

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

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24 **ABSTRACT**

25 The family Strombidae is one of the twenty-three families and subfamilies of gastropods associated with
26 tropical environmental conditions, and therefore useful as a biogeographical and palaeoclimatic proxy.
27 Today, the strombid genus *Persististrombus* is represented in the NE Atlantic by a single species
28 restricted to the tropical Mauritanian-Senegalese Province. This work reports the occurrence of
29 *Persististrombus coronatus* from the lower Pliocene of Santa Maria Island in the Azores Archipelago.
30 Based on this occurrence, and on the Mio-Pliocene fossil record of the NE Atlantic oceanic islands,
31 palaeoclimatological considerations are discussed, which allow, for the first time, to include the Azores
32 and the other Macaronesian islands in a wider context of the NE Atlantic palaeobiogeographical
33 molluscan provinces. Late Miocene to present day molluscan biogeographic units, ranging in latitude
34 from 60°N down to 17°S, are here defined and the boundaries of the proposed climatic zones are outlined.
35 We suggest that during the upper Miocene-lower Pliocene, the palaeoclimate at Santa Maria Island was
36 drastically different from that seen at those latitudes today, with mean annual sea surface temperatures
37 (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
38 from 20°C to 28°C, with six months with mean SST's over 24°C, conditions typical of a tropical setting.

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

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45 **1. Introduction**

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

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

66 Global and more geographically restricted studies on the recent Atlantic marine biogeographic
67 units have been produced by several authors (Forbes and Godwin-Austen, 1859; Ekman, 1953; Hedgpeth,
68 1957; Stephenson and Stephenson, 1972; Hayden et al., 1984; Briggs, 1995; Petuch, 2004, Cook and
69 Auster, 2007; Spalding et al., 2007; Waters et al., 2010; Briggs and Bowen, 2012; Belanger et al., 2012),
70 whereas for periods as recent as the Neogene and the Quaternary, similar studies for the NE Atlantic are
71 comparatively scarce (Raffi and Monegatti, 1993; Monegatti and Raffi, 2001; Hall, 2002; Berning, 2006;
72 Landau et al., 2007, 2011; Silva & Landau, 2007; Silva et al., 2010, 2011; Lozouet, 2014).

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

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

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

88 Situated in the central Atlantic, the easternmost and oldest island of the Azores Archipelago,
89 Santa Maria, yields numerous fossiliferous sedimentary deposits of lower Pliocene to Pleistocene age.
90 Zbyszewski and Ferreira (1962), based on their own sampling and on previous information from the
91 works of Bronn (1860), Hartung (1860), Reiss (1862), Mayer (1864), Cotter (1888-1892), and Ferreira
92 (1952, 1955), reported 188 specific taxa (179 invertebrate and 9 vertebrate species). The lower Pliocene
93 Brachiopoda (Kroh et al., 2008), Echinodermata (Madeira et al., 2011), Chordata (Cetacea: Estevens &
94 Ávila, 2007; sharks: Ávila et al., 2012), and Ostracoda (Meireles et al., 2012) as well as some of the
95 Mollusca (Heteropoda and Pteropoda: Janssen et al., 2008) have been recently revised, whereas other
96 invertebrate groups such as the Bryozoa, the Cnidaria (Anthozoa) and most of the Mollusca are in need of
97 revision.

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

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

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111 **2. Geological setting**

112 *2.1. Azores Archipelago*

113 The Azores Archipelago is located in the NE Atlantic Ocean and comprises nine volcanic
114 oceanic islands younger than ~6 Ma (Ramalho et al., 2014). The islands and their submarine volcanic
115 edifices lay on top of the Azores Plateau (Needham and Francheteau, 1974), an area of seafloor with a
116 complex tectonic setting and an average depth of 2,000 m, near the triple junction between the Eurasian,
117 Nubian and North American plates (Luis et al., 1994; Fig. 1). Santa Maria and Corvo are the only two
118 islands of the archipelago whose volcanic activity is considered ceased (e.g. França et al., 2003; Ávila et
119 al., 2012), but only Santa Maria holds outcrops of marine fossiliferous sequences (Zbyszewski and
120 Ferreira, 1962; Serralheiro, 2003; Ávila et al., 2002, 2009, 2012, 2015c; Janssen et al., 2008; Kroh et al.,
121 2008; Winkelmann, 2010; Madeira et al., 2011; Meireles et al., 2012, 2013; Rebelo et al., 2014).

122

123 *2.2. Santa Maria Island*

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

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

144 Many of the sediments in outcrops such as Pedreira do Campo, Figueiral, Malbusca, Pedra-que-
145 pica and Ponta do Castelo, were deposited at depths around 40-60 m (Cachão et al., 2003; Meireles et al.,
146 2013; Ávila et al., 2015b) or even deeper (Cré; Jansen et al., 2008). In the present-day, these outcrops are
147 exposed at different altitudes, ranging from the intertidal (e.g., Pedra-que-pica; Ávila et al. 2015b) to 95
148 m above sea-level (Figueiral; Ávila et al., 2015c) due to the uplift of the island (Ramalho et al., 2014).

