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Pliocene Atlanto-Mediterranean biogeography of *Patella pellucida* (Gastropoda, Patellidae): Palaeoceanographic implications

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Abstract

Patella pellucida is a north-western Atlantic shallow water grazing gastropod typically living and feeding on laminarian algae. It is an Upper Cenozoic species, known from the Icelandic and Iberian Pliocene to Recent. Today the species is usually considered to be primarily a northern cooler water species, inhabiting the Atlantic coasts of Europe, but rarely found off the Atlantic NW African coast and westernmost Mediterranean. Its presence in the warm, subtropical to tropical, Pliocene Atlantic and Mediterranean Iberian waters is thus unexpected. *P. pellucida* lives on laminarian algae, which occur in cold or temperate nutrient-rich ocean waters. At higher sea surface temperatures laminarian algae become physiologically stressed and are found only where seasonal upwelling of cooler nutrient-rich waters occurs. Such oceanographic conditions exist today, e.g., off the western coast of Iberia. It is suggested that similar upwelling conditions were already in place in western Iberia and in the Alboran Sea during Pliocene times and that the distribution of *P. pellucida* was dictated by upwelling of nutrient-rich, cooler waters, and high productivity conditions rather than sea surface temperature alone. Thus, the unexpected Pliocene geographic distribution of *P. pellucida* demonstrates that high productivity associated with upwelling may, at least in the Atlanto-Mediterranean area, override the dominant biogeographic pattern resulting from the latitudinal sea surface temperature gradient of water masses.

Keywords: *Patella pellucida*; Laminarian algae; Pliocene; Iberia; North-eastern Atlantic; Western Mediterranean; Upwelling; Palaeoceanography

1. Introduction

Patella pellucida Linnaeus, 1758 = [*Helcion* (*Ansates*) *pellucidum*], the blue-rayed limpet, is a well-known and easily recognised NE Atlantic herbivorous grazing gastropod species nowadays commonly occurring in almost all Atlantic European coasts, typically living and feeding on laminarian algae.

Despite its abundance in present day European Atlantic coastal environments, it is seldom referred to in the palaeontological literature. The species is known in the fossil record from the European Pliocene (Zanclean) to Recent (Harmer, 1921; Knight et al., 1960; Gladenkov et al., 1980; Silva, 2001; Landau et al., 2003). Until recently, it had been recorded in the Pliocene only from the Tjörnes deposits of Iceland, *Serripes* zone (Gladenkov et al., 1980), dated as Middle Pliocene (see Leifsdóttir and Símonarson, 2002).

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Extensive sampling works on the Neogene of the Iberian Peninsula have yielded *P. pellucida* from the Lower–Middle Pliocene of the Atlantic Mondego basin, central-west Portugal, (Silva, 2001) and the Lower and Middle Pliocene (Guerra-Merchán et al., 2002) of the western Mediterranean, southern Spain, Estepona basin (Vera-Peláez et al., 1995; Landau et al., 2003).

In the Pleistocene it is recorded from the Atlantic coasts of the British Isles, in Selsey, Bridlington, Scotland and in Ireland (Harmer, 1921; Glibert, 1962), and from the "Ancient Quaternary" of the Atlantic coast of NW Morocco (Lecointre, 1952). It also occurs in the French Pleistocene, in the "Marnes du Bosc d'Aubigny" of Marchésieux (Normandy, Manche department) (A. Janssen, pers. comm., 2003). *P. pellucida* is also reported from the post-glacial deposits of Christiania fiord, Norway (Harmer, 1921).

Today *P. pellucida* is usually considered to be a northern cooler water species. It occurs in all European Atlantic coasts (Fig. 1), from northern Norway to Portugal and south-western Spain, including Iceland and the British Isles (Fretter and Graham, 1976; Graham, 1988). In the western Mediterranean it is very rare (Thorson, 1941; D'Angelo and Gargiullo, 1978) and is not recorded in several major taxonomic works (Bucquoy et al., 1882; Giannuzzi-Savelli et al., 1994). *P. pellucida* was recorded from the Canaries (Nordsieck and García-Talavera, 1979) and northwest Africa, at least as far as Essaouira, Morocco (Harmer, 1921; Lecointre, 1952). It is absent off the east coast of England surrounding the Wash (Tyler-Walters, 2000), where laminarian algae are also absent (Birkett et al., 1998). *P. pellucida* is not present along the coasts of Belgium, Holland, the east coast of Denmark, and the Baltic Sea (Fretter and Graham, 1976; Poppe and Goto, 1991), nor is it present in the Azores (S. Ávila, pers. comm., 2003) or Madeira (D. Abreu, pers. comm., 2003).

The typical association of *P. pellucida* with laminarian algae stresses its cooler water character. Its presence in the warm, subtropical to tropical, Early–Middle Pliocene Atlantic and Mediterranean Iberian waters is thus unexpected, its palaeoceanographic implications being discussed herein.

