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

Antonietta Rosso, 1,2 Emanuela Di Martino, 3* and Andrew N. Ostrovsky 4,5

1 Dipartimento di Scienze Biologiche, Geologiche e Ambientali, University of Catania, Corso Italia 57, 95129, Catania, Italy <croso@unict.it>
2 CoNISMa (Consorzio Interuniversitario per le Scienze del Mare), Piazzale Flaminio 9, 00196, Roma, Italy
3 Natural History Museum, University of Oslo, Blindern, P.O. Box 1172, Oslo 0318, Norway <e.d.martino@nhm.uio.no>
4 Department of Invertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaja nab. 7/9, 199034, Saint Petersburg, Russia <a.ostrovsky@spbu.ru>
5 Department of Paleontology, Faculty of Earth Sciences, Geography and Astronomy, University of Vienna, Althanstr. 14, 1090, Vienna, Austria <andrei.ostrovsky@univie.ac.at>

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 figuraris 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 mikela n. comb.. The diagnosis of the genus Figularia was amended to include a erect growth morphology in addition to the encrusting form, and the occurrence of ooecia formed by the distal kenozooid. Following a literature revision of all species currently assigned to Figularia, the new combinations Vitrimurella capitifera (Canu and Basslier, 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 (Borning, 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...
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 heteropitic 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), interfingered with calcarenites and carbonate sands containing scattered isidid octocorals, and locally truncated by erosional surfaces and overlain 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 erosionally capped by Upper Pleistocene fluvo-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 foraminifera 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; 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 Tyrrenian Sea (Fig. 1).

At Capo Milazzo, cribrilinid 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, cribrilinids were found in a test sample associated with a *Scillaelepas*-rich layer, and in the sample “Scoppo 24 top” coming from uncremented marly sediment.

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).
At the Apollo Bank, coarse sediments associated with the kelp *Laminaria rodriguezii* Bornet, 1888 were collected at about 60 m depth. Living and dead bryozoans associated 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 Paleoecological 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 backsaturated-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 ooecia produced by the distal autozooid or kenozooid, interzooidal avicularia of variable size and shape, usually five (4–8) oral spines, and relatively large uncalcified windows of pore-chambers; *Glabrilaria* has non-pseudoporous ooecia that are exclusively produced by the distal kenozooid, 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 interzooidal 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 Cribrilinoidea Hincks, 1879
- Family Cribrilinidae Hincks, 1879
- Genus *Cribrilaria* Canu and Bassler, 1929

*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 oviellate zooids and interzooidal 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 oviellate zooids. Interzooidal avicularia with elongate, triangular or parallel-sided, raised rostrum, crossbar lacking. Ovicell hyperstomial, presumably cleithral. Ooecium formed by distal autozooid, 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). Interzooidal 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
bridges leaving 4–11, regularly spaced, subrectangular lacunae, 8–16 μm 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. Ooecium 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 autozooid; (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 interzooidal avicularium; (6) ovicellate zooid, avicularium, and ooecium showing longitudinal carina. Scale bars: (1) 500 μm; (2, 6) 200 μm; (3–5) 100 μm.
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, ascribing 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 Glaibriliria Bishop and Househam, 1987

Type species.—Puellina pedunculata Gautier, 1956, by original designation.
Glabrilaria cf. G. pedunculata Gautier, 1956, Capo Milazzo, Gelasion, Rosso Collection collective code PMC I. Pl. B.81a. (1–5) Cala Sant’Antonio 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 ooecia; (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 ooecium 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’Antonio 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 μm; (3–5) 100 μm.

Glabrilaria cf. G. pedunculata (Gautier, 1956) | cf. 1966 Colletosia pedunculata; Prenant and Bobin, p. 596, fig. 207 III.
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Glabrilaria transversocarinata n. sp. | cf. 1970 Cribilaria pedunculata; Harmelin, p. 93, fig. lg, h, pl. 2, fig. 6.

