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# ON THE VALIDITY OF THE GENUS *ENANTIOSULA* CANU & BASSLER AND A NEW DESCRIPTION OF *ENANTIOSULA VIALLII* POLUZZI, 1975 LATE-PLIOCENE SPECIES OF THE MEDITERRANEAN BASIN

(Bryozoa Gymnolaemata Cheilostomata Adeonidae)

#### Riassunto

[Sulla validità del genere Enantiosula Canu & Bassler (Bryozoa, Cheilostomata) e una nuova descrizione di Enantiosula viallii Poluzzi, una specie mediterranea del Pliocene Superiore] Viene descritta Enantiosula viallii, specie istituita da Poluzzi nel 1975 su colonie raccolte nella sezione pliocenica di Monte Padova affiorante a sud-ovest di Castell'Arquato (Piacenza). Le colonie qui descritte dovrebbero provenire dagli stessi livelli da cui Poluzzi raccolse gli esemplari utilizzati per istituire i tipi della sua specie. Dalla sua istituzione questa specie non è più stata segnalata in altri affioramenti neogenici italiani, solo la Microporella (Fenestrulina) ciliata var. senensis Neviani (1900), probabilmente, potrebbe essere da attribuire alla E. viallii, così la specie poteva essere presente anche nel Pliocene di Siena. E. viallii viene comparata a specie fossili ed attuali ritenute qui contenute nel genere Enantiosula Canu & Bassler (1930), che spesso però dagli autori sono state considerate appartenenti al genere Triporula Canu & Bassler (1927) o ad altri generi. Si danno anche i motivi per cui il genere Enantiosula è da considerarsi un genere valido e non un sinonimo più recente di Triporula Canu & Bassler.

#### Abstract

[On the validity of the genus *Enantiosula* Canu & Bassler and a new description of *Enantiosula viallii* Poluzzi, 1975, Late-Pliocene species of the Mediterranean basin (Bryozoa Gymnolaemata Cheilostomata Adeonidae)]

New colonies of *Enantiosula viallii* Poluzzi have been collected in Pliocene terrigenous sediments cropping out in the Monte Padova section, located near Castell'Arquato (Piacenza Province, N Italy), and so they are described. This species was instituted by Poluzzi in 1975 upon material collected from the Pliocene Monte Padova section, thus the colonies described here should come from the same layers in which Poluzzi found the types of the species. After its foundation this species has never been collected in other Neogene Italian outcrops. Only *Microporella (Fenestrulina) ciliata* var. *senensis* Neviani (1900) might pertain to *E. viallii*, thus Poluzzi's species could perhaps be present also in the Pliocene of Siena. *E. viallii* is compared with fossil and Recent species belonging to genus *Enantiosula* Canu & Bassler (1930), which have sometimes been thought by some authors as pertaining to the genus *Triporula* Canu & Bassler (1927) or to other different genera. *Enantiosula* is thought here as a valid genus, thus it cannot be regarded as a junior synonym of *Triporula* Canu & Bassler and the reasons of this assertion are given.

Key words: Bryozoa, Cheilostomata, *Enantiosula*, Pacific, Atlantic, Mediterranean, Paratethys, *Enantiosula viallii*, Pliocene.