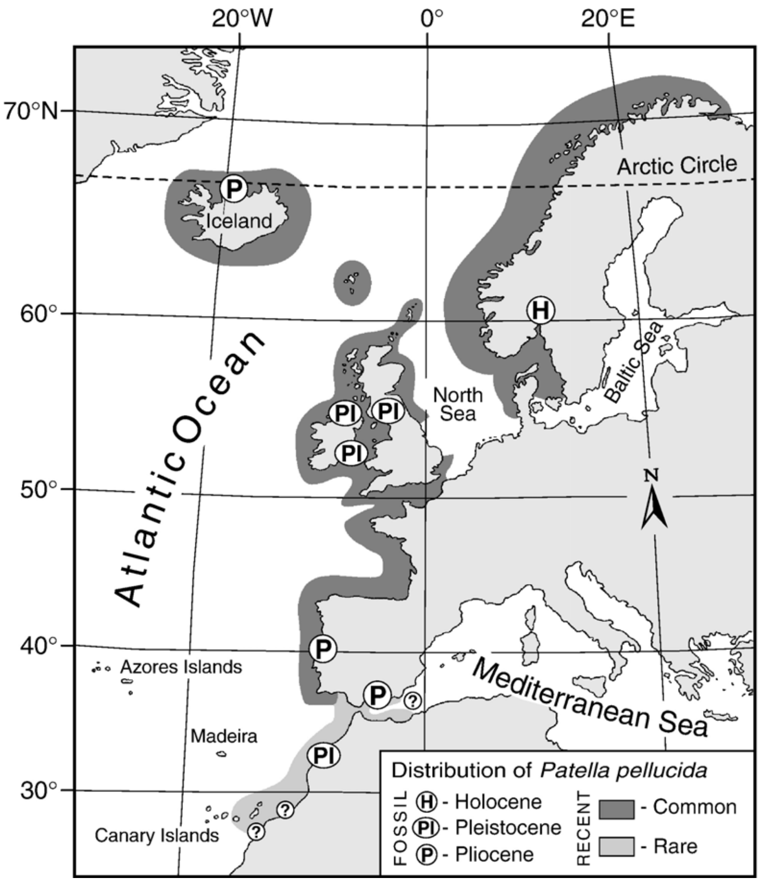

Fig. 1. Geographic distribution of *Patella pellucida* Linnaeus, 1758 in the north-eastern Atlantic.

2. General geological and stratigraphical setting

2.1. Vale de Freixo, Mondego basin, W Portugal

Vale de Freixo is located in the Pombal region, central-west Portugal in the Mondego Cenozoic basin (Fig. 2). This locality is Pliocene, uppermost Zanclean to lower Piacenzian, in age. The calcareous nannofossils assemblage from its fossiliferous beds indicate placement in biozone CN12a of Okada and Bukry (1980), after Cachão (1990). For more details, general stratigraphical setting, graphic columnar section, and additional references see Gili et al. (1995), Nolf and Silva (1997), Silva et al. (2000), and La Perna et al. (2003).

The Atlantic marine malacofauna of Vale de Freixo, and of all the Pliocene sites of the Mondego basin, corresponds to the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) as defined by Monegatti and Raffi (2001) for the Mediterranean (Silva, 2001).

2.2. Padrón, Velerín and El Lobillo, Estepona basin, SW Spain

Padrón, Velerín and El Lobillo are located in the Malaga region, Southern Spain, in the Estepona basin (Fig. 2). Until recently the Estepona–Málaga Upper Neogene deposits were considered to represent a single sedimentary cycle of Lower Pliocene age by some authors (Aguirre, 1995) and Lower Pliocene to lower Middle Pliocene age by others (Sanz de Galdeano and Lopez Garrido, 1991).

Guerra-Merchán et al. (2002) suggested these deposits were comprised of three lithostratigraphic units, which in turn represent three transgressive cycles. The first (Lower Pliocene I unit) they assigned to the Mediterranean Pliocene MPL1 zone as defined by Cita (1975), which corresponds to lowermost Zanclean. The second (Lower Pliocene II unit) is lower Zanclean in age (MPL2 zone). No deposits corresponding to the upper part of the Zanclean (MPL3 and MPL4a) were found in the study area by Guerra-Merchán et al. (2002). The third (Middle Pliocene unit) was dated as lower Piacenzian (upper part of the MPL4b zone).

In the Estepona basin, specimens of *P. pellucida* where found in three localities, Rio del Padrón, dated as lower Zanclean, Lower Pliocene II unit; Velerín conglomerates, dated as lower Piacenzian, Middle Pliocene unit, and El Lobillo (also known as Finca). This Pliocene locality has not yet been formally assigned to any of the lithostratigraphic units so far defined (for further details see Landau et al., 2003).

The malacofauna of all these deposits fall within the unit MPMU1, as defined by Monegatti and Raffi (2001).

3. Material and methods

The fossil material examined and discussed in this study results from extensive field samplings performed over the last 20 years in the main Pliocene western and south-western Iberian sedimentary basins (Mondego: Gili et al., 1995; Silva et al., 2000; see Silva, 2001 for extensive references; Guadalquivir: Landau, 1984; Estepona: Landau et al., 2003, also see Landau et al., 2004 for extensive references) and consists of five well-preserved specimens and two partials from Vale de Freixo, Mondego basin, four well-preserved shells from Padrón, three well-preserved shells, from the Velerín conglomerates, and three well-preserved shells from El Lobillo, all from the Estepona basin.

The Recent material used for comparison was collected in Portugal, both on the western (Peniche region, Estremadura) and southern shores (Lagos region, Algarve).

For the identification, systematics and the present day geographic distribution of *P. pellucida* the following works have been used: Wenz (1938), Nordsieck (1968), Powell (1973), Nordsieck and García-Talavera (1979), Rolán (1983), and Graham (1988).

4. Results. The Iberian Pliocene specimens of *P. pellucida*

4.1. P. pellucida Linnaeus, 1758

The shells of the blue-rayed limpet exist in two forms: one found on the fronds and stipes of laminarian algae, the other in the holdfast under the stipe (Fig. 3.1–3.8). The former, referred herein as the "P morph", is usually known as "*P. p. pellucida*" or "pellucida morphotype", the latter as the "L morph", is known as "*P. p. laevis*" or "laevis morphotype" (see, e.g., Fretter and Graham, 1976; Graham, 1988; Tyler-Walters, 2000).