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151 **3. Materials and methods**

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

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

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Institutional Abbreviations Used

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

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

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

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168 **4. Results**

169 *Systematics*

170 Phylum MOLLUSCA Linnaeus, 1758

171 Class GASTROPODA Cuvier, 1795

172 Order LITTORINIMORPHA Golikov & Starobogatov, 1975

173 Family STROMBIDAE Rafinesque, 1815

174 Genus *Persististrombus* Kronenberg & Lee, 2007

175 *Persististrombus coronatus* (Defrance, 1827)

176 (Fig. 2A-H)

177

178 *Type material*

179 Lectotype: specimen illustrated in Walch (1768, pl. 38, figs 1–2) (Harzhauser and Kronenberg,
180 2008).

181

182 *Type locality*

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

184

185 *Material examined*

186 (1) Ponta Negra outcrop: one permineralized shell imbedded in strongly cemented volcanoclastic
187 calcarenite, viewed in cross-section, 67.5 mm in length, 52.5 mm in width. (2) Ponta do Cedro outcrop:
188 one permineralized shell imbedded in strongly cemented sandstone, viewed in cross-section, 122.4 mm in
189 length, 71.4 mm in width. (3) Pedra-que-pica outcrop: DBUA-F 318; DBUA-F 332-2, one internal mould
190 108.0 mm in length, 80.0 mm in width; DBUA-F 419, one internal mould. (4) Baía de Nossa Senhora
191 outcrop: DBUA-F 849, four internal mould fragments; DBUA-F 936, one internal mould 75.0 in length,
192 52.2 mm in width; DBUA-F 938, one internal mould; DBUA-F 966-1, a permineralized shell fragment;
193 DBUA-F 969, several internal mould fragments; DBUA-F 1006-1, seven internal mould fragments;

194 DBUA-F 1006-1-1, broken permineralized shell 88.0 mm in length, 65.1 mm in width; DBUA-F 1006-1-
195 2, broken permineralized shell 80.1 mm in length, 50.3 mm in width; DBUA-F 1006-1-3, broken
196 permineralized shell 100.0 mm in length, 65.0 mm in width; DBUA-F 1006-2, broken permineralized
197 shell 110.0 mm in length, 54.03 mm in width; DBUA-F 1007-1-1, one permineralized shell fragment. (5)
198 Figueiral outcrop: CIADP-F 32 (Fig 2a-c), one well-preserved permineralized shell, 119.1 mm in length,
199 107.2 mm in width. (6) Santa Maria Island (outcrop location unknown): LAQ-F21, one internal mould,
200 88.0 mm in length, 79.0 mm in width; LAQ-F62, one permineralized shell, 149.0 mm in length, 83.6 mm
201 in width.

202

203 *Description*

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

215

216 *Habitat and bathymetric range of Strombidae*

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

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

228

229 *Geological history and geographic distribution*

230 *Persististrombus coronatus* is an extinct species (see below), the youngest reported occurrences
231 come from the mid-Piacenzian (upper Pliocene) of the Mediterranean basin (Harzhauser and Kronenberg,
232 2008). The species disappeared from the Mediterranean Sea as consequence of the late Pliocene (mid-
233 Piacenzian) cooling event that occurred circa 3.0 Ma (Raffi et al., 1985; Monegatti and Raffi, 2001),
234 marking the upper boundary of the Mediterranean Pliocene Molluscan Unit 1 (MPMU1) of Monegatti
235 and Raffi (2001). The extant congeneric *P. latus* lives today at the Cape Verde Archipelago, at São Tomé
236 and Príncipe Archipelago, and along the West African coast, from Rio d'Oro (Senegal) south to Angola
237 (Guerreiro and Reiner, 2000; Rolán, 2005), where it inhabits flat sandy bottoms interspersed with stones
238 covered by algae, in waters with mean winter SST's $\geq 20^{\circ}\text{C}$ (Silva et al., 2010). Its distribution is limited
239 in the north by the cold Canary Current and in the south by the Benguela Current.

240 The fossil record of the genus *Persististrombus* extends from the Oligocene to the Holocene
241 (Harzhauser and Kronenberg, 2013). *Persististrombus coronatus* is reported from the upper Miocene of
242 the Mediterranean (Tortonian), from Italy and Turkey (Sacco, 1893; Stchepinsky, 1939, 1946), lower
243 Pliocene of the Mediterranean (Fontannes, 1879; Palla, 1967; Malatesta, 1974; Pavia, 1975; Martinell,
244 1979; Martinell and Marquina, 1981; Cavallo and Repetto, 1992; Landau et al., 2004; Harzhauser and
245 Kronenberg, 2008) and Pliocene (Zanclean and lower Piacenzian) of the Mediterranean (Chirli and
246 Richard, 2008). In the Atlantic, it has been reported from the Miocene of Angola (?) (Brébion, 1983, no
247 description nor illustration provided), upper Miocene of Portugal (Costa, 1867), Pliocene of Morocco
248 (Lecointre, 1952), Miocene and lower Pliocene of the Canaries (Meco, 1977, 2007), and Pliocene (?) of
249 Madeira (Mayer, 1864). Here we report it from the lower Pliocene of the Azores.

