***Persististrombus coronatus* (Mollusca: Strombidae) in the lower Pliocene of Santa
Maria Island (Azores, NE Atlantic): palaeoecology, palaeoclimatology and
palaeobiogeographic implications**

Sérgio P. Ávila ^{1,2,*}, Carlos Melo ^{2,3}, Björn Berning ⁴, Ricardo Cordeiro ^{1,2}, Bernie
Landau ^{5,6} & Carlos Marques da Silva ⁶

¹ CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado,
Pólo dos Açores, Departamento de Biologia da Universidade dos Açores, Campus de Ponta Delgada,
Apartado 1422, 9501-801 Ponta Delgada, Açores, Portugal

² MPB-Marine PalaeoBiogeography group, University of the Azores, Ponta Delgada, Portugal

³ Departamento de Geociências, Universidade dos Açores, Ponta Delgada, Portugal

⁴ Oberösterreichisches Landesmuseum, Geowissenschaftliche Sammlungen, Welser Str. 20, 4060
Leonding, Austria

⁵ Naturalis Biodiversity Center, Leiden, The Netherlands

⁶ Departamento de Geologia, Instituto Dom Luiz, Faculdade de Ciências da Universidade de Lisboa,
Campo Grande, 1749-016, Lisboa, Portugal

*** Corresponding author, e-mail address: avila@uac.pt (Sérgio Ávila).**

ABSTRACT

The family Strombidae is one of the twenty-three families and subfamilies of gastropods associated with tropical environmental conditions, and therefore useful as a biogeographical and palaeoclimatic proxy. Today, the strombid genus *Persististrombus* is represented in the NE Atlantic by a single species restricted to the tropical Mauritanian-Senegalese Province. This work reports the occurrence of *Persististrombus coronatus* from the lower Pliocene of Santa Maria Island in the Azores Archipelago. Based on this occurrence, and on the Mio-Pliocene fossil record of the NE Atlantic oceanic islands, palaeoclimatological considerations are discussed, which allow, for the first time, to include the Azores and the other Macaronesian islands in a wider context of the NE Atlantic palaeobiogeographical molluscan provinces. Late Miocene to present day molluscan biogeographic units, ranging in latitude from 60°N down to 17°S, are here defined and the boundaries of the proposed climatic zones are outlined. We suggest that during the upper Miocene-lower Pliocene, the palaeoclimate at Santa Maria Island was drastically different from that seen at those latitudes today, with mean annual sea surface temperatures (SST's) about 3.7°C to 6.3°C higher than the present-day 20.6°C, and with mean monthly SST's ranging from 20°C to 28°C, with six months with mean SST's over 24°C, conditions typical of a tropical setting.

Keywords: Strombidae, *Persististrombus coronatus*, Macaronesian islands, palaeobiogeographical molluscan provinces, palaeoclimatology, NE Atlantic.

1. Introduction

The distribution of life on Earth is non-random in both space and time, and the description and formulation of hypotheses that explain the detected spatio-temporal patterns and processes of that distribution are the very foundations of the science of biogeography (Crother and Murray, 2011). In an attempt to classify the aforementioned patterns, marine biogeographical provinces were first defined in a qualitative manner by Johnston (1856) and Woodward (1856), both defining 25 different molluscan provinces worldwide, and later defined within a terrestrial framework by Neumayr (1883) as large areas characterized by a common fauna, and largely conditioned by geographical/physical boundaries (e.g. temperature, sea currents). Since then, the definition and concept of biogeographic units have changed, but the concept is still a cornerstone in palaeo- and neobiogeographic studies, as it allows establishing relationships between different regions (Briggs, 1995; Harzhauser et al., 2002).

Palaeobiogeographic units were first classified in a quantitative manner by Kauffmann (1973), based on percentages of endemism (25-50% for provinces). Valentine (1973) considered palaeoprovinces as the main descriptive biogeographical unit and was the first to use cluster analysis and other statistical methods in the definition and individualization of biogeographical provinces. As biogeographic provinces are dynamic units, their ranges (and ranks) vary with time and in extreme cases (e.g., due to mass-extinction events), some may even disappear (Cecca, 2002) or are newly formed. For example, in the North Atlantic Ocean, the once similar Late Cretaceous faunas in the western and eastern sides of the newly-opened Atlantic Ocean progressively diverged to such an extent, as time passed and the distance between both margins of the ocean steadily increased, that endemic, and thus different faunas, formed on both sides of the Atlantic, thus creating distinct biogeographic palaeoprovinces.

Global and more geographically restricted studies on the recent Atlantic marine biogeographic units have been produced by several authors (Forbes and Godwin-Austen, 1859; Ekman, 1953; Hedgpeth, 1957; Stephenson and Stephenson, 1972; Hayden et al., 1984; Briggs, 1995; Petuch, 2004; Cook and Auster, 2007; Spalding et al., 2007; Waters et al., 2010; Briggs and Bowen, 2012; Belanger et al., 2012), whereas for periods as recent as the Neogene and the Quaternary, similar studies for the NE Atlantic are comparatively scarce (Raffi and Monegatti, 1993; Monegatti and Raffi, 2001; Hall, 2002; Berning, 2006; Landau et al., 2007, 2011; Silva & Landau, 2007; Silva et al., 2010, 2011; Lozouet, 2014).

In the marine realm, Hall (1964) demonstrated that temperature is an important feature in shaping biogeographical provincial boundaries. More so, when latitudinal boundaries and variations are

involved. Raffi et al. (1985) improved earlier studies and concluded that for bivalve molluscs, the key factor was not the minimum water temperature but the duration and values of summer temperatures necessary for reproduction. Petuch (2004) linked marine biogeographical units with temperature, and defined “eutropical provinces” as tropical regions where sea surface temperatures (SST’s) never fall below 20°C, whereas “paratropical provinces” were defined as subtropical or warm-temperate seas where SST’s are below 20°C in the winter, but never dropping below 10°C. In the eastern Atlantic, the present-day Mediterranean-Moroccan Province (from southern Portugal to Mauritania, West Africa, including the Mediterranean Sea) is an example of a paratropical province, while the Mauritanian–Senegalese Province is an example of a eutropical province.

A number of molluscan genera and families are associated to all tropical areas worldwide. Among these “provincial indicators” *sensu* Petuch (2013), the family Strombidae is one of the twenty-three families and subfamilies of gastropods associated to tropical environmental conditions and therefore, useful as a biogeographical and palaeoclimatic proxy.

Situated in the central Atlantic, the easternmost and oldest island of the Azores Archipelago, Santa Maria, yields numerous fossiliferous sedimentary deposits of lower Pliocene to Pleistocene age. Zbyszewski and Ferreira (1962), based on their own sampling and on previous information from the works of Bronn (1860), Hartung (1860), Reiss (1862), Mayer (1864), Cotter (1888-1892), and Ferreira (1952, 1955), reported 188 specific taxa (179 invertebrate and 9 vertebrate species). The lower Pliocene Brachiopoda (Kroh et al., 2008), Echinodermata (Madeira et al., 2011), Chordata (Cetacea: Estevens & Ávila, 2007; sharks: Ávila et al., 2012), and Ostracoda (Meireles et al., 2012) as well as some of the Mollusca (Heteropoda and Pteropoda: Janssen et al., 2008) have been recently revised, whereas other invertebrate groups such as the Bryozoa, the Cnidaria (Anthozoa) and most of the Mollusca are in need of revision.

Molluscs are by far the best represented group in the Santa Maria geological record. Ávila et al. (2015b) made a preliminary revision of the mollusc checklist of Zbyszewski and Ferreira (1962) and accepted 99 species of Mio-Pliocene fossils as valid, with over 40 other specific taxa waiting to be added to the list after appropriate identification and description. Whereas none of the previous authors has ever reported any Strombidae, fieldwork at Santa Maria Island in the Azores Archipelago yielded specimens of *Persististrombus* from several lower Pliocene beds (Fig. 1).

This study reports and describes *Persististrombus coronatus* (Defrance, 1827) for the first time from the Pliocene of Santa Maria Island (Azores Archipelago), and discusses the palaeoecology and palaeoclimatic implications, palaeobiogeography and ecostratigraphical consequences of this occurrence for the understanding of the evolution of the biogeographical provinces defined for the eastern Atlantic from the late Miocene-early Pliocene to the present.

2. Geological setting

2.1. Azores Archipelago

The Azores Archipelago is located in the NE Atlantic Ocean and comprises nine volcanic oceanic islands younger than ~6 Ma (Ramalho et al., 2014). The islands and their submarine volcanic edifices lay on top of the Azores Plateau (Needham and Francheteau, 1974), an area of seafloor with a complex tectonic setting and an average depth of 2,000 m, near the triple junction between the Eurasian, Nubian and North American plates (Luis et al., 1994; Fig. 1). Santa Maria and Corvo are the only two islands of the archipelago whose volcanic activity is considered ceased (e.g. França et al., 2003; Ávila et al., 2012), but only Santa Maria holds outcrops of marine fossiliferous sequences (Zbyszewski and Ferreira, 1962; Serralheiro, 2003; Ávila et al., 2002, 2009, 2012, 2015c; Janssen et al., 2008; Kroh et al., 2008; Winkelmann, 2010; Madeira et al., 2011; Meireles et al., 2012, 2013; Rebelo et al., 2014).