The Iberian Pliocene "P morph" shells are small to medium in size (Table 1), patelliform, antero-posteriorly elongated, fragile, translucent, without marginal fissura, apical orifice or internal septum. Protoconch not preserved. The aperture is elliptical, base slightly concave in profile. Apex consists of a small rounded eminence, somewhat narrower in the large specimen from Padrón (Estepona), placed mid-line, far towards the anterior margin, but not surpassing it. The surface is covered by numerous, fine, concentric growth lines and

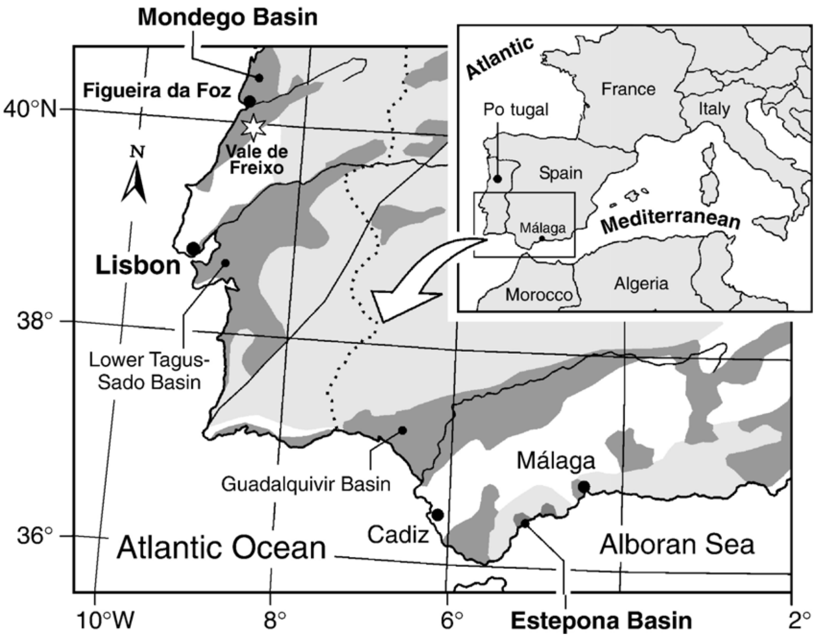

Fig. 2. Main Cenozoic basins of south-western Iberia and location of Mondego and Estepona Pliocene basins. Dark grey areas: Cenozoic basins; white areas: Mesozoic sediments; light grey areas: Palaeozoic sediments.

very fine radial striae almost restricted to the anterior and posterior margins, only visible under magnification; shell margin simple, sharp and internally smooth; inner aspect smooth and shiny; muscle scar, clearly marked in the specimen from Padrón, horse-shoe shaped, open at the anterior end.

Our specimens show well-preserved remnants of the typical original colour pattern, consisting of about 23 radial rows of minute elongated to rounded dark purple spots, originating at the apex and continuing to the edge. The width of the spots is variable, often alternating from row to row, but always narrower than the intervals between the rows.

The colour pattern preserved in our "P morph" Pliocene specimens from Portugal and Spain are similar to that seen in Recent specimens. There are some minor differences. The radial colour pattern seen in the modern shell consists of an interrupted line, whereas in the fossil specimens, from both Estepona and Vale de Freixo, the rays are made up of a series of elongated dots.

The "L morph" shells are medium-sized (Table 1), somewhat conico-truncated, antero-posteriorly elongated, fragile (although less so than "P morph" shells), without marginal fissura, apical orifice or internal septum. Protoconch not preserved. The aperture is elliptical, base slightly concave in profile. The dorsal side is rounded, rather truncated in profile. Apex mid-line, placed very anteriorly, almost overhanging the anterior edge. The shell is covered by numerous, fine growth lines; shell margin simple, sharp and internally smooth; inner aspect smooth and shiny; muscle scar horse-shoe shaped, open at the anterior end, but not clearly preserved. The upper part of the shell is smooth resembling a small specimen of a "P morph" shell placed on top of a truncated cone. The lower portion, below a strong growth line, ornamented by evenly spaced, numerous, fine radial ribs, of alternate strength.

5. Discussion

5.1. The west and south Iberian Pliocene malacofaunas

It has long been recognised that the Mediterranean and adjacent Atlantic Early–Middle Pliocene waters were significantly warmer than in the present, with mean sea surface temperatures (SST) 1 to 5 °C higher than today, and supported a molluscan fauna with a strong thermophilous character (e.g., Dowsett et al., 1996, 1999; Monegatti and Raffi, 2001; Silva, 2001). The presence of *P. pellucida*, considered to be a northern cooler water species in the warm, subtropical to tropical, Early–Middle Pliocene Atlantic and Mediterranean Iberian waters is thus unexpected.

The Iberian Pliocene malacofaunas from the Mondego and Estepona basins, as expected, show strong affinities with the typical Mediterranean ones found, e.g., in Italy. However, some remarkable differences are also evident.