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

| Species | Locality | Glabrilaria cf. G. pedunculata (Gautier, 1956) | Glabrilaria transversocarinata n. sp. |
|---------|----------|---------------------------------|----------------------------------|
| Number of costae | Capo Milazzo | 13–17; 15 ± 1 (N = 11) | 14–16; 15 ± 1 (N = 10) |
| Zood length | | 252–425; 337 ± 67 (N = 10) | 407–457; 436 ± 23 (N = 5) |
| Zood width | | 211–323; 263 ± 37 (N = 10) | 271–337; 302 ± 27 (N = 5) |
| L/W | 1.28 | 1.44 |
| Proximal gymnocyast length | narrow and sloping | narrow and sloping, proximal tip |
| Costate shield length | 166–257; 201 ± 28 (N = 10) | 227–268; 250 ± 19 (N = 5) |
| Costate shield width | 192–277; 238 ± 31 (N = 10) | 244–264; 254 ± 9 (N = 5) |
| Orifice length | 46–56; 50 ± 3 (N = 7) | 45–70; 59 ± 9 (N = 4) |
| Orifice width | 69–79; 74 ± 4 (N = 7) | 63–99; 83 ± 12 (N = 4) |
| Number of articulated oral spines | 7 (4 on ovicellate ones) | 6 (4 on ovicellate ones) |
| Ooeicum length | 134–148; 139 ± 8 (N = 3) | 139–165; 151 ± 11 (N = 4) |
| Ooeicum width | 159–185; 170 ± 13 (N = 3) | 153–240; 194 ± 19 (N = 4) |
| Ooeicum length with kenozooid | 197 | 186–213; 200 ± 19 (N = 2) |
| Ooeicum width with kenozooid | 195 | 199–265; 232 ± 47 (N = 2) |
| Oivicellate orifice length | 44–47; 46 ± 2 (N = 2) | 60 |
| Oovicellate orifice width | 80–86; 83 ± 4 (N = 2) | 74 |
| Kenozooid length | 108–173; 119 ± 28 (N = 4) | 92 |
| Kenozooid width | 94–144; 103 ± 24 (N = 4) | 78 |
Glabrilaria pedunculata; Bishop and Househam, figs. 95–97, tab. 13.
cf. 1988 Puelлина (Glabrilaria) pedunculata; Harmelin, p. 31, figs. 9–11.
cf. 2013a Puelлина (Glabrilaria) pedunculata; Rosso et al., tab. 17.1.
cf. 2015 Puelлина (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; Lesbos: 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’Onglia 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). Interzoooidal communication through basal pore-chambers, more than 10 visible only in some marginal zooids, with longitudinally elongate windows ~10 × 20 μm (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, ~7–8 μm 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. Ooeicum 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, ooeia, 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 ooeicum 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 Atlantic-Mediterranean region and the Gibraltar Strait area, respectively. However, the former species shows an ooeicum 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 ooeicum. 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 ooeicum 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.
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. Gymnocyst 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. Ooecium formed by distal kenozooid, surface smooth, with transverse rib. Avicularia not observed. Kenozooids rare.

