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Persististrombus coronatus (Mollusca: Strombidae) in the lower Pliocene of Santa Maria Island (Azores, NE Atlantic): Paleoecology, paleoclimatology and paleobiogeographic implications

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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 paleoclimatic 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, paleoclimatological 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 paleobiogeographical 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 paleoclimate at Santa Maria Island was drastically different from that seen at those latitudes today, with mean annual sea surface temperatures (SSTs) about 3.7 °C to 6.3 °C higher than the present-day 20.6 °C, and with mean monthly SSTs ranging from 20 °C to 28 °C, with six months with mean SSTs over 24 °C, conditions typical of a tropical setting.

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 paleo- and neobiogeographic studies, as it allows establishing relationships between different regions (Briggs, 1995; Harzhauser et al., 2002).

Paleobiogeographic units were first classified in a quantitative manner by Kauffmann (1973), based on percentages of endemism (25–50% for provinces). Valentine (1973) considered paleoprovinces 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,

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formed on both sides of the Atlantic, thus creating distinct biogeographic paleoprovinces.

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; Belanger et al., 2012; Briggs and Bowen, 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 and 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 (SSTs) never fall below 20 °C, whereas "paratropical provinces" were defined as subtropical or warm-temperate seas where SSTs 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 paleoclimatic 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 and 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. (2015) 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 paleoecology and paleoclimatic implications, paleobiogeography 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 2000 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; Ávila et al., 2002, 2009, 2012, in press-a; Serralheiro, 2003; Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 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 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 volcaniclastic 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., 2015) 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., 2015) to 95 m above sea-level (Figueiral; Ávila et al., in press-b) 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., in press-b). Five of these outcrops (Ponta Negra, Ponta do Cedro, Pedra-que-pica,

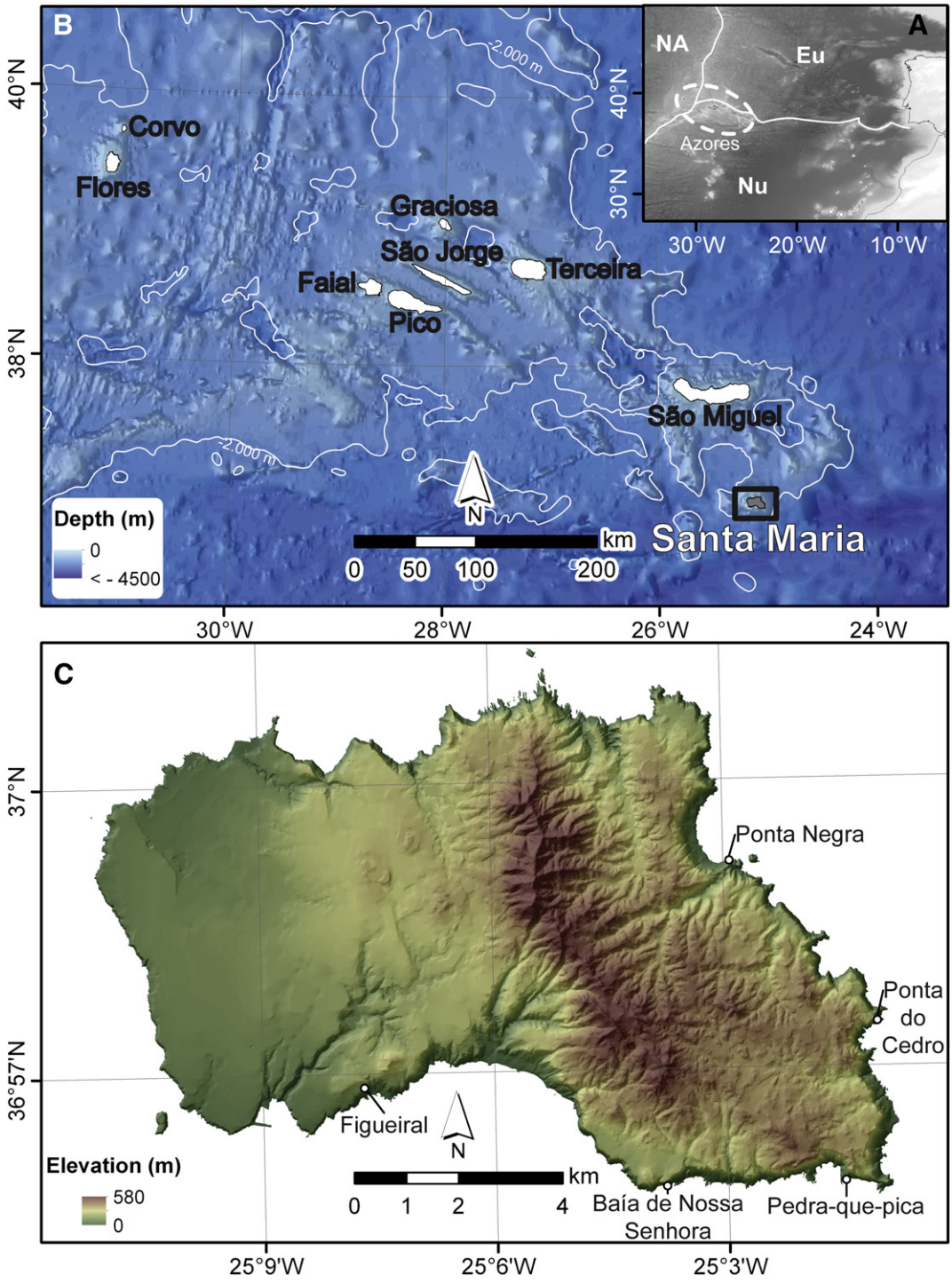

Fig. 1. A: Location of the Azores Archipelago within the NE Atlantic. NA — North American plate; Eu — Eurasian plate; Nu — Nubian (African) plate. B: Location of the Azores Archipelago in the NE Atlantic and location of Santa Maria Island, within the Azores Archipelago. C: Map of Santa Maria with the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

Baía de Nossa Senhora (Malbusca), and Figueiral), all lower Pliocene in age (Fig. 1), yielded both permineralized shells and moulds of *P. 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).

