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PALAEOECOLOGY AND TAPHONOMY OF BIVALVES, MAINLY *Glycymeris insubrica* (BROCCHI), AND BRYOZOANS FROM THE HUELVA SANDS FM. (LOWER PLIOCENE, SW SPAIN)

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ABSTRACT

The fossiliferous Huelva Sands Formation belonging to the Upper Neogene complex (Lower Pliocene), that is located at the outfall of Tinto and Odiel rivers, southwestern end of Guadalquivir Basin (SW Spain), consists of fine silty and sandy beds with abundant molluscan faunas. These suffered predation and successive colonisation events during their life span and also after death. Eight bivalve communities are distinguished on the basis of their taxonomic contents and trophic classification. Focussing on the abundant species *Glycymeris insubrica* (Brocchi), we analysed the borings produced as result of predator-prey interaction, and also the commensalism relationships, and colonisation sequences, both when *G. insubrica* was still alive and *post-mortem*. The abundant evidence of encrusting on bivalve shells and also free-living bryozoans, gives a detailed view of the scenario after death of most bivalve faunas. The final skeletal concentrations are described using the nomenclature of Kidwell *et al.* (1986).

Keywords: Bivalves, Bryozoans, Borings, Palaeoecological and Taphonomic analysis, Huelva Sands Formation, Lower Pliocene, Guadalquivir Basin.

RESUMEN

La Formación Arenas de Huelva de edad Neógeno superior (Plioceno inferior), se extiende a lo largo de las márgenes de los ríos Tinto y Odiel, en el extremo suroccidental de la Cuenca del Guadalquivir (SO de España). Está representada por arenas finas y limos arenosos que contienen una fauna mayoritaria de moluscos con evidencias notables de bioerosión. Se han diferenciado ocho comunidades de bivalvos en función de su composición taxonómica y estructuración trófica. El estudio detallado de los aspectos bioerosivos pone de manifiesto la existencia de fenómenos de depredación (analizando las perforaciones producidas en la interacción depredador-presa) y de comensalismo que sirven para establecer las secuencias de colonización en vida y *post-mortem* en uno de los sustratos orgánicos más abundantes y representativos: *Glycymeris insubrica* (Brocchi). La gran abundancia de fauna de briozoos incrustantes colonizando las conchas, así como de formas libres, permite tener una visión muy completa del escenario después de la muerte de la mayoría de los bivalvos y en especial del taxón seleccionado. De esta forma, se pueden reconstruir los episodios previos al depósito final de cada nivel dentro de la evolución transgresivo-regresiva general de la secuencia estudiada. Los tipos de concentraciones esqueléticas resultantes de todos estos procesos se han resumido utilizando la nomenclatura de Kidwell *et al.* (1986).

Palabras clave: Bivalvos, Briozoos, Perforaciones, Análisis Paleoecológico y Tafonómico, Formación Arenas de Huelva, Plioceno Inferior, Cuenca del Guadalquivir.

INTRODUCTION

From the geologic point of view all organisms living in a definite area, together with inorganic elements presents in it, constitute the initial stage of the potential formation of some definite kind of rock. This rock may be formed in the same area or elsewhere and, through a more or less complicated process may be part of the future stratigraphic record.

According to this concept, each stratigraphic formation is the terminal stage of the history starting as indicated. This is particularly apparent if the organisms had hard parts and if the later evolution favours the stratigraphic formation to be fossiliferous.

The Pliocene Huelva Sands Formation of the Tinto-Odiel basin (Huelva, SW Spain), which is a very fossil-rich formation provides very good materials with which to attempt some paleoecological and taphonomic analysis. Taking into account the molluscan communities (mainly of bivalves) and their evolution from their life-time to final contribution in the stratigraphic record, we aim to describe the main milestones of this specific short history. The presence of the abundant bryozoan colonies, most of them encrusting bivalve shells, suggested that we might study the content and the significance of bryozoan fauna.

The fossil rich clays and sands of this area have been known since the end of the last century. Recently a lot of research was made by sedimentologists, paleontologist and biostratigraphers. Civis *et al.* (1987) gave an historical report of these contributions. Mayoral (1986a) made a substancial contribution to the taphonomy and paleoecology of the Pliocene of Huelva-Bonares. Reguant & Mayoral (1992) and Reguant & Mayoral (1994) are two contributions to the paleogeographic and paleoecologic analysis based on the bryozoan fauna.

GEOGRAPHICAL AND STRATIGRAPHICAL CONTEXT

The area surveyed is located at the outfall of Tinto and Odiel rivers into Atlantic Ocean, southwestern end of Guadalquivir Basin. It belongs to Huelva province, from Huelva city to Bonares (Fig. 1). The clayey and sandy formations from the Upper Neogene-Lower Quaternary have been sampled in five geographic sectors: Bonares (BO); Lucena del Puerto (LU); Moguer (MO); Palos de la Frontera (PF), and Huelva (HU).

The composite stratigraphical section (Fig. 1), based on many local individual sections, may be summarized as follows, from bottom to top:

1. **Gibraleon Clays Fm** (Civis *et al.*, 1987). Upper Tortonian-Lower Pliocene.

This Formation consists of bluish-grey clays, sometimes black, silty near the top, with a rich micro-fossiliferous content. The macrofauna appears scarce, disperse, and fragmented. In the uppermost part there are abundant biogenic structures belonging to different ichnospecies of *Skolitos, Planolites, Ophiomorpha, Gyrolithes* and *Thalassinoides.* Its visible thickness is 80 m.

2. **Huelva Sands Fm** (Civis *et al.*, 1987). Lower Pliocene.

This very fossiliferous Formation consists of fine, silty in the lower part and brown-yellowish sands with a glauconitic horizon near the bottom. (Fig. 1). The fauna consists mainly of mollusk, associated with fish teeth and vertebrae, crabs, bryozoans, echinoids, corals and a lot of biogenic structures. The thickness of this Formation reachs 10 to 30 m and it is concordant in relation to the underlying formation.

3. **Bonares Sands Fm** (Mayoral & Pendón, 1986-87). Lower Pliocene (upper part) - Pleistocene?

The contact between this Formation and the underlying Huelva Sands

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Fm. is erosional. It consists of coarsening upwards sands with some conglomeratic intercalated beds. The fossiliferous content is poor and consists chiefly of mollusk moulds and some biogenic structures. The thickness is very variable, from 1 to 20 meters.

4. The **"Alto nivel aluvial"** (Alluvial high horizon) (Pendon & Rodriguez-Vidal, 1986-87) is the top unit and consists of 0.5 to 9 m of red clayey sands and sandy clays with some conglomerate intercalated beds. It belongs to Pliocene-Pleistocene age. The contact with the underlying formation is erosional.

This study deals with the paleobiology of Huelva Sands Fm. The paleoenvironmental characteristics of this unit have been fully examined by different authors (Andrés, 1982; Antunes *et al.,* 1989; Castaño *et al.,* 1988; Civis *et al.,* 1987; Dabrio *et al.,* 1988; Galán *et al.,* 1989; González Delgado, 1983; González Delgado *et al.,* 1993, in press; Mayoral 1986a & b, 1987, 1988a & b, 1989; Porta & González Delgado, 1980, 1983; Sierro, 1984; Sierro *et al.,* 1990). The lower part of the formation, consisting of glauconitic sands and silts, was deposited in a low energy open marine environment. These deposits were the result of transgressive pulsation. In contrast, the upper part of the formation, predominantly sandy, is the result of a regressive situation with a very important biological activity under high energy subtidal conditions.

THE BIVALVE COMMUNITIES

According to the criteria expressed by Scott (1976), it was possible to distinguish 8 bivalve communities either on the basis of their taxonomic content (Table 1) or their trophic features (Fig. 2).

The first 4 bivalve paleocommunities in which *Glycymeris insubrica* is a frequent species, are particularly important to analyze the contribution of the bryozoans to the Huelva Sands Fm, because more than 70 % of encrusting bryozoan colonies were encountered on shells of this mollusk (Reguant & Mayoral, 1994).

1. *Glycymeris* community

This community is characteristic of sandy environments with strong bottom currents producing high material agitation. The opportunistic species, chiefly suspension feeders, dominate the environment. The diversity and equitability indices are low (0.42 and 0.28 respectively) (Mayoral, 1986a). The predation and commensalism phenomena is also strongly reduced. The *Glycymeris* community is well represented in the middle upper part of the formation.

2. *Corbula* community

This community is similar to *Glycymeris* community, as the suspension feeders are the dominant species. However, there are included species tolerant with the absence of clastic material. This feature results in a higher diversity (0.77) and equitability (0.67) respect to the former community (Mayoral 1986a). The phenomena of commensalism are rare and predation pressure is somewhat higher if compared with preceding community. The *Corbula* community replace to the *Glycymeris* community towards the top and it is generally well represented in the middle upper part of the formation. It is lateral and progressively replaced by *Spisula* community.

3. *Lucina* community

Lucina community marks the upper part of the formation. It presents some mixed characters with *Corbula* community. The sea floor is sandy with moderate energy. This community shows the highest diversity index (1.08) (Mayoral, 1986a), presumably as a consequence of greater stability conditions. It favours the settlement of epifauna and, consequently the frequent presence of predation phenomena. The mollusk species are mainly suspension feeders.

4. *Acanthocardia* community

This community is restricted to the upper part of the formation. It is characterized by variable energy of sea bottom resulting in rather restrictive conditions. General features are a lowered value of diversity index (0.63), significant decrease in epifaunal organisms and a simultaneous decrease in predation pressure. The boring and encrusting activities developed in post-mortem stages, are relatively high.

5. *Venus* community

The community is restricted to the lower part of the formation. The sea floor is characterized by silty sands with glauconite and low levels of hydrodynamic energy. The diversity and equitability indices are low (0.49 and 0.48, respectively) as are the bioerosive phenomena.

6. *Spisula* community

This community also present in the middle upper part of the formation, indicates a more fluctuating energy condition. The bioerosive phenomena are similar to that of the precedent communities. Diversity and equitability indices are 0.79 and 0.58 respectively.

7. *Ostrea* community

This and the latter communities are dominated by epifaunal animals. The Ostrea community is present in silty sandy sea floors with variable conditions of energy. The diversity index is low (0.35), but not the bioerosive phenomena which are the most important into Huelva Sands Fm. *Ostrea* community appears in different scattered parts of the formation, but chiefly in the upper part.

8. *Neopycnodonte* community

Community is restricted to the lower part of the formation, in silty-sandy, glauconitic sea floor with low energy. The diversity index is low (0.47). The bioerosive phenomena are relevant, due to the kind of life of the main taxon.

SEDIMENTOLOGICAL OBSERVATIONS

Before considering the palaeoecological aspects deduced from the study of the predation and commensalism relationships and before establishing the colonization sequences on the valves of *G. insubrica,* it is

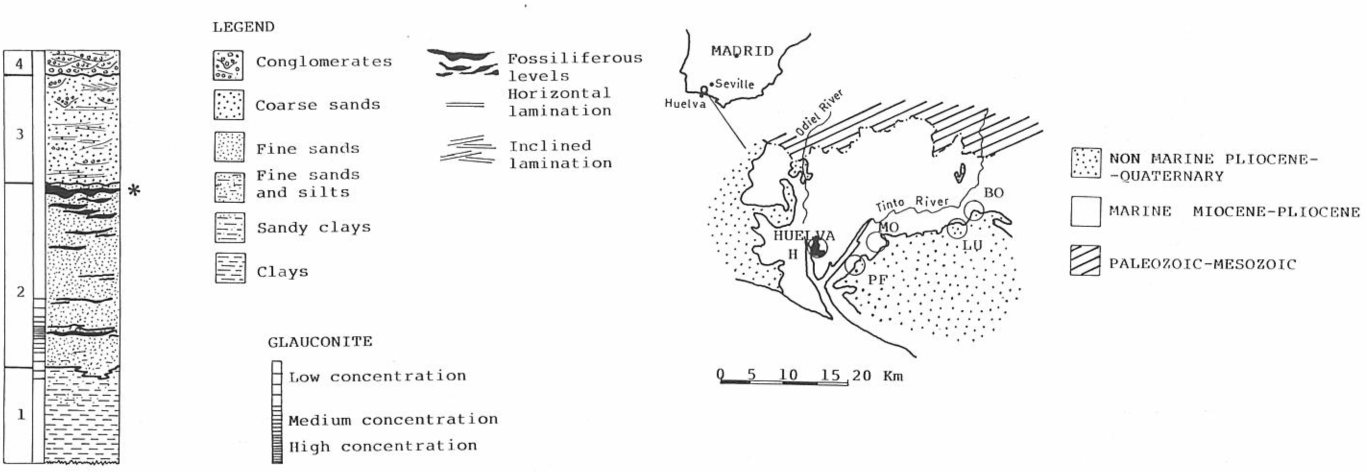


Figure 1. Geographic and geologic situation of the studied area and synthetic stratigraphic section in Huelva-Bonares sector. H: Huelva; PF: Palos de la Frontera; MO: Moguer; LU: Lucena del Puerto; BO: Bonares. The star-like signal represent the stratigraphic horizons where the samples were obtained.