**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 ooecium 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.
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 × 18 μm (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 subimmerses. Ooecium formed by the distal kenozooid, with frontally visible costa (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 margin is distinctive of this species. Ooecia with a transverse ridge are known in a few species only. One is the extant *Glabrilaria hirsuta* Rosso in 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 *Glabrilaria cristata* (Harmelin, 1978) from the Hyères and Meteor banks south of the Azores, the ooeccal 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 *Glabrilaria 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 subimmerses, 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).
| Species                          | Distr | Costate shield | N of costae | Intercostal pores | Pelmata | Occlusion | Orig | Fenestrae | Suture | Dim Or | Vicarious avicularia | Additional notes                                                                 |
|---------------------------------|-------|----------------|-------------|-------------------|---------|-----------|-------|-----------|---------|--------|---------------------|----------------------------------------------------------------------------------|
| *Figularia arnouldi* Buigé, 1956 | P     | Extensive      | 12          | numerous          | 1       | *§*       | Transv. triangular | *carina | Spathulate with bar | Duckfeet-shaped *oecum also formed by vicarious avicularia.*                      |
| *F. carinata* (Waters, 1887)    | R     | 2/3 ZL; <1/2 ZW | 10–12       | fissure           | 1 (slit-like) | *          | Transv. drop-shaped to elliptical | *       | Spathulate with bar | Specimens in Souto et al. (2014) possibly different species. Likely a species complex (see Harmer, 1926, figs 20–23 and Ryland and Hayward, 1992). |
| *F. clithridiata* (Waters, 1887) | R     | 1/2 ZL; 1/2 ZW  | 7–10        | ?                 | 1 (oval) | *§*       | Transv. drop-shaped | *       | Duckfeet-shaped *oecum with peripheral semicircle of pelma seemingly belonging to the distal kenozooid.* |
| *F. dimorpha* Figuerola et al., 2018 | R     | 2/3 ZL; 1/2 ZW  | 16          | numerous          | 1       | *          | Transv. oval to pear-shaped | *       | Spathulate with bar | *oecum with peripheral semicircle of pelma seemingly belonging to the distal kenozooid.* |
| *F. figularis* (Johnston, 1847)  | M–R   | 2/3 ZL; 4/5 ZW  | 9–13        | ~5                | 1 (circular) | *§*       | Transv. drop-shaped to irregularly oval | *       | Spathulate with bar | F. figularis by some morphometrics (see Berning, 2006) Plastic colony morphology including an encrusting phase (var. *adnata*) and bilamellar erect parts. |
| *F. fissata* Hincks, 1880        | R     | 1/3 ZL; 1/2 ZW  | 8–10        | 1 (triangular)    | 1 (circular) | *          | Transv. crescentic | *       | Spoon-like with bar | Colony erect, flabelliform, very large *oecum.* |
| *F. fissurata* Canu and Bassler, 1929 | R     | 1/2 ZL; 2/3 ZW  | 3–12        | fissure           | 1 (circular) | *          | Transv. crescentic | *       | Spoon-like with bar | Colony erect, flabelliform, very large *oecum.* |
| *F. haueri* Reuss, 1848          | M     | Extensive      | 14–18       | numerous          | Not mentioned or visible in fig. | *          | Not mentioned or visible in fig. | *       | Spathulate | Plastic colony morphology including an encrusting phase (var. *adnata*) and bilamellar erect parts. |
| *F. hilli* (Osburn, 1950)        | R     | 3/4 ZL; 4/5 ZW  | 5–7         | 1–2 (slit-like)   | 1 (drop-shaped) | *          | Transv. oval | *       | Absent | Ooecium including a pair of proximo-lateral costae. |
| *F. japonica* Silén, 1941        | R     | 3/4 ZL; 4/5 ZW  | 11–13       | 1–3 (circular)    | 1 (drop-shaped) | *          | 2 pairs, transv. triangular | *       | Duckfeet-shaped | 7–10 costae in Yang et al., 2018. |
| *F. mernae* Uttley and Bullivant, 1972 | R     | 2/3 ZL; 1/2 ZW  | 12–18       | 1 (slit-like)     | 1 (circular) | *          | Longit. drop-shaped | *       | Lanceolate | Colony erect, flabelliform, very large *oecum.* |
| *F. pelmatifera* Gordon, 1984    | R     | 3/4 ZL; 3/4 ZW  | 24–30       | fissure + 1–2 (elliptical) | 1 (elliptical) | *          | Diagonal elliptical to transv. drop-shaped | *       | Spathulate | Colony erect, flabelliform, very large *oecum.* |
| *F. philomela* Busk, 1884        | R     | Extensive      | 14–16       | numerous          | Not mentioned or visible in figs. | *          | Diagonal elliptical to transv. drop-shaped | *       | Spathulate | Colony erect, flabelliform, very large *oecum.* |
| *F. rhodanica* Li, 1990          | M     | Extensive      | 14–20       | 2                 | Not mentioned or visible in fig. | *          | Not mentioned or visible in fig. | *       | Spathulate | Colony erect, flabelliform, very large *oecum.* |
| *F. speciosa* Hincks, 1881       | R     | 4/5 ZL; 3/4 ZW  | 12–18       | 3 (slit-like)     | 1 (slit-like) | *          | Longit. slit-like | *       | Absent | Colony erect, flabelliform, very large *oecum.* |
| *F. spectabilis* n. sp.          | PI    | 3/4 ZL; 3/4 ZW  | 8–13        | 3–4? (subcircular) | 1 (drop-shaped) | §          | Large quadrangular | *       | Slightly | Colony erect, flabelliform, very large *oecum.* |
| *F. tenuicosta* MacGillivray, 1895 | M, R  | 2/3 ZL; >1/2 ZW | 19–20       | 1 (slit-like)     | 1 (slit-like) | *          | Transv. slit-like | *       | Not observed | Colony erect, flabelliform, very large *oecum.* |
| *F. triangula* Powell, 1967b     | R     | 2/3 ZL; <1/3 ZW | 12–14       | 1 (slit-like)     | Absent   | ?          | Transv. slit-like | *       | Not observed | Colony erect, flabelliform, very large *oecum.* |
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 columns Orig: * ooecium formed by the distal autozooid; § ooecium 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), Bugé (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                      | Vicarious avicularia | New combination          | Additional notes                                      |
|--------------------------|-------------|----------------|-------------|-------------------|---------|------------------------------|---------------------|--------------------------|-------------------------------------------------------|
| *Figularia ampla*        | R           | 2/3 ZL; 1/3 ZW | 10          | fissure           | none    | * Absent                     | *carina             | Not mentioned           | Frontal shield densely pseudoporous                   |
| *F. capitifera*          | R           | Vestigial, suboral | 2+2         | 1 (elliptical)    | *       | Single, central              | Spathulate          | *                       | Frontal shield and ooecium with massive pseudopores   |
| *F. contraria*           | R           | 2/3 ZL; 1/2 ZW | 8–11        | 2                  | 1 (circular) | Two pairs of small membranous areas | *carina             | *                       | Not observed                                          |
| *F. echinoides*          | O           | Extensive      | 22–24       | numerous          | 2–3 spine-like | Ovicells not observed/Absent |                      |                         | Ovicell submersed. Ooecium with a pair of small oval membranous areas centrally. Two more membranous areas are situated on the ectooecium laterally. |
| *F. juconda*             | R           | 2/3 ZL; 3/5 ZW | 8–9         | 1 (triangular)    | 1 (circular) | § Pseudopores and/or pelmatidia | *carina             | *                       | Ooecium with pseudopores and/or pelmatidia            |
| *F. kenley*              | M           | 1/2 ZL; 4/5 ZW | 14–16       | 1 (slit-like)     | Visible/present only on suboral costae? | ? 2 large | *carina             | Erect bilaminar; pelma only on suboral costae |
| *F. peltata*             | M           | Extensive      | 15–18       | numerous          | Absent/not visible | * Absent |                      | Flat ooecium                                        |
| *F. planicostulata*      | M           | Extensive      | 17          | several, large    | Absent/not visible | ? Absent/not visible | Spathulate          | Smooth ooecium.                                      |
| *F. pulcherrima*         | 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. cl. *F. tahitiensis.* |
| *F. quaylei*             | R           | Extensive      | 10–12       | fissure           | 2 (circular) | * 4–7 | Not observed | Hayumiellina quaylei | Costate ooecium                                      |
| *F. rugosa*              | M           |                |             | Absent/not visible | ?       | * Lancerate no bar | * Not mentioned | Pseudopores                                           |
| *F. ryukienensis*        | PI          | Extensive      | 8–10        | 1 (slit-like)     | Absent/not visible | * Pseudopores | Not mentioned | Pseudoporous ooecium with ill-defined keel           |
| *F. tahitiensis*         | 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. cl. *F. pulcherrima.* |
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 ooecium (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 ooecium in Figularia is generally described as bivalved/bifenestrate (Ostrovsky, 2013). In F. figularis, the prominent bilobate ooecium 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 ooecia 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 ooecia produced by the distal autozooid and kenozooid is known in other cribrilinids, such as Cribrilina 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.
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 kenozoid producing the ooecium 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 ooecia formed by the distal kenozoid 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 ooecium) 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 ooecia (see also Ostrovsky, 2002). Winston et al. (2014) remarked that the occurrence of costate ooecia in F. pulcherrima possibly suggests a better allocation of this species in a distinct genus. Inclusion of costae in the
construction of the ooecium 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 ooecial halves (see Table 3).