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5. Discussion

5.1. Palaeoecology

254 As their present-day congeners, the large-shelled *Persististrombus coronatus* was probably an
255 epifaunal herbivorous or detritivorous inhabitant of sandy and rocky shores covered by algae (Wells,
256 1998). As typical shallow-water species, the shells of these large strombids would be prone to be swept
257 ashore post-mortem in large numbers by spring tides or storm events, as can be seen in the present times
258 at Ponta Braço de Sirena (Sal Island, Cape Verde Archipelago; Zazo et al., 2010), or in the upper
259 Pleistocene (MIS 5e) deposits at Matas Blancas (Fuerteventura Island, Canaries; Meco et al., 2002) and at
260 La Marina, Alicante (East Spain) (Goy et al., 2006), where specimens of the congeneric *P. latus* occur in
261 large numbers. However, at Santa Maria Island, no similar deposits were found, all *P. coronatus*
262 specimens representing shells transported downslope into deeper marine environments, as at Pedra-que-
263 pica or at Baía de Nossa Senhora outcrops (Fig. 2F-H) (Ávila et al., 2015b).

264 The common occurrence of Strombidae in the fossil record, apart from the fact that they usually
265 have large and sturdy shells, may also be related with the usual discrete aggregation pattern of the
266 animals, e.g., *Lobatus gigas*, which may reach hundreds or even thousands of specimens/ha (McCarthy,
267 2007). Juvenile individuals of extant *Persististrombus* usually feed during the night, and predation is
268 decreased by diurnal burial in sandy bottoms, congregation in large numbers, and rapid growth (Savazzi,
269 1988, 1989; Ray and Stoner, 1995; Freiheit and Geary, 2009). However, the spines and knobs in the shell
270 of adult *P. coronatus* probably prevented a complete burial (but see Orr and Berg (1987) who note that
271 adult *L. gigas* can bury themselves completely). In addition, extant larger *Persististrombus* specimens are
272 usually seen in rocky bottoms covered by algae, thus in habitats with almost no sediment available for
273 burial (Pecharde, 1968, 1970). Palmer (1979) attributed a defensive function to the spines present on the
274 shells of gastropods and several authors suggested a correlation between the intensity of durophagous
275 predation and the selection for mollusc defensive shell structures such as spines and knobs (Vermeij,
276 1978, 1987; Herbert et al., 2004; Landau et al., 2011).

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

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

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295 5.2 Palaeoclimatology

296 As today, Mio-Pliocene SST's played a key role in the geographical distribution of shallow
297 marine gastropods in the NE Atlantic. In fact, SST's are one of the most important limiting factors
298 affecting both the reproductive phase of adult marine organisms (i.e., their spawning period) and the
299 successful development of embryos to the veliger state (Raffi, 1986). Global climate was warmer than
300 today during the late Miocene and also during most of the early Pliocene (Zanclean age, 5.33-3.6 Ma;
301 Lysieck and Raymo, 2005). A cooling trend affected the end of the Zanclean after ca. 3.7 Ma and,
302 coupled with a long-term steady weakening of the Atlantic meridional overturning circulation caused by
303 an increased Pacific-to-Atlantic flow via the Central American Seaway, ended in the Glacial M2, 3.312-
304 3.264 Ma ago (de Schepper et al., 2013). This was a short but intense global glaciation during the early
305 Piacenzian (late Pliocene), with fully glacial conditions from 3.305 to 3.285 Ma (de Schepper et al.,
306 2013). The following mid-Piacenzian Warm Period (3.265-2.970 Ma) is characterized by about 3 °C
307 warmer global temperatures than preindustrial era ones, 10-40 m higher sea levels and reduced
308 continental ice sheets (de Schepper et al., 2013).

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

314 SST's in the area of Santa Maria Island would be at least equal to those reported nowadays for the
315 northern distribution limit of the extant *P. latus* in the west African shores at Cape Blanc (21°N), with
316 mean monthly SST's always higher than 19°C and seven months with SST's equal or higher than 20°C
317 (Silva et al., 2010). As Cape Blanc is located at the border of the transition zone between the recent
318 Mauritanian-Senegalese Province (MSP) and Mediterranean-Moroccan Province (MMP; cf. Fig 3C), the
319 above-mentioned temperatures were probably the values of SST's in Santa Maria shores during the early
320 Pliocene (5.33-3.6 Ma; cf. Fig. 3B), when the transition zone would be located just north of the island. In
321 fact, SST estimates based on alkenones (surface water 0-10 m depth) from IODP U1313 site (41°0.1'N
322 32°57.4'W), located about 800 km WNW from Santa Maria Island, indicate that prior to the Glacial M2
323 (3.332-3.305 Ma), mean annual SST's (20.0 °C) were about 3-4 degrees higher than today. During the
324 Glacial M2 (3.305-3.285 Ma), SST's dropped to 18.4 °C, while increasing to 21.2 °C during the mid-
325 Piacenzian Warm Period (de Schepper et al., 2013).