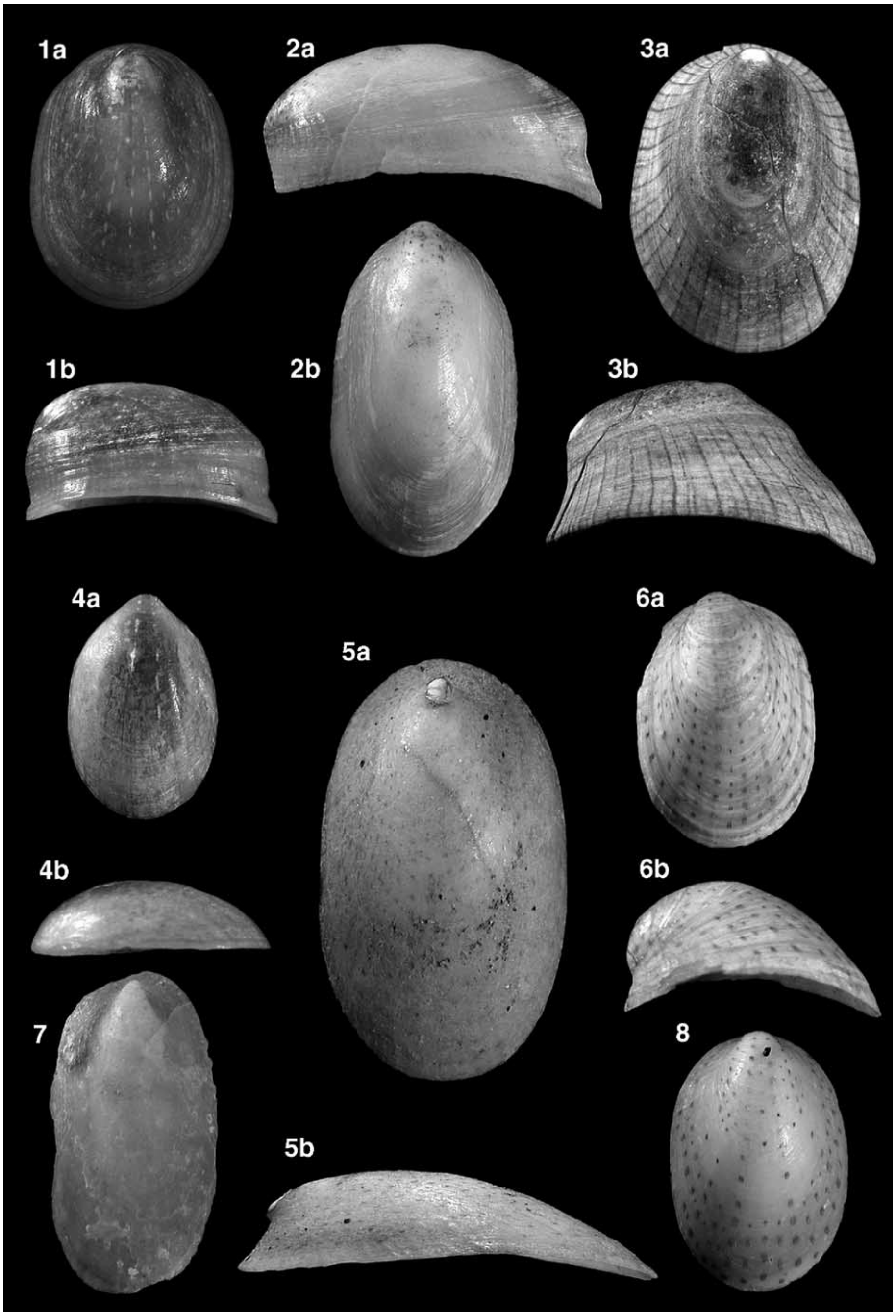

Fig. 3. *Patella pellucida* Linnaeus, 1758. (1) L morph shell, a — dorsal view, b — lateral view, Lagos, Algarve (S Portugal), Modern; (2) L morph shell, a — lateral view, b — dorsal view, Vale de Freixo, Mondego Basin, Pliocene; (3) L morph shell, a — dorsal view, b — lateral view, Vale de Freixo, Mondego Basin, Pliocene; (4) P morph shell, a — dorsal view, b — lateral view, Lagos, Algarve (S Portugal), Modern; (5) P morph shell, a — dorsal view, b — lateral view, Padrón, Estepona Basin; (6) P morph shell, a — dorsal view, b — lateral view, Vale de Freixo, Mondego Basin; (7) P morph shell, El Lobillo, Estepona Basin, Pliocene; (8) P morph shell, Vale de Freixo, Mondego Basin, Pliocene. Measurements of all specimens are given in Table 1.

In the Atlantic Pliocene of the Mondego basin the presence of gastropod taxa, such as *Cymbium* Röding, *Scaphella* Swainson, *Amalda* H. and A. Adams, and *Persicula* Schumacher must be explained (Silva, 2001). These are all thermophilous genera. They are present in the Atlantic Mondego basin, but they do not penetrate into the warmer Pliocene Mediterranean further than the Alboran Sea region (i.e., the Estepona basin).

Table 1
Measurements (mm) of representative specimens of *Patella pellucida* studied herein

Specimen	Fig.	Locality	Chronology	Shell type	H	L	W	L/W
CMS coll.	2.4	LAG	Modern	P	2.7	8.8	5.8	1.52
CMS coll.	–	LAG	Modern	P	3.5	11.8	7.4	1.59
CMS coll.								
VFX.03.014	2.6	VFX	L./M. Pliocene	P	5.1	10.0	6.9	1.44
BML coll.	–	VFX	L./M. Pliocene	P	4.1	9.8	6.8	1.44
BML coll.	2.8	VFX	L./M. Pliocene	P	3.6	12.4	7.7	1.61
BML coll.	2.7	ELB	L. Pliocene	P	3.2	14.4	7.4	1.95
BML coll.	2.5	PDR	L. Pliocene	P	5.5	17.9	10.5	1.70
CMS coll.	2.1	LAG	Modern	L	7.4	13.4	10.4	1.29
CMS coll.	–	LAG	Modern	L	7.3	14.7	11.5	1.28
CMS coll.	–	LAG	Modern	L	6.0	10.9	8.3	1.31
CMS coll.								
VFX.03.267	2.2	VFX	L./M. Pliocene	L	6.8	14.4	8.2	1.76
BML coll.	2.3	VFX	L./M. Pliocene	L	7.8	15.0	10.9	1.38

Specimens: CMS coll.—Carlos Marques da Silva collection; BML coll.—Bernard M. Landau collection.
Localities: VFX—Vale de Freixo; PDR—Padrón; VLR—Velerín; ELB—El Lobillo; LAG—Lagos.
Measurements: H—Height; L—Length; W—Width.

In the Estepona basin the malacofauna is even more remarkable, not only in the wealth of taxa of tropical affinity, common to other typical Lower Pliocene Mediterranean assemblages, but by a greater biodiversity, by the presence of thermophilous taxa which do not extend further into the Mediterranean, by the occurrence of taxa suggesting an Atlantic influence and the existence of a Miocene relict fauna (Landau and Marquet, 2000; Landau et al., 2003, 2004).

