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Cenozoic Atlanto-Mediterranean biogeography of *Spiricella* (Gastropoda, Umbraculidae) and climate change: Filling the geological gap

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Abstract. *Spiricella unguiculus* Rang & Des Moulins, 1828 is a thermophilic opisthobranch species, occurring today in the eastern Atlantic from southern Portugal to Mauritania, and the Mediterranean. However, during its geological history, the species had a much broader geographic distribution, including also the North Sea basin and more northern Atlantic coasts of Western Europe.

For more than 150 yr the species was known from a single specimen from the Atlantic Lower Miocene of the Aquitaine basin, France. More recently the species has been recorded from the European Oligocene, Miocene and Recent faunas. The discovery of *Spiricella unguiculus* in the Pliocene of the Mondego Basin (central-west Portugal) fills the gap existing in the geological distribution of the species. Although the overall recorded occurrences of the species are rare, the Cenozoic geographical distribution of *S. unguiculus* appears to have undergone a sharp southward contraction. This contraction is in accordance with the general biogeographic trend observed for other Atlanto-Mediterranean gastropod taxa and with the Neogene to Recent Northern Atlantic cooling scenario.

Key Words: Gastropoda, Opisthobranchia, Umbraculidae, *Spiricella unguiculus*, Pliocene, Atlantic, Portugal, Palaeobiogeography.

INTRODUCTION

Opisthobranch mollusks have reduced thin-walled shells or no shell at all. Consequently, these mollusks have a low fossilization potential and a relatively poor fossil record, when compared with most groups of gastropods. Therefore, as stressed by Valdés & Lozouet (2000), with the exception of the Cephalaspidea and the pteropods, little is known about fossil Opisthobranch molluscs.

Spiricella Rang & Des Moulins, 1828, a monospecific opisthobranch gastropod genus, is a good example of this. *Spiricella unguiculus* Rang & Des Moulins, 1828, an Atlanto-Mediterranean thermophilic species, has a remarkably long geological history, spanning from the Oligocene to Recent, yet probably more papers have been written on this enticing little gastropod than there are specimens, fossil or Recent.

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Until twenty years ago the species was known only from one specimen from the Lower Miocene of Aquitaine. Since then, a series of papers have increased its geochronological range dramatically, making it one the most long lived Cenozoic gastropod species known and, more important, an excellent biogeography case study. *Spiricella unguiculus* has been reported from the Lower Oligocene, Rupelian stage, of the Aquitaine basin, south-western France (Valdés & Lozouet, 2000), from the Lower Miocene, Aquitanian and Burdigalian stages, of the Aquitaine basin (Rang & Des Moulins, 1828; Peyrot, 1932; Dekker, 1987; Valdés & Lozouet, 2000; Lozouet, Lesport & Renard, 2001); from the Middle Miocene, Hemmoorian stage, Aalten Member, Netherlands (Janssen, 1984) and from the Pliocene, uppermost Zanclean to lower Piacenzian stages, of the Mondego basin, central-West Portugal (this paper).

At the same time, the species has seen its geographical occurrences expanded from south-western France (Oligocene-Miocene: Rang & Des Moulins, 1828; Valdés & Lozouet, 2000) to the North Sea basin (Miocene: Janssen, 1984), and Western Iberia (Pliocene: this paper). *Spiricella*