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

334

335 *5.3 Palaeobiogeography*

336 Based on previous works by Raffi et al. (1985), Raffi and Monegatti (1993), Silva (2002), Silva
337 and Landau (2006), Silva et al. (2006, 2010, 2011), Monegatti and Raffi (2007, 2010), and Landau et al.
338 (2009, 2011), we use several NE Atlantic Biogeographic Molluscan Provinces from the late Miocene (6
339 Ma) to the Present (Fig. 3). The names attributed to these biogeographic molluscan provinces are in
340 accordance with the International Code of Area Nomenclature, as defined by Ebach et al. (2008), and are
341 intended to unequivocally identify areas in space and time, delimited by the distribution range of taxa
342 (Cecca and Westermann, 2003).

343 According to the fossil record, *P. coronatus* seems to have originated in the Miocene of West
344 Africa, from where it migrated northward to the Mediterranean Sea, during the Tortonian. The
345 Mediterranean populations were probably exterminated during the Messinian Salinity Crisis (MSC,
346 5.971-5.33 Ma; Hsü et al., 1973, 1978; Krijgsman et al., 1999; Berning, 2006; Manzi et al., 2013; Pérez-
347 Asensio et al., 2013), surviving in the Eastern Atlantic shores and in the Macaronesian archipelagos,
348 namely at the Azores (this work), Madeira (Mayer, 1864; reported as *Strombus italicus*) and Canaries
349 (Meco et al., 2007). After the MSC, and until the mid-Piacenzian (upper limit of the Mediterranean Plio-
350 Pleistocene Marine Molluscan Unit 1, MPPMU1, 5.0-3.0 Ma of Raffi and Monegatti, 1993; Monegatti &
351 Raffi, 2001), *P. coronatus* recolonized the Mediterranean Sea, where it abundantly thrived in practically
352 all seashores (Harzhauser and Kronenberg, 2008). Other thermophilic mollusc genera such as *Cheilea*,
353 *Gigantopecten* and *Hinnites*, as well as thermophilic species (e.g., *Spondylus concentricus* Bronn, 1831;
354 *Ficus condita* (Brongniart, 1832); *Solenocurtus basteroti* (Des Moulins, 1832); *Pecten laevicostatus*
355 Seguenza, 1880), together with *P. coronatus*, became extinct or disappeared locally from the Pliocene
356 Mediterranean as a result of the mid-Piacenzian cooling event (Raffi and Monegatti, 1993, Monegatti and
357 Raffi, 2001). *Cheilea equestris* (Linnaeus, 1758), *Spondylus* cf. *concentricus*, *F. condita*, *Gigantopecten*
358 *latissimus* (Brocchi, 1814), *Pecten dunkeri* Mayer, *P. laevicostatus* and *Hinnites ercolanianus* Cocconi,
359 1873, are all known from the lower Pliocene of the Azores (Santa Maria Island; Fig. 4). The tropicity of
360 the late Miocene-early Pliocene fauna of Santa Maria is also attested by other thermophilic elements of
361 the fossil assemblages such as the echinoderms, described by Madeira et al. (2011): the extant regular
362 sea-urchin *Euclidaris tribuloides* (Lamarck, 1816) that today occurs in the Eastern Atlantic (Guinea Gulf
363 and Cape Verde Archipelago); the extant irregular sea-urchin *Echinoneus cyclostomus* Leske, 1778, today
364 restricted to the tropical shallow waters of the Caribbean and the Indo-Pacific; and the extinct *Clypeaster*
365 *altus* (Leske, 1778) and the spatangoid *Schizobrissus* sp., both also typically tropical taxa. The possible
366 existence of *Echinometra* spp. in the late Miocene-early Pliocene of Santa Maria Island, suggested by
367 Santos et al. (2015) is another example of a thermophile rock-boring echinoid that locally disappeared
368 from the Azores. Among the Bryozoa, representatives of the genera *Biflustra* and *Crepidacantha* are
369 indicative for tropical to subtropical temperatures (Ávila et al., 2015b).

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

373 knowledge, Dollfus (1909) was the first to suggest that, during the Miocene, a single, vast tropical
374 biogeographical province (here named Miocene European-West African Province, MEWAP, after
375 Brébion (1974)) extended along the eastern Atlantic coasts, from the NW tip of France (38°30'N) south
376 to Angola. This view was supported by the molluscan fossil record (Brébion, 1974, 1983; Lozouet, 1991;
377 Lozouet and Gourgues, 1995; Silva and Landau, 2007; Silva et al., 2011) and is depicted in Fig. 3A,
378 which portrays the climatic zones and the Atlantic biostratigraphic molluscan provinces between 6.0 and
379 5.33 Ma.

