Pliocene and Late Pleistocene actinopterygian fishes from Santa Maria Island, Azores (NE Atlantic Ocean): palaeoecological and palaeobiogeographical implications

Sérgio Ávila, José M.N. Azevedo, Patrícia Madeira, Ricardo Cordeiro, Carlos Melo, Lara Baptista, Paulo Torres, Markes Johnson, Romain Vullo

Plio-Pleistocene actinopterygian fishes from Santa Maria Island (Azores: North-eastern Atlantic Ocean): palaeoecological and palaeobiogeographical implications

SÉRGIO P. ÁVILA[*,1,2,3], JOSÉ M.N. AZEVEDO[2,4] , PATRÍCIA MADEIRA[1,2,3], RICARDO CORDEIRO[1,2,3], CARLOS S. MELO[1,3,5,6], LARA BAPTISTA[1,2,3], PAULO TORRES[1,2,3], MARKES E. JOHNSON[7] & ROMAIN VULLO[8]

[1]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores, Azores, Portugal. [2]Departamento de Biologia, Faculdade de Ciências e Tecnologia da Universidade dos Açores, 9501-801 Ponta Delgada, Açores, Portugal. [3]MPB-Marine PalaeoBiogeography working group of the University of the Azores, Rua da Mãe de Deus, 9501-801 Ponta Delgada, Açores, Portugal. [4]Grupo de Biodiversidade dos Açores and cE3c - Centro de Ecologia, Evolução e Alterações Ambientais, Portugal. [5]Departamento de Geologia, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal. [6]Instituto Dom Luiz, Faculdade de Ciências, Universidade de Lisboa, 1746-016 Lisboa, Portugal. [7]Department of Geosciences, Williams College, Williamstown, Massachusetts 01267, USA. [8]Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France.

Correspondence and request for materials should be addressed to S.P.A. (email: avila@uac.pt)

Abstract

Fossil fish are among the rarest in volcanic oceanic islands, their presence providing invaluable data for the understanding of more general (palaeo)biogeographical patterns and processes. Santa Maria Island (Azores Archipelago) is renowned for its palaeontological heritage, with representatives of several phyla, including the Chordata. Herein, we report on the fossil fishes, resulting in an increase of the number of Pliocene fish from the Azores to 11 taxa: 7 Chondrichthyes and 4 Actinopterygii. The genus *Sparisoma* is reported for the first time in the fossil record. The presence of fossil remains of the parrotfish *Sparisoma cretense* in Last Interglacial outcrops is significant, because it posits a setback for the theory that most of the present-day Azorean marine species colonized the area after the last glacial episode. Our multidisciplinary approach combines palaeontological data with ecological and published genetic data, offering an alternative interpretation. We suggest that most of the Azorean shallow-water subtropical and temperate marine species living in the archipelago during the Last Interglacial were not affected by the decrease in sea surface temperatures during the last glacial episode. We also predict low genetic diversity for fish species presently living in the Azores and ecologically associated with fine sediments. These are viewed as post-glacial colonizers or as 'bottleneck' survivors from the Last Glaciation.

Keywords

Actinopterygii; Azores archipelago; glacial-interglacial cycles; sea-surface temperature; *Sparisoma cretense*; *Labrodon pavimentatum*; Sparidae

Introduction

Oceanic islands have long been considered as ideal places to study biogeographical patterns and processes, and to test evolutionary theories (Darwin, 1859; Wallace, 1880). A detailed knowledge of an island's geological history and evolution is of paramount importance, influenced by the ontogenic state of the island as determined by a series of factors [e.g. geological age of the oldest subaerial lavas, terrestrial area, maximum altitude, latitude; see Whittaker et al. (2010); Fernández-Palacios et al. (2016)]. Such factors ultimately regulate and explain both the number of species that live on the island, as well as the functional composition of the biological assemblage itself. The marine fossil record for volcanic oceanic islands may be considered as rare or poor, especially when compared to that for vastly larger continentes (Ávila et al., 2018). However, the dating of an island's fossil fauna and flora when coupled with checklists validated by experts provides valuable insights for a number of disciplines such as palaeobiogeography, palaeoceanography, phylogenetic and climate-change studies (Ávila et al., 2019).

The remarkable marine fossil record of Santa Maria Island in the Azores Archipelago has been intensively studied over the last decades (for a review, see Ávila et al. (2018) and references therein). The result has been 204 Pliocene and 146 Pleistocene (Last Interglacial) species and 15–20 further ichnospecies reported for the island (Santos et al., 2015; Uchman et al., 2016, 2017; Raposo et al., 2018). The vast majority of specimens collected are invertebrates: molluscs (Zbyszewski & Ferreira, 1962; Ávila et al., 2002, 2015a, 2015b, 2016; Janssen et al., 2008), brachiopods (Kroh et al., 2008), crustacean balanids (Winkelmann et al., 2010), echinoderms (Madeira et al., 2011) and ostracods (Meireles et al., 2012). A small number of fossil vertebrate