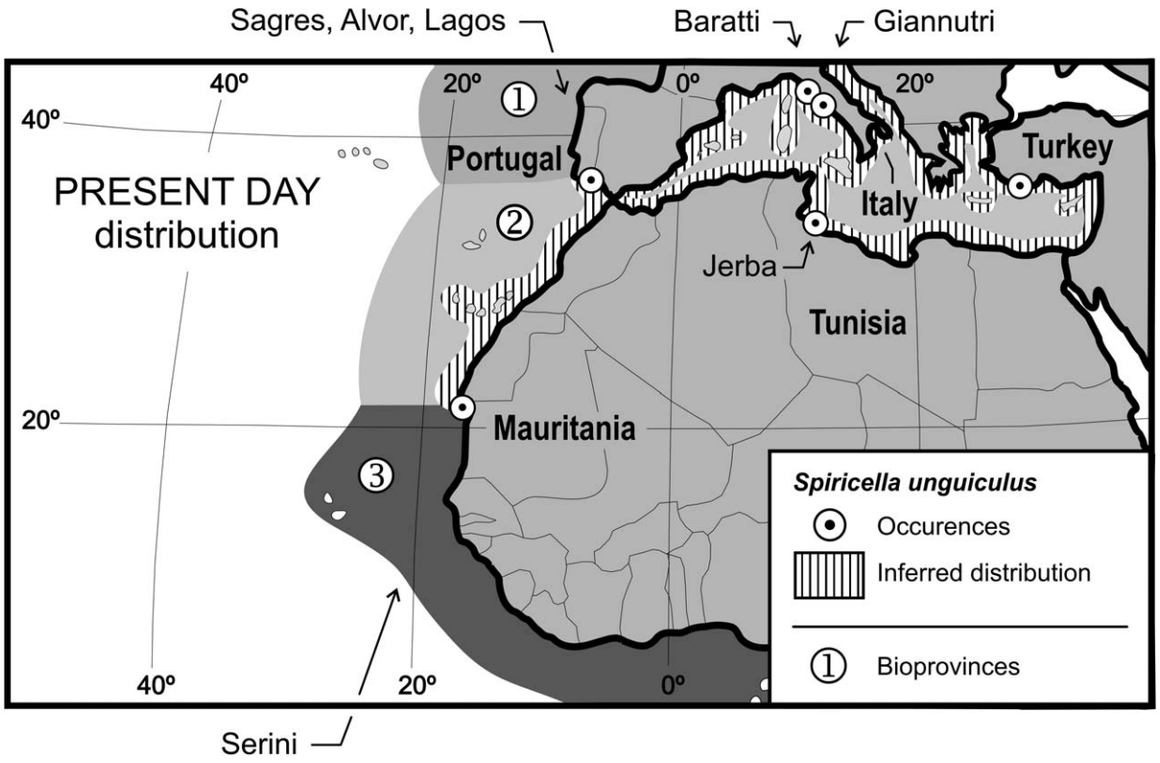

Figure 1. Present day geographic distribution of *Spiricella unguiculus* and molluscan biogeographic provinces (after Raffi, Stanley & Marasti, 1985). 1 - French-Iberian province; 2 - Mediterranean-Moroccan province; 3 - Mauritanian-Senegalese province.

unguiculus is essentially subtropical in distribution. In the present day, it occurs in the Eastern Atlantic, in the southern coast of Portugal (between Alvor and Lagos: Hoeksema & Janssen, 1984; Geuze & Hoeksema, 1994) and in Mauritania, West Africa (Serini: Geuze & Hoeksema, 1994), and in the Mediterranean, in Italy (bay of Baratti, south of Livorno: Carozza & Rocchini, 1987; island of Giannutri: Angioy & Nikolay, 1993), in Tunisia (island of Djerba: Carozza & Rocchini, 1987) and in Turkey (locality unknown; see Valdés & Lozouet, 2000) (Figure 1).

Although described from several Oligocene to Pliocene localities, and reported from the present day Atlanto-Mediterranean region, the species always seems to be uncommon, known from less than a dozen fossil and Recent shells. What is more, nothing is known of the animal.

Until now, there was a gap in the geological history of the genus. *Spiricella* was unknown from Upper Neogene formations. Recent work on the Atlantic Pliocene of the Mondego basin, at the Vale de Freixo outcrop, central-west Portugal, has yielded one specimen of *S. unguiculus*. This exciting find, reported herein, fills the existing gap in the genus geological history, making it possible to trace its entire biogeographical evolution and, more important, to correlate it to late Cenozoic Atlanto-Mediterranean molluscan biogeography and global climatic change.