380 The present-day subtropical Mediterranean-Moroccan Province (MMP) includes the
381 Mediterranean Sea, the Azores, Madeira, Selvagens, and Canary archipelagos, and the eastern Atlantic
382 coasts between the transition zone with the tropical MSP and the transition zone with the warm-temperate
383 French-Iberian Province (FIP), which is located between Sagres and Lisbon in mainland Portugal (37°N–
384 39°N; Fig. 3C). Between 5.33–2.95 Ma (i.e., the end of the mid-Piacenzian Warm Period; de Schepper et
385 al., 2013), the tropical Pliocene Mediterranean-West African Province (PMWAP) extended north,
386 including all Macaronesian archipelagos, with the transition zone with the subtropical Pliocene French-
387 Iberian Province (PFIP) in the exact location of the modern MMP-FIP transition zone (Monegatti and
388 Raffi, 2001; Silva, 2001; Monegatti and Raffi, 2007; Silva and Landau, 2007; Silva et al., 2011). In a
389 similar manner, the transition zone between the subtropical PFIP and the warm-temperate Pliocene
390 Boreal-Celtic Province (PBCP) was in place in the same location of the modern FIP transition zone with
391 the cool-temperate Boreal-Celtic Province (BCP; Fig. 3B; Monegatti and Raffi, 2007; Silva and Landau,
392 2007). The subtropical PFIP is also supported by the presence of thermophilic taxa such as Conidae,
393 Terebridae and the opisthobranch *Spiricella unguiculus* Rang, 1828, as well as by its poor diversity and
394 lack of *Persististrombus* (Silva and Landau, 2007).

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

403 located in the subtropical MMP). This southwards withdrawal of the biogeographical provinces resulted
404 as a consequence of global climatic deterioration, which caused the pattern of extinction or local
405 disappearance of thermophilic species from the northern latitudes. Despite this southwards shift of the
406 biogeographical provinces that has occurred in the NE Atlantic since the late Miocene, the geographical
407 position of the transition zones between provinces at about 38°–40° and 48°–50° latitude North has not
408 changed. This fact was already mentioned by authors (Dowsett et al., 1996; Monegatti and Raffi, 2001,
409 2007; Silva, 2002; Berning, 2006; Silva et al., 2006, 2011; Silva and Landau, 2007), and poses an
410 exciting biogeographical problem still unresolved.

411

412

413 **6. Conclusions**

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

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

423 2. The presence of *Persististrombus* is characteristic of the Pliocene Mediterranean molluscan
424 assemblages (Raffi and Monegatti, 1993, reported as *Strombus*), being a common element in Pliocene
425 (Zanclean to mid-Piacenzian) Mediterranean fossil assemblages of the MPPMU1 sensu Landau et al.
426 (2011), modified from the MPMU1 of Raffi and Monegatti (1993) and Monegatti and Raffi (2001). The
427 presence of this species in the lower Pliocene of the Azores allows enlarging the geographical scope of
428 the biogeographical provinces, which were formerly restricted to the eastern Atlantic coastline, into a
429 wider biogeographical model, incorporating continental and insular shores between latitudes 50°N and
430 17°S;

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

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

438

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

443

444

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832

833 **Figures and tables**

834

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

839

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

845

846 **Fig. 3.** A–C. NE Atlantic Biogeographic Molluscan Provinces from late Miocene to Pliocene (A, 6.0-
847 5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm Period (B, 5.33-2.95 MA) and the
848 Present (C), modified from Raffi et al. (1985), Monegatti and Raffi (2007) and Silva and Landau (2007).
849 The names attributed to these biostratigraphic molluscan provinces are in accordance with the
850 International Code of Area Nomenclature, as defined by Ebach et al. (2008). Colours refer to the climatic
851 zones as defined in Silva and Landau (2007), Landau et al. (2011) and Silva et al. (2011), here expanded
852 to the NE Atlantic, in order to include the archipelagos of the Azores, Madeira, Selvagens, Canaries and
853 Cape Verde. D–F. Hypothetical reconstruction of the palaeo-NE Atlantic islands, modified from
854 Fernández-Palacios et al. (2011). Numbers follow the most recent geochronological age of the islands,
855 and are ordered from oldest to youngest (cf. Table 1): 1–Gettysburg; 2–Ormonde; 3–Dacia; 4–Ampere;
856 5–Coral Patch; 6–Unicorn; 7–Mahan *; 8–Fuerteventura; 9–Seine; 10–Porto Santo; 11–Great Meteor;
857 12–Concepcion Bank; 13–Sal; 14– Amanay; 15–Gran Canaria; 16–Lanzarote; 17–Maio; 18–Selvagens;
858 19–Tenerife; 20–La Gomera; 21–Boavista; 22–Santa Maria; 23–Santiago; 24–Desertas; 25–Madeira; 26–
859 Adeje; 27–Anaga; 28–Santa Luzia; 29–Teno; 30–São Nicolau; 31–Formigas; 32–São Vicente; 33–São
860 Miguel; 34–Brava; 35–Fogo; 36–Santo Antão; 37–Flores; 38–La Palma; 39–Corvo; 40–São Jorge; 41–El
861 Hierro; 42–Faial; 43–Graciosa; 44–Terceira; 45–Pico. * Mahan refers to a former island composed by