Yang et al. (2018), while including pseudoporous ooecia in the diagnosis of Figularia, also suggested the examination of species with multiple ectooecial 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 pelmata 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 pelmata (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 x 0.67 mm) and the absence of spines are rare and remarkable among cribrilinids, which usually have small, tatifom 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 Calliporidae (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 ooecia, 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 ooecia formed by the distal kenozooid without a visible frontal part. Figularia duvergieri Bassler, 1936 has an unusual denticulate proximal orifice margin, and lacks costal pelmata and fenestrae in the ooecium. 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                  | Figularia figularis (Johnston, 1847) | Figularia spectabilis n. sp. Capo Milazzo |
|--------------------------|-------------------------------------|------------------------------------------|
| Locality                 | Scoppo                               |                                          |
| Number of costae         | 10–20; 14 ± 5 (N = 3)*               | 7–14; 10 ± 2 (N = 18)                    |
| Zoid length              | 858                                  | 588–1057; 759 ± 135 (N = 16)             |
| Zoid 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, MN19b-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 ooezial fenestra with narrow horizontal part and could represent a different species.

Figularia spectabilis new species

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 ooeicum-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
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 (~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 ooeicum formed by

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 pelmas); (4) wider autozooid with large wedge-shaped costae and very large drop-shaped pelma; (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.
Remarks above), while the remaining three species, including *Bryobaculum carinatum* Rosso, 2002a, occurring in the same portion may develop through “sites of articulation” as in *Bryobaculum carinatum* Rosso, 2002a, occurring in the same sediment.

**Discussion**

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

*Figularia figuraris* 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.

Cribrilinids 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 cribrilinid taxa were previously reported (Di Geronimo et al., 1997, 2005; Rosso, 2005; Rosso et al., 2015). Thus, this study raises the total number of cribrilinids 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 cribrilinids: *Cribrilaria radiata* (Moll, 1803), *C. hincksi* (Friedl, 1917), *C. innominata* (Couch, 1844), *Puellina gautyae* (Landsborough, 1832), *Distansescharella seguenza* Cipolla, 1921, *Gephyrotes moissetei* 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 cribrilinid 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, cribrilinids 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 cribrilinids usually occur with 2–3 species (Rosso et al., 2018). However, the Gelasian of Capo Milazzo includes at least 46 cheilostome species, and the cribrilinid 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. figuralis*; 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. chithridiata* 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. figuralis* and *F. dimorpha*, fall outside this area, being recorded in the Atlantic-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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