GEOLOGICAL SETTING

Vale de Freixo is located in central-west Portugal (Pombal region) in the Mondego Cenozoic basin (Figure 2). The fossiliferous beds of this locality are Pliocene, uppermost Zanclean to lower Piacenzian, in age (Cachão, 1990; Silva, 2001). The calcareous nannofossil assemblage from these beds indicates placement in the biozone CN12a of Okada & Bukry (1980), after Cachão (1990).

The Atlantic marine malacofauna of Vale de Freixo, as well as all the marine Pliocene macrofossil assemblages of the Mondego basin, correlate to the Pliocene MPMU1 (Mediterranean Pliocene Molluscan Unit 1) as defined by Monegatti & Raffi (2001) for the Mediterranean (Silva, 2001).

During the very end of the Zanclean and the beginning of the Piacenzian the Caldas da Rainha - Marinha Grande - Pombal region corresponded, generally speaking, to a shallow sea of warm waters, significantly warmer than today at that latitude, and

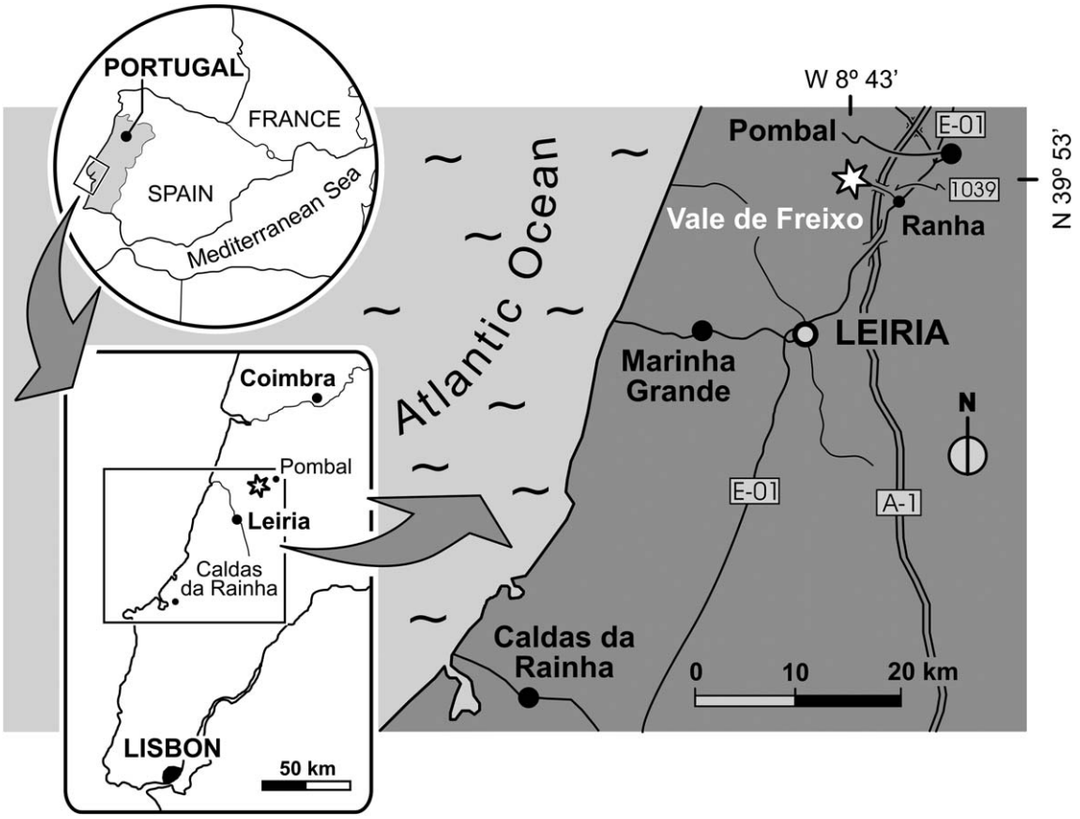

Figure 2. Geographic location of the Vale de Freixo outcrop. Central-West Portugal.

normal marine salinity, somehow protected from the direct influence of the open Atlantic ocean (Nolf & Silva, 1997; Silva et al., 2000; Silva, 2001).