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

864

865 **Fig. 4.** Thermophilic species that disappeared locally since the early Pliocene of Santa Maria Island. **A.**

866 *Cheilea equestris* (Linnaeus, 1758), internal moulds, Pedra-que-pica outcrop, Touril Complex. **B.**

867 *Spondylus cf. concentricus* Brönn, 1831, Ponta do Cedro outcrop, Touril Complex. **C.** *Ficus condita*

868 (Brongniart, 1832), Ponta do Castelo outcrop, Touril Complex. **D.** *Pecten dunkeri* Mayer, 1864, Pedra-

869 que-pica outcrop, Touril Complex. **E.** *Trivia parvicosta* Brönn in Reiss, 1862, Ponta do Castelo outcrop,

870 Touril Complex. **F.** *Gigantopecten latissimus* (Brocchi, 1814), Pedra-que-pica outcrop, Touril Complex.

871

872 **Table 1.** NE Atlantic islands ordered from oldest to youngest and corresponding geochronological ages.

873 Data collated from Rad (1974, Abdel-Monem et al. (1975), Demand et al. (1982), Azevedo (1998),

874 França et al. (2002), Geldmacher et al. (2006), Fernández-Palacios et al. (2011), Ramalho (2011),

875 Bogaard (2013), Mata et al. (2013), Hildenbrand et al. (2014), Ramalho et al. (2014), Sibrant et al.

876 (2014), and references therein. † – plausible ages.

877

878

879

880 **Table 1.** NE Atlantic (palaeo)islands ordered from oldest to youngest and corresponding
881 geochronological ages. Data collated from von Rad (1974), Abdel-Monem et al. (1975), Demand et al.
882 (1982), Azevedo (1998), França et al. (2002), Geldmacher et al. (2006), Fernández-Palacios et al. (2011),
883 Ramalho (2011), Bogaard (2013), Mata et al. (2013), Hildenbrand et al. (2014), Ramalho et al. (2014),
884 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