72 remains also have been studied, most notably cetaceans (Estevens & Ávila, 2007; Ávila
73 et al., 2015c) and sharks (Ávila et al., 2012). Fossil bony fishes are known from the
74 island, but the last account for Santa Maria fossil Actinopterygii fishes' dates from the
75 1950's and 60's (Zbyszewski & Ferreira, 1962; Ferreira, 1955). With few exceptions
76 (Ávila et al., 2012; Betancort et al., 2016), the majority of the published
77 palaeoecological and palaeobiogeographical studies on the marine fauna and flora of
78 the Macaronesian archipelagos targeted sessile or low-motility species, such as the
79 marine molluscs, echinoderms, bryozoans, barnacles, ostracods and algae (Meco,
80 1977; Meco et al., 1997, 2015, 2016; Ávila et al., 2008a, 2008b, 2009; 2015a;
81 Winkelmann et al., 2010; Madeira et al., 2011; Santos et al., 2011, 2012a, 2012b;
82 Meireles et al., 2012; Ávila et al., 2013; Baarli et al., 2013, 2017; Betancort et al., 2014;
83 Johnson et al., 2014; Meireles et al., 2014; Rebelo et al., 2014; Tuya et al., 2017). Still
84 largely unresolved, an interesting question is how the evolutionary patterns and
85 processes inferred from these studies do relate with species' dispersal capabilities
86 (Ávila et al., 2019). Therefore, this study aims to: 1) review and update the status of all
87 existing Actinopterygii fossil material from Santa Maria Island; 2) use this new data to
88 test previous statements by several authors (e.g., Briggs, 1974; Santos et al., 1995;
89 Domingues et al., 2006, 2008) who concluded that the shallow littoral fauna of the
90 Azores was extirpated during the Last Glacial episode; and 3) compare the
91 palaeobiogeographical and palaeoecological patterns known from sessile and low-
92 dispersive species (e.g. non-planktotrophic marine molluscs), with that of highly motile
93 species such as fishes.
94
95 **Geographical and Geological Setting**

Azores Archipelago

The nine volcanic oceanic islands that form the Azores Archipelago are located in the north-eastern Atlantic Ocean (Fig. 1) and rise from a bathymetric anomaly (the Azores Plateau) with depths of about 2,000 m. The most distant islands (Flores, in the western group, and Santa Maria in the eastern group) are 615 km apart. Flores and Corvo belong to the North American tectonic plate, whereas the other seven islands are located around the most-studied area called the Azores Triple Junction (Laughton & Whitmarsh, 1974), a place where three major tectonic plates, North American, Nubian and Eurasian, interact. The Azores Triple Junction is limited by the East Azores Fracture Zone to the south, the Mid-Atlantic Ridge (MAR) to the west and the Terceira's Rift and Gloria Fault to the northeast and east (Searle, 1980) (Fig. 1A). This area (i.e. the Azores Plateau, the Azores Triple Junction and the islands that compose the Azores Archipelago), was named the 'Azores Geosyndrome' (Vogt & Jung, 2018), which is derived from a series of anomalies related to 'crustal thickness, rock composition, basement depth, plate boundary morphology, seismicity, gravity and geoid, and upper mantle seismic velocity structure'.

Santa Maria Island

This island has a complex geological history (see Ramalho et al. (2017) for a review). It is the oldest island of the Azores Archipelago, first rising above sea level at about 6 Ma, initially by Surtseyan activity (the Cabrestantes Formation), and then by subaerial, monogenetic volcanism associated to the Porto Formation. High rates of magma production formed a shield volcano (the Anjos volcanic complex, dating from 5.8 to 5.3 Ma), which substantially increased the area of the Santa Maria protoisland, as attested

120 by the present-day insular shelf (Ricchi et al., 2018). Although the entire volcanic
121 edifice likely has undergone subsidence since extrusion of the first lavas of the
122 submarine edifice, at around 5.3 Ma, a prolonged subsidence rate of about 100 m/myr
123 lasted until 3.5 Ma (Ramalho et al., 2017). Volcanic activity associated with the Anjos
124 shield volcano ceased at about 5.3 Ma and was followed by a period of about 1.2 myr
125 with almost no volcanism, during which the protoisland nearly vanished due to erosion
126 (Ávila et al., 2012; Ramalho et al., 2017), thus originating a large, flat, shallow
127 seamount. The sediments of this unit (the Touril volcano-sedimentary complex, 5.30 to
128 4.13 Ma) are highly fossiliferous and correspond to early Pliocene outcrops formerly
129 described in the literature as of Miocene in age (see Madeira et al. (2007) for a
130 review). Volcanic activity initiated again at about 4.1 Ma, during the first rejuvenated
131 stage, with eruptive foci associated with the Pico Alto volcanic successions, first
132 submarine and later subaerial in nature (Ramalho et al., 2017), thus originating the
133 revival of Santa Maria as an island. This stage lasted to 3.5 Ma, when the subsidence
134 trend was reversed, and the island's volcanic edifice initiated an uplift trend continuing
135 to the present day. Initially, a rate of 59 m/myr occurred from 3.5 to 2.15 Ma,
136 thereafter at a slower rate of 42 m/myr between 2.15 Ma and the present (Ricchi et
137 al., 2018). This uplift trend, coupled with Pleistocene glacio-eustatic sea-level
138 fluctuations, produced a staircase of 10 subaerial and of 5 submerged marine terraces,
139 the former particularly evident across the island's western sector at elevations ranging
140 from 7–11 to 210–230 m (Ramalho et al., 2017), and the latter on the shelf all around
141 the island at depths ranging between -40/-50 and -120/-140 m (Ricchi et al., 2018). A
142 second rejuvenated stage occurred from 3.2 to 2.8 Ma, associated with monogenetic
143 volcanism of the Feteiras Formation. Uplift has continued until today, but erosion