3.1. Institutional abbreviations used

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.

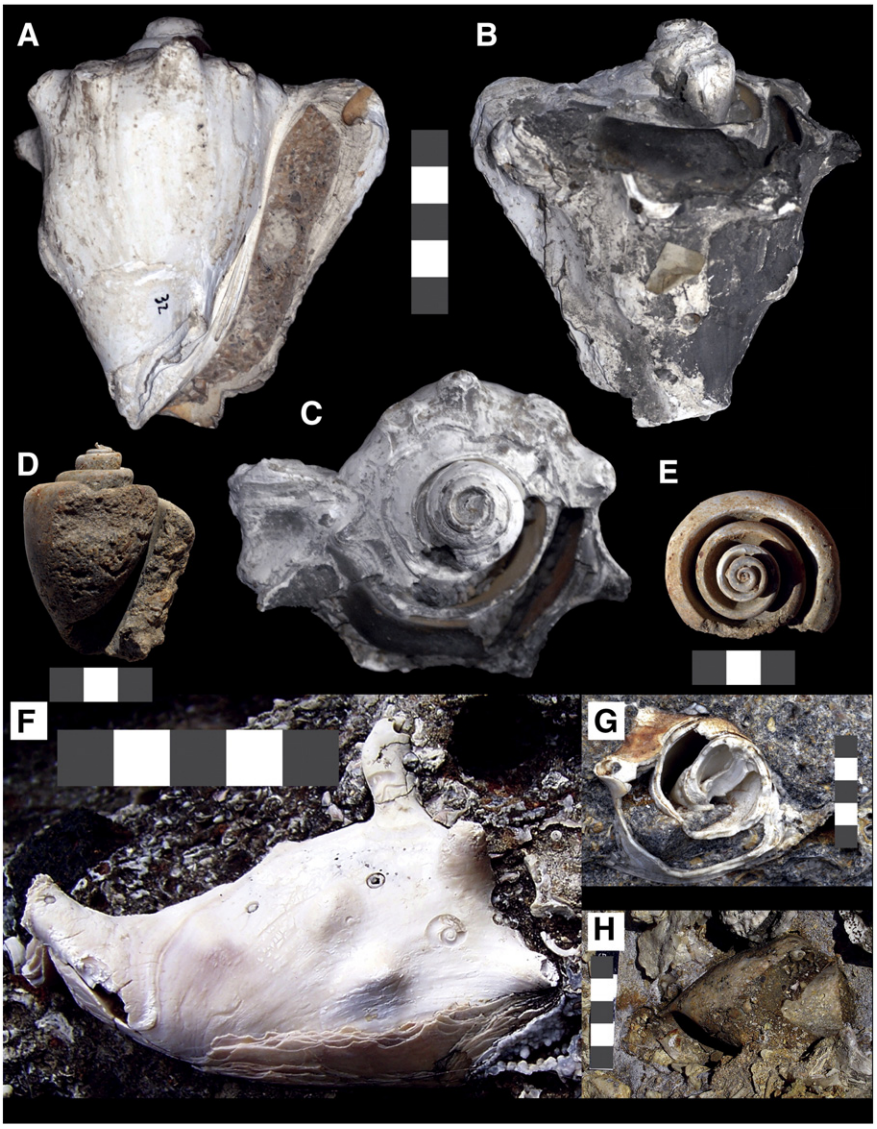

Fig. 2. *Persististrombus coronatus*. A–C: CIADP 32, Figueiral outcrop, Touril Complex, Mio-Pliocene. A: Ventral view. B: Dorsal view. C: Apical view. D, E: Internal mould, Figueiral outcrop, Touril Complex, Mio-Pliocene. F, G: Shells at Baía de Nossa Senhora outcrop, Touril Complex, early Pliocene.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

4. Results

4.1. Systematics

Phylum MOLLUSCA Linnaeus, 1758
Class GASTROPODA Cuvier, 1795
Order LITTORINIMORPHA Golikov & Starobogatov, 1975
Family STROMBIDAE Rafinesque, 1815
Genus *Persististrombus* Kronenberg & Lee, 2007
P. coronatus (Defrance, 1827)
(Fig. 2A–H)

4.2. Type material

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

4.3. Type locality

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

4.4. Material examined

(1) *Ponta Negra outcrop*: one permineralized shell imbedded in strongly cemented volcaniclastic 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.

4.5. 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.

4.6. 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, *Persististrombus 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).

4.7. Geological history and geographic distribution

P. 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 Principe 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 SSTs ≥20 °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). *P. 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; Meco et al., 2007), and Pliocene (?) of Madeira (Mayer, 1864). Here we report it from the lower Pliocene of the Azores.

5. Discussion

5.1. Paleoecology

As their present-day congeners, the large-shelled *P. 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., 2015).

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., *L. 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 sauciatus* (Koch, 1845), which has recently successfully reached and colonized Santa Maria Island (Ávila et al., in press-a). Moreover, during the late Miocene and early Pliocene, the number and distribution of volcanic oceanic islands in the eastern Atlantic were 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

