

# THE DISTRIBUTION OF PLIOCENE NASSARIIDAE (MOLLUSCA, GASTROPODA) FROM THE WESTERN MEDITERRANEAN: PALAEOECOLOGICAL AND HISTORICAL CONSIDERATIONS

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The palaeobiogeography and palaeoecology (and possible factors determining these) of twenty-seven species of nassariid gastropod which inhabited the Mediterranean and parts of the Atlantic Ocean during the Pliocene are analysed. Tables of presence-absence for these species and faunal affinity indexes are presented. The study of the causal factors of this distribution is based on ecological aspects, mainly relying on available outcrop data, and historical aspects with regard to the present knowledge of conditions and general changes prevailing in the area during the Pliocene.

Key words — Mollusca, Gastropoda, Nassariidae, Pliocene, Mediterranean, palaeobiogeography, palaeoecology.

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## INTRODUCTION

The aim of this study is to present a description of the geographical distribution patterns of twenty-seven species of nassariid gastropod which inhabited parts of the Mediterranean and the Atlantic Ocean during the Pliocene. The palaeobiogeographical distribution is interpreted with the aid of the causal factors, both ecological and historical, which underlie such distribution patterns.

As a starting point, reference is made to the systematic revision of the species studied by Martinell

(1976, 1982b), Gili & Martinell (1990) and Gili (1991). A taxonomic revision, based on modern criteria, is a necessary step in order to deal with more general palaeontological problems, especially when working at the specific level.

The present study comprises a qualitative and quantitative analysis of presence-absence tables of the species within the study area (western Mediterranean) and relates the results obtained to data available on the ecological conditions expressed in the strata from which the species have been collected, and on the historical modifications having occurred in the area during the Pliocene.

## MATERIAL AND METHODS

The material under study consists of locality data for twenty-seven species of the genus *Nassarius* Duméril, 1806 s. lat. (Table 1) in outcrops in the eastern and western Mediterranean and in some Atlantic localities close to the Strait of Gibraltar; they have been grouped in the fourteen basins or zones indicated in Fig. 1.

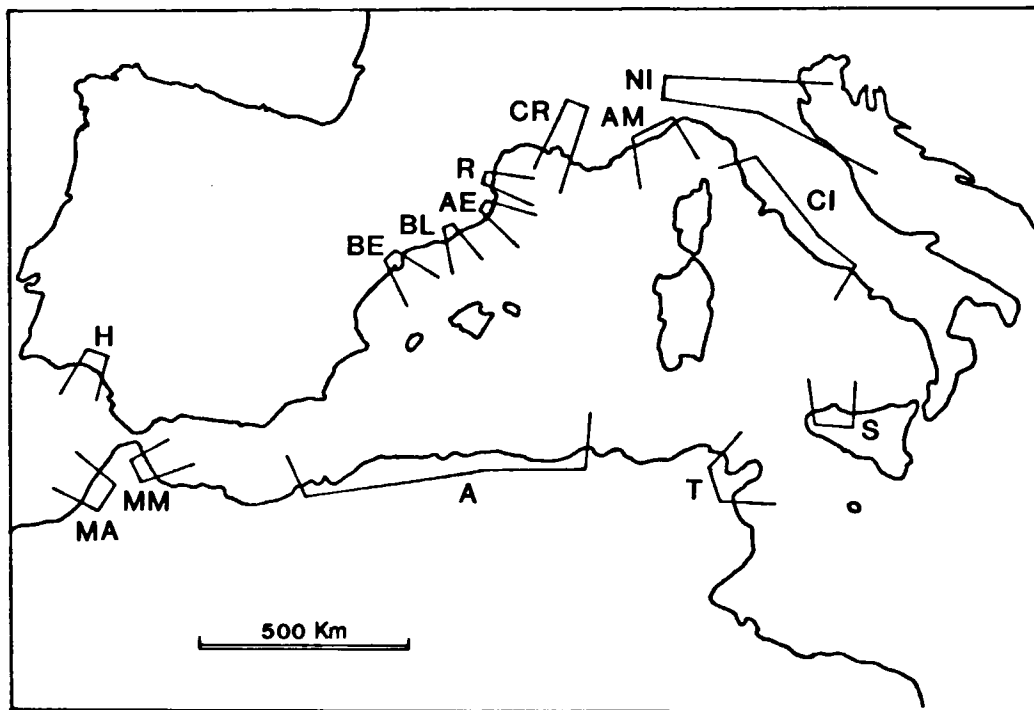


Fig. 1. Map showing the location of the basins studied. Abbreviations are as follows: MA - Atlantic Morocco; H - Huelva; MM - Mediterranean Morocco; A - Algeria; BE - Baix Ebre; BL - Baix Llobregat; AE - Alt Empordà; R - Roussillon; CR - Rhône basin; AM - Alpes Maritimes; CI - western Italian basin; S - Sicily; T - Tunisia; NI - northern Italy.