TAXON	A	B	C	D	E	F	G	H
Nuculana (Lembulus) pella (Linné)	*	*	*					
Nuculana (Sacella) fragilis (Chemnitz)		*						
Glycymeris (G.) insubrica (Brocchi)	*	*	*	*				
Amusium cristatum (Bronn)								*
Palliolum (Lissochlamys) excisum (Bronn)		*		*			*	
Chlamys (C.) multistriata (Poli)				*		*	*	*
Chlamys (Aequipecten) radians (Nyst)			*	*		*		
Pecten (P.) cf. planariae Simonelli						*		
Neopycnodonte cochlear (Poli)	*	*						*
Ostrea (O.) edulis lamellosa Brocchi	*	*	*	*	*		*	*
Lucina (L.) orbicularis Deshayes		*			*			
Megaxinus (M.) transversus (Bronn)		*			*			
Myrtea (M.) spinifera (Montagu)	*	*	*	*	*			
Gonimyrtea meneghinii (De Stefani & Pantanelli)		*			*			
Lucinoma borealis (Linné)		*			*			
Anodontia (Loripinus) fragilis (Philippi)		*		*	*			
Lucinella divaricata (Linné)	*	*						
Diplodonta (D.) rotundata (Montagu)	*		*					
Acanthocardia (A.) paucicostata (Sowerby)	*	*	*	*	*	*	*	
Laevicardium (L.) crassum (Gmelin)		*	*					
Glans cf.*intermedia* (Brocchi)				*		*		
Spisula (S.) subtruncata (Da Costa)	*	*	*				*	
Tellina (Arcopagia) corbis (Bronn)		*						
Tellina (Laciolina) incarnata Linné					*			
Tellina (Ouardia) compressa Brocchi	*	*			*			
Tellina (Peronidia) planata Linné	*	*	*		*			
Tellina (Tellinella) distorta Poli		*			*			
Tellina (Peronidia) bipartita Basterot		*						
Macoma (Psammacoma) elliptica (Brocchi)	*	*	*		*			
Abra (Syndosmya) alba (Wood)		*						
Abra (Syndosmya)prismatica (Montagu)		*						
Venus (Ventricoloidea) multilamella (Lamarck)					*	*	*	*
Circomphalus foliaceolamellosus (Dillwyn)		*			*			
Pitar (P.) rudis (Poli)	*	*	*		*			
Pelecyora (P.) brocchi (Deshayes)				*	*			
Pelecyora (P.) gigas (Lamarck)			*					
Dosinia (Asa) lupinus (Linné)					*			
Paphia (Callistotapes) vetula (Basterot)			*		*			
Corbula (Varicorbula) gibba (Olivi)	*	*	*		*		*	*

Table 1. Main bivalve taxonomic composition of the bivalves communities. A: ***Glycymeris*** community. B: ***Corbula*** community. C: ***Spisula*** community. D: ***Acanthocardia*** community. E: ***Lucina*** community. F: ***Venus*** community. G: ***Ostrea*** community. H: ***Neopycnodonte*** community.

necessary to make some remarks on the sedimentological model, which is based on the taphonomic study.

According to Dabrio *et al.* (1988); Sierro *et al.* (1990) and our observations, bivalve shells are well preserved in all communities with various stages of growth, showing delicate structures, not or poorly abraded and fragmented. However, their valves are disorganized and disarticulate. Some of the shells have clearly been reworked (See Table 5), but others occur almost in life position with both valves articulate and closed. This features suggest reduced transport for the shells. The paleocommunities studied here lived on a sandy-silty bottom which was modified by erosion under the high energy conditions related to repeated storm surges. This represents removal to a variable degree according to the intensity of the wave-induced surges on the bottom. The living communities included in the uppermost centimeters of the water-sediment interface can be removed and redeposited under these conditions. Removed remains were winnowed and mainly accumulated in the vertical, with very short lateral transport. This characteristic explains the apparent inconsistency between the high desarticulation degree (it normaly involves long transport, Kornicker *et al.,* 1963; Stewart, 1967; Raup & Stanley, 1971) and the very fine states of conservation of the shells. The fragments can be numerous, but their preservation (colour, ornamentation, etc.) is excellent! In spite of this energetic disturbance, present in all cases, *Glycymeris insubrica* constitutes autochthonous assemblages, where the *in situ* specimens (in "life position") are mixed with the vertical winnowed valves. The results is a near equivalent percentage in right and left valves (Fig. 3). This peculiar transport could explain also, the statistical significant differences observed in *Spisula* community (Table 3c), where this mechanism is more accentuated. For these reasons, the paleoecologic observations are valid, so the fossil assemblages can be considered paleocommunities *sensu lato.*

BIOEROSIONAL STRUCTURES: PREDATION

The bivalves belonging to the former quoted communities support many bioerosive structures that supply basic information to the progressive stages of the history we try to retrace.

BORINGS RELATED TO *Oichnus*

Number of borings

We can limit now our attention to the borings produced as a result of interaction predator-prey when the prey is *Glycymeris insubrica.* The borings are represented by several ichnospecies of *Oichnus* Bromley. (Plate I, Fig. 2) Taking into account the four communities in which the *Glycymeris* is the dominant species or an important subordinate, we measured the bored and unbored valves, either in right or left valves (Fig. 3).

Distribution of borings

To identify areas of boring, left and right valves were

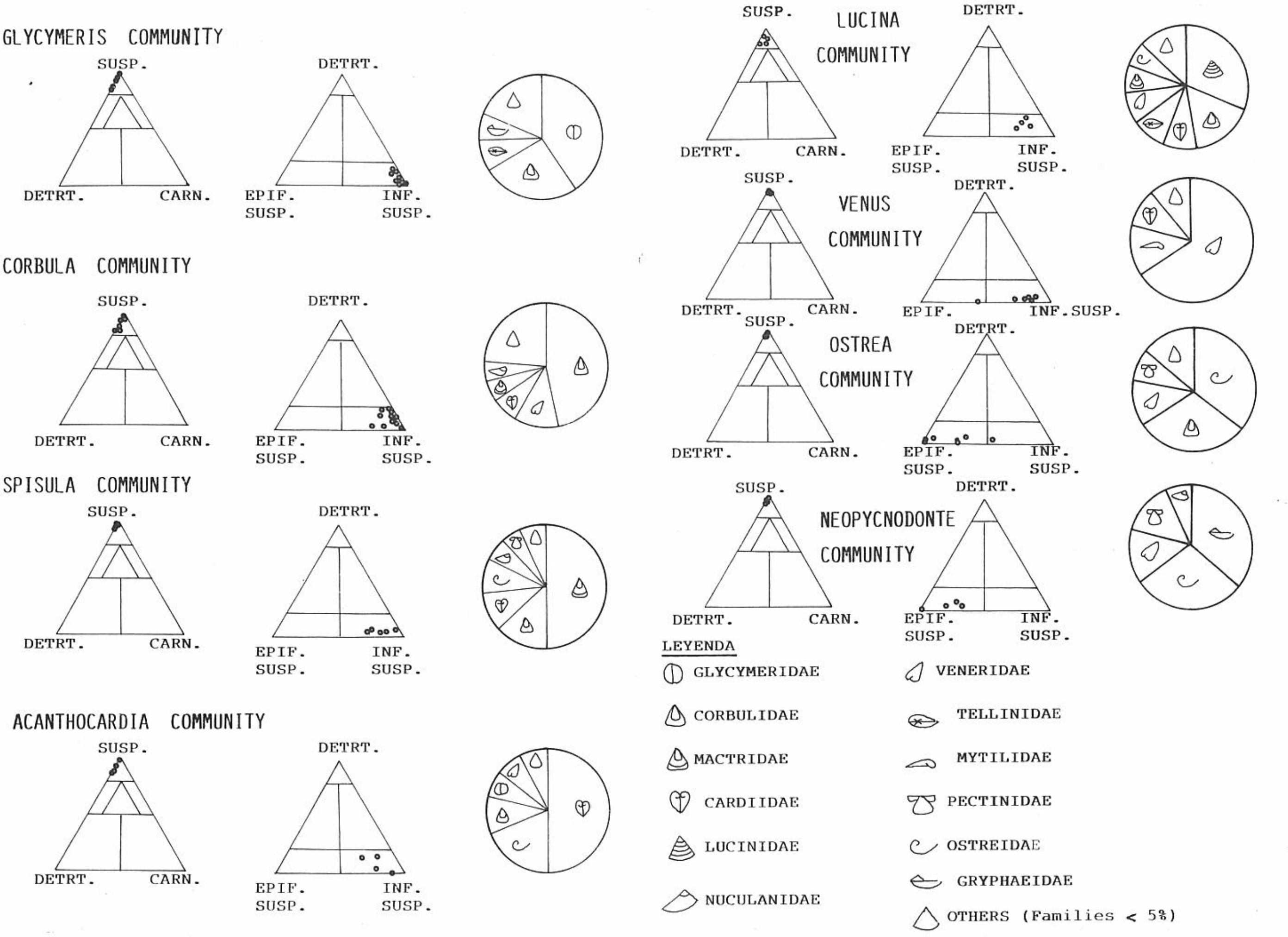


Figure 2. Trophic classification of the *Glycymeris, Corbula, Spisula, Acanthocardia, Lucina, Venus, Ostrea* and *Neopycnodonte* benthic communities (According to Scott's model, 1976). SUS: Suspensivorous, DETRT: Detritivorous, CARN: Carnivorous, EPIF SUSP: Epifaunal suspensivorous, INF SUSP: Infaunal suspensivorous.

subdivided into anterior-medial-posterior and dorsal-medial-ventral zones. Fig. 4 shows diagrams of areal location (According to modified Sohl's model, 1969) and frequency of counted borings *(Oichnus)*. Table 2 show in a double tabulation for each community, first the exact number of borings (different ichnospecies of *Oichnus*) and their location on the valves, and secondly the number of bored and unbored valves together with two indeces. The predation index is Cd = 2D/N (proposed by Kelley, 1984) where D = number of bored valves and N = total number of valves. The reparation index is Cr = Nf/N where Nf = number of repaired valves and N = total number of valves.

Table 3 shows the contingency tables test (χ^2 test) between unbored-bored left and right valves for each community.

Interpretations

Comparing the results showed in Fig. 3, we may conclude that the near equivalent number of borings in perforated right and left valves is probably demonstrative of predominant vertical life position, where the predator has a 50% of probability to bore both. This fact is well known in recent individuals of the same or closed species.