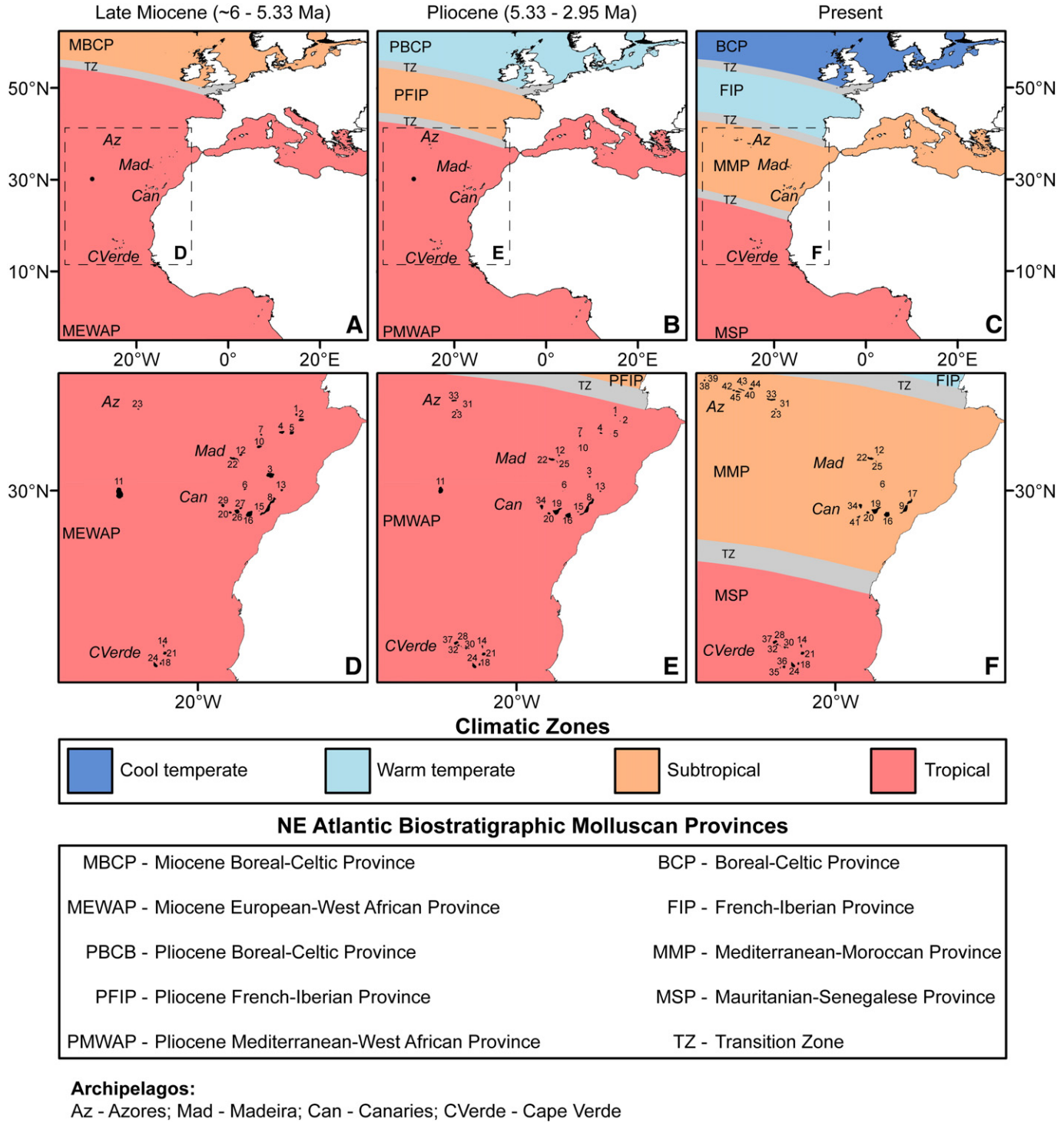

Fig. 3. A–C: NE Atlantic Biogeographic Molluscan Provinces from late Miocene to Pliocene (A, 6.0–5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm Period (B, 5.33–2.95 MA) and the present (C), modified from Raffi et al. (1985), Monegatti and Raffi (2007) and Silva and Landau (2007). The names attributed to these biostratigraphic molluscan provinces are in accordance with the International Code of Area Nomenclature, as defined by Ebach et al. (2008). Colors 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 paleo-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).

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.

Table 1
NE Atlantic (paleo)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.

ID	Island	Age (Ma)	Geographical region	Author	Present Status
1	Gettysburg	67	Madeiran	Fernández-Palacios et al. (2011)	Seamount
2	Ormonde	67	Madeiran	Fernández-Palacios et al. (2011)	Seamount
3	Dacia	47	Canarian	Fernández-Palacios et al. (2011)	Seamount
4	Ampere	31	Madeiran	Fernández-Palacios et al. (2011)	Seamount
5	Coral Patch	31	Madeiran	Fernández-Palacios et al. (2011)	Seamount
6	Selvagens	29.5	Madeiran	Geldmacher et al. (2001)	Island
7	Unicorn	27	Madeiran	Fernández-Palacios et al. (2011)	Seamount
8	Mahan	25	Canarian	Fernández-Palacios et al. (2011)	Not applicable
9	Fuerteventura	23	Canarian	Bogaard (2013)	Island
10	Seine	22	Canarian	Fernández-Palacios et al. (2011)	Seamount
11	Great Meteor	22	Great Meteor	Von 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[a]	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	Fernández-Palacios et al. (2011)	Seamount
27	Anaga	5[a]	Canarian	Fernández-Palacios et al. (2011)	Seamount
28	Santa Luzia	5[a]	Cape Verdian	Ramalho (2011)	Island
29	Teno	5[a]	Canarian	Fernández-Palacios et al. (2011)	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[a]	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

[a] Plausible ages.

5.2. Paleoclimatology

As today, Mio-Pliocene SSTs played a key role in the geographical distribution of shallow marine gastropods in the NE Atlantic. In fact, SSTs 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; Lisiecki 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 *P. 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), SSTs 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 SSTs always higher than 19 °C and seven months with SSTs 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 SSTs 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 SSTs (20.0 °C) were about 3–4° higher than today. During the Glacial M2 (3.305–3.285 Ma), SSTs 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, SSTs should have been even higher, probably comparable to those nowadays occurring around Dakar (14°44′N), where mean monthly SSTs range from 20 °C to 28 °C while six months have mean SSTs over 24 °C (Silva et al., 2010). These values compare with the present mean SSTs at Santa Maria Island, which range from 16 °C to 22.7 °C, and only four months having mean SSTs 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. Paleobiogeography

Based on previous works by Raffi et al. (1985), Raffi and Monegatti (1993), Silva (2002), Silva et al. (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 Plio-Pleistocene Marine Molluscan Unit 1, MPPMU1, 5.0–3.0 Ma of Raffi and Monegatti, 1993; Monegatti and 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); and *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 tropicality 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* (de Lamarck, 1816) that today occurs in

