

Systematic revision and scanning electron microscopic study of some critical cheilostome bryozoan species of Arthur Waters from the Pleistocene of Brucoli (Siracusa, Sicily)

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ABSTRACT - In 1878, Arthur Waters described a bryozoan fauna from a Pleistocene (Calabrian) outcrop, at that time considered as Pliocene, located near the town of Brucoli in southeast Sicily (Italy). Waters' work on bryozoans was based on the material collected four years earlier by Theodor Fuchs, curator of the Imperial-Royal Mineralogical Court-Cabinet in Vienna, now the Natural History Museum, and currently housed in the palaeontological collection of the same museum. Since its first description, Waters' material has never been revised and his new species never recorded again. Here, we employ scanning electron microscopy (SEM) to study Waters' new species that are still valid today, and some other critical taxa present in the same collection. Based on this revision, *Eschara lunaris* Waters, 1878 is synonymized with *Microporella verrucosa* (Peach, 1868), and *Lepralia auriculata* var. *leontiniensis* Waters, 1878 is confirmed to be a valid species, i.e., *Stephanotheca leontiniensis* (Waters, 1878) comb. nov. We also highlight that *Biflustra rynchota* Waters, 1878 fits better in the genus *Amphiblestrum*, showing a close affinity with *A. lyrulatum* (Calvet, 1907). Additional specimens in Waters' collection identified as *Onychocella angulosa* (Reuss, 1847) were compared with Reuss' Miocene syntypes to confirm their identification and the distinction of this species from the Recent *Onychocella marioni* (Jullien, 1882). Lastly, a specimen identified by Waters as Busk's *Microporella morrisiana* (Busk, 1859) from the Pliocene Coralline Crag is now regarded as *M. appendiculata* Heller, 1867, a common Pliocene-to-Recent Mediterranean species, after comparison with a topotypic colony of the former species.

INTRODUCTION

In 1878 Arthur Waters, a British naturalist and bryozoologist based in Manchester, published a taxonomic work on fossil bryozoans from Brucoli, a town near Siracusa in southeast Sicily (Italy), using the material he borrowed from Theodor Fuchs, the curator at the Imperial-Royal Mineralogical Court-Cabinet in Vienna. Waters (1878) described a total of 43 species, including two species and two subspecies new to science. After completing his study, he returned the specimens to the original collector and, since then, the material has been housed in the palaeontological collection of the Natural History Museum Vienna, Austria (NHMW) (see Tab. 1 for a comprehensive list of the material available). Founded in 1876, the NHMW integrated the former Imperial-Royal Mineralogical Court-Cabinet, splitting it between two constituent departments, i.e., Mineralogy & Petrography, and Geology & Palaeontology, appointing T. Fuchs as the head of the latter department (Hochstetter, 1884).

The historical sampling locality has never been visited since 1874, and the new taxa described by Waters never recorded again, not even from coeval deposits in the vicinity of the original sampling site. Some of the new taxa of Waters (1878) were mentioned in past and recent publications (e.g., Harmer, 1957; Gautier, 1962; Reverter-Gil et al., 2015; Di Martino & Rosso, 2021) as presumed synonyms of well-known Mediterranean Pleistocene-Recent species, but these synonymies were never formalized, pending a proper description and illustration of the type specimens. A recent SYNTHESYS+ funded visit

to the palaeontological collection of the NHMW by one of us (EDM) revealed the presence of Waters' specimens, and allowed the taxonomic revision of some critical taxa.

The aim of this work is threefold: 1) revise and illustrate, for the first time since the advent of scanning electron microscopy (SEM) as the standard tool for bryozoan taxonomy, the two new species and a new subspecies introduced by Waters (1878), in order to ascertain their synonymy and clarify their nomenclatural status (i.e., *Biflustra rynchota* Waters, 1878 as *Amphiblestrum* cf. *lyrulatum* [Calvet, 1907]; *Eschara lunaris* Waters, 1878 as *Microporella verrucosa* [Peach, 1868]), or confirm their validity (i.e., *Stephanotheca leontiniensis* [Waters, 1878] comb. nov.); 2) illustrate the syntypes and other fossil specimens of *Onychocella angulosa* (Reuss, 1847), including some from Brucoli studied by Waters (1878) and others newly collected for this study, to clarify the differences with *O. marioni* (Jullien, 1882) and the currently doubtful status of the latter species; 3) compare specimens from Brucoli attributed to *Microporella morrisiana* (Busk, 1859) with the nominal species from the Coralline Crag Formation to ascertain their conspecificity.

MATERIAL AND METHODS

The bulk of material studied here is part of the historical collections of the Department of Geology and Palaeontology of the Natural History Museum Vienna, Austria (NHMW). The material was collected in 1874 by Theodor Fuchs, at that time curator of the Imperial-

	Inventory Number	Original label	Accepted as
Cheilostomatida	2021/0166/...		
	0001	<i>Salicornaria farciminoidea</i> (Ellis & Solander)	<i>Cellaria fistulosa</i> (Linnaeus)
	0002	<i>Membranipora angulosa</i> (Reuss)	<i>Onychocella angulosa</i> (Reuss) *
	0003	<i>Membranipora lacroixii</i> (Audouin)	<i>Conopeum lacroixii</i> (Audouin)
	0004	<i>Biflustra rhynchota</i> Waters	<i>Amphiblestrum</i> cf. <i>lyrulatum</i> (Calvet) *
	0005	<i>Membranipora bidens</i> (von Hagenow)	<i>Steraechemella buski</i> Lagaaij
	0006	<i>Membranipora andegavensis papyracea</i> (Reuss)	<i>Micropora coriacea</i> (Esper)
	0007	<i>Eschara lunaris</i> Waters	<i>Microporella verrucosa</i> (Peach) *
	0008	<i>Lepralia ciliata</i> (Pallas)	<i>Microporella ciliata</i> (Pallas)
	0009	<i>Lepralia innominata</i> (Couch)	<i>Cribrilaria innominata</i> (Couch)
	0010a	<i>Eschara foliacea fascialis</i> Pallas	<i>Pentapora fascialis</i> (Pallas)
	0010b	<i>Cellepora tubigera</i> Busk	<i>Turbicellepora tubigera</i> (Busk)
	0011	<i>Eschara foliacea fascialis</i> Pallas	<i>Pentapora fascialis</i> (Pallas)
	0012	<i>Lepralia cupulata</i> Manzoni	<i>Hagiosynodos cupulata</i> (Manzoni)
	0013	<i>Lepralia auriculata leontiniensis</i> Waters	<i>Stephanotheca leontiniensis</i> (Waters) *
	0014	<i>Lepralia ansata porosa</i> Reuss	<i>Schizoporella dunkeri</i> (Reuss)
	0015	<i>Hippothoa catenularia</i> Fleming	<i>Pyripora catenularia</i> (Fleming)
	0016	<i>Lepralia vulgaris</i> (Moll)	<i>Escharina vulgaris</i> (Moll)
	0017	<i>Eschara pertusa</i> Milne Edwards	<i>Pentapora pertusa</i> (Milne Edwards)
	0018	<i>Lepralia ansata porosa</i> Reuss	<i>Schizoporella dunkeri</i> (Reuss)
	0019	<i>Myrionozoon truncatum</i> (Pallas)	<i>Myriapora truncata</i> (Pallas)
	0020	<i>Lepralia auriculata</i> Hassall	<i>Schizomavella</i> (S.) <i>auriculata</i> (Hassall)
	0021	<i>Cellepora ramulosa</i> Linnaeus	<i>Omalosecosa ramulosa</i> (Linnaeus)
	0023	<i>Cellepora coronopus</i> Wood	<i>Turbicellepora coronopus</i> (Wood)
	0024	<i>Cellepora coronopus</i> Wood	<i>Turbicellepora coronopus</i> (Wood)
	0025	<i>Lepralia coccinea</i> (Abildgaard)	<i>Escharoides coccinea</i> (Abildgaard)
	0026a	<i>Cellepora tubigera</i> Busk	<i>Turbicellepora tubigera</i> (Busk)
	0027	<i>Lepralia arrecta</i> (Reuss)	<i>Hippoporina arrecta</i> (Reuss)
	0028a	<i>Lepralia innominata</i> (Couch)	<i>Cribrilaria innominata</i> (Couch)
	0028b	<i>Lepralia arrecta</i> (Reuss)	<i>Hippoporina arrecta</i> (Reuss)
	0029	<i>Lepralia bowerbankiana</i> (Busk)	<i>Schizomavella</i> (S.) <i>auriculata</i> (Hassall)
	0030	<i>Eschara cervicornis</i> (Ellis & Solander)	<i>Smittina cervicornis</i> (Pallas)
	0031	<i>Lepralia pallasiana</i> (Moll)	<i>Cryptosula pallasiana</i> (Moll)
0032	<i>Lepralia morrisiana</i> (Busk)	<i>Microporella appendiculata</i> (Heller) *	
0044	<i>Lepralia resupinata</i> Manzoni	<i>Escharoides coccinea</i> (Johnston)	
0051	<i>Retepora cellulosa</i> Linnaeus	<i>Reteporella cellulosa</i> (Linnaeus)	
Cyclostomatida	0022	<i>Pustulopora rugosa</i> d'Orbigny	<i>Filisparsa rugosa</i> (d'Orbigny)
	0026b	<i>Pustulopora proboscidea</i> Milne Edwards	<i>Mecynoezia proboscidea</i> (Milne Edwards)
	0034a	<i>Discoporella radiata</i> (Audouin)	<i>Patinella radiata</i> (Audouin)
	0034b	<i>Diastopora flabellum</i> Reuss	<i>Mesenteripora flabellum</i> (Reuss)
	0037	<i>Discoporella mediterranea</i> Blainville	<i>Patinella mediterranea</i> (de Blainville)
	0038	<i>Discoporella radiata</i> (Audouin)	<i>Patinella radiata</i> (Audouin)
	0039	<i>Fron dipora reticulata verrucosa</i> (Lamouroux)	<i>Fron dipora verrucosa</i> (Lamouroux)
	0040	<i>Alecto major</i> Landsborough in Johnston	<i>Annectocyma major</i> (Johnston)
	0041	<i>Diastopora flabellum</i> Reuss	<i>Mesenteripora flabellum</i> (Reuss)
	0042	<i>Mesenteripora</i> sp.	<i>Mesenteripora</i> sp.
	0043	<i>Diastopora cupula</i> (d'Orbigny)	<i>Discosparsa cupula</i> d'Orbigny
0052	<i>Hornera frondiculata</i> (Lamarck)	<i>Hornera frondiculata</i> (Lamarck)	

Tab. 1 - List of bryozoan species collected in 1874 at Brucoli (Sicily) by T. Fuchs and studied by Waters in 1878, housed in the palaeontological collection at the NHMW. Specimens are ordered based on the inventory number. Asterisks (*) indicate the species/material studied here. Specimens labelled as *Diastopora/Mesenteripora* (predominantly Mesozoic cyclostome genera with erect, frondose or tubular colonies) have encrusting, circular colonies, and are likely to be species of *Plagioecia*.

Royal Mineralogical Court-Cabinet (*k.k. mineralogisches Hofcabinet*; NHMW founding constituent 1876), in Brucoli (Siracusa) in SE Sicily (Italy) (Fig. 1), and subsequently lent to Arthur Waters in Manchester (United Kingdom) to be studied (Waters, 1878; Pergens, 1887). It includes

the type specimens of two species and a subspecies newly described by Waters (1878): *Biflustra rynchota* (syntypes NHMW 2021/0166/0004, two specimens/fragments), *Eschara lunaris* (syntype NHMW 2021/0166/0007, one branch fragment), *Lepralia auriculata* var. *leontiniensis*



Fig. 1 - (color online) Location of the historical sampling site of Fuchs & Bittner (1875) in Brucoli, southeast Sicily, between the cities of Siracusa and Catania (Italy). The site location is pinpointed on the maps with its geographical coordinates. a) Satellite overview. b) Position of the site on the geological map (ISPRA, 2015; see https://www.isprambiente.gov.it/Media/carg/641_AUGUSTA/Foglio.html for the map legend). c) Close-up of site location in satellite view with the lower (N) and upper (S) boundary of the lower Calabrian Villasmundo subsynthem indicated in red. d-e) Views of the railway cutting exposing the Pleistocene strata. Maps are from Google Earth, earth.google.com/web/.