Diagrams showed in Fig. 4 and the values of Table 3 allows us to suggest the following interpretations:

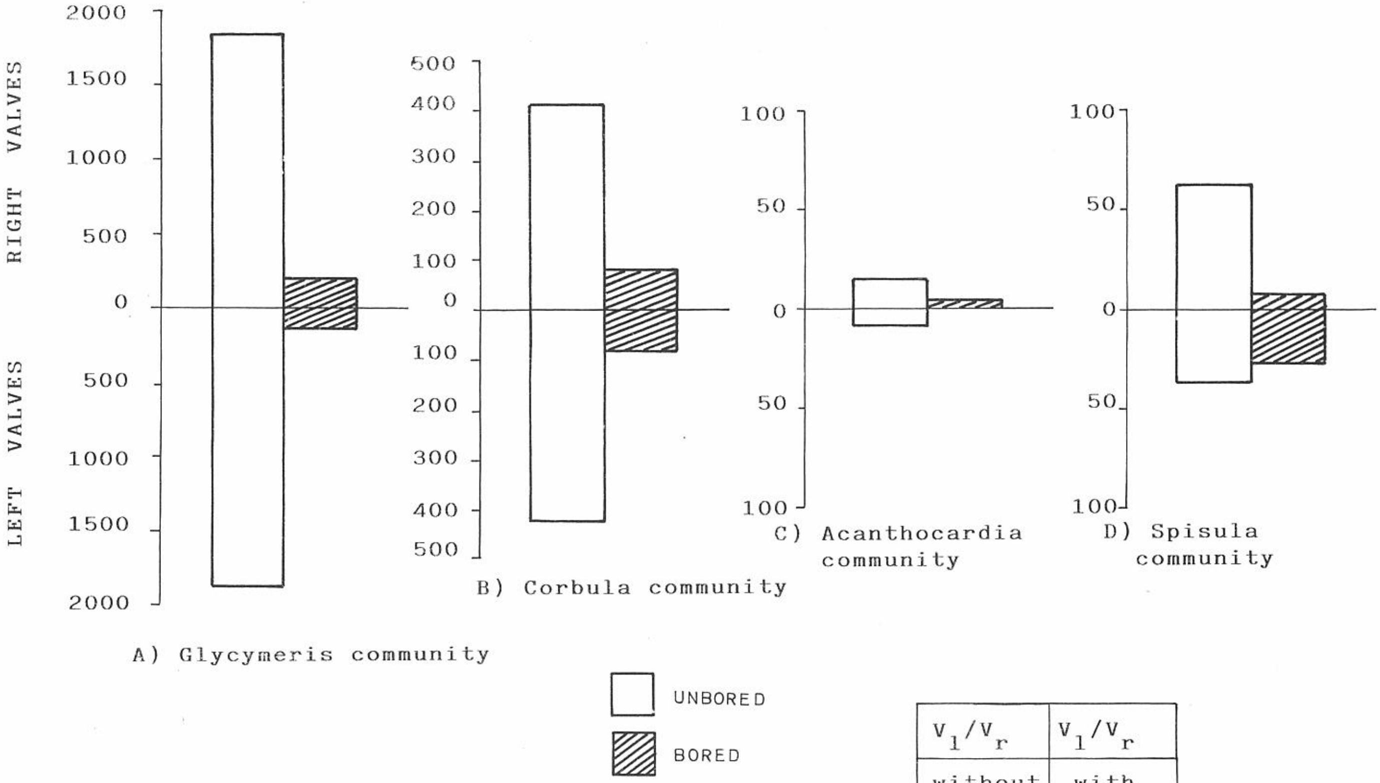
1. The predominant distribution of maximum boring in dorso-medial (near the umbo) and medial areas were in agreement with a definite position of the valves. The antero-posterior axis of them were in perpendicular position relative to sea floor. This situation is congruent with the work of Thomas (1975) assessing that *Glycymeris* are in vertical position with umbonal area near the surface.

2. The predators' attacks are preferentially directed to the areas mentioned, not to the posterior ones. These back areas are the best exposed in vertical position but have a thick periostracum giving a good protection against the predators attack. All this demonstrates that most of the predators' attacks can be produced when the preys are still alive. In fact, the behaviour of predators (naticids and/or muricids gastropoda) are very specific (Carriker & Zandt, 1972; Berg, 1975, 1976; Mueller, 1974; Adegoke & Tevesz, 1974; Berg & Nishenko, 1975; Kitchell *et al.,* 1981, 1986; Taylor *et al.,* 1983; Hoffman & Martinell, 1984; Kelley, 1988, 1991; Guerrero & Reyment, 1988a-b; Kabat, 1990; Mayoral, 1990) and easily recognizable. In fact, the morphology of the naticids and muricids boreholes constitute a very reliable behavioral criterion, because of their living representatives make exactly the same kind of borings. So, the discrimination of this kind of behaviour attains the reliability rank 2B from Boucot (1990). These attack areas are chosen by predators to weaken the device of valve plugging or to damage the visceral body of the prey.

3. The significant differences existing in *Spisula* community are due to the peculiar transport suffered by the *Glycymeris* on the bottom. This feature has been clarified in the former chapter.

OTHER BORINGS AND BIOEROSIVE STRUCTURES

For practical reasons, the contour-diagrams and histo-



	V_l/V_r without OICHNUS	V_l/V_r with OICHNUS
A) Glycymeris community......	1.02	0.91
B) Corbula community.........	1.00	0.98
C) Acanthocardia community...	0.60	0.00
D) Spisula community.........	0.67	1.81

Figure 3. Left/right valves ratio without/with *Oichnus* Bromley on *Glycymeris (G.) insubrica* (Brocchi) for each community where it is an important taxon.

2 a. *Glycymeris* Community

DORSO-VENTRAL SUBDIVISIONS	Op	Os	Op	Os	Op	Os
DORSAL	10	0	219	0	12	0
MEDIUM	36	0	58	1	25	0
VENTRAL	5	0	13	0	3	0
	ANT.		MEDIUM		POST.	

VALVE	Unbored	Bored	$C_d=2D/N$	$C_r=N_f/N$
Left	1906	182		
Right	1861	200		
	3767	382	0.18	0.18
TOTAL	**4149**			

2 b. *Corbula* Community

DORSO-VENTRAL SUBDIVISIONS	Op	Os	Op	Os	Op	Os
DORSAL	3	0	106	0	2	0
MEDIUM	2	0	28	1	10	0
VENTRAL	2	0	8	0	3	0
	ANT.		MEDIUM		POST.	

VALVE	Unbored	Bored	$C_d=2D/N$	$C_r=N_f/N$
Left	419	81		
Right	419	82		
	838	163	0.32	0.07
TOTAL	**1001**			

2 c. *Acanthocardia* Community

DORSO-VENTRAL SUBDIVISIONS	Op	Os	Op	Os	Op	Os
DORSAL	0	0	0	0	1	0
MEDIUM	0	0	0	1	0	0
VENTRAL	0	0	0	0	0	0
	ANT.		MEDIUM		POST.	

VALVE	Unbored	Bored	$C_d=2D/N$	$C_r=N_f/N$
Left	6	0		
Right	10	1		
	16	1	0.11	0.00
TOTAL	**17**			

2 d. *Spisula* Community

DORSO-VENTRAL SUBDIVISIONS	Op	Os	Op	Os	Op	Os
DORSAL	1	0	18	0	1	0
MEDIUM	2	1	7	2	0	0
VENTRAL	0	0	0	0	0	0
	ANT.		MEDIUM		POST.	

VALVE	Unbored	Bored	$C_d=2D/N$	$C_r=N_f/N$
Left	37	20		
Right	55	11		
	92	31	0.50	0.20
TOTAL	**123**			

Table 2. Quantitative analysis of *Oichnus* Bromley on *Glycymeris (G.) insubrica* (Brocchi) based on the areal division of the valves. Further information in the text. **2 a.** *Glycymeris* Community. **2 b.** *Corbula* Community. **2 c.** *Acanthocardia* Community. **2 d.** *Spisula* Community. Op: *Oichnus paraboloides* Bromley; Os: *Oichnus simplex* Bromley.

Plate I

Life-stage colonization:

1 *Caulostrepsis-Maeandropolydora* (annelid borings) restricted on the posterior edge of the bivalve. To see the orientation towards the external margin of the shell. Scale bar: 1 cm.

2 *Oichnus paraboloides* Bromley (naticid gastropods predation). Scale square: 1 mm.

3 Shells repaired after fracturing presumed due to Crustacea. Scale bar: 1 cm.

Post-mortem colonization:

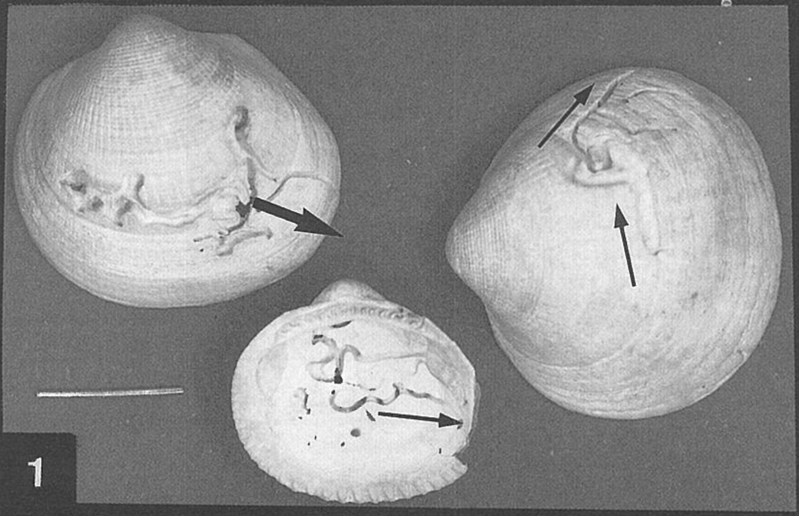
4 *Stellichnus radiatus* Mayoral (scar atribuited to Ctenostomate bryozoans) on the internal side of *Glycymeris (G.) insubrica* (Brocchi). Scale bar: 200 µm.

5 B_4 morphotype (Thallophyte ramified microborings), *Entobia* sp (sponge microborings: large and small rounded holes) and *Iramena bonaresi* (bryozoan microborings: the smallest rounded holes). Scale bar: 1 cm.

6 *Gastrochaenolites* sp. External moulds in plastic material. Scale bar: 1 cm.

7 *Maeandropolydora* sp on the external side of the broken shell of *Glycymeris (G.) insubrica* (Brocchi) near the ventral margin. Scale square: 1 mm.

Plate I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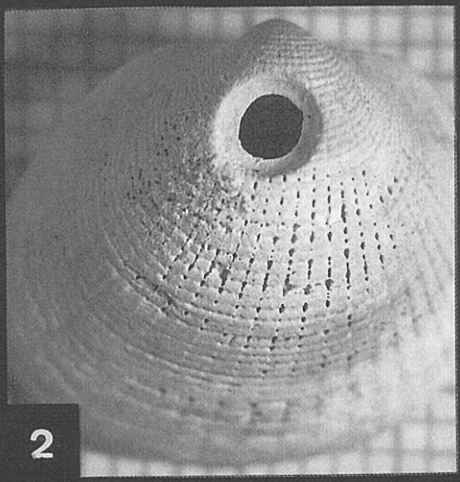
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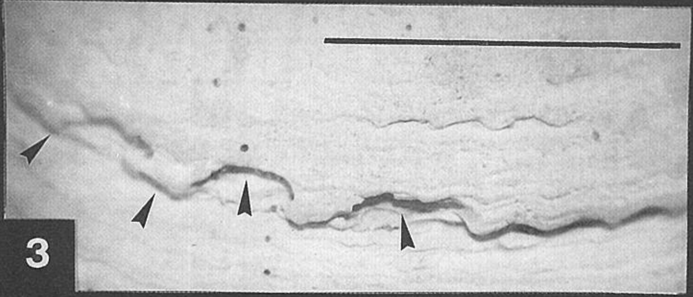
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grams presented here are referred to all marks, mainly after death, recorded on surface valves of *Glycymeris insubrica* in the 4 bivalve communities in which this species is the dominant or a main taxon.

The concentration degree of several marks on different areas of surface valves in distinct identified communities are shown in contour-diagrams of Fig. 5.

The histograms of the Fig. 6 show the global contents on each community of different marks and also the frequency of these ones on separate right and left valve surfaces.