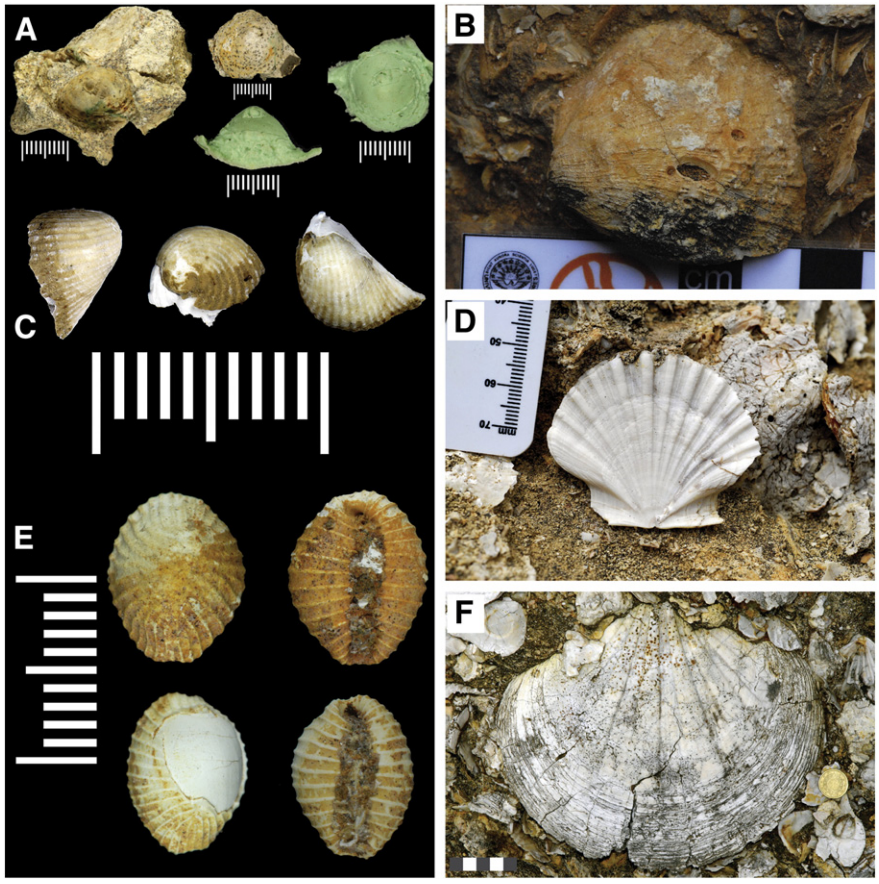

Fig. 4. Thermophilic species that disappeared locally since the early Pliocene of Santa Maria Island. A: *Cheilea equestris* (Linnaeus, 1758), internal moulds, Pedra-que-pica outcrop, Touril Complex. B: *Spondylus* cf. *concentricus* Brönn, 1831, Ponta do Cedro outcrop, Touril Complex. C. *Ficus condita*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

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., 2015).

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 and 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 (*G. latissimus*, *C. 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 the 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 paleoenvironmental reconstruction of the SSTs for the area.

1. *Persististrombus* is characteristic of tropical marine environments, and is used as a paleoclimatic 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 paleoclimate of the island was characterized by mean annual SSTs about 3.7 °C to 6.3 °C higher than the present-day 20.6 °C, and by mean monthly SSTs ranging from 20 °C to 28 °C, with six months with mean SSTs 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 (Lisiecki 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) paleobiogeographic 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. (in press-b). 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 paleoclimatic conclusions.

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References

Abbott, R.T., 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pac. Mollusca 1, 33–146.

Abdel-Monem, A.A., Fernandez, L.A., Boon, G.M., 1975. K–Ar ages from the eastern Azores group (Santa Maria, São Miguel and the Formigas Islands). Lithos 8, 247–254.

Ávila, S.P., Amen, R., Azevedo, J.M.N., Cachão, M., García-Talavera, F., 2002. Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). Açoreana 9, 343–370.

Ávila, S.P., Ramalho, R., Vullo, R., 2012. Systematics, palaeoecology and palaeobiogeography of the Neogene fossil sharks from the Azores (Northeast Atlantic). Ann. Paleontol. 98, 167–189.

Ávila, S.P., Madeira, P., Rebelo, A.C., Melo, C., Hipólito, A., Pombo, J., Botelho, A.Z., Cordeiro, R., 2015. *Phorcus sauciatus* (Koch, 1845) (Mollusca: Gastropoda) in the Archipelago of the Azores (NE Atlantic Ocean): the onset of a biological invasion. J. Molluscan Stud. http://dx.doi.org/10.1093/mollus/eyv012 (in press-a).

Ávila, S.P., Cachão, M., Ramalho, R.S., Botelho, A.Z., Madeira, P., Rebelo, A.C., Cordeiro, R., Melo, C., Hipólito, A., Ventura, M.A., Lipps, J.H., 2015. The palaeontological heritage of Santa Maria Island (Azores: NE Atlantic): a revaluation of the geosites in GeoPark Azores and its use in geotourism. Geoheritage http://dx.doi.org/10.1007/s12371-015-0148-x (in press-b).

Ávila, S.P., Ramalho, R., Habermann, J., Quartau, R., Kroh, A., Berning, B., Johnson, M., Kirby, M., Zanon, V., Titschack, J., Goss, A., Rebelo, A.C., Melo, C., Madeira, P., Cordeiro, R., Meireles, R., Bagaço, L., Hipólito, A., Uchman, A., Silva, C.M. da, Cachão, M., Madeira, J., 2015. Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores). Palaeogeogr. Palaeoclimatol. Palaeoecol. 430, 57–73.

Azevedo, J., 1998. Geologia e Hidrogeologia da Ilha das Flores (Açores — Portugal). Universidade de Coimbra. Unpublished Ph.D. thesis, 148 pp.

Belanger, C.L., Jablonski, D., Roy, K., Berke, S.K., Krug, A.Z., Valentine, J.W., 2012. Global environmental predictors of benthic marine biogeographic structure. Proc. Natl. Acad. Sci. 109, 14046–14051.

Berning, B., 2006. The cheilostome bryozoan fauna from the Late Miocene of Niebla (Guadalquivir Basin, SW Spain): environmental and biogeographic implications. Mitteilungen aus dem Paläontologischen Institut der Universität Hamburg 90 pp. 7–156.