(holotype NHMW 2021/0166/0013, one colony encrusting a fragment of a pectinid shell), as well as non-type material of two additional species identified by Waters (1878) as *Onychocella angulosa* and *Microporella morrisiana*. The type specimens of another new subspecies, *Eschara biaperta eschariformis* Waters, 1878, were not found.

New material from the historical sampling site was also collected by one of us (EDM) on the 27th of December 2021. However, given that the historical outcrop is part of an active railway (see Geological setting for details), accessibility was limited, and the new sampling restricted to specimens hand-picked from float material.

Additional material used for comparison includes: 1) the specimens of *Onychocella angulosa* from Nußdorf acquired by the NHMW in 1867 from its author August Emanuel Reuss (NHMW 1867/0040/0203; 13 poorly preserved fragments of which nine fragments were imaged using SEM); 2) specimens of *Porina columnaris* (Manzoni, 1875) (NHMW 2021/0168/0001) and *Onychocella angulosa* (NHMW 2021/0168/0002) from the Pleistocene of Rhodes, illustrated in Pergens (1887, fig. 1a-c); 3) photographs of the type specimen of *Eschara columnaris* Manzoni, 1875 (Catalogue Number 13454) made available by Drs L. Bellucci and S. Dominici, housed in the palaeontological collections of the Museo di Storia Naturale, Università di Firenze (Italy); 4) SEM images of *Microporella morrisiana* made available by Dr P.D. Taylor, and housed in the palaeontological bryozoan collection of the Natural History Museum London, UK (NHMUK); 5) fossil and Recent specimens of *Amphiblestrum lyrulatum* and *Microporella verrucosa* housed in the Rosso Collection of the Museo di Paleontologia dell'Università di Catania (PMC). The fossil material of the latter two species originates from deposits coeval with those of Brucoli, cropping out in the close vicinity (i.e., Castelluccio, Madonna di Adonai, San Marcellino River), or other Calabrian localities of southern Italy (see Rosso 1989a, b, 2002 and references therein; Costa et al., 1991; Di Geronimo et al., 2000).

Scanning electron microscopy was conducted on uncoated specimens using a JEOL JSM-661 OLV at the Central Research Laboratories of NHMW and a TESCAN VEGA 2 LMU at the Microscopical Laboratory of the University of Catania in backscattered-electron/low-vacuum mode. Measurements were taken from SEM images using the image processing program ImageJ (available from <https://imagej.nih.gov>), and are given either in the species description, in the Remarks or in tables as mean±standard deviation and, in parentheses, size ranges. Abbreviations for the measurements are: AvL: avicularium length, AvW: avicularium width, AvOpL: avicularium opesia length, AvOpW: avicularium opesia width, N: number of traits measured, OL: orifice length, OW: orifice width, OpL: opesia length, OpW: opesia width, OvL: ovicell length, OvW: ovicell width, ZL: autozooid length, ZW: autozooid width.

GEOLOGICAL SETTING AND AGE OF THE BRUCOLI SITE

Theodor Fuchs collected the fossil material loaned to Waters on the 25th of May 1874, during one of

his numerous study-travels into the Cenozoic of the Mediterranean region on behalf of the Austrian Academy of Sciences in Vienna (Hochstetter, 1884). The precise geographical position of the locality, in the railway cutting between Brucoli (transcribed there Brucoli) and Agnone, near Catania in southern Sicily, as well as its geological setting were subsequently published (Fuchs & Bittner, 1875). Cross-checking of the regional geological map at 1:50,000 scale (ISPRA, 2015) and the Google Earth Pro topographic model allowed a most precise approximation of the geographical coordinates of the bryozoan collecting site as WGS84 37°16'59.24"N, 15°9'51.09"E (Fig. 1). In particular, the railway heading from Brucoli towards Agnone to which the authors refer, was exclusively built on Pleistocene marine strata. The position of the sampling site is marked immediately above the transgressive contact of Pleistocene marine strata with Cretaceous basalt, indicated on the geological map by a railway cutting c. 2.3 km (300°, WNW) from Brucoli train station (ISPRA, 2015).

On top of the Cretaceous basaltic rocks, the sedimentary succession starts with the lower Calabrian Villasmundo subsynthem, grading upwards into the upper Calabrian Scordia subsynthem. Together, they constitute the Lower Pleistocene Lentini synthem, itself transgressively overlain by the Middle-Upper Pleistocene Augusta synthem, which is poorly exposed along the last kilometre of the railroad to Brucoli train station (ISPRA, 2015).

Accordingly, Fuchs' collection-site appears to be the flanks of a c. 8-m-deep railway cutting spanned by an overbridge, positioned close to the lower Calabrian transgressive boundary over the basaltic basement (Fig. 1d-e). The whitish-yellowish, unconsolidated tuffaceous deposits (from which the material studied here originates) are extraordinarily rich in bryozoans, corals, brachiopods and molluscs, indicating a mid-outer shelf depositional environment. Among the molluscs, the ostreid *Neopycnodonte cochlear* (Poli, 1795) and the pectinids *Pseudamussium peslutrae* (Linnaeus, 1771) and *Aequipecten opercularis* (Linnaeus, 1758) are the most frequent therein. On top of these strata, at a horizontal distance of c. 120 m from the transgressive base, the start of a thick succession of bluish marls, barren of macrofossils, points to the continued environmental deepening at the site, and the establishment of open marine depositional conditions during the late Calabrian.

SYSTEMATIC PALAEOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Order CHEILOSTOMATIDA Busk, 1852
Suborder FLUSTRINA Smitt, 1867
Superfamily CALLOPOROIDEA Norman, 1903
Family CALLOPORIDAE Norman, 1903

Genus *Amphiblestrum* Gray, 1848
Type species *Membranipora flemingii* Busk, 1854

Amphiblestrum cf. *lyrulatum* (Calvet, 1907)
(Figs 2-5)

1878 *Biflustra rynchota* WATERS, p. 478, Fig. 1.

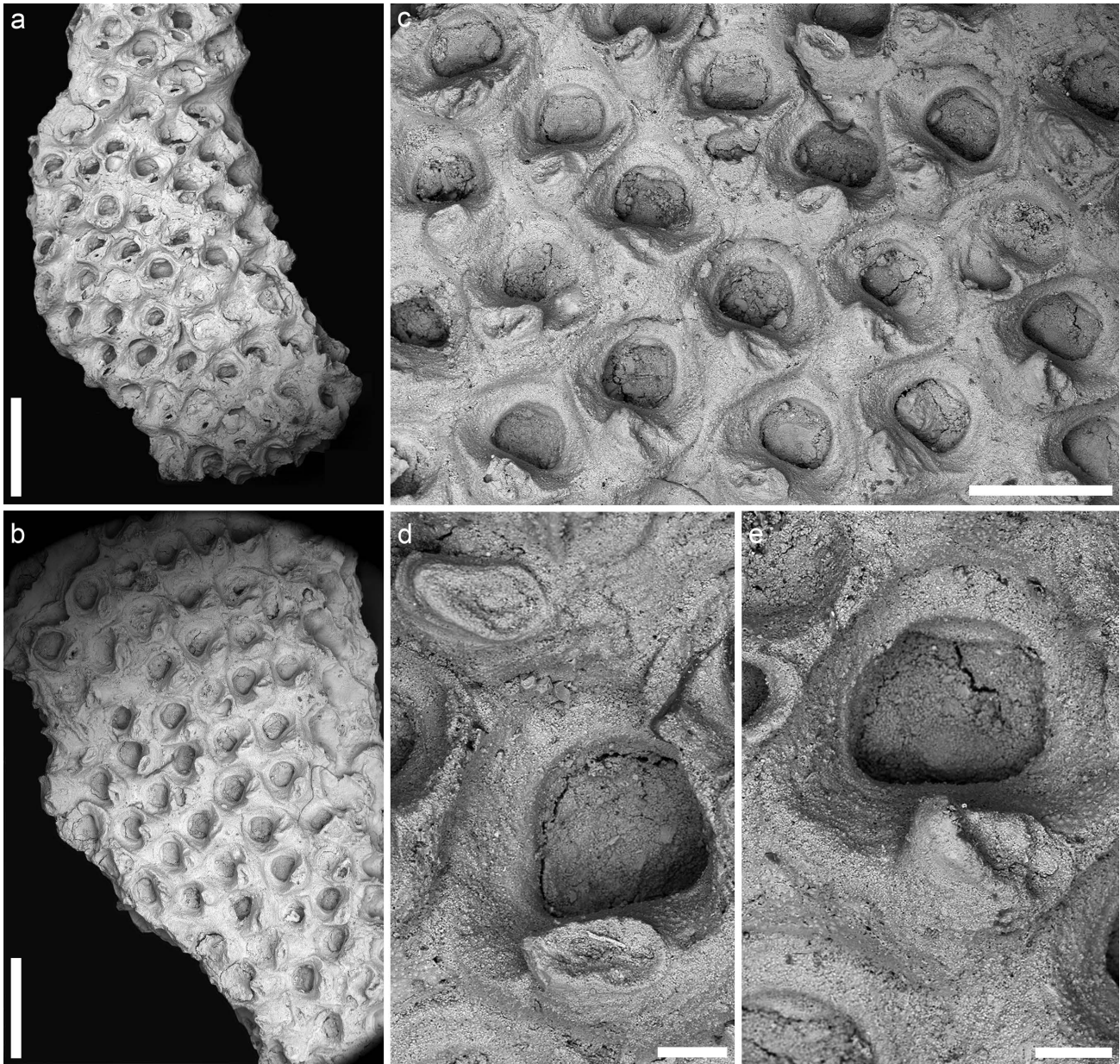


Fig. 2 - Syntypes of *Biflustra rynchota* Waters, 1878 here considered as *Amphiblestrum* cf. *lyrulatum* (Calvet, 1907). Paralectotype NHMW 2021/0166/0004b (a) and lectotype NHMW 2021/0166/0004a designated here (b-e), Calabrian, Pleistocene, Brucoli, Sicily. a-b) General view of the two type specimens consisting of two flat, bilamellar, erect fragments. c) Group of autozooids and avicularia. d) Close-up of two adventitious avicularia showing intramural budding (top left) and the serrated rostrum (bottom right). e) Close-up of an autozooid and associated avicularium with raised and slightly upturned rostrum preserved. Scale bars: 1 mm (a-b); 500 µm (c); 100 µm (d-e).

Material - Pleistocene (Calabrian): lectotype (designated here) NHMW 2021/0166/0004a (Fig. 2b-e), and paralectotype NHMW 2021/0166/0004b (Fig. 2a) of *Biflustra rynchota*, Brucoli, Italy; PMC Rosso-Collection I. Ps. B.89b one colony with developing erect branches and ovicells encrusting an erect cheilostome bryozoan, and an encrusting base on a brachiopod, Brucoli, Italy (Fig. 3); PMC Rosso-Collection I. Ps. B.89c, Musalà, Reggio Calabria, Italy (Fig. 4a-c), as *Ramphonotus minax* (Busk, 1860a) in Costa et al. (1991); PMC Rosso-Collection I. Ps. B.89d, Madonna di Adonai, Brucoli, Augusta, Siracusa, Italy (Fig. 4d-e). Recent: *Amphiblestrum minax* in Rosso (1989a), PMC Rosso-Collection F. H. B.89a: Stn CL-74-84, off Calvi, Corse, France, 42°47'32"N, 9°08'17"E;

110-150 m (not figured); PMC Rosso-Collection I. H. B.89e, off south-eastern Sicily: Vega 6, 125 m (Fig. 5a-b); Vega 14, 115 m (Fig. 5c-f).

