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BRYOZOANS AS SEDIMENTARY INSTABILITY INDICATORS

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Riassunto. In numerose sezioni stratigrafiche italiane di età neogenica, contenenti faune a Briozoi, si è osservata una elevatissima dominanza dei Briozoi lunulitiformi in livelli caratterizzati da una abbondante componente pelitico-siltosa del sedimento. Tutti i casi considerati riguardano sempre Popolamenti Eterogenei. Questi popolamenti si sviluppano ed evolvono molto rapidamente in substrati caratterizzati da velocità di sedimentazione irregolare, dovuta a cambiamenti climatici o ad attività tettonica. Indagini preliminari su questo argomento mostrano che i Briozoi lunulitiformi sono indicatori di instabilità, caratteristici della fase iniziale dei Popolamenti Eterogenei.

Abstract. In several Neogene stratigraphic sections of Italy bearing bryozoan assemblages, a great dominance of lunulitiform bryozoans was recorded in those levels characterized by the abundant muddy fraction of the sediment, and by the presence of Heterogeneous Communities. These latter settle and quickly evolve on sea-floors where anomalous sedimentation rates occur, caused by climatic or tectonic factors. Research carried out so far shows that lunulitiform bryozoans may be regarded as instability indicators, characterizing the early phase of Heterogeneous Communities.

Introduction.

Recently, the paleoecological methods have been increasingly used in the study of neotectonic evolution of Plio-Pleistocene basins, combined with usual geologic, stratigraphic, structural, and seismic methodologies.

In this case, the paleoecological approach is mainly concerned with the structure of fossil communities and their evolution in time and space. In fact, evidence does exist that tectonic activity, causing variations of the nature and rate of sediment production, strongly influences the composition and trophic structure of benthic marine communities (Di Geronimo, 1984). Moreover, the paleoecological method allows to notice also those minor events of slight tectonic instability, which are always accurately recorded by modifications of paleocommunities (Di Geronimo & Robba, 1989). Several examples in this respect, connected with Plio-Pleistocene tectonics, are to be

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found in Central Sicily (Di Geronimo, 1984; Amore et al., 1985; Di Geronimo & Robba, 1989), Southern Italy (Barrier et al., 1985), and in some localities of Northern Italy (Pelosio & Raffi, 1977; Benigni & Corselli, 1981). They concern fossiliferous sequences in which normal and well structured paleocommunities are suddenly replaced by more or less unstructured (in the sense of Picard, 1965) ones.

Bryozoans are generally lacking from such paleocommunities; if present, they form low diversity to oligospecific associations. It is of note that lunulitiform colonies become the dominant morphologic type when instability occurs, and are the only represented in more extreme conditions.

The heterogeneous communities and paleoenvironment reconstruction.

Changes in composition and structure of soft bottom benthic communities occur as a consequence of variations of sediment supply: thus, specific biocoenoses may gradually replace one another (Picard, 1965). A sudden change, often involving an increased turbidity, can quickly alter a previous biocoenotic equilibrium bringing to an unstructured biocoenosis. In this case, the original biocoenosis is replaced by a transitional association which settles temporarily in between the previous community and a subsequent one corresponding to a newly achieved equilibrium (Di Geronimo & Robba, 1989).

These transitional associations, described for the first time as "Biocoenosis of unstable soft bottoms" by Pérès & Picard (1957), and later named Heterogeneous Communities by Picard (1965), are affected by a permanent instability as regards both qualitative and quantitative faunal and floral composition. The impoverished fauna is largely dominated by filter feeders while deposit feeders are strongly reduced or even absent. As regards this latter aspect, it is worthy of note that tectonic activity commonly results in an increased sediment load of rivers involving an increase of turbidity. The latter causes the destruction of the alimentary film on the sea-bottom surface (Di Geronimo, 1984), and alters significantly the trophic structure of benthic communities.

According to Di Geronimo & Robba (1989), three main phases can be recognized in the development of Heterogeneous Communities (Fig. 1).

- The first phase (PE 1) is characterized by: diversity usually very high; dominance of suspension-feeders; presence of several stocks of characteristic species pertaining to different biocoenoses; appearance of some species which positively indicate instability (in the sense of Pérès & Picard, 1957) such as the molluscs *Nuculana pella*, *Lucinoma borealis*, *Lunatia guillemini*, *Dentalium rubescens*. The community exactly corresponds to Picard's (1965) PE, and can easily evolve toward a specific, stable biocoenosis which can be predicted in most cases.

- The second phase (PE 2) develops concomitant with a further increase of water turbidity, and is characterized by: distinct drop down of species diversity due to strong reduction or complete disappearance of detritus feeders and decrease of suspen-

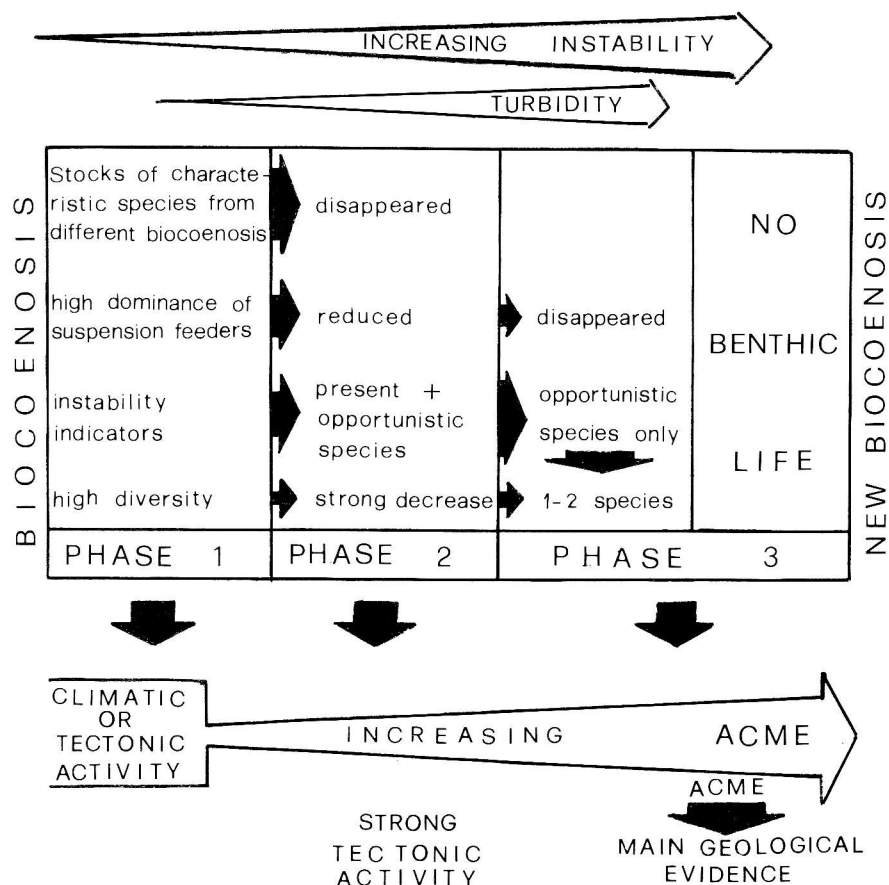


Fig. 1 - Instability model according to Di Geronimo & Robba (1989).

sion-feeders; absence of species characteristic of specific biocoenoses; settlement of a few opportunistic species represented by a great number of specimens.

- The third phase (PE 3) is characterized only by opportunistic taxa whose number tends to reduce to 1-2 species and later to disappear. When turbidity reaches its maximum, a condition commonly observed near river mouths, no benthic organisms can survive (Di Geronimo & Robba, 1989).

Typic Mediterranean opportunistic species are the small bivalve *Corbula gibba* and the polychaete *Ditrupa arietina* which are found in high turbidity stress conditions both in modern environments and Neogene deposits.

The establishment of Heterogeneous Communities can be caused by two different types of instability, 1) climatic of 2) tectonic (Di Geronimo, 1984; Di Geronimo & Robba, 1989).

The climatic instability is linked to long rainy periods resulting in an increased load and consequent rivers discharge. The sedimentation rate becomes very high, and

a predominantly silt and clay deposition occurs. The tectonic instability (activity), through the rise of a land area or the downthrow or sinking of the continental shelf, produces the lowering of rivers base level, thus a more active erosion, and basically the same sedimentary consequences as in the previous case.

The two types of instability are recognizable within sedimentary sequences, on the basis of inferred paleobathymetry and thicknesses combined; criteria have been discussed by Di Geronimo & Robba (1989). It results that the identification of an Heterogeneous Community within a stratigraphic unit provides evidence of instability, and can be effectively used in order to reconstruct the tectonic history of a given area.

Lunulitiform bryozoans.

Lunulitiform bryozoans comprise cup-shaped forms usually ranging in diameter from a few millimeters to few centimeters. Lunulitiform zoaria are free-living and simply need small sand particles ensuring the larval settlement and metamorphosis. These sand grains may have both organic or inorganic nature, and are quickly encrusted and subsequently envelopped by the adult colonies. Zooids and vibracula are regularly arranged in radial rows, and their frontal walls form the convex frontal surface of the zoarium. The basal surface, which can be flat or concave, becomes increasingly thick during the growth.

Lunulitiform colonies of several species are always associated with soft bottoms (Cook, 1963). Their strong and flexible vibracular setae are able to execute wide movements in order to remove fine sedimentary particles from the zoarial frontal surface (Lagaaij, 1963; Greeley, 1967). According to Cook (1965), lunulitiform zoaria can rise from the substratum standing on peripheral vibracular setae; in such a position, colonies increase their virtual supporting surface and become very stable.

According to Schopf (1969), this zoarial type, because of its peculiar features, can withstand moderate (10-100 cm/1000 years) to high (1000 cm/1000 years) sedimentation rates. Moreover, Cook's (1965) observations on lunulitiform bryozoans show that living colonies are able to get the sediment surface even if dispersed within a washed sand layer in shallow trays of sea-water. Several lunulitiforms reach the interface, always with their convex side upward, in about 40 hours. Cook noted that "colonies emerged gradually removing the sand placed on their top by means of regular sweeping movements of the frontal setae while the peripheral ones remain open. So, small grains were dislodged by the setae and rolled down the sloping sides of the zoarium".

The same process ensures lunulitiform colonies to regain the sea-bottom surface if suddenly buried, even by some centimeters of sedimentary particles. Moreover, lunulitiform colonies are able to survive in such unfavourable conditions for a relatively long period. The possession of these abilities accounts for the modern geographical distribution of lunulitiform bryozoans which, according to Lagaaij (1963), Cook (1965), Greeley (1967), and Cadée (1975), are particularly abundant in the circumtropi-

cal deltaic areas (viz., Mississippi, Niger, Amazon etc.) where they always form oligospecific communities. In these areas, lunulitiform bryozoans reach very high abundance values, up to several thousands of specimens per square meter.

A high dominance of lunulitiform bryozoans, up to 30% of the whole benthic fauna, has been observed on the Guayana continental shelf, at depths of 20-60 meters within the "middle shelf" (Cadée, 1975). There, lunulitiforms inhabit a bottom swept by moderate currents (34-66 cm/s); the sedimentation rate is moderate to low in respect to the "inner shelf" where it exceeds 100 cm/1000 years, over a substrate entirely made of very fine particles. The extremely soft nature of the substrate as well as the lack of grains large enough to allow the larval settlement would prevent lunulitiform bryozoans from growing in the "inner shelf". Nevertheless, lunulitiforms are very abundant in the Mississippi deltaic area, also on bottoms with a great quantity of suspended matter (Greely, 1967).

As regards the Mediterranean region, lunulitiforms (*Cupuladria canariensis* and *Reussirella doma*) resulted to be very abundant off Oran (Caulet, 1972). There, lunulitiform death assemblages including abraded specimens as well were recovered from bottoms of pure mud in the outer shelf, whereas populations are present in the inner shelf only. Number of bottom samples from this latter sector contain a mud proportion of 15-35%. In these samples, lunulitiform bryozoans result to be members of true Heterogeneous Communities including high-dominance molluscan species that are currently regarded as instability indicators (*Nuculana pella* and *Tellina distorta*).

It is of note that the just reported examples concern areas characterized by quite different climatic conditions. A higher turbidity concomitant with moderate sedimentation rates is more likely to occur in rainy intertropical regions, i.e. Guayana, than in relatively arid regions such as Algeria.

Examples from the fossil record.

We have studied some Neogene and Quaternary stratigraphic sections of Italy (Fig. 2), with the aim of pointing out the meaning of lunulitiform bryozoans and their role within Heterogeneous Communities.

The sediment containing the considered Heterogeneous Communities is predominantly fine sand with a mud proportion ranging from 20% to 71%; the muddy fraction is exceptionally reduced to 3-7% only in samples from Monte Navone Section (Tab. 1).

Benestare. It is a classic locality of Calabria (southern Italy) that yielded a very rich fauna of probable Late Tortonian age, formerly described by Seguenza (1879). The sedimentary sequence (Fig. 2, 3) is made of clay, 100 m thick, with thin layers of silty sand and sandy silt intercalated in the uppermost part; a bed of siliceous sand very rich in fossils makes the top, and is overlain by Messinian gypsiferous layers. Two silty intercalations in the uppermost part of the clayey body have been sampled. The megafaunas are characterized by a significantly high dominance of *Ditrupea* sp. and

Corbula gibba which together exceed 60% of the whole assemblages; other relevant members of the abundant, high-diversity mollusc fauna are arcids and limopsids. The fossil associations can be referred to circalittoral Heterogeneous Communities (Tab. 2). In particular, they testify a mature stage of the first phase (PE 1) of Di Geronimo & Robba (1989) previously referred to. Evidence in this respect are the significant dominance figures pertaining to the opportunistic taxa and the high diversity (compare Fig. 1).

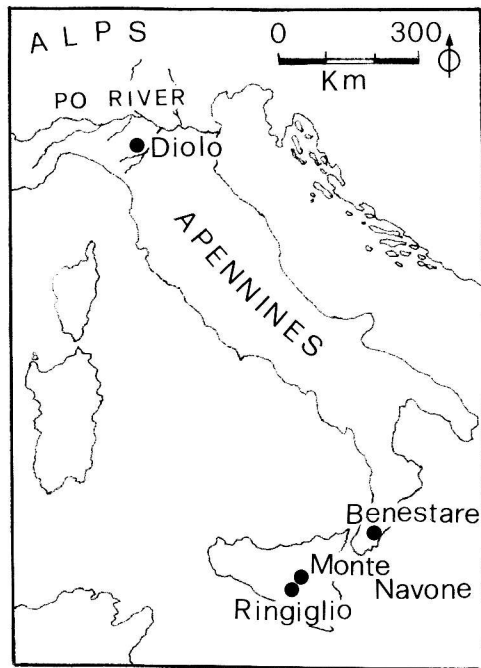


Fig. 2 - Location of the considered stratigraphic sections.

GRANULOMETRY	GRAVEL	SAND				MUD	
		coarse & very coarse	medium	fine	very fine	silt	clay
Monte Navone 3	2.8	4.1	4.7	60.8	19.8	4.8	3
Monte Navone 2	4.2	5.1	15.3	59.1	13.1	2.1	1.1
Monte Navone 1	0.4	0.3	4.8	75.6	13.6	2.6	2.7
Ringiglio D	7.1	2.1	3.6	20.6	13.1	44.6	8.9
Ringiglio C		4.8	3.2	42.5	13.8	27.9	7.8
Ringiglio A	8.9	2.8	3.5	40.2	14.2	2.2	8.4
Diolo 4	1.8	36.2	1.1	14.5	16.9	20.3	9.2
Diolo 2	2.3	17.8	19.7	14.9	15.1	21.9	8.3
Benestare 2	0.6	2.3	5.5	53.6	16.1	13.7	8.2
Benestare 1		4.1	2.5	9.5	12.6	49.1	22.2

Tab. 1 - Granulometric composition of the analyzed samples.

SAMPLES	Litology	Number of Bryozoans species	% Bryozoans in relation to other organisms	Bryozoans specimens in 1 l of sediment	% Lunulitiform Bryozoans in relation to all Bryozoans	% instability indicators other than Bryozoans	Palaeobionomy
Monte Navone 3	Sands	9	10	107	98.02	14	SFBC
Monte Navone 2	Sands	10	8	91	96.26	70	PE1
Monte Navone 1	Sands	3	10	28	98.79	74	PE2 / PE1
Ringiglio D	Sandy silts	22	6	76	64.10	90	PE1
Ringiglio C	Silty sands	22	8	165	52.67	84	PE1
Ringiglio A	Silty sands	11	8	268	41.68	86	PE1
Diolo 4	Silty sands	29	20	183	97.22	53	PE1
Diolo 2	Silty sands	35	35	511	94.78	20	DC / PE1
Benestare 2	Silty sands	17	10	208	97.17	62	PE1
Benestare 1	Sandy silts	19	15	232	87.84	80	PE1

Tab. 2 - Composition of the analyzed fossil communities and respective biocoenotic meaning (right). SFBC) Biocoenosis of the Fine Well Sorted Sands; PE) Heterogeneous Community; DC) Biocoenosis of Coastal Detritic.

In the two samples, bryozoans with 17 and 19 species respectively, represent 10% and 15% of the whole fauna (Tab. 3). Lunulitiforms, largely dominated by *Reusirella doma* and *Cupuladria vindobonensis*, show very high dominance values (87% and 97%) within the bryozoan assemblages (Tab. 2).

Diolo. This Pliocene locality is located along the Stramonte River in western Emilia (northern Italy) (Fig. 2, 3). The fossil content was studied by Mayer (1889) and Sacco (1900), and paleoecological reconstructions were recently offered by Monegatti & Raineri (1989). The lower part of the sedimentary sequence here analyzed is composed by alternating clayey silt and silty sand layers, and reaches 30 meters in thickness. The first lithotype contains assemblages that can be assigned to a biocoenosis comparable to the modern VTC (Biocoenosis of the Terrigenous Muds). Two samples were taken from the silty sand beds (Diolo 2 and 4). The upper part (not represented in Fig. 3) is made of sand and slightly muddy sand. The sampled levels should be earliest Middle Pliocene (Piacenzian) in age because of the presence of *Globorotalia crassaformis*.

The first (lower) considered level (sample Diolo 2), 2 metres thick, bears a circalittoral association referable to a Coastal Detritic Paleocommunity (Tab. 2). The presence of instability indicators such as *Nuculana pella* and *Tellina distorta* concomitant with the low cumulative dominance (about 18%) of *Ditrupea arietina* and *Corbula gibba* firmly suggests an incipient turbidity (cf. Di Geronimo & Robba, 1989). The bryozoans (Tab. 2, 3) are represented by 35 species, and make up 35% of the whole fossil community. Lunulitiforms (6 species) total 94.78% of the bryozoan assemblage; the dominant species is *Lunulites androsaces* (52.07%).

The upper level (sample Diolo 4), 4.5 metres thick, contains a circalittoral Heterogeneous Community referable to phase 1 (PE 1) of Di Geronimo & Robba (1989). The presence of the instability indicators *Nuculana pella* and *Lunatia guillemini* is to

SAMPLES	Benestere		Diolo		Ringiglio			Monte Navone		
	1	2	2	4	A	C	D	1	2	3
SPECIES										
<i>Crisia denticulata</i> Lamarck				0.04						
<i>Crisia</i> spp.			0.11							
<i>Ybseleocia typica</i> (Manzoni)				1.79						
<i>Annectocyma indistincta</i> (Canu & Bassler)						0.10				
<i>Annectocyma major</i> (Johnston)					0.50	0.30	0.88			
<i>Annectocyma tubulosa</i> (Busk)						0.20				
<i>Annectocyma</i> spp.			0.92							
<i>Entalophora</i> spp.	0.08		0.14	0.61						
" <i>Cardioecia</i> " <i>watersi</i> (O'Don. & de Wat.)			0.01							
<i>Diplosolen obelium</i> (Johnston)							0.22			
<i>Plagioecia sarniensis</i> (Norman)				0.04						
<i>Tervia irregularis</i> (Meneghini)				0.08						
<i>Tervia</i> sp.	0.08									
<i>Idmidronea atlantica</i> (Forbes in John.)						0.10	0.44			
<i>Idmonea</i> spp.	0.15		0.18							
<i>Tubulipora notomale</i> (Busk)						0.10				
<i>Tubulipora plumosa</i> Harmer			0.01	0.19	0.06					
<i>Fron dipora verrucosa</i> (Lamoroux)						1.21	0.44			
<i>Fron dipora</i> sp.		0.15								
<i>Disporella hispida</i> Fleming									0.86	0.22
<i>Hornera frondiculata</i> (Lamoroux)							1.76			
<i>Fasciculipora</i> sp.			0.73	0.11						
<i>Fungella</i> sp.				0.15						
<i>Membranipora savartii</i> (Audouin)			0.24	0.27	48.20	1.61	0.66			
<i>Chapperia annulus</i> (Manzoni)			0.10	0.30	1.06	4.53	11.45			0.22
<i>Cupuladria gr. canariensis</i> (Busk)					1.80	7.45	22.91	1.20	0.58	31.21
<i>Cupuladria vindobonensis</i> Baluk & Radw.	25.43	17.23	2.52	3.65						
<i>Reussirella doma</i> (d'Orbigny)	45.36	59.32	1.04	0.46						
? <i>Reussirella haidingeri</i> (Reuss)	5.58	10.46	3.77	14.52						
<i>Reussirella reussiana</i> (Manzoni)			6.19	21.57	39.88	45.22	41.19	97.59	95.68	66.81
<i>Reussirella</i> spp.			27.49	38.39						
<i>Discoporella umbellata</i> (DeFrance)			1.71	0.27						
<i>Calpensia nobilis</i> (Esper)						0.40	0.88			0.29
<i>Rosseliana rosselli</i> (Audouin)			0.39	0.27						
<i>Setosella vulnerata</i> (Busk)	0.08		0.03	0.27						
<i>Lunulites androsaces</i> Michelotti	7.85	5.76	52.07	18.36						
<i>Lunulites</i> sp.1	2.49	4.30								
? <i>Selenaria miocenica</i> Sequenza	1.13	0.10								
<i>Cellaria crassa</i> (Wood)				0.46						
<i>Cellaria fistulosa</i> Auct.	4.53		0.01						0.86	0.22
<i>Cellaria normani</i> Hastings			0.01		0.12	1.01	3.08			
<i>Cellaria salicornia</i> (Pallas)							0.44			
<i>Cellaria sinuosa</i> (Hassall)						0.70				
<i>Cellaria</i> spp.	0.30	0.15				0.81				
<i>Scrupocellaria scruposa</i> (Linne')			0.01							
<i>Scrupocellaria</i> sp.									0.29	
<i>Puellina innominata</i> (Couch)			0.01							
<i>Escharoides coccinea</i> (Abildgaard)							1.98			
<i>Escharoides infundibulata</i> (Busk)				0.11						
<i>Adeonella polystomella</i> (Reuss)	0.75									
<i>Reptadeonella violacea</i> (Johnston)		0.05	0.07							
<i>Pentapora foliacea</i> (Ellis & Solander)					1.93	0.50	3.08			
<i>Pentapora</i> sp.			0.01							
<i>Porella cervicornis</i> (Pallas)						0.30	1.10			
<i>Porella</i> sp.	0.23									
<i>Buffonellaria divergens</i> (Smitt)			0.01							

SAMPLES	Benestare		Diolo		Ringiglio			Monte Navone		
	1	2	2	4	A	C	D	1	2	3
SPECIES										
Schizobrachiella sanguinea (Norman)										0.44
Schizomavella rudis (Manzoni)			0.14							
Characodoma sp.1	0.08									
Hippopodinella sp.	0.08						0.22			
Calloporina decorata (Reuss)				0.11						
Trypostega venusta (Normann)			0.01	0.04						
Metrarabdotos sp.				0.08	4.97	23.97	0.22		0.58	0.22
Alysidotella cipollai Buge			1.20	1.06						
Rhynchozon spp.			0.03							
Sertella couchi (Hincks)					0.12	0.70	1.10			
Sertella cf. septentrionalis Harmer			0.20		0.50	3.63				
Sertella spp.			0.03	0.08		3.73	2.64			
Margaretta cereoides (Ellis & Solander)									0.29	
? "Cellepora" compressa Busk			0.50							
Celleporaria sp.				0.11						
Celleporina caminata (Waters)		0.15		0.04			0.22	1.20	0.29	0.22
Celleporina hassalli (Johnston)						0.50	0.88			0.44
Celleporina spp.			0.03	0.11		1.51	2.64			
Omalosecosa ramulosa (Linne')						0.20				
? Turbicellepora armata (Hincks)						0.10				
Turbicellepora coronopus (Wood)				0.34						
Batopora rosula Reuss	2.19	0.51								
Orbitulipora excentrica Seguenza	1.21	0.15								
Undetermined	2.42	1.67	0.04	2.58		1.01	0.44		0.29	

Tab. 3 - Percentage of bryozoan species in the analyzed samples.

be noticed together with the medium cumulative dominance (50%) of the opportunistic species *Ditrupea arietina* and *Corbula gibba*. The 29 bryozoan species (Tab. 2, 3) form 20% of the whole fauna, and lunulitiform colonies make up 90% of the bryozoan assemblage. *Reussirella reussiana* is the dominant species (57.02%) followed by *Lunulites androsaces* (18.36%).

Ringiglio. This sequence, located in Central Sicily, has been recently dealt with by Di Geronimo et al. (1989). The stratigraphic succession (Fig. 3), about 200 meters thick, includes the Pliocene blue marly clay (Argille Marnose Azzurre) and the overlying sandy deposits of Early Pleistocene age. The topmost stratigraphic interval has been considered, slightly exceeding 4 meters in thickness, and composed of fine sandy layers having different silt and clay contents (Tab. 1). These layers bear fossil assemblages that reflect different phases or stages of the Heterogeneous Communities.

Three samples have been studied in detail (A, C, D) whose fauna (Tab. 2 and 3) is characterized by the great abundance of *Ditrupea arietina* and *Corbula gibba* (cumulative dominance ranging from 84% to 90%), and by the presence of the instability indicators *Nuculana pella*, *Tellina distorta*, *Turbonilla rufa* and *Dentalium rubescens*. On the basis of their composition, the recognized Heterogeneous Communities are referable to a mature stage of the first phase (PE 1), in the sense of Di Geronimo & Robba (1989). Moreover, an increase of turbidity along the section (Fig. 4) can be inferred, mainly suggested by the upward decrease of *Ditrupea arietina*, and by the concomitant

increase of *Corbula gibba*. The cumulative dominance pertaining to lunulitiform bryozoans significantly augments upward, and this is consistent with the just mentioned inference; calculated figures, ranging from 41% to 64%, are in comparison smaller than those recorded in all the other considered sections (Tab. 2). *Reussirella reussiana* and *Cupuladria gr. canariensis* are the only recovered species.

Monte Navone. The Plio-Pleistocene stratigraphic section (Di Geronimo, 1969) is located in Central Sicily. A 4 meters thick level of Earliest Pleistocene age has been considered, made of sand with decimetric sandstone intercalations.

Three samples (1, 2, 3) (Tab. 1, 2 and 3) have been analyzed that yielded slightly different fossil associations, all pertaining to infralittoral Heterogeneous Communities. An upward decreasing turbidity of the depositional environment can be pointed out. In fact, the lower sample contains an Heterogeneous Community which may be considered transitional between phases 1 and 2 of Di Geronimo and Robba (1989). The

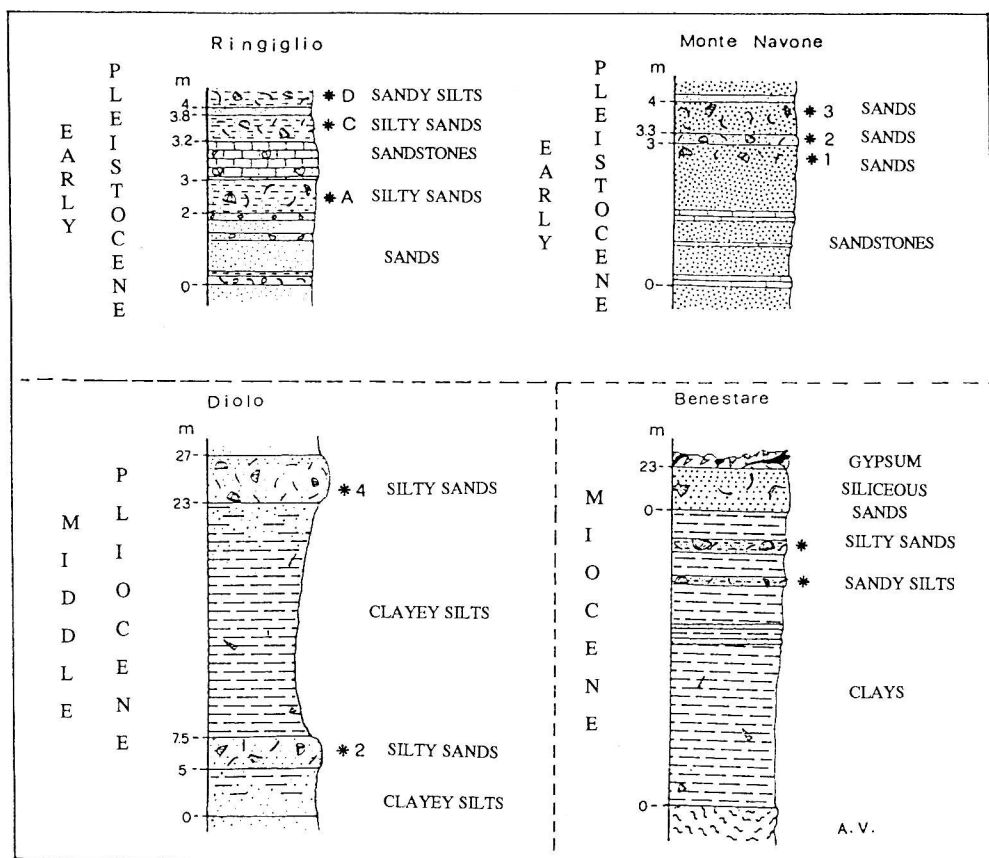


Fig. 3 - Lithologic logs of the stratigraphic sections showing the location (*) of sampled layers.

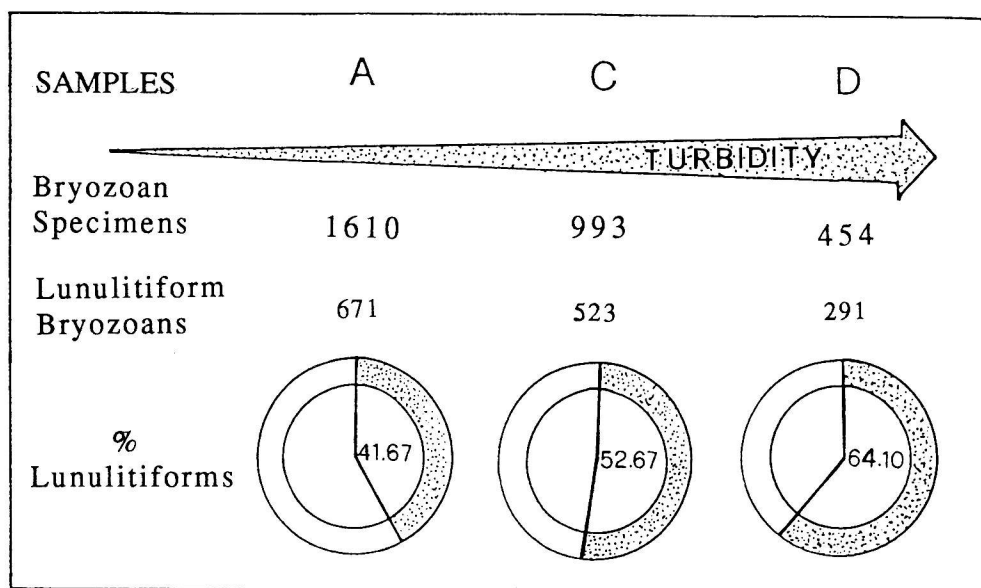


Fig. 4 - Inferred relationship between turbidity and lunulitiform percentage of the bryozoan paleocommunities of the Ringiglio Early Pleistocene section (Sicily).

upper third sample provided a fossil association belonging to a paleobiocoenosis comparable to the modern SFBC (Biocoenosis of the Fine Well Sorted Sands); little evidence of instability still persists. Bryozoans constitute a small proportion of the whole assemblages, and are mainly represented by lunulitiform colonies all belonging to the two species *Reussirella reussiana* and *Cupuladria* gr. *canariensis*. The cumulative dominance pertaining to lunulitiforms remains basically unchanged, whereas their abundance markedly increases with the decreasing instability.

Conclusions.

A preliminar interpretation of the ecological and paleoecological meaning of lunulitiform bryozoans has been proposed, based on literature data concerning their life-habit and habitat, and detailed research on selected Neogene and Quaternary stratigraphic sections of Italy.

In modern seas, lunulitiforms have been found on continental shelves of circum-tropical regions influenced by river discharge, where the sedimentation rate is moderate (see Cadée, 1975 for the Amazon River), or where the peculiar pluviometric regime causes a continuous input of suspended material and, thence, a nearly persistent turbidity (cf. Lagaaij, 1963 as regards the Mississippi River). In the Mediterranean

Sea, similar environments can be found in the area influenced by the Rhone delta; there, only cellariforms persist instead of lunulitiforms (Lagaaij & Gautier, 1965).

Usually, both the number of bryozoan species and the variety of zoarial forms decrease as a response to the increasing sedimentation rate. When turbidity onto the sea-bottom becomes considerable, causing environmental instability (see above), stress conditions establish. Such being the case, only a very small number of bryozoan species are able to survive, and a single zoarial type is found, namely lunulitiform or cellariform. Lunulitiform ability to sweep sedimentary particles from the colony surface, and to regain the interface if suddenly buried, allow them to survive on soft substrates as well, where the growth of other morphotypes is impossible. In strongly unstable environments a monotypic bryozoan community will be found.

If Italian fossil communities are considered, lunulitiforms are present, and sometimes significantly abundant, only within Heterogeneous Communities. It is worthy of note that all the examined situations are to be referred to the first phase (PE 1) of Di Geronimo & Robba (1989) which exactly fits in with the definition of Heterogeneous Communities originally given by Pérès & Picard (1964) and Picard (1965). Regardless of the examples discussed above, other personal data and field observations support the constant association of lunulitiform bryozoans with Heterogeneous Communities or, at least, with fossil communities dominated by the opportunistic species *Ditrupa arietina* and *Corbula gibba*. Finally, some Miocene assemblages of Algeria (Moisette, pers. comm.), Germany (Buge, 1973), Poland (Hoffman, 1977; Baluk & Radwanski, 1984) and Florida (Scolaro, 1970) seem to have an identical meaning.

The constant presence of lunulitiforms within fossil communities always having the same environmental and biocoenotic meaning (Heterogeneous Communities), and, conversely, their absence from communities inferred to have inhabited stable bottoms devoid of or with little turbidity, strongly suggest that: 1) these bryozoans are strictly linked to Heterogeneous Communities, and 2) they can be regarded as instability indicators having the same value of those molluscan and crustacean species selected as such by Picard (1965).

Moreover, bryozoans and in particular lunulitiforms, because of their peculiar response to the increasing turbidity, might be an efficient tool in discriminating stages of first phase Heterogeneous Communities; examples in this respect have been considered in the preceding pages (Ringiglio, Monte Navone). Of course, much work is still to be done.

In the examined stratigraphic sections, species appear to replace each other over the time, and these events are likely to be of real evolutionary meaning. In fact, we observed that the ecological niche of lunulitiform bryozoans remained one and the same at least from Miocene onwards. So far we can point out that *Lunulites* sp. and *Selenaria miocenica* are of strict Miocene age, while *Cupuladria vindobonensis*, *Reussirella haidingeri* and *Lunulites androsaces* reached extinction during Pliocene; the *Cupuladria canariensis* group seems to be restricted to Pleistocene.

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