Bogaard, P., 2013. The origin of the Canary Island Seamount Province — new ages of old seamounts. Sci. Rep. 3, 2107. http://dx.doi.org/10.1038/srep 02107.

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

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

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

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

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

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

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

Brownell, W.N., 1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and *S. pugilis* in Los Roques, Venezuela. Bull. Mar. Sci. 27, 668–680.

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

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

Cecca, F., 2002. Palaeobiogeography of Marine Fossil Invertebrates — Concepts and Methods. Taylor and Francis, London (273 pp.).

Cecca, F., Westermann, G.E.G., 2003. Towards a guide to palaeobiogeographic classification. Palaeogeogr. Palaeoclimatol. Palaeoecol. 201, 179–181.

Chirli, C., Richard, C., 2008. Les mollusques plaisanciens de la Cote d'Azur. Devaye Imprimeurs, Cannes la Bocca.

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

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

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

Cotter, J.C.B., 1888–1892. Noticia de alguns fosseis terciarios da Ilha de Santa Maria no archipelago dos Açores. Communicações da Commissão dos Trabalhos Geológicos de Portugal 2 pp. 255–287.

Crother, B.I., Murray, C.M., 2011. Ontology of areas of endemism. J. Biogeogr. 38, 1009–1015.

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

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

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

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

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

Ebach, M.C., Morrone, J.J., Parenti, L.R., Viloria, Á.L., 2008. International code of area nomenclature. J. Biogeogr. 35, 1153–1157.

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

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

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

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

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

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

Forbes, E., Godwin-Austen, R., 1859. The natural history of the European seas. Outlines of the Natural History of Europe. John Van Voorst, London (reprinted 1977).

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

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

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

Geldmacher, J., Hoernle, K., van den Bogaard, P., Zankl, G., Garbe-Scho¨nberg, D., 2001. Earlier history of the > 70-Ma-old Canary hotspot based on temporal and geochemical evolution of the Selvagens Archipelago and neighbouring seamounts in the eastern North Atlantic. J. Volcanol. Geotherm. Res. 111, 55–87.

Geldmacher, J., Hoernle, K., Klügel, A., van den Bogaard, P., Wombacher, F., Berning, B., 2006. Origin and geochemical evolution of the Madeira–Tore Rise (eastern North Atlantic). J. Geophys. Res. 111, B09206.

Gmelin, J.F., 1791. Vermes. In: Gmelin, J.F. (Ed.), Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Editio Decima Tertia, Aucta Reformata. Tome 1, Pars 6 (Vermes). G.E. Beer, Lipsiae, Leipzig, pp. 3021–3910.

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

Guerreiro, A., Reiner, F., 2000. Moluscos marinhos da ilha de S. Vicente (Arquipélago de Cabo Verde). Câmara Municipal de Oeiras (279 pp.).

Hall, C., 1964. Shallow-water marine climates and molluscan provinces. Ecology 45, 226–234.

Hall Jr., C.A., 2002. Nearshore marine paleoclimatic regions, increasing zoogeographic provinciality, molluscan extinctions, and paleoshorelines, California: late Oligocene (27 Ma) to late Pliocene (2.5 Ma). Geol. Soc. Am. Spec. Pap. 357, 1–489.

Hartung, G., 1860. Die Azoren in ihrer äusseren Erscheinung und nach ihrer geognostischen Natur. Verlag von Wilhelm Engelmann, Leipzig, pp. 1–350.

Harzhauser, M., Piller, W.E., Steininger, F.F., 2002. Circum-Mediterranean Oligo-Miocene biogeographic evolution — the gastropod's point of view. Palaeogeogr. Palaeoclimatol. Palaeoecol. 183, 103–133.

Harzhauser, M., Kronenberg, G.C., 2008. A note on *Strombus coronatus* Defrance, 1827 and *Strombus coronatus* Röding, 1798 (Mollusca: Gastropoda). Veliger 50, 120–128.

Harzhauser, M., Kronenberg, G.C., 2013. The Neogene strombid gastropod *Persististrombus* in the Paratethys Sea. Acta Palaeontol. Pol. 58, 785–802.

Hayden, B.P., Ray, G.C., Dolan, R., 1984. Classification of coastal and marine environments. Environ. Conserv. 11, 199–207.

Hedgpeth, J.W., 1957. Marine biogeography. Geol. Soc. Am. Mem. 67, 359–382.

Herbert, G.S., Dietl, G.P., Vermeij, G.J., 2004. Pleistocene escalation in strombid gastropods of Florida and a possible catalyst role for glacial "super-El Niño" conditions. Geol. Soc. Am., Abstr. with Program 36, 480.

Hildenbrand, A., Weis, D., Madureira, P., Marques, F.O., 2014. Recent plate reorganization at the Azores Triple Junction: evidence from combined geochemical