Although the molluscan assemblages of both these basins suggest significantly higher water temperatures during Pliocene times than nowadays, the Estepona waters, located in the western Mediterranean, were, as today, warmer than those of western Iberia. Nevertheless, the Mondego and Estepona assemblages share some traits not found elsewhere in the Pliocene Mediterranean basin. First, they share genera such as *Cymbium*, *Persicula*, and *Amalda*, second, they share taxa suggesting a northern Atlantic influence, e.g., *Scaphella*, and third, the unexpected presence of 'cooler water' taxa, such as *P. pellucida*. It is this last question we mean to address herein.

5.2. Laminarian algae, kelp forests and *P. pellucida*

Laminarian algae are large photophyllic brown seaweeds, also known as kelp, which dominate much of the shallow rocky sublittoral habitats of the world's cold to temperate-water mid-latitude coasts, approximately between 40° and 60° (Little and Kitching, 1996; Birkett et al., 1998; Steneck et al., 2002). The distribution of laminarian forests is basically constrained by light penetration at high latitudes and by nutrient availability, temperature, and other macroalgae at low latitudes. Warm sea water temperatures, higher than 20 °C, and low nutrient concentrations generally prevent kelp from developing in subtropical or tropical regions (Steneck et al., 2002).

Nowadays, laminarian beds occur in warmer waters, at lower latitudes, lower than 40°, only when ocean currents flowing toward the equator, or periodic upwelling, advect cooler, nutrient-rich water to the kelp (Steneck et al., 2002).

P. pellucida typically lives and feeds on laminarian algae, though it has also sporadically been reported from other algae (Vahl, 1971; Fretter and Graham, 1976; McGrath, 1992; Poppe and Goto, 1991; Tyler-Walters, 2000). In the British Isles, e.g., other than the kelp species themselves, *P. pellucida* is deemed to be highly typical of kelp beds, being among the keystone species of kelp biotopes (Birkett et al., 1998). Its modern distribution, therefore, follows that of its host laminarian algae. For example, although the Azores are at the same latitude as the western coast of Portugal, rich in laminarian beds, *P. pellucida* does not occur in the Azores (S. Ávila, pers. comm., 2003), where laminaria beds are practically absent, due to reduced nutrient availability and higher medium SSTs (Tempera and Cardigos, 2001). The only restricted occurrence of laminarian algae in the Azores, the Formigas Islets, is associated with the local upwelling of deeper, cooler, nutrient-rich waters (Tempera and Cardigos, 2001). Similarly, *P. pellucida* does not occur along the coasts of Belgium, Holland, and the east coast of Denmark, and in the Baltic Sea, where laminarian algae are rare or absent.

The presence, albeit not common, of *P. pellucida* along the present day West African coast of north-western Morocco (Lecointre, 1952) and the Canary Islands (Nordsieck and García-Talavera, 1979), in areas where shallow water kelps, namely the warm-temperate species *Phyllariopsis brevipes* (C. Agardh) Henry and South, *Laminaria ochroleuca* de la Pylaie, and the opportunist *Saccorhiza polyschides* (Lightfoot) Batters (Little and Kitching, 1996; Birkett et al., 1998), are found in association with upwelling currents, demonstrates that both *P. pellucida* and laminarian algae can live in warmer waters, provided nutrient availability is high.

5.3. *P. pellucida* in the European Pliocene: palaeoceanographic implications

Today, the Icelandic malacofauna is part of the north Atlantic Boreal–Celtic molluscan province (after Raffi et al., 1985) and kelp forests with *P. pellucida* are a common feature in the Icelandic shallow waters (Tyler-Walters, 2000; Steneck et al., 2002). Due to the extreme northern geographic location of Iceland, a similar biogeographic situation would be expected in the Pliocene. Therefore, the presence of *P. pellucida* in the Icelandic northern Atlantic Pliocene is not controversial.

The western Iberian coast today is subject to moderate seasonal upwelling (e.g., Cachão and Moita, 2000). Upwelling occurs in the spring and summer along the coasts of Portugal and western Galicia, and summer mean monthly SSTs do not exceed 20 °C. Laminarian beds, mainly with *S. polyschides*, but also with *Laminaria hyperborea* and *L. ochroleuca*, whenever the substrate is adequate, are a normal feature of the western Iberian margin, hence the frequent occurrence of *P. pellucida*.

The presence of the species in the Pliocene Mondego basin, with estimated summer mean maximum SSTs reaching 23.5 °C (Silva, 2001), suggests that in the Early to Middle Pliocene laminarian beds already existed and, therefore, that the Pliocene western Iberian subtropical coast was subject to seasonal upwelling of cooler, nutrient-rich deep waters, giving rise to high biological productivity. Cachão (1995) reached a similar conclusion based on the abundance of *Coccolithus pelagicus* (Wallich) Schiller in the Pliocene marine sediments of the Mondego basin. *C. pelagicus* is a coccolithophore that seems to consistently occupy a particular ecological niche related to moderate turbulence conditions combined with higher nutrient availability. Therefore Cachão and Moita (2000) propose that *C. pelagicus* can be used as a proxy for the location of productivity enhanced areas, namely upwelling induced ones.

Today in the Alboran Sea, unlike most of the Mediterranean, a similar oceanographic situation occurs with two systems of high biological productivity associated with the Western Anticyclonic Gyre (WAG) and the Almeria–Oran density front. In the northern extremity of the WAG an upwelling of cooler, nutrient-rich subsurface waters occurs, the North Alboran upwelling system (the high productivity cell of the Malaga Front of Colmenero-Hidalgo et al., 2004), which fertilises the sea surface levels along the Mediterranean coast of Andalusia, in the Estepona–Malaga–Almuñecar sector (Fig. 4) (Bárcena et al., 2001).