Remarks - *Biflustra* d'Orbigny, 1852 is a malacostegine genus and, as such, lacks avicularia and ovicells. In the syntypes of *Biflustra rynchota*, consisting of two bilamellar, flat erect fragments, robust adventitious avicularia are associated with each autozooid, although ovicells were not observed, the two fragments being infertile. SEM examination of the type material suggests that this species fits better into the genus *Amphiblestrum* and, moreover, that it shows a close affinity with *A. lyrulatum*.

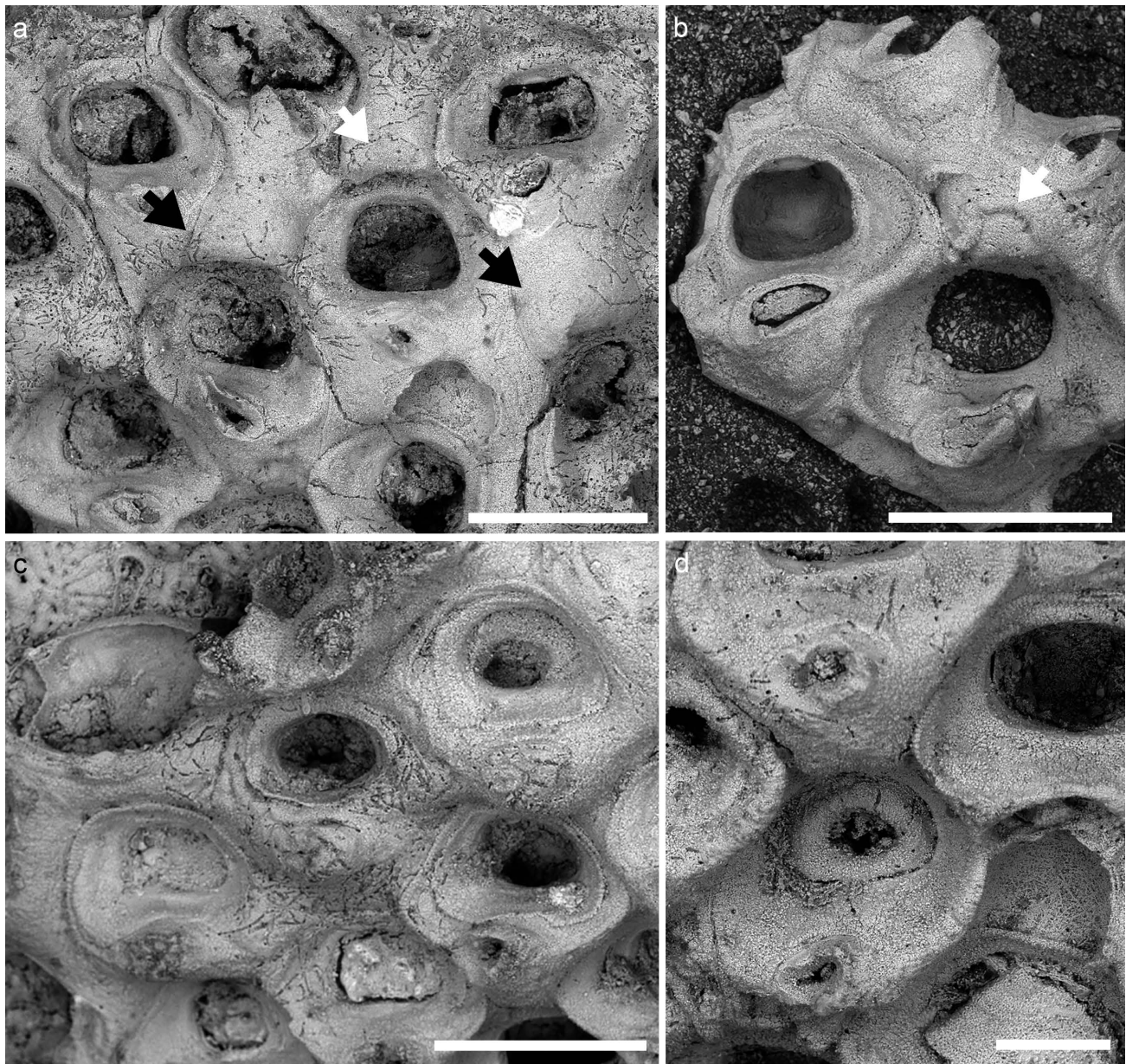


Fig. 3 - *Amphiblestrum* cf. *lyrulatum* (Calvet, 1907) newly collected from Brucoli historical sampling site. PMC Rosso-Collection I. Ps. B.89b A (a-b, d) and B (c), Calabrian, Pleistocene, Brucoli, Sicily. a-b) Ovicellate zooids with either an apparent reduced area of uncalcified ectooecium (white arrows) or ectooecium fully calcified (black arrows). c-d) Group of autozooids with intramural budding and structures interpreted as either closure plates or intramurally budded kenozooids. Scale bars: 500 μ m (a-c); 200 μ m (d).

While Recent Mediterranean records of *Amphiblestrum lyrulatum*, traditionally synonymised with *Ramphonotus minax*, were undoubtedly distinguished from the Atlantic species after comparison among populations from the two areas (López de la Cuadra & García-Gómez, 1994), a certain caution was suggested when dealing with fossil occurrences (Rosso, 2002). The Pleistocene specimens examined here from Brucoli and other localities in Sicily and Calabria (Rosso, 2002 and references therein) fit well into the description of this species. In agreement with the description of *A. lyrulatum*, based on both Recent Mediterranean and Pleistocene southern Italian colonies in Rosso (2002), they show: autozooids with a deeply immersed cryptocyst surrounded by a prominent gymnocyst (Figs 2c, 3a-b and 4a, d); a trapezoidal

opesia that is wider than long (Figs 2d-e, 3a-b and 4a, d); ancestrula with six spines (illustrated here for the first time in both fossil [see Fig. 4a-b] and Recent colonies [see Fig. 5a-b]); four oral spine bases in periancestrular autozooids (Fig. 4a) but spines absent in later autozooids (Fig. 2c); and suboral avicularia with a robust columnar base and an upturned, serrated rostrum (Fig. 2e). Ovicells are usually characterized by a crescentic area of uncalcified ectooecium (Fig. 4d-e). Ovicells were absent in the syntypes from Brucoli but were observed in some fragments newly collected in 2021 from the historical sampling site. In this case, the uncalcified ectooecial area seems extremely reduced (Fig. 3a-b, see white arrows) or the ectooecium appears fully calcified (Fig. 3a, see black arrows). Size of autozooids (including opesia), avicularia

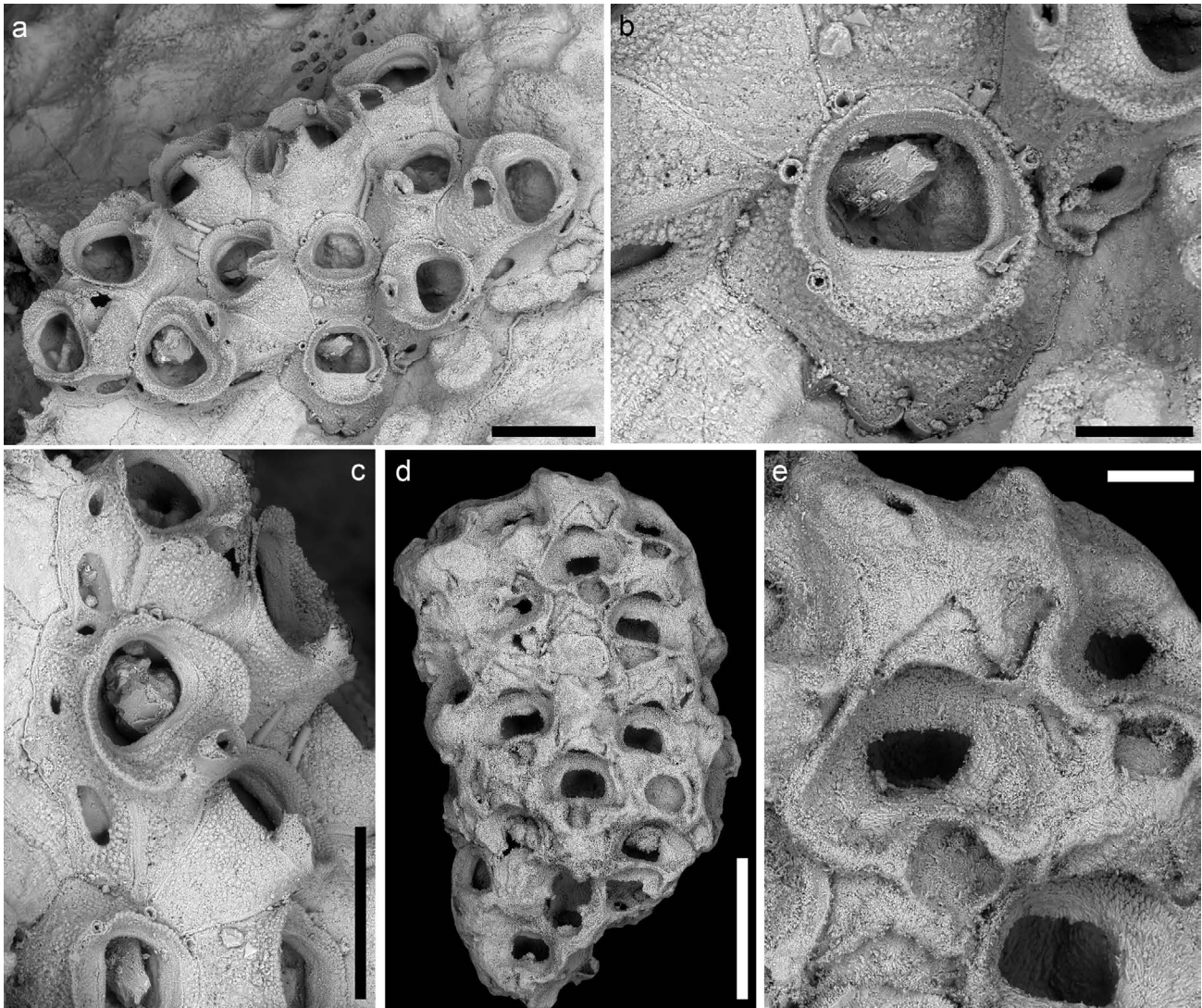


Fig. 4 - *Amphiblestrum lyrulatum* (Calvet, 1907), Calabrian (Pleistocene), Italy. a-c) PMC Rosso-Collection I. Ps. B.89c Musalà, Reggio Calabria. a) Encrusting base and early astogeny. b) Close-up of the ancestrula. c) Close-up of autozooids at the growing edge of the colony, showing pore-chamber windows and avicularia with serrated rostrum. d-e) PMC Rosso-Collection I. Ps. B.89d Madonna di Adonai, Brucoli, Siracusa. d) General view of a fertile, erect fragment. e) Close-up of ovicells. Scale bars: 500 μm (a, c); 200 μm (b, e); 1 mm (d).

and ovicells are on average smaller in the fossil specimens compared to the Recent but their size ranges partially overlap (see Tab. 2). In some zooids, the development of structures that can be interpreted either as closure plates or intramurally budded kenozooids was observed (Fig. 3c-d). Intramural budding of autozooids seems also to be frequent (Fig. 3d).

The colony form of this species is highly variable (López de la Cuadra & García-Gómez, 1994). It usually starts with an encrusting base that can be more or less extensive depending on the size of the substrate (Fig. 5a, c). It later becomes erect, forming either strap-like branches with three-ten longitudinal series of zooids (Figs 2a-b and 3d), or cylindrical branches (Fig. 5c) formed by eight wedge-shaped zooids with vertical walls converging towards the centre of the branch (Fig. 5e). The zooids at the tip of the branch show that interzooidal communication happens through multiporous (five-eight pores) septula (Fig. 5f). Irregularly-shaped autozooids with extensive

cryptocyst may occur along the contact between lobes of the same colony or because of anomalies in the substrate (Fig. 5d).