and geochronological data on Faial, S. Jorge and Terceira volcanic islands. Lithos 210–211, 27–39.
Hsü, K.J., Ryan, W.B.F., Cita, M.B., 1973. Late Miocene desiccation of the Mediterranean. Nature 242, 240–244.
Hsü, K.J., Montadert, L., Bernoulli, D., Cita, M.B., Erickson, A., Garrison, R.E., Kidd, R.B., Mélières, F., Müller, C., Wright, R., 1978. History of the Mediterranean Salinity Crisis. Initial Report Deep Sea Drilling Project 42, pp. 1053–1078.
Instituto Hidrográfico, 2010. Roteiro da costa de Portugal. Arquipélago dos AçoresGrupos Oriental e Ocidental vol. 1 (3ª edição, Lisboa).
Janssen, A.W., Kroh, A., Ávila, S.P., 2008. Early Pliocene heteropods and pteropods (Mollusca, Gastropoda) from Santa Maria (Azores, Portugal): systematics and biostratigraphic implications. Acta Geol. Pol. 58, 355–369.
Johnston, A.K., 1856. The Physical Atlas of Natural Phenomena. W. Blackwood, Publisher, Edinburgh (420 pp.).
Kauffman, E.G., 1973. Cretaceous Bivalvia. In: Haallam, A. (Ed.), Atlas of Paleobiogeography. Elsevier, New York, pp. 353–382.
Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J., Wilson, D.S., 1999. Chronology, causes and progression of the Messinian salinity crisis. Nature 400, 652–655.
Kroh, A., Bitner, M.A., Ávila, S.P., 2008. *Novocrania turbinata* (Brachiopoda) from the early Pliocene of the Azores (Portugal). Acta Geol. Pol. 58, 473–478.
de Lamarck, J.-B.M., 1816. Histoire naturelle des animaux sans vertèbres. Paris: Vol. 3 [suite des Radiaires; les Tuniciers; les Vers]: Verdièrepp. 1–586.
Landau, B.M., Beu, A., Marquet, R., 2004. The Early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 5 Tonnoidea, Ficoidea. Palaeontos 5, 35–102.
Landau, B., Capelo, J.C., Silva, C.M. da, 2007. Patterns of extinction and local disappearance of tropical marine gastropods: contrasting examples from across the North Atlantic. Açoreana Suplemento 5, 50–58.
Landau, B., Silva, C.M. da, Gili, C., 2009. The early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 8: Nassariidae. Palaeontos 17, 1–101.
Landau, B., Kronenberg, G.C., Herbert, G.S., Silva, C.M. da, 2011. The genus *Strombus* (Mollusca: Caenogastropoda: Strombidae) in the Neogene of the Bocas del Toro area, Panama, with the description of three new species. J. Paleontol. 85, 337–352.
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 pp. 5–170.
Leske, N.G., 1778. Jacobi Theodori Klein naturalis dispositio echinodermatum, edita et descriptionibus novisque inventis et synonomis auctorem aucta. Addimenta ad I. T. Klein naturalem dispositionem echinodermatum. G.E. Beer, Leipzig (pp. i–xxii + 1–278).
Linnaeus, C., 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. *Laurentius Salvius: Holmiae* ii (824 pp.).
Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic 18O records. Paleoceanography 20, PA1003. http://dx.doi.org/10.1029/2004PA001071.
Lozouet, P., 1991. Mollusca Gastropoda: *Eumitra* recentes de la région néo-calédonienne et *Charitodoron* fossiles de l'Oligocène supérieur d'Aquitaine (Mitridae). Mémoires du Muséum National d'Histoire Naturelle (A) 15 pp. 205–222.
Lozouet, P., 2014. Temporal and latitudinal trends in the biodiversity of European Atlantic Cenozoic gastropod (Mollusca) faunas. A base for the history of biogeographic provinces. Carnets de Géologie 14, 273–314.
Lozouet, P., Gourgues, D., 1995. *Senilia* (Bivalvia: Arcidae) et *Anazola* (Gastropoda: Olividae) dans le Miocène d'Angola et de France, témoins d'une paléo-province Ouest-Africaine. Haliotis 24, 101–110.
Luis, J., Miranda, J.M., Galdeano, A., Patriat, P., Rossignol, J.C., Mendes-Victor, L.A., 1994. The Azores triple junction evolution since 10 Ma from an aeromagnetic survey of the Mid-Atlantic Ridge. Earth Planet. Sci. Lett. 125, 439–459.
Madeira, P., Kroh, A., Cordeiro, R., Meireles, R., Ávila, S.P., 2011. The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). Acta Geol. Pol. 61, 243–264.
Malatesta, A., 1974. Malacofauna pliocenica umbra. Memorie per Servire alla Carta Geologica d'Italia 13 pp. 1–498.
Manzi, V., Gennari, R., Hilgen, F., Krijgsman, W., Lugli, S., Roveri, M., Sierro, F.J., 2013. Age refinement of the Messinian salinity crisis onset in the Mediterranean. Terra Nova 25, 315–322.
Martinell, J., 1979. Mesogastropoda del Plioceno del Empordà (Girnoa). I. Descriptiva y Sistemática. Studia Geologica Salmaticensia 15, 85–165.
Martinell, J., Marquina, J., 1981. Malacofauna Pliocenica de St. Vicenç dels Horts (Baix Llobregat, Barcelona). Iberus 1, 9–22.
Mata, J., Fonseca, P.E., Prada, S., Rodrigues, D., Martins, S., Ramalho, R., Madeira, J., Cachão, M., Silva, C.M. da, Matias, M.J., 2013. O arquipélago da Madeira. Geologia de Portugal. Escolar Editora vol. 2 pp. 691–746.
Mayer, K., 1864. Die Tertiär-Fauna der Azoren und Madeiren. Systematisches Verzeichniss der fossilen Reste von Madeira, Porto Santo und Santa Maria nebst Beschreibung der neuen Arten. In: Hartung, G. (Ed.), Geologische Beschreibung der Inseln Madeira und Porto Santo. W. Engelmann, Leipzig, pp. 183–298.
McCarthy, K., 2007. A review of queen conch (*Strombus gigas*) life-history. Sustainable Fisheries Division Contribution SFD-2007-008pp. 1–8.
Meco, J., 1977. Los *Strombus* néogenos y cuaternarios del Atlántico euroafricano (taxonomia, biostratigrafia y paleoecologia). Paleontología de Canarias vol. 1. Excmo. Cabildo Insular de Gran Canaria (142 pp.).
Meco, J., Gillou, H., Carracedo, J.C., Lomoschitz, A., Ramos, A.J.G., Rodríguez-Yánez, J.J., 2002. The maximum warmings of the Pleistocene world climate recorded in the Canary Islands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 185, 197–210.
Meco, J., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J.C., Ballester, J., Betancort, J.-F., Cilleros, A., 2007. Evidence for long-term uplift on the Canary Islands from emergent Mio-Pliocene littoral deposits. Glob. Planet. Chang. 57, 222–234.