For further details, general stratigraphical setting of the Mondego basin, graphic columnar section of Vale de Freixo, and additional palaeomalacological references see Gili et al. (1995), Silva et al. (2000), Dell'Angelo & Silva (2003).

SYSTEMATIC PALAEONTOLOGY

Subclass Opisthobranchia Milne-Edwards, 1848

Order Notaspidea P. Fischer, 1883

Superfamily Umbraculoidea Dall, 1889

Family Umbraculidae Dall, 1889

Genus *Spiricella* Rang & Des Moulins, 1828

Spiricella unguiculus Rang & Des Moulins, 1828

Figure 3

1928 *Spiricella unguiculus* Rang, 1828 - Rang & Des Moulins, p. 227, pl. 1, figs. 1–5.
1932 *Spiricella unguiculus* Rang, 1827 - Peyrot, p. 297, pl. 18, figs. 38–39, 42 (holotype).
1984 *Spiricella unguiculus* Rang, 1827 - Janssen, p. 386, pl. 19, fig. 19a–d.
1984 *Spiricella unguiculus* Rang, 1827 - Hoeksema & Janssen, p. 7, figs. 1–8.
1987 *Spiricella unguiculus* Rang, 1827 - Carozza & Rocchini, p. 63, fig. 1a–c.
1987 *Spiricella unguiculus* Rang, 1827 - Dekker, p. 225, fig. 1.
1994 *Spiricella unguiculus* Rang, 1827 - Geuze & Hoeksema, p. 225, fig. 1–3.
2000 *Spiricella unguiculus* Rang and Des Moulins, 1828 - Valdés & Lozouet, p. 459, pl. 2, figs. 7–10.
2001 *Spiricella unguiculus* Rang, 1828 - Lozouet, Lesport & Renard, p. 84, figs. 19d–e.
2001 *Spiricella unguiculus* Rang, 1827 - Silva, p. 590, fig. 3.201.

Material: One specimen (N° VFX.03.381, Carlos Marques da Silva coll., Geology Department, Sciences Faculty of the University of Lisbon), relatively well-preserved, from bed 3 of the Vale de Freixo outcrop, Pombal region, central-west Portugal. Pliocene, uppermost Zanclean to lower Piacenzian; calcareous nannofossils biozone CN12a of Okada & Bukry (1980); Mediterranean Pliocene Molluscan Unit 1 of Monegatti & Raffi (2001).