# Introduction

Investigations of bryozoan assemblages, from Late-Pliocene sedimentary layers cropping out in the Monte Padova section located near Castell'Arguato (Piacenza Province, N. Italy), have yielded new colonies of *Enantiosula viallii* Poluzzi. Poluzzi assigned his species to the genus *Enantiosula* Canu & Bassler (1930), which had been established by its authors upon the Recent type-species *Enantio*sula manica Canu & Bassler (1930) from Galapagos Islands (Eastern Pacific). As per the records of Osburn (OSBURN, 1952), E. manica has been collected in the Central Eastern Pacific, from Galapagos Islands to California. Poluzzi's generic attribution seems to be appropriate, because E. viallii shares a suite of characters with the type-species E. manica Canu & Bassler. Before the foundation of Enantiosula manica, in 1923 Canu and Bassler (CANU & BASSLER, 1923) instituted Adeonel*lopsis coccinella* from the Lower Miocene of Florida, but this species should be assigned to genus *Enantiosula* (see WINSTON, 2005), and, in 1927, these authors (CANU & BASSLER, 1927) established also the genus Triporula upon the type-species "Triporula (Escharipora) stellata Smitt, 1873", a Recent species from the Central Western Atlantic, which is a little similar to the type-species of *Enantiosula*, but different enough from the latter to do Triporula stellata (Smitt) to be thought here pertaining to a different genus. In the Bock Ed. 'triporula' (2002) the two species, Enantiosula manica Canu & Bassler and Triporula stellata (Smitt), are regarded as different species, but are both inserted in the genus *Triporula* Canu & Bassler, because in the Bock Ed. 'triporula' (2002) genus Enantiosula is thought as a "subjective synonym" of Triporula. Maybe this synonymy could have been induced by Cook (COOK, 1967), who synonymised the genus *Enantiosula* with *Triporula* and also Enantiosula manica Canu & Bassler with Triporula stellata (Smitt). Besides Canu and Bassler (CANU & BASSLER, 1927), among characters of the genus Triporula, referred: "avicularia adjacent to the aperture, two proximal with the beak oriented superiorily". This disposition of lateral avicularia is that always occurring in *Enantiosula*, whereas in type-species *Triporula stellata*, the two lateral avicularia are placed almost horizontally and oriented toward mid-line. As a result of the synonymies by Cook (Cook, 1967) and the direction of lateral avicularia given by Canu & Bassler (CANU & BASSLER, 1927) in genus Triporula, subsequent authors probably thought the genus *Enantiosula* as a synonym of *Triporula* Canu & Bassler and consequently E. manica, the type-species of Enantiosula, to belong to genus Triporula. Cook (COOK, 1967) gave the reasons of her assertion relating to the two synonymies only with "Enantiosula, with the type-species E. manica, was defined with the frontal 'a tremocyst'. Examination of specimens shows that the frontal shield of E. manica is of the same nature as that of T. stellata and that the two species are not only congeneric but synonymous". This opinion of Cook's seems to be little useful and very vague. Before and after COOK (1967), no author defined, in detail, the synonymy between the two genera. Objectively, in line with the Bock Ed. 'triporula' (2002), Enantiosula manica and Triporula stellata are rather different, because of the several characters doing the two species to be separable. Fallen the synonymy between the species *Enantiosula manica* and *Triporula stellata* given by Cook (Cook, 1967), also the synonymy between the two genera can be rejected.

In my opinion, the Pliocene *Microporella (Fenestrulina) ciliata* var. *senensis* Neviani (1900), Lower Miocene *Adeonellopsis coccinella* Canu & Bassler (1923), Recent *Enantiosula manica* Canu & Bassler (1930), Recent *Enantiosula manica* Canu & Bassler in OSBURN (1952), Recent *Enantiosula plana* Osburn (1952), Recent *Anarthropora coccinella* (Canu & Bassler) in RUCKER (1967), Recent *Triporula stellata* (Smitt) in COOK (1967, ? *pars*), Recent *Triporula stellata* (Smitt) in COOK (1968), Pliocene *Enantiosula viallii* Poluzzi (1975), Recent *Triporula stellata* (Smitt) in COOK (1985), Pleistocene *Triporula stellata* (Smitt) in the Smithsonian Institution Ed. 'tripstel' (1998), Badenian ''? *Triporula* sp.'' in VAVRA (2002) and Recent, Australian South Pacific *Triporula biarmata* (Waters) in the Bock Ed. 'tribia' (2002), belong all to the genus *Enantiosula*. Maybe also the Mid-Miocene *Lepralia strenuis* Manzoni, that in 1869 (not in 1876), should pertain to the genus *Enantiosula*.

The Recent species of the genus Enantiosula occur in the tropical Atlantic (RUCKER, 1967; COOK 1967, 1968, 1985), in the Central Eastern Pacific (CANU & BASSLER, 1930; OSBURN, 1952; Bock Ed. 'tripman', 2002) and in the Australian South Pacific (Bock Ed. 'tripbia', 2002). While in the Miocene, Enantiosula species were present in the Central Atlantic (CANU & BASSLER, 1923), Mediterranean (? MANZONI, 1869) and Europe Paratethys (VAVRA, 2002). Maybe this genus had its origin in one of these three sea-regions. In Pliocene, only the species Enantiosula viallii has been recorded (? NEVIANI, 1900; POLUZZI, 1975) and has been found in sediments of the Central Mediterranean. The Triporula stellata (Smitt), figured in the Smithsonian Institution Ed. 'tripstel' (1998), if it is confirmed to pertain to genus *Enantiosula*, may be the only record of a Pleistocene (within biozone NN19, by MARTINI, 1971) Enantiosula species and has been found in sediments of the Western Central Atlantic, at Moin Formation, Limon (Costa Rica). The genus Triporula might consist of two species only, Recent T. stellata (Smitt), the type-species of the genus, and, perhaps, Miocene Australian Triporula biarmata (Waters), if it is confirmed to pertain to genus Triporula, because also the Miocene specimen figured in the Bock Ed. 'tripbia' (2002) might pertain to Enantiosula. The genus *Triporula*, even if its Recent type-species occurs in the Central Atlantic (SMITT, 1873; BASSLER, 1953; Bock Ed. 'triporula', 2002; WINSTON, 2005), could perhaps have had its origin in the Miocene of Australia or New Zealand (Cook, 1985; Bock Ed. 'tripbia', 2002), probably due to the records of Early Miocene Microporella macropora var. biarmata Waters (WATERS, 1882) from Mount Gambier (South Australia) and Middle Miocene Triporula biarmata (Waters) from Muddy Creek (Victoria, South Australia), the latter is that of the Bock Ed. 'tripbia' (2002). As a result, the origin region of *Triporula* should be very distant from the probable origin region of *Enantiosula*. Besides, in the Miocene and Lower Pliocene of the Atlantic, Mediterranean and Paratethys, *Triporula* species have never been collected. Maybe an *Enantiosula* species had to have migrated from the Central Atlantic in the Easter Central Pacific, where the ancestor of *E. manica* and *E. plana* settled. This migration had to have obligatorily happened when the Atlantic and the Pacific were still communicating, that was till around 3 million years ago, in the Late-Pliocene. Maybe also a species of *Triporula*, if this genus really had origin in the Pacific, had to have migrated from the Pacific to the Atlantic when the two oceans were still communicating, and *Triporula stellata* or its ancestor settled. The presence of the genus *Enantiosula* species (the ancestor of or one's *E. viallii*) from the Atlantic, after the Messinian Salinity Crisis (Hsü et al., 1972, Hsü et al., 1978) happened in the Mediterranean in the uppermost Miocene. Thus, in accordance with this assertion, the genus *Enantiosula* had to be present also in the Pliocene of the Atlantic.

The living species of *Enantiosula* are encrusting from infralittoral to shallow circalittoral (OSBURN, 1952; RUCKER, 1967; COOK, 1967, 1968, 1985) and can be also epiphytic (CANU & BASSLER, 1930; COOK, 1968, 1985). Also fossil species had to be of shallow-water and, maybe, epiphytic too.

## Sample location and stratigraphic setting

The specimens of *Enantiosula viallii* here described are usually well-preserved, are not very common within the inspected silty pelite sediments, come from the Late-Pliocene Monte Padova section, located near Castell'Arguato (Piacenza Province, N. Italy) (see: BARBIERI, 1967; POLUZZI, 1975; RIO et al., 1988; RAFFI et al., 1989; Pizzaferri & Berning, 2007), and have been collected in those layers interbedded between the First and Second Monte Giogo Biocalcarenites in RAFFI et al. (1989) and including also the First Monte Giogo Biocalcarenite. In the stratum corresponding to the Second Monte Giogo Biocalcarenite and in the layer just below it, Enantiosula viallii would seem to be wanting. These new colonies of Enantiosula viallii should come from the same layers where Poluzzi found his specimens, used to establish the species in 1975. The stratigraphic position of the samples 115 and 123, from the drawn stratigraphic section in POLUZZI (1975), seems to agree with that of my findings. Due to a transcription mistake perhaps, sample 122, in Enantiosula viallii text in POLUZZI (1975), was not recorded by the author in his sample description and drawn stratigraphic section, thus it might correspond to Poluzzi's sample 112. The sedimentary layers, containing this species of Poluzzi's, are Piacenzian (Late-Pliocene) in age, within planktonic foraminifera biozone MPI5a (CITA, 1975, emend.) and calcareous nannoplankton biozone MNN16a (Rio et al., 1990) (Rio et al., 1988; RAFFI et al., 1989; ROVERI et al., 1998; MONEGATTI et al., 2001; MONEGATTI et al., 2002; ROVERI & TAVIANI, 2003) and comprised between 2,7 and 3,1 million years according to RAFFI et al. (1989), but, more probably, these layers are 2,8 to 3 million years old (MONEGATTI et al., 2001; MONEGATTI et al., 2002). These terrigenous sediments consist of silt or muddy silt and can sometimes include an abundant biogenetic fraction, they were of shallow circalittoral environments (around 50-70 m deep), rich in vegetation and having also some episodes of low oxygenation (RIO et al., 1988).

## Material and methods

The studied material consists only of *Enantiosula viallii* specimens collected at the Late-Pliocene Monte Padova section. The sampled sediments were dried, broken into little pieces, treated initially with water and hydrogen peroxide ( $H_2O_2$ ), then, in succession, with sodium hypochlorite (NaClO), very little sodium hydroxide (NA(OH)) and still hydrogen peroxide, washed and sieved to remove the fine-grained matrix. Part of the studied material is stored at the Museo Geologico "Giuseppe Cortesi" of Castell'Arquato (Piacenza Province, Italy), sample with inventory number MG0995; the remaining material is in a private collection. A complete quotation sequence, relating to the species pertaining to the genera *Enantiosula* and *Triporula*, has helped to prove the validity of genus *Enantiosula* Canu & Bassler, and also that *Enantiosula* and *Triporula* are two different genera. Besides, with this quotation sequence, I have been able to assign to the genus *Enantiosula* some species in past times regarded as belonging to other genera.

# Systematics and description of the species

Bryozoa suprageneric systematics follows that of D.P. Gordon, (Bock Ed. 'treat-fam.pdf', 2007)

Suborder	Neocheilostomina d'Hondt, 1985		
Infraorder	Ascophora Levinsen, 1909		
"Grade"	Umbonulomorpha Gordon, 1989.		
Superfamily	Adeonoidea Busk, 1884.		
Family	Adeonidae Busk, 1884.		
Genus	Enantiosula Canu & Bassler, 1930.		

Gordon did not insert genus *Enantiosula* Canu & Bassler in the Bock Ed. 'treat-fam.pdf' (2007) and 'treatgen.pdf' (2007).

#### Enantiosula viallii Poluzzi, 1975.

? 1900 Microporella (Fenestrulina) ciliata var. senensis n. var. - Neviani, p. 363, text-fig. 2.
1975 Enantiosula viallii n. sp. - Poluzzi, p. 66, T. 19, fig. 7, T. 21, figs. 7-9.

Text of Poluzzi (Poluzzi, 1975).

Enantiosula viallii n. sp.

Materiali. Val d'Arda, Piacenza:

*Holotypus*: I.B. 390, camp. 122. Esemplare illustrato a t. 19, f. 7, e a t. 21, ff. 7, 8 e 9. Zoario cupuliforme del diametro di 8 mm, sviluppato su un frammento conchigliare.

*Paratipi*: I.B. 391, camp. 115, I.B. 392, camp. 123, M. Padova, Pliocene medio (zona a *Globorotalia* gr. *crassaformis*). Frammenti multilamellari isolati.

*Locus typicus et status typicus*: M. Padova, Pliocene medio (zona a *G*. gr. *crassaformis*), camp. 122, argille alternate a sabbie, circa 12 m. sopra le argille *s.s.* che costituiscono la base dello spezzone di serie.

*Derivatio nominis*: in onore del Prof. Vittorio Vialli, il quale ha promosso ed incoraggiato nel nostro Istituto lo studio dei Briozoi neogenici.

Collocazione dei materiali: Museo dell'Istituto di Geologia e Paleontologia di Bologna.

Diagnosi. Aechmella con zoario massivo, vibracoli (?) talora bilaterali, tangenti all'arco superiore dello zoecio, pseudo-spiramen stretto e asimmetrico.

Descrizione. *Zoario* a cupola emisferica, sviluppato su di un frammento organogeno (I.B. 390) in lamine di zoeci fortemente convesse, sovrapposte e coassiali. *Zoeci* di forma subesagonale o rombica con lati superiori curvilinei, ben distinti solo dal peristoma distale rilevato e dalle camere avicolariane, disposti in file longitudinali alternanti, discendenti dall'apice della cupola verso la base. *Apertura esterna* semicircolare con labbro inferiore retto o lievemente inflesso. *Avicolario* bilaterale « unguicolato », piazzato sul peristoma, occupante quasi metà lato dell'apertura, il rostro leggermente ricurvo e puntato verso l'alto, provvisto, se integro, di due piccoli condili pivotali. Grossi *eterozoeci (vibracoli ?)*, occasionalmente sdoppiati, tangenti all'arco superiore dello zoecio. *Pseudospiramen* stretto e asimmetrico presente solo nelle celle meno calcificate. *Muro frontale* porcellanaceo, depresso rispetto la linea degli avicolari, leggermente rigonfio e perforato da una decina di profondi tremopori che ai bordi possono assumere disposizione ordinata e lineare. *Septule* in doppia fila, una percorrente l'intero perimetro zoeciale nell'intersezione col muro di base, l'altra parallela e spostata verso l'alto di 0,08 mm. Occasionalmente le file sono sostituite da grosse septule uniporose irregolari. *Dietelle* presenti. *Ovicelle* non osservate.

Osservazioni: *Variabilità*: come già indicato nella descrizione, *E. viallii* porta un pseudospiramen poco profondo sotto il labbro inferiore del peristoma; tale struttura è tuttavia occasionale e pare confinata di preferenza nelle zone meno calcificate della colonia. Le fotografie al microscopio JSM-2 di sezioni trasversali del peristoma leggermente abraso, hanno mostrato come attorno alle camere avicolariale affiorino almeno tre strati distinti

## del muro frontale (t. 21, f. 7).

*Sistematica e affinità*: *E. Viallii* presenta le maggiori affinità con *E. manica* Canu & Bassler 1930 b (p. 23, t. 3, ff. 6-11). Di questa però non possiede la differenziazione stadiale dei tessuti (« The frontal is ... ornamented with tremopores on the young cells and with radial costules on calcified ones », op. cit. p. 23), né i caratteristici tremopori tubulari e salienti che, al contrario, nella specie italiana sono sempre piuttosto affondati. Nella descrizione originale di *E. manica* inoltre non si fa cenno ai grossi eterozoeci, da me indicati dubitativamente come vibracoli, alla fila di septule uniporose sui muri verticali e al pseudospiramen. Il carattere peculiare del genere, cioè l'inversione degli zoeci e la loro tendenza ad orientarsi verso la base della colonia, è invece sempre presente e facilmente rilevabile (t. XIX, f. 7).

Misure. Olotipo I.B. 390. Estremi di variabilità e medie (tra parentesi).

Ø base	= 8 mm	lap	= 0,09-0,15 (0,12)
altezza	= 6,5 mm	Lav	= 0,16-0,24 (0,20)
Lz	= 0,45-0,53 (0,48)	lav	= 0,10-0,15 (0,13)
lz	= 0,36-0,42 (0,40)	Ø tremopori	= (0,03)
Lap	= 0,09-0,15 (0,13)		

Distribuzione stratigrafica. Pliocene medio della Val d'Arda.

Surely due to a mistake, Poluzzi begins his "Diagnosi" with Aechmella.

## Description

Colony encrusting, multiserial, plurilaminar, sometimes small unilaminar colonies can occur. Zooecia oval to oval-hexagonal, from almost flat to convex, gradually increasing in size, smaller in periancestrular area and wider in the peripheral one, distinct by shallow grooves. In the studied material a probable ancestroecium has only been recognized in one small colony, this zooecium regarded to be an ancestroecium is like a small normal zooecium with also the small distal peristomial avicularium and one marginal avicularium (see Pl. 1, fig. A, B, C). In regular substrata, zooecia can be arranged more or less quincuncially, but also almost radially in ancestrular area or in the first grown zooecia of superposed layers. Basal wall entirely calcified, while, in some small unilaminar colonies lacking substratum, it can be incomplete in its central part. Frontal wall almost smooth to more often finely grained, pierced by small to mid-wide scattered pores; when the frontal area is affected by thick secondary calcification pores are usually very small, but can sometimes be moderately wider. In frontal wall pores can be 8-9 in number, if mid-wide, to 21-22 when they are tiny. Stellate pores would sometimes seem be present, but might be non-frequent or very rare. Fractal edge of lots of stellate perforations may be non-visible due to fact that pores are usually filled by

fine grained sediments or granular diagenetic calcification, or because colonies have been treated with hydrogen peroxide, whose action can have detached the thin fractal edge. With mid-wide marginal pores, which are more evident in early ontogeny, some of them can be very reduced in size or overlaid by secondary calcification in later ontogeny. Marginal pores arranged in a single row between frontal walls of neighbouring zooecia and appear to be the opening of areolar tubules inserted within the vertical zooecium wall. Marginal pores might be regarded as frontal septular pores. Zooid did not produce its proximal vertical wall, but produced, together with the basal wall, only the distal piece of the vertical wall, that closing the zooecial chamber distally, then the frontal wall was added ("nonlineal budding process" in "nonlineal geometry" in LIDGARD, 1985). Tubules of marginal pores are inserted into the vertical wall, consequently each zooid produced only those marginal pores contained within the vertical wall that was produced by it. In vertical wall, next to level of the basal wall, there is a series of interzooecial pores and a second series of them occurs little below the level of the exit of marginal pores, the latter are connected to the tubules of marginal pores. Due to connection existing between interzooecial pores and marginal pores, the utilization of the marginal pores could perhaps be shared by both the neighbouring zooecia. Probably this species had to have also a frontal budding, from which at least the first zooecia of superposed layers grew and also the others zooecia of superposed layers could perhaps be helped in their growth. Secondary calcification affects frontal area of zooecia and, initially, can sometimes make a series of wide peripheral radial ribs, interposed between marginal pores. Zooecia of these Pliocene ephebastic and gerontastic colonies would seem to have none of these radial ribs. Orifice Dshaped, longer than wide, anter arched and poster almost straight; having a short lyrula with a slightly convex to straight border. Peristome well developed, very raised laterally and distally, proximally marked by a thin, low and straight rim. The peristome is formed laterally by the vertical wall of the chamber of the two lateral avicularia. Two lanceolate avicularia occur at both proximal corners of the peristome, with palate almost slender, acuminate, often with a slightly lateral curve, directed distally or distointernally when following the direction of the peristomial rim, and with risen vertex. The chamber of two lateral avicularia is closely applied to the peristome. All the avicularium types develop onto single or paired marginal pores. In these lateral avicularia there is a small tooth-shaped thickening placed on both the beginnings of the palate borders, and it is inside directed. This thickening can be regarded as a small pivotal condyle. The palate border usually has a thin rim. Rarely enough, some of these lateral avicularia (seen four in zooecia of several colonies) can be horizontally placed and directed toward the longitudinal midline, but this horizontal disposition should be due to a reparative growth after a breakage of the zooecium surface. In some zooecia one of the two lateral avicularia can sometimes be wanting, because not reconstructed after a breakage on the zooecium surface and so it has been overlaid by secondary calcification. In

zooecia of some colonies, one or both lateral peristomial avicularia can sometimes have a regeneration, where a new small subtriangular avicularium is reconstructed onto the wide original avicularian chamber, this small avicularium preserves almost the same direction of the underlying one. There can sometimes be also a small lanceolate avicularium, placed on the median area of the outside distal wall of the peristome. This distal avicularium is directed proximally and placed almost perpendicularly compared to the peristome border. In these Pliocene colonies this avicularium type does not developed on all zooecia, it is very little frequent. In zooecia of some colonies there can be also one or both of the lateral peristomial avicularia that are small in size, they seem to be like those described and figured by Osburn (OSBURN, 1952) in Enantiosula plana, but in these Pliocene colonies, having zooecia with small lateral avicularia, usually the small, distal avicularium is very little frequent to very rare, in contrast to as it is frequent in E. plana. In some zooecia another type of avicularium can occur, this further type of avicularium is small, subtriangular to almost suboval, placed on the peripheral border of frontal area and present in few zooecia, thus it is little frequent or very rare. Also these marginal avicularia develop onto marginal pores. The "pseudospiramen", referred by Poluzzi, is very rare, it can be present in almost all the zooecia of a colony, but in the great majority of colonies this "pseudospiramen" is absent. Ovicell absent, maternal zooecia not recognized.

# Remarks

Presence of the small unilaminar colonies, lacking substratum and with incomplete basal wall, may mean these colonies had also to be epiphytic probably. This can be accordant with the sedimentary layers regarded to be vegetation-rich (RIO et al., 1988), occurring in the inspected part of the Monte Padova section. In these populations of *E. viallii*, colonies, having zooecia with wider pores in frontal area, are low in number, colonies usually have frontal zooecium wall pierced by more numerous tiny pores. The characters shared between E. viallii and E. manica, the type-species of genus *Enantiosula*, are: D-shaped orifice, lateral peristomial avicularia directed almost distally, an inconstant distal peristomial avicularium, areolar tubules inserted in vertical wall, marginal pores in a single row placed between frontal walls of neighbouring zooecia and production only of the distal part of vertical wall (see fig. 10 in CANU & BASSLER, 1930). None of modern authors, including Poluzzi, referred the presence of a lyrula at the orifice of the species related to genus *Enantiosula* here. In these colonies of *E. viallii*, presence of a lyrula is indisputable, besides its presence agrees with the lyrula figured by Neviani (NEVIANI, 1900) in the zooecia of Microporella (Fenestrulina) ciliata var. senensis. A small lyrula would seem to occur also in the Pleistocene Triporula stellata figured in the Smithsonian Institution Ed. 'tripstel' (1998), and in Recent, Australian South Pacific, Triporula biarmata specimen figured in the Bock Ed.



Explanation of Plate 1.

*Enantiosula viallii* Poluzzi. figs. A, B, C - Probable ancestroecium in a small unilaminar colony; fig. B. magnification of the probable ancestroecium. fig. D - Zooecia with mid-wide pores in frontal wall. fig. E - Fragment of an unilaminar colony. fig. F - Zooecia with marginal avicularia. fig. G - Zooecia with raised lateral avicularia. fig. H - Young zooecia in which a row of marginal pores is visible. 'tripbia' (2002). When an *E. viallii* colony overspread a sub-cylindrical to elongate-hemispherical hard substratum it was growing in regular way toward the top of substratum; after the closing of the zoarium in the substratum top, beginning from the last grown zooecia, a new layer of zooecia was superposed with zooecia placed in inverse direction that is directed toward the substratum base. When other new superposed layers were added, usually zooecia were directed like those of the first superposed layer.

Microporella (Fenestrulina) ciliata var. senensis Neviani (1900) would seem to be very close morphologically to *E. viallii*, but should be it also geographically and stratigraphically, because coming from the Pliocene of Siena. In the text of Neviani (NEVIANI, 1900), the oral spines and the ascopore should do the Neviani's variety to be different from an *Enantiosula* species. However the oral spines of Neviani might be marginal pores and/or the hole of a small, distal, peristomial avicularium chamber. Besides Neviani could regard a central, large, orbicular pore of the frontal wall to be the ascopore. In the frontal wall of Neviani's variety there are few and mid-wide perforations like those occurring in some colonies from Monte Padova section. Orifice form, disposition and form of the two lateral avicularia and pores in frontal area do to suppose that the zooecia figured by Neviani should belong to an *Enantiosula* species, thus the Neviani's variety may pertain to Enantiosula viallii. The Badenian "? Triporula sp." from Forchtenstein (Austria) in VAVRA (2002) no doubt belongs to the genus Enantiosula, but seems to be slightly different from E. viallii, it may be allied to Lepralia strenuis Manzoni (1869). Unfortunately the poor condition of preservation of this Badenian figured specimen does not give the possibility of a detailed comparison with other species. Disposition and direction of the two lateral avicularia, in the figured zooecia of the Mid-Miocene Lepralia strenuis Manzoni (1869), remind those occurring in *Enantiosula* species, but this species of Manzoni's seems to be different from E. viallii and very similar to the Badenian "? Triporula sp." in VAVRA (2002). In the diagnosis and scarce description of Manzoni (MANZONI, 1869) there are some characters that may be attributable to an *Enantiosula* species. Among these characters the wide and deep channels, placed along the mural rim and containing the pores, may mean that in frontal area there are peripheral radial ribs. If this species of Manzoni's belongs to the genus *Enantiosula*, in that case *Enantiosula* was present also in the Mediterranean Miocene, thus it could be coeval with the Badenian "? Triporula sp." in VAVRA (2002) and, perhaps, also to be allied to it or belonging to the same species. A new finding of Lepralia strenuis specimens, in the Mid-Miocene of Serravalle Scrivia (Alessandria Province, N. Italy), may help to verify if this species of Manzoni's belongs to genus *Enantiosula* and is synonymous with the "? Triporula sp." in VAVRA (2002). Poluzzi's species appears to be also slightly different from the Recent Pacific Enantiosula manica Canu & Bassler (1930), owing to a different morphology of frontal area, where in the latter pores often can be in the centre of salient surfaces, whereas in Pliocene

colonies of *E. viallii* pores are placed in small to mid-wide and suborbicular to irregularly-shaped dimples. Instead the Recent Pacific *Enantiosula plana* Osburn (1952) would appear to be very close morphologically to some colonies collected in the Monte Padova section, because, in specimens of the two species, the small pores of frontal wall might be very similar in size, but the two species differ because the two, lateral, peristomial avicularia might be smaller in the Recent species from the Pacific, and in *E. viallii* the small, distal, peristomial avicularium is very rare. The Recent species, more closed to *E. viallii*, might be *E. plana*, but the little iconography concerning the latter does not permit to confirm it.

*Enantiosula viallii* went into the Mediterranean from the Atlantic in the Zanclean (Lower Pliocene) or lower Piacenzian (Late-Pliocene) and, maybe, its disappearance could be due to the climatic cooling coinciding with the Glacial Pliocene of SHACKLETON & al. (1984), begun in upper Piacenzian. In Italy the only certain record of *Enantiosula viallii* is that from the Piacenzian of the Monte Padova section (Poluzzi, 1975), outcropping near Castell'Arquato, but also the *Microporella (Fenestrulina) ciliata* var. *senensis* Neviani of the Pliocene of Siena (NEVIANI, 1900) may probably belong to *Enantiosula viallii*. This species of Poluzzi's has never been discovered in other Pliocene outcrops of Emilia Region and Italy.

# Ecology

Encrusting in shallow circalittoral, maybe also epiphytic.

# Stratigraphic distribution

Piacenzian (Late-Pliocene).

# Conclusions

The several Miocene to Recent records of *Enantiosula* species should do to think *Enantiosula* as a valid genus. In the time that is at least 15 million years due to Early Badenian in VAVRA (2002) (the oldest certain dating), the species of this genus have maintained all of peculiar and basic genus characters, and besides its probable origin region should be very distant from that of *Triporula*, if the origin region of the latter really results from the South Pacific. Lots of species, assigned to the genus *Triporula* in past times, have almost all characters occurring in the type-species of *Enantiosula*, thus they must be assigned to the genus established by Canu & Bassler (CANU & BASSLER, 1930). Characters of the two genera *Enantiosula* and *Triporula* might appear to be similar, but should actually be rather different orifice shape, different location and direction of the two lateral peristomial avicularia and different morphology of the frontal area. In all species regarded here to belong to *Enantiosula*, the peculiar and basic genus characters have been constant in the time, always present and fairly different from those occurring in

the type-species of *Triporula*, to do the two genera to be separable. Marginal pores in a single row, due to areolar tubules inserted into vertical wall, zooecial growth with production only of the distal part of the vertical wall and presence in some species of a small lyrula have never been related in the type-species of *Triporula*. Thus it is fairly rash to relate *Triporula stellata*, the type-species of genus *Triporula*, with the characters occurring in the type-species of *Enantiosula*.

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