The present day occurrence of laminarian algae in the Mediterranean is scarce and very localised, most often found in the Alboran Sea, represented by *Laminaria rodriguezii* Bornet, *L. ochroleuca*, *P. brevipes*, *Ph. purpurascens* (C. Agardh) Henry et South, and *S. polyschides* (Birkett et al., 1998), hence explaining the possible occurrence, albeit very rare, of *P. pellucida* in this westernmost restricted area of the Mediterranean. Moreover, in a study on the biodiversity patterns of marine benthic fauna on the Atlantic coast of tropical Africa, Le Loeuff and Cosel (1998) found that on coasts under the influence of periodical upwelling of cooler, nutrient-rich waters the biodiversity was higher than in those where hydrological structure remains stable, stratified, and warmer SSTs prevail. Therefore, the occur-

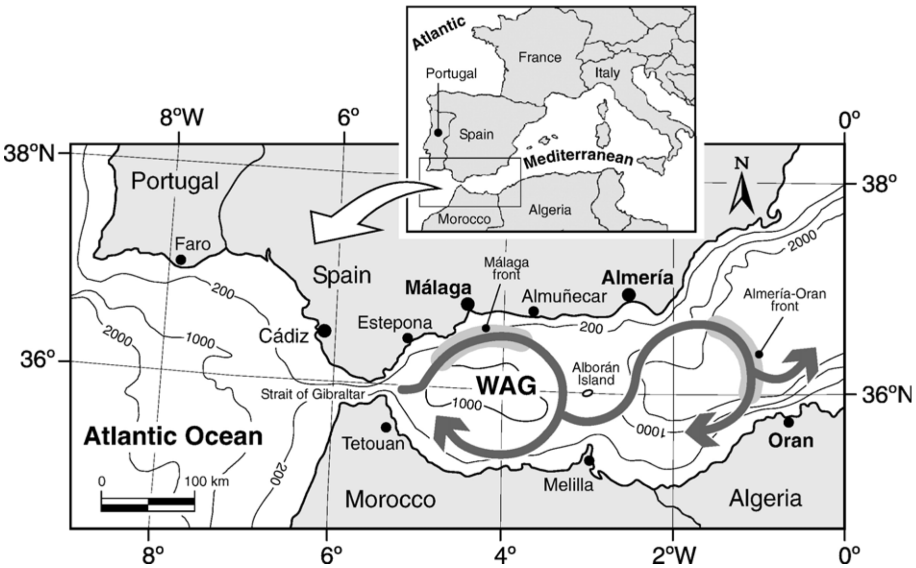

Fig. 4. Predominant oceanographic features of the Alboran Sea, the western Anticyclonic Gire (WAG) and the Almeria–Oran density front. Shaded areas represent today's high fertility zones. Adapted from Bárcena et al. (2001) and Colmenero-Hidalgo et al. (2004).

rence of *P. pellucida* in the Estepona deposits implies the presence of laminarian algae. This, together with the very high gastropod biodiversity, strongly suggest that similar hydrological conditions were present in the Pliocene Alboran Sea.

According to Monegatti and Raffi (2001), during Early–Middle Pliocene time (during MPMU1), the Mediterranean was a tropical sea, with mean maximum SSTs over 24–25 °C for at least five to six months every year. In the western end of the Mediterranean, in the Alboran Sea, although tropical conditions prevailed, slightly lower SSTs would be expected due to the occurrence of periodical upwelling, as observed today in some coastal areas of tropical West Africa (Le Loeuff and Cosel, 1998).

The fact that, seemingly, back then *P. pellucida* was more common in this westernmost area of the Mediterranean Sea than nowadays, since its fossils are found in several fossiliferous outcrops of the Estepona basin, suggests that during Pliocene times the North Alboran upwelling system could have been more active than today and the productivity rates higher.

6. Conclusion

Although sea surface temperature plays a major role in controlling the latitudinal distribution of shallow marine benthic molluscs (Monegatti and Raffi, 2001), other factors influence, sometimes dramatically, their biogeography.

The Mediterranean and adjacent Atlantic Early–Middle Pliocene waters were significantly warmer than they are in the present, tropical to subtropical, and supported a molluscan fauna with a strong thermophilous character (e.g., Monegatti and Raffi, 2001; Silva, 2001).

The grazing gastropod *P. pellucida* lives and feeds on laminarian algae. Kelp, although generally present only in cold to temperate mid-latitude waters, can thrive at lower latitudes and in warmer water conditions, warmer than 20 °C, provided there is a high enough supply of nutrients, normally conveyed by the upwelling of cooler nutrient-rich waters.

The occurrence of upwelling is a feature of the present day Atlantic west Iberian coast and upwelling also occurs today, albeit at a lesser scale, in the Alboran Sea. The presence of *P. pellucida* in the Pliocene of western Iberia and in the westernmost Mediterranean suggests that, back then, although SSTs where significantly warmer, periodical upwelling conditions where already active in these areas, enhancing nutrient availability, enabling the existence of laminarian algae and, e.g., in the tropical northern Alboran Sea, dramatically boosting molluscan biodiversity.

These findings are consistent with the conclusions of Suc et al. (1995), Fauquette et al. (1999), and Dowsett et al. (1996, 1999). According to these authors Early to Mid Pliocene times represent the last interval of earth history when climate was significantly warmer than today, yet many other boundary conditions, i.e., position of the continents, general oceanographic conditions, faunal and phytogeographic provinces, etc., were essentially unchanged.

In this context, the unexpected Pliocene geographic distribution of the "cooler water" gastropod *P. pellucida*, present in the subtropical to tropical waters of Atlantic and Mediterranean Iberia, demonstrates that high productivity associated with upwelling may, at least in specific areas, namely in the Atlanto-Mediterranean area, override the dominant biogeographic pattern generally resulting from the latitudinal SST gradient of water masses.