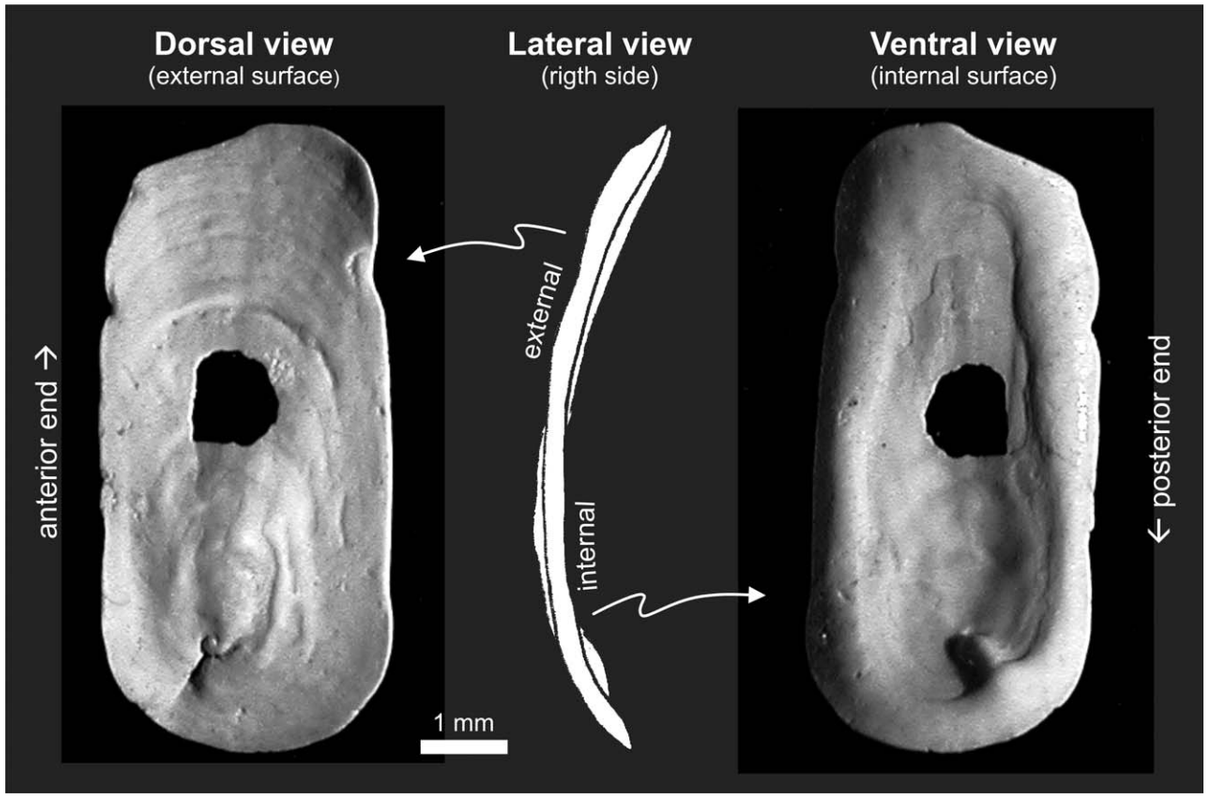

Figure 3. *Spiricella unguiculus* Rang & Des Moulins, 1828. Specimen VFX.03.381. Length: 7,3 mm. Vale de Freixo, Mondego Basin, Portugal. Pliocene.

Description: Shell small, 7.3 mm long, 3.4 mm width, thin, fragile, unguiform, subrectangular, antero-posteriorly elongate, with parallel sides and rounded extremities, convex profile on the dorsal side. Apex eccentric, placed approximately one sixth of the total length from the posterior edge and slightly to the left. A narrow rectilinear sulcus runs obliquely from the apex to the edge of the posterior border. Protoconch paucispiral, naticiform, sinistrally coiled, arranged in the horizontal plane, consisting of 1.5 smooth whorls, diameter 333 μm, with a medium-sized nucleus, diameter 88 μm. The protoconch is partially embedded within the surface of the shell. Transition to teleoconch sharply delimited. Sculpture of the teleoconch absent, except for concentric growth lines, more strongly developed on the anterior part of the dorsum, giving it a rugose appearance. The growth lines are much finer and sometimes subobsolete on the anterior part. Edge sharp. Ventrum smooth and shiny, with a rounded, thickened rim of variable width (about ¼ the shell width: 0.6–0.8 mm). A tenuous horseshoe-shaped continuous muscle scar is present on the posterior part on the inner edge of the rim, with the open end facing forward. The apex and sulcus are represented on the inner aspect by a rounded ridge.

Remarks: Traditionally, the monospecific genus *Spiricella* has been placed in the Umbraculidae (Janssen, 1984; Hoeksema & Janssen, 1984; Carrozza & Rocchini, 1987; Valdés & Lozouet, 2000). Willan (1984) described members of this family as having patelliform shells, with a more or less centrally placed blunt apex and the protoconch arranged in a vertical plane. As previously pointed out by Valdés & Lozouet (2000), the shell shape of *S. unguiculus* is quite different, flattened, elongated, with the apex not prominent and the protoconch arranged in a horizontal plane. This and other differences in the shell ontogeny led Valdés & Lozouet (2000) to consider *Spiricella* to belong to a separate superfamily from Umbraculoidea, but postponed its definitive assignment until soft parts become available to study.