144 became the dominant agent impacting the island's landscape during the last 2.8 myr
145 (Ramalho et al., 2017).
146
147 **Institutional Abbreviations**
148 **DBUA-F**: fossil collection of the Department of Biology of the University of the Azores
149 (Portugal).
150 **LAQ-F**: fossil collection of the Liceu Antero de Quental, Ponta Delgada, São Miguel Island
151 (Azores, Portugal).
152 **MGM**: fossil collection of the former Museu Geológico e Mineiro, now Museu Geológico,
153 LNEG, Lisbon (Portugal).
154
155 **Methods**
156 Most of the 20 known fossiliferous outcrops on Santa Maria Island are early Pliocene in
157 age, but scattered Last Interglacial deposits from the Pleistocene also are known from
158 the north (Lagoinhas; Ávila et al., 2009a, 2009b) and southern shores (Prainha, Praia
159 do Calhau and Vinha Velha outcrops (Ávila et al., 2002, 2015a; Fig. 1B). The fossil fish
160 specimens reported, herein, were found in sedimentary layers from a total of eight
161 outcrops (cf. Table 1). Six of these contain fauna that deposited during the early
162 Pliocene: Cré (Kroh et al., 2008; Fig. 2A), Figueiral (Rebelo et al., 2016a; Ávila et al.,
163 2018a; Fig. 2B), Malbusca (Rebelo et al., 2016b; Johnson et al., 2017; Fig. 3A), West
164 Fault of Malbusca (Uchman et al., 2017 Fig. 3B), Pedra-que-pica (Ávila et al., 2015b,
165 2018a; Uchman et al., 2016; Fig. 3C), and the yet undescribed Ponta dos Frades
166 outcrop. The two remaining outcrops [Prainha (Fig. 2C) and Vinha Velha (Fig. 2D)]
167 include faunas from the Last Interglacial period (*c.* 116–130 kyr), of which the warmest

168 interval is known as MIS 5e (Marine Isotopic Stage 5e) (Ávila et al., 2015a). Figure 1B
169 shows the geographical location of each outcrop and Figure 4 displays representative
170 composite sections of the studied outcrops.
171 All specimens described were collected during fourteen fieldwork campaigns of
172 the *Palaeontology in Atlantic Islands* workshops, held on Santa Maria Island from 2002
173 to 2017. In compliance with the legislation that rules the "PalaeoPark Santa Maria", all
174 fossil specimens collected were deposited in the fossil collection at the Department of
175 Biology of the University of the Azores (DBUA-F). Over 1,300 lots containing fossil
176 specimens collected at Santa Maria Island were screened for fossil Actinopterygii
177 fishes, yielding a total of 42 lots. Systematics for Actinopterygii conform to the World
178 Register of Marine Species (WoRMS, 2018). As the oral and pharyngeal tooth plates
179 are frequently well preserved in the fossil record and as they display diagnostic
180 features (Bellwood & Schultz, 1991), direct comparisons of the fossil remains with
181 fossil and recent remains (whenever available) were used to classify our material. The
182 teeth terminology for Scaridae is in accordance with Day (2002).
183 All data generated or analysed during this study are included in this published
184 article.
185
186
187 **Results**
188 Actinopterygian fish taxa were found in the fossilliferous sediments of Santa Maria
189 Island: at least two extinct Sparidae species with a probable Mio-Pliocene temporal
190 range (Fig. 5A-Q); *Sparisoma cretense* (Linnaeus, 1758) (Fig. 6), an extant Scaridae
191 herein reported for the Pliocene and Pleistocene (Last Interglacial, MIS 5e) of the

Azores; and *Labrodon pavimentatum* Gervais, 1857 (Fig. 7), an extinct Labridae with a Mio-Pliocene temporal range. In total, 54 teeth and several pharyngeal plates were found.

SYSTEMATIC PALAEONTOLOGY

Class ACTINOPTERYGII Klein, 1885

Order PERCIFORMES Bleeker 1859

Family SPARIDAE Rafinesque, 1818

Genus and species indet.

Figure 5A–Q

Material Examined—54 teeth in total: Pedra-que-pica (26 teeth), Malbusca (17), Cré (4), West Fault of Malbusca (2), Figueiral (1): DBUA-F 165-1, 165-2, 204-2, 205-2, 250-1, 260, 286, 313, 344-2, 350, 382, 448, 460-1, 477-2, 508-1, 508-2, 595, 596, 597, 598, 599, 601, 647, 667, 668, 669, 671, 672, 673, 674, 966-2, 991, 1014, 1017, 1073, 1083. Cré, formerly also known as Pedreira dos Frades (2): MGM 11311, 11312 (one spheroidal and one oval molariform teeth, respectively); Santa Maria Island (4 teeth), no locality: MGM 11313.

Description—The 50 teeth examined from the DBUA collection represent three types of dentition: molariform, conical and incisiform teeth. We have examined a total of 39 molariform teeth, corresponding to the lingual series (36 spheroidal in shape (Fig. 5A-F, 5L), ranging from 2.87 to 17.34 mm in diameter; and 3 oval in shape, 5.89–11.51 mm), 9 conical teeth (Fig. 5G-K), corresponding to the labial series (2.41–7.93 mm in diameter) and 2 ‘spatulate’ incisiform teeth (1.45–1.53 mm in diameter; DBUA-F 668, 671). Some

of the largest spheroidal molariform teeth exhibit a central depression; these are considered to belong to the upper lingual series (Fig. 5A-C, 5F). Some of the largest teeth show radial grooves at the base of the crown. The general shape and size resemble some of the teeth described by (Betancort et al., 2016).

The four teeth housed at MGM (Lisbon) that we examined are all lateral teeth, with a conical shape, and rounded, worn crowns (Fig. 5M–Q).

Remarks—this material represents at least two taxa, including a small one and a larger one (possibly *Diplodus* and *Pagrus*, respectively). Some of these teeth might also belong to *Archosargus* (Cutwa & Turingan, 2000). However, any generic/specific assignment would be highly tentative without any additional osteological evidence.