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886

Figure 1

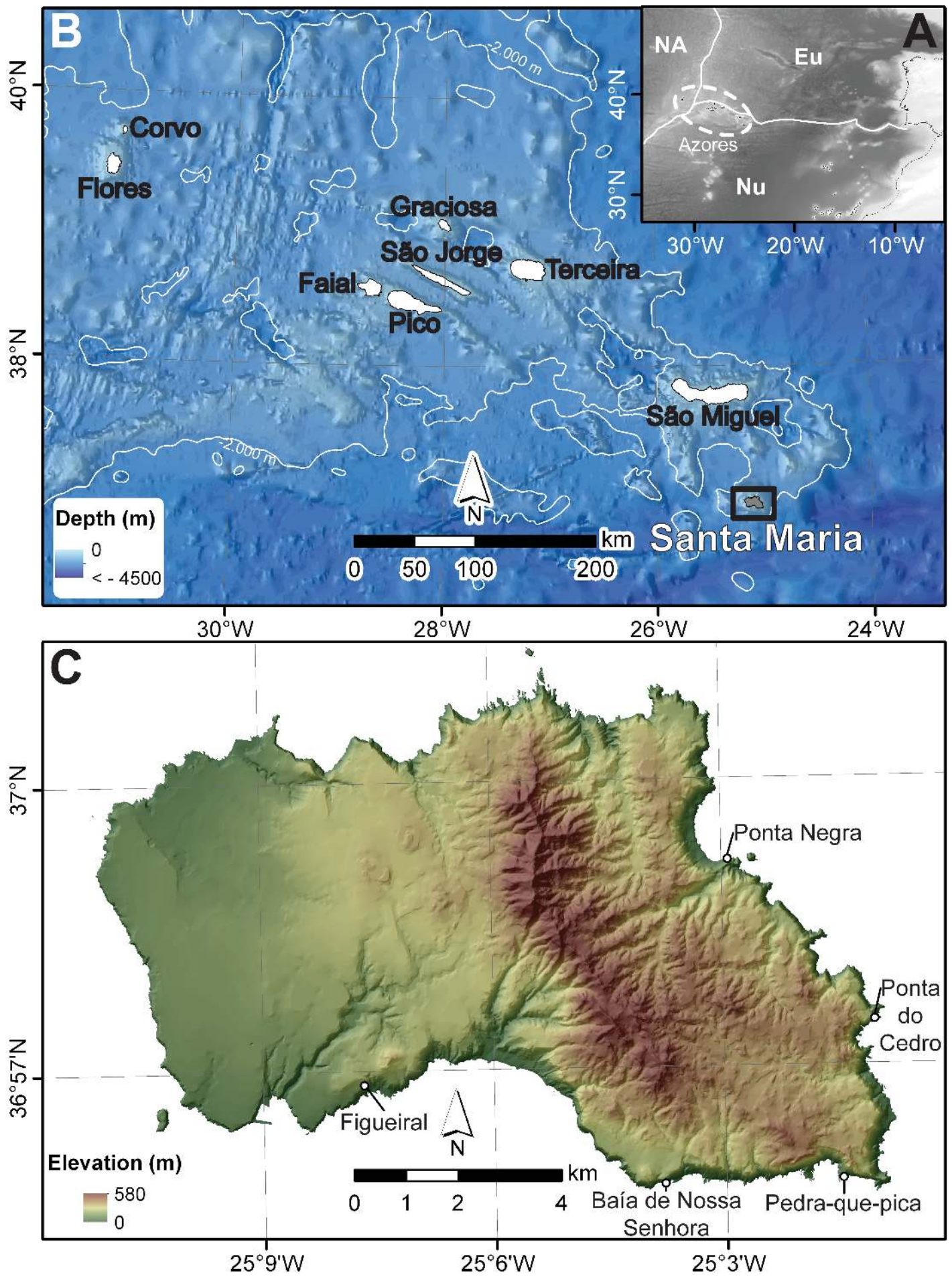


Figure 2

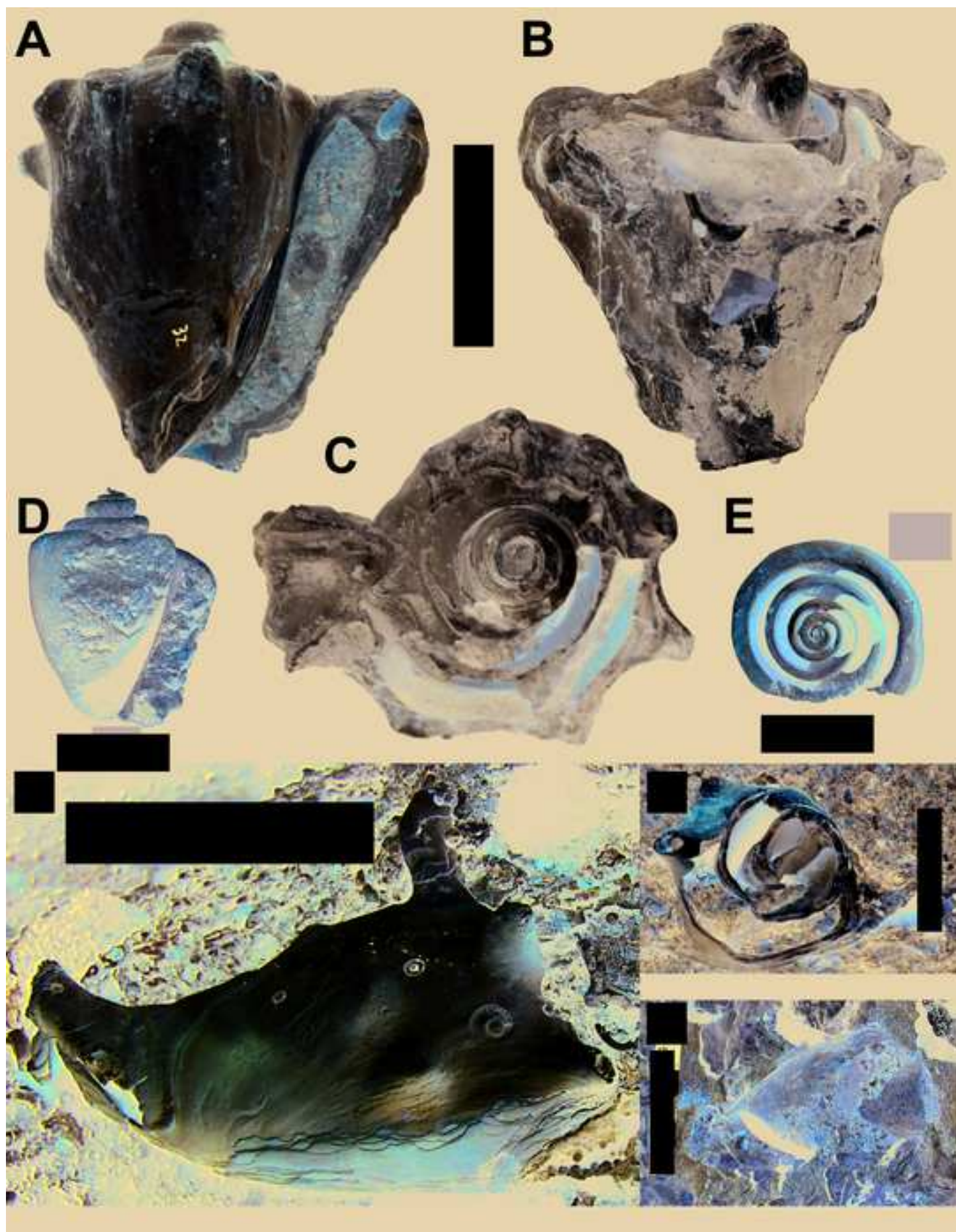