Part of the present study has focused on outcrops in northwestern Mediterranean basins, as indicated in Table 2. Data have been obtained from a direct comparison of our own fossil collections with specimens housed in various museums and universities (Museu de Geologia de Barcelona; Institut Royal des Sciences naturelles de la Belgique, Brussels; Département des Sciences de la Terre, Université Claude Bernard, Lyon; and Muséum national d'Histoire naturelle, Paris), making sure that locality data could be verified and taphonomic characteristics were known. These data have been complemented with bibliographical data thought to be relevant with regard to the species studied (Gili, 1991).

Literature data should be used with caution if one is working at species level as it is quite common to encounter uncertainty as to whether the specific name used by one author corresponds to that applied to our material. Consequently, these data have been used only sparingly as they do not allow a more precise discrimination.

The following course was taken: a qualitative analysis based on presence-absence tables was carried out, in relation to the basins in which the

species were located (Table 1), and another study of the strata in which the species occur (Table 2). In addition, a quantitative analysis based on these tables using faunal affinity matrices as calculated according to the Dice index (Cheetham & Hazel, 1969) was carried out (Tables 3 and 4). Every table was used for the analysis of different aspects of the biogeographical study.

By grouping the data available for all deposits of any one basin distinguished (Table 1), it is possible to determine whether problems result from 'non-significant' absences or collection failure. This procedure permits the inclusion in the same register of those species which lived at all or many of the localities in one basin, but are found only in one or few localities. This table results from a direct study of the material and from a literature search.

To ensure a maximum reliability of the data, those for the various zones need to be as homogeneous as possible. Therefore, we have fewer data for the following basins: Moroccan Atlantic, Moroccan Mediterranean, Algeria and Tunisia, mainly because these are the basins that have been studied in the least detail. This fact must be taken into account when interpreting the results and when

SPECIES	H	BE	BL	AE	R	CR	AM	CI	S	T	A	MM	MA	NI	N. Bas.
<i>N. pliomagnus</i> (SACCO, 1904)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	14
<i>N. companyoi</i> (FONTANNES, 1879)	+			+	+	+	+	+	+	+				+	9
<i>N. obliquatus</i> (BROCCHI, 1814)														+	1
<i>N. clathratus</i> (BRONN, 1788)	+			+	+	+	+	+	+			+	+	+	10
<i>N. prismaticus</i> (BROCCHI, 1814)	+	+	+	+	+	+	+	+	+	+	+			+	11
<i>N. bisotensis</i> (DEPONTAILLER, 1879)								+							1
<i>N. ligusticus</i> (BELLARDI, 1882)								+							1
<i>N. aff. ligusticus</i> (BELLARDI, 1882)								+							1
<i>N. semistriatus</i> (BROCCHI, 1814)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	14
<i>N. elatus</i> (GOULD, 1845)			+	+	+	+	+		+	+	+	+		+	11
<i>M. martinelli</i> (GILI, 1992)								+							1
<i>N. cabrierensis</i> (FISC. & TOURN., 1873)			+	+	+	+	+	+			+			+	8
<i>N. macrodon</i> (BRONN, 1831)			+		+	+	+		+		+	+		+	8
<i>N. reticulatus</i> (LINNÉ, 1758)	+		+	+	+	+	+	+	+	+			+	+	11
<i>N. corrugatus</i> (BROCCHI, 1814)														+	1
<i>N. bugellensis</i> (BELLARDI, 1882)				+					+					+	3
<i>N. angulatus</i> (BROCCHI, 1814)	+	+	+	+	+	+	+	+	+	+			+	+	12
<i>N. asperulus</i> (BROCCHI, 1814)	+							+	+	+	+			+	6
<i>N. serraticosta</i> (BRONN, 1830)	+		+	+	+	+	+	+	+		+	+		+	11
<i>N. catulloi</i> (BELLARDI, 1882)			+	+	+		+							+	5
<i>N. productus</i> (BELLARDI, 1882)	+									+				+	3
<i>N. turbinellus</i> (BROCCHI, 1814)			+					+		+				+	4
<i>N. quadriserialis</i> (BON. in MICH., 1838)								+						+	2
<i>N. bollenensis</i> (TOURNOUER, 1838)		+	+	+		+									4
<i>N. gibbosulus</i> (LINNÉ, 1758)	+		+	+			+	+		+			+	+	8
<i>N. pyrenaicus</i> (FONTANNES, 1879)			+		+	+	+					+		+	6
<i>N. turritus</i> (BORSON, 1820)	+			+	+	+	+	+	+			+		+	9
N. Sp.-Basin	12	5	14	15	14	14	22	12	13	10	8	8	6	22	