Stratigraphic and geographic range—Extinct *Archosargus* species are reported from the Miocene and Pliocene of the Mediterranean Sea (Obrador & Mercadal, 1973; Vicens & Rodríguez-Perea, 2003; Mas & Antunes, 2008) and from the Miocene of France (Gagnaison, 2017). In the Atlantic, *Archosargus* species are reported from the Miocene of Portugal (Zbyszewski & Moitinho d'Almeida, 1950; Jonet et al., 1975) and Morocco (Lecointre, 1952), the Pliocene of Canary Islands (Gran Canaria Island) (Betancort et al., 2016) and from the Pliocene of the Azores (Santa Maria Island) (Zbyszewski & Moitinho d'Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962; Ávila et al., 2015b). The extinct species formerly known as *D. jomnitanus* is reported from the Miocene of France (Gagnaison, 2017), Portugal (Zbyszewski & Moitinho d'Almeida, 1950; Jonet et al., 1975) and the Mediterranean Sea (Vicens & Rodríguez-Perea, 2003), and from the Pliocene of the Azores (Santa Maria Island) (Zbyszewski & Moitinho d'Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962). Extinct *Pagrus* species are reported from Mio-Pliocene

239 sediments from the Mediterranean Sea and from Europe (Arambourg, 1927; Bauzá,
240 1948; Menesini, 1969; Bauzá & Plans, 1973; Jonet, 1975; Antunes et al., 1981).
241
242
243 Family LABRIDAE Cuvier, 1816
244 Tribe SCARINI Rafinesque, 1810
245 Genus *SPARISOMA* Swainson, 1839
246 *Sparisoma cretense* (Linnaeus, 1758)
247 Figure 6
248 **Material Examined**—Seven pharyngeal plates (4 lower and 3 upper) plus one
249 fragmentary tooth plate: Ponta dos Frades (3 lower and 3 upper pharyngeal plates),
250 Vinha Velha (1 lower pharyngeal plate) and Pedra-que-pica (one fragmentary tooth
251 plate): DBUA-F 825, 1030, 1069, 1214-1 to 1214-5.
252 **Description**—This species has a jaw formed from modified hindmost gill-arch, with
253 tooth-bearing bones above, denominated upper pharyngeal plates, and a large, single
254 bone below, the lower pharyngeal plate. Our fossil specimens' pharyngeal plates are
255 very similar to those of Recent specimens of *Sparisoma cretense*. The tooth rows of the
256 lower pharyngeal plate range from 11 to 12 in the fossil material, and from 10 to 14 in
257 the recent material. As all fossil lower pharyngeal plates examined are smaller than the
258 recent ones (see below), we attribute the intraspecific variation of the pharyngeal jaw
259 elements (i.e., the lower number of tooth rows in the fossil material, as well as the
260 slightly different angles of the lateral bony articulation in smaller fossil specimens) to
261 ontogeny. A fresh specimen of *S. cretense* was weighted and measured (1.585 kg; 45.50
262 cm in total length; 40.50 cm standard length). Its lower pharyngeal plate was 4.11 cm
263 wide, which compares with those from fossil material, which measured 2.62 cm wide

(DBUA-F 1030), 2.82 cm (DBUA-F 1214-1), 2.84 cm (DBUA-F 1214-2) and an inferred 3.82 cm (DBUA-F 825 broken specimen measuring 2.84 cm). The fragmentary tooth plate collected at Pedra-que-pica (DBUA-F 1069) measures 1.22 cm.

Today, there are 15 species of *Sparisoma* in the Atlantic Ocean and the Mediterranean Sea (Table 2). Of these, only 3 species are reported for the Eastern Atlantic: two tropical species (*Sparisoma choati* Rocha, Brito & Robertson, 2012, reported for Cabo Verde, São Tomé and Príncipe and to the tropical west African shores; *S. frondosum* (Agassiz, 1831), endemic to Cabo Verde); and the eurythermic *S. cretense*, with a wider geographical distribution, occurring in all the Macaronesian archipelagos, the Mediterranean Sea, Iberian shores and Senegal (Abecasis et al., 2008; Randall, 1990).

Ecology—The parrotfish *Sparisoma cretense* is an omnivorous daytime feeder species with specialized pharyngeal bones and muscles (Bullock & Monod, 1997). It is a sexually dimorphic species that lives on rocky bottoms covered by algae and sea grass beds, where it feeds on algae, sea grass and small invertebrates with its fused, beak-like jaw (Quignard & Pras, 1986; Abecasis et al., 2008). This shallow-water species is common to about 50 m depth (Guidetti & Boero, 2002).

Stratigraphic and geographic range—This extant species is presently reported from the Mediterranean Sea and from the eastern Atlantic shores of Portugal, the Azores, Madeira, Canary Islands, Cabo Verde and Senegal (Abecasis et al., 2008; Randall, 1990). A search for fossil *Sparisoma* species on the PaleoBiology Database and on Bellwood et al. (2019) yielded no occurrences. With the exception of otolithes from the Late Eocene of France referred to *Sparisoma* [Nolf (1988) but see remarks by Bellwood et al. (2019), in whose opinion these otoliths are not secure evidence of *Sparisoma*], this genus is reported herein for the first time from the fossil record based on dental remains. *S.*

cretense is herein reported from the Pliocene (Pedra-que-pica and Ponta dos Frades outcrops) and Pleistocene (Vinha Velha outcrop; Last Interglacial, MIS 5e) of Santa Maria Island, Azores.

Tribe HYPSIGENYINI Günther, 1861

Genus *LABRODON* Gervais, 1857

† *Labrodon pavimentatum* Gervais, 1857

Figure 7

Material Examined—Two lower pharyngeal plates, both from Pedra-que-pica outcrop (Fig. 7A–E): DBUA-F 386, 678. One lower pharyngeal plate from Santa Maria Island (no locality; Fig. 7F–G): MGM 11318.

