

LATE NEOGENE MOLLUSCAN FAUNAS FROM THE NORTHEAST ATLANTIC (PORTUGAL, SPAIN, MOROCCO)

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ABSTRACT

The age of the main Neogene molluscan deposits from Lisboa, Algarve (Portugal), Sevilla, Huelva (Guadalquivir Basin, SW of Spain) to Dar bel Amri (South Rifian Basin, NW of Morocco) has been established and correlated with the global sea level changes on the basis of micropaleontological event-stratigraphic evidence. The time period ranges from the Early Tortonian to the Late Zanclean. The deposits consist of sands with levels of concentration of molluscs that are generally shell-supported, with a variable morphology and arrangement. They deposited in infralittoral environments, and are included in Transgressive Systems tracts or in Highstand Systems tracts. The taphonomic, sedimentologic and paleogeographic characteristics of most of the deposits suggest they originated by discontinuous processes of winnowing and bypassing of sediment, probably due to the action of storms in shallow waters (mainly in bay environments). From the paleoecologic point of view, a greater richness in the molluscan diversity is seen in the Pliocene outcrops with respect to the Tortonian ones. Also, there is a difference in the abundance of specimens from several families: Turritellidae and Veneridae are more abundant in Tortonian outcrops, whereas Naticidae, Nassariidae and Lucinidae are in Pliocene ones. In the Miocene deposits the filter feeding molluscs are dominant, while in the Pliocene the carnivorous, sedimentivores and scavengers are abundant as well. These changes in the trophic structure are probably related to changes in substratum, hydrodynamics, and climatic conditions from the Tortonian to the Pliocene.

KEY-WORDS : MOLLUSCS, TAPHONOMY, GLOBAL SEA LEVEL CHANGES, PALEOECOLOGY, NEOGENE, NE ATLANTIC.

RÉSUMÉ

L'âge des principaux gisements contenant des Mollusques a été établi depuis Lisbonne, l'Algarve (Portugal), Seville, Huelva (Bassin du Guadalquivir, Espagne) jusqu'à Dar bel Amri (Bassin Sud-Rifain, Maroc) à partir d'études stratigraphiques des événements et il a été corrélé avec les changements globaux du niveau de la mer. La période étudiée est comprise entre le Tortonien inférieur et le Zancien supérieur. Les gisements sont formés par des concentrations de coquilles dans des sédiments sableux infra-littoraux ; elles ont en général peu de matrice sédimentaire et présentent une morphologie et une disposition variable. En relation avec les changements eustatiques, ils forment des complexes transgressifs ou des complexes de haut niveau de la mer. Les caractéristiques taphonomiques, sédimentologiques et paléogéographiques de la plupart des gisements suggèrent que leur origine se trouve dans les processus discontinus de lessivage du sédiment dans des zones de baies affectées par les tempêtes. Du point de vue paléocologique, il y a une plus haute diversité de mollusques dans les gisements du Pliocène que dans ceux du Tortonien. D'après l'abondance des individus d'une même famille, on observe aussi des changements temporels : les Turritellidés et les Vénéridés sont plus abondants au Tortonien, les Naticidés, Nassaridés et Lucinidés au Pliocène. On observe aussi des changements dans les catégories trophiques en relation avec des différences d'habitat sédimentaire et les conditions climatiques entre le Tortonien et le Pliocène.

MOTS-CLÉS : MOLLUSQUES, TAPHONOMIE, CHANGEMENTS EUSTATIQUES, PALÉOÉCOLOGIE, NÉOGÈNE, ATLANTIQUE NORD-ORIENTAL.

RESUMEN

Se ha establecido la edad de los principales yacimientos con Moluscos de Lisboa y el Algarve (Portugal), Sevilla y Huelva (Cuenca del Guadalquivir), y Dar bel Amri (Cuenca Surifeña, Marruecos), correlacionandose con los cambios globales del nivel del mar, a partir de estudios micropaleontológicos evento-estratigráficos. El tiempo comprendido abarca desde el Tortonense inferior al Zancliense superior. Los yacimientos están formados por concentraciones de conchas, generalmente con poca matriz sedimentaria, de morfología y disposición variable, en sedimentos arenosos infralitorales. Se incluyen en cortejos transgresivos o en cortejos de alto nivel del mar. Las características tafonómicas, sedimentológicas y paleogeográficas de la mayoría de los yacimientos sugieren que se originaron por procesos discontinuos de lavado de sedimento en zonas de bahía afectadas por tormentas. Desde el punto de vista paleoecológico, se aprecia una mayor diversidad de Moluscos en los yacimientos del Plioceno con respecto a los del Tortonense. También se observan cambios en la abundancia de individuos de varias familias : los Turritellidae y Veneridae son más abundantes en los yacimientos del Tortonense, mientras que los Naticidae, Nassariidae y Lucinidae lo son en los del Plioceno. Los moluscos filtradores dominan en los yacimientos del Tortonense, y en los pliocénicos son abundantes también los carnívoros, sedimentívoros y carroñeros. Estos cambios en la estructura trófica probablemente están relacionados con variaciones en el sustrato y en las condiciones hidrodinámicas y climáticas en la región desde el Tortonense al Plioceno.

PALABRAS CLAVE : MOLUSCOS, TAFONOMÍA, EUSTATISMO, PALEOECOLOGÍA, NEÓGENO, NE ATLÁNTICO.

INTRODUCTION

A study has been made in the deposits with molluscan fauna from the Upper Miocene and Lower Pliocene, which are situated in a geographic range close to the current NE Atlantic coastline, including an area extending from Central Portugal (the Lisboa region, deposits of Foz do Rego and Fonte da Telha), the Algarve (Cacela), SW of Spain (Sevilla, Arroyo Trujillo outcrop, Huelva), to the NW of Morocco (Dar-bel-Amri) (Fig. 1).

The lithology of such deposits is sandy. Unlike the situation in many beds with molluscs from the Mediterranean Neogene, including the Tortonian and Tabianian stratotypes (Kobba 1968, 1990 ; Pelosio 1967), the silt and clay facies contain very few molluscs in this zone.