Table 1. Presence of species in the various basins. Abbreviations are as follows: N. Bas. - number of basins; N. Sp.-Basin - number of species in each basin.

drawing conclusions. The table of presence per outcrops (Table 2) permits to distinguish more concrete aspects of the distribution within each basin or between different zones. Yet, not only must our knowledge of the fauna then be comparable for all deposits, but also a uniformity of sampling must be ensured. Therefore, this table depends exclusively on the material and deposits studied personally. Thus, only twenty-three of the twenty-seven species have been considered. Another essential factor, taphonomy, must be considered when evaluating ecological factors of distribution. Only those beds for which a taphonomic study has demonstrated the fossil fauna to correspond to a palaeocommunity or 'census assemblage' (Hallam, 1972; Kidwell & Bosence, 1991) are useful. Others not meeting this criterion must be disregarded. Thus, the fauna from the Can Albareda outcrop (Baix Llobregat basin) has not been considered as it represents an accumulation level, its record corresponding to a thanatocoenosis (Fürsich, 1990).

The use of the affinity index permits a quantification of the relationships that exist between faunas of different basins (Table 3), or between different outcrops within the same basin or between different zones (Table 4). Data obtained allow to test diverse hypotheses as to distribution patterns and underlying causes.

#### DISTRIBUTION CHARACTERISTICS

The overall distribution of the twenty-seven species used in the present investigation is as follows:

- twenty are found both in the eastern and western Mediterranean;
- fifteen are found also in the Atlantic adjacent to the Mediterranean;
- five are restricted to the western Mediterranean;
- two are restricted to deposits in northern Italy (the Adriatic Pliocene of the eastern Mediterranean).

Relevant in the presence table for the species found in the different zones (Table 1) is the strikingly high number of species present in the majority of these basins. Only in five zones has a low number of species (fewer than ten) been found. The Baix Ebre basin has yielded only five species. Fifty percent of all basins yield between twelve and fifteen species. In two zones, up to twenty-two species have been encountered, this being the maximum number observed.

On the other hand, the number of species that are widely distributed is also high. Two species have been found in fourteen of the zones considered, six species are found in between ten and twelve zones and another eight in between five and nine basins. A low, albeit, important number of five species are found in few basins, and six species have been located exclusively in only one of the zones considered.

In total, these data suggest a certain degree of homogeneity in the distribution of the twenty-seven species within the study area. Yet, some cases of restricted or strongly discontinuous distribution must be considered in causal analysis.

The study of the faunal affinity matrix among the zones (Table 3) allows a quantitative evaluation of this distribution. As a set the values are high or very high. Only 12.1% of the indices is found between 0.3 and 0.45; values between 0.46 and 0.61 (quite high) account for 29.6%. Values between 0.62 and 0.77 account for 40.7% of all data; values between 0.78 and 0.93 are considered very high, and account for 17.6% of the indices. In total, 81.3% of all values are in excess of 0.5, and if indices are taken as equal or higher than 0.5, the percentage rises to 86.8%. The mean value of all the indices obtained is 0.62. This confirms the view that the distribution of the twenty-seven species is strongly homogeneous.

The way in which the zones have been situated on the matrix (Table 3) allows to formulate various simple hypotheses. For example, if the faunal affinity were an inverse function of the distance which separates the basins, its values would diminish regularly from left to right in each row, and would increase regularly from top to bottom in each column of the matrix. However, as may be seen, this is not the case: no regularity or tendency to such is observed. It may thus be concluded that the affinity amongst the zones, in relation to the species under discussion, is not a function of distance.

Secondly, the sudden and discontinuous increases

or decreases of affinity indices between adjacent rows and columns, which result in strongly different sectors of the matrix, would indicate the existence of geographical regions (sets of basins) distinguishable by populations. The sudden changes in the indices would correspond to the fringes, for which a causal explanation is needed. No phenomenon of this type is observed in Table 3. Thus, if the values of the faunal affinity indices are not governed by either of these hypotheses, it must be concluded that the zones established within the study area do not represent geographical areas, nor palaeobiogeographical transcendence; they should be considered as points of reference only. This strengthens the basic uniformity of distribution of the species. These nassariid faunas may thus be considered to have been part of a unique Pliocene biogeographical province, which included the western Mediterranean, a part at least of the eastern Mediterranean and the adjacent Atlantic closest to the Strait of Gibraltar.