Description—The dentition of Labridae is characterized by subtriangular pharyngeal plates composed by small, contiguous, flattened teeth, which may be rounded or sub-oval in shape (Jonet, 1968). The two lower pharyngeal plates collected from the Pedra-que-pica coquina in Santa Maria Island (Azores), as well as that deposited at MGM collection (Lisbon), conform with both the figures and the description provided by Betancort et al. (2016). Cocchi (1864) was the first to describe pharyngeal plates similar to our samples, which were attributed to *Labrodon multidens* (Sacco, 1916), and to *L. pavimentatum* (Simonelli, 1889).

Stratigraphic and geographic range—This extinct species is reported from the Miocene of France (Sauvage, 1875; Gagnaison, 2017), Portugal (Jonet et al., 1975), Poland (Bellwood et al., 2019), and the Mediterranean (Cocchi, 1864; Mas & Antunes, 2008). It is also reported from the western Atlantic, from the Miocene of Costa Rica (Laurito et al., 2014) and also from the Pliocene of Morocco (Lecointre, 1952), France (de Lumley,

1988) and the Azores (Santa Maria Island: Zbyszewski & Moitinho d'Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962; this work).

Discussion

During the late Miocene, the once continuous and large tropical Miocene European-West African palaeobiogeographical molluscan province (Ávila et al., 2016) stretched between about 50° N to the equator and further south to Angola (Baarli et al., 2017), at about 15° S (Fig. 8A). The waters around the Azores thus exhibited tropical temperatures during the late Miocene/early Pliocene, with mean annual sea surface temperatures (SSTs) estimated to be about 3.7–6.3°C higher than the present-day 20.6°C (Ávila et al., 2016). The extinct Pliocene fish species reported from the fossiliferous sediments of Santa Maria Island in the Azores (two Sparidae indet. and *Labrodon pavimentatum*) add at least three more taxa to an increasing number of known thermophilic taxa that went extinct or locally disappeared from this volcanic oceanic island (as well as from other Atlantic islands/archipelagos) during the pronounced climatic cooling events that characterized the mid-Piacenzian stage, towards the end of the Pliocene at about 3.3–3.6 Ma (or sometime prior), consequence of a global glaciation (the MIS M2; see Lisiecki & Raymo, 2005; Fig 8B). Several warm-water species are also known to have disappeared from the Canary Islands at about 4.2–4.1Ma (Meco et al., 2007). As a direct consequence of the MIS M2 glaciation, a southward geographical range contraction of the biogeographical provinces took place (Ávila et al., 2016; Fig. 8B). Table 3 lists examples of several extinctions or extirpations of Pliocene species from the marine fauna of Santa Maria

Island across a wide spectrum of phyla: molluscs (5 bivalves, 1 benthic macrogastropod, 1 neustonic gastropod and 4 holoplanktonic gastropods; Janssen et al., 2008; Beu, 2017; Ávila et al., 2015, 2016, 2018a), 4 echinoderms (Madeira et al., 2011), 1 brachiopod (Kroh et al., 2008), 1 barnacle (Winkelmann et al., 2010) and 5 sharks (Ávila et al., 2012). This pattern of extinctions/extirpations from volcanic oceanic islands during the late Pliocene also is reported for other Atlantic archipelagos, such as Madeira (Santos et al., 2012), Canary Islands (Meco et al., 2007, 2015, 2016; Baarli et al., 2017) and Cabo Verde (Baarli et al., 2017).

Between 5.3 and 4.13 Ma, the protoisland of Santa Maria probably was entirely destroyed, originating a large seamount where marine sediments rich in organic debris were deposited. In a broader palaeoceanographical context, the pattern of sea surface and bottom circulation in the area should have been different from the present day, as the connection between the Atlantic and the Pacific oceans was still open at the Central American Seaway (Garcia-Castellanos et al., 2009), and the Gibraltar Seaway had just reopened at 5.33 Ma, in an event known as the Zanclean or post-Messinian flood (Blanc, 2002). As attested by the fossil record of their geographical distribution, most of the Actinopterygii (this work) and Chondrichthyes fishes (Ávila et al., 2012) reported from the Pliocene of the Azores are also reported from Pliocene deposits in the northeast Atlantic and the Mediterranean Sea, with some species being reported as well from Pliocene sediments along the north-western shores of Africa, and no Western Atlantic species reported. This predominantly eastern Atlantic pattern of biogeographical relationships for the Azorean Pliocene marine fauna derives from the sea surface currents set in place by the easterly trade winds that facilitated dispersal of marine species from European shores towards the western Atlantic, a few reaching

and colonizing American Atlantic shores (Harzhauser et al., 2002; Baarli et al., 2017) and even the Pacific (Meco et al., 2016).

The final closure of the Central American Seaway, caused by re-emergence of the Panamanian land bridge (Briggs, 1995) at about 2.8 Ma (O'Dea et al., 2016), and the associated strengthening of the Gulf Stream, altered the north Atlantic system of sea surface circulation. The effect of a stronger Gulf Stream is testified by the shallow-water (<50 m depth) marine molluscs of the Azores, which show a gradual increase in the number of Western-Atlantic related species from 10.0% to 12.3%, when Last Interglacial (MIS 5e) checklists of fossil marine molluscs from the Azores (Ávila et al., 2002, 2009a, 2009b, 2015a) are compared to recent checklists available from this archipelago (Ávila, 2000; Cordeiro et al., 2015; Fig. 8C).