From a nomenclatural point of view, if the conspecificity of the species from Brucoli with *Amphiblestrum lyrulatum* is confirmed, the new combination *Amphiblestrum rynchotum* could co-exist with *Amphiblestrum rynchotum* (Busk, 1859), given the different spelling of the two specific names, although unfortunate. Busk's species, described from the Pliocene Coralline Crag Formation of England, differs mainly in having avicularia, sometimes paired, directed proximolaterally (see SEM images available at <https://neogenebryozoans.myspecies.info/taxonomy/term/316/media>; accessed 10.11.2021). Waters (1878, p. 479) acknowledged the similarity between his new species and Busk's species, as well as the similarity of it with *Ramphonotus minax*.

Given that the syntypes of Waters' species are infertile, and given the differences in ovicell morphology observed

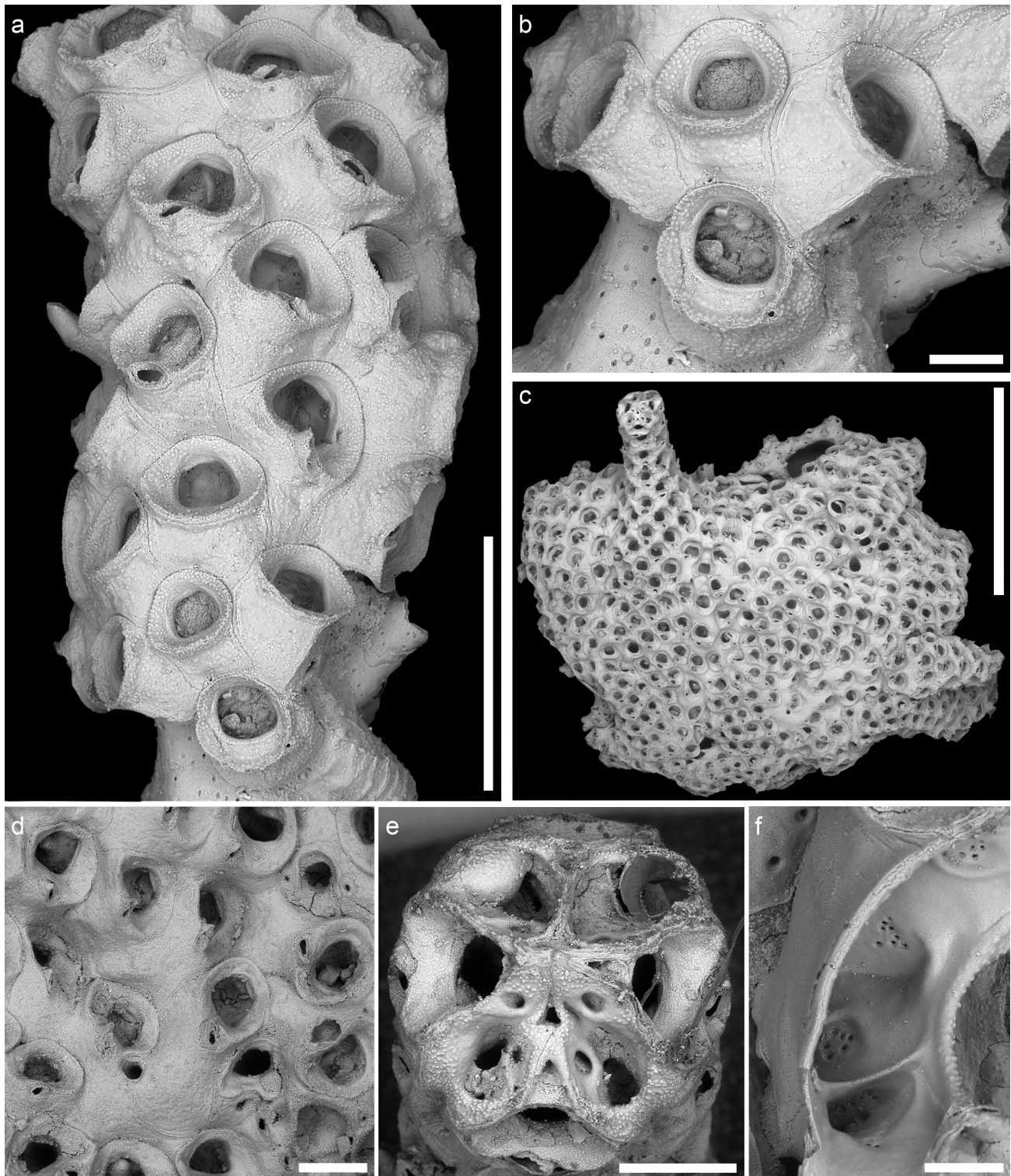


Fig. 5 - *Amphiblestrum lyrulatum* (Calvet, 1907), Recent, off south-eastern Sicily. a-b) PMC Rosso-Collection I. H. B.89e1 Vega 6 (depth: 125 m). a) Encrusting base of a young colony. The substrate is a cyclostome bryozoan. b) Close-up of the ancestrula and first budded autozooids. c-f) PMC Rosso-Collection I. H. B.89e2 Vega 14 (depth: 115 m). c) General view of the colony including the encrusting base and the first erect branch. d) Group of irregularly shaped autozooids with extensive proximal cryptocyst, likely owing to the encounter of different lobes of the same colony. e) Frontal view of the tip of the branch. f) Interzooidal communication through multiporous septula. Scale bars: 1 mm (a); 200 µm (b, f); 0.5 cm (c); 500 µm (d-e).

between the newly collected specimens from Brucoli and other fossil and recent material from the area, we await better preserved specimens, hopefully showing a transition

from ovicells with a largely uncalcified ectooecium to a fully calcified ectooecium, to confirm with certainty the conspecificity of the two species.

	<i>Amphiblestrum cf. lyrulatum</i> (Calabrian, Brucoli)	<i>Amphiblestrum lyrulatum</i> (Recent, Mediterranean)
ZL	673±48 (594-789) N = 14	774±64 (650-913) N = 20
ZW	542±41 (482-612) N = 14	637±54 (569-760) N = 20
OpL	240±23 (204-279) N = 14	281±19 (245-325) N = 20
OpW	302±26 (254-344) N = 14	329±30 (259-377) N = 20
AvL	231±21 (172-276) N = 20	289±19 (264-338) N = 20
AvW	133±14 (112-161) N = 20	164±22 (131-238) N = 20
OvL	273±24 (239-316) N = 8	330±50 (234-414) N = 9
OvW	321±41 (262-397) N = 8	385±42 (328-447) N = 9

Tab. 2 - Measurements in μm of specimens of *Amphiblestrum cf. lyrulatum* (Calvet, 1907) from the Calabrian of Brucoli (Italy) (NHMW 2021/0166/0004, Waters' Collection; PMC Rosso-Collection I. Ps. B.89b), and *A. lyrulatum* from the Recent Mediterranean (PMC Rosso-Collection I. H. B.89e1; PMC Rosso-Collection I. H. B.89e2). Note that in order to obtain measurements that are comparable between fossil and Recent specimens, avicularium length (AvL) is measured at the base not at the tip of the raised rostrum, which is broken in most fossil specimens.

Family ONYCHOCELLIDAE Jullien, 1882

Genus *Onychocella* Jullien, 1882

Type species *Cellepora angulosa* Reuss, 1847

Onychocella angulosa (Reuss, 1847) (Figs 6-8)

1847 *Cellepora angulosa* REUSS, p. 93, Pl. 11, fig. 10.

1878 *Membranipora angulosa* (REUSS) - WATERS, p. 468.

Material - Middle Miocene (Badenian): lectotype (designated here) NHMW 1867/0040/0203g; paralectotypes 12 residual specimens from the same lot NHMW 1867/0040/0203a-f, h-m, Nußdorf, Austria (Fig. 8); Pleistocene (Gelasian): NHMW 2021/0166/0051 (not figured) and 2021/0168/0002 (one of two fragments; Fig. 7), Rhodes, Greece; Pleistocene (Calabrian): NHMW 2021/0166/0002 (Fig. 6a-b), PMC Rosso-Collection I. Ps. B.90a some colonies mostly encrusting *N. cochlear* (one figured, Fig. 6c-f) Brucoli, Italy.

Remarks - The only registered syntypes part of the original collection described by Reuss (1847) is lot NHMW 1848/0038/0080 labelled as *Cellepora angulosa* Reuss from Nußdorf (NHMW inventory-book entry from the 23rd of October 1848). While the syntypes from localities such as Steinabrunn, Kroisbach, and Bischofswart were absent from the type collection since its acquisition, the lot from Nußdorf is not available at present probably misplaced in the collection or lost. The second collection acquired by NHMW from Reuss on the 18th of December 1867 comprised 318 lots of bryozoan species from different Mesozoic and Cenozoic localities. The inventory-book registered the present species as *Lepralia angulosa* Reuss in lots from Wurzing (NHMW 1867/0040/0202), Bischofswart (1867/0040/0227), and Nußdorf (1867/0040/0203).

In their revision of Reuss' Collection, David & Pouyet (1974) listed one colony fragment as the "neolectotype", and the remaining 12 colony fragments as the "paralectotypes" of *Onychocella angulosa* constituting altogether the single lot registered as NHMW 1867/0040/0203. The fact that these authors did not explicitly designate the lectotype or illustrate the species, and kept all type specimens together under the same collection number, prevents the distinction between the designated "neolectotype" and the "paralectotypes", making their action invalid. Consequently, we imaged the best preserved of those fragments in order to choose a lectotype from this lot. We designate the specimen NHMW 1867/0040/0203g as the lectotype (Fig. 8g), and illustrate the best preserved paralectotypes (NHMW 1867/0040/0203a-f, h-i).

Based on Reuss' drawing (1847, pl. 11, fig. 10), Rosso et al. (2020) considered *O. angulosa* and *O. marioni* as two distinct species pending the examination of the type material. The differences apparent from the drawing included autozooids with centrally placed, polygonal opesiae, and small heterozooids with reduced opesiae in *O. angulosa*. However, none of the fragments available from the original material (Fig. 8) corresponds to the specimen illustrated by Reuss (1847), which was probably part of the misplaced/lost specimen lot NHMW 1848/0038/0080. The specimen was unavailable also to David & Pouyet (1974), thus the use of the term "neolectotype" to indicate their chosen type specimen. Here, we confirm the distinction between these two species with the main difference being the reduced size of the autozooidal opesia, which is also more polygonal-shaped with a straight proximal margin. On the other hand, the opesia is still placed distally, although not terminally, at about two-thirds of zooidal length and seems to be placed more centrally when partially obliterated by sediment. The small heterozooids, like those depicted by Reuss (1847), were not observed in the remaining fragments. A structure that we interpret as a heterozooid was, however, observed in one of the colonies newly collected by one of us (EDM) from Brucoli (Fig. 6e-f). This single, putative heterozooid is lozenge-shaped with a rounded distal margin, the texture of the cryptocyst similar to that of autozooids and avicularia but with a reduced, elliptical opening placed centrally. Its morphology is clearly distinct from that of autozooids and avicularia. The presence of a single heterozooid in a single fairly large colony (Fig. 6c) out of several specimens suggests that this character is rare. In the same specimen, we also observed the ancestrula and early astogeny (Fig. 6d), which is consistent with that of other *Onychocella* species; the ancestrula is rhomboidal, smaller than later autozooids but proportionally wider, and buds three autozooids, one distal and two distolateral. The size of autozooids and avicularia (including their opesiae) are similar in the Miocene and Pleistocene specimens from Rhodes, while autozooids are slightly larger in the Pleistocene specimens from Brucoli, although size ranges partially overlap across all the specimens (see Tab. 3).