2.2. Santa Maria Island

Santa Maria Island emerged during the Messinian (~6 Ma; Ramalho et al., 2014). The first subaerial volcanic edifices formed two islands whose remnants can be seen in the northwest (Cabrestantes Formation) and in the southwest of the island (Porto Formation). These volcanic products were capped by a subaerial shield volcano (Anjos Complex) that formed during the late Messinian. The island experienced a subsidence rate estimated by Ramalho et al. (2014) at around 100 m/Ma during the late late Miocene until the early late Pliocene, from 5.5 to 3.5 Ma. After the extrusion of the lavas that formed the Anjos Complex, a period of volcanic quiescence in the late Miocene-early Pliocene followed during which the first island of Santa Maria was probably completely eroded and submerged, producing heterogeneous volcanoclastic deposits, with synchronous low-volume submarine lava effusions on the eastern side of the island. A large volume of scattered, very fossiliferous submarine sediments (included

in the Touril Complex) deposited at shallow depths on top of the seamount during this period (Ávila et al., 2012), reaching a total thickness of 130 m. Since the late Pliocene (3.5 Ma to present) the subsidence trend reversed to an uplift trend for reasons still unknown. After a large period of deposition, these 130 m-thick sediments were entombed by submarine lavas (and thus preserved) during a subsequent intensification of the volcanic activity, which gradually shifted from submarine to subaerial. Lava deltas formed along coeval coastlines and an elongated NNW-SSE-trending edifice (Facho-Pico Alto Complex) emerged during the early Pliocene. The last period of volcanism occurred during the late Pliocene, at about 3.2-2.9 Ma, producing a set of monogenetic cinder cones (Feteiras Formation). After that, continuing uplift at an estimated rate of about 60 m/Ma (Ramalho et al., 2014) and erosion were the main factors affecting the volcanic edifice from the early Pleistocene to the present.

Many of the sediments in outcrops such as Pedreira do Campo, Figueiral, Malbusca, Pedra-que-pica and Ponta do Castelo, were deposited at depths around 40-60 m (Cachão et al., 2003; Meireles et al., 2013; Ávila et al., 2015b) or even deeper (Cré; Jansen et al., 2008). In the present-day, these outcrops are exposed at different altitudes, ranging from the intertidal (e.g., Pedra-que-pica; Ávila et al. 2015b) to 95 m above sea-level (Figueiral; Ávila et al., 2015c) due to the uplift of the island (Ramalho et al., 2014).

3. Materials and methods

During eleven international workshops “Palaeontology in Atlantic Islands” held yearly at Santa Maria Island, twenty exposures of Mio-Pliocene sediments scattered around the shores of the island were surveyed for the presence of fossil molluscs (Ávila et al., 2015c). Five of these outcrops (Ponta Negra, Ponta do Cedro, Pedra-que-pica, Baía de Nossa Senhora (Malbusca), and Figueiral), all lower Pliocene in age (Fig. 1), yielded both permineralized shells and moulds of *Persististrombus coronatus*, which were photographed and measured as described by Freiheit and Geary (2009) (Fig. 2).

In compliance with the legislation of the Regional Government of the Azores, all fossil specimens collected during this study were deposited in the Fossil Collection at the Department of Biology of the University of the Azores (DBUA-F).

DBUA-F, fossil collection of the Department of Biology of the University of the Azores.

CIADP, Centro de Interpretação Ambiental Dalberto Pombo, Vila do Porto, Santa Maria Island.

LAQ-F, fossil collection of the Liceu Antero de Quental, Ponta Delgada, São Miguel Island.

4. Results

Systematics

Phylum MOLLUSCA Linnaeus, 1758

Class GASTROPODA Cuvier, 1795

Order LITTORINIMORPHA Golikov & Starobogatov, 1975

Family STROMBIDAE Rafinesque, 1815

Genus *Persististrombus* Kronenberg & Lee, 2007

Persististrombus coronatus (Defrance, 1827)

(Fig. 2A-H)

Type material

Lectotype: specimen illustrated in Walch (1768, pl. 38, figs 1–2) (Harzhauser and Kronenberg, 2008).

Type locality

Siena, Italy, lower Pliocene? (Defrance, 1827: 124).

Material examined

(1) Ponta Negra outcrop: one permineralized shell imbedded in strongly cemented volcanoclastic calcarenite, viewed in cross-section, 67.5 mm in length, 52.5 mm in width. (2) Ponta do Cedro outcrop: one permineralized shell imbedded in strongly cemented sandstone, viewed in cross-section, 122.4 mm in length, 71.4 mm in width. (3) Pedra-que-pica outcrop: DBUA-F 318; DBUA-F 332-2, one internal mould 108.0 mm in length, 80.0 mm in width; DBUA-F 419, one internal mould. (4) Baía de Nossa Senhora outcrop: DBUA-F 849, four internal mould fragments; DBUA-F 936, one internal mould 75.0 in length, 52.2 mm in width; DBUA-F 938, one internal mould; DBUA-F 966-1, a permineralized shell fragment; DBUA-F 969, several internal mould fragments; DBUA-F 1006-1, seven internal mould fragments;

DBUA-F 1006-1-1, broken permineralized shell 88.0 mm in length, 65.1 mm in width; DBUA-F 1006-1-2, broken permineralized shell 80.1 mm in length, 50.3 mm in width; DBUA-F 1006-1-3, broken permineralized shell 100.0 mm in length, 65.0 mm in width; DBUA-F 1006-2, broken permineralized shell 110.0 mm in length, 54.03 mm in width; DBUA-F 1007-1-1, one permineralized shell fragment. (5) Figueiral outcrop: CIADP-F 32 (Fig 2a-c), one well-preserved permineralized shell, 119.1 mm in length, 107.2 mm in width. (6) Santa Maria Island (outcrop location unknown): LAQ-F21, one internal mould, 88.0 mm in length, 79.0 mm in width; LAQ-F62, one permineralized shell, 149.0 mm in length, 83.6 mm in width.

Description

Shell fusiform, very large, thick, heavy, solid, up to 149.0 mm in height. Protoconch and first teleoconch whorls eroded. Spire low, concave. Five teleoconch whorls preserved. Last whorl about 90% total height, greatly expanded, with fine axial lines and ornamented with a row of eight well-developed, elevated, solid spines at the shoulder of the conical spire (Fig. 2A-C, F, G), producing a stellate pattern in apical view (Fig. 2C). One or two further rows of smaller, rounded knobs are discernible on the last whorl, the first row in the mid-whorl, the second row at about the base (Fig. 2A-C, F). Aperture elongated, about 80% total height, large, about 1/6 total width. Outer lip expanded adapically and thickened by a strong labial varix, delimited adapically by a wide posterior anal canal, abapically by an anterior notch (the “stromboid notch”), and with a dorsally recurved siphonal anterior canal, which might be present in some specimens (Fig. 2F). Columella straight and smooth. Expanded columellar callus over the base.

Habitat and bathymetric range of Strombidae

Strombid gastropods are megathermal organisms. Recent strombid gastropods live in shallow depths in tropical and subtropical marine environments with clear waters and normal marine salinity (Abbott, 1960). The preferred habitats of these epifaunal omnivore-grazing gastropods (Robertson, 1961) are seagrass meadows, algal plains, coral rubble and sandy bottoms (McCarthy, 2007). The only extant species of the genus *Persististrombus* in the Atlantic, *P. latus* (Gmelin, 1791), has a well-known ecology in the Guinea Gulf (very low salinity, migration in large groups towards the mouth of rivers in the rainy season, buried in sand (detritivorous) and a habitat so close to the coast that they appear on the shore

when the tide is low). However, in the Cape Verde Islands (where no river mouths occur) specimens of *P. latus* occur by the thousands in infralittoral environments with full marine salinity conditions (CMS, personal observation). Strombids usually occur at depths of less than 30 m, although there are records of strombids occurring as deep as 150 m, such as the queen conch *Lobatus gigas* (Linnaeus, 1758).

Geological history and geographic distribution

Persististrombus coronatus is an extinct species (see below), the youngest reported occurrences come from the mid-Piacenzian (upper Pliocene) of the Mediterranean basin (Harzhauser and Kronenberg, 2008). The species disappeared from the Mediterranean Sea as consequence of the late Pliocene (mid-Piacenzian) cooling event that occurred circa 3.0 Ma (Raffi et al., 1985; Monegatti and Raffi, 2001), marking the upper boundary of the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) of Monegatti and Raffi (2001). The extant congeneric *P. latus* lives today at the Cape Verde Archipelago, at São Tomé and Príncipe Archipelago, and along the West African coast, from Rio d'Oro (Senegal) south to Angola (Guerreiro and Reiner, 2000; Rolán, 2005), where it inhabits flat sandy bottoms interspersed with stones covered by algae, in waters with mean winter SST's $\geq 20^{\circ}\text{C}$ (Silva et al., 2010). Its distribution is limited in the north by the cold Canary Current and in the south by the Benguela Current.

The fossil record of the genus *Persististrombus* extends from the Oligocene to the Holocene (Harzhauser and Kronenberg, 2013). *Persististrombus coronatus* is reported from the upper Miocene of the Mediterranean (Tortonian), from Italy and Turkey (Sacco, 1893; Stchepinsky, 1939, 1946), lower Pliocene of the Mediterranean (Fontannes, 1879; Palla, 1967; Malatesta, 1974; Pavia, 1975; Martinell, 1979; Martinell and Marquina, 1981; Cavallo and Repetto, 1992; Landau et al., 2004; Harzhauser and Kronenberg, 2008) and Pliocene (Zanclean and lower Piacenzian) of the Mediterranean (Chirli and Richard, 2008). In the Atlantic, it has been reported from the Miocene of Angola (?) (Brébion, 1983, no description nor illustration provided), upper Miocene of Portugal (Costa, 1867), Pliocene of Morocco (Lecointre, 1952), Miocene and lower Pliocene of the Canaries (Meco, 1977, 2007), and Pliocene (?) of Madeira (Mayer, 1864). Here we report it from the lower Pliocene of the Azores.

5. Discussion

5.1. Palaeoecology

As their present-day congeners, the large-shelled *Persististrombus coronatus* was probably an epifaunal herbivorous or detritivorous inhabitant of sandy and rocky shores covered by algae (Wells, 1998). As typical shallow-water species, the shells of these large strombids would be prone to be swept ashore post-mortem in large numbers by spring tides or storm events, as can be seen in the present times at Ponta Braço de Sirena (Sal Island, Cape Verde Archipelago; Zazo et al., 2010), or in the upper Pleistocene (MIS 5e) deposits at Matas Blancas (Fuerteventura Island, Canaries; Meco et al., 2002) and at La Marina, Alicante (East Spain) (Goy et al., 2006), where specimens of the congeneric *P. latus* occur in large numbers. However, at Santa Maria Island, no similar deposits were found, all *P. coronatus* specimens representing shells transported downslope into deeper marine environments, as at Pedra-que-pica or at Baía de Nossa Senhora outcrops (Fig. 2F-H) (Ávila et al., 2015b).