However, some observations on the affinity values of a few of the basins are possible. The affinity values between the Baix Ebre basin (BE) and the others form the lowest set of the matrix, with a unique value of 0.55, some being equal to 0.5, the rest below this value. This does not occur with such regularity in other cases. Other zones, in particular the Moroccan Mediterranean (MM) and Algeria (A) produce low and not very high values. From these basins no or only very little material has been studied and literature data are few. It is therefore possible that the lower values are due to the lack of data. However, the Tunisia (T) and Moroccan Atlantic (MA) zones, for which literature data are also few, the affinity values do not appear to have been affected adversely. These results seem to be quite correct.

In some zones an overestimation of the real affinity values may have taken place since only twenty-seven species have been considered and not all nassariids. This holds especially true for northern Italy (NI) from where more species than studied herein have been recorded (not recorded from the western Mediterranean).

Once the basic uniformity of these twenty-seven species was established, the distribution in the set of basins yielding the data was considered in more detail. The table illustrating the presence by outcrops (Table 2) considers twenty-one deposits in five basins with twenty-three species. Here, it may be seen that the majority of the deposits yield between six and ten species. This does not represent a high

SPECIES	SO	VH	ET	PB	TT	PV	P	CS	MF	MS	MB	FT	VR	N	ND	M	SI	V	MV	C	AB	N. Out.
<i>N. phiomagnus</i>	+		+	+			+	+		+					+	+	+					9
<i>N. companyoi</i>										+	+							+				3
<i>N. clathratus</i>								+							+							2
<i>N. prismaticus</i>		+	+				+	+			+		+	+	+	+						9
<i>N. bisolensis</i>																					+	1
<i>N. ligusticus</i>																					+	1
<i>N. aff. ligusticus</i>																		+	+			2
<i>N. semistriatus</i>	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+			17
<i>N. elatus</i>	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+		+	19
<i>N. martinelli</i>																		+				1
<i>N. cabrierensis</i>		+	+	+	+	+	+	+										+		+	+	11
<i>N. macrodon</i>		+	+				+															3
<i>N. reticulatus</i>		+	+	+	+	+	+	+			+					+						10
<i>N. bugellensis</i>								+	+	+	+	+										5
<i>N. angulatus</i>	+	+	+				+	+		+					+	+						8
<i>N. serraticosta</i>		+	+					+	+						+	+		+				8
<i>N. catulloi</i>		+	+		+			+	+			+			+	+						8
<i>N. turbinellus</i>							+											+	+		+	5
<i>N. quadriserialis</i>																		+			+	2
<i>N. bollenensis</i>	+	+	+	+		+	+	+		+	+											9
<i>N. gibbosulus</i>			+				+	+		+	+							+				6
<i>N. pyrenaicus</i>			+	+		+								+	+	+						6
<i>N. turritus</i>								+			+				+	+						4
N. Sp.-Outcrop	5	10	13	7	5	6	11	14	5	8	9	4	1	8	9	10	9	5	1	6	3	

Table 2. Presence of species in the various outcrops. N. Out. - number of outcrops; N. Sp.-Outcrop - number of species in each outcrop.

Key of outcrops:

- Baix Ebre (BE) basin: SO - Sant Onofre;
- Baix Llobregat (BL) basin: VH - St. Vicenç dels Horts; ET - El Tarc; PB - Plaça de les Bruixes; TT - Torrent del Terme; PV - Pi d'En Valls; P - Papiol;
- Alt Empordà (AE) basin: CS - Cementiri de Siurana; MF - St. Miquel de Fluvià; MS - Mas Siurana; MB - Mas la Brava; FT - Feixa Torta; VR - Vila-robau;
- Roussillon (R) basin: N - Néfiach; ND - Nidolères; M - Millas;
- Alpes Maritimes (AM) basin: SI - Saint Isidore; V - Vence; MV - St. Martin du Var; C - Costamagna; AB - Cava di Villanova.