David & Pouyet (1974) erroneously included in the synonymy of *O. angulosa* two tentative syntypes of *Eschara excavata* Reuss, 1847 from the lot NHMW 1848/0038/0066 attributed to Nußdorf, although Reuss (1847) referred to an unknown Middle Miocene site in

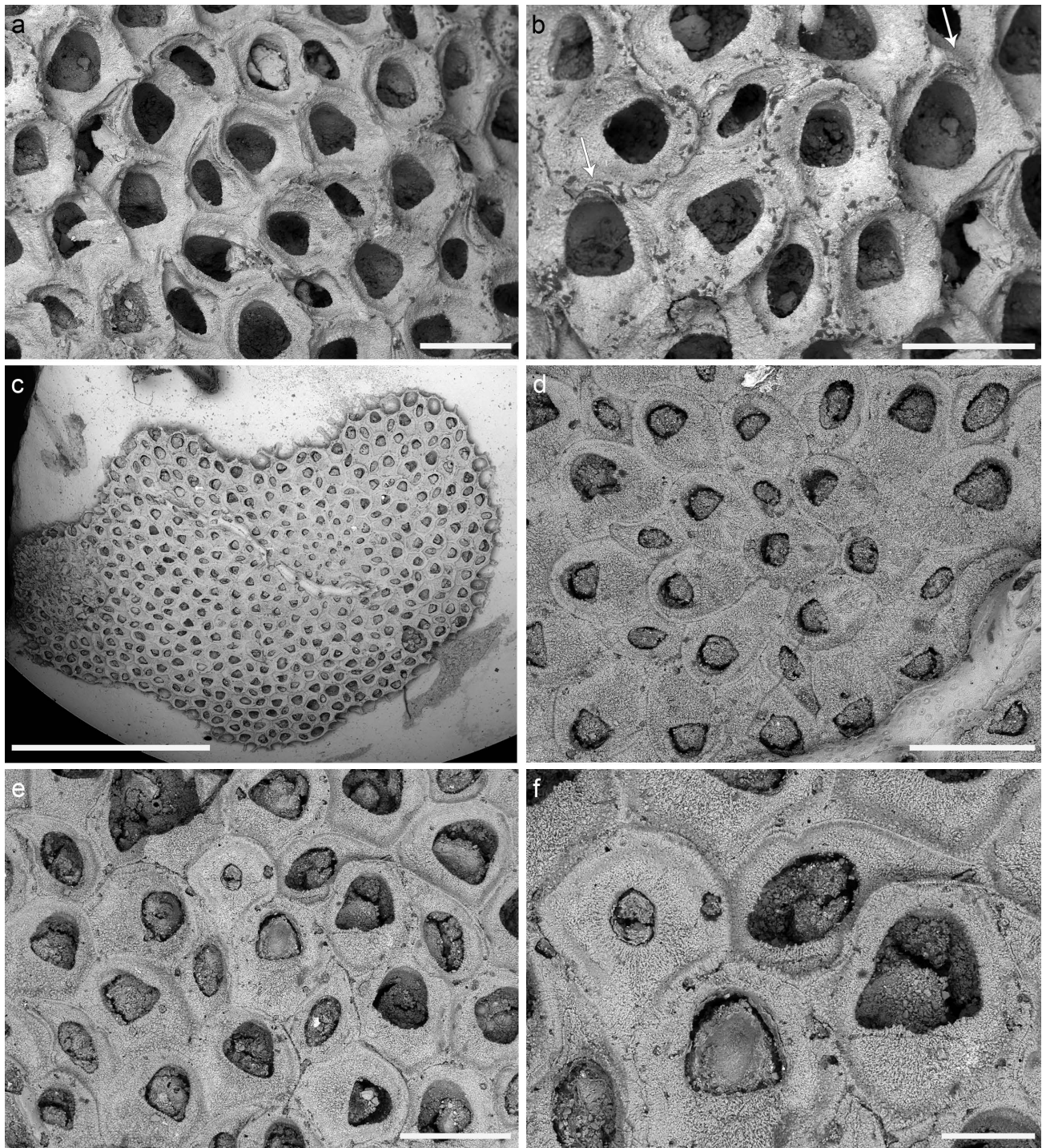


Fig. 6 - *Onychocella angulosa* (Reuss, 1847), Pleistocene (Calabrian), Brucoli. a-b) NHMW 2021/0166/0002. a) General view of the best preserved portion of the colony. b) Group of autozooids, two of which ovicellate (arrowed), and vicarious avicularia. c-f) PMC Rosso-Collection I. Ps. B.90a. c) General view of one of the colonies collected in 2021 from the historical sampling site. d) Ancestrula and early astogeny. e) Portion of the colony with autozooids, avicularia and a putative heterozooid. f) Close-up of the putative heterozooid. Scale bars: 500 μ m (a-b, d-e); 5 mm (c); 200 μ m (f).

the Vienna Basin. Nevertheless, their syntype status is well supported by the fact that this is the only lot of *E. excavata* in Reuss' Collection acquired by the NHMW in 1848, and comprising in total 50 bryozoan species described in Reuss (1847). In contrast, the locality designation (as Nußdorf), which is indeed a Middle Miocene locality in the Vienna Basin, proved to be an

erroneous deduction. Schmid (1989, p. 13) assumed that the specimens under the number NHMW 1848/0038/0066 were instead from the Eocene locality Val di Lonte in northern Italy (Reuss, 1874), based on the state of preservation, completely atypical for Nußdorf, and that no further finds of *Onychocella* with erect colony form were known from the Miocene of the Vienna Basin.

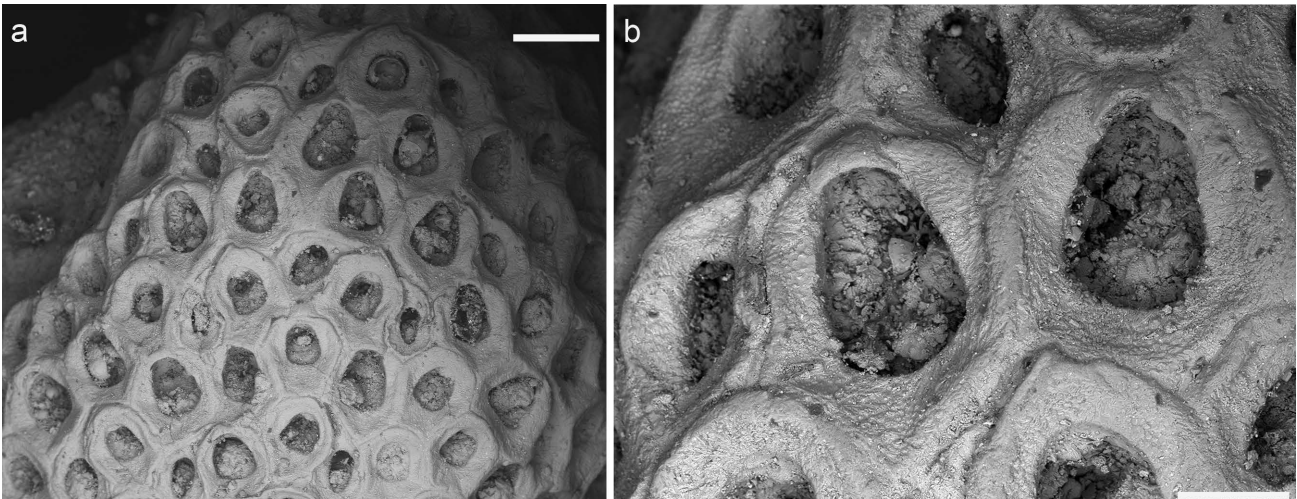


Fig. 7 - *Onychocella angulosa* (Reuss, 1847). a-b) Pleistocene (Gelasian), Rhodes, NHMW 2021/0168/0002 (one of two colony fragments). a) General view of the best preserved colony fragment. b) Close-up of two ovicellate zooids and a vicarious avicularium. Scale bars: 500 µm (a); 200 µm (b).

Braga in Schmid (1989) identified the specimens as *Onychocella subpyriformis* (d'Archiac, 1846) (oldest synonym of *O. geometrica* [Reuss, 1869]) and, confirming Schmid's observations about preservation, suggested Val di Lonte as the original locality. Schmid (1989, p. 35) also mentioned a specimen of *O. angulosa* found among specimens of *Adeonella polystomella* (Reuss, 1847), part of Mr Lukasch's Collection, as the potential type specimen figured by Reuss (1847). Such specimen (now registered as NHMW 2022/0092/0002), however, does not seem to correspond with Reuss' (1847) drawing. In addition, the NHMW acquired some Neogene fossil material (including a brachiopod collection from Nußdorf) from Mr Lukasch in 1852 but there is no mention of Lukasch's material in Reuss (1847, 1874).

Superfamily SCHIZOPORELLOIDEA Jullien, 1882
Family MICROPORELLIDAE Hincks, 1877

Genus *Microporella* Hincks, 1877
Type species *Eschara ciliata* Pallas, 1766

Microporella verrucosa (Peach, 1868)
(Figs 9-10)

1878 *Eschara lunaris* WATERS, p. 475, Fig. 9.
1887 *Porina columnaris* (Manzoni) - PERGENS, p. 23, Pl. 1, fig. 1a-c.

Material - Pleistocene (Gelasian): NHMW 2021/0168/0001 (Fig. 9d-i; two branch fragments) *Porina columnaris*, Rhodes, Pergens' Collection; Pleistocene (Calabrian): NHMW 2021/0166/0007 (Fig. 9a-c; one branch fragment), syntype of *Eschara lunaris*, Brucoli, Italy; Pleistocene: PMC. Rosso Collection I. Ps. B-17f (Fig. 10), Monte dell'Apa, Gela (Caltanissetta), Italy (Rosso, 1989b); Pleistocene (Sicilian): PMC. Rosso Collection I. Ps. B-17g (not figured), Castelluccio, Augusta (Siracusa), Italy.

Remarks - Di Martino & Rosso (2021) proposed the genus *Diporula* as a junior synonym of *Microporella*, and resurrected the combination *M. verrucosa*, based solely on morphology, now corroborated also by molecular data (Orr et al., 2022). However, this synonymy left out Waters'

	Miocene (Austria) NHMW 1867/0040/0203a-i	Gelasian (Rhodes)	Calabrian (Brucoli)
ZL	525±41 (424-588) N = 20	545±32 (503-588) N = 8	572±62 (475-704) N = 20
ZW	454±40 (382-513) N = 20	412±20 (368-432) N = 8	494±43 (412-589) N = 20
OpL	243±26 (229-289) N = 5	249±33 (212-310) N = 8	294±31 (230-341) N = 20
OpW	240±20 (214-269) N = 5	206±17 (186-240) N = 8	257±25 (200-308) N = 20
AvL	586±56 (473-661) N = 10	523±51 (454-595) N = 8	614±70 (502-728) N = 20
AvW	328±34 (272-382) N = 10	292±26 (249-326) N = 8	299±25 (240-344) N = 20
AvOpL	166±13 (152-177) N = 3	200±22 (155-228) N = 8	274±28 (227-351) N = 20
AvOpW	113±6 (108-119) N = 3	127±18 (100-148) N = 8	150±21 (110-185) N = 20

Tab. 3 - Measurements in µm of specimens of *Onychocella angulosa* (Reuss, 1847) from the Miocene (Badenian) of Nußdorf (Austria) (NHMW 1867/0040/0203a-i), from the Gelasian of Rhodes (Greece) (NHMW 2021/0168/0002), and the Calabrian of Brucoli (Italy) (NHMW 2021/0166/0002, Waters' Collection; PMC Rosso-Collection I. Ps. B.90a).