The common occurrence of Strombidae in the fossil record, apart from the fact that they usually have large and sturdy shells, may also be related with the usual discrete aggregation pattern of the animals, e.g., *Lobatus gigas*, which may reach hundreds or even thousands of specimens/ha (McCarthy, 2007). Juvenile individuals of extant *Persististrombus* usually feed during the night, and predation is decreased by diurnal burial in sandy bottoms, congregation in large numbers, and rapid growth (Savazzi, 1988, 1989; Ray and Stoner, 1995; Freiheit and Geary, 2009). However, the spines and knobs in the shell of adult *P. coronatus* probably prevented a complete burial (but see Orr and Berg (1987) who note that adult *L. gigas* can bury themselves completely). In addition, extant larger *Persististrombus* specimens are usually seen in rocky bottoms covered by algae, thus in habitats with almost no sediment available for burial (Pecharde, 1968, 1970). Palmer (1979) attributed a defensive function to the spines present on the shells of gastropods and several authors suggested a correlation between the intensity of durophagous predation and the selection for mollusc defensive shell structures such as spines and knobs (Vermeij, 1978, 1987; Herbert et al., 2004; Landau et al., 2011).

Strombidae are dioecious species with a planktotrophic larval development deduced from fossil and extant representatives, which consistently have three or more protoconch whorls with a small nucleus (Robertson, 1959; Wells, 1998; Landau et al., 2011; Harzhauser and Kronenberg, 2013), their pelagic larva lasting for two to three weeks in the water column, although in undernourished veligers, this time can be extended (Brownell, 1977). Species with similar larval lifetimes in the water column have been reported to reach isolated archipelagos by natural means, e.g., the intertidal non-planktotrophic trochid gastropod *Phorcus sauciatu*s (Koch, 1845), which has recently successfully reached and colonized Santa

Maria Island (Ávila et al., 2015a). Moreover, during the late Miocene and early Pliocene, the number and distribution of volcanic oceanic islands in the eastern Atlantic was different from what we witness today (Fig. 3D-F). Many of these older islands have now vanished (e.g., Gettysburg, Ormonde, Dacia, Ampere, Seine; cf. Table 1) as the result of erosion (e.g., Ramalho et al., 2013) and are presently represented by seamounts, but back then, in a triangle area defined by Santa Maria, the Iberian Peninsula and Porto Santo (Madeira Archipelago), the number of islands was higher than nowadays, and these islands provided additional shorelines and submarine shelves for the stepping-stone dispersal of shallow-water and intertidal marine species, thus diminishing the distance between continental (and insular) populations and isolated islands, such as Santa Maria, in the future Azores Archipelago.

5.2 Palaeoclimatology

As today, Mio-Pliocene SST's played a key role in the geographical distribution of shallow marine gastropods in the NE Atlantic. In fact, SST's are one of the most important limiting factors affecting both the reproductive phase of adult marine organisms (i.e., their spawning period) and the successful development of embryos to the veliger state (Raffi, 1986). Global climate was warmer than today during the late Miocene and also during most of the early Pliocene (Zanclean age, 5.33-3.6 Ma; Lysieck and Raymo, 2005). A cooling trend affected the end of the Zanclean after ca. 3.7 Ma and, coupled with a long-term steady weakening of the Atlantic meridional overturning circulation caused by an increased Pacific-to-Atlantic flow via the Central American Seaway, ended in the Glacial M2, 3.312-3.264 Ma ago (de Schepper et al., 2013). This was a short but intense global glaciation during the early Piacenzian (late Pliocene), with fully glacial conditions from 3.305 to 3.285 Ma (de Schepper et al., 2013). The following mid-Piacenzian Warm Period (3.265-2.970 Ma) is characterized by about 3 °C warmer global temperatures than preindustrial era ones, 10-40 m higher sea levels and reduced continental ice sheets (de Schepper et al., 2013).

The fossil record of Santa Maria does not allow us to know exactly when *Persististrombus coronatus* locally disappeared from the island. This species might have disappeared from Santa Maria during the Glacial M2, or even before, as it happened in the Canary Islands, where the warm-water fauna disappeared at 4.2-4.1 Ma. Nevertheless, the very existence of the genus *Persististrombus* in the Azores during the late Miocene-early Pliocene implies that during that time interval (6.0-3.6 Ma; Fig. 3A-B),

SST's in the area of Santa Maria Island would be at least equal to those reported nowadays for the northern distribution limit of the extant *P. latus* in the west African shores at Cape Blanc (21°N), with mean monthly SST's always higher than 19°C and seven months with SST's equal or higher than 20°C (Silva et al., 2010). As Cape Blanc is located at the border of the transition zone between the recent Mauritanian-Senegalese Province (MSP) and Mediterranean-Moroccan Province (MMP; cf. Fig 3C), the above-mentioned temperatures were probably the values of SST's in Santa Maria shores during the early Pliocene (5.33-3.6 Ma; cf. Fig. 3B), when the transition zone would be located just north of the island. In fact, SST estimates based on alkenones (surface water 0-10 m depth) from IODP U1313 site (41°0.1'N 32°57.4'W), located about 800 km WNW from Santa Maria Island, indicate that prior to the Glacial M2 (3.332-3.305 Ma), mean annual SST's (20.0 °C) were about 3-4 degrees higher than today. During the Glacial M2 (3.305-3.285 Ma), SST's dropped to 18.4 °C, while increasing to 21.2 °C during the mid-Piacenzian Warm Period (de Schepper et al., 2013).

As during the late Miocene the transition zone between the Miocene-European-West-African Province (MEWAP) and the Miocene-Boreal-Celtic Province (MBCP) was located much further north of Santa Maria Island, SST's should have been even higher, probably comparable to those nowadays occurring around Dakar (14°44'N), where mean monthly SST's range from 20°C to 28°C while six months have mean SST's over 24°C (Silva et al., 2010). These values compare with the present mean SST's at Santa Maria Island, which range from 16°C to 22.7°C, and only four months having mean SST's higher than 20°C (Instituto Hidrográfico, 2010). Accordingly, the mean annual SST in the late Miocene at Santa Maria Island would have been about 3.7°C to 6.3°C higher than the present day 20.6°C.

5.3 *Palaeobiogeography*

Based on previous works by Raffi et al. (1985), Raffi and Monegatti (1993), Silva (2002), Silva and Landau (2006), Silva et al. (2006, 2010, 2011), Monegatti and Raffi (2007, 2010), and Landau et al. (2009, 2011), we use several NE Atlantic Biogeographic Molluscan Provinces from the late Miocene (6 Ma) to the Present (Fig. 3). The names attributed to these biogeographic molluscan provinces are in accordance with the International Code of Area Nomenclature, as defined by Ebach et al. (2008), and are intended to unequivocally identify areas in space and time, delimited by the distribution range of taxa (Cecca and Westermann, 2003).

According to the fossil record, *P. coronatus* seems to have originated in the Miocene of West Africa, from where it migrated northward to the Mediterranean Sea, during the Tortonian. The Mediterranean populations were probably exterminated during the Messinian Salinity Crisis (MSC, 5.971-5.33 Ma; Hsü et al., 1973, 1978; Krijgsman et al., 1999; Berning, 2006; Manzi et al., 2013; Pérez-Asensio et al., 2013), surviving in the Eastern Atlantic shores and in the Macaronesian archipelagos, namely at the Azores (this work), Madeira (Mayer, 1864; reported as *Strombus italicus*) and Canaries (Meco et al., 2007). After the MSC, and until the mid-Piacenzian (upper limit of the Mediterranean Pliocene Marine Molluscan Unit 1, MPPMU1, 5.0-3.0 Ma of Raffi and Monegatti, 1993; Monegatti & Raffi, 2001), *P. coronatus* recolonized the Mediterranean Sea, where it abundantly thrived in practically all seashores (Harzhauser and Kronenberg, 2008). Other thermophilic mollusc genera such as *Cheilea*, *Gigantopecten* and *Hinnites*, as well as thermophilic species (e.g., *Spondylus concentricus* Bronn, 1831; *Ficus condita* (Brongniart, 1832); *Solenocurtus basteroti* (Des Moulins, 1832); *Pecten laevicostatus* Seguenza, 1880), together with *P. coronatus*, became extinct or disappeared locally from the Pliocene Mediterranean as a result of the mid-Piacenzian cooling event (Raffi and Monegatti, 1993; Monegatti and Raffi, 2001). *Cheilea equestris* (Linnaeus, 1758), *Spondylus* cf. *concentricus*, *F. condita*, *Gigantopecten latissimus* (Brocchi, 1814), *Pecten dunkeri* Mayer, *P. laevicostatus* and *Hinnites ercolanianus* Cocconi, 1873, are all known from the lower Pliocene of the Azores (Santa Maria Island; Fig. 4). The tropicity of the late Miocene-early Pliocene fauna of Santa Maria is also attested by other thermophilic elements of the fossil assemblages such as the echinoderms, described by Madeira et al. (2011): the extant regular sea-urchin *Eucidaris tribuloides* (Lamarck, 1816) that today occurs in the Eastern Atlantic (Guinea Gulf and Cape Verde Archipelago); the extant irregular sea-urchin *Echinoneus cyclostomus* Leske, 1778, today restricted to the tropical shallow waters of the Caribbean and the Indo-Pacific; and the extinct *Clypeaster altus* (Leske, 1778) and the spatangoid *Schizobrissus* sp., both also typically tropical taxa. The possible existence of *Echinometra* spp. in the late Miocene-early Pliocene of Santa Maria Island, suggested by Santos et al. (2015) is another example of a thermophile rock-boring echinoid that locally disappeared from the Azores. Among the Bryozoa, representatives of the genera *Biflustra* and *Crepidacantha* are indicative for tropical to subtropical temperatures (Ávila et al., 2015b).