Intensification of the Pleistocene glacial episodes clearly impacted the Azorean fish pool in a similar manner to that described for the marine molluscs (Ávila et al., 2008a, 2008b, 2009a). We here expand on those conclusions, which were based on the MIS 5e mollusc fossil record from Santa Maria Island, and we postulate that range expansions of tropical and subtropical fishes with a Cabo Verdean origin probably occurred during 'windows of opportunity' towards the end of glacial Terminations (i.e. the short periods of time, *c.* 6 kyr, between the end of a glacial episode and the inception of a full interglacial episode). During those intervals, some fish species might have been able to reach, colonize and establish viable populations in the Canaries, Madeira and, in less numbers, the Azores Archipelago (Fig. 8D). We further hypothesize that, again in a similar manner to the marine molluscs (Ávila et al., 2008a, 2008b, 2009a), during the subsequent glacial episode, (1) all tropical species with a Cabo Verdean provenience that became established in the northern archipelagos

(Azores, Madeira and Canaries) during the previous interglacial were extirpated (Ávila et al., 2019; Fig. 8E), and (2) shallow-water fish species associated with fine sediments were functionally extirpated (i.e. locally disappeared from most volcanic oceanic islands) or their insular populations passed through a 'bottleneck' effect, resulting in a substantial net decrease in population size. The latter event occurs because the fine-sand habitat is mostly lost whenever sea level falls below the erosive edge of the insular shelf during glacial episodes (Ávila et al., 2008b, 2015a; Fig. 8G-I). The trigger for this outcome resides with the slope of the insular volcanic edifice being so steep below the erosive shelf edge, that it no longer becomes possible to physically retain fine sediments around the island, ultimately being lost to the abyssal depths (Fig. 8H). Either way, be it post-glacial colonizers or 'bottleneck' glacial survivors, we predict lower genetic diversity of the populations of shallow-water insular fish species associated with sandy bottoms [e.g. the following extant species in the Azores: the European finless eel *Apterichtus caecus* (Linnaeus, 1758); the wide-eyed flounder *Bothus podas* (Delaroche, 1809); the striped red mullet *Mullus surmuletus* Linnaeus, 1758; the Atlantic lizard fish *Synodus saurus* (Linnaeus, 1758); the greater weever *Trachinus draco* Linnaeus, 1758; and the pearly razorfish *Xyrichtys novacula* (Linnaeus, 1758)], when compared with continental populations. This prediction can be tested using molecular tools.

In contrast, fish species associated with algae-covered rocky shores, such as the omnivorous parrotfish *Sparisoma cretense*, were not affected by the drop in SSTs associated with the inception of glacial episodes, which was estimated at about 2–3°C (Crowley, 1981) in the region of the Azores. The lineage that led to the two eastern Atlantic species, *S. cretense* (presently reported from the Mediterranean Sea and from

408 the eastern Atlantic shores of mainland Portugal, the Azores, Madeira, Canaries, Cabo
409 Verde and Senegal; cf. Table 2), and *S. strigatum* (Günther, 1862) (endemic to Saint
410 Helena and Ascension islands; Table 2), originated at about 10 Ma from a West Atlantic
411 ancestor (Bernardi et al., 2000). The oldest known fossil specimens of *S. cretense* were
412 collected in two Pliocene outcrops from Santa Maria Island (Pedra-que-pica and Ponta
413 dos Frades) and dated as 4.78±0.13 to 4.13±0.19 myr in age (Table 1), thus our data
414 are in agreement with the estimates of Bernardi and colleagues (2000).
415 Last interglacial (MIS 5e) fossils of *S. cretense* were also collected from a
416 Pleistocene outcrop (Vinha Velha; cf. Table 1). Today, *S. cretense* lives as far north as
417 the eastern Atlantic shores of mainland Portugal, where it breeds during the summer,
418 from July to September (Abecasis et al., 2008; Froese & Pauly, 2018), with mean SSTs
419 varying from 17 to 19°C. The present average SSTs range in the Azores from 15° C in
420 the winter, to about 23–24°C in the summer (Ávila et al., 2008c). The gonadosomatic
421 index of *S. cretense* (which is closely associated with mean temperature) increases in
422 the Azores from June to August and then drops to a minimum in November (Afonso et
423 al., 2008). Hence, although it mainly breeds from mid-July to mid-September, it is
424 possible that this species extends its reproductive activity through October (Afonso et
425 al., 2008). Therefore, in our opinion, neither temperature nor habitat shift were an
426 impediment for the survival of this species in the Azores throughout the last glacial
427 episode. Our view differs from that of previous authors, who suggested that 'the drop
428 of sea temperatures (…) that occurred during the Pleistocene probably resulted in
429 mass extinctions' (of fishes) and so 'most of the organisms now present would have
430 reached the Azores in the last 17,000 years' (Santos et al., 1995). Our reasoning also
431 contradicts the conclusions of Domingues et al. (2008), who stated that 'persistence of

(…) *S. cretense* in the Azores archipelago during the Pleistocene glaciations is difficult to admit'. Moreover, the very abundant and well-studied MIS 5e (i.e. Last Interglacial) fossil record from Santa Maria Island disproves the conclusions of these former authors.