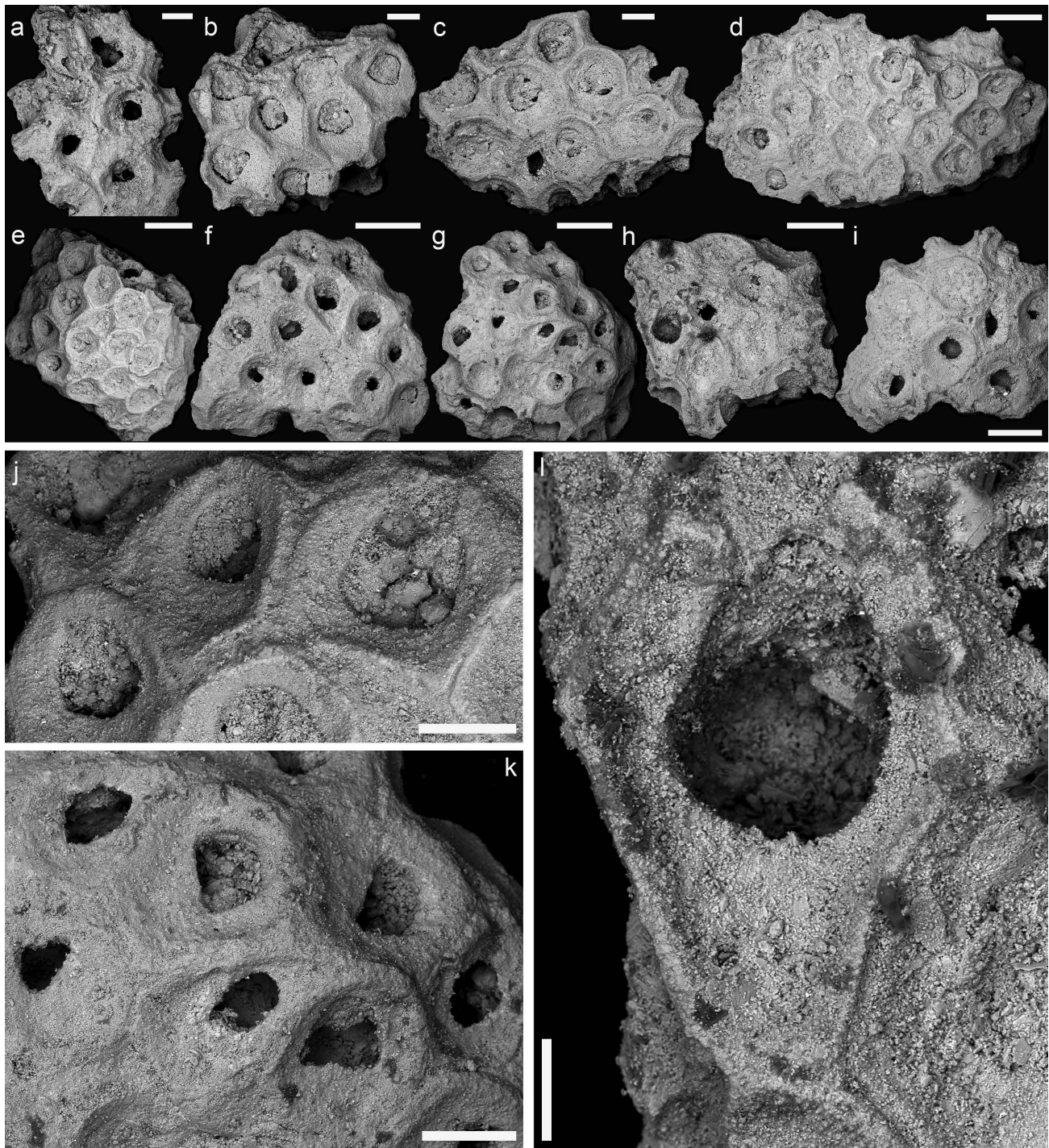


Fig. 8 - *Onychocella angulosa* (Reuss, 1847), lectotype (designated here) (Fig. 8g; NHMW 1867/0040/0203g) and the selected paralectotypes from the same lot (Fig. 8a-f, h-i; NHMW 1867/0040/0203a-f, h-i), Middle Miocene (Badenian), Nußdorf, Austria. a-i) Best preserved fragments among the 13 syntypes available in the original collection from Reuss acquired by NHMW in 1867. j) Close-up of the paralectotype in e (NHMW 1867/0040/0203e) showing the dimorphic opesiaie of autozooids and fertile zooids. k) Close-up of the lectotype in g (NHMW 1867/0040/0203g) showing both autozooids and vicarious avicularia. l) Close up of the paralectotype in h (NHMW 1867/0040/0203h) showing a fertile zooid. Scale bars: 200 μ m (a-c, j-k); 500 μ m (d-g); 400 μ m (h-i); 100 μ m (l).

fossil specimens described as *Eschara lunaris*, pending a re-examination of the type material (Di Martino & Rosso, 2021, p. 32). Here, we confirm the conspecificity of *E. lunaris* and *M. verrucosa* in agreement with Hincks (1880). In addition, the specimens of *Porina columnaris* illustrated in Pergens (1887) from the Pleistocene (Gelasian) of Rhodes (formerly regarded as Pliocene; see

Moissette & Spjeldnaes, 1995, fig. 2; Rosso & Sciuto, 2019) also proved to be conspecific with *M. verrucosa*.

The original material described by Manzoni (1875) from the Pliocene of Castrocaro (northern Apennines, Italy) as *Eschara columnaris* was first revised by Neviani (1893) who re-assigned it to the genus *Porina*, and later by Poluzzi (1971, p. 565, note 66), who suggested the

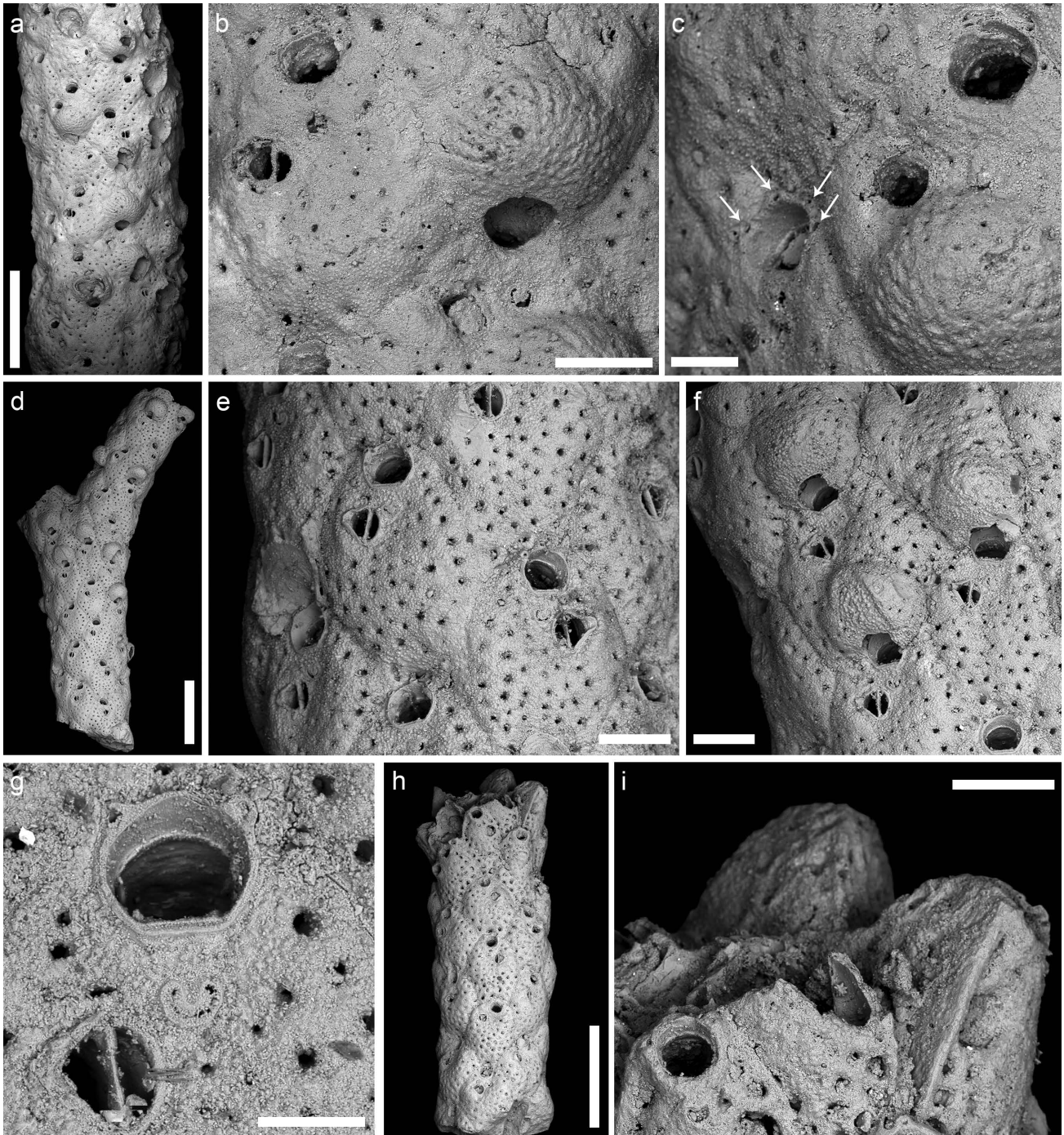


Fig. 9 - *Microporella verrucosa* (Peach, 1868). a-c) Syntype of *Eschara lunaris* Waters, 1878, Pleistocene (Calabrian), Brucoli, NHMW 2021/0166/0007. a) General view of the branch fragment. b) Close-up of two autozooids showing oral spine bases, avicularium, ascopore and ovicell. c) Close-up of two autozooids showing four oral spine bases (arrowed) and scattered pseudopores on the ovicell. d-i) Specimens of *Porina columnaris* sensu Pergens (1887), Pleistocene (Gelasian), Rhodes, NHMW 2021/0168/0001. d, h) General view of the fragments. e) Group of autozooids. f) Group of ovicellate zooids. g) Close-up of orifice, avicularium and ascopore. i) Growing tip of the branch fragment. Scale bars: 1 mm (a, d, h); 200 μ m (b, e-f, i); 100 μ m (c, g).

synonymy of Manzoni's species with *Microporella verrucosa* (see also Dominici, 2010, fig. 9.15). The suggestion of Poluzzi (1971) has been neglected over the years. After examination of photographs of the type specimen of *Eschara columnaris* (Catalogue Number 13454) obtained through the kindness of Luca Bellucci and Stefano Dominici, curators of the geological and palaeontological collections of the Museo di Storia

Naturale, Università di Firenze (Italy), we refrain from synonymising this species with *M. verrucosa*. Despite the poor preservation of the specimen, we can confirm that the main characters of the species are consistent with Manzoni's (1875, pl. 5, fig. 65) illustration. It differs from *M. verrucosa* in the shape of the orifice (with a bowl-shaped sinus in *E. columnaris*), and in the absence of avicularia and ascopore.

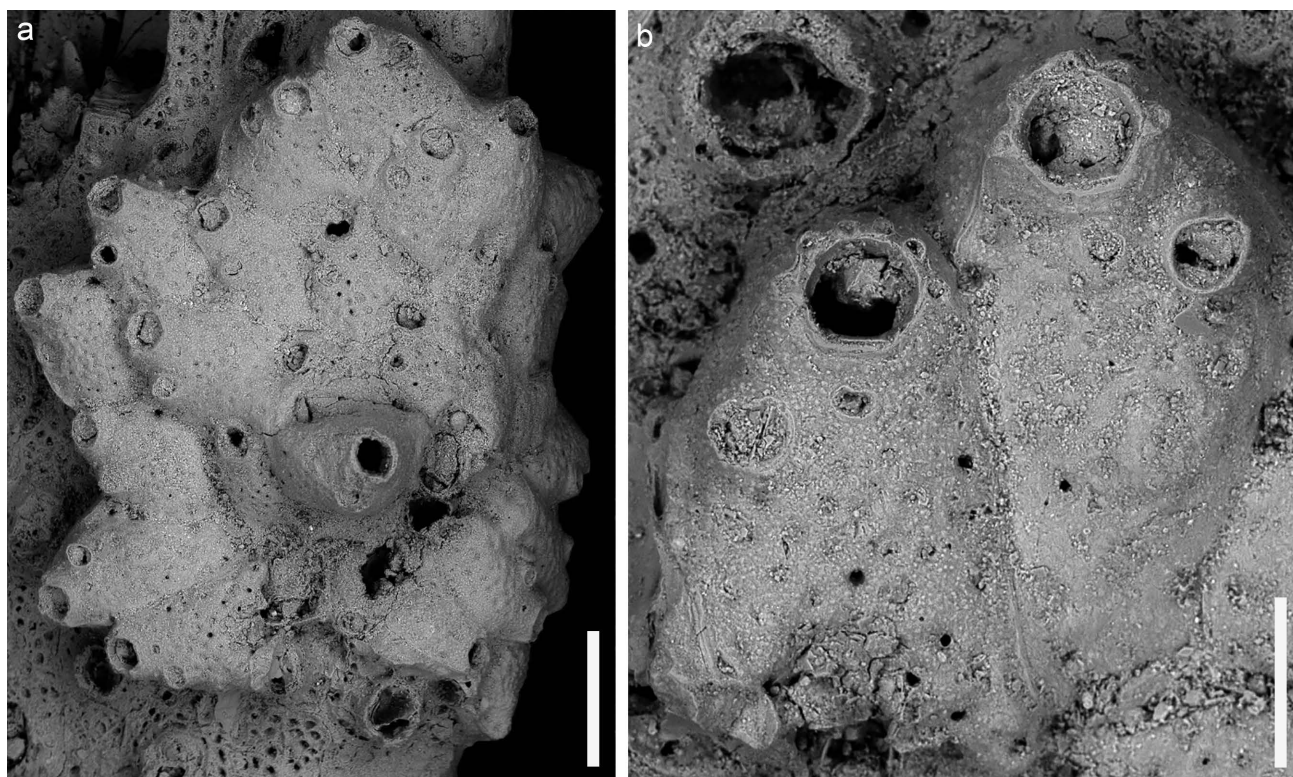


Fig. 10 - *Microporella verrucosa* (Peach, 1868), Pleistocene (Calabrian), PMC. Rosso Collection I. Ps. B-17f, Monte dell'Apa, Gela, Sicily. a) Encrusting base with ancestrula. b) Close-up of two autozooids. Scale bars: 500 μ m (a); 200 μ m (b).

