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PATTERNS OF EXTINCTION AND LOCAL DISAPPEARANCE OF TROPICAL MARINE GASTROPODS; CONTRASTING EXAMPLES FROM ACROSS THE NORTH ATLANTIC

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ABSTRACT

In the North Atlantic, Pliocene times were marked by sharp climatic cooling events, causing pulses of extinction and local disappearance of thermophilic taxa among shallow marine gastropods. These events were not followed by recovery phases. Hence a step by step reduction of thermophilic taxa and of molluscan diversity in general occurred. This was not the case of the Pliocene of the Caribbean.

In this paper preliminary data on the Pliocene gastropod assemblages of the Atlantic Caribbean Island of Cubagua are presented and their relevance for the definition of patterns of extinction and local disappearances in the Atlantic portion of the tropical American Gatunian Province discussed.

Since the Pliocene, the generic composition of the Cubagua gastropod fauna – namely thermophilic taxa – is little changed. At more northern latitudes, at generic level, a southwards range contraction of thermophilic taxa driven by cooling events occurred, whereas in the Caribbean a westwards range contraction of some taxa took place – paciphile taxa – accompanying the closure of the Central American Seaway (CAS). The driving forces of these extinctions and local disappearances in the Caribbean are still unclear, and have been ascribed to various environmental factors.

Unlike the North Atlantic and the Mediterranean, where a steep diversity decline occurred since the Early Pliocene, these Caribbean extinctions and local disappearances are accompanied by a high species turnover. The fact that the generic composition of the gastropod assemblages in Cubagua changed less than in the rest of the Caribbean might suggest that the Cubagua region was more stable than the Gatunian Province as a whole. At specific level, however, a drastic extinction occurred, equal if not higher than that seen in the Gatunian region as a whole. What forces led to these extinctions are, at present, unclear.

INTRODUCTION

In the North Atlantic, Pliocene times were marked by a series of sharp climatic cooling events, causing pulses of extinction and local disappearance, not followed by recovery phases (Stanley, 1986; Stanley & Ruddiman, 1995; Monegatti & Raffi, 2001). As a consequence progressive reduction of ther-

mophilic taxa and general diversity reduction occurred (Monegatti & Raffi, 2001).

Based on the Mediterranean Pliocene fossil assemblages of Italy, Monegatti & Raffi (2001) recognised four Mediterranean Pliocene Molluscan Units (MPMUs), separated by disappearance events. These units are ecobiostratigraphic faunistic units based on local disappearance and true extinction events of shallow marine benthic molluscs. Since changes in the distribution of shallow marine thermophilic molluscs are a proxy for SSTs variations, the boundaries of the MPMUs approximate the major Pliocene climatic changes (cooling events) of the Northern Hemisphere affecting the Atlanto-Mediterranean region (Monegatti & Raffi, 2001).

In this paper we present preliminary observations on Pliocene patterns of extinction and local disappearances in the southern part of the Atlantic portion of the Gatunian Province, and compare them to the Province as a whole, and to patterns observed along the Atlantic European frontage and Western Mediterranean. These results are from an ongoing study of the Pliocene fauna of the Atlantic Caribbean Island of Cubagua, with the cooperation of the Instituto La Salle, Margarita, Venezuela, and the Departamento e Centro de Geologia da Faculdade de Ciências da Universidade de Lisboa, Portugal.

Northeastern Atlantic pattern of extinction and local disappearance

MPMUs, being ecobiostratigraphic units, are heavily dependent on the biogeography of shallow marine molluscs. Therefore, they are valid exclusively within the Mediterranean region, or within the limits of the Pliocene Mediterranean – West African Pliocene Province (Fig. 1). The criteria used to define these ecobiostratigraphic units do not apply, directly, to Pliocene molluscan assemblages outside the Mediterranean, such as the coeval Pliocene Western Iberian Atlantic assemblages. On the other hand, once a sound temporal equivalence between Mediterranean and non-Mediterranean assemblages has been established, MPMUs are a powerful tool for interprovincial palaeoclimatic and palaeoceanographic correlations, as well as for the definition of Pliocene Atlanto-Mediterranean palaeobiogeographic boundaries.

Raffi & Monegatti (1993) and Monegatti & Raffi (2001), based on data from Italian Pliocene molluscan assemblages, estimated the specific extinction and disappearance rates for Mediterranean Pliocene bivalves marking MPMU boundaries. Until now, no detailed figures are available for gastropods for these faunal units, but gastropod extinction and local disappearances, in the Mediterranean and in the adjacent European Atlantic, from Early Pliocene to Recent times runs at around 70-85% for thermophilic species (Marasti & Raffi, 1976; Silva, 2001).

The eastern Atlantic component of the present work is centred on rich Pliocene fossiliferous deposits on southern and western Iberian Peninsula; from just within the Mediterranean in the Estepona Basin (Southern Spain), just outside in the

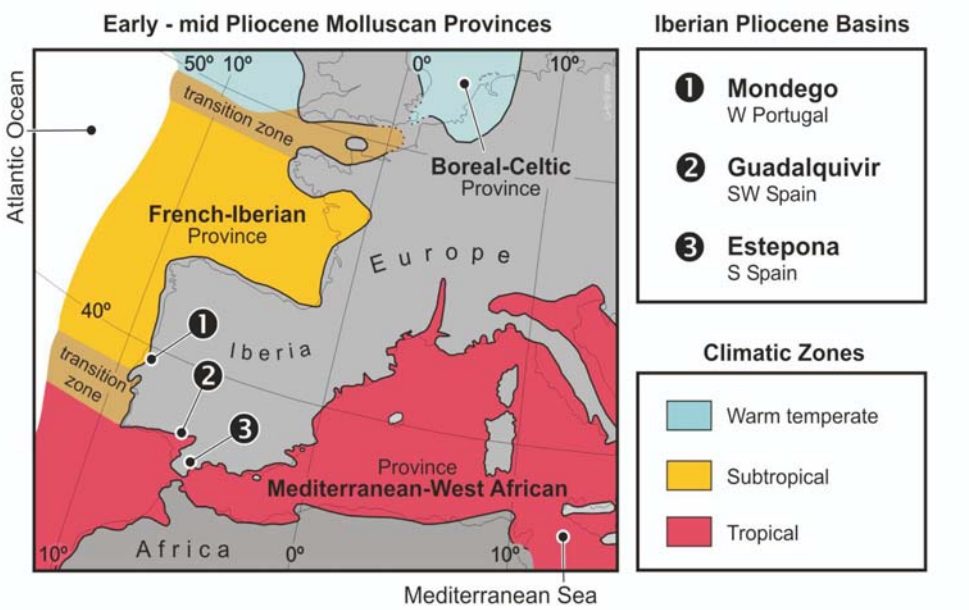

FIGURE 1. Geographic position of the Iberian Pliocene Basins, with Early to mid Pliocene biogeographic provinces superimposed (adapted from Landau & Silva, 2006).

Atlantic in the Guadalquivir Basin (SW Spain), and further north in the central West Portugal, the Mondego Basin (Fig. 1).

The Pliocene assemblages from these deposits, ranging in age from Zanclean to lower Piacenzian, although not strictly synchronous, fall within the frame of MPMU1. They all precede the mid Pliocene 3.0 Ma cooling event that, after Monegatti & Raffi (2001), triggered the first Pliocene event of extinction and local disappearance in the Mediterranean region. Therefore, they are all ecobiostratigraphically coeval. Both Guadalquivir and Estepona Pliocene sites, straddling the Strait of Gibraltar have frankly tropical gastropod assemblages, typical for MPMU1 as defined for the Mediterranean (Silva, 1995; Raffi & Monegatti, 2001, Landau *et al*., 2003). The Atlantic Mondego Basin Pliocene assemblage, although coeval, is not a typical MPMU1 assemblage as it is located well outside the Mediterranean, at a more northern latitude than the Atlantic Guadalquivir Basin, lacks most of the thermophilic indicators described by Monegatti & Raffi (2001), and has a subtropical character (Silva, 2001; Silva & Landau, 2007).

Within the Estepona assemblage, for instance, we find extinction and local disappearance rates of 60% at the species level and 37% at generic level (all taxa, not just thermophilic) in comparison with Recent faunas (B. Landau unpubl. data). The genera that have disappeared from Iberian

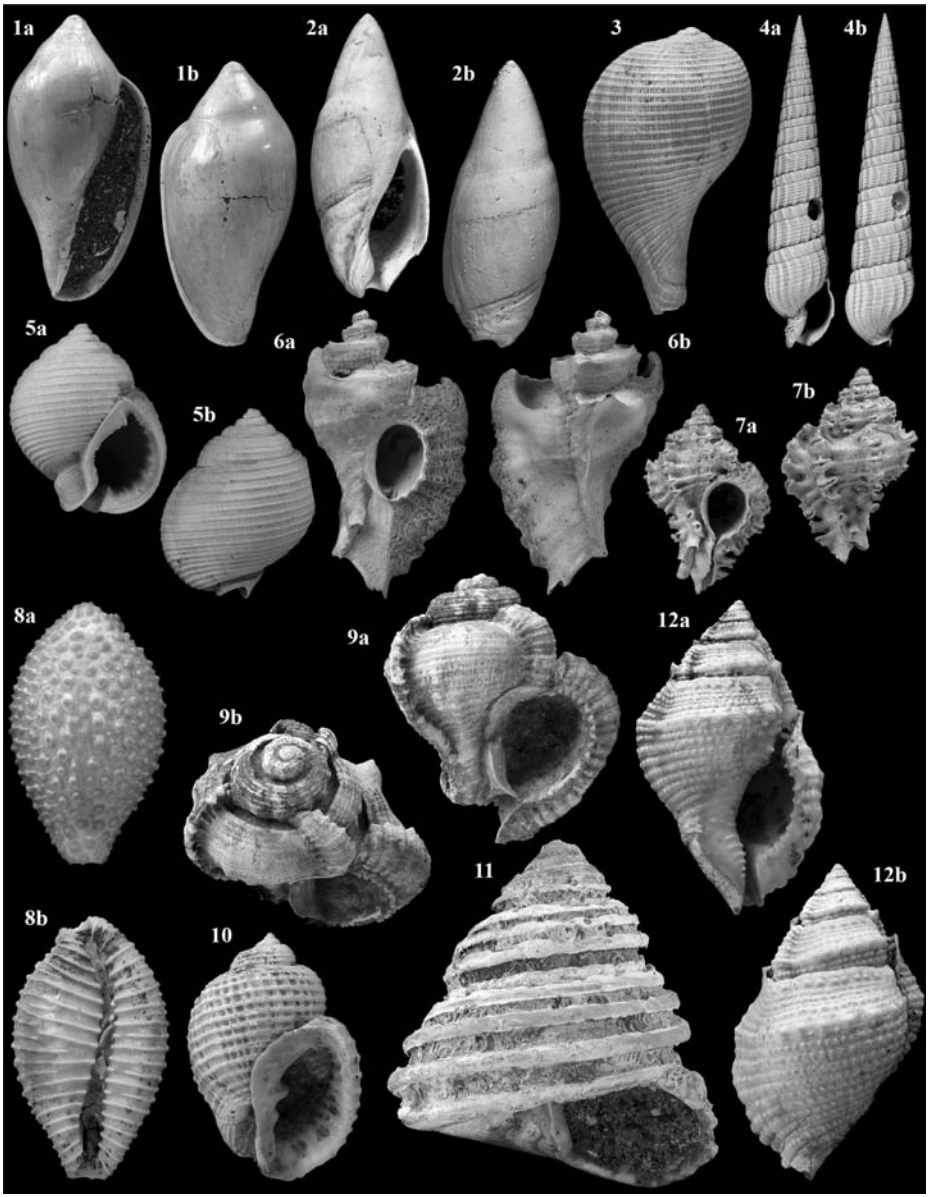

FIGURE 2.
1. *Marginella aurisleporis* (Brocchi, 1814). Height 43.1 mm. Uppermost Zanclean to lower Piacenzian, Vale de Freixo, Pombal region, Mondego Basin, central-west Portugal. (CMS coll.).
2. *Amalda glandiformis* morphotype *elongata* (Deshayes, 1830). Height 39.5 mm. Uppermost Zanclean to lower Piacenzian, Nadadouro, Caldas da Rainha region, Modego Basin, central-west Portugal. (CMS coll.).

3. *Ficus subintermedia* (D'Orbigny, 1852). Height 22.1 mm. Uppermost Zanclean to lower Piacenzian, Vale de Freixo, Pombal region, Mondego Basin, central-west Portugal. (CMS coll.).
4. *Strioterebrum reticulare* (Pecchioli ms. in Sacco, 1891). Height 51.6 mm. Uppermost Zanclean to lower Piacenzian, Vale de Freixo, Pombal region, Mondego Basin, central-west Portugal. (CMS coll.).
5. *Demoulia conglobata* (Brocchi, 1814). Height 23.4 mm. 'Grey sands', Zanclean, Santa Catalina near Lucena del Puerto, Huelva, Guadalquivir Basin, southern Spain, (BLP coll.).
6. *Jaton helenae* (Landau, 1984). Height 33.6 mm. 'Yellow sands', Zanclean, Lucena del Puerto, Huelva, Guadalquivir Basin, southern Spain (BLP coll.).
7. *Favartia excisa* (Grateloup, 1833). Height 18.2 mm. lower Piacenzian, Velerín conglomerates, Velerín, Estepona Basin, southern Spain (BLP coll.).
8. *Jenneria loxahatcheensis* (M. Smith, 1934). Height 23.2 mm. Zanclean, Cañon de las Calderas, Cubagua Island, Venezuela. (BLP coll.).
9. *Haustellum mimiwilsoni* E. VOKES, 1990. Height 48.8 mm. Zanclean, Cañon de las Calderas, Cubagua Island, Venezuela. (BLP coll.).
10. *Cancellaria (Massyla) cubaguensis* Landau, Petit & Silva, 2007. Height 25.9 mm. Zanclean, Cañon de las Calderas, Cubagua Island, Venezuela. (BLP coll.).
11. *Heteroninella bertarellii* (Andreoli & Marsigli, 1997). Height 18.2 mm. lower Piacenzian, Velerín conglomerates, Velerín, Estepona Basin, southern Spain (BLP coll.).
12. *Marsupina bufo* (Bruguière, 1792). Height 53.4 mm. Zanclean, Cañon de las Calderas, Cubagua Island, Venezuela. (BLP coll.).

waters since the Pliocene are mainly thermophilic in character, and are now either extinct (e.g. Fig.2/11), absent from the eastern Atlantic (e.g. Fig.2/3) or, as in most cases, emigrated southwards to warmer latitudes, or suffered a range contraction, becoming restricted to the southern part of their original distribution (e.g. Fig.2/1, 2, 4, 5, 6, 7). The species which have disappeared are in the vast majority within these thermophilic genera.

Therefore, the pattern for extinction and local disappearances which emerges along the Atlantic European frontage is one of a stepwise extinction and southwards withdrawal of thermophilic taxa (Brébion, 1972, 1981, 1988; Silva & Landau, 2007). These extinctions and local disappearances are especially evident at generic level. Relatively few species within genera still extant in the European coasts became extinct or emigrated southwards. This left in the region an impoverished residual fauna, depleted of the majority of the typically Pliocene thermophilic elements.

These observations give us a pattern for extinction and local disappearances of gastropods throughout the Pliocene at Eastern Atlantic northern latitudes, but what is the situation at more southern latitudes. Unfortunately there are no outcropping Neogene shell-bearing marine deposits known at tropical latitudes along the Atlantic African frontage, however, on the other side of the Atlantic, the tropical Caribbean is rich in marine fossiliferous deposits, which might shed light on this subject.

Western Atlantic tropical pattern of extinction and local disappearance

A similar extinction/local disappearance and southward range contraction pattern is observed along the north-eastern coast of North America during the Neogene (Stanley, 1986; Stanley & Ruddiman, 1995).

However, quite a different scenario is seen in the tropical Caribbean region. Vermeij & Petuch (1986) noted that 32% of genera became locally extinct in the Atlantic portion of the Gatunian region (roughly equivalent to the Caribbean and the Gulf of Mexico, excluding the southern coasts of North America) after the closure of the Central American Seaway (CAS). Most of these genera absent in the Recent Caribbean are now found only on the Pacific side of Tropical America, these are known as paciphile taxa (Woodring, 1928) (e.g. Fig. 2/8, 10). At species level, it runs roughly at about 80-90%.

The western Atlantic component of the present study is centred in the Pliocene molluscan assemblages of the Caribbean Island of Cubagua. The island is located just off the northern coast of Venezuela, between the mainland and Margarita Island. The location and the stratigraphic section of the site of Cañon de las Calderas, in Cubagua, were given by Padrón *et al*. (1993), who assigned the fossiliferous beds to the Pliocene.

The molluscan assemblage from the lower beds of the Cañon de las Calderas is typically soft-bottom, shallow marine and of normal salinity. The molluscs represented are tropical in character, with numerous frankly thermophilic taxa present, such as *Barycypraea* (Muracypraea), *Jenneria* (Fig.2/8), *Marsupina* (Fig.2/12), *Strombus*, *Oliva*.

The extinction and local disappearance rates seen in Cubagua are of 21% at generic level, but 90% at the species level, in comparison with Recent faunas. Of these genera 3.5% are totally absent from the Tropical American region (e.g. Pl. 1, Fig. 9), the rest, 17.5%, are now found only in the Tropical American Pacific (e.g. Pl. 1, Figs 8, 10). Therefore, in Cubagua we see quite a different pattern, with a brutal extinction rate at the species-level, but the generic composition altered less than in the whole of the Atlantic portion of the Gatunian Province and far less than in the Atlanto-Mediterranean region.

CONCLUSIONS

At more northern latitudes, at generic level, a gradual southwards range contraction of thermophilic taxa driven by cooling events is observed since the Miocene, whereas in the Caribbean there is relative generic stability within the Atlantic portion of the Gatunian region during the Miocene and Pliocene, followed by a pulsed Plio-Pleistocene westwards range contraction associated with the closure of the CAS (Landau *et al*., in prep).

In the Pliocene, as today, the Cubagua region was tropical, based on the molluscan assemblage, and the generic composition of the fauna, since then, is little changed. This sug-

gests that temperature change, unlike what seen at higher latitudes, was not a driving force for these extinctions and local disappearances. It was not a driving force for extinction in the Gatunian Province as a whole either, although the extinction rate at generic level is greater there than in Cubagua.

These high extinction and local disappearance rates in the Atlantic portion of the Gatunian Province have been ascribed to shifts in oceanographic conditions after and during the closure of the CAS (Maier-Reimer *et al*., 1990); sea level fluctuations and changes in patterns of upwelling and nutrient distribution (Vermeij & Petuch, 1986; Jackson *et al*., 1993).

Unlike the Atlanto-Mediterranean region, where an important diversity decline occurred since Early Pliocene times, these Caribbean extinctions and local disappearances are accompanied by high rates of speciation (Allmon *et al*., 1993; Jackson *et al*., 1993), although some maintain that there has also been a substantial impoverishment in the marine biota since the Pliocene (Vermeij & Petuch, 1986; Petuch, 2004; G. Vermeij, pers. com. 14/12/2005).

The fact that the generic composition of the gastropod assemblages in Cubagua changed less than in the rest of the Caribbean might suggest that the Cubagua region was more stable than the Atlantic portion of the Gatunian Province as a whole (Landau et al., submitted). At specific level, despite this relative generic stability, a drastic extinction (far more significant than the local disappearances) occurred, equal if not higher than that seen in the Province as a whole. What forces led to these extinctions are, at present, unclear.

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