The finding of fossil pharyngeal plates belonging to *S. cretense* in MIS 5e sediments does not necessarily exclude the hypothesis that this species locally disappeared during the Last Glaciation, only to recolonize the archipelago post-glacially. Nevertheless, we consider it more plausible to argue that such extirpation did not happen, taking in consideration the following: (1) detailed studies on the Azorean MIS 5e and recent marine molluscs showed that the drop of the SSTs during the Last Glaciation only affected two groups of species: the tropical species that reached the Azores probably during a 'window of opportunity' associated with the final phase of Termination 2, and bivalve species associated to fine-sand sediments; both groups were extirpated (Ávila et al., 2008a, 2008b, 2009b, 2015a); (2) as temperature is known to play a key role on marine fish species biology (Pepin, 1991; van der Kraak & Pankhurst, 1997; Pankhurst & Porter, 2003; Dolomatova et al., 2013; Poloczanska et al., 2016) and in light of the premises pointed above, the drop of SSTs was not sufficient enough to severely affect the survival, growth and reproduction of the temperate parrotfish *S. cretense* in the Azores during the Last Glacial episode; (3) finally, if *S. cretense* was a post-glacial colonizer of the Azores, the genetic diversity of the Azorean populations should be low, in comparison with southern Madeiran populations (postulated to have not been affected by the drop of SSTs), but that is not the case, as pointed out by Domingues et al. (2008). Thus, combining our palaeontological data with ecological and genetic data from other authors (Abecasis et

al., 2008; Afonso et al., 2008; Domingues et al., 2008), we believe the most plausible scenario is the survival of most (if not all) temperate and subtropical fish species in the Azores during the Last Glacial episode, so long as their ecological traits are not tied on sandy habitats.

This contribution expands the number of Pliocene fishes reported from the Azores to at least 11 taxa: seven taxa of Chondrichthyes (Ávila et al., 2012): *Carcharias acutissima* (Agassiz, 1833), *Carcharhinus* cf. *leucas* (Valenciennes, 1839 in Müller and Henle, 1839–1841), *Cosmopolitodus hastalis* (Agassiz, 1833), *Isurus oxyrinchus* Rafinesque, 1810, *Otodus (Megaselachus) megalodon* (Agassiz in Charlesworth, 1837), *Notorynchus primigenius* (Agassiz, 1833) and *Paratodus benedenii* (Le Hon, 1871); and four of Actinopterygii (this work): at least two Sparidae indet. taxa, *Labrodon pavimentatum* and *Sparisoma cretense*. Most of these are also reported for the Pliocene of Canaries (Betancort et al., 2016), the exceptions being *Carcharhinus* cf. *priscus* (Agassiz, 1843), *Diodon scillae* Agassiz, 1843 and *Galeocerdo* cf. *aduncus* Agassiz, 1843, only reported for Canary Islands; and Sparidae indet., *N*. *primigenius* and *S*. *cretense*, only reported for the Azores. The high number of shared species on archipelagos over 1,100 km apart is understandable if it is taken into consideration that during the Pliocene both archipelagos were part of the same Atlantic biostratigraphic molluscan province [the Pliocene Mediterranean-West African Province of Ávila et al. (2016); see Fig.8B] sharing similar tropical palaeoclimatic conditions.

Conclusions

479 The genus *Sparisoma* Swainson, 1839 is reported, herein, for the first time in
480 the fossil record. The discovery of several pharyngeal plates of *S*. *cretense* on Pliocene
481 and on MIS 5e sediments (Last Interglacial) of Santa Maria Island challenges former
482 authors (Briggs, 1974; Santos et al., 1995; Domingues et al., 2006, 2008) who argued
483 that mass extinctions affected the shallow-water marine fauna of the Azores during
484 the course of the Last Glaciation and that, as a consequence, most of the present
485 Azorean marine species colonized the area during the last 17–18 kyr. A
486 multidisciplinary approach, merging our palaeontological data with ecological and
487 genetic data, offers an alternative, more plausible explanation, suggesting that most (if
488 not all) of the Azorean shallow-water subtropical and temperate marine species living
489 in the archipelago during the Last Interglacial (and probably in previous interglacials as
490 well) and associated to non-mobile sediments (e.g., rocky shores, covered or not by
491 algae), were not affected by the drop of the SSTs during the Last Glacial episode.
492 Finally, we also predict that the only marine fish species that were extirpated
493 from the Azores during the course of the Last Glaciation were those associated with
494 fine sand (Fig. 8G-I), and the thermophilic species that colonized the archipelago
495 during the Last Interglacial/Termination 2 'window of opportunity' (Fig. 8D-F).
496 Whether fish species ecologically associated with fine sediments and presently living in
497 the Azores are post-glacial colonizers or 'bottleneck' survivors from the Last Glaciation
498 should be assessed by genetic tools, as we anticipate low genetic diversity of the
499 Azorean populations, when compared with continental counterparts.
500
501 **Acknowledgments**

We thank Direcção Regional da Ciência e Tecnologia (Regional Government of the Azores), FCT (Fundação para a Ciência e a Tecnologia) of the Portuguese Government, and Câmara Municipal de Vila do Porto for financial support, and acknowledge the field assistance of Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto. We are grateful to the organizers and participants of all editions of the International Workshop *Palaeontology in Atlantic Islands* who helped with fieldwork (2002–2017). We thank F. Couto (Hobby Factor) for the aerial/drone photos. We thank M. Ramalho and J. Anacleto (Museu Geológico, LNEG, Lisbon), for allowing access to their historical collections. SPA acknowledges his research contract (IF/00465/2015) funded by the Portuguese Science Foundation (FCT). LB acknowledges her PhD Grant from FCT (SFRH/BD/135918/2018). CSM is benefiting from a PhD grant M3.1.a/F/100/2015 from Fundo Regional para a Ciência e Tecnologia (FRCT). This research also received substantial support from the SYNTHESYS Project (http://www.synthesys.info/), which is financed by the European Community Research Infrastructure Action under the FP7 'Capacities' Program: SPA studied fossil collection at the Museum für Naturkunde, Berlin (DE-TAF-1071). This work also was supported by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE, and by National Funds through FCT under the UID/BIA/50027/2013, POCI-01-0145-FEDER-006821 and under DRCT-M1.1.a/005/Funcionamento-C-/2016 (CIBIO-A) project from FRCT. This work was also supported by FEDER funds (in 85%) and by funds of the Regional Government of the Azores (15%) trough Programa Operacional Açores 2020, in the scope of the project "AZORESBIOPORTAL – PORBIOTA": ACORES-01-0145-FEDER-000072.