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References

Aguirre, J., 1995. Tafonomía y evolución sedimentaria del Plioceno marino en el litoral sur de España entre Cádiz y Almería. Ph.D. Thesis, University of Granada, Spain.

Bárcena, M.A., Cacho, I., Abrantes, F., Sierro, F.J., Grimalt, J.O., Flores, J.-A., 2001. Paleoproductivity variations related to climatic conditions in the Alboran Sea (western Mediterranean) during the last glacial–interglacial transition: the diatom record. Palaeogeography, Palaeoclimatology, Palaeoecology 167, 337–357.

Birkett, D.A., Maggs, C.A., Dring, M.J., Boaden, P.J.S., 1998. Infralittoral Reef Biotopes with Kelp Species (VII). An Overview of Dynamic and Sensitivity Characteristics for Conservation Management of Marine SACs. Scottish Association of Marine Science, UK Marine SACs Project.

Bucquoy, E., Dautzenberg, Ph., Dollfus, G., 1882. Les mollusques marins du Roussillon. Gastéropodes, vol. I. J.-B. Baillière & Fils, Paris.

Cachão, M., 1990. Posicionamento biostratigráfico da jazida Pliocénica de Carnide (Pombal). Gaia 2, 11–16.

Cachão, M., 1995. Utilização de nanofósseis calcários em biostratigrafia, paleoceanografia e paleoecologia. Aplicações ao Neogénico do Algarve (Portugal) e do Mediterrâneo Ocidental (ODP 653) e à problemática de *Coccolithus pelagicus*. Ph.D. Thesis, University of Lisbon, Portugal.

Cachão, M., Moita, M.T., 2000. *Cocolithus pelagicus*, a productivity proxy related to moderate fronts off western Iberia. Marine Micropaleontology 39, 131–155.

Cita, M.B., 1975. Studi sul Pliocene e sugli strati di passaggio dal Miocene al Pliocene. VIII Planktonic foraminiferal biozonation of the Mediterranean Pliocene deep sea record. A revision. Rivista Italiana di Paleontologia 81, 527–544.

Colmenero-Hidalgo, E., Flores, J.-A., Sierro, F.J., Bárcena, M.A., Löwemark, L., Schönfeld, J., Grimalt, J.O., 2004. Ocean surface water response to short-term climate changes revealed by coccolithophores from the Gulf of Cadiz (NE Atlantic) and Alboran Sea (W Mediterranean). Palaeogeography, Palaeoclimatology, Palaeoecology 205, 317–336.

D'Angelo, G., Gargiullo, S., 1978. Guida alle conchiglie mediterranee. Fabri Editori, Milan.

Dowsett, H.J., Barron, J.A., Poore, R.Z., 1996. Middle Pliocene sea surface temperatures: a global reconstruction. Marine Micropaleontology 27, 13–25.

Dowsett, H.J., Barron, J.A., Poore, R.Z., Thompson, R.S., Cronin, T.M., Ishman, S.E., Willard, D.A., 1999. Middle Pliocene paleoenvironmental reconstruction: PRISM2. U.S. Geological Survey Open File Report, 99–535. (Available at http://pubs.usgs.gov/openfile/of99-535 [cited 01/04/2004]).

Fauquette, S., Suc, J.-P., Guiot, J., Diniz, F., Feddi, N., Zhuo, Zh., Bessais, E., Drivaliari, A., 1999. Climate and biomes in the west Mediterranean area during the Pliocene. Palaeogeography, Palaeoclimatology, Palaeoecology 152, 15–36.

Fretter, V., Graham, A., 1976. The prosobranch molluscs of Britain and Denmark: Part 1—Pleurotomariacea, Fissurellacea and Patellacea. Journal of Molluscan Studies (suppl. 1), 1–37.

Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A., Ebreo, C., 1994. Atlante delle conchiglie marine del Mediterraneo. Archaeogastropoda, vol. 1. La Conchiglia, Rome.

Gili, C., Silva, C.M. da, Martinell, J., 1995. Pliocene nassariids (Mollusca: Neogastropoda) of central-west Portugal. Tertiary Research 15 (3), 95–110.

Gladenkov, Yu.B., Norton, P., Spaink, G., 1980. Verkhnii Kainozoi Islandii. Upper Cenozoic of Iceland (stratigraphy of Pliocene–Pleistocene and Paleontological assemblages). Trudy Akademii Nauk CCCP, Transactions of the Academy of Sciences of the USSR 345, 1–114 (in Russian, with English abstract).

Glibert, M., 1962. Les Archaeogastropoda fossiles du Cénozoïque étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. Mémoires de l'Institut Royal des Sciences Naturelles de Belgique, 2nd Series 68, 1–131.

Graham, A., 1988. Molluscs: prosobranch and pyramidellid gastropods: keys and notes for the identification of the species. E.J. Brill/Dr. W. Backhuys, Leiden.

Guerra-Merchán, A., Serrano, F., Ramallo, D., 2002. Evolución sedimentaria y paleogeográfica Pliocena del borde septentrional de la cuenca de Alborán en la área de Estepona (Provincia de Málaga Cordillera Bética). Pliocénica 2, 31–43.

Harmer, F.W., 1921. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's monograph of the Crag Mollusca, vol. II. Monographs of the Palaeontographical Society of London 2, 705–856.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L., Robertson, R., 1960. Systematic descriptions. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Geological Society of America: Part I. Mollusca, vol. 1. University of Kansas Press, Lawrence, Kansas, pp. I 169–I 331.

Landau, B.M., 1984. A discussion of the molluscan fauna of two Pliocene localities in the Province of Huelva (Spain), including descriptions of six new species. Tertiary Research 6 (4), 135–155.