Meireles, R.P., Faranda, C., Gliozzi, E., Pimentel, A., Zanon, V., Ávila, S.P., 2012. Late Miocene marine ostracods from Santa Maria Island, Azores (NE Atlantic): systematics, palaeoecology and palaeobiogeography. Rev. Micropaleontol. 55, 133–148.
Meireles, R.P., Quartau, R., Ramalho, R., Rebelo, A.C., Madeira, J., Zanon, V., Ávila, S.P., 2013. Depositional processes on oceanic island shelves — evidence from storm-generated Neogene deposits from the mid-North Atlantic. Sedimentology 60, 1769–1785.
Monegatti, P., Raffi, S., 2001. Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. Palaeogeogr. Palaeoclimatol. Palaeoecol. 165, 171–193.
Monegatti, P., Raffi, S., 2007. Mediterranean–middle eastern Atlantic façade: molluscan biogeography and ecobiostratigraphy throughout the late Neogene. Açoreana Supplement 5, 126–139.
Monegatti, P., Raffi, S., 2010. The Messinian marine molluscs record and the dawn of the eastern Atlantic biogeography. Palaeogeogr. Palaeoclimatol. Palaeoecol. 297, 1–11.
Needham, H.D., Francheteau, J., 1974. Some characteristics of the rift valley in the Atlantic Ocean near 36°48′ north. Earth Planet. Sci. Lett. 22, 29–43.
Neumayr, M., 1883. Über klimatische Zonen während der Jura- und Kreidezeit. Denkschriften der Kaiserlichen Akademie der Wissenschaften 47 pp. 277–310.
Oliver, P.G., Cosel, R. von, 1993. Taxonomy of tropical West African Bivalves. IV. Arcidae. Bulletin du Muséum National d'Histoire Naturelle 14 pp. 293–381.
Orr, K.S., Berg Jr., C.J., 1987. The Queen Conch. Windward Publishing, Miami (32 pp.).
Palla, P., 1967. Gasteropodi Pliocenici della bassa Val d'Elsa (Toscana Occidentale). Riv. Ital. Paleontol. 73, 931–1020.
Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33, 697–713.
Pavia, G., 1975. I molluschi del Pliocene Inferiore di Monteu Roero (Alba, Italia NW). Boll. Soc. Paleontol. Ital. 14, 99–175.
Pecharde, P.L., 1968. Notes on distribution and underwater observations on the molluscan genus *Strombus* as found in the waters of Trinidad and Tobago. Caribb. J. Sci. 8, 47–55.
Pecharde, P.L., 1970. Further underwater observations on the molluscan genus *Strombus* as found in the waters of Trinidad and Tobago. Caribb. J. Sci. 10, 73–81.
Pérez-Asencio, J., Aguirre, J., Jiménez-Moreno, G., Schmiedl, G., Civis, J., 2013. Glacioeustatic control on the origin and cessation of the Messinian salinity crisis. Glob. Planet. Chang. 111, 1–8.
Petuch, E.J., 2004. Cenozoic Seas: The View From Eastern North America. CRC Press, Boca Raton, Florida (308 pp.).
Petuch, E.J., 2013. Biogeography and Biodiversity of Western Atlantic Mollusks. CRC Press, Boca Raton, Florida (234 pp.).
Von Rad, U., 1974. Great Meteor and Josephine Seamounts (eastern North Atlantic): composition and origin of bioclastic sands, carbonate and pyroclastic rocks. "Meteor" Forsch. results 19, 1–61.
Raffi, S., 1986. The significance of marine boreal molluscs in the early Pleistocene faunas of the Mediterranean area. Palaeogeogr. Palaeoclimatol. Palaeoecol. 52, 267–289.
Raffi, S., Monegatti, P., 1993. Bivalve taxonomic diversity throughout the Italian Pliocene as a tool for climatic–oceanographic and stratigraphic inferences. Proceedings 1st. R.C.A.N.S. Congress, Lisboa, 1992. Ciências da Terra (UNL) 12, pp. 45–50.
Raffi, S., Stanley, S.M., Marasti, R., 1985. Biogeographical patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. Paleobiology 11, 368–388.
Ramalho, R., 2011. Building the Cape Verde Islands. 1st edition. Springer (260 pp.).
Ramalho, R., Quartau, R., Trenhaile, A.S., Mitchell, N.C., Woodroffe, C.D., Ávila, S.P., 2013. Coastal evolution in oceanic islands: a complex interplay between volcanism, erosion, sedimentation and biogenic production. Earth-Sci. Rev. 127, 140–170.
Ramalho, R., Helffrich, G., Madeira, J., Cosca, M., Quartau, R., Thomas, C., Hipólito, A., Ávila, S.P., 2014. The emergence and evolution of Santa Maria Island (Azores) — the conundrum of uplifting islands revisited. AGU Fall Meeting, San Francisco, 15–19 December: Abstract V11B-4697.
Ramalho, R., da Silveira, A.B., Fonseca, P.E., Madeira, J., Cosca, M., Cachão, M., Fonseca, M.M., Prada, S.N., 2015. The emergence of volcanic oceanic islands on a slow-moving plate: the example of Madeira Island, NE Atlantic. Geochem. Geophys. Geosyst. 16, 522–537. http://dx.doi.org/10.1002/2014GC005657.
Rang, P.C., 1828. Description de trois genres nouveaux de coquilles fossiles du terrain tertiaire de Bordeaux, savoir: *Spiricella*, par M. Rang, correspondant Grateloupia et Jouannetia, par M. Charles des Moulins, président. Bulletin d'Histoire Naturelle de la Société Linnéenne de Bordeaux 2 pp. 226–255.
Ray, M., Stoner, A.W., 1995. Predation on a tropical spinose gastropod: the role of shell morphology. J. Exp. Mar. Biol. Ecol. 187, 207–222.
Rebelo, A.C., Rasser, M.W., Riosmena-Rodríguez, R., Neto, A.I., Ávila, S.P., 2014. Rhodolith forming coralline algae in the Upper Miocene of Santa Maria Island (Azores, NE Atlantic): a critical evaluation. Phytotaxa 190, 370–382.
Reiss, W., 1862. Mittheilungen über die tertiären Schichten von Santa Maria, der südlichsten der Azoren, und ihre organischen Einschlüsse. Neues Jarhrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkundepp. 1–22.
Robertson, R., 1959. Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. Proc. Malacol. Soc Lond. 33, 164–170.
Robertson, R., 1961. The feeding of *Strombus* and related herbivorous marine gastropods. Notula Natura 343, 1–9.
Rolán, E., 2005. Malacological Fauna From the Cape Verde Archipelago. Part 1. Polyplacophora and Gastropoda. Conchbooks, Hackenheim (455 pp.).
Sacco, F., 1893. I Molluschi dei terreni terziari del Piemonte e della Liguria. Memoria della Reale Accademia delle Scienze 14 pp. 1–38.
Santos, A., Mayoral, E., Dumont, C.P., Silva, C.M. da, Ávila, S.P., Baarli, B.G., Cachão, M., Johnson, M.E., Ramalho, R.S., 2015. Rock-boring echinoid: a new trace fossil controlled by environmental conditions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 432, 1–14. http://dx.doi.org/10.1016/j.palaeo.2015.04.029.