The present-day tropical Mauritanian-Senegalese Province (MSP) extends from Cape Blanc (Mauritania, 21°N) south to Baía dos Tigres (Angola, 17°S), with a transition zone north of Cape Blanc that extends up to Rio de Oro (western Sahara, 23°N) (Oliver and Cosel, 1993; cf. Fig. 3F). To our

knowledge, Dollfus (1909) was the first to suggest that, during the Miocene, a single, vast tropical biogeographical province (here named Miocene European-West African Province, MEWAP, after Brébion (1974)) extended along the eastern Atlantic coasts, from the NW tip of France (38°30'N) south to Angola. This view was supported by the molluscan fossil record (Brébion, 1974, 1983; Lozouet, 1991; Lozouet and Gourgues, 1995; Silva and Landau, 2007; Silva et al., 2011) and is depicted in Fig. 3A, which portrays the climatic zones and the Atlantic biostratigraphic molluscan provinces between 6.0 and 5.33 Ma.

The present-day subtropical Mediterranean-Moroccan Province (MMP) includes the Mediterranean Sea, the Azores, Madeira, Selvagens, and Canary archipelagos, and the eastern Atlantic coasts between the transition zone with the tropical MSP and the transition zone with the warm-temperate French-Iberian Province (FIP), which is located between Sagres and Lisbon in mainland Portugal (37°N–39°N; Fig. 3C). Between 5.33–2.95 Ma (i.e., the end of the mid-Piacenzian Warm Period; de Schepper et al., 2013), the tropical Pliocene Mediterranean-West African Province (PMWAP) extended north, including all Macaronesian archipelagos, with the transition zone with the subtropical Pliocene French-Iberian Province (PFIP) in the exact location of the modern MMP-FIP transition zone (Monegatti and Raffi, 2001; Silva, 2001; Monegatti and Raffi, 2007; Silva and Landau, 2007; Silva et al., 2011). In a similar manner, the transition zone between the subtropical PFIP and the warm-temperate Pliocene Boreal-Celtic Province (PBCP) was in place in the same location of the modern FIP transition zone with the cool-temperate Boreal-Celtic Province (BCP; Fig. 3B; Monegatti and Raffi, 2007; Silva and Landau, 2007). The subtropical PFIP is also supported by the presence of thermophilic taxa such as Conidae, Terebridae and the opisthobranch *Spiricella unguiculus* Rang, 1828, as well as by its poor diversity and lack of *Persististrombus* (Silva and Landau, 2007).

The Pliocene cooling event (mid-Piacenzian, ~3.0 Ma) dramatically impacted the Mediterranean (Monegatti and Raffi, 2001) and the Atlantic shallow faunas of Africa north of Cape Blanc, as well as the ones from the archipelagos of the Azores, Madeira, Selvagens and Canaries, eradicating many thermophilic species (*Gigantopecten latissimus*, *Clypeaster altus*, etc.). As a consequence, the northern limit of the tropical PMWAP contracted to the present position of the eastern Atlantic tropical molluscan bioprovince (MSP). Another important consequence that will be dealt in a forthcoming paper was that, for the first time and from a marine biogeographic point of view, the Cape Verde Archipelago (since that time located in the tropical MSP) became isolated from the rest of the Macaronesian archipelagos (all

located in the subtropical MMP). This southwards withdrawal of the biogeographical provinces resulted as a consequence of global climatic deterioration, which caused the pattern of extinction or local disappearance of thermophilic species from the northern latitudes. Despite this southwards shift of the biogeographical provinces that has occurred in the NE Atlantic since the late Miocene, the geographical position of the transition zones between provinces at about 38°–40° and 48°–50° latitude North has not changed. This fact was already mentioned by authors (Dowsett et al., 1996; Monegatti and Raffi, 2001, 2007; Silva, 2002; Berning, 2006; Silva et al., 2006, 2011; Silva and Landau, 2007), and poses an exciting biogeographical problem still unresolved.

6. Conclusions

The occurrence of a diversified group of thermophilic taxa in the Mio-Pliocene of Santa Maria Island allows putting forward a palaeoenvironmental reconstruction of the SST's for the area.

1. *Persististrombus* is characteristic of tropical marine environments, and is used as a palaeoclimatic proxy. Its modern presence in tropical waters from Cape Verde to Angola suggests that in the late Miocene the climatic conditions in the Azores region were greatly different from the ones that are registered today. Based on the molluscan assemblage found at Santa Maria it is thus possible to suggest that the palaeoclimate of the island was characterized by mean annual SST's about 3.7°C to 6.3°C higher than the present-day 20.6°C, and by mean monthly SST's ranging from 20°C to 28°C, with six months with mean SST's over 24°C, thus representing conditions typical of a tropical setting;

2. The presence of *Persististrombus* is characteristic of the Pliocene Mediterranean molluscan assemblages (Raffi and Monegatti, 1993, reported as *Strombus*), being a common element in Pliocene (Zanclean to mid-Piacenzian) Mediterranean fossil assemblages of the MPPMU1 sensu Landau et al. (2011), modified from the MPMU1 of Raffi and Monegatti (1993) and Monegatti and Raffi (2001). The presence of this species in the lower Pliocene of the Azores allows enlarging the geographical scope of the biogeographical provinces, which were formerly restricted to the eastern Atlantic coastline, into a wider biogeographical model, incorporating continental and insular shores between latitudes 50°N and 17°S;

3. As first stated by Raffi and Monegatti (1993), *P. coronatus* disappeared from the Mediterranean with the mid-Piacenzian cooling event, around 3.0 Ma. Our data indicates that, along with

other thermophilic species, it probably disappeared as well from the Azores islands at the same time (about 3.6-3.3 Ma), as a result of the global glaciation during the marine isotope stage (MIS) M2 (Lysieck and Raymo, 2005), or even before (the warm fauna disappeared from Canary Islands at 4.2-4.1 Ma; Meco et al., 2007). The mid-Piacenzian cooling event terminated at 2.95 Ma and marks the end of the Miocene Mediterranean-West-African Province (MMWAP) palaeobiogeographic unit as defined in this work.

A total of 196 marine species from eight different phyla, have been reported from the upper Miocene-lower Pliocene outcrops of Santa Maria Island by Ávila et al. (2015c). Hopefully, many of the over 50 mollusc species collected in these outcrops, which remain to be identified, will help to fuel this line of research with new data that may be used to test our palaeoclimatic conclusions.

Acknowledgements

We are grateful to Joana Pombo, who provided access to the Dalberto Pombo collection, housed at the Centro de Interpretação Ambiental Dalberto Pombo (Vila do Porto, Santa Maria Island) and Liceu Antero de Quental (Ponta Delgada). We thank the Direcção Regional da Ciência, Tecnologia e Comunicações (Regional Government of the Azores), FCT (Fundação para a Ciência e a Tecnologia) of the Portuguese government, and Câmara Municipal de Vila do Porto for financial support. We also thank the Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto for field assistance. We are grateful to the organizers and participants of several editions of the International Workshops “Palaeontology in Atlantic Islands” who helped in fieldwork (2002, 2005-2014). Sérgio Ávila acknowledges his Ciência 2008 research contract funded by FCT. Sérgio Ávila also acknowledges a SYNTHESYS Application DE-TAF-1071 “Systematics and taxonomy of the Miocene malacofauna of Santa Maria Island (Azores)” (<http://www.synthesys.info/>) which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Program. Ricardo Cordeiro benefited from PhD grant SFRH/BD/60366/2009 by FCT, Portugal.

References

- Abbott, R.T., 1960. The genus *Strombus* in the Indo-Pacific. *Indo Pacific Mollusca* 1: 33–146.
- 463 Abdel-Monem, A.A., Fernandez, L.A., Boon, G.M., 1975. K-Ar ages from the eastern Azores group
464 (Santa Maria, São Miguel and the Formigas Islands). *Lithos* 8, 247–254.
- 465 Ávila, S.P., Amen, R., Azevedo, J.M.N., Cachão, M., García-Talavera, F., 2002. Checklist of the
466 Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). *Açoreana*
467 9, 343–370.
- 468 Ávila, S.P., Ramalho, R., Vullo, R., 2012. Systematics, palaeoecology and palaeobiogeography of the
469 Neogene fossil sharks from the Azores (Northeast Atlantic). *Annales de Paléontologie* 98
470 167–189.
- 471 Ávila, S.P., Madeira, P., Rebelo, A.C., Melo, C., Hipólito, A., Pombo, J., Botelho, A.Z., Cordeiro, R.,
472 2015a. *Phorcus sauciatatus* (Koch, 1845) (Mollusca: Gastropoda) in the Archipelago of the
473 Azores (NE Atlantic Ocean): the onset of a biological invasion. *Journal of Molluscan Studies*
474 (in press). doi:10.1093/mollus/eyv012.
- 475 Ávila, S.P., Ramalho, R., Habermann, J., Quartau, R., Kroh, A., Berning, B., Johnson, M., Kirby, M.,
476 Zanon, V., Titschack, J., Goss, A., Rebelo, A.C., Melo, C., Madeira, P., Cordeiro, R., Meireles,
477 R., Bagaço, L., Hipólito, A., Uchman, A., Silva, C.M. da, Cachão, M., Madeira, J., 2015b.
478 Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a
479 volcanic oceanic island (Santa Maria Island, Azores). *Palaeogeography, Palaeoclimatology,*
480 *Palaeoecology* 430, 57–73.
- 481 Ávila, S.P., Cachão, M., Ramalho, R.S., Botelho, A.Z., Madeira, P., Rebelo, A.C., Cordeiro, R., Melo, C.,
482 Hipólito, A., Ventura, M.A., Lipps, J.H., 2015c. The palaeontological heritage of Santa Maria
483 Island (Azores: NE Atlantic): a revaluation of the geosites in GeoPark Azores and its use in
484 geotourism. *Geoheritage* (in press). doi:10.1007/s12371-015-0148-x.
- 485 Azevedo, J., 1998. *Geologia e Hidrogeologia da Ilha das Flores (Açores – Portugal)*. Universidade de
486 Coimbra. Unpublished Ph.D. thesis, 148 pp.
- 487 Belanger, C.L., Jablonski, D., Roy, K., Berke, S.K., Krug, A.Z., Valentine, J.W., 2012. Global
488 environmental predictors of benthic marine biogeographic structure. *Proceedings of the*
489 *National Academy of Sciences* 109, 14046–14051.
- 490 Berning, B., 2006. The cheilostome bryozoan fauna from the Late Miocene of Niebla (Guadalquivir
491 Basin, SW Spain): environmental and biogeographic implications. *Mitteilungen aus dem*
492 *Paläontologischen Institut der Universität Hamburg* 90, 7–156.

493 Bogaard, P., 2013. The origin of the Canary Island Seamount Province – New ages of old seamounts.
 494 Scientific Reports 3, 2107, DOI: 10.1038/srep 02107.

495 Brébion, P., 1974. Les Gastéropodes du Miocène atlantique. Mémoires du Bureau de Recherches
 496 Géologiques et Minières 78, 279–285.

497 Brébion, P., 1983. Etude d’une faune de Gastéropodes Miocènes récoltés par M.M. Feio dans le Sud de
 498 l’Angola. Comunicações dos Serviços Geológicos de Portugal 63, 161–171.

499 Briggs, J., 1995. Global Biogeography. Elsevier Press, Amsterdam, 452 pp.

500 Briggs, J.C., Bowen, B.R., 2012. A realignment of marine biogeographic provinces with particular
 501 reference to fish distributions. Journal of Biogeography 39, 12–30.

502 Brocchi, G.B., 1814. Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul
 503 suolo adiacente. Milano Vol. I: pp. LXXX + 56 + 240; Vol. II, p. 241–712, pl. 1–16.

504 Bronn, H.G., 1831. Übersicht der fossilen Überreste in den tertiären subapenninischen Gebirgen. Italiens
 505 Tertiär-Gebilde und deren organische Einschlüsse. Heidelberg pp. XII + 176.

506 Bronn, H.G., 1860. Die fossilen Reste von Santa Maria, der südlichsten der Azorischen Inseln. In G.
 507 Hartung (Ed.), Die Azoren in ihrer äusseren Erscheinung und nach ihrer geognostischen Natur
 508 (pp. 1-350). Leipzig: Verlag von Wilhelm Engelmann.

509 Brownell, W. N. 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and
 510 *S. pugilis* in Los Roques, Venezuela. Bulletin of Marine Science 27, 668–680.

511 Cachão, M., Madeira, J., Silva, C.M. da, Azevedo, J., M., Cruz, A.P., Garcia, C., Sousa, F., Melo, J.,
 512 Aguiar, M., Silva, P., Amen, R., Ávila, S.P., 2003. Pedreira do Campo (Santa Maria, Açores):
 513 monumento natural, Actas do VI Congresso Nacional de Geologia. Ciências da Terra (UNL) 5,
 514 120-123.

515 Cavallo, O, Repetto, G., 1992. Conchiglie Fossili del Roero. Atlante Iconografico. Memoire del
 516 Associazione Naturalistica Piemontese 2, 1–251.

517 Cecca, F., 2002. Palaeobiogeography of Marine Fossil Invertebrates – Concepts and Methods. Taylor and
 518 Francis, London, 273 pp.

519 Cecca, F., Westermann, G.E.G., 2003. Towards a guide to palaeobiogeographic classification.
 520 Palaeogeography, Palaeoclimatology, Palaeoecology 201, 179–181.

521 Chirli, C., Richard, C., 2008. Les mollusques plaisanciens de la Cote d’Azur. Cannes la Bocca: Devaye
 522 Imprimeurs.

523 Cocconi, G., 1873. Enumerazione sistematica dei molluschi miocenici e pliocenici delle provincie di
524 Parma e di Piacenza. Memoire della Accademia delle Scienze dell'Instuto di Bologna, serie 3 3,
525 409-776.

526 Cook, R.R., Auster, P.J., 2007. A bioregional classification of the continental shelf of northeastern North
527 America for conservation analysis and planning based on representation. Marine Sanctuaries
528 Conservation Series NMSP-07-03. U.S. Department of Commerce, National Oceanic and
529 Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD. 14 pp.

530 Costa, F.A. da C., 1867. Molluscos Fosseis. Gasteropodes dos Depositos Terciarios de Portugal. Memória
531 Comissão Geologica de Portugal 4 part 2, 117–252.

532 Cotter, J.C.B., 1888-1892. Noticia de alguns fosseis terciarios da Ilha de Santa Maria no archipelago dos
533 Açores. Comunicações da Comissão dos Trabalhos Geológicos de Portugal 2, 255–287.

534 Crother, B.I., Murray, C.M., 2011. Ontology of areas of endemism. Journal of Biogeography 38, 1009–
535 1015.

536 Defrance, J.L.M., 1827. Dictionnaire des sciences naturelles, dans lequel on triate méthodiquement des
537 différents êtres de la nature, Tome 51, 1. F.G. Levrault Éditeur, Strasbourg.

538 Demand, J., Fabriol, R., Gerard, F., Lundt, F., Chovelon, P., 1982. Prospection géothermique, îles de
539 Faial et de Pico (Açores). Rapport géologique, geochimique et gravimétrique. Technical report,
540 BRGM 82 SGN 003 GTH.

541 Des Moulins C., 1832. Description d'un genre nouveau de coquille bivalve. Actes de la Société Linnéenne
542 de Bordeaux 5, 48-58.

543 Dollfus, G., 1909. Essai sur l'étage Aquitanien. Bulletin pour server d' explication à la carte géologique
544 de France 19 124, 379–506.

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

547 Ebach, M.C., Morrone, J.J., Parenti, L.R., Vilorio, Á.L., 2008. International code of area nomenclature.
548 Journal of Biogeography 35, 1153–1157.

549 Ekman, S., 1953. Zoogeography of the Sea. Sidgwick and Jackson Publishers, London, 417 pp.

550 Estevens, M., Ávila, S.P., 2007. Fossil whales from the Azores. In Ávila, S.P., Martins, A.M.F. (Eds.),
551 Proceedings of the “1st Atlantic Islands Neogene”, International Congress, Ponta Delgada, 12-
552 14 June 2006. Açoreana Suplemento 5, 140–161.

553 Fernández-Palacios, J.M., Nascimento, L. de, Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R.,
 554 Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the
 555 long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* 38, 226–
 556 246.

557 Ferreira, O. da V., 1952. Os pectinídeos do Miocénico da ilha de Santa Maria (Açores). *Revista da*
 558 *Faculdade de Ciências de Lisboa, 2ª Série C* 2(2), 243–258.

559 Ferreira, O. da V., 1955. A fauna Miocénica da ilha de Santa Maria. *Comunicações dos Serviços*
 560 *Geológicos de Portugal* 36, 9–44.

561 Fontannes, F., 1879. Les invertébrés du bassin tertiaire du sud-est de la France. Les mollusques pliocènes
 562 de la vallée du Rhône et du Roussillon. t 1, Gasteropodes. Paris: F. Savy, 278 pp.

563 Forbes, E., Godwin-Austen, R., 1859. *The Natural History of the European Seas. Outlines of the Natural*
 564 *History of Europe.* John Van Voorst, London (reprinted 1977).

565 França, Z., Nunes, J.C., Cruz, J.V., Duarte, J.F., Forjaz, V.H., 2002. Preliminary study of the Corvo
 566 Island volcanism, Azores. 3º Assembleia Luso-Espanhola de Geodesia e Geofísica (S09), 727–
 567 730.

568 França, Z., Cruz, J.V., Nunes, J.C., Forjaz, V.H., 2003. *Geologia dos Açores: uma perspectiva actual.*
 569 *Açoreana*, 10(1): 11-140.

570 Freheit, J.R., Geary, D.H., 2009. Neogene paleontology of the northern Dominican Republic. Strombid
 571 gastropods (genera *Strombus* and *Lobatus*; Mollusca: Gastropoda: Strombidae) of the Cibao
 572 Valley. *Bulletin of American Paleontology* 376, 1–54.

573 Geldmacher, J., Hoernle, K., Klügel, A., Bogaard, P. van den, Wombacher, F., Berning, B., 2006. Origin
 574 and geochemical evolution of the Madeira-Tore Rise (eastern North Atlantic). *Journal of*
 575 *Geophysical Research* 111, B09206.

576 Gmelin, J.F., 1791. Vermes. In Gmelin J.F. (Ed.) *Caroli a Linnaei Systema Naturae per Regna Tria*
 577 *Naturae, Editio Decima Tertia, Aucta Reformata. Tome 1, Pars 6 (Vermes).* G.E. Beer, Lipsiae
 578 [Leipzig], 3021-3910.

579 Goy, J.L., Hillaire-Marcel, C., Zazo, C., Ghaleb, B., Dabrio, C.J., González, A., Bardají, T., Civis, J.,
 580 Preda, M., Yébenes, A., Forte, A.M., 2006. Further evidence for a relatively high sea level
 581 during the penultimate interglacial: open-system U-series ages from La Marina (Alicante, East
 582 Spain). *Geodinamica Acta* 19, 409-426.

583 Guerreiro, A., Reiner, F., 2000. Moluscos marinhos da ilha de S. Vicente (Arquipélago de Cabo Verde).
 584 Câmara Municipal de Oeiras, 279 pp.
 585 Hall, C., 1964. Shallow-water marine climates and molluscan provinces. *Ecology* 45, 226–234.
 586 Hall Jr., C.A., 2002. Nearshore marine paleoclimatic regions, increasing zoogeographic provinciality,
 587 molluscan extinctions, and paleoshorelines, California: late Oligocene (27 Ma) to late Pliocene
 588 (2.5 Ma). *Geological Society of America, Special Paper* 357, 1–489.
 589 Hartung, G., 1860. Die Azoren in ihrer äusseren Erscheinung und nach ihrer geognostischen Natur (pp.
 590 1–350). Leipzig: Verlag von Wilhelm Engelmann.
 591 Harzhauser, M., Piller, W.E., Steininger, F.F., 2002. Circum-Mediterranean Oligo-Miocene
 592 biogeographic evolution – the gastropod’s point of view. *Palaeogeography, Palaeoclimatology,*
 593 *Palaeoecology* 183, 103–133.
 594 Harzhauser, M., Kronenberg, G.C., 2008. A note on *Strombus coronatus* Defrance, 1827 and *Strombus*
 595 *coronatus* Röding, 1798 (Mollusca: Gastropoda). *The Veliger* 50, 120–128.
 596 Harzhauser, M., Kronenberg, G.C., 2013. The Neogene strombid gastropod *Persististrombus* in the
 597 Paratethys Sea. *Acta Palaeontologica Polonica* 58, 785–802.
 598 Hayden, B.P., Ray, G.C., Dolan, R., 1984. Classification of coastal and marine environments.
 599 *Environmental Conservation* 11, 199–207.
 600 Hedgpeth, J.W., 1957. Marine biogeography. *Geological Society of America Memoirs* 67, 359–382.
 601 Herbert, G.S., Dietl, G.P., Vermeij, G.J., 2004. Pleistocene escalation in strombid gastropods of Florida
 602 and a possible catalyst role for glacial “super-El Niño” conditions. *Geological Society of*
 603 *America, Abstracts with Program* 36, 480.
 604 Hildenbrand, A., Weis, D., Madureira, P., Marques, F.O., 2014. Recent plate re-organization at the
 605 Azores Triple Junction: evidence from combined geochemical and geochronological data on
 606 Faial, S. Jorge and Terceira volcanic islands. *Lithos* 210–211, 27–39.
 607 Hsü, K.J., Ryan, W.B.F., Cita, M.B., 1973. Late Miocene desiccation of the Mediterranean. *Nature* 242,
 608 240–244.
 609 Hsü, K.J., Montadert, L., Bernoulli, D., Cita, M.B., Erickson, A., Garrison, R.E., Kidd, R.B., Mélières, F.,
 610 Müller, C., Wright, R., 1978. History of the Mediterranean Salinity Crisis. Initial Report Deep
 611 Sea Drilling Project 42, 1053–1078.

612 Instituto Hidrográfico, 2010. Roteiro da costa de Portugal. Arquipélago dos Açores. Grupos Oriental e
 613 Ocidental. Vol. 1., 3ª edição, Lisboa.

614 Janssen, A.W., Kroh, A., Ávila, S.P., 2008. Early Pliocene heteropods and pteropods (Mollusca,
 615 Gastropoda) from Santa Maria (Azores, Portugal): systematics and biostratigraphic
 616 implications. *Acta Geologica Polonica* 58, 355–369.

617 Johnston, A.K., 1856. *The Physical Atlas of Natural Phenomena*. W. Blackwood, Publisher, Edinburgh,
 618 420 pp.

619 Kauffman, E.G., 1973. Cretaceous Bivalvia. In: Haallam, A. (ed.), *Atlas of Paleobiogeography*, 353–382.
 620 Elsevier, New York.

621 Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J., Wilson, D.S., 1999. Chronology, causes and
 622 progression of the Messinian salinity crisis. *Nature* 400, 652–655.

623 Kroh, A., Bitner, M.A., Ávila, S.P., 2008. *Novocrania turbinata* (Brachiopoda) from the early Pliocene of
 624 the Azores (Portugal). *Acta Geologica Polonica* 58, 473–478.

625 de Lamarck, J.-B.M., 1816. *Histoire naturelle des animaux sans vertèbres*. Paris: Vol. 3 [suite des
 626 Radiaires; les Tuniciers; les Vers]: Verdière, 1–586.

627 Landau, B.M., Beu, A., Marquet, R., 2004. The Early Pliocene Gastropoda (Mollusca) of Estepona,
 628 Southern Spain. Part 5 Tonnoidea, Ficoidea. *Palaeontos* 5, 35–102.

629 Landau, B., Capelo, J.C., Silva, C.M. da, 2007. Patterns of extinction and local disappearance of tropical
 630 marine gastropods: contrasting examples from across the North Atlantic. *Açoreana Suplemento*
 631 5, 50–58.

632 Landau, B., Silva, C.M. da, Gili, C., 2009. The early Pliocene Gastropoda (Mollusca) of Estepona,
 633 Southern Spain. Part 8: Nassariidae. *Palaeontos* 17, 1–101.

634 Landau, B., Kronenberg, G.C., Herbert, G.S., Silva, C.M. da, 2011. The genus *Strombus* (Mollusca:
 635 Caenogastropoda: Strombidae) in the Neogene of the Bocas del Toro area, Panama, with the
 636 description of three new species. *Journal of Paleontology* 85, 337–352.

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

639 Leske, N.G., 1778. *Jacobi Theodori Klein naturalis dispositio echinodermatum, edita et descriptionibus*
 640 *novisque inventis et synonymis auctorem aucta. Addimenta ad I. T. Klein naturalem*
 641 *dispositionem echinodermatum*, pp. i–xxii+1–278. G.E. Beer; Leipzig.

642 Linnaeus, C., 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species,
643 cum characteribus, differentiis, synonymis, locis. *Editio decima, reformata. Laurentius*
644 *Salvius: Holmiae*. ii, 824 pp.

645 Lozouet, P., 1991. Mollusca Gastropoda: *Eumitra* recentes de la région néo-calédonienne et *Charitodoron*
646 fossiles de l'Oligocène supérieur d'Aquitaine (Mitridae). Mémoires du Muséum National
647 d'Histoire Naturelle (A) 15, 205–222.

648 Lozouet, P., 2014. Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic
649 gastropod (Mollusca) faunas. A base for the history of biogeographic provinces. Carnets de
650 Géologie 14, 273–314.

651 Lozouet, P., Gourgues, D., 1995. *Senilia* (Bivalvia: Arcidae) et *Anazola* (Gastropoda: Olividae) dans le
652 Miocène d'Angola et de France, témoins d'une paléo-province Ouest-Africaine. Haliotis 24,
653 101–10.

654 Luis, J., Miranda, J.M., Galdeano, A., Patriat, P., Rossignol, J.C., Mendes-Victor, L.A., 1994. The Azores
655 triple junction evolution since 10 Ma from an aeromagnetic survey of the Mid-Atlantic Ridge.
656 Earth and Planetary Science Letters 125, 439–459.

657 Madeira, P., Kroh, A., Cordeiro, R., Meireles, R., Ávila, S.P., 2011. The fossil echinoids of Santa Maria
658 Island, Azores (Northern Atlantic Ocean). Acta Geologica Polonica 61, 243–264.

659 Malatesta, A., 1974. Malacofauna pliocenica umbra. Memorie per Servire alla Carta Geologica d'Italia
660 13, 1–498.

661 Manzi, V., Gennari, R., Hilgen, F., Krijgsman, W., Lugli, S., Roveri, M., Sierro, F.J., 2013. Age
662 refinement of the Messinian salinity crisis onset in the Mediterranean. Terra Nova 25, 315–
663 322.

664 Martinell, J., 1979. Mesogastropoda del Plioceno del Empordà (Girona). I. Descriptiva y Sistemática.
665 Studia Geologica Salmaticensia 15, 85–165.

666 Martinell, J., Marquina, J., 1981. Malacofauna Pliocenica de St. Vicenç dels Horts (Baix Llobregat,
667 Barcelona). Iberus 1, 9–22.

668 Mata, J., Fonseca, P.E., Prada, S., Rodrigues, D., Martins, S., Ramalho, R., Madeira, J., Cachão, M.,
669 Silva, C.M. da, Matias, M.J., 2013. O arquipélago da Madeira. – Geologia de Portugal. Escolar
670 Editora, vol. 2, 691–746.

671 Mayer, K., 1864. Die Tertiär-Fauna der Azoren und Madeiren. Systematisches Verzeichniss der fossilen
672 Reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. In:
673 Hartung, G., 1864. Geologische Beschreibung der Inseln Madeira und Porto Santo, pp. 183–
674 298. W. Engelmann; Leipzig.

675 McCarthy, K., 2007. A review of queen conch (*Strombus gigas*) life-history. Sustainable Fisheries
676 Division Contribution SFD-2007-008, 1–8.

677 Meco, J., 1977. Los *Strombus* néogenos y cuaternarios del Atlántico euroafricano (taxonomía,
678 biostratigrafía y paleoecología). Paleontología de Canarias, Vol. 1, Excmo. Cabildo Insular de
679 Gran Canaria, 142 pp.

680 Meco, J., Gillou, H., Carracedo, J.C., Lomoschitz, A., Ramos, A.J.G., Rodríguez-Yáñez, J.J., 2002. The
681 maximum warmings of the Pleistocene world climate recorded in the Canary Islands.
682 Palaeogeography, Palaeoclimatology, Palaeoecology 185, 197–210.

683 Meco, J., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J.C., Ballester, J., Betancort, J.-F., Cillerós,
684 A., 2007. Evidence for long-term uplift on the Canary Islands from emergent Mio-Pliocene
685 littoral deposits. Global and Planetary Change 57, 222–234.

686 Meireles, R.P., Faranda, C., Gliozzi, E., Pimentel, A., Zanon, V., Ávila, S.P., 2012. Late Miocene marine
687 ostracods from Santa Maria island, Azores (NE Atlantic): Systematics, palaeoecology and
688 palaeobiogeography. Revue de Micropaléontologie 55, 133–148.

689 Meireles, R.P., Quartau, R., Ramalho, R., Rebelo, A.C., Madeira, J., Zanon, V., Ávila, S.P., 2013.
690 Depositional processes on oceanic island shelves – evidence from storm-generated Neogene
691 deposits from the mid-North Atlantic. Sedimentology 60, 1769–1785.

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

694 Monegatti, P., Raffi, S., 2007. Mediterranean-middle eastern Atlantic façade: molluscan biogeography
695 and ecobiostatigraphy throughout the late Neogene. Açoreana Supplement 5, 126-139.

696 Monegatti, P., Raffi, S., 2010. The Messinian marine molluscs record and the dawn of the eastern Atlantic
697 biogeography. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 1–11.

698 Needham, H. D., Francheteau, J., 1974. Some characteristics of the rift valley in the Atlantic Ocean near
699 36°48' north. Earth and Planetary Science Letters 22, 29-43.

700 Neumayr, M., 1883. Über klimatische Zonen während der Jura- und Kreidezeit. Denkschriften der
701 Kaiserlichen Akademie der Wissenschaften 47, 277–310.

702 Oliver, P.G., Cosel, R. von, 1993. Taxonomy of tropical West African Bivalves. IV. Arcidae. Bulletin du
703 Muséum National d'Histoire Naturelle 14, 293–381.

704 Orr, K.S., Berg, C.J. Jr., 1987. The Queen Conch. Miami, Windward Publishing, 32 pp.

705 Palla, P., 1967. Gasteropodi Pliocenici della bassa Val d'Elsa (Toscana Occidentale). Rivista Italiana de
706 Paleontologia 73, 931–1020.

707 Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and
708 geographic evidence. Evolution 33, 697–713.

709 Pavia, G., 1975. I molluschi del Pliocene Inferiore di Monteu Roero (Alba, Italia NW). Bolletino della
710 Società Paleontologica Italiana 14, 99–175.

711 Pecharde, P.L., 1968. Notes on distribution and underwater observations on the molluscan genus
712 *Strombus* as found in the waters of Trinidad and Tobago. Caribbean Journal of Science 8, 47–
713 55.

714 Pecharde, P.L., 1970. Further underwater observations on the molluscan genus *Strombus* as found in the
715 waters of Trinidad and Tobago. Caribbean Journal of Science 10, 73–81.

716 Pérez-Asencio, J., Aguirre, J., Jiménez-Moreno, G., Schmiedl, G., Civis, J., 2013. Glacioeustatic control
717 on the origin and cessation of the Messinian salinity crisis. Global and Planetary Change 111,
718 1–8.

719 Petuch, E.J., 2004. Cenozoic Seas: The View from Eastern North America. CRC press, Boca Raton,
720 Florida, 308 pp.

721 Petuch, E.J., 2013. Biogeography and Biodiversity of Western Atlantic Mollusks. CRC press, Boca
722 Raton, Florida, 234 pp.

723 Rad, U. von, 1974. Great Meteor and Josephine Seamounts (eastern North Atlantic): Composition and
724 origin of bioclastic sands, carbonate and pyroclastic rocks. "Meteor" Forsch.-Ergebnisse 19, 1–
725 61.

726 Raffi, S., 1986. The significance of marine boreal molluscs in the early Pleistocene faunas of the
727 Mediterranean area. Palaeogeography, Palaeoclimatology, Palaeoecology 52, 267–289.

728 Raffi, S., Monegatti, P., 1993. Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for
729 climatic-oceanographic and stratigraphic inferences. Proceedings 1st. R.C.A.N.S. Congress,
730 Lisboa, 1992. Ciências da Terra (UNL) 12, 45–50.

731 Raffi, S., Stanley, S.M., Marasti, R., 1985. Biogeographical patterns and Plio-Pleistocene extinction of
732 Bivalvia in the Mediterranean and southern North Sea. Paleobiology 11, 368–388.

733 Ramalho, R., 2011. Building the Cape Verde Islands. 1st Edition, Springer, 260 pp.

734 Ramalho, R., Quartau, R., Trenhaile, A.S., Mitchell, N.C., Woodroffe, C.D., Ávila, S.P., 2013. Coastal
735 evolution in oceanic islands: a complex interplay between volcanism, erosion, sedimentation
736 and biogenic production. Earth Science Reviews 127, 140–170.

737 Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Quartau, R., Thomas, C., Hipólito, A., Ávila, S.P.,
738 2014. The emergence and evolution of Santa Maria Island (Azores) - the conundrum of
739 uplifting islands revisited. AGU Fall Meeting, San Francisco, 15-19 December: Abstract
740 V11B-4697.

741 Ramalho, R., da Silveira, A.B., Fonseca, P.E., Madeira, J., Cosca, M., Cachão, M., Fonseca, M.M., Prada,
742 S.N., 2015. The emergence of volcanic oceanic islands on a slow-moving plate: The example
743 of Madeira Island, NE Atlantic. Geochemistry Geophysics Geosystems 16, 522–537.
744 DOI:10.1002/2014GC005657.

745 Rang, P.C., 1828. Description de trois genres nouveaux de coquilles fossiles du terrain tertiaire de
746 Bordeaux, savoir: *Spiricella*, par M. Rang, correspondant Grateloupia et Jouannetia, par M.
747 Charles des Moulins, président. Bulletin d'Histoire Naturelle de la Société Linnéenne de
748 Bordeaux 2, 226–255.

749 Ray, M., Stoner, A.W., 1995. Predation on a tropical spinose gastropod: the role of shell morphology.
750 Journal of Experimental Marine Biology and Ecology 187, 207–222.

751 Rebelo, A.C., Rasser, M.W., Riosmena-Rodríguez, R., Neto, A.I., Ávila, S.P., 2014. Rhodolith forming
752 coralline algae in the Upper Miocene of Santa Maria Island (Azores, NE Atlantic): a critical
753 evaluation. Phytotaxa 190, 370–382.

754 Reiss, W., 1862. Mittheilungen über die tertiären Schichten von Santa Maria, der südlichsten der Azoren,
755 und ihre organischen Einschlüsse. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und
756 Petrefactenkunde, 1–22.

757 Robertson, R., 1959. Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas.
 758 Proceedings of the Malacological Society of London 33, 164–170.
 759 Robertson, R., 1961. The feeding of *Strombus* and related herbivorous marine gastropods. Notula Naturae
 760 343, 1–9.
 761 Rolán, E., 2005. Malacological Fauna from the Cape Verde Archipelago. Part 1. Polyplacophora and
 762 Gastropoda. Hackenheim: Conchbooks, 455 pp.
 763 Sacco, F., 1893. I Molluschi dei terreni terziari del Piemonte e della Liguria. Memoria della Reale
 764 Accademia delle Scienze 14, 1–38. Santos, A. Mayoral, E., Dumont, C.P., Silva, C.M. da,
 765 Ávila, S.P., Baarli, B.G., Cachão, M., Johnson, M.E., Ramalho, R.S., 2015. Rock-boring
 766 echinoid: a new trace fossil controlled by environmental conditions. Palaeogeography,
 767 Palaeoclimatology, Palaeoecology 432, 1–14. doi:10.1016/j.palaeo.2015.04.029.
 768 Savazzi, E., 1988. Burrowing behaviour in Recent Indo-Pacific strombid Gastropods. Neues Jahrbuch für
 769 Geologie und Paläontologie Monatshefte 7, 415–430.
 770 Savazzi, E., 1989. New observations on burrowing in stromboid gastropods. Stuttgarter Beiträge zur
 771 Naturkunde Serie A 434, 1–10.
 772 de Schepper, S., Groeneveld, J., Naafs, B.D.A., van Renterghem, C., Hennissen, J., Head, M.J., Louwye,
 773 S., Fabian, K., 2013. Northern Hemisphere Glaciation during the globally warm early Late
 774 Pliocene. PLOS ONE 8(12), e81508. doi:10.1371/journal.pone.0081508
 775 Seguenza, G., 1880. Le formazioni terziarie nella provincia di Reggio (Calabria). Memorie della Classe di
 776 Scienze Fisiche Matematiche e Naturali della Regia Accademia del Lincei, serie 3 6, 1–445.
 777 Serralheiro, A., 2003. A geologia da ilha de Santa Maria, Açores. Açoreana 10, 141–192.
 778 Sibrant, A., Marques, F.O., Hildenbrand, A., 2014. Construction and destruction of a volcanic island
 779 developed inside an oceanic rift: Graciosa Island, Terceira Rift, Azores. Journal of
 780 Volcanology and Geothermal Research 284, 32–45.
 781 Silva, C.M. da, 2002. Novos dados sobre os Moluscos Pliocénicos de Portugal: implicações
 782 paleoceanográficas e paleobiogeográficas. Pliocénica 2, 117–125.
 783 Silva, C M. da, Landau, B., 2007. Cenozoic Atlanto-Mediterranean biogeography of *Spiricella*
 784 (Gastropoda, Umbraculidae) and climate change: Filling the geological gap. The Veliger 49,
 785 19–26.

786 Silva, C.M. da, Landau, B., Domènech, R., Martinell, J., 2006. Pliocene Atlanto-Mediterranean
787 biogeography of *Patella pellucida* (Gastropoda, Patellidae): palaeoceanographic implications.
788 Palaeogeography, Palaeoclimatology, Palaeoecology 233, 225–234.

789 Silva, C.M. da, Landau, B., Domènech, R., Martinell, J., 2010. Pliocene Atlantic molluscan assemblages
790 from the Mondego Basin (Portugal): age and palaeoceanographic implications.
791 Palaeogeography, Palaeoclimatology, Palaeoecology 285, 248–254.

792 Silva, C.M. da, Landau, B., Perna, R. la, 2011. Biogeography of Iberian Atlantic Neogene marginelliform
793 gastropods (Marginellidae, Cystiscidae): global change and transatlantic colonization. Journal
794 of Paleontology 85, 1052–1066.

795 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge,
796 M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A.,
797 Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf
798 areas. BioScience 57, 573–583.

799 Stchepinsky, V. 1939. Faune miocene du vilayet de Sivas (Turquie). Publications de l’Institut d’E’tudes
800 et de Recherches minières de Turquie, série C 1, 1–63.

801 Stchepinsky, V. 1946. Fossiles Caractéristiques de Turquie Maden tetkik ve arama enstitüsü
802 yayinlarindan, jeolojik harta materyelleri 1, 1–151.

803 Stephenson, T.A., Stephenson, A., 1972. Life between tidemarks on rocky shores. San Francisco: W.H.
804 Freeman, xiv+426 pp.

805 Valentine, J.W., 1973. Evolutionary Palaeoecology of the Marine Biosphere. Prentice-Hall, Englewood,
806 New Jersey, 511 pp.

807 Vermeij, G.J., 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press,
808 Cambridge, U.S.A., 332 pp.

809 Vermeij, G.J., 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press,
810 New Jersey, U.S.A., 527 pp.

811 Walch, J.E.I., 1768. Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorr’schen
812 Sammlung von Merkwürdigkeiten der Natur. Des zweyten Theils erster Abschnitt, 1–184,
813 Raspe, Nürnberg.

814 Waters, J.M., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., Sanderson,
 815 J.C., West, J.A., Gurgel, C.F.D., 2010. Australia's marine biogeography revisited: back to the
 816 future? *Austral Ecology* 35, 988–992.

817 Wells, F.E., 1998. Superfamily Stromboidea. In: Beesley, P.L., Ross, G.J.B., Wells, A. (eds.), *Mollusca:*
 818 *The Southern Syntehsys. Fauna of Australia*, vol. 5. CSIRO Publishing, Melbourne, Part B,
 819 766–768.

820 Winkelmann, K., Buckeridge, J.S., Costa, A.C., Dionísio, M.A.M., Medeiros A., Cachão, M., Ávila, S.P.,
 821 2010. *Zullobalanus santamariaensis* sp. nov. a new late Miocene barnacle species of the family
 822 *Archeobalanidae* (Cirripedia: Thoracica), from the Azores. *Zootaxa* 2680, 33–44.

823 Woodward, S.P., 1856. *Manual of Mollusca: Or a Rudimentary Treatise of Recent and Fossil Shells*. John
 824 Weale, London, 484 pp.

825 Zazo, C., Goy, J.L., Hillaire-Marcel, C., Dabrio, C.J., González-Delgado, J.A. Cabero, A., Bardají, T.,
 826 Ghaleb, B., Soler, V., 2010. Sea level changes during the last and present interglacials in Sal
 827 Island (Cape Verde archipelago). *Global and Planetary Change* 72, 302–317.

828 Zbyszewski, G., Ferreira, O. da V., 1962. La faune Miocène de l'île de Santa Maria (Açores).
 829 *Comunicações dos Serviços Geológicos de Portugal* 46, 247–289.

830
 831
 832

Figures and tables

Fig. 1. A: location of the Azores Archipelago within the NE Atlantic. NA-North American plate; Euroasian plate; Nu-Nubian (African) plate. B: location of the Azores Archipelago in the NE Atlantic and location of Santa Maria Island, within the Azores Archipelago. C: map of Santa Maria with the location of Mio-Pliocene outcrops with *Persististrombus coronatus*.

Fig. 2. *Persististrombus coronatus*. A–C: CIADP 32, Figueiral outcrop, Touril Complex, Mio-Pliocene; A. Ventral view. B. Dorsal view. C. Apical view. D,E. Internal mould, Figueiral outcrop, Touril Complex, Mio-Pliocene. F,G. Shells at Baía de Nossa Senhora outcrop, Touril Complex, early Pliocene. H. Internal mould, Pedra-que-pica outcrop, Touril Complex, early Pliocene. Scale bar: A-C, F-H = 5 cm; D-E = 3 cm.

Fig. 3. A–C. NE Atlantic Biogeographic Molluscan Provinces from late Miocene to Pliocene (A, 6.0–5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm Period (B, 5.33–2.95 MA) and the Present (C), modified from Raffi et al. (1985), Monegatti and Raffi (2007) and Silva and Landau (2007). The names attributed to these biostratigraphic molluscan provinces are in accordance with the International Code of Area Nomenclature, as defined by Ebach et al. (2008). Colours refer to the climatic zones as defined in Silva and Landau (2007), Landau et al. (2011) and Silva et al. (2011), here expanded to the NE Atlantic, in order to include the archipelagos of the Azores, Madeira, Selvagens, Canaries and Cape Verde. D–F. Hypothetical reconstruction of the palaeo-NE Atlantic islands, modified from Fernández-Palacios et al. (2011). Numbers follow the most recent geochronological age of the islands, and are ordered from oldest to youngest (cf. Table 1): 1–Gettysburg; 2–Ormonde; 3–Dacia; 4–Ampere; 5–Coral Patch; 6–Unicorn; 7–Mahan *; 8–Fuerteventura; 9–Seine; 10–Porto Santo; 11–Great Meteor; 12–Concepcion Bank; 13–Sal; 14–Amanay; 15–Gran Canaria; 16–Lanzarote; 17–Maio; 18–Selvagens; 19–Tenerife; 20–La Gomera; 21–Boavista; 22–Santa Maria; 23–Santiago; 24–Desertas; 25–Madeira; 26–Adeje; 27–Anaga; 28–Santa Luzia; 29–Teno; 30–São Nicolau; 31–Formigas; 32–São Vicente; 33–São Miguel; 34–Brava; 35–Fogo; 36–Santo Antão; 37–Flores; 38–La Palma; 39–Corvo; 40–São Jorge; 41–El Hierro; 42–Faial; 43–Graciosa; 44–Terceira; 45–Pico. * Mahan refers to a former island composed by

Fuerteventura and Lanzarote. Present seasonal variations not shown (e.g., the winter upwelling that forms a cold water strip between the oriental Cape Verde Islands and the African coast).

Fig. 4. Thermophilic species that disappeared locally since the early Pliocene of Santa Maria Island. **A.** *Cheilea equestris* (Linnaeus, 1758), internal moulds, Pedra-que-pica outcrop, Touril Complex. **B.** *Spondylus* cf. *concentricus* Brönn, 1831, Ponta do Cedro outcrop, Touril Complex. **C.** *Ficus condita* (Brongniart, 1832), Ponta do Castelo outcrop, Touril Complex. **D.** *Pecten dunkeri* Mayer, 1864, Pedra-que-pica outcrop, Touril Complex. **E.** *Trivia parvicosta* Brönn in Reiss, 1862, Ponta do Castelo outcrop, Touril Complex. **F.** *Gigantopecten latissimus* (Brocchi, 1814), Pedra-que-pica outcrop, Touril Complex.

Table 1. NE Atlantic islands ordered from oldest to youngest and corresponding geochronological ages. Data collated from Rad (1974, Abdel-Monem et al. (1975), Demand et al. (1982), Azevedo (1998), França et al. (2002), Geldmacher et al. (2006), Fernández-Palacios et al. (2011), Ramalho (2011), Bogaard (2013), Mata et al. (2013), Hildenbrand et al. (2014), Ramalho et al. (2014), Sibrant et al. (2014), and references therein. † – plausible ages.

Table 1. NE Atlantic (palaeo)islands ordered from oldest to youngest and corresponding geochronological ages. Data collated from von Rad (1974), Abdel-Monem et al. (1975), Demand et al. (1982), Azevedo (1998), França et al. (2002), Geldmacher et al. (2006), Fernández-Palacios et al. (2011), Ramalho (2011), Bogaard (2013), Mata et al. (2013), Hildenbrand et al. (2014), Ramalho et al. (2014), Sibrant et al. (2014), and references therein. † – plausible ages.

ID	Island	Age (Ma)	Geographical region	Author	Present Status
1	Gettysburg	67	Madeiran	Fernandéz-Palacios et al., 2010	seamount
2	Ormonde	67	Madeiran	Fernandéz-Palacios et al., 2010	seamount
3	Dacia	47	Canarian	Fernandéz-Palacios et al., 2010	seamount
4	Ampere	31	Madeiran	Fernandéz-Palacios et al., 2010	seamount
5	Coral Patch	31	Madeiran	Fernandéz-Palacios et al., 2010	seamount
6	Selvagens	29.5	Madeiran	Geldmacher et al., 2001	island
7	Unicorn	27	Madeiran	Fernandéz-Palacios et al., 2010	seamount
8	Mahan	25	Canarian	Fernandéz-Palacios et al., 2010	not applicable
9	Fuerteventura	23	Canarian	Bogaard, 2013	island
10	Seine	22	Canarian	Fernandéz-Palacios et al., 2010	seamount
11	Great Meteor	22	Great Meteor	van Rad, 1974	seamount
12	Porto Santo	18.8	Madeiran	Mata et al., 2013	island
13	Conception	18	Canarian	Bogaard, 2013	seamount
14	Sal	15.8	Cape Verdian	Ramalho, 2011	island
15	Amanay	15	Canarian	Bogaard, 2013	seamount
16	Gran Canaria	15	Canarian	Bogaard, 2013	island
17	Lanzarote	15	Canarian	Bogaard, 2013	island
18	Maio	12	Cape Verdian	Ramalho, 2011	island
19	Tenerife	12	Canarian	Bogaard, 2013	island
20	La Gomera	11	Canarian	Bogaard, 2013	island
21	Boavista	10 †	Cape Verdian	Ramalho, 2011	island
22	Madeira	7	Madeiran	Ramalho et al., 2015	island
23	Santa Maria	6.3	Azorean	Ramalho et al., 2014	island
24	Santiago	6	Cape Verdian	Ramalho, 2011	island

25	Desertas	5.5	Madeiran	Mata et al., 2013	island
26	Adeje	5	Canarian	Fernandéz-Palacios et al., 2010	seamount
27	Anaga	5 †	Canarian	Fernandéz-Palacios et al., 2010	seamount
28	Santa Luzia	5 †	Cape Verdian	Ramalho, 2011	island
29	Teno	5 †	Canarian	Fernandéz-Palacios et al., 2010	seamount
30	São Nicolau	4.7	Cape Verdian	Ramalho, 2011	island
31	Formigas	4.65	Azorean	Abdel-Monem et al., 1975	islets
32	São Vicente	4.43	Cape Verdian	Ramalho, 2011	island
33	São Miguel	4.01	Azorean	Abdel-Monem et al., 1975	island
34	La Palma	4	Canarian	Staudigel et al., 1986	island
35	Brava	3 †	Cape Verdian	Ramalho, 2011	island
36	Fogo	< 3	Cape Verdian	Ramalho, 2011	island
37	Santo Antão	3	Cape Verdian	Ramalho, 2011	island
38	Flores	2.16	Azorean	Azevedo, 1998	island
39	Corvo	1.5	Azorean	França et al., 2002	island
40	São Jorge	1.32	Azorean	Hildenbrand et al., 2014	island
41	El Hierro	1.1	Canarian	Bogaard, 2013	island
42	Faial	0.85	Azorean	Hildenbrand et al., 2014	island
43	Graciosa	0.7	Azorean	Sibrant et al., 2014	island
44	Terceira	0.4	Azorean	Hildenbrand et al., 2014	island
45	Pico	0.27	Azorean	Demand et al., 1982	island

885

886

Figure 1

Figure 2

Figure 3

NE Atlantic Biostratigraphic Molluscan Provinces

MBCP - Miocene Boreal-Celtic Province	BCP - Boreal-Celtic Province
MEWAP - Miocene European-West African Province	FIP - French-Iberian Province
PBCB - Pliocene Boreal-Celtic Province	MMP - Mediterranean-Moroccan Province
PFIP - Pliocene French-Iberian Province	MSP - Mauritanian-Senegalese Province
PMWAP - Pliocene Mediterranean-West African Province	TZ - Transition Zone

Archipelagos:

Az - Azores; Mad - Madeira; Can - Canaries; CVerde - Cape Verde

Figure 4