number of the total amount of studied species. The majority of species are not found in a large number of localities, 86.95% being found in between one and ten outcrops (Table 2). Only few species are widely distributed. Generally, this distribution is highly heterogeneous and contrasts with the homogeneity observed in the comparison of the zones/basins where the different deposits are situated (Tables 1, 3). The heterogeneity is apparent also in the populations in the matrix of affinity between deposits (Table 4). Low values are quite common, being lower than or just over 0.5. High or very high values are very rare. Deposits in some of the zones, e.g. Baix Llobregat (VH, ET, PB, TT, PV and P), and in particular, Roussillon (N, ND and M), present strong affinities (mean affinities of 0.64 and 0.81, respectively). In the Alt Empordà (CS, MF, MS, MB, FT and VR) and Alpes Maritimes (SI, V,

MV, C and AB), diversity is high in this respect; both high and low affinities amongst their deposits (in the case of the Alt Empordà, affinity mean of 0.41); or principally low (Alpes Maritimes, affinity mean of 0.39) are seen.

A comparison of the affinity indices between the outcrops of one basin and those of other basins indicate that low values are always found in relation to Alpes Maritimes deposits, and diverse values, never regularly high or low, in relation to deposits of other zones.

Even though sampling of these deposits has been uniform and extensive, the possibility that some species have escaped attention cannot be ruled out (Gili & Martinell, 1989; Gili *et al.*, in press), we believe that the heterogeneity observed is an expression of a peculiar distribution characteristic, rather than of collection failure. Diverse faunal assem-

	MA	H	MM	A	BE	BL	AE	R	CR	AM	CI	S	T	NI	sum
MA	---	,67	,43	,29	,55	,60	,57	,50	,50	,43	,66	,53	,63	,43	6,79
H		---	,60	,50	,35	,54	,74	,69	,62	,65	,92	,80	,73	,65	7,79
MM			---	,63	,46	,55	,52	,73	,64	,53	,50	,66	,33	,53	6,08
A				---	,46	,64	,52	,64	,64	,53	,60	,66	,44	,53	5,66
BE					---	,53	,50	,42	,53	,30	,35	,44	,53	,30	3,90
BL						---	,76	,79	,79	,72	,62	,59	,66	,72	5,65
AE							---	,83	,83	,70	,81	,79	,64	,76	5,36
R								---	,93	,77	,77	,81	,58	,72	4,58
CR									---	,72	,77	,81	,58	,72	3,60
AM										---	,71	,69	,56	,82	2,78
CI											---	,80	,64	,71	2,15
S												---	,61	,74	1,35
T													---	,63	,63
NI														---	---

Table 3. Faunal affinity between basins (see key of basins in Fig. 1.).

blages are in support of the overall homogeneity. Thus, low affinities between deposits, either in close geographical proximity or not, correspond to significant faunal differences which must be explained by ecological or historical factors.

#### ECOLOGICAL CONSIDERATIONS

In order to study this causal aspect of distribution the greatest possible number of abiotic data for each outcrop have been compiled. Only deposits studied personally and containing 'census assemblages' have been considered. Data include water temperature, salinity, sedimentation depth and sediment type (Table 5).

Early Pliocene (Zanclean) temperature was higher than at present and differed slightly during the Late Pliocene (Piacenzian) (Suc, 1984; Cravatte & Suc, 1985; Demarcq, 1985). Because of a lack of notable differences in this respect between the different localities in the study area, this factor cannot have played an important role in nassariid distribution. Temperature differences due to water depth have not been taken into account.

All outcrops, with the exception of Sant Onofre (SO) expose strata laid down in marine haline water (Martinell, 1988; Martinell & Domènech, 1984, 1990; Clauzon *et al.*, 1990). Despite the various palaeodepths recorded in the literature for the outcrops, we think it possible to differentiate between sediments of shallow depth (between 0 and -50 m) and those of greater depths (between -100 and -200 m) (Robba & Ostinelli, 1975; Martinell & Domènech, 1984, 1985, 1990; Martinell & Marquina, 1984; Nolf & Cappetta, 1988; Clauzon *et al.*, 1990).

For all deposits studied four types of sediments have been distinguished, *viz.* blue-grey clays, sandy clays, limey clays and yellow sands (Robba & Ostinelli, 1975; Andres, 1980; Martinell & Domènech, 1986a, 1990; Gonzalez Delgado, 1987; Martinell, 1988). As may be seen in Table 5, a large number of outcrops, especially those situated in the central part of the study area, display quite uniform characteristics.

Amongst the nassariid species studied, there are ten which have been found in strata that present quite different ecological factors [*Nassarius pliomagnus* (Sacco, 1904), *N. companyoi* (Fontannes, 1879), *N. clathratus* (Bronn, 1788), *N. prismaticus* (Brocchi, 1814), *N. semistriatus* (Brocchi, 1814), *N. elatus* (Gould, 1845), *N. angulatus* (Brocchi, 1814), *N. serraticosta* (Bronn, 1830), *N. turritus* (Borson, 1820) and *N. reticulatus* (Linné, 1758)]. They are here considered to be species with a wide ecological tolerance. Another seven species are found also in a certain environmental type, although in fewer numbers than the previous ones [*N. macrodon* (Bronn, 1831), *N. cabrierensis* (Fischer & Tournouer, 1873), *N. pyrenaicus* (Fontannes, 1879), *N. turbinellus* (Brocchi, 1814), *N. catulloi* (Bellardi, 1882), *N. bol-lenensis* (Tournouer, 1838) and *N. gibbosulus* (Linné, 1758)]. These species are tolerant in some aspects but not in others. Finally, there are six species, the least tolerant, which have only been found in one setting [*N. bisotensis* (Depontailleur, 1879), *N. ligusticus* (Bellardi, 1882), *N. aff. ligusticus*, *N. martinelli* Gili, 1992, *N. productus* (Bellardi, 1882) and *N. quadri-serialis* (Bonelli in Michelotti, 1838)].

The overall homogeneity of the distribution is thus a function of two factors: the important

	SO	VH	ET	PB	TT	PV	P	CS	MF	MS	MB	FT	VR	N	ND	M	SI	V	MV	C	AB	sum.
SO	---	,53	,55	,66	,40	,55	,66	,53	,40	,77	,46	,40	0	,62	,43	,53	,29	,40	0	,20	,25	8,63
VH		---	,87	,59	,66	,63	,76	,75	,27	,44	,55	,40	,18	,66	,53	,60	,32	,32	,40	,18	,25	9,36
ET			---	,70	,55	,63	,83	,81	,44	,57	,57	,33	,14	,76	,64	,78	,36	,33	,14	,21	,25	9,04
PB				---	,66	,92	,66	,57	,33	,53	,53	,33	0	,66	,50	,59	,38	,33	,25	,31	,40	7,95
TT					---	,73	,63	,53	,60	,31	,46	,60	0	,46	,43	,53	,43	,40	,30	,55	,50	7,46
PV						---	,59	,50	,36	,43	,57	,36	0	,57	,40	,50	,40	,36	,29	,33	,44	6,10
P							---	,72	,25	,63	,63	,25	,17	,63	,50	,57	,50	,38	,16	,35	,43	6,17
CS								---	,53	,64	,73	,42	,13	,64	,70	,75	,35	,42	,13	,20	,24	5,88
MF									---	,46	,46	,80	0	,46	,57	,53	,29	,60	0	,18	,25	4,60
MS										---	,63	,62	0	,50	,35	,44	,47	,31	0	,14	,18	3,64
MB											---	,46	,22	,50	,47	,55	,35	,31	0	,14	,18	3,18
FT												---	0	,31	,43	,40	,43	,40	0	,18	,25	2,40
VR													---	,22	,20	,18	0	0	0	0	0	,60
N														---	,71	,89	,24	,46	0	,14	,25	2,69
ND															---	,84	,22	,43	0	,13	,17	1,79
M																---	,21	,40	0	,13	,15	,89
SI																	---	,53	,20	,53	,50	1,76
V																		---	0	,18	,50	,68
MV																			---	,29	,50	,79
C																				---	,66	,66
AB																					---	---

Table 4. Faunal affinity between outcrops (see key of outcrops in Table 2).

number of species with a notable ecological tolerance level, and the fact that the majority of the outcrops present similar physicochemical characteristics.

A particular event noted above may now be explained on the basis of the ecological analysis. The low affinity indices between the Baix Ebre (BE) and all other basins may be interpreted to be the result of this being the only zone where strata had been laid down in saline waters. This effect is not produced by the occurrence of some exclusive species, but by the low number of species that are able to survive under such conditions. The majority of these (four out of five) display maximum tolerance. The study of the affinity matrix (Table 4) resulting from the presence of the species in the deposits (Table 3), may help explain other aspects of distribution, especially those referring to the heterogeneity of the affinity indices between deposits.

In two of the basins, Baix Llobregat (BL) and Roussillon (R), faunal affinities between outcrops are high (mean values of 0.64 and 0.81, respectively). This matches the homogeneous abiotic characteristics for all localities within each zone (identical depth, salinity and sediments), and also in the same type of basin (in both cases estuarine settings).

The low affinities between outcrops, either in close geographical proximity or not, which cannot

be explained by ecological factors, are attributable to other factors not evaluated, but it is quite possible that we will not be able to determine their nature.

The Alt Empordà (AE) and Alpes Maritimes (AM) basins have lower faunal affinity indices, even though ecologically similar conditions prevailed, 0.41 and 0.39 on average, respectively. To explain this, it is necessary to consider aspects not taken into consideration here. Alt Empordà is a bay setting with quite distinctive environments. Martinell (1982a) distinguished fifteen different faunal associations; nassariid faunas in certain of these associations differed from those found in others, but no exclusive species were found. The Alpes Maritimes sediments were laid down in a prograding deltaic front enclosed in a ria (Gilbert delta), which would explain the range of highly different ecological environments which have not been evaluated directly. The existence of four species found only in one or two outcrops and restricted to this basin exaggerates the differences between the faunas of each deposit within this basin. This is the only zone where deep-water sediments have been found. This, together with the presence of these exclusive species, causes the low affinities in the Alpes Maritimes basin in relation to the levels of the other zones, and also to its own deposits.

The deposits of the Baix Llobregat zone (BL)

yield quite high affinity indices (between 0.4 and 0.78) in comparison with those of the Roussillon zone (R). The Alt Empordà basin outcrops have diverse affinity indices in comparison to those of Baix Llobregat and Roussillon, with values ranging from very low (0) to very high (0.81).

All this indicates similarities and differences amongst the populations of the species considered here which are not caused by ecological factors considered above, but probably by biotic factors. Certainly in some cases, 'non-significant' absences may affect the affinities. However, these are insufficient to offer explanations for these similarities and differences.

In general, high values in comparisons of affinity indices for outcrops of different basins, are the result of similarities in basin type, whereas oscillating or low values characterise dissimilar basin types. The discontinuity in the distribution of certain species may be explained by ecological characteristics considered for the outcrops. For example, *N. productus* (Bellardi, 1882), and probably also *N. asperulus* (Brocchi, 1814), are only found in sandy deposits (Tables 1, 5). For other species, such as *N. bugellensis* (Bellardi, 1882), *N. quadriserialis* or *N. turbinellus*, however, their discontinuous distribution with respect to ecological data considered, cannot be explained. Other species such as *N. bollenensis* show a highly continuous but restricted distribution (Table 1), and data available do not offer any explanation either. Three explanations may be considered:

- the distribution may be determined by a certain ecological factor not detected during the present study;
- absences are 'non-significant'; the species lived in special places and has not yet been found;
- a problem of taxonomic nature exists; our species concept differs from that in the literature.

All that has been pointed above may explain the heterogeneity of the affinity indices amongst outcrops, in spite of a strong homogeneity of the population of the various basins.

#### HISTORICAL CONSIDERATIONS

The majority of the twenty-seven nassariids from the Zanclean (Early Pliocene) in the western Mediterranean probably were of Atlantic origin, having entered the Mediterranean on the definitive re-opening of the Strait of Gibraltar subsequent to the

Messinian. At least twelve species are common to the Mediterranean and the Atlantic Pliocene. Moreover, the Mediterranean Pliocene has ten species in common with the Atlantic Miocene, in which are found an additional seven forms which are very similar to Pliocene species from the Mediterranean. These Miocene forms may be considered direct predecessors (Gili, 1991). During the Messinian-Zanclean transition an extension of the Atlantic area was thus produced.

From the data available (Caprotti, 1973; Riba, 1981; Peres, 1989) it appears that climatic conditions were very constant during the Zanclean, and changes leading to differentiation of the Late Pliocene (climatic warming, marine regression) arose gradually and progressively, without marked discontinuities, although with certain pulsations (Martinell & Domènech, 1986b). These stable conditions are also an important factor in terms of providing an explanation for the homogeneous nature of the distribution of the species studied, which was previously explained by ecological factors.

Above, the existence of four species found exclusively in the Alpes Maritimes basin (*N. bisotensis*, *N. ligusticus*, *N. aff. ligusticus* and *N. martinelli*) was also indicated. These have been considered, from an ecological viewpoint, to have had a very limited tolerance. However, such an important restriction in their distribution cannot be explained solely by that factor, since other species equally limited in tolerance are found more commonly. Except for *N. ligusticus*, it is possible that this is due to the fact that the deposits in which they are found are the only ones to have been laid down in deep water. But yet another aspect has to be considered. As these four species appear in the Pliocene fossil record, they may be considered to represent endemic Alpes Maritimes zone species. Their restricted distribution may be no more than a reflection of their recent appearance (neo-endemic or non-relict species).

Amongst those studied, two other species (*N. obliquatus* and *N. corrugatus*) have been found in one of the basins only, viz. the northern Italian zone. Again, their restricted distribution may be considered to reflect their neo-endemic nature, rather than be a reflection of their low ecological tolerance.

Consequently, the Mediterranean Pliocene includes six neo-endemic species amongst those studied. A closer look at the distribution reveals that these species do not appear at random in the area,



OUTCROP	LITHOLOGY	BATHYMETRY	SALINITY	BASIN	ZONE
Sant Onofre (SO)	Blue clays	<20m.	brackish	Bay	BE
Plaça de les Bruixes (PB)	Blue clays	10m. to cms.	marine	Estuary	BL
El Tarc (ET)	Blue clays	<40m.	marine		
Pi de'n Valls (PV)	Blue clays	<40m.	marine		
Torrent del Terme (TT)	Blue clays	<40m.	marine		
St. Vincenç dels Horts (VH)	Blue clays	<40m.	marine		
Papiol (P)	Blue clays	<40m.	marine		
St. Miquel de Fluvià (MF)	Blue clays	<25m.	marine	Bay	AE
Vila Robau (VR)	Silty clays	<25m.	marine		
Feixa Torta (FT)	Blue clays	<25m.	marine		
Mas Siurana (MS)	Blue clays	<25m.	marine		
Mas la Brava (MB)	Blue clays	<25m.	marine		
Cementiri Surana (CS)	Blue clays	<25m.	marine		
Nidolères (ND)	Sandy clays	10 to 25m.	marine	Estuary	R
Néfiach (N)	Sandy clays	10 to 25m.	marine		
Millas (M)	Sandy clays	<25m.	marine		
St. Isidore (SI)	Blue clays	100 to 200m.	marine	Delta	AM
Costamagna (C)	Blue clays	100 to 200m.	marine		
Vence (V)	Blue clays	100 to 200m.	marine	Bay	
St. Martin du Var (MV)	Blue clays	100 to 200m.	marine		
Cava di Villanova (AB)	Blue clays	<50m.	marine		
Zona Huelva (H)	Yellow sands	<30m.	marine	Estuary	H

Table 5. Characteristics of outcrops.

but are concentrated in two basins: the Alpes Maritimes, and the north of Italy. These alpine zones have been strongly affected by tectonic changes during the Neogene, which may be related to the appearance of new species. For the Alpes Maritimes area, more concrete data as to the sedimentology and geological structure are available. The structural complexity of the zone is related to tectonic processes of the Alpine range (Clauzon *et al.*, 1990). The existence of a Gilbert type delta in the River Var basin could reflect strong environmental instability, with frequent formation of enclaves, more or less isolated from the open sea and from other locations in the delta (Gili, 1992). The isolation of populations in enclaves of these types could have favoured the appearance of new species. This then would be reflected in the irregular distribution of these species in the different outcrops of the basin.

What has occurred in these zones (environmental variability and strong speciation) contrasts with what is seen in the rest of the basins studied (environmental stability and lack of speciation). All these historical data are of importance in interpreting the heterogeneity when comparing populations of specific outcrops in relation to the twenty-seven species

studied, which heterogeneity was also explained by ecological considerations.

#### CONCLUSIONS

The distribution in the western Mediterranean of the species studied is a result of ecological and historical factors, which are intimately related. In some cases one factor appears to have become dominant over others. In the majority of cases both types of factors combine, which makes it difficult to distinguish one type from the other, especially in an overall interpretation of palaeobiogeographical distribution.

Therefore, both the homogeneity of the distribution, taking into account the populations of the different basins, and the heterogeneity, comparing faunas of outcrops in particular, have an ecological as well as a historical aspect. The homogeneity between basins is produced by a high number of species with a wide ecological tolerance, local conditions of little diversification with a notable number of different zones with very similar abiotic characteristics (ecological aspects), and an important climatic uniformity in the study area during the

Pliocene, in which the changes were gradual and progressive with time (historical aspects).

The heterogeneity between outcrops is produced by basins with diverse environments, in some cases more diverse than what may be evaluated on abiotic factors. Along with a few species with low tolerance and others with discontinuous distributions (ecological aspects), neo-endemic species are observed which are not randomly distributed in deposits of the various basins, but concentrated in two localities with strong local environmental instability during the Pliocene (historical factors).

To sum up, it should be realised that any determined geographical distribution of an assemblage of species (or of any other taxon) has an ecological as well as a historical aspect. Both components may act simultaneously and the effects they have on distribution may increase or decrease reciprocally.

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