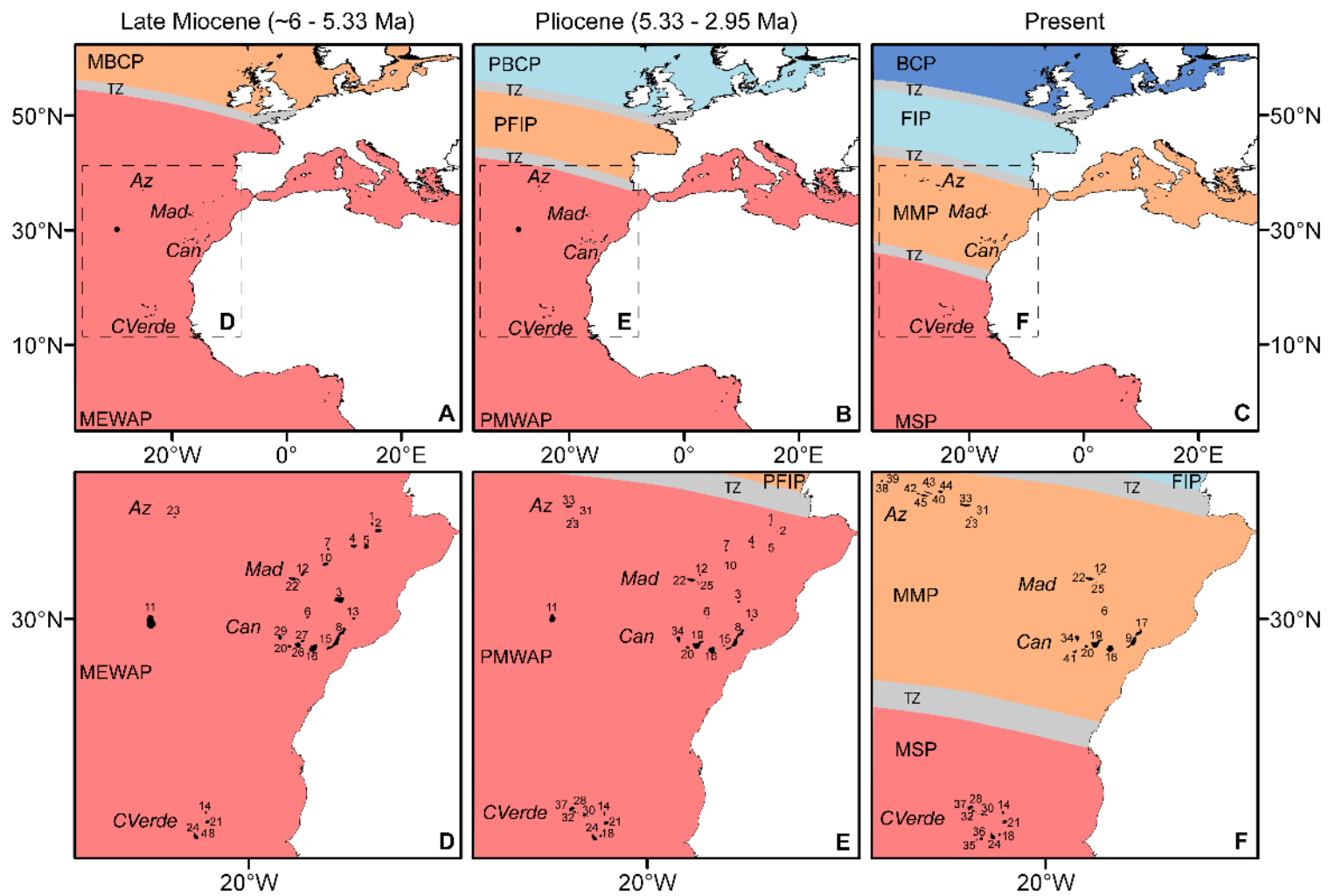
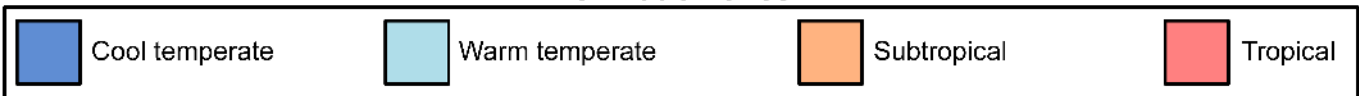


Figure 3



Climatic Zones



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

