Seguenza (1880), the loss of the type material makes it difficult to confirm the status of some cribrilininid species, such as *Lepralia thiara*, *L. mitrata*, and *L. mitrata* v. *radians*, in addition to the previously mentioned *L. elegantissima* and *L. planicosta*. Analogously, the real identity of some other species (briefly described and lacking illustrations) in Waters (1878), De Stefani (1884), Hincks (1884), and Neviani (1900, and references therein) is doubtful.

Focusing only on deep-water assemblages, cribrilininids are present with three species in both the Gelasian associations from Capo Milazzo and the Calabrian (MNN19b-19c biozones) of Scoppo. These figures are comparable to those found in present-day deep-water associations from the Mediterranean and Atlantic (Bahama Bank), in which cribrilininids usually occur with 2–3 species (Rosso et al., 2018). However, the Gelasian of Capo Milazzo includes at least 46 cheilostome species, and the cribrilininid relative percentage is ~6%, which is lower than the 10–18% found in present-day assemblages (Rosso and Sciuto, 2019). No comparison can be made for

the Calabrian of Scoppo whose bryozoans are still under investigation.

Discovery of a new species of *Figularia*, *F. spectabilis* n. sp., led to the emendation of the genus diagnosis and the re-examination of the 32 species and one variety currently assigned to the genus, based on drawings and photographic material available from the literature. This preliminary survey allows us to confidently reassign two species based on published scanning electron micrographs of the type material. The newly proposed combinations are *Vitrimurella capitifera* (Canu and Bassler, 1929) n. comb. and *Hayamiellina quaylei* (Powell, 1967a) n. comb., as also suggested by Kukliński et al. (2015). Thirteen species remain doubtful and their assignment to more suitable genera requires examination of the type material (Table 4).

At present, 18 species, including *Figularia spectabilis* n. sp., match the diagnosis of the genus. This figure will likely change further after a more detailed revision of some fossil species and species left in open nomenclature (see Berning, 2006 for *F. haueri* and *F. figularis*; Di Martino et al., 2017 and Cook et al., 2018 for two different *Figularia* spp.) as well as cryptic species/species complexes (e.g., *F. clithridiata* and *F. fissa*). Based on our literature review, the diversity of *Figularia* is reduced by about one-half, from 33 (including *F. spectabilis* n. sp.) to 18 species, with a revision in the stratigraphic range, but only little variation in the geographic distribution of the genus. The genus possibly appeared in the Cenozoic of Europe and Australia, and commonly occurred in sediments in the European-Mediterranean area during the Miocene. Of the 12 species of *Figularia* living today, 10 species are found in the Pacific and Australasian region. Only two species, *F. figularis* and *F. dimorpha*, fall outside this area, being recorded in the Atlanto-Mediterranean and southwestern Atlantic regions, respectively.

A twofold future investigation is sought. This includes an examination of the type material of all the species in the genus to confirm their status, prioritizing those that appear to remain problematic (see Table 4; issue partially addressed by López Gappa et al., in press), and an accurate re-examination of all species records to refine both the temporal and spatial distribution of the genus and reconstruct its diversification history, as well as disentangle species complexes.

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