Savazzi, E., 1988. Burrowing behaviour in Recent Indo-Pacific strombid Gastropods. Neues Jb. Geol. Paläontol. Monat. 7, 415–430.
Savazzi, E., 1989. New observations on burrowing in stromboid gastropods. Stuttgarter Beiträge zur Naturkunde Serie A 434 pp. 1–10.
de Schepper, S., Groeneveld, J., Naafs, B.D.A., van Renterghem, C., Hennissen, J., Head, M.J., Louwye, S., Fabian, K., 2013. Northern Hemisphere Glaciation during the globally warm early Late Pliocene. PLoS One 8 (12), e81508. http://dx.doi.org/10.1371/journal.pone.0081508.
Seguenza, G., 1880. Le formazioni terziarie nella provincia di Reggio (Calabria). Memorie della Classe di Scienze Fisiche Matematiche e Naturali della Regia Accademia del Lincei, serie 3 6 pp. 1–445.
Serralheiro, A., 2003. A geologia da ilha de Santa Maria, Açores. Açoreana 10, 141–192.
Sibrant, A., Marques, F.O., Hildenbrand, A., 2014. Construction and destruction of a volcanic island developed inside an oceanic rift: Graciosa Island, Terceira Rift, Azores. J. Volcanol. Geotherm. Res. 284, 32–45.
Silva, C.M. da, 2001. Gastrópodes Pliocénicos marinhos de Portugal. Sistemática, Paleoecologia, Paleobiologia, Paleobiogeografia. Fac. Sciences, Univ., Lisbon (714pp, Unpublished PhD thesis).
Silva, C.M. da, 2002. Novos dados sobre os Moluscos Pliocénicos de Portugal: implicações paleoceanográficas e paleobiogeográficas. Pliocénica 2, 117–125.
Silva, C.M. da, Landau, B., 2007. Cenozoic Atlanto-Mediterranean biogeography of *Spiricella* (Gastropoda, Umbraculidae) and climate change: filling the geological gap. Veliger 49, 19–26.
Silva, C.M. da, Landau, B., Domènech, R., Martinell, J., 2006. Pliocene Atlanto-Mediterranean biogeography of *Patella pellucida* (Gastropoda, Patellidae): palaeoceanographic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 233, 225–234.
Silva, C.M. da, Landau, B., Domènech, R., Martinell, J., 2010. Pliocene Atlantic molluscan assemblages from the Mondego Basin (Portugal): age and palaeoceanographic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 285, 248–254.
Silva, C.M. da, Landau, B., la Perna, R., 2011. Biogeography of Iberian Atlantic Neogene marginelliform gastropods (Marginellidae, Cystiscidae): global change and transatlantic colonization. J. Paleontol. 85, 1052–1066.
Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57, 573–583.
Stchepinsky, V., 1939. Faune miocene du vilayet de Sivas (Turquie). Publications de l'Institut d'Études et de Recherches minières de Turquie, série C 1 pp. 1–63.
Stchepinsky, V., 1946. Fossiles Caractéristiques de Turquie Maden tetkik ve arama enstitüsä yayinlarindan. jeolojik harta materyelleri 1 pp. 1–151.
Stephenson, T.A., Stephenson, A., 1972. Life Between Tidemarks on Rocky Shores. W.H. Freeman, San Francisco (xiv + 426 pp.).
Valentine, J.W., 1973. Evolutionary Palaeoecology of the Marine Biosphere. Prentice-Hall, Englewood, New Jersey (511 pp.).
Vermeij, G.J., 1978. Biogeography and adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, U.S.A. (332 pp.).
Vermeij, G.J., 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, New Jersey, U.S.A. (527 pp.).
Walch, J.E.I., 1768. Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur. Des zweyten Theils erster Abschnitt. Raspe, Nürnberg, pp. 1–184.
Waters, J.M., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., Sanderson, J.C., West, J.A., Gurgel, C.F.D., 2010. Australia's marine biogeography revisited: back to the future? Austral Ecol. 35, 988–992.
Wells, F.E., 1998. Superfamily Stromboidea. In: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), Mollusca: The Southern SynthesysFauna of Australia vol. 5. CSIRO Publishing, Melbourne, pp. 766–768 (Part B).
Winkelmann, K., Buckeridge, J.S., Costa, A.C., Dionísio, M.A.M., Medeiros, A., Cachão, M., Ávila, S.P., 2010. *Zullobalanus santamariaensis* sp. nov. a new late Miocene barnacle species of the family Archeobalanidae (Cirripedia: Thoracica), from the Azores. Zootaxa 2680, 33–44.
Woodward, S.P., 1856. Manual of Mollusca: Or a Rudimentary Treatise of Recent and Fossil Shells. John Weale, London (484 pp.).
Zazo, C., Goy, J.L., Hillaire-Marcel, C., Dabrio, C.J., González-Delgado, J.A., Cabero, A., Bardají, T., Ghaleb, B., Soler, V., 2010. Sea level changes during the last and present interglacials in Sal Island (Cape Verde archipelago). Glob. Planet. Chang. 72, 302–317.
Zbyszewski, G., Ferreira, O. da V., 1962. La faune Miocène de l'île de Santa Maria (Açores). Comunicações dos Serviços Geológicos de Portugal 46 pp. 247–289.