The single Pliocene specimen available from the Portuguese Vale de Freixo outcrop is very similar to those described and figured by other authors (Janssen, 1984; Hoeksema & Janssen, 1984; Carrozza & Roc-

chini, 1987; Valdés & Lozouet, 2000) and agrees with the original description of the species and the holotype (Rang & Des Moulins, 1828; Peyrot, 1932). The protoconch is almost identical in form and dimension to that described and figured by Valdés & Lozouet (2000: pl. 2, fig. 7). Unfortunately, in the Portuguese Pliocene specimen, the protoconch is somewhat worn and, therefore, does not show the distinctive narrow ribbon at its border with the teleoconch described by these authors.

Almost nothing is known of the ecology of this species. In the Pliocene of Vale de Freixo it occurs in fine sandy sediments, in association with a fossil assemblage indicating a subtropical normal salinity marine infralittoral habitat, with a fine sandy substrate (Silva, 2001). The North Sea basin Miocene specimen belongs to an assemblage indicative of an open marine environment of rather shallow water in a subtropical to temperate-subtropical climate (Hoeksema & Janssen, 1984). The Recent Italian specimen was collected from dredgings on a muddy bottom at a depth of about 30 m (Carrozza & Rocchini, 1987) and the specimen from the island of Giannutri, Djerba, Tunisia, at a depth of about 54 m (Angioy & Nicolay, 1993). Both the single specimen collected from the Recent southern Portuguese coast and that found in Serini, Mauritania, were found in fine shell grit taken from a beach also suggesting a shallow marine habitat (Hoeksema & Janssen, 1984; Geuze & Hoeksema, 1994).

BIOGEOGRAPHY OF *SPIRICELLA* AND CLIMATIC CHANGE

Today, the thermophilic gastropod *S. unguiculus* occurs in the Northern Hemisphere on the Eastern Atlantic coast, from Southern Portugal to northernmost Mauritania, and in the Mediterranean (Figure 1). Its distribution basically encompasses the Mediterranean-Moroccan province and the northernmost part of the Mauritano-Senegalese Province (as defined in Raffi, Stanley & Marasti, 1985) or the northernmost part of the northern alternance zone of tropical West Africa (as defined in Le Loeuff and Von Cosel, 1998).

The most northerly records of *Spiricella* are those of the Lower Miocene of the North Sea basin. Janssen (1984) reported the occurrence of the species from the Aalten Member, Miste Bed of Winterswijk-Miste, which is equivalent to the North Sea Hemmorian stage (= Burdigalian, see Kowalewski et al., 2002).

The Early-Middle Miocene was a time of global warming (Zachos et al. 2001; Kowalewski et al., 2002) and in the Eastern Atlantic, according to Brébion (1974), Lozouet & Gourges (1995) and Le Loeuff & Von Cosel (1998) a Euro-West African tropical molluscan province stretched from the West coast of France southwards to Angola. This Euro-West African province corresponds to the Eastern Atlantic expression of the broader Early Miocene Proto-Mediterranean-Atlantic Region of Harzhauser et al. (2002), which according to the palaeogeography of Rögl (1998), would have roughly included the entire area of the Modern Mediterranean and part of the Eastern Atlantic coast, from the coast of Western France southwards. Earlier, during Oligocene times, again according to Harzhauser et al. (2002), a tropical Mediterranean-Iranian Province, part of the broader Western Tethys Region, covered the area of the modern Mediterranean Sea and probably included the European Atlantic coast up to the Bay of Biscay. Therefore, the presence of the subtropical *Spiricella* in the Oligocene of the Aquitaine basin, approximately on the northern limit of this tropical province is not controversial.

Lower Miocene North Sea basin molluscan assemblages show a strong thermophilic character, well established by the presence of taxa such as Conidae, Ficidae, Olividae, Terebridae, Architectonicidae, and Xenophoridae, amongst others (see, e.g., Sorgenfrei, 1958; Anderson, 1964; Rasmussen, 1968; Janssen, 1984). The low diversity of gastropods such as Conidae, with a maximum of three species, and Terebridae, with a maximum of five species, together with the absence of other typically megathermic gastropod taxa such as *Strombus*, strongly suggests that tropical conditions were not present in the North Sea region during Early to Middle Miocene times. Indeed, during Early-Middle Miocene, the North Sea region was part of a separate northern biogeographical unit from the Euro-West African tropical province: the Boreal province (of Kowalewski et al., 2002) or the Proto-Eastern Atlantic Boreal Region (of Harzhauser et al., 2002), roughly equivalent to the Recent Boreal-Celtic province of Raffi, Stanley & Marasti (1985). According to Hoeksema & Janssen (1984) and Zagwijn & Hager (1987), the southern coast of the Miocene North Sea was characterized by warm temperate or even subtropical climate as indicated, e.g., by the presence of thermophilic molluscs and extensive peats. Again, the presence of *Spiricella* in these deposits agrees with the general thermophilic character of the fossil mollusc assemblages.

Taking the presence of the megathermic gastropod *Strombus* as a proxy of tropical conditions, during the Miocene the northern limit of the Euro-West African tropical province would be located somewhere north of the Aquitaine basin, possibly even farther north than the Loire basin. This assumption is based in the reported presence of several species of *Strombus* in the Aquitaine basin (Peyrot, 1932; Lozouet et al., 2001) and the possible occurrence of a single species of the genus in the Loire basin (Glibert, 1949). Harzhauser et al. (2002) assumed a similar northern extension (up to

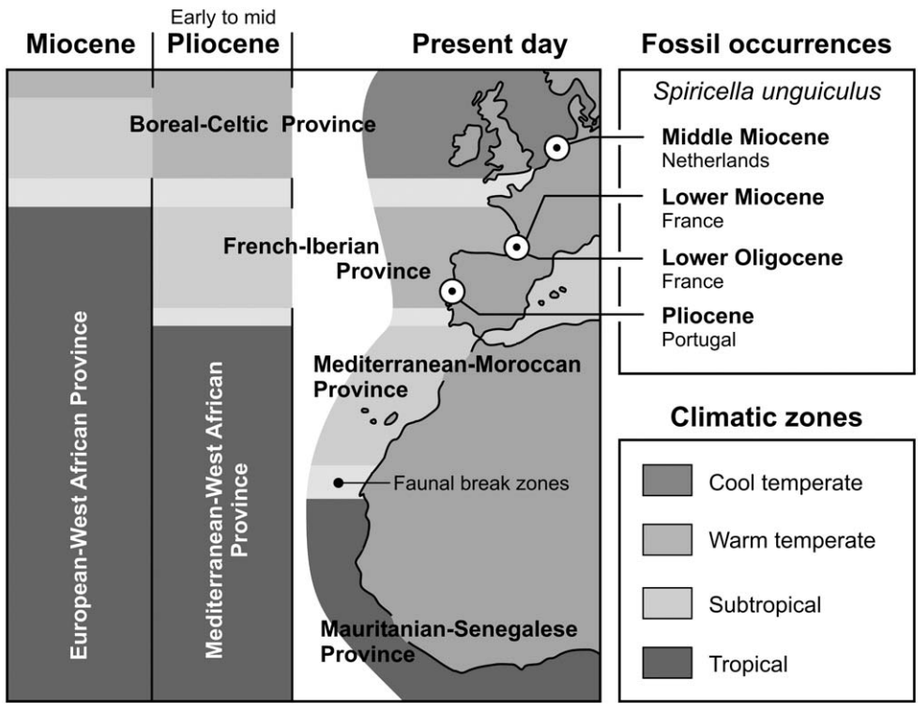

Figure 4. Fossil occurrences of *Spiricella unguiculus* and Neogene molluscan biogeographic provinces of the Atlanto-Mediterranean region. Present day bioprovinces after Raffi, Stanley & Marasti (1985).

the Bay of Biscay) for their Early Miocene Proto-Mediterranean-Atlantic Region.

Hence, since Early-Middle Miocene, north-western France and the Channel region might have represented the southern boundary of the Boreal-Celtic province. Back then, from a climatic point of view, this biogeographic province was characterized by warm temperate to subtropical waters, at least in its southern area, and bordered, to the south-west, with the Miocene Euro-West African tropical province (Figure 4).

In the Pliocene *Spiricella* is recorded only from the Mondego basin, central-west Portugal. The Pliocene malacofauna of the Mondego basin shows strong thermophilic affinity, again with the presence of taxa such as Conidae and Terebridae, but with poor diversity and lacking *Strombus* (Silva, 2001). Once more the presence of *Spiricella* in these deposits agrees with the subtropical character of the fauna.

Cenozoic climate in the Atlanto-Mediterranean region, and indeed in the Northern Hemisphere, is marked by a relatively steady long term Oligocene to mid Pliocene cooling (Stanley & Ruddiman, 1995). After the Middle Miocene climatic optimum (Zachos et al., 2001), this cooling trend probably led to a step-by-step breakdown of the original European-West African tropical province, as its northern limit contracted southwards, and to the individualization of the present day Atlanto-Mediterranean warm temperate and subtropical bioprovinces.

The Mondego assemblage shows that, during mid Pliocene times, the Atlantic mollusk faunas of West Iberia, at this latitude, were already part of a different subtropical biogeographical unit (Silva, 2001), homologous to the Recent French-Iberian province of Raffi, Stanley & Marasti (1985). The Pliocene Western Iberian region was, as nowadays, characterized by cooler SSTs (Sea Surface Temperatures) than the more southern Mediterranean and West African areas (Silva, 2001). In the Early to mid Pliocene (corresponding to the faunistic Mediterranean Pliocene Molluscan Unit 1) everywhere in the Mediterranean tropical conditions prevailed (Monegatti & Raffi, 2001). Therefore, at least since the late Early Pliocene, South-Western Atlantic Iberia represented the northern boundary of what was left of the broad Miocene Euro-West African tropical province (Monegatti & Raffi, 2001; Silva 2001), by then merely encompassing the Atlantic Southern Iberian and West African coasts and the Mediterranean: the Mediterranean-West African Pliocene tropical province.

According to Monegatti & Raffi (2001), the mid Pliocene cooling event, registered around 3.0 Ma, has had a dramatic impact on Mediterranean Pliocene thermophilic taxa. This cooling event was responsible

for yet another geographic distribution contraction southwards and, this time, for the consequent individualization of the Mediterranean-Moroccan molluscan bioprovince and the narrowing of the Eastern Atlantic tropical area, generally speaking, to its present day limits (Figure 4). It seems that after this cooling event, *Spiricella unguiculus* disappeared from West Iberian coasts, and became restricted to the warmer southern province: the present day Mediterranean-Moroccan subtropical province.

CONCLUSION

The discovery of *Spiricella unguiculus* in the Pliocene of the Mondego Basin fills the gap up until now existing in the Oligocene to Recent geological distribution of the species.

Although the overall recorded occurrences of the species are rare, the Oligocene to Recent geographical distribution of *S. unguiculus* appears to have undergone a sharp southward contraction. This contraction is in accordance with the general biogeographic trend observed with other Atlanto-Mediterranean mollusk taxa (e.g., Silva et al., 2000; Monegatti & Raffi, 2001; La Perna et al. 2003), and supports the hypothesis of a Neogene Northern Atlantic cooling scenario (e.g., Stanley & Ruddiman, 1995; Monegatti & Raffi, 2001; Zachos et al. 2001).

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