526

527 **Author Contributions**

528 S.P.A and R.V. designed the research plan. S.P.A., P.M., R.C. and R.V. collected the

529 fossil material. C.S.M. constructed all figures. S.P.A., M.E.J and R.V. wrote the

530 manuscript, with input from all authors, who discussed and commented on the

531 manuscript.

532

533

534 **Additional Information**

535 **Competing Interests:** The authors declare no competing interests.

536

537

538 **References**

539 Abecasis, D., Bentes, L., Ribeiro, J., Machado, D., Oliveira, F., Veiga, P., Gonçalves, J. M.

540 S. & Erzini, K., 2008. First record of the Mediterranean parrotfish, *Sparisoma*

541 *cretense* in Ria Formosa (south Portugal). *Marine Biodiversity Records* **1**, e27.

542 Afonso, P., Morato, T. & Santos, R. S., 2008. Spatial patterns in reproductive traits of

543 the temperate parrotfish *Sparisoma cretense*. *Fisheries Research* **90**, 92–99.

544 Antunes, M.T., Jonet, S. & Nascimento, A., 1981: Vertébrés (crocodiliens, poissons) du

545 Miocène marin de l'Algarve occidentale. Ciências da Terra, 6: 9-38.

546 Arambourg, C., 1927: Les poissons fossiles d'Oran. Matériaux pour la carte géologique

547 de l´Algérie, Paléontologie, Alger, 6: 1-293.

548 Ávila, S. P., 2000. Shallow-water marine molluscs of the Azores: biogeographical
549 relationships. *Arquipélago* Life and Marine Sciences. **Supplement 2(Part A)**,
550 99–131.
551 Ávila, S. P., 2013. Unravelling the patterns and processes of evolution of marine life in
552 oceanic islands: a global framework; pp. : 95–125 in: J. M. Fernández-Palacios,
553 L. de Nascimento, J. C. Hernández, S. Clemente, A. González, and J. P. Díaz-
554 González (Eds.), Climate Change perspectives from the Atlantic: past, present
555 and future. Universidad de La Laguna, Tenerife.
556 Ávila, S. P., Amen, R., Azevedo, J. M. N., Cachão, M. & García-Talavera, F., 2002.
557 Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa
558 Maria Island, Azores). *Açoreana* **9**, 343–370.
559 Ávila, S. P., Madeira, P., Mendes, N., Rebelo, A. C., Medeiros, A., Gomes, C., García-
560 Talavera, F., da Silva, C. M., Cachão, M., Hillaire-Marcel, C. & Martins, A. M. F.,
561 2008a. Mass extinctions in the Azores during the last glaciation: fact or myth?
562 *Journal of Biogeography* **35**, 1123–1129.
563 Ávila, S. P., da Silva, C. M., Cachão, M., Landau, B., Quartau, R. & Martins, A. M. F.,
564 2008b. Local disappearance of bivalves in the Azores during the last glaciation.
565 *Journal of Quaternary Science* **23**, 777–785.
566 Ávila, S. P., Melo, P. J., Lima, A., Amaral, A., Martins, A. M.F. & Rodrigues, A., 2008c.
567 The reproductive cycle of the rissoid *Alvania mediolittoralis* Gofas, 1989
568 (Mollusca, Gastropoda) at São Miguel Island (Azores, Portugal). *Journal of*
569 *Invertebrate Reproduction and Development* **52**, 31–40.
570 Ávila, S. P., da Silva, C. M., Schiebel, R., Cecca, F., Backeljau, T. & Martins, A. M. F.,
571 2009a. How did they get here? Palaeobiogeography of the Pleistocene marine

molluscs of the Azores. *Bulletin of the Geological Society of France* **180**, 295–307.

Ávila, S. P., Madeira, P., Zazo, C., Kroh, A., Kirby, M., da Silva, C. M., Cachão, M. & Martins, A. M. F., 2009b. Palaeoecology of the Pleistocene (MIS 5.5) outcrops of Santa Maria Island (Azores) in a complex oceanic tectonic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology* **274**, 18–31.

Ávila, S. P., Rebelo, A. C., Medeiros, A., Melo, C., Gomes, C., Bagaço, L., Madeira, P., Borges, P. A., Monteiro, P., Cordeiro, R., Meireles, R. & Ramalho, R. S., 2010. Os fósseis de Santa Maria (Açores). 1. A jazida da Prainha, 103 pp. OVGA – Observatório Vulcanológico e Geotérmico dos Açores, Lagoa (2010).

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

Ávila, S. P., Melo, C., Silva, L., Ramalho, R. S., Quartau, R., Hipólito, A., Cordeiro, R., Rebelo, A. C., Madeira, P., Rovere, A., Hearty, P. J., Henriques, D., da Silva, C. M., Martins, A. M. F. & Zazo, C., 2015a. A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews* **114**, 126–148.

Ávila, S. P., Ramalho, R. S., Habermann, J. M., Quartau, R., Kroh, A., Berning, B., Johnson, M. E., Kirby, M. X., Zanon, V., Titschack, J., Goss, A., Rebelo, A. C., Melo, C., Madeira, P., Cordeiro, R., Meireles, R., Bagaço, L., Hipólito, A., Uchman, A., da Silva, C. M., Cachão, M. & Madeira, J., 2015b. Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a

596 volcanic oceanic island (Santa Maria Island, Azores, NE Atlantic Ocean).
597 *Palaeogeography, Palaeoclimatology, Palaeoecology* **430**, 57–73.
598 Ávila, S. P., Cordeiro, R., Rodrigues, A. R., Rebelo, A. C., Melo, C., Madeira, P. &
599 Pyