Paleobiogeography of turrid gastropods in the Pliocene of Catalonia

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Gili, C. & Martinell, J. 1994. Paleobiogeography of turrid gastropods in the Pliocene of Catalonia. *Acta Palaeontologica Polonica* 38, 3/4, 349–358.

The distribution of the Tumdae in the Pliocene of Catalonia (NE Spain) is heterogeneous. It appears to be determined to a greater extent by the particular autoecological traits of each species than by more general environmental factors. The area formed by the Pla de Barcelona and the Baix Llobregat may be regarded as a bio-geographical unit due to turrid species, which do not occur in other basins. The turrid distribution in the Alt Emporda basin manifests a high degree of environmental diversity among the different outcrops of the area, thus confirming the earlier provided taphonomic and biogeographic data. Species of the Turridae from Poble de Siurana (Alt Emporda) are also present in different parts of the Pla de Barcelona and Baix Llobregat areas. This indicates the existence of similar ecological enclaves in both basins, within a quite different general context.

Key words: paleoecology, paleobiogeography, Mollusca, Turridae, Pliocene, N.E. Spain (Catalonia).

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Introduction

The principal Pliocene marine basins of Catalonia (Spain) are those situated in the Baix Ebre, Baix Llobregat, in the Pla de Barcelona and the Alt Emporda (Fig. 1). Their recognition dates to the last century (Vezian 1856). Subsequently, Porta *et al.* (1979) described a small exposure with deposits, attributed to the Pliocene, within the municipal boundaries of Sant Viceng de Calders (Baix Penedès). Martinell (1985) provided an exhaustive bibliography refemng to the marine Pliocene of these basins.

From a lithological point of view, these outcrops present, in general, three major types of sediments. These are blue marls, argillaceous in places, which dominate in the Baix Llobregat, Pla de Barcelona and Baix Ebre; yellow sands more or less clayey, very abundant in the Alt Emporda and Baix Penedès and conglomeratic levels of Baix Ebre and Alt Emporda.

The facies transition is recognizable both horizontaly and verticaly. The latter is an expression of the Pliocene regression. The outcropped strata represent shallow-water marine environments. The coccoliths and molluscs shows that the age of the sediments forming these basins is Early Pliocene (Zanclean) (Martinell 1988; Matias 1990).

The molluscs of these beds were studied intensively at the end of the last and at the beginning of the present century (Almera & Bofill 1898; Almera 1907). Few works have been published since then, and it was not until the end of the seventies that interest in mollusc fossils of the Catalonian Pliocene was revived.

The material used in this study was either collected personally by the authors and is stored now in the Laboratori de Paleontologia, Facultat de Geologia, Universitat de Barcelona, or was earlier deposited by J. Almera and collaborators in the Museum Martorell and in the Museum of the 'Seminari Conciliar', both in Barcelona.

Distribution of the turrids

Among the studied basins, the Baix Ebre Pliocene presents a very poor fossil record, in both diversity and richness (Martinell & Domènech 1984a). Only one species of the Turridae has been found.

The number of species collected in the Baix Llobregat Pliocene is very high, despite the progressive destruction of the outcrops (Almera 1907; Martinell & Marquina 1981). This region is the richest in the Turridae; a total of 34 species have been identified (Marquina 1988a). The Pliocene in the Pla de Barcelona has been for a long time inaccessible and is only sporadically exposed (Martinell 1985). Its malacological fauna contains 12 species of the Turridae (Almera & Bofill 1898; Almera 1907; Marquina 1988a). The number of fossil species found in the Alt Emporda Pliocene is also considerable, yet still lower than cited from the Baix Llobregat. However, it must be stressed that the outcrops of the Alt Emporda represent several different fossil assemblages. Martinell (1982a, b) recognized fourteen faunistic associations of shallow environments with 22 species of the Turridae.

All together 39 species of the Turridae have been identified in the 16 Pliocene localities in Catalonia (see Tabs 1 and 2). In Roussillon (SE France) 28 species have been found (Martinell & Domenech 1984b; unpublished data). In the Tunisian Pliocene Fekih (1975) listed 60 species, and Bellardi (1877) counted 89 species for the whole of Liguria and Piemonte (Italy). In the outcrops of the west of Liguria, Bernasconi and Robba (1984) cite 28 species in the five subfamilies of Tumdae studied. On the other hand, Glibert (1960) counted 57 species from the Mediterranean Pliocene in the collections of the Institut Royal des Sciences Naturelles in Brussels. This family is thus quite well represented in the region studied.

Fig. 1. Geographical location of the studied Pliocene basins of Catalonia.

Except for one species (*T.* contigua) which has also been found in yellow limy clays (at Vila-robau, Alt Emporda) all the tumds discussed in the present paper have been collected from blue clays. The other types of sediments have not provided any specimen attributable to the family.

The number of turrid species in each of the studied localities is usually small. No site contains more than 18 species which is less than half of the total number of species. The number of localities containing less than 6 species is eight, with 7 to 12 species is five, and only in three localities the number of species found is greater.

Particular species occur in few localities, most frequent being the presence of one species in less than three sites (29 species, 74% of those studied). Only two species are presents in 9 outcrops and one appears in 13 of them. Although all Spanish species have been cited from other areas of the Mediterranean Pliocene (except for ***C. acuticostulata***; Marquina 1988b), very few species are widely distributed. Even at the level of geographic zones or basins (Tab. 1), the turrid fauna continues to present a high degree of heterogeneity. Only one species has been found in all four basins (B. *brachystoma*) and no more than 7 species have been identified in three of the basins. In fact, 19 species are found exclusively in one and 12 in two basins.

This coincidence in results derived from different kinds of analysis of species presence-absence data is relevant, given that grouping sites together one reduces the effect of insignificant absences resulting from sampling. When data on all localities within one basin are lumped together, the species that in reality occupy *all* of the area but have been

Tab. 1. Repartition of the species in particular basins. Abbreviations: BE – Baix Ebre; BL – Baix Llobregat; B – Pla de Barcelona; AE – Alt Empordà.

	BE	BL	B	AE	No. of basins
Gemmula rotata (Brocchi 1814)		+			1
Tunis *contigua* (Brocchi 1814)		+	+	+	3
Turricula dimidiata (Brocchi 1814)		+	+	+	3
Tumcula intermedia (Bronn 1831)		+		+	2
Tumcula allionii (Belardi in Seguenza 1875)		+	+		2
Clavatula cf. *gradata* (Defrance 1826)		+		+	2
Clauatula *interrupta* (Brocchi 1814)		+		+	2
Clavatula rustica (Brocchi 1814)		+		+	2
Clauatula *acuticostulata* (Marquina 1988)		+			1
Clavatula ditissima (Mayer 1877)				+	1
Genota *intorta* (Brocchi 1814)		+	+	+	3
Clavus maravignae (Bivona 1838)		+	+	+	3
Clavus sigmoideus (Bonn 1837)		+			1
Crassispira bifida (Bellardi 1877)		+			1
Crassispira matheroni (Bellardi 1877)		+			1
Brachytoma obtusangula (Brocchi 1814)		+	+		2
Haedopleura maitreja (Semper in Von Koen 1872)		+			1
Haedropleura septangularis (Montagu 1804)		+			1
Mangelia *angusta* (Jan 1842)		+			1
Mangeliu *quadrilum* (Dujardin 1837)		+			2
Mangelia *attenuata* (Montagu 1803)		+			2
Mangeliu tenuicosta (Brugnone 1862)					1
Cythara frumentum (Brugnone 1874)		+			2
Cythara rugosissima (Brugnone 1862)		+			1
Bela brachystoma (Philippi 1844)	+	+	+	+	4
Bela harpula (Brocchi 1814)		+	+		2
Bela aff. *hispida* (Bellardi 1877)		+		+	2
Bela hispidula (Jan in Bellardi 1847)		+	+	+	3
Bela turgida (Forbes 1843)		+	+		2
Bela vulpecula (Brocchi 1814)		+	+	+	3
Bela nebula (Montagu 1803)				+	1
Pleurotomoides *scalaria* (De Cristofori & Jan 1832)		+			1
Pleurotomoides *ringens* (Bellardi 1847)		+			1
Paphitoma *cordieri* (Payraudeau 1826)		+	+	+	3
Paphitoma montagui (Bellardi 1847)		+			1
Paphitoma semicostata (Bellardi 1847)		+			1
Raphitoma stria (Calcara 1840)				+	1
Epalxis cataphracta (Brocchi 1814)				+	1
Daphnella salinasi (Calcara 1841)		+			1
Number of species	1	34	12	22	

found in as single locality are still included in the information. Then if a strong heterogeneity in the distribution survives such procedure, it proves that there is *a* truly heterogenous distribution. It is not an artifact of the sampling method.

The comparison may be done quantitatively with a use of affinity matrices. Here the DICE index is used (Cheetham & Hazel 1969) to measure the affmity between the assemblages of the Tumdae of different sites (Tabs 3 and 4). It appears that The Baix Ebre indices are extremely low in relation to all other areas, the reason for this being the identification of only one species in this basin.

The indices for other areas approach or slightly surpass 0.5. These are not high affinity values and they indicate the presence of appreciably different turrid fauna. In the case of Baix Llobregat-Pla de Barcelona the difference is merely quantitative, as all those species found in the Pla de Barcelona are also found in the Baix Llobregat. Yet between the Baix Llobregat and the Alt Emporda a qualitative difference also exists as there are 22 species which have only been found in one basin.

In affmity matrix based on data from each outcrop (Tab. 4) four sectors can be distinguished:

(1) At Sant Onofre (Baix Ebre) the only species found was B. *brachystoma*, and only with few individuals. The affinity to other localities is very low. A unique case of identity exists in respect to Feixa Torta (Alt Emporda) where no other species has been found either, even though here the number of individuals is higher.

(2) Pla de Barcelona and the Baix Llobregat indices are often higher than 0,5 or come very close. Sant Vicenq dels Horts (the only outcrop on the right side of river Llobregat) and Can Albareda (accumulation level) are those outcrops giving the lowest affinities in relation to the others. Pla de Barcelona gives high indices with respect to the set of outcrops in the Baix Llobregat. The indices arising among the sites of the Baix Llobregat themselves are similar.

(3) Affinities of the Pla de Barcelona and Baix Llobregat in relation to those of the Alt Emporda are low or very low. What is striking are higher values for the outcrop at Poble Siurana (PS) in Alt Emporda and three outcrops in other basins (Pla de Barcelona, St. Vicenq dels Horts and Can Albareda). In two cases (St. Vicenq dels Horts and Can Albareda) this affinity is higher than with any of the outcrops of its own zone.

(4) Among the outcrops of the Alt Emporda very low affinity indices are given in general; much lower than those among the localities of the Baix Llobregat. Only three values equal 0.5, and one is higher (0.57).

Paleoecological interpretation

The information provided in the previous section can be analysed with the aid of the paleoecological data available for the outcrops. Yet the characteristics of the outcrops of the basins studied are so varied that it was impossible to take a comparable sample in each of them. This in turn impedes a quantitative paleoecological analysis, like the one carried out

Tab. 2. Repartition of the species in particular outcrops. Abbreviations: SO – Sant Onofre; B – Pla de Barcelona; SV – Sant Vicenq dels Horts; TT – Torrent del Terme; CA – Can Albareda; T – El Tarc; PB – Plaqa de les Bruixes; PV – Pi d'En Valls; P – El Papiol; V – Vila-robau; FT – Feixa Torta; SM – Sant Miquel de Fluvià; MS – Mas Siurana: BA – Baseia; CS – Cementiri de Siurana; PS – Poble de Siurana.

	SO	B	SV	TT	CA	T	PB	PV	P	V	FT	SM	MS	BA	CS	PS	No. of occur.
G. rotata									+								1
T. *contigua*		+	+	+	+	+	+	+	+	+		+		+	+	+	13
T. dimidiata		+	+	+	+	+	+	+	+							+	9
T. intermedia							+		+					+	+	+	5
T. allwnii		+	+		+	+	+	+	+								7
C. cf. gradata			+												+	+	3
C. *interrupta*									+							+	2
C. *rustica*					+											+	2
C. *acuticostulata*			+						+								2
C. *ditissima*																+	1
G. *intorta*		+	+		+		+		+							+	6
C. *maravignae*		+	+													+	3
C. *sigmoideus*			+														1
C. bifida									+								1
C. matheroni			+														1
B. *obtusangula*		+	+	+	+	+	+	+	+								8
H. *maitreja*					+												1
H. *septangularis*					+												1
M. *angusta*				+													1
M. *quadrilum*			+		+											+	3
M. *attenuata*			+									+			+	+	4
M. tenuicosta															+		1
C. *frumentum*					+										+	+	3
C. *rugosissima*			+		+												2
B. brachystoma	+	+	+	+					+		+	+			+	+	9
B. *harpula*		+		+	+												3
B. aff. *hispida*				+	+											+	3
B. hispidula		+	+		+												3
B. *turgida*		+	+											+	+		3
B. uulpecula		+			+								+		+	+	5
B. nebula															+	+	2
P. scalaria							+										1
P. ringens						+								+			1
R. *cordieri*		+	+		+				+							+	5
R. *montagui*			+													+	1
R. *semicostata*					+											+	1
R. stia																+	1
E. cataphracta														+			1
D. salinasi					+												1
No. of species	1	12	17	7	18	5	7	5	12	1	1	3	1	3	10	18	

among some of the localities of the Alt Emporda (De Renzi & Martinell 1979). As a result, only qualitative ecological aspects are considered.

Tab. 3. Indices of affinity between basins (see Tab. **1** for abbreviations).

	BE	BL	B	AE
BE	–	0.06	0.15	0.09
BL		–	0.52	0.57
B			–	0.47
AE				–

Tab. 4. Affinityindex between outcrops (see Tab. 2 for abbreviations).

BAS.	BE	B			BL						AE					
OUT.	SO	B	SV	TT	CA	T	PB	PV	P	V	FT	SM	MS	BA	CS	PS
SO	–	0.15	0.11	0.25	0	0	0	0	0.15	0	1	0.50	0	0	0.18	0.11
B		–	0.62	0.53	0.53	0.47	0.53	0.59	0.58	0.15	0.15	0.27	0.15	0.13	0.27	0.53
SV			–	0.33	0.51	0.36	0.42	0.36	0.48	0.11	0.11	0.30	0.11	0.10	0.30	0.51
TT				–	0.40	0.50	0.43	0.50	0.42	0.25	0.25	0.40	0	0.20	0.24	0.32
CA					–	0.35	0.40	0.35	0.40	0.11	0	0.10	0.11	0.10	0.21	0.50
T						–	0.67	0.80	0.47	0.33	0	0.25	0	0.25	0.13	0.17
PB							–	0.67	0.41	0.25	0	0.20	0	0.40	0.24	0.32
PV								–	0.47	0.33	0	0.25	0	0.25	0.13	0.26
P									–	0.15	0.15	0.27	0	0.27	0.27	0.47
V										–	0	0.50	0	0.50	0.18	0.11
FT											–	0.50	0	0	0.18	0.11
SM												–	0	0.33	0.46	0.29
MS													–	0	0.18	0.11
BA														–	0.31	0.19
CS															–	0.57
PS																–

All the outcrops studied correspond to a depth of water in no way deep and, in some cases, evidently shallow (Martinell & Marquina 1981, 1984). The average temperature of the water during the Early Pliocene was higher than the current temperature in the Mediterranean (Suc & Zagwijn 1983; Suc 1984; Cravatte & Suc 1985; Demarcq 1985) and it remained constant until its decrease at the boundary with the Late Pliocene. The sediment is blue clay. Only in Vila-robau (Alt Emporda) are yellow limy clays found (Martinell & Domenech 1985), in which we have only found *T. contigua*, the species with broadest distribution. Depth, temperature and sediment type could not thus have played any important part in controlling the distribution of the Turridae in the area, as they are quite uniform among the outcrops.

Therefore, we have to look for other possible ecological factors which may be responsible for the observed distribution (salinity, other local abiotic conditions, trophic specializations, competitive relations, etc.). Unfortunately, current knowledge about the influence of these factors on living turrids is very poor. Many of the recent turrid species, such as those of the Pliocene, have a wide geographical distribution and rarely form abundant populations. The sediments in which one species is found are frequently of diverse kinds.

Among the litoral forms, some species are found associated with sea grass or *Laminaria* meadows, others are more typical of the corallinaceous

circalittoral zone. The depths indicated by different authors fall within a wide range, with variations of hundreds of metres. With respect to their feeding habits, the turrids are considered predatory carnivores, their prey being principally small polychaetes (Bucquoy *et al.* 1882; Sabelli & Spada 1977; Bouchet & Waren 1980; Templado 1983; Rolan 1983; Graham 1988). Therefore, no more than general conclusions can be made in any particular case.

The low faunistic affinity between St. Onofre and all the other deposits appears to be clearly determined by the salty environment of this outcrop of the Baix Ebre (Martinell & Domenech 1984a). As has been seen, it only has maximum affinity with Feixa Torta (Alt Emporda) due to the fact that the only species present in both localities is *B. brachystoma.* The basically marine environment assumed for Feixa Torta (Alt Emporda) (Martinell & Domènech 1982) indicates that this coincidence cannot result from any environmental similarity, but expresses rather the ecological plasticity of this species, which is the only one to be identified in all the four basins. The low affinities among the outcrops of the Alt Emprda area indicate a greater diversification of physical-biological environments (Martinell 1982a). On the contrary, the assemblage of the Turridae is much more homogeneus within the ensemble formed by the Pla de Barcelona and the Baix Llobregat, in spite of their peculiarities, and greatly differs from that of the Alt Emporda as a whole. This may be interpreted as showing a high degree of uniformity among the ecosystems of the Baix Llobregat, which would be noticeably different from those of the Alt Emporda. Following from this, the similarity between the Turridae population of the Poble de Siurana and various outcrops from the Baix Llobregat and Pla de Barcelona areas above mentioned is remarkable. It is possible that in the case of Poble de Siurana there existed ecological conditions very similar to those of some parts of the Baix Llobregat.

Biogeographic subdivisions

One may consider that a biogeographic unit is defined on the basis of certain species which are not found in other geographical areas. In the Pla de Barcelona-Baix Llobregat unit *Brachytoma obtusangula* and *Turricula allionii* (the latter only being absent at Torrent del Terme) have been found in all the outcrops of this basin and in none of the localities of the other basins. Also, *Turricula dimidiata, Raphitoma cordieri* and *Genota intorta* have been identified in all or in a high number of the outcrops of the Pla de Barcelona-Baix Llobregat and in none of the other basins, with the exception of Poble de Siurana (Alt Emporda).

In the remaining basins the ensemble of Tumdae does not show such a minimum uniformity. The only species present in all of them, *Bela brachystorna,* is a species with a wide distribution (Graham 1988) thanks to a strong ecological plasticity. It is, therefore, not a good indicator of

faunistic affinity. Apart from this, in the Alt Emporda, only *Turris contigua* is found in a high number of outcrops, yet it is present in all the other sites of the Pla de Barcelona-Baix Llobregat, being common in the Mediterranean Pliocene in various sediments. Thus, its occurrence is similar to that of B. *brachystoma*. The Pla de Barcelona-Baix Llobregat presents a certain degree of coherence as a biogeographical zone. Also the similarity of the Poble de Siurana outcrop (Alt Emporda) to the former zones is evident.

The species occurring in restricted number of different geographic areas may serve as good indicators of special conditions. *Clavatula interrupta* is present at El Papiol (Baix Llobregat) and at Poble de Siurana (Alt Emporda). *Clavatula rustica* is found at Can Albareda (Baix Llobregat) and at Poble de Siurana. *Beh hispidula* has been identified at Pla de Barcelona and Pi d'en Valls (Baix Llobregat) and at Poble de Siurana. *Clavus maravignae* has been found at Pla de Barcelona and St. Vicenç dels Horts (Baix Llobregat), and at Poble de Siurana. In all these cases one outcrop from the Baix Llobregat is involved and Poble de Siurana is invariably among them.

Acknowledgments

The authors would like to express their gratitude to Prof. Dr. A. Hallam (Univ. of Birmingham) for his helpful comments on the text and to Dr. R. Domenech (University of Barcelona) for comments and assistance with the draft. Constructive criticism of review by Prof. Wacław Bałuk (Warsaw University) is gratefully appreciated. This research is within the range of investigation of the Project DGICYT no. PB90-0489.

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