The group of *Caulostrepsis-Maeandropolydora* borings are located chiefly on posterior margins of the bivalve (Figs. 5.3 and 7a$_{1-2}$; Plate I, Fig. 1) and they can show an oriented or unoriented arrangement respect to these margins. Several microborings are present, too. These one are related to thallophytes, belong to B1, B2 and B4 morphotypes Mayoral (1988a) and bryozoans: *Iramena bonaresi* and *Pinaceocladichus onubensis* (Mayoral, 1988b) (Figs. 5.4 and 7a$_2$-d) together with traces of boring sponges belonging to *Entobia* (Figs. 5.2 and 7a$_2$-d). These borings are located in external and/or internal valve surfaces. In relation to the encrusting activity, bryozoans organism are the most important by far. In fact, the abundant encrusting bryozoans settling on concave internal surface of disarticulated valves of *G. insubrica* (Fig. 7b-d) and on other mollusk species have been the subject of two previous studies (Reguant & Mayoral, 1992, 1994). Some outstanding aspects

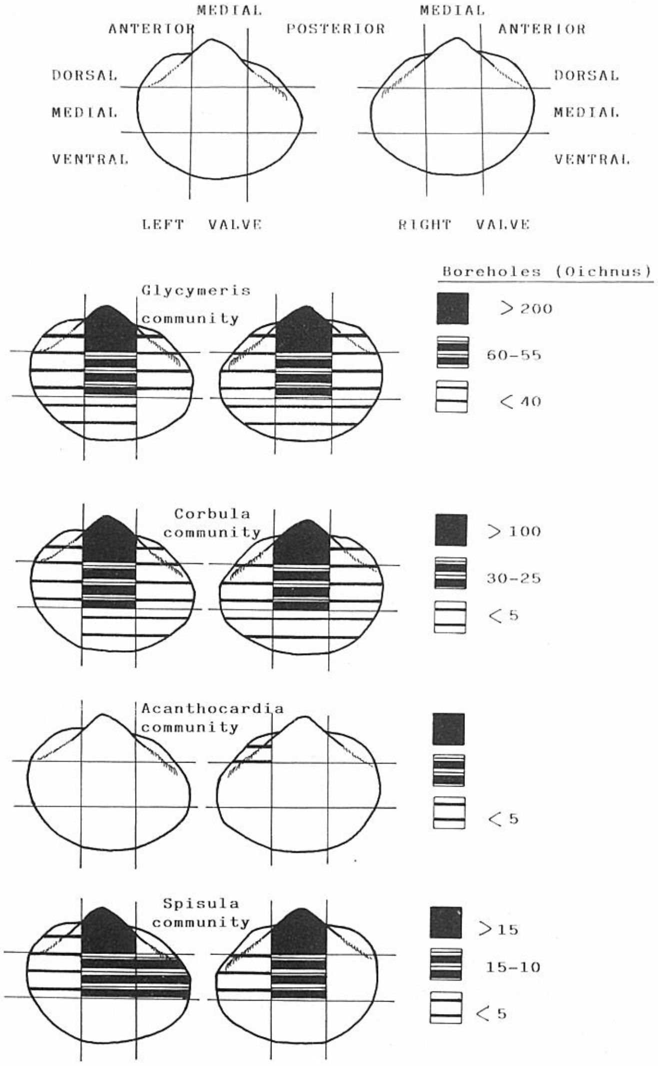


Figure 4. Graphical and numerical evaluation of *Oichnus* Bromley on *Glycymeris (G.) insubrica* (Brocchi) based on schematic contour diagrams.

3 a. *Glycymeris* Community.

Contingence Table Analysis
Summary Statistics

DF:	1
Total Chi-square:	1.21 p= 0.2713
G Statistic:	1.21
Contingency Coefficient:	0.017
Phi:	0.017
Chi square with continuity correction:	1.095 p= 0.2954

3 b. *Corbula* Community.

Contingence Table Analysis
Summary Statistics

DF:	1
Total Chi-square:	0.005 p= 0.9429
G Statistic:	0.005
Contingency Coefficient:	0.002
Phi:	0.002
Chi square with continuity correction:	1.943 p= 0.9889

3 c. *Acanthocardia* Community.

Contingence Table Analysis
Summary Statistics

DF:	1
Total Chi-square:	0.58 p= 0.4465
G Statistic:	♦
Contingency Coefficient:	0.182
Phi:	0.185
Chi square with continuity correction:	0.101 p= 0.7511

3 d. *Spisula* Community.

Contingence Table Analysis
Summary Statistics

DF:	1
Total Chi-square:	5.506 p= **0.019**
G Statistic:	5.536
Contingency Coefficient:	0.207
Phi:	0.212
Chi square with continuity correction:	4.572 p= 0.325

Table 3. Contingency table analysis (X^2 test) for the four bivalve communities in which *Glycymeris insubrica* (Brocchi) is a frequent species.

of Huelva Sands Fm. bryozoan assemblages, including also erect forms, will be discussed in a subsequent chapter.

Another scars produced by encrusting organism are balanomorphs (Figs. 5.9 and 7d), serpulids (Figs. 5-6 and 7c-d) and bryozoans (*Stellichnus radiatus,* Mayoral, 1987; Plate I, Fig. 4 and Fig. 7d). Finally, very rare borings are due to lithophagous bivalves (*Gastrochaenolites,* Plate I, Fig. 6) and *Trypanites solitarius,* borings of phoronids (Fig. 5.7; Plate II, Fig. 4). Scarce shallow traces are represented by *Gnathichnus* and *Radulichnus* (Fig. 5.5; Plate II, Figs. 1,2 and Fig. 7d).

INTERPRETATION AND COLONIZATION SEQUENCES

The study of marks recorded on surface valves *Glycymeris insubrica* (Brocchi) suggest that most of them are produced after death in disarticulated valves, clearly removed from their original position. Some of the marks recorded, however, are the result of commensalism relationships when the bivalves are still alive.

Life-stage colonization

The group of *Caulostrepsis-Maeandropolydora* borings, ascribed largely to Polychaeta annelids (Bromley & D'Alessandro, 1983) are located chiefly on posterior margins of the bivalve (Figs. 7a$_{1-2}$). These marginal zones are directed to the sediment surface, and if water fluxes are created nutrients are easy caught by settling organisms. This boring activity is realized when *G. insubrica* is alive, because of blocking marks and anomalous shell thickenings or corns produced as response to the annelids infestation.

In this stage, the colonization may be interrupted by the presence of fishes or decapoda (Fig. 7a$_1$) attacking the bivalve, breaking its shell and, in some cases, causing its death. Perhaps, the star-fishes or other predators may provoke the same wastes. This interruption is clearly demonstrated by the presence of cicatrices and traumatisms repaired. (Plate I, Fig. 3).

Colonization sequences *post-mortem*

After their death, the bivalves, mainly those living near the sediment-water interface, are quickly exhumed. In the

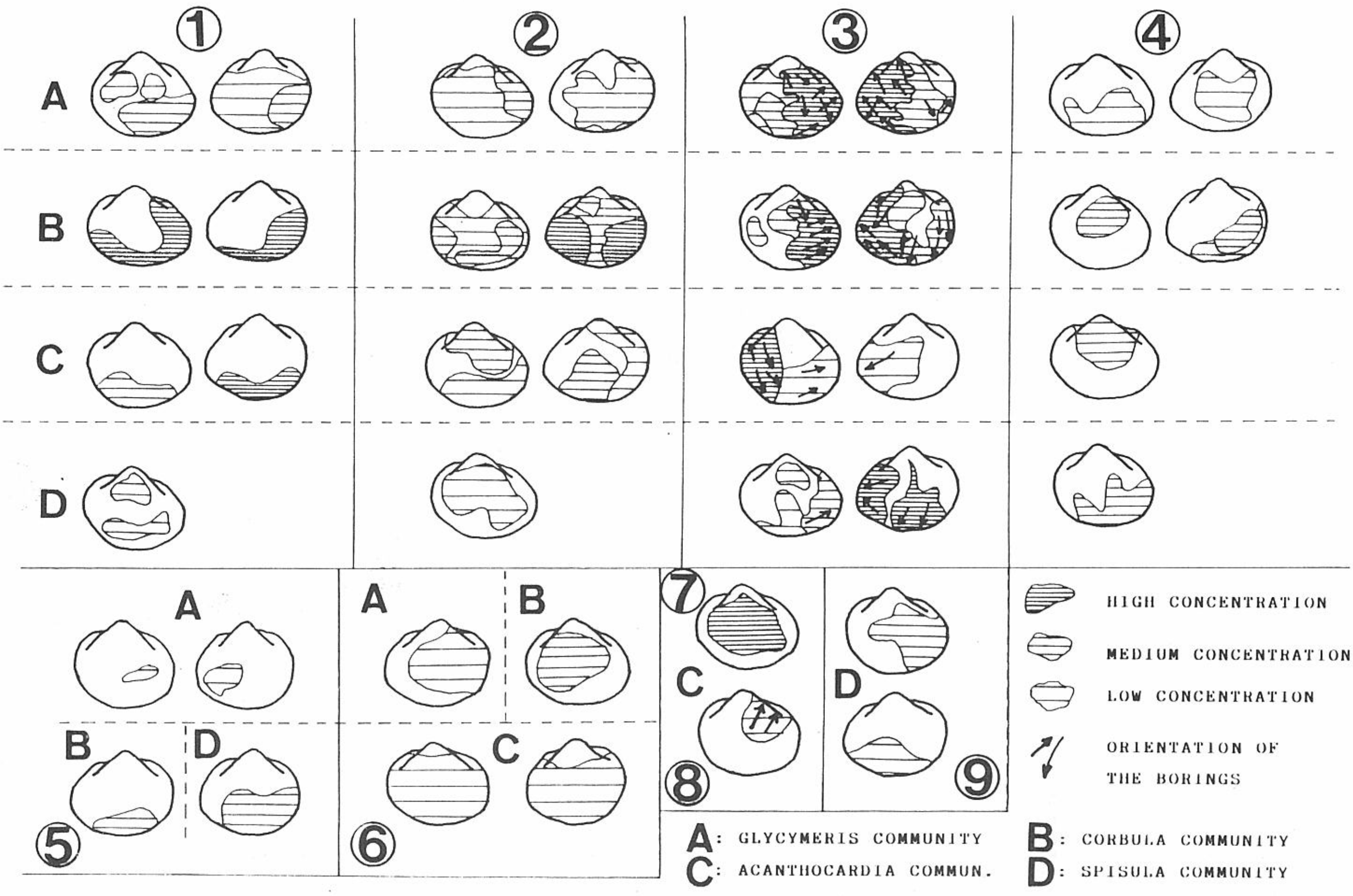


Figure 5. Schematic contour diagrams to evaluate the most important commensalism relationships on *Glycymeris (G.) insubrica* (Brocchi). 1: Thallophytes microborings; 2: *Entobia* (sponges' borings); 3: *Caulostrepsis-Maeandropolydora* (annelids borings); 4: *Iramena, Pennatichnus, Pinaceocladichnus* (ctenostomates bryozoans microborings); 5: *Gnathichnus-Radulichnus* (gastropods and equinoids scratching marks); 6: Encrusting serpulids; 7: *Trypanites* (phoronid borings); 8: *Gastrochaenolites* (lithophagous bivalves borings); 9: Balanomorphes scars marks.

first stage they remain in a near life position (Fig. 7a$_2$). In this conditions, when the light and space are favourable, there are microborings produced by different kinds of thallophyte commonly associated with the *Caulostrepsis-Maeandropolydora* borings. Sometimes, borings of *Entobia* class produced by sponges settlement are also present. It is also possible to find microborings produced by bryozoans. All these borings are always restricted to the valve areas above or immediately below the interface water-sediment. (Fig. 7a$_2$).

In a second stage, depending on hydrodynamic energy, the valves are disarticulated and dispersed over the sandy bottom (Figs. 7b-c). Consequently, all the zones of the shells are potentially available by colonizers. In this stage, many colonial organisms, chiefly encrusting bryozoa cover the surface valves. The encrusting bryozoans tend to occupy the more sheltered areas, but through shell movements by water currents, these areas can be overturned towards the external turbulent surfaces.

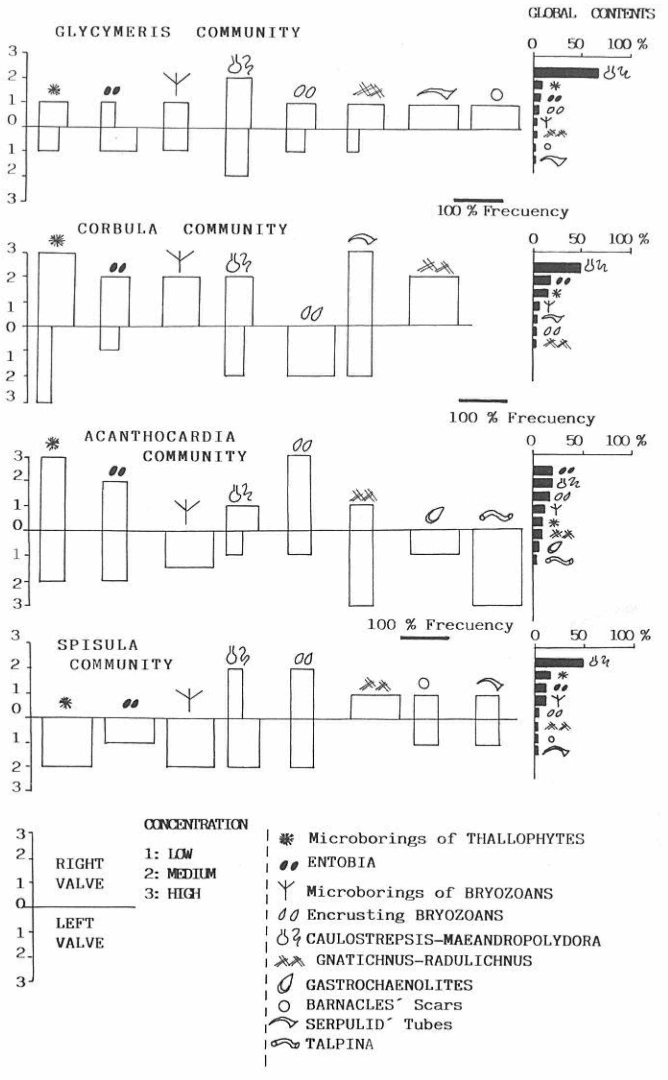


Figure 6. Frequency/intensity histograms for the most significant commensalism phenomena for every valve of *Glycymeris (G.) insubrica* (Brocchi) and real percentage with regard to the global content of them.

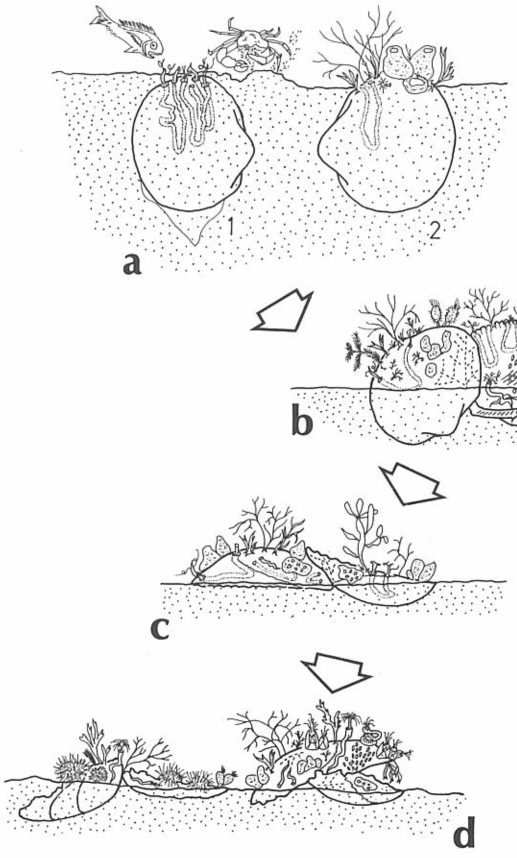


Figure 7. Idealized colonization sequence of *Glycymeris (G.) insubrica* (Brocchi) deduced from the palaeoecologic data refered in the text. 7a$_1$: Initial phase, live susbstratum and life position; 7a$_2$: First phase of the *post-mortem* stage: dead substratum still in "life position" with articulate valves; 7b: Valves in disarticulation processes. Internal and external colonization is beginning; 7c: Secondary phase of the *post-mortem* stage: completely disarticulated valves and starting of stabilitation of the substratum on the bottom; 7d: Final phase of the *post-mortem* stage: mature substratum in evolutioned colonization situation.

Plate II

1 *Gnathichnus pentax* Bromley (echinoid bioerosion) on the internal central side of *Glycymeris (G.) insubrica* (Brocchi). Scale bar: 4 mm.

2 *Radulichnus* sp (gastropods or chitons bioerosion) on the internal central side of *Glycymeris (G.) insubrica* (Brocchi). Scale bar: 4 mm.

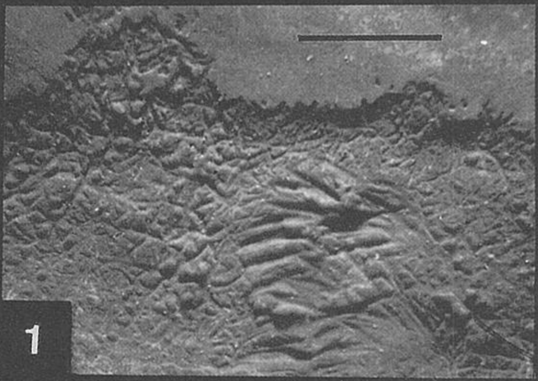
3 Meandroids scars attributed to encrustings annelids (serpulids). Scale bar: 1 cm.

4 *Trypanites solitarius* (phoronid microborings) on the external central surface. Scale bar: 1 cm.

5 Normal state of clustering (nesting) in the most of the skeletal concentrations studied. *Glycymeris (G.) insubrica* (Brocchi) operate as a trap for himself. Scale bar: 1 cm.

6-7 Settings of *Neopycnodonte cochlear* (Poli) on the internal side of *Glycymeris (G.) insubrica* (Brocchi). Scale bar: 1 cm.

Plate II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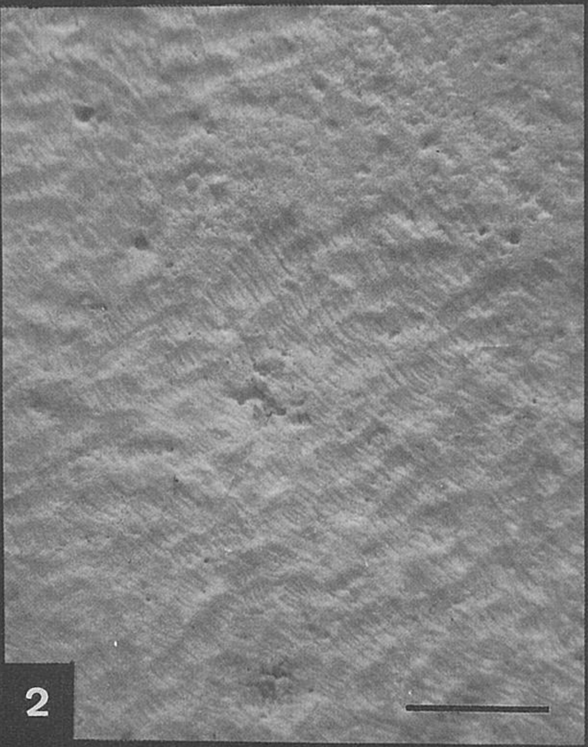
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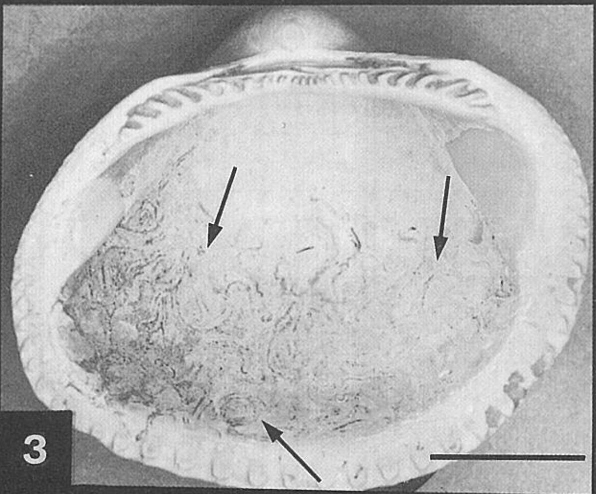
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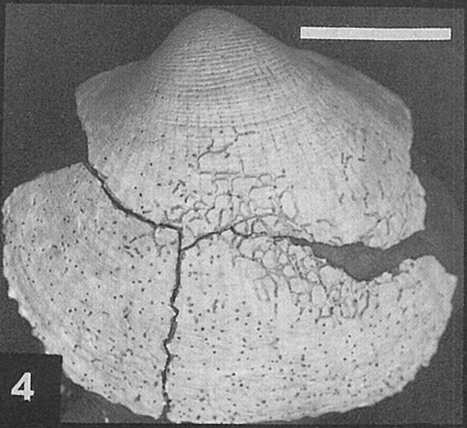
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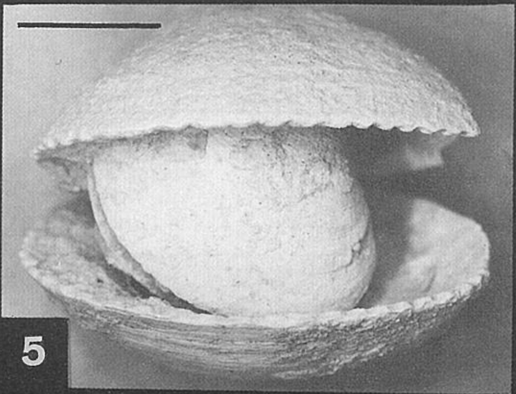
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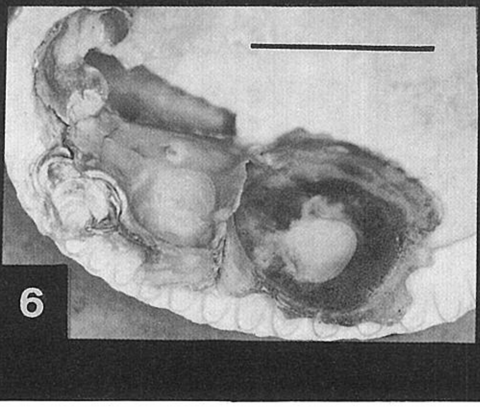
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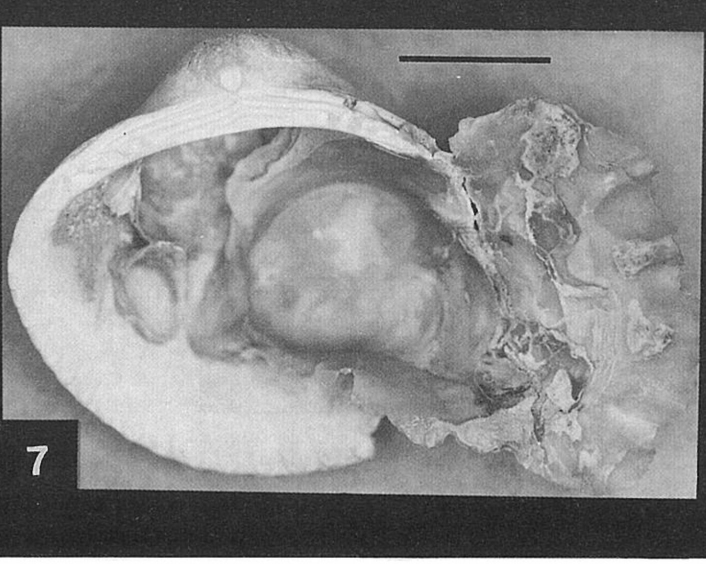
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bryozoan species / samples	ENCRUSTING COLONIES												NON - ENCRUSTING COLONIES								
	Biflusta savartii (Sav.-Audouin)	*Electra monostachys* (Busk) *	*Calpensia gracilis* (Munster)	cf. *Manzonella fissurata* (Busk)	*Chorizopora brongniarti* (Sav.-Audouin)	*Reptadeonella violacea* (Johnston)	*Microporella utriculus* (Manzoni)	*Schizoporella* aff. *tetragona* (Reuss)	*Prenantia cheilostoma* (Manzoni)	*Smittina* sp. A	*Rhynchzoon* sp.	unidentified species	*Biflusta savartii* (Sav.-Audouin)	*Cupuladria vindobonensis* Baluk & Rad	*Cupuladria onubensis* nov. sp.	*Reussirella reussiana* (Manzoni)	*Reussirella haidingeri* (Reuss)	*Lunulites androsaces* Michelotti	*Metrarabdotos moniliferum* (Milne-Edw)	*Metrarabdotos* aff. *elegans* Buge & Gal	*Rhynchozoon* sp.
BO_1 3/2				1 1																	
BO_2 1												1 2 AN									
BO_3 1/1		5 5		3 3	5 5			3 3	2 3	24 47		5 5 CY									
BO_3 1/3	1 1	3 3								8 19											
BO_3 1/4										1 1		1 1 AS									
BO_5 1/5						1 1			$\boxed{1}$ 1	1 1 2 2	$\boxed{1}$ 1										
BO_3 1/6		3 3								5 10	1 1										
BO_3 1/7										3 3											
BO_3 1/8		1 1							1 1		1 3										
BO_4 2/1										3 3	2 2										
BO_4 2/2		4 4		5 5	2 2		2 2	13 14		26 41	7 10										
BO_4 2/3										1 1			1								
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BO_5 1/3								1 1		① 1 1 2	8 9						2				
BO_5 1/4	1 2																3				
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BO_6 3/2		1 1 2 2		1 1 1 1		① 1			① 1	① 4 1 1	② 3				1	16					
BO_6 4/1		① 1								② 2											
BO_6 4/2		① 2																			
BO_6 4/3	1 1	② 2 2 2								1 1	① 1 1 1										
LU_1 1/1										1 1			1			2					
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LU_3 1														1			3				
LU_3 2/1										① 1						4					
LU_3 3										1 1	1 1				4						
MO_2 3/1				1 3															3		
MO_2 3/2																			1		
MO_5 1	1 1	1 1		1 3								1 1 CY									
MO_6 3		7 7				3 3				3 3	3 4 1 2	1 1 CY				2					
MO_6 4											① 1							1			
PF_4 1	1 2			2 2								3 3 AN 1 1 CY									
H_1 1			$\boxed{1}$ 1																		
H_1 8				2 4								3 11 CY									
H_1 10				1 2								1 2 AN 1 1 CY									

Table 4. General distribution of the bryozoans in the samples studied. For an explanation of the figures in the cells see text. (AN: Anascan; CY: Cyclostomata; AS: Ascophoran).

In a third and last stage (Fig. 7d), the valves remain near steady in the sea floor. The borings increase, and a lot of traces are present. These traces are produced by encrusting organisms like balanomorphs, serpulids, bryozoans and borings as some lithophagous bivalves and phoronids.

The borings and traces are distributed in all available valve surfaces, both external and internal, producing a very complex laberynthic print or also destroying the shells. In these last stages, the destruction is favourized by scraping action of sea-urchins, chitons and so on. These organisms find their food source between the cavities and residual products of prior borings.

BRYOZOANS IN HUELVA SANDS FM.

The bryozoans are one of the major contributors to Huelva Fm beds. Table 4 shows the distribution of bryozoans in different samples. Each cell corresponds to one determinate sample and to one specific bryozoan species. The left-hand side of the table is devoted to encrusting bryozoan species. Each cell contains between one and three pairs of figures. The first figure in each pair indicates the number of encrusted bivalve shells and the species to which they belong. The figures corresponding to *Glycymeris insubrica* shells are indicated by numbers in standard print; the smaller print numbers correspond to *Ostrea (O.) edulis lamellosa*; the figures within a circle *Acanthocardia* sp; and the figures within a square to other species. The second figure in each pair indicates the number of bryozoan species encrusting disarticulated bivalve shells of each of the species considered. In a large number of cases the two figures are equal, indicating that there is only one bryozoan species on each bivalve shell. It can be seen that most of the shells encrusted belong to the species *Glycymeris insubrica* (63 %); followed by *Ostrea (O.) edulis lamellosa* (25 %), *Acanthocardia* sp (10 %) and only 2 % to other species.

Reguant (1993) and Reguant & Mayoral (1994) described the general conditions of these encrusting bryozoa, in a detailed study of encrustation on *Glycymeris insubrica* shells. Their main conclusions are: **(1)** There are both externally and internally encrusted valves. The number of internally encrusted valves is higher than the number of externally encrusted ones; **(2)** Most colonies are found in the edge position as defined by Ward & Thorpe (1989); **(3)** The number of colonies in each individual valve ranges from 1 to 6, very few valves support more than two; **(4)** The areal occupancy ratios (100 **a/A**) where **a** is the area covered by bryozoan colonies, and **A** the total area available to be covered, are very small. In 27 % of encrusted valves the encrusting bryozoans occupy less than 1 % of the area available; in 59 % less than 3 %, and in 99 % less than 28 %.

The right hand side of the Table 4 shows the content of non-encrusting bryozoan colonies in the samples. Most of these colonies are free-living (*Cupuladria, Reussirella* and *Lunulites*).

PALAEOECOLOGIC OBSERVATIONS ON BRYOZOAN ENCRUSTING BIVALVES

Cyclostomata forms

Thirty-one encrusting, linear or flabelliform cyclostome colonies were found, most of them (28) on *Ostrea edulis lamellosa* valves. None of the Cyclostomata species has been identified. The preserved fragments are very small and they do not possess the diagnostic features for correct identification. Nevertheless 5 fragments of an adnate zooid system of *Crisiidae* have been found, four of them on an unique smooth internal surface of the *Ostrea edulis lamellosa,* and one in a wedge part of the internal surface of a *Glycymeris insubrica* valve.

The structure and phylogenetic significance of this kind of zooid adnate system is discussed by Silén (1987). The samples taken in Huelva present some differences with regard to the forms described by the latter author (Plate III, Figs. 1, 2). In Huelva forms the autozooids are fully adnate, without a proximal adnate part and a distal region raised into a peristome as in Silen's forms. We have not seen the formation of an erect branch from ancestrula. The number of buds formed from the basal disc of the ancestrula is 3 instead of 4 described by Silen. The respective angles range from 90° to 170°. The length of adnate autozooids is highly variable (from 0.233 to 1.540 mm) most of them being between 0.4 to 0.7 mm (arithmetic mean of 13 measurements, 0.678 mm).

It seems (personal communication by Harmelin) that the extensive development of adnate systems constitutes a strategy to occupy the greatest area of available space on the smooth flat surface of the disarticulated valves remaining on the sea floor.

Cheilostomata forms

All encrusting cheilostome species present, except *Electra monostachys* whose colonies are often "runners", form "sheets" according to the nomenclature by Jackson (1979). There are two kinds of sheet formed by the encrusting colonies: flabelliform and radial. Flabelliform sheets are the result of growth with predominant proximal direction. The lateral expansion of the colony is by wider zooecia producing two new rows in the same proximal direction. This growth pattern is apparent in *?Manzonella fissurata,* in *Biflustra savartii* and in *Calpensia gracilis* (Plate III, Fig. 3).

Radial growth is typical of the obligatory multiserial colonies, termed by Silén (1987) "unitary multiserial". It is more apparent if the colonies are small, due either to premature death or because the species are characterized by a short life-span. In Huelva shells the colonies of *Chorizopora brongniarti, Schizoporella* cf. *tetragona, Prenantia cheilostoma, Smittina* sp. A and *Rhynchozoon* sp. are clearly of this type even showing a more or less circular outline (Plate III. Fig. 4). *Reptadeonella violacea* and *Microporella utriculus* also show radial growth, but in our specimens they tend to occupy all the available space with adaptations that produce irregular non-circular outlines of the whole colonies.

The uniserial (Silén, 1987) or runner (Jackson, 1979) type, considered in its strictest sense, consists of a single row of zooecia branching and sometimes colliding, but as Silén (1987) points out there are also bi-, tri- or pluriserial rows. In Huelva *Electra monostachys* growth is made by flabelliform uniserial rows but mainly bi- and triserial, which sometimes produce small areas with pluriserial fan-like sheets, in central or lateral situation with respect to the central growth-line (Plate III. Fig. 5).

The preservation of the traces of *Electra monostachys* on bivalve shells in which the skeletal remains of the same species have been destroyed by *post-mortem* processes, gives us a better understanding of both the growth type and the behavior of this species in the environment of the Huelva Sea in Lower Pliocene times. It seems that *Electra monostachys* in Huelva Sands Fm. found an extremely poor nutritional environment (Poluzzi, 1981). On the other hand, this species encrusts both internal and external valve surfaces and sometimes it is possible to see that a runner colony crossed the boundary of the shell separating the external from the internal surface. This constitutes some of the clearest evidence of overturning of shells in a high energy environment.

This species is, in many cases, an estuarine form. This seems to be the case in Huelva, as the presence of some ichnospecies of *Entobia* corroborate. If so, this species lived in Huelva Sea at a different time to the other encrusting species, which are clearly marine. As has been pointed out, some trace-maker bryozoans lived in Huelva Sea during the last stage of the shelly sea-bottom before the fixed position of all material by sedimentation.

THE FINAL EVENT: THE SKELETAL CONCENTRATIONS

The different biogenic parts acummulated in the sedimentary record reflect the succesive environmental conditions derived from the palaeogeographic context existing in the different past times. This results in the acquisition of a taphonomic code which allows us to decipher the biostratinomic history of each concentration of remains.

To simplify and make homogeneous the study of these concentrations we follow, with some modifications, the des-

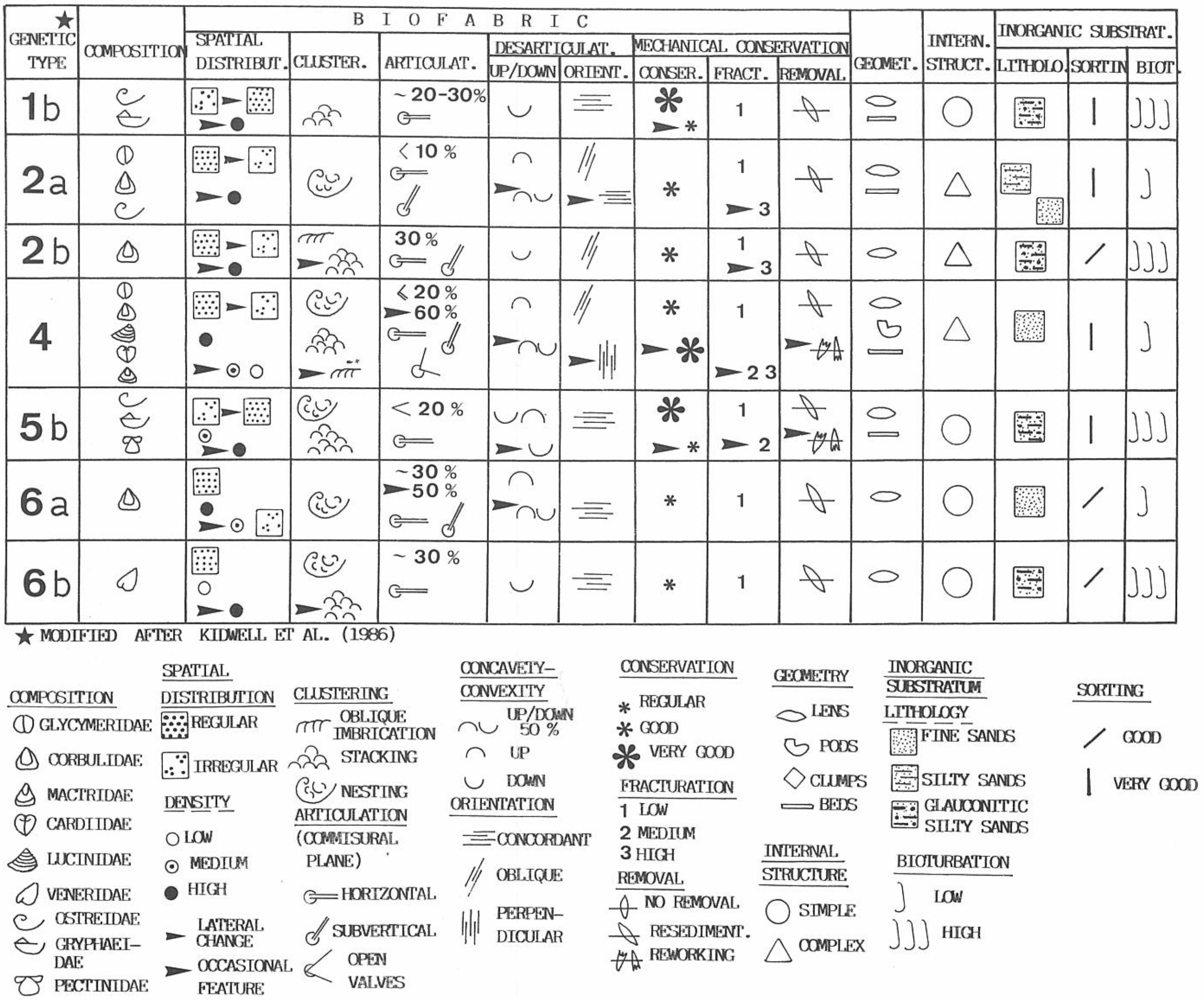


Table 5. Genetic types of the skeletal concentrations.

Plate III

1 Branching adnate zooid system of a Crisiidae specimen. Scale bar: 500 µm.

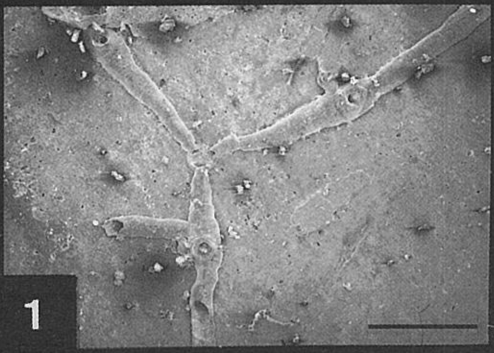
2 Basal disc of a Crisiidae species showing three buds emerging from him. Scale bar: 100 µm.

3 Partial aspect of a flabelliform colony of *Calpensia gracilis* showing (in the right part of the photo) the production of two new rows of zooecia from one wider zoecium. Scale bar: 1 mm.

4 Small circular colony of *Smittina* sp with typical radial growth. Scale bar: 1 mm.

5 Etching scars of unpreserved *Electra monostachys* colonies showing uniserial growth as discussed in the text. Scale bar: 4 mm.

Plate III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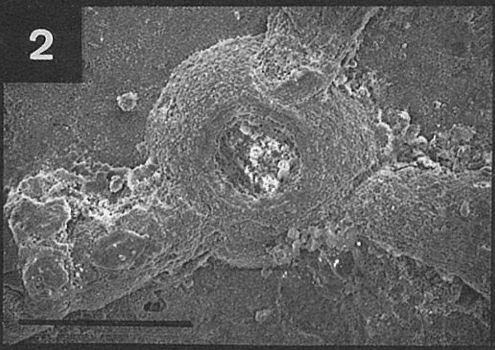
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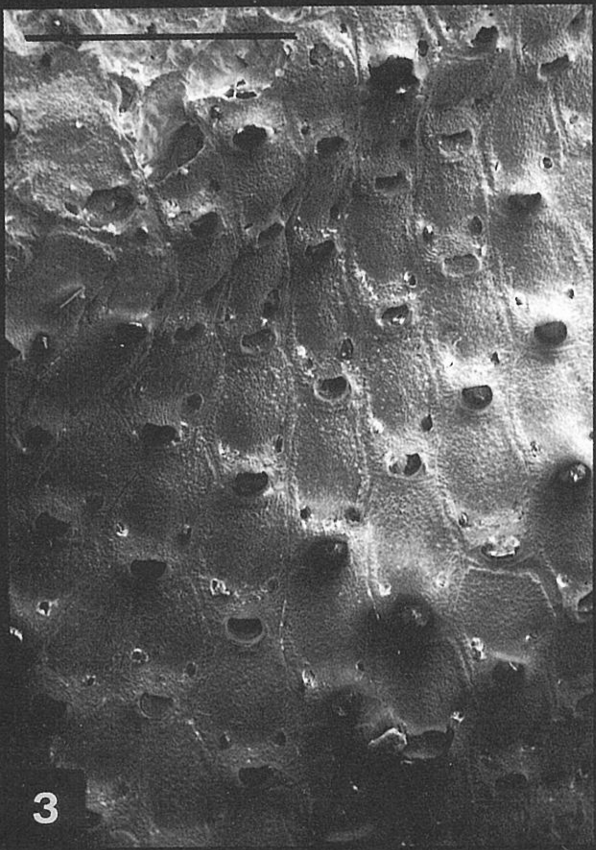
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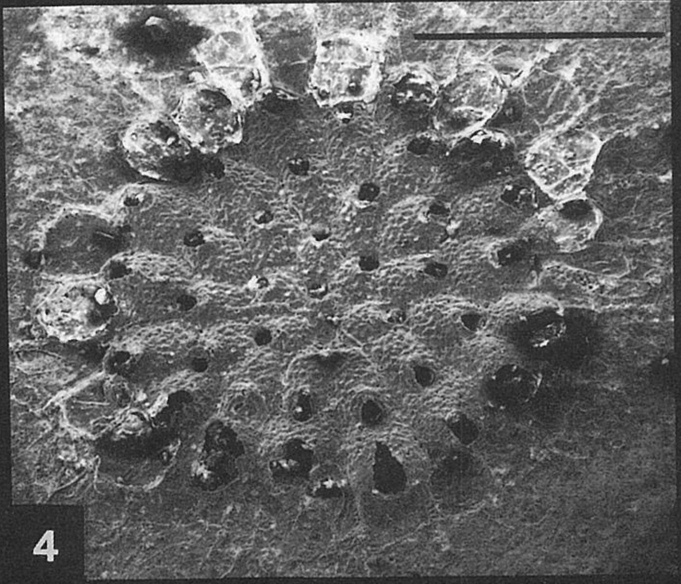
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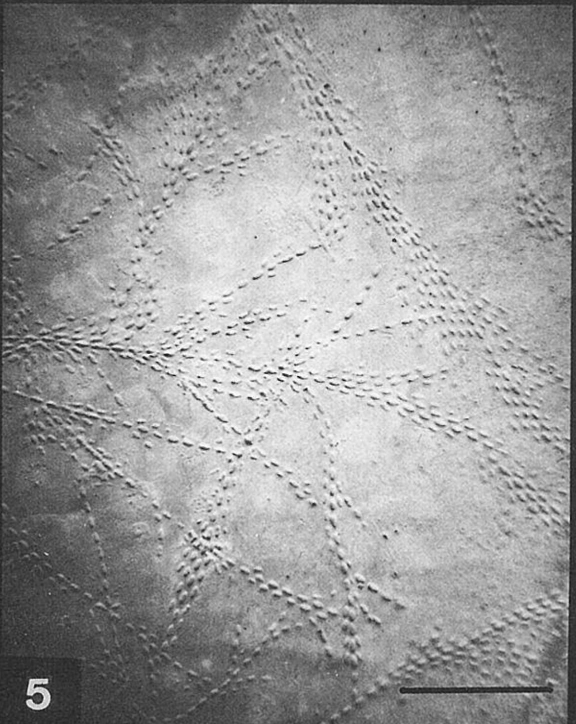
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criptive nomenclature of Kidwell *et al.* (1986). We have added some supplementary taxonomic and sedimentologic criteria with the introduction of the *a* and *b* suffixes to differentiate between substrates constituted by fine sands with no or low bioturbation and they glauconitic and very bioturbed respectively. The types resulting are summarized in Table 5.

Five genetic types *sensu* Kidwell *et al.* (1986) have been distinguished: **biogenic concentrations** (1b); **sedimentological concentrations** (2a and 2b), and 3 types of mixed concentrations; the more abundant **biogenic-sedimentologic concentrations** (4); and **sedimentologic-diagenetic** (5b) and **biogenic-diagenetic concentrations** (6a and 6b).

In general all skeletal concentrations studied correspond to an evolutive model with a common origin. The different final evolution derives from the different nature and strength of physical processes they have been subject.

The bivalve communities living in stable and low energy bottoms (*Venus* and *Neopycnodonte* communities) produce biogenic concentrations, mainly intrinsic (*sensu* Kidwell *et al.*, 1986). These concentrations remain in the same type until the last taphonomic processes. The recent dissolution shift them to a mixed biogenic-diagenetic type.

The communities living in, more or less fluctuating, high energy environments, it is nearly all remaining communities (*Glycymeris, Corbula, Spisula, Acanthocardia, Lucina* and *Ostrea* communities), start as biogenic concentrations of high density, but often have been subjected to a resedimentation. This resedimentation, intense in short time spans coinciding probably with storm events (Dabrio *et al.* 1988) was unsufficient to produce alloctonous accumulations within the lumachelic beds. In fact, this layers are constituted by remains in different degree of removal with an *in situ* fossil assemblages. In some cases the chemical dissolution processes are apparent (southern part of the studied region) and then they shift to biogenic-diagenetic type.

The biogenic-sedimentologic concentrations, mainly these derived from epifaunal bivalve communities, constitute a subtype characterized by a recolonization produced by new organisms. These organisms can modify continuously the feedback taphonomic processes. The study of the bioerosive structures and the encrusting organisms, mainly bryozoans, allowed us to discover these complex processes.

CONCLUDING REMARKS

The fossiliferous beds of the Huelva Sands Formation (Lower Pliocene) characteristic in the SW area of the Guadalquivir Basin, were deposited through a transgressive-regressive cycle. The presence of these levels in the uppermost part of this Formation allows the collection of interesting data on several palaeoecologic aspects of the fossil assemblages. *Glycymeris insubrica* (Brocchi) one of the most abundant bivalves in the main communities differentiated, has been chosen to illustrate some examples related with these subjects. So, the borings *(Oichnus)* on the valves permit us to establish that: **(1)** most of the predators attacks were produced when the prey *(G. insubrica)* was still alive, **(2)** life position was vertical with the umbonal area near the surface, corroboring previous observations (Thomas, 1975), **(3)** the existence of a first stage *post-mortem* without transportation, **(4)** when transport was present, this was in connection with high energy conditions related to repeated storm surges, confirming the Sierro *et al.* (1990) assumptions.

The bioerosional structures, except *Oichnus,* allow us to show the existence of a commensalism relationship when the bivalves were still alive, and also the sequence of colonization of the disarticulated valves in *post-mortem* stages. The steps were the following: **(a) life stage:** settling of boring organisms on the posterior margins of *Glycymeris*: polychaeta annelids *(Caulostrepsis-Maeandropolydora).* The sequence may be interrupted by the attack of fishes or crustacea decapoda, normally crabs (traumatisms repaired). **(b) *post-mortem* stages:** Advance of the boring activity from the posterior areas in partial exhumed still articulated valves: borings of thallophytes *(B_1, B_2, B_4 morphotypes),* sponges *(Entobia),* bryozoans *(Pinaceocladichnus onubensis, Iramena bonaresi).* The valves are disarticulated and practically exhumed. The former boring organisms provoke an extensive and unoriented colonization of the valves. Lithophagous bivalves *(Gastrochaenolites),* phoronids *(Talpina)* and others encrusting: balanomorphs, serpulids and above all, bryozoans, finish the sequence. The last stages were characterized by scraping actions of sea-urchins *(Gnathichnus)* or chitons *(Radulichnus).*

The encrusting bryozoans mainly colonize the valves in *post-mortem* stages and they generally occupy a very small area respect to the total available. Cyclostomata form linear or flabelliform colonies and settle normally on the bivalve *Ostrea (O.) edulis lamellosa.* Cheilostomata form sheets (flabelliform and radial) and "runner" colonies (uniserial). The most important *runner* colony is *Electra monostachys,* the growth of which evidences a clear overturning of shells in a high energy, extremely poor nutritional estuarine environment developed at a different time to the other marine encrusting species. Finally, the skeletal concentrations correspond largely to biogenic concentrations which were modified to mixed types (biogenic-sedimentologic, sedimentologic-diagenetic or biogenic-diagenetic) on the basis of the energy on the bottom or of the relatively recent ulterior diagenetic processes.

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BIBLIOGRAPHY

Adegoke, O.S. and Tevesz, M.J.S. 1974. Gastropod predation patterns in the Eocene of Nigeria. *Lethaia,* **7,** 17-24.

Andrés, I. 1982. *Estudio malacológico (Clase Bivalvia) del Plioceno marino de Bonares (Huelva).* Tesis Doctoral. Universidad de Salamanca (Unpublished), 410 pp.

Antunes, M.T., Civis, J., Dabrio, C.J., Pais, J., Sierro, F.J., González Delgado, J.A., Flores, J.A. y Valle, M.F. 1989. El Neógeno del Algarve (Portugal) y de la Cuenca del Guadalquivir (España). *Actas IV Jornadas de Paleontología.* Salamanca, 65-72.

Berg, C.J. 1975. A comparison of adaptative strategies of predation among naticid gastropods. *Biological Bulletin,* **149,** 420-421.

Berg, C.J. 1976. Ontogeny of predatory behaviour in marine snails (Prosobranchia: Naticidae). *Nautilus,* **90,** 1-4.

Berg, C.J. and Nishenko, S. 1975. Stereotypy of predatory boring behaviour of Pleistocene naticid gastropods. *Paleobiology,* **1,** 258-260.

Boucot A.J. 1990. *Evolutionary Paleobiology of Behaviour and Coevolution.* Elsevier Scientific Publishing, 725 p.

Bromley, R.G. and D'Alessandro, A. 1983. Bioerosion in the Pleistocene of Southern Italy: ichnogenera *Caulostrepsis* and *Maeandropolydora. Rivista Italiana di Paleontologia e Stratigrafia,* **89,** 283-309.

Carriker, M.R. and Zandt, D. Van 1972. Predatory behaviour of a shell-boring muricid gastropod. *In: Behaviour of marine animals* (Eds. H.E. Winn and B.L. Olla). Plenum Press. New York, 157-24.

Castaño, M.J., Civis, J. y González Delgado, J.A. 1988. Los Moluscos del Plioceno de la Palma del Condado y Moguer (Huelva). Aproximación paleoecológica. *Iberus,* **8** (2), 173-186.

Civis, J., Sierro, F.J., González Delgado, J.A., Flores, J.A., Andrés, I., Porta, J. de y Valle, M.ª. F. 1987. El Neógeno marino de la provincia de Huelva. Antecedentes y definición de las unidades litoestratigráficas. *In: Paleontología del Neógeno de Huelva,* Ediciones Universidad de Salamanca, 9-21.

Dabrio, C.J., González Delgado, J.A., Civis, J. y Sierro, F.J. 1988. Influencia de las tempestades en la generación de niveles e interniveles fosilíferos en las Arenas de Huelva (Plioceno). *Resúmenes IV Jornadas de Paleontología.* Salamanca, 34-36.

Galán, E., González, I., Mayoral, E. y Vázquez, M.A. 1989. Caracterización y origen de la facies glauconítica de la Cuenca del Guadalquivir. *Estudios Geológicos,* **45**, 169-175.

González Delgado, J.A. 1983. *Estudio de los gasterópodos del Plioceno de Huelva.* Tesis Doctoral. Universidad de Salamanca, 474 p.

González-Delgado, J.A., Sierro, F.J. y Civis, J. 1993. Cambios globales del nivel del mar y concentraciones de megafaunas marinas someras en el Neógeno del Oeste de la Península Ibérica. *Comunicaciones de las IX Jornadas de Paleontología,* 33-36.

González Delgado, J.A., Andrés, I. and Sierro, F.J. *in press.* Late Miocene and Early Pliocene molluscan faunas from the Northeast Atlantic (Lisbon, the Algarve, W Guadalquivir, NW Morocco). *Procedings First RCANS Congress,* Lisbon 92. Springer Verlag.

Guerrero, S. and Reyment, R.A. 1988a. Predation and feeding in the naticid gastropod *Naticarius intricatoides* (Hidalgo). *Palaeogeography, Palaeoclimatology, Palaeoecology,* **68** (1), 49-52.

Guerrero, S. and Reyment, R.A. 1988b. Differentation between the traces of predation of muricids and naticids in Spanish Pliocene *Chlamys. Estudios Geológicos,* **44** (3-4), 317-328.

Hoffman, A. and Martinell, J. 1984. Prey selection by naticid gastropod in the Pliocene of Emporda (Northeast Spain). *Neues Jahrbuch Geologie und Paläontologie, Monatshefte* **(7)**, 393-399.

Jackson, J.B.C. 1979. Morphological strategies of sessile animals. *In: Biology and Systematics of Colonial Organisms.* (Eds. G. Larwood & B. R. Rosen). *Systematics Association Special Vol.* **11**, 499-555.

Kabat, A.R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia,* **32** (1), 155-193.

Kelley, P.H. 1984. Coevolution in a naticid gastropod predator-prey system: relation of predation intensity to rates of prey evolution. *Geological Society of America Abstracts with Programs,* **19**, 724.

Kelley, P.H. 1988. Predation by Miocene gastropods of Cheasapeake Group: stereotyped and predictable. *Palaios,* **3**, 436-448.

Kelley, P.H. 1991. Apparent cannibalism by Chesapeake Group naticid gastropods: a predictable result of selective predation. *Journal of Paleontology,* **65**, 75-79.

Kidwell, S.M., Fürsich, F.T. and Aigner, Th. 1986. Conceptual framework for the analysis and classification of fossil concentrations. *Palaios,* **1**, 228-238.

Kitchell, J.A., Boggs, C.H., Kitchell, J.F. and Rice, J.A. 1981. Prey selection by naticid gastropods: experimental test and application to the fossil record. *Paleobiology,* **7**, 522-533.

Kitchell, J.A., Boggs, C.H., Rice, J.A., Kitchell, J.F., Hoffman, A. and Martinell, J. 1986. Anomalies in naticid predatory behaviour: a critique and experimental observations. *Malacologia,* **27**, 291-298.

Kornicker, L.S., Wise, Ch. D. and Wise, J. M. 1963. Factors affecting the distribution of opposing mollusk valves. *Journal of Sedimentary Petrology,* **33** (3), 703-712.

Mayoral, E. 1986a. *Tafonomía y Paleoecología del Plioceno de Huelva-Bonares.* Tesis Doctoral. Universidad de Sevilla, 599 p. (Unpublished).

Mayoral, E. 1986b. Icnofacies de *Skolitos* y *Cruziana* en el Neógeno superior (Plioceno marino) del sector de Huelva-Bonares (Valle del río Guadalquivir, España). *Revista Española de Paleontología,* **1**, 13-28.

Mayoral, E. 1987. *Stellichnus* nov. icnogen. Huellas de incrustación atribuidas a *Paravinella* nov. gen. (Bryozoa, Ctenostomata) de la Formación Arenas de Huelva (Plioceno inferior) en la Cuenca del Bajo Guadalquivir. *Revista Española de Paleontología,* **2**, 33-40.

Mayoral, E. 1988a. Microperforaciones (Tallophyta) sobre Bivalvia en el Plioceno del Bajo Guadalquivir. *Estudios Geológicos,* **44**, 301-316.

Mayoral, E. 1988b. *Pennatichnus* nov. icnogen.; *Pinaceocladichnus* nov. icnogen. e *Iramena.* Huellas de bioerosión debidas a Bryozoa perforantes (Ctenostomata, Plioceno inferior) en la Cuenca del Bajo Guadalquivir. *Revista Española de Paleontología,* **3**, 13-22.

Mayoral, E. 1989. Dinámica sedimentaria y concentraciones fósiles: implicaciones en la realimentación tafonómica. *Revista de la Sociedad Geológica de España,* **2**, 31-40.

Mayoral, E. 1990. Implicaciones etológicas y significado de la estereotipicidad en *Oichnus* Bromley durante el Plioceno en la Cuenca del Bajo Guadalquivir (SO, España). *Estudios Geológicos,* **46**, 347-354.

Mayoral, E., y Pendón, J.G. 1986-1987. Icnofacies y sedimentación en zona costera. Plioceno superior (?), litoral de Huelva. *Acta Geológica Hispánica,* **21-22**, 507-513.

Mueller, H.G. 1974. The development of prey recognition and predatory behaviour in the American Kestrel. *Falco Sparverius Behaviour,* **49**, 313-324.

Pendón, J.G., y Rodríguez Vidal, J. 1986-1987. Caracteres sedimentológicos y geomorfológicos del Alto Nivel Aluvial cuaternario en el litoral de Huelva. *Acta Geológica Hispánica,* **21-22**, 107-111.

Poluzzi, A. 1981. *Electra monostachys* (Busk): un Cheilostoma Anasca nelle acque costiere del Mare Adriatico (Bryozoa). *Atti della Società italiana di Scienze naturali. Museo civico di Storia naturale, Milano,* **122** (1-2), 3-20.

Porta, J., y González Delgado, J.A. 1980. Algunos aspectos tafonómicos y paleoecológicos en el Plioceno de Niebla. I (Bivalvos). *Resumen II Congreso Nacional de Malacología,* Barcelona, 3.

Porta, J., y González Delgado, J.A. 1983. Relación fauna - sedimento de los Bivalvia en el Plioceno de Huelva (Sección de la Autovía Sevilla-Huelva). *Resúmenes. X Congreso Nacional de Sedimentología.* Menorca, 7.1-7.3

Raup, D.M. and Stanley, S.M. 1971. *Principles of Paleontology.* W.H. Freeman & Co. San Francisco, 451 p.

Reguant, S. 1993. The Cheilostome Bryozoa from the Huelva Pliocene (SW Spain) in the Western Mediterranean context. *Memorie di Scienze Geologische,* **45**, 125-138.

Reguant, S. and Mayoral, E. 1992. The time of postmessinian opening of the Mediterranean: evidence from Pliocene bryozoans. *In: Mar de Alborán-Golfo de Cádiz: Conexiones atlántico-mediterráneas* (Ed. A. Maldonado). *III Congreso Geológico de España y VIII Congreso Latinoamericano de Geología.* Salamanca 1992. Simposios **2.** 532-535.

Reguant, S. and Mayoral, E. 1994. The encrusting Bryozoa on disarticulated bivalve shells (chiefly of *Glycymeris insubrica*) in the Lower Pliocene of Huelva (SW Spain). *In: Biology and Paleobiology of Bryozoans* (Eds. P.J. Hayward, J.S. Ryland & P.T. Taylor). Olsen & Olsen. Fredensborg, 157-160.

Schopf, T.J.M. 1969. Paleoecology of Ectoprocts (Bryozoans). *Journal of Paleontology,* **43**, 234-2442.

Scott, R.W. 1976. Trophic classification of benthonic communities. *In: Structure and Classification of Paleocommunities* (Eds. R. W. Scott and West), 29-66.

Sierro, F.J. 1984. *Foraminíferos planctónicos y bioestratigrafía del Mioceno superior-Plioceno del borde occidental de la Cuenca del Guadalquivir (SO de España).* Tesis Doctoral. Universidad de Salamanca, 391 pp. (Unpublished). Abstract TC 325, 34 p. Ed. Universidad de Salamanca.

Sierro, F.J., González Delgado, J.A., Flores, J.A., Dabrio, C.J. and Civis, J. 1990. The Neogene of the Guadalquivir Basin (SW Spain). *Paleontologia i Evolució.* Memoria Especial, **2**, 209-250.

Silén, L. 1987. Colony growth pattern in *Electra pilosa* (Linnaeus) and comparable encrusting cheilostome bryozoans. *Acta Zoológica,* **68** (1), 17-34.

Sohl, N.F. 1969. The fossil record of shell boring by snails. *American Zoologist,* **9**, 725-734.

Stewart, J. 1967. Wave and current orientation of shells. *Journal of Sedimentary Petrology,* **37**, 1124-1138.

Taylor, J.D., Cleevely, R.J. and Morris, N.J. 1983. Predatory gastropods in a Tertiary (Eocene) molluscan assemblage from Paris Basin. *Palaeontology,* **26**, 521-553.

Thomas, R.D.K. 1975. Functional morphology, ecology and evolutionary conservation in the Glycymeridae (Bivalvia). *Paleontology,* **18**, 217-255.

Ward, M.A. and Thorpe, J.P. 1989. Assessment of space utilisation in a subtidal temperate bryozoan community. *Marine Biology,* **103**, 215-224.

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