In order to better compare the data, only the deposits with similar depositional conditions were considered (those with the greatest species richness and good preservation both for calcite and for aragonite shells). The calcarenitic facies, which are very common in the Northeastern part of the Guadalquivir basin and Morocco (i.e. calcarenite of Niebla Formation, of Upper Tortonian age, Huelva, Spain ; Oued-Akrech calcarenite, of similar age, Morocco), underwent important processes of fossil-diagenetic dissolution that favored the preservation of Ostreids and Pectinids, and corroded the main components of the molluscan assemblage.

CHRONOSTRATIGRAPHIC SETTING

Many of the outcrops studied here are well known in the paleontologic literature since the

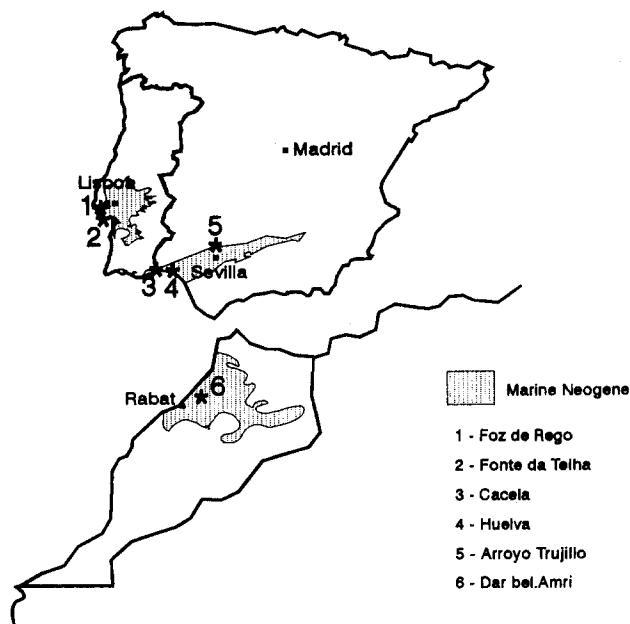


Figure 1 - Geographical situation of the area studied. *Situation géographique de la zone étudiée.*

end of the last century by their molluscan richness (Pereira da Costa 1866-67 ; Dollfus *et al.* 1903-04 ; Wenz 1942 ; Lecoindre 1952).

The age of the deposits was obtained by planktic Foraminifera event-stratigraphy (Fig. 2). The Neogene foraminiferal record has left a series of isochronous events (Sierro 1985 ; Sierro *et al.* 1993) defined by changes in the coiling direction or the replacement of populations of keeled Globorotaliids. These events have been correlated

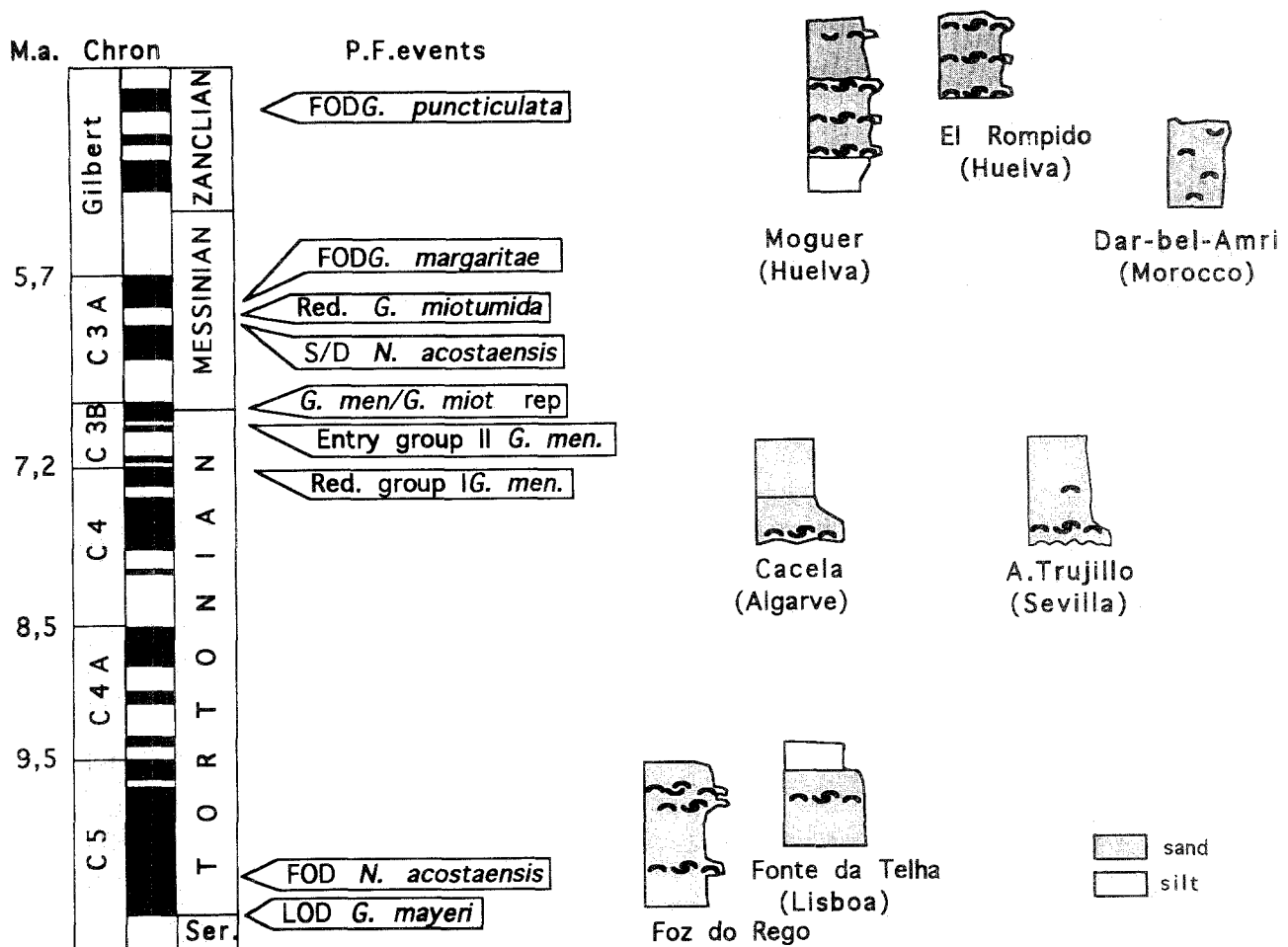


Figure 2 - Chronostratigraphic setting of the molluscan deposits. Planktic foraminiferal events from Sierro (1985) and magnetostratigraphical scale from Cande & Kent (1992). *Chronostratigraphie des gisements de mollusques. Evénements chez les foraminifères planctoniques de Sierro (1985). Echelle magnétostratigraphique de Cande & Kent (1992).*

with the curve of global changes in sea level from Haq *et al.* (1987). They were also correlated with the magnetostratigraphic scale (Cande & Kent 1992) and thus calibrated with the geochronologic scale. Based on these data, the molluscan deposits studied in this paper range from Early Tortonian to Late Zancian. The Messinian sediments (only outcropping in the Guadalquivir basin) are very scarce in molluscs. The oldest deposits analysed are located in the region of Lisboa (Foz do Rego and Fonte da Telha) and were dated as Lower Tortonian. In them, it has been possible to recognize the first dextral specimens of *Neoglobobadrina acostaensis* immediately above the last occurrence of *Globorotalia mayeri*. The Cacela outcrop (the Algarve, Portugal) and that of Arroyo Trujillo (Sevilla, Spain) are almost synchronous and correspond to the same transgressive

system tract of the Upper Tortonian (immediately before event 1 of Sierro *et al.* 1993). The molluscs of the Huelva region belong to the Lower Zancian (biozones of *G. margaritae* and *G. puncticulata* of Sierro 1984) and those of Dar-bel-Amri are probably Lower Zancian, within the biozone of *G. margaritae*.

The accurate datation of the molluscan deposits also give us the opportunity for interpreting the relationships and differences between them and other classic deposits from adjacent areas, such as those of the Mediterranean. Moreover, this may help to clarify the changes that, upon observing the literature, have been undergone by some deposits with respect to their chronostratigraphic position (Lecointre 1952 ; Viguier 1974 ; Wernli 1989 ; Antunes & Pais 1992).

	TAPHONOMIC SIGNATURE				SEDIMENTARY SETTING	
	Abrasion	Pre-burial fragmentation	Bioerosion	Encrustation	Matrix	Systems Tracts
Dar-bel-Amri	↘	≈	↘↘	↘	sand	?TR
Huelva	↘	↘	≈	↘↘	fine sand (100 mm)	HS
Sevilla (A.Trujillo)	↗	↗	≈	↘	coarse sand	TR
Cacela	≈	↗↗	↘	↘	conglomerate to sand	TR
Fonte da Telha	↘	↗↗	↘	↘	sand	HS
Foz do Rego	↗	↗↗	≈	↘	coarse sand	HS

↗↗ very high ↗ high ≈ moderate
 ↘ low ↘↘ very low

Figure 3 - Taphonomic signature and sedimentary setting of the molluscan deposits. TR : Transgressive System tract ; HS : Highstand System tract. *Taphonomie et contexte sédimentaire des gisements de mollusques.* TR : complexe transgressif ; HS : complexe de haut niveau de la mer.

TAPHONOMIC AND SEDIMENTARY SETTING

In all the deposits, the fossils are not uniformly distributed in the sediment but rather occur in lenticular layers of shell-accumulation that alternate with other intervals in which the shells are more scattered. The horizons that are rich in molluscs are shell-supported in the zone of Huelva, Foz do Rego and Fonte da Telha and generally matrix-supported in Arroyo Trujillo and Dar-bel-Amri. The lithology of the matrix ranges from conglomerate to fine-sands and, by deposits, the following decreasing order is seen : Cacela, Foz do Rego, Arroyo Trujillo, Fonte da Telha, Dar-bel-Amri and Huelva ; that is, the matrix is finer in the Pliocene deposits than in those of Miocene age. Most outcrops are formed of shell concentrations of the multiple-event concentration type *sensu* Kidwell (1991).

The deposits are rarely more than a dozen meters thick. Cyclic fining upward sequences are common, decimeter in size, with frequent erosive surfaces at the base, marked by the molluscs.

The degree of pre-burial fragmentation and the abrasion of the shells is not the same in all the deposits (Fig. 3) ; it is higher in the Tortonian deposits than in those of Pliocene age. Within a single area, differences can be seen ; thus, it is greater in Foz do Rego than in Fonte da Telha.

Bioerosion varies, reaching higher values in Huelva, Arroyo Trujillo and Foz do Rego than in Fonte da Telha. The gastropod borers, Clionid sponges, Annelids, Bryozoans, Decapod crustaceans and fishes are the most representative bioeroders. In all the outcrops the degree of encrustation is low, mainly produced by Balanids

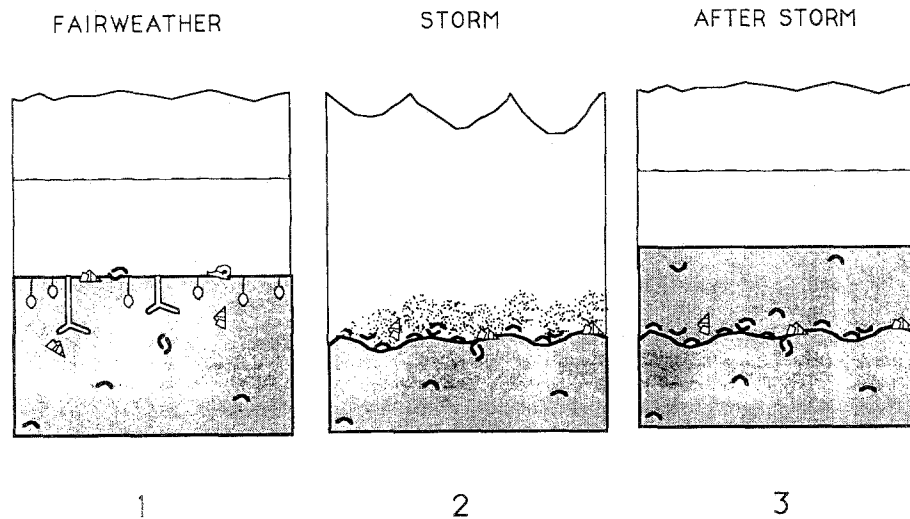


Figure 4 - Origin of a single concentration of shells in relation with storm activity. Dashed line marks the wave base level. *Origine d'une concentration simple de mollusques par rapport à l'activité des orages. Le trait discontinu représente le niveau de base des vagues.*

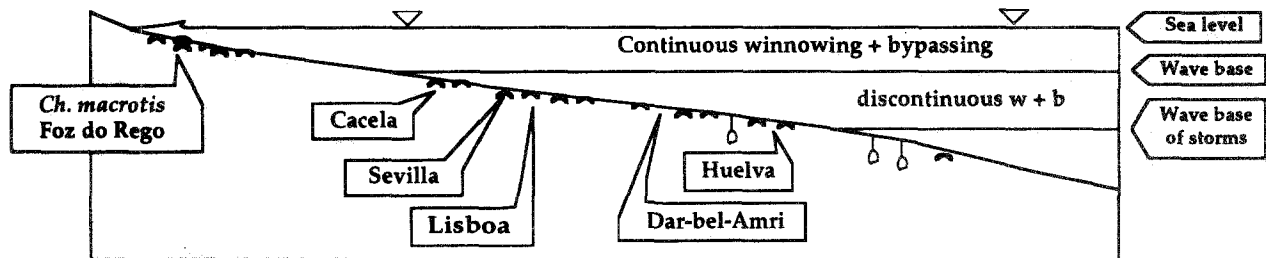


Figure 5 - Depositional environment of the Molluscan-rich areas. *Conditions de dépôt des gisements étudiés.*

on Bivalves and Gastropods (Pl. 63). This suggests that the molluscs did not form shelly pavements.

In the light of the foregoing, we interpret that the deposits were formed on inner siliciclastic shelves through the accumulation of shells owing to the sporadic action of storms which led to a remobilization of the bottom and a redeposition of the molluscs. Dabrio *et al.* (1988) suggested this for the deposits of Huelva, and Civis *et al.* (1990) for Arroyo Trujillo.

Figure 4 shows a simple scheme of the origin of the shell concentrations; in the infralittoral zone the molluscs live normally in their corresponding habitats during fairweather times. When affected by wave action due to storms, the profile of the bottom is reduced, leading to an erosive surface at the base, and a subsequent accumulation of molluscs, many of them corresponding to shells already buried, others to shallow infaunal ones and yet others to epifaunal ones. After the storm, which has led to that concentration of shells, the sand subjected to winnowing re-sediments and the cycle begins again. The repetition of this si-

tuation gives rise to shell concentrations up to 1 m thick.

The interpretation of the depositional environment of the different deposits can be seen in the Figure 5. Most of the deposits were formed by sedimentary progradation during periods of relative sea level rise and high sedimentary input (Sierra *et al.* 1990; Antunes *et al.* 1990). For example, the deposits of Foz do Rego and Fonte da Telha are related to the deltaic progradation of the River Tagus; those of Huelva and Dar-bel-Amri with the filling of a basin whose geometry decreased over time (Guadalquivir and South Rifian basins, respectively).

The processes of winnowing and bypassing of sediment, continuous or discontinuous according to whether one is in the zone affected by waves or the zone only affected by storms, would be mainly responsible for the genesis of concentrations of molluscan shells. In general, these processes were discontinuous in the deposits studied here, and their intensity was slightly different, as suggested by the particular taphonomic signatures.

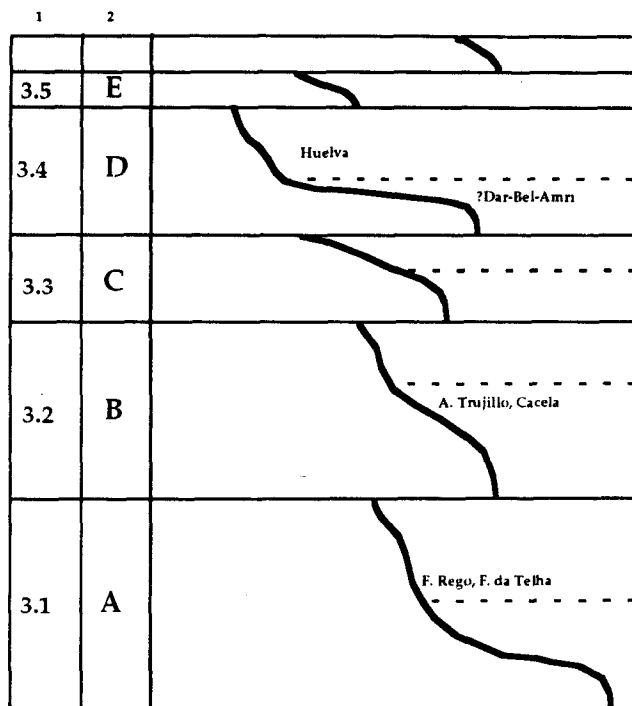


Figure 6 - Situation of the molluscan deposits in relation with the cycles of global sea-level changes from Haq *et al.* (1987) (1) and the depositional sequences of Sierro *et al.* (1990) (2). *Situation des gisements de mollusques par rapport aux cycles de changements du niveau de la mer de Haq et al. (1987) (1), et les séquences de dépôt de Sierro et al (1990) (2).*

To a lesser extent there are some accumulations (such as *Chlamys macrotis* at Foz do Rego) with a higher package of shells, cross-lamination, and orientation of the shells, that probably resulted from processes of bypassing and winnowing of sediment produced by permanent currents.

The fossil-diagenetic processes of carbonate dissolution in these sandy facies have sometimes affected the preservation of the molluscs, as is the

case of certain zones in Huelva such as Moguer, or in the Asilah area (NW Morocco). Calcite shells of pectinids, ostreids and cirripeds are preserved (González Delgado 1983 ; Ben Moussa 1991), while the aragonite test of gastropods, scaphopods and most bivalves have been destroyed.

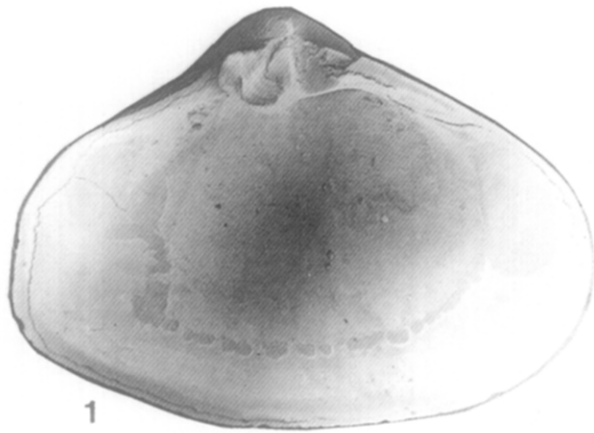
Taking into account the paleogeographic context within which the deposits were formed, the most likely sedimentary environment would be a more or less protected shallow sea. The most protected zone, according to the taphonomic signatures of their beds, seems to have been at Huelva, which probably formed part of a large bay during the Pliocene in the Guadalquivir basin (González Delgado 1983).

The identification of five (A to E) depositional sequences in the Guadalquivir basin dated by planktic foraminiferera and correlated with eustatic changes (Sierra *et al.* 1990) provided us with an interesting tool to analyse the relationship between the major episodes of shell concentration and the record of Global Sea level changes (Haq *et al.* 1987).

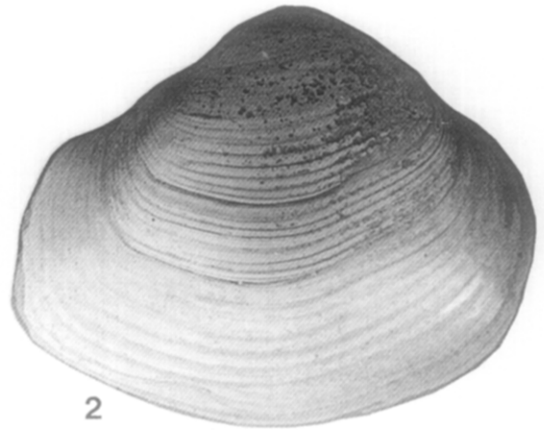
All the molluscan-rich sediments were deposited within Transgressive or Highstand Systems tracts (Fig. 6). The outcrops of Foz do Rego and Fonte da Telha (Lisboa) were formed within the Highstand Systems tract of cycle 3.1 (Lower Tortonian) of Haq *et al.* (1987) (sequence A of Sierro *et al.* 1990), whereas those of Cacela and Arroyo Trujillo correspond to the Transgressive Systems tract of the Upper Tortonian (cycle 3.2, lower part of Sequence B). Those of Huelva are encompassed within the Highstand Systems tract of Lower Pliocene age (cycle 3.4, upper part of Sequence D). So far it is not possible to pinpoint the position of Dar-bel-Amri, although it is probably related to the Transgressive Systems tract of the same cycle (Lower Pliocene age).

PLATE 63

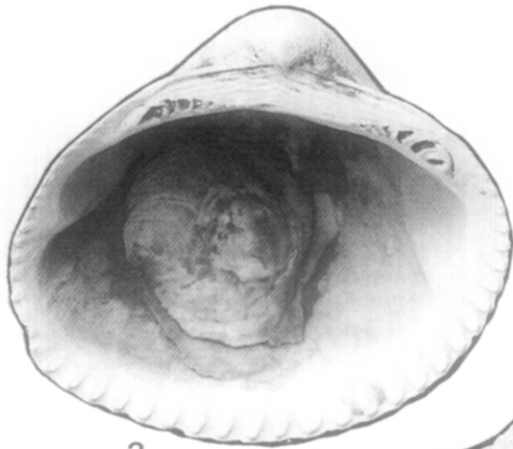
- Fig. 1-2 - *Corbula (Varicorbula) gibba*. Left (x 1.2) and right (x 1.3) valves. Pliocene of Huelva. *Valve gauche, valve droite. Pliocène de Huelva.*
- Fig. 3 - *Glycymeris insubrica*. Left valve (x 1.2). Pliocene of Huelva. Note the inner shell cemented by *Ostrea lamellosa*. *Valve gauche of G. insubrica avec, à l'intérieur, cimentation par O. lamellosa.*
- Fig. 4 - *Spisula (S.) subtruncata*. Left valve (x 9). Pliocene of Huelva. *Valve gauche. Pliocène de Huelva.*
- Fig. 5 - Incrustation of barnacles on right valve of *Limaria tuberculata* (x 1.5). *Encroûtements de cirripèdes dans une valve droite de L. tuberculata.*
- Fig. 6 - *Acanthocardia paucicostata*. Left valve (x 1.5). Pliocene of Huelva. *Valve gauche. Pliocène de Huelva.*
- Fig. 7-8 - *Chlamys macrotis*. Right and left valves (x 1.7). Lower Tortonian of Foz do Rego. *Valve droite et gauche. Tortonien inférieur de Foz do Rego.*
- Fig. 9-11 - Boring (*Oichnus paraboloides*) in *Naticarius tigrinus* from Upper Tortonian of Cacela (Fig. 9) and Arroyo Trujillo (Fig. 10), and from Pliocene of Huelva (Fig. 11). (x 1.5). *Bioérosion (O. paraboloides) dans N. tigrinus du Tortonien supérieur de Cacela et Arroyo Trujillo, et du Pliocène de Huelva.*



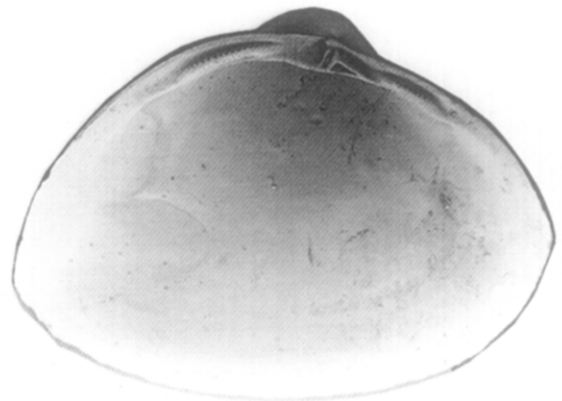
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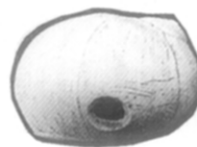
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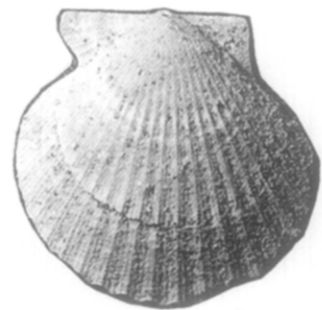
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So far, the studies about the relationship between the molluscan rich deposits and global sea level changes are scarce, although they could be a powerful tool for the regional or global correlation. In this way, the deposits of the Lisboa region could be correlated with some of the shell concentrations described by Kidwell (1989) in the Miocene of Maryland (USA), in particular to those called Drumcliff or Boston cliffs (Choptank Formation) which occur in the bottom of the depositional sequences (transgressive lags).

PALEOECOLOGY

In order to avoid additional biases, homogeneous taxonomic criteria have been used along with similar sampling (bulk-samples) and sieving techniques, studying the residues larger than 1 mm mesh size.

The extent of study of the molluscs has not been the same in all the deposits. The Pliocene region of Huelva has been studied most intensively, including data from 7,319 gastropod specimens, and 63,798 bivalve specimens (González Delgado 1983, 1987 ; Andrés 1982, 1986 ; Castaño *et al.* 1992).

In each region the molluscan assemblage (especially the number of species and specimens recorded) varies from one place to another. In the region of Lisboa, the outcrops of Foz do Rego show the highest diversity, with 143 species of molluscs. Half of these species are Gastropods, mainly represented by the following families : Turridae (10 species), Nassariidae (9), Trochidae (5) and Conidae and Pyramidellidae (4). The abundance of specimens is greater in Turritellidae (57%), followed by Naticidae (15%), Nassariidae (7%) and Turridae (5%). Among the Bivalves, the Veneridae are the best represented at species level (9), followed by Tellinidae (8) and Pectinidae, Lucinidae and Cardiidae (6). The greatest number of specimens corresponds to Veneridae (19%), Corbulidae (18%) and Ostreidae, Mactridae and Tellinidae with percentages close to 11%. The remaining families do not surpass 5%.

In the Cacela deposit, 154 species have been documented, of which 78 correspond to gastropods. The Turritellidae (6 species), Nassariidae (6), Naticidae (6) and Turridae (4) are the families with the greatest number of species. The families most abundant in specimens are Turritellidae (50%), Naticidae (15%), Trochidae (11%) and Ringiculidae (5%). The best represented in bivalves (76 species) are the Veneridae (11), Lucinidae and Tellinidae (6), and the Cardiidae (4). As regards

the number of specimens, the most abundant are Veneridae, with 18%, Nuculidae (9%), and Lucinidae and Tellinidae which reach almost 5%.

The Arroyo Trujillo (Sevilla) deposit display the lowest diversity, with only 92 species of molluscs recorded, corresponding to gastropods (58) and bivalves (34). Turritellidae (5) and Naticidae, Nassariidae and Turridae (4) are the best represented in number of species, while Naticidae is the most abundant in specimens, followed by Turritellidae, Nassariidae, Turridae and Ringiculidae. The bivalves include 8 species of Veneridae, 4 of Lucinidae, and 3 of Pectinidae and Cardiidae, and the Veneridae and Nuculanidae are the families with the greatest numbers of specimens.

In Pliocene deposits, the Huelva region is the richest with 266 species of molluscs, of which 147 are gastropods and 116 bivalves. The greatest richness of species of gastropods corresponds to Turridae (20), Pyramidellidae (14) and Nassariidae (13), whereas in the bivalves they are Pectinidae (16), Veneridae (13) and Tellinidae (9). The highest abundances of specimens in the gastropods correspond to Naticidae (24,4%), Nassariidae (16,2%) and Ringiculidae (15,5%), and in bivalves to Mactridae (33,2%), Corbulidae (24,5%) and, although to a much lesser extent, Nuculanidae (7,5%) and Lucinidae (7,2%).

In Dar-bel-Amri (Morocco), the molluscs (currently being studied by El Alami), are less abundant, both in the number of species (about 100) and the number of specimens.

As may be seen in the Figure 7, in the zone studied there is an increase in the number of species of molluscs belonging to the Pliocene with respect to the Tortonian ; this can be seen when a comparison is made between the diversity of the outcrops recorded in Huelva and that of Lisboa, Cacela and Sevilla. Similarly, in all the deposits there are higher number of gastropod species than bivalves, although the number of bivalve specimens is higher (gast./biv. ratio of 0.26 in Huelva, 0.37 in Cacela, 0.94 in Lisboa).

It should be noted as well the remarkable differences observed between the molluscan assemblages of Arroyo Trujillo and Cacela, which are coetaneous and were deposited under similar lithologic, taphonomic and paleogeographic conditions. These differences, probably due to the slightly higher bathymetry in Arroyo Trujillo, are related to the different situation of both deposits within the same Transgressive Systems tract ; the Cacela assemblage was deposited during the

	Total species MOLLUSCA	GASTROPODA	BIVALVIA	Monospecific Concentrations	Relative Abundance Gast./Biv.	Trophic chains			
							<i>G. Insubrica</i>	<i>S. subtruncata</i>	<i>A. paucicostata</i>
Huelva	266	147	116		0.26	long			
Sevilla	92	58	34	no	0.59	long			
Cacela	154	78	76	no	0.37	long			
Lisboa	143	74	69	<i>Ch. macrotis</i>	0.94	long			

Figure 7 - Some paleoecological characters of the molluscan-rich deposits studied. *Caractères paléocologiques des gisements étudiés.*

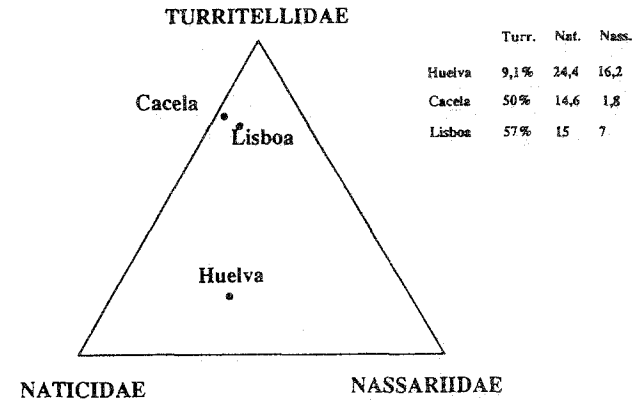
first stage of the transgression, while that of the Arroyo Trujillo was deposited within the upper part of the Transgressive Systems tract.

As reported above, the layers of shell-accumulation are characterized by a higher number of species, related to the intervals in which the molluscs are more diluted. However, sometimes a single species is the main component of one of these layers of shell-accumulation. In the deposits studied, monospecific concentrations are very rare in the Tortonian, with the exception of the high concentration of *Chlamys macrotis* in one level of the outcrop of Foz do Rego. However, this type of accumulation is very common in the Pliocene, with *Glycymeris insubrica*, *Spisula subtruncata* or *Acanthocardia paucicostata* (Pl. 63).

All type of shell-concentrations are produced by taphonomic and/or ecological processes, including a certain degree of time-averaging. However, in the monospecific concentrations studied here, the biostratinomical signature (abrasion, pre-burial fragmentation, bioerosion and incrustation) and the minor diversity of the assemblages allow us to interpret them as ecologically controlled, as an adaptation to particular stress environmental conditions (*Glycymeris*, *Spisula*), or facilities to larval settlement (*Chlamys*).

From the Miocene to the Pliocene, the following trends in abundance are seen in the gastropods : there is an increase in the number of specimens of Naticidae, Nassariidae and Ringiculidae in the Pliocene deposits (Fig. 8). In Foz do Rego and Cacela the Naticids represent 15% and 14.6% of the

GASTROPODA



BIVALVIA

	Veneridae	Lucinidae
Huelva	5,5%	7,2%
Cacela	18%	4,7%
Lisboa	18,8%	2,9%

Figure 8 - Relative abundance of representative families of Gastropods and Bivalves in the Tortonian deposits of Lisboa and Cacela, and the Zanclean deposits of Huelva. *Abondance relative des familles représentatives de gastéropodes et de bivalves dans les sédiments du Tortonien de Lisboa et Cacela, et dans ceux du Pliocène de Huelva.*

total number of gastropod shells respectively, whereas in Huelva they reach 24.4%. On the other hand, the Turritellids, which reach 57% in Foz do Rego and 50% in Cacela, decrease to 9% in the Pliocene outcrops of Huelva. Some authors (Allmon 1988, 1992) relate the abundance of Turritellids to high productivity surface waters ; so that the change in their abundance, and the probable lower temperature of the Tortonian waters related to that of the Pliocene, (see below) may be due to productivity differences. However, siliciclastic turritelline-dominated shelves have low molluscan diversity (around 20 species, Allmon & Knight 1993) while in the studied areas diversity is remarkably higher (see Fig. 7).

Also outstanding is the increase observed in the number of species of Turridae and Pyramidellidae in the Pliocene deposits as compared with those of Miocene age, probably related with environmental differences.

Regarding the bivalves, in all the deposits studied, a great abundance of specimens belonging to Mactridae and Corbulidae is due to the massive presence of *Spisula subtruncata* and *Corbula gibba* (Pl. 63). These two taxa are very common in Neogene molluscan-rich beds of the Mediterranean and adjacent Atlantic realms. *Spisula subtruncata* is abundant in environments of high phytoplankton concentration and good water circulation (Moholenberg & Biorboe 1981, in Di Geronimo *et al.* 1987); the grain-size of the substratum also affects the larval metamorphosis and juvenile stage (Benigni & Corselli 1981). *Corbula gibba* is considered an opportunistic taxon (Martinell *et al.* 1983; Di Geronimo *et al.* 1987), related to high levels of organic matter in the sea bottom. It preferentially lives in environments of greater instability and lower grain-size than *S. subtruncata*.

Apart from these two families, also outstanding is the abundance of Veneridae in the Tortonian deposits (reaching 18.8% in Lisboa and 18% in Cacela), whereas in the Pliocene deposits decrease to 5.5%. An opposite trend may be seen with the Lucinids, which reach 2.9% in Lisboa, 4.7% in Cacela, and 7.2% in Huelva (Fig. 8).

There are also spatial variations in the malacological associations. For example, in the Huelva region the dominant association in shallow deposits (i.e. Moguer) is different with respect to other onshore associations (i.e. La Palma del Condado, some 30 km to the NE). Apart from *C. gibba*, in Moguer the association is dominated by *Nuculana pella*, *N. fragilis* and *Ringicula buccinea* (along with the foraminifer *Ammonia inflata*). However, in the outcrop of La Palma del Condado the assemblage is mainly characterized by *Venus lamellosa*, *Chamellea gallina* and *Naticarius tigrinus* (along with the foraminifer *Ammonia beccarii*) (Castaño *et al.* 1992).

The presence of stenotherms and stenohalines in all the deposits is suggestive of higher temperatures than the present ones and normal salinities, although in certain zones, owing to their position with respect to bay environments, salinity would have been variable. Bivalves such as *Nuculana pella*, *Linga columbella* and *Circomphalus foliaceolamellosus* that inhabit warm environments, along with the presence of *Paphia*, considered to be tropical, and of *Callista italica* and *Pelecycora gigas* with morphometric characteristics of tropical environments (Brambilla 1976; Glemarec 1978; Marasti & Raffi 1980), support the afore-mentioned thermal conditions.

A study of the oxygen and carbon stable isotopes (González and Sierro, in prep.) indicate $\delta^{18}\text{O}$ (PDB) heavier values in bivalves of the Cacela and Arroyo Trujillo deposits compared to those of Huelva, so that the paleotemperature must have been higher in the Pliocene than in the Late Tortonian in this area. Ontogenetic sampling (see Jones, 1985, for review of the technical description and applications of this type of sampling) in one specimen of *Callista italica* belonging to Huelva outcrop shows ranges of 0.40 δ , whereas ranges of 0.90 δ correspond to specimens of *Callista italica* of Cacela and Arroyo Trujillo outcrops. These results agree with higher seasonality in the Tortonian sea with respect to that of the Pliocene. Moreover, the $\delta^{13}\text{C}$ (PDB) analyses of the same samples show higher values in Tortonian samples which respect to the Pliocene ones, and corroborate the differences in seasonality, because they range from 0.41 δ to 0.70 δ in the Huelva specimen, and from 0.88 δ to 1.70 δ , and from 1.01 δ to 1.32 δ in *C.italica* belonging to Cacela and Arroyo Trujillo, respectively.

All the deposits contain abundant specimens of *Nuculana fragilis*, which is a stenohaline species of at least 28‰ water-salinity (Svagrösky in Malatesta 1974). Moreover, *Acanthocardia paucicostata* and *Plagiocardium papillosum*, that do not tolerate influxes of fresh water (Brambilla 1976), and *Dosinia lupinus*, relatively stenohaline at 28-30‰ of salinity (Nevesskaja in Malatesta 1974), are suggestive of environments with a normal degree of salinity.

Among the gastropods, mainly the Terebridae and Olividae (see Bouchet 1982; Davoli 1976, 1989 for an extensive review) corroborate the data on the bivalves.

All the beds seem to reflect the existence of complex trophic chains; among the bivalves, there is a general dominance of filter-feeders over detritivores, while within the gastropods, the carnivorous dominate over the scavengers, sedimentivores, filter-feeders and herbivores. Nevertheless, there are differences in the trophic structure between the Tortonian and the Pliocene assemblages; in the Tortonian, the filter-feeders (Veneridae, Turritellidae) are abundant, whereas in the Pliocene, the gastropods carnivorous and the bivalves sedimentivores like Nuculacea and Lucinidae (see Freneix *et al.* 1987 for discussion on feeding habits of Lucinacea) increase. These changes can be related to better climatic conditions and variations in grain-size of the substratum. The taphonomic signature of the faunas, and the coar-

ser grain of the sand of Tortonian deposits suggest higher hydrodynamic conditions than those of the Pliocene, where the substratum is finer, and there is a more protected depositional environment (Fig. 4).

Another general characteristic of the molluscan assemblages is the presence of traces of breakage on the bivalve and scaphopod shells performed by crustaceans or fishes, and on gastropods such as *Turritella subarchimedis*, *Mesalia cochleata*, or *Naticarius tigrinus*. Borings (*Oichnus paraboloides* of Bromley 1981) on Naticids are common in the Huelva deposits and, to a lesser extent, in Cacela and Arroyo Trujillo (Pl. 63). They reflect probable evidences of cannibalism (Kitchell *et al.* 1986).

CONCLUDING REMARKS

The molluscan Neogene deposits in the NE Atlantic realm (Lisboa to Rabat) ranges from Early Tortonian to the Late Zanclean, on the basis of micropaleontological evidence. A high resolution event-stratigraphy study of the basins allowed us to locate the main molluscan deposits within the different sequences recognized and correlate them with global sea level changes.

Most deposits (Huelva, Lisboa) form concentrations of shells that are shell-supported (coquina) with a variable morphology and arrangement. They originated in a infralittoral sandy environments, although the hydrodynamic conditions were probably more intense and water-depth lower in the Tortonian deposits than in the Pliocene ones.

The taphonomic, sedimentologic and paleogeographic characteristics of most of the deposits suggest they originated by discontinuous processes of winnowing and bypassing of sediment, probably due to the action of storms in shallow protected zones (bays). The abrasion and pre-burial fragmentation are more pronounced in the Tortonian than in the Pliocene deposits.

Although the amount of paleontologic information differs from outcrop to outcrop, a greater richness in molluscan species is seen in the Pliocene with respect to the Atlantic Tortonian, allways with larger numbers of species of gastropods than of bivalves and more specimens of bivalves than of gastropods.

There are some bivalves that accumulate in monospecific patches ecologically originated, such as *Chlamys macrotis* in the Tortonian deposits, or

Spisula subtruncata, *Acanthocardia paucicostata* and *Glycymeris insubrica* in Pliocene outcrops.

A striking observation is the abundance of Turritellidae, Veneridae and Naticidae in Tortonian sediments, the latter family increasing in importance during the Late Neogene until it becomes the most important in terms of number of specimens within the Pliocene gastropods. On the other hand, during the same period, the number of specimens of Turritellidae decreases drastically.

These changes in the abundance of specimens of several families from Miocene to Pliocene reflect changes in the community structure. In the Tortonian deposits, filter feeders are abundant (Turritellidae, Veneridae), whereas in the Pliocene there is an increase in carnivorous gastropods (Naticidae) and sedimentivorous bivalves (Nuculacea, Lucinidae). These changes relate to better climatic conditions, low hydrodynamics, and finer substratum during the Pliocene.

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