The size of autozooids, orifice, avicularia and ovicells are similar among the Gelasian, Calabrian and Recent specimens of *M. verrucosa* (see Tab. 4).

Microporella appendiculata (Heller, 1867)
(Fig. 11a-g)

1867 *Lepralia appendiculata* HELLER, p. 107, Pl. 2, fig. 8.

1878 *Lepralia morrisiana* Busk - WATERS, p. 469, Fig. 2.

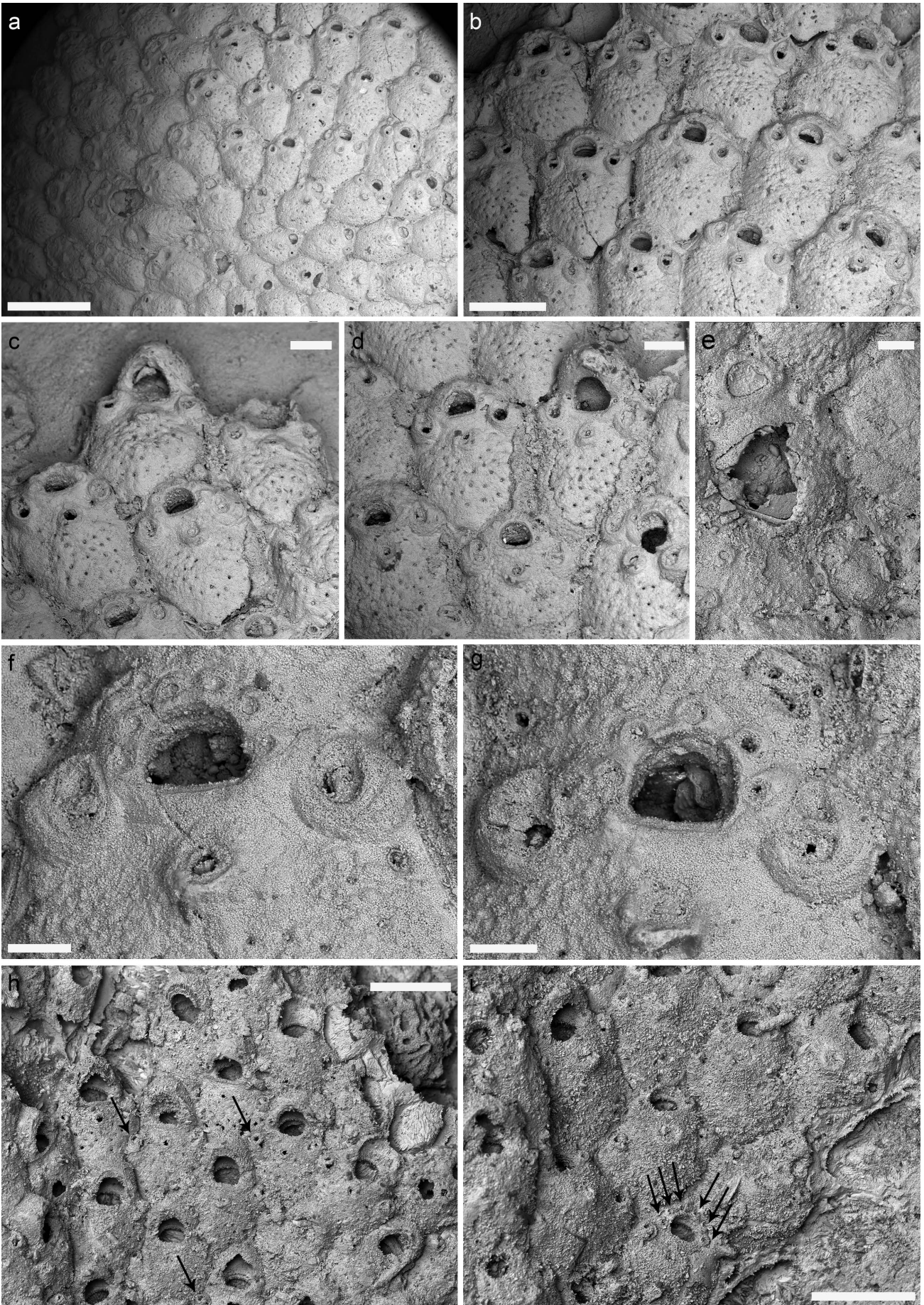
Material - Pliocene: *Microporella morrisiana*, Coralline Crag Formation, late Zanclean-early Piacenzian, Crag Pit Nursery, Aldeburgh, Suffolk, United Kingdom

(Fig. 11h-i); collected by P.D. Taylor & J.D. Bishop in 1983-1984, housed in the palaeontological bryozoan collection of NHMUK. Pleistocene (Calabrian): *Microporella appendiculata*, NHMW 2021/0166/0032, Brucoli, Italy.

Remarks - The type specimen of *Microporella morrisiana* is apparently missing from the palaeontological bryozoan collection of the NHMUK where it was supposed to be housed. However, we have been able to examine SEM images kindly provided by Dr P.D. Taylor of a topotypic colony available in the same collection and identified as *M. morrisiana* by J.D. Bishop (Fig. 9h-i), and which is consistent with Busk's (1859, pl. 7, fig. 8) drawing. In the original label accompanying this

	Gelasian (Rhodes)	Calabrian (Brucoli)	Recent (Mediterranean)
ZL	705 \pm 41 (650-803) N = 11	712 \pm 80 (648-864) N = 6	661 \pm 93 (477-779) N = 18
ZW	476 \pm 27 (428-536) N = 11	578 \pm 49 (541-675) N = 6	493 \pm 68 (389-615) N = 18
OL	131 \pm 5 (125-137) N = 8	123 \pm 5 (116-128) N = 4	143 \pm 6 (130-151) N = 10
OW	149 \pm 6 (137-156) N = 8	140 \pm 10 (132-151) N = 4	161 \pm 10 (145-177) N = 10
AvL	124 \pm 11 (110-143) N = 18	158 \pm 14 (141-175) N = 5	142 \pm 9 (121-156) N = 20
AvW	110 \pm 9 (90-125) N = 18	125 \pm 4 (122-132) N = 5	130 \pm 7 (119-133) N = 20
OvL	270 \pm 21 (253-303) N = 6	292 \pm 13 (280-304) N = 4	286 \pm 36 (250-327) N = 4
OvW	365 \pm 26 (320-392) N = 6	416 \pm 10 (405-429) N = 4	402 \pm 20 (384-430) N = 4

Tab. 4 - Measurements in μ m of specimens of *Microporella verrucosa* (Peach, 1868) from the Gelasian of Rhodes (Greece) (NHMW 2021/0168/0001, Pergens' Collection), the Calabrian of Brucoli (Italy) (NHMW 2021/0166/0007, Waters' Collection), and the Recent Mediterranean. Measurements of Recent colonies are from Di Martino & Rosso (2021).



specimen, Bishop suggested a comparison between this species and the Recent *M. marsupiata* (Busk, 1860b) from Madeira, which is considered as a senior synonym of *M. appendiculata* (see Di Martino & Rosso, 2021, and references therein).

The specimen from Brucoli identified as *Lepralia* (now *Microporella*) *morrisiana* by Waters (1878) is similar to the nominal species from the Pliocene Coralline Crag Formation in having up to six oral spine bases (although more commonly five), kenozooidal ovicells, a circular ascopore and paired avicularia. The main difference between the two species is in the position and direction of the avicularia, which are placed lateral to the orifice and directed distally in the Pleistocene specimen from Brucoli, while avicularia are placed laterally at zooidal mid-length and directed laterally to disto-laterally in the Pliocene Coralline Crag species. In addition, in the Pliocene species autozooids, avicularia and ovicells are smaller (ZL 543±29 [499-576] µm, ZW 434±18 [404-447] µm, N = 6 vs ZL 804±65 [720-894] µm, ZW 668±51 [613-769] µm, N = 10; AvL 91±4 [85-95] µm, AvW 67±6 [61-75] µm, N = 5 vs AvL 145±14 [124-167] µm, AvW 114±14 [91-127] µm, N = 10; OvL 131±10 [116-143] µm, OvW 270±16 [254-289] µm, N = 6 vs OvL 187±21 [172-201] µm, OvW 363±9 [356-369] µm, N = 6).

Waters' specimen fits well into the description of *Microporella appendiculata* (see Di Martino & Rosso, 2021, p. 6), and here we re-assign it to this species. *Microporella appendiculata* is found in several other Pliocene and Pleistocene deposits of southern Italy (e.g., Calabria [Pliocene]: Pavigliana [Reggio Calabria; Barrier et al., 1987]; Sicily [Pleistocene]: Monte dell'Apa [Gela; Rosso, 1989b], Catallarga [Grammichele; Rosso, 1987], Belice [Di Geronimo et al., 1994]) reported as *Microporella coronata* (Audouin, 1826) and *M. pseudomarsupiata* Aristegui, 1984. The Pleistocene specimen from Brucoli shares with the Recent Mediterranean colonies of *M. appendiculata* all the main diagnostic characters including the shape of the orifice (transversely D-shaped, smooth without denticles and condyles) and of the ascopore (circular with radial spines, developing a mucro proximally), the number of oral spines (more commonly five but sometimes six), and the type of avicularia (paired, distally directed, placed lateral to the orifice with crossbar at the level of the proximal margin of the orifice, with truncated, open rostrum). Ovicells in *M. appendiculata* can be either of the kenozooidal type or produced by the distal zooid. In the specimen from Brucoli, we only observed kenozooidal ovicells of comparable size to those of the Recent *M. appendiculata* (fossil: 172-201 × 356-369 µm; Recent: 143-235 × 262-378 µm; see Di Martino & Rosso, 2021). The sizes of autozooids and avicularia of the Pleistocene specimen fall into the size range of the Recent colonies but on average autozooids are slightly larger (fossil: 804 × 668 µm; Recent: 698 × 458 µm).

The above-mentioned differences between *M. morrisiana* and the fossil *M. appendiculata* from Brucoli

also confirm that the former species is not conspecific with *M. marsupiata*. A lectotype/neotype should be designated for *M. morrisiana*, hopefully using a better preserved specimen than the one illustrated here, but this is out of the scope of this paper.

Superfamily SMITTINOIDEA Levinsen, 1909

Family LANCEOPORIDAE Harmer, 1957

Genus *Stephanotheca* Reverter-Gil, Souto & Fernández-Pulpeiro, 2012

Type species *Stephanotheca barrosoi* Reverter-Gil, Souto & Fernández-Pulpeiro, 2012

Stephanotheca leontiniensis (Waters, 1878) comb. nov. (Fig. 12)

1878 *Lepralia auriculata* var. *leontiniensis* WATERS, p. 472, Fig. 5.

Material - Pleistocene (Calabrian): a single specimen NHMW 2021/0166/0013, encrusting a fragment of a pectinid shell, Brucoli, Italy, holotype by monotypy.

Description - Colony encrusting, multiserial, multilaminar. Autozooids distinct with thin furrows and/or a raised outline, irregularly hexagonal to rectangular, slightly longer than wide (ZL 667±42 [583-714] µm, ZW 524±117 [412-727] µm, N = 10, mean L/W 1.27), arranged in linear series (Fig. 12a) or irregularly (Fig. 12e). Frontal shield flat, nodular, evenly and densely perforated by 30-40 large, circular pseudopores (20-50 µm in diameter) with raised outline (Fig. 12c-d). Orifice rounded (OL 144±7 [136-156] µm, OW 153±5 [146-160] µm, N = 5), seemingly with a small, U-shaped sinus (Fig. 12c-d); condyles not observed owing to sediment infilling; an uncertain number of oral spine bases still visible in some zooids (Fig. 12d, see arrows). Adventitious avicularium commonly present but absent in some cases such as, for instance, in ovicellate zooids and those placed distally of ovicellate zooids, positioned in the centre of the frontal shield, about 50-70 µm below the orifice, usually occupying two-thirds of the frontal shield, sometimes the entire length (AvL 327±37 [270-384] µm, AvW 134±21 [112-175] µm, N = 10); rostrum either elongate triangular with a rounded tip (Fig. 12b), or elliptical (Fig. 12c), directed proximally; crossbar complete. Ovicell wider than long (OvL 325±28 [305-345] µm, OvW 440±31 [418-462] µm, N = 2), seemingly cleithral with the proximolateral oocelial margins reaching the proximal orifice margin; calcification spreading from the distal zooid over the distal and lateral portions of the oocium but not proximally; the cover of secondary calcification bearing the same type of pseudopores as the autozooidal frontal shield; exposed ectooecium seemingly smooth and imperforate (Fig. 12f). Ancestrula and early astogeny unknown.

Fig. 11 (previous page) - a-g) *Microporella appendiculata* (Heller, 1867) previously *Lepralia morrisiana* Busk, 1859 sensu Waters (1878), Pleistocene, Brucoli, NHMW 2021/0166/0032. a) General view of the colony. b) Group of autozooids. c-d) Group of zooids showing the kenozooidal ovicell developed either at the margin of (c) or within (d) the colony. e) Ancestrula and first budded autozooid. f-g) Close-up of the orifice showing six (f) or five (g) oral spine bases. h-i) *Microporella morrisiana*, Pliocene, Coralline Crag Formation, Suffolk, United Kingdom. h) Group of ovicellate zooids (some avicularia arrowed). i) Group of non-ovicellate zooids showing the six oral spine bases (see arrows). SEM images (h-i) are courtesy of Dr P.D. Taylor. Scale bars: 1 mm (a); 500 µm (b); 200 µm (c-d); 100 µm (e-g); 400 µm (h-i).

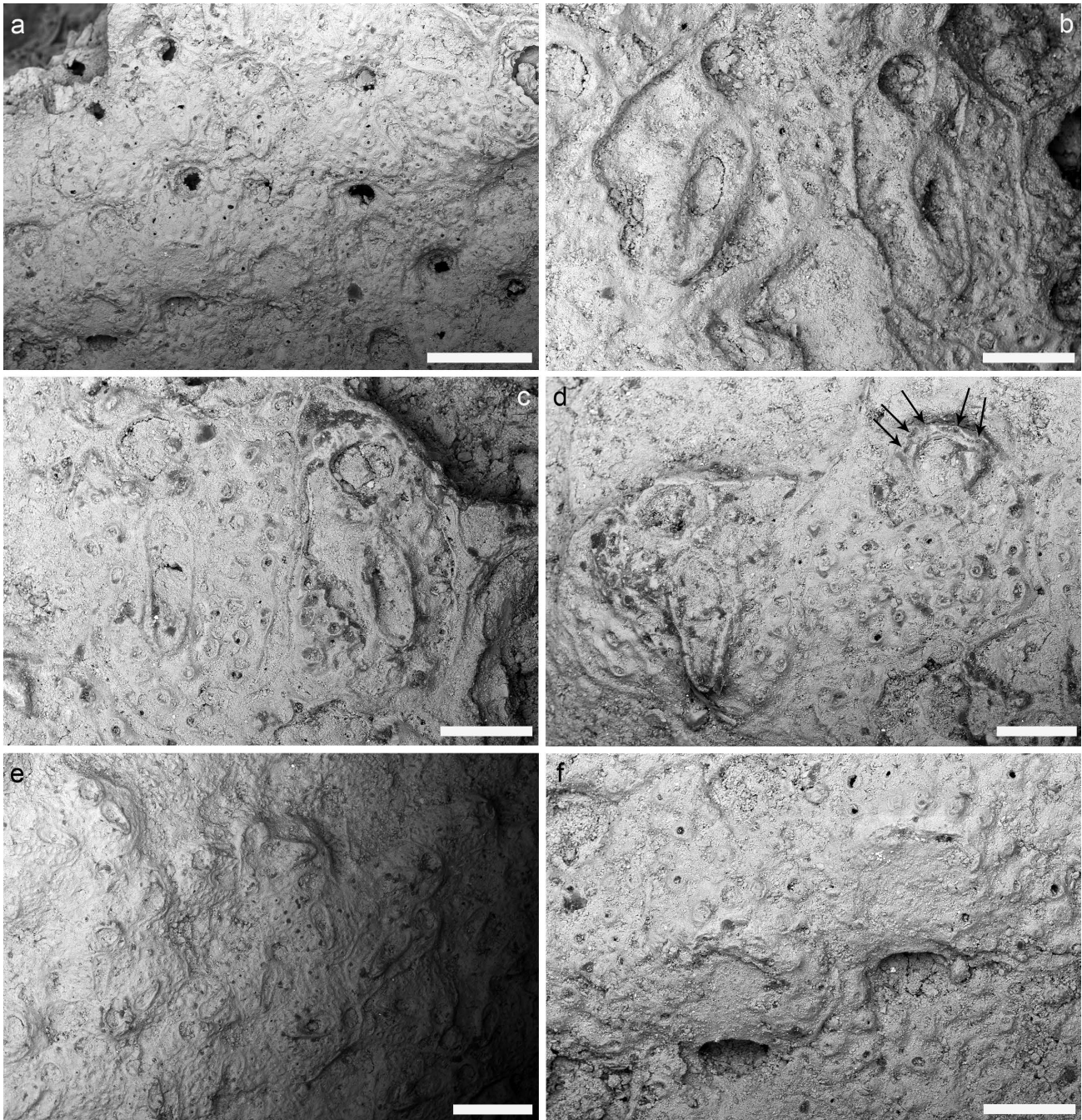


Fig. 12 - Holotype of *Stephanotheca leontiniensis* (Waters, 1878) comb. nov., Pleistocene, Brucoli, NHMW 2021/0166/0013. a) View of the best preserved portion of the colony. b-c) Close-up of autozooids showing the large, adventitious avicularia either elongate triangular with rounded tip or elliptical. d) Close-up of two autozooids showing the outline of the orifices; the autozoid on the right lacks the frontal avicularium and shows distal oral spine bases (arrowed). e) View of a portion of the colony showing the irregular arrangement of the zooids. f) Close-up of two ovicells. Scale bars: 500 μ m (a, e); 200 μ m (b-d, f).

Remarks - *Stephanotheca leontiniensis* comb. nov. was reported living in the Mediterranean by Rosso (2003, as *Schizomavella leontiniensis*) but subsequently removed from the checklist by Rosso & Di Martino (2016). This decision was based on Reverter-Gil et al. (2015) who synonymised the Recent records of this species in Gautier (1962) and in Waters (1879) from the Bay of Naples (erroneously reported as Taranto Bay, Naples) (southern Italy) with *S. (S.) cornuta* (Heller, 1867), after examination of two specimens in Waters' Collection in the Manchester Museum.

The fossil species from Brucoli was also considered to be a senior synonym of *Schizomavella cuspidata* (Hincks, 1880), now accepted as junior synonym of *S. (S.) cornuta*, by Reverter-Gil & Fernández-Pulpeiro (1996). However, Reverter-Gil et al. (2015, p. 7) only tentatively synonymized Waters' variety with *S. (S.) cornuta* because of its unclear identity and the impossibility to check the original material. These authors acknowledge that the figure in Waters (1878, fig. 5) shows a different-shaped orifice and avicularia somewhat triangular in shape and frequently detached from the orifice, features that suggest

a close resemblance with *Stephanotheca arrogata* (Waters, 1879) (Reverter-Gil et al., 2012), as previously pointed out by Harmer (1957). Although poorly preserved, both these differences are still visible in the holotype of *S. leontiniensis* (Fig. 12), while the main recognizable differences with *S. arrogata* are: 1) the ovicell, with the seemingly smooth and imperforate central area (although it should be acknowledged that this could be an effect of diagenesis), peripheral pseudopores (as in the autozooidal frontal shield), and with the secondary calcification present only distally and distolaterally, not extended proximally; and 2) the size and shape of the frontal shield pseudopores, small and funnel-shaped in *S. arrogata*, but larger with a raised rim in *S. leontiniensis*. However, the species is here reassigned to *Stephanotheca* based on its ovicell closure, which seems cleithral (i.e., ovicell closed by the zooidal operculum), while it is acleithral in *Schizomavella*.

Stephanotheca leontiniensis is known to date only from its type locality.

DISCUSSION

Restudy of historical museum collections is of paramount importance to clarify the taxonomic identity and status, and consequently the stratigraphical and geographical distribution, of species described in early taxonomic works. As in other early bryozoan works (e.g., Canu, 1922; Vigneaux, 1949), the new species described by Waters (1878) have never been recorded since their first description, either because the type localities have not been resampled due to inaccessibility/disappearance or the difficulty in precisely locating them, or because they are rare or their identities could not be clearly understood from the original descriptions and figures (Di Martino & Taylor, 2017; Di Martino et al., 2018).

This revision has focused on the new species and subspecies introduced by Waters (1878) as well as some other critical specimens. Application of SEM has allowed clarification of the identities of *Biflustra rhynchota*, *Eschara lunaris* and *Lepralia auriculata* var. *leontiniensis* for the first time. While *B. rhynchota* and *E. lunaris* are either formally recognized as synonyms or shown to have close affinity with well-known, widely recorded Atlantic/Mediterranean species (i.e., *Amphiblestrum lyrulatum* and *Microporella verrucosa*, respectively), *L. auriculata* var. *leontiniensis* is reassigned to *Stephanotheca* and confirmed as a valid species, only recorded from the type locality by a single colony. In addition, the re-examination of the syntypes of *Onychocella angulosa*, a Reuss species first described from the Middle Miocene of Austria and subsequently considered as widespread in Cenozoic to Recent Mediterranean deposits, has allowed the designation of a lectotype, confirming the presence of this species also in the Pleistocene of Brucoli, and better defining the differences with the Recent *Onychocella marioni*. On the other hand, the specimen identified by Waters as *Microporella morrisiana*, a Busk species from the Pliocene Coralline Crag of England, not recorded anywhere else in the Mediterranean area, was revealed to be instead *Microporella appendiculata*, a common Pliocene-Recent Mediterranean species.

Of the 43 species recorded by Waters (1878), only four were considered as new taxa or varieties, while most of the specimens were attributed to previously described species, spanning from the Late Cretaceous/Eocene to the Recent. Several species were identified as species commonly found in the Pliocene Coralline Crag, and some also in the Upper Cretaceous Chalk. Such an extensive geographical and stratigraphical distribution is highly unlikely, as already seen for some of the taxa re-examined here, highlighting the need for further studies of historical palaeontological collections. The use of this rich data source is important to better define the distributional boundaries (both geological and spatial) and abundance patterns of the species recorded, both parameters essential for meaningful biodiversity studies (e.g., Meineke et al., 2018; Gotelli et al., 2021).

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