Landau, B.M., Marquet, R., 2000. The genus *Cymbium* (Gastropoda, Volutidae) in the Iberian Neogene. Contributions to Tertiary and Quaternary Geology 37 (1–2), 23–34.

Landau, B.M., Marquet, R., Grigis, M., 2003. The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain: Part 1. Vetigastropoda. Palaeontos 3, 1–87.

Landau, B.M., Marquet, R., Grigis, M., 2004. The Early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain: Part 2. Orthogastropoda, Neotaenioglossa. Palaeontos 4, 1–108.

La Perna, R., Landau, B.M., Silva, C.M.da, 2003. The genus *Granulina* (Gastropoda, Marginellidae) from the Atlantic Iberian Neogene with description of a new Pliocene species from Portugal. Iberus 21 (1), 35–42.

Lecointre, G., 1952. Recherches sur le Néogène et le Quaternaire marins de la côte atlantique du Maroc: II. Paléontologie. Notes et Mémoires du Service Géologique du Maroc 99, 5–170.

Le Loeuff, P., Cosel, R.von., 1998. Biodiversity patterns of the marine benthic fauna on the Atlantic coast of tropical Africa in relation to hydroclimatic conditions and paleogeographic events. Acta Oecologica 19 (3), 309–321.

Leifsdóttir, Ó.E., Símonarson, L.A., 2002. The mesogastropod *Littorina littorea* (Linné, 1758) in Iceland: palaeobiogeography and migration. Cainozoic Research 1 (1–2), 3–12.

Linnaeus, C., 1758. *Systema Naturæ per Regna Tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. Editio Decima, Reformata. L. Salvii, Holmiæ.

Little, C., Kitching, J.A., 1996. The Biology of Rocky Shores. Oxford University Press, Oxford.

McGrath, D., 1992. Recruitment and growth of the blue-rayed limpet, *Helcion pellucidum* (L.), in south east Ireland. Journal of Molluscan Studies 58, 425–431.

Monegatti, P., Raffi, S., 2001. Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 171–193.

Nolf, D., Silva, C.M. da, 1997. Otolithes de poissons Pliocènes (Plaisancien) de Vale de Freixo. Portugal. Revue de Micropaléontologie 40 (3), 273–282.

Nordsieck, F., 1968. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia). Vom Eismeer bis Kapverden und Mittelmeer. Gustav Fischer Verlag, Stuttgart.

Nordsieck, F., García-Talavera, F., 1979. Moluscos Marinos de Canarias y Madera (Gastropoda). Aula de Cultura de Tenerife, Ediciones Selecciones Gráficas, Madrid.

Okada, H., Bukry, D., 1980. Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation. Marine Micropaleontology 5, 321–325.

Poppe, G.T., Goto, Y., 1991. European seashells. Polyplacophora, Caudofoveata, Solenogastra, Gastropoda, vol. I. Verlag Christa Hemmen, Wiesbaden.

Powell, A.W.B., 1973. The patellid limpets of the world (Patellidae). Indo-Pacific Mollusca 3 (15), 75–206.

Raffi, S., Stanley, S., Marasti, R., 1985. Biogeographic patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. Paleobiology 1 (4), 368–388.

Rolán, E., 1983. Moluscos de la Ria de Vigo. I Gasterópodos. Thalassas 1 (1), 1–383.

Sanz de Galdeano, C., Lopez Garrido, A.G., 1991. Tectonic evolution of the Málaga basin (Betic Cordillera). Regional implications. Geodinamica Acta 5 (3), 173–186.

Silva, C.M. da, 2001. Gastrópodes Pliocénicos marinhos de Portugal: sistemática, paleoecologia, paleobiologia, paleobiogeografia. Ph.D. Thesis, University of Lisbon, Portugal.

Silva, C.M. da, Landau, B.M., Martinell, J., 2000. The genus *Solariella* (Mollusca: Archaeogastropoda) from the Pliocene of Vale de Freixo, Portugal: palaeobiogeographic and palaeoclimatic implications. Contributions to Tertiary and Quaternary Geology 37 (3–4), 57–65.

Steneck, R., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29 (4), 436–459.

Suc, J.-P., Diniz, F., Leroy, S., Poumot, C., Bertini, A., Dupont, L., Clet, M., Bessais, E., Zhuo, Zh., Fauquette, S., Ferrier, J., 1995. Zanclean (~Brunssumian) to Early Piacenzian (~Early–Middle Reuverian) climate from 4° to 54° north latitude (west Africa, west Europe and west Mediterranean areas). Mededelingen Rijks Geologische Dienst 52, 43–56.

Tempera, F., Cardigos, F., 2001. As algas laminárias. Mundo Submerso 56, 30–31.

Thorson, G., 1941. Marine Gastropoda Prosobranchiata. Zoology of Iceland 4 (60), 1–150.

Tyler-Walters, H., 2000. *Helcion pellucidum*. Blue-Rayed Limpet. Marine Life Information Network: Biology and Sensitivity Key Information Sub-Programme On-Line. Marine Biological Association of the United Kingdom, Plymouth. Available at: http://www.marlin.ac.uk/species/Helpel.htm (cited 19/06/2003).

Vahl, O., 1971. Growth and density of *Patina pellucida* (L.) (Gastropoda: Prosobranchia) on *Laminaria hyperborea* (Gunnerus) from western Norway. Ophelia 9, 31–50.

Vera-Peláez, J.L., Lozano-Francisco, M.C., Muñiz-Solís, R., Gili, C., Martinell, J., Domènech, R., Palmqvist, P., Guerra-Merchán, A., 1995. Estudio preliminar de la malacofauna del Plioceno de Estepona (Málaga España). Iberus 13 (2), 93–117.

Wenz, W., 1938. Gastropoda, Teil I: Allgemeiner Teil und Prosobranchia. Handbuch der Paläozoologie. Band, vol. 6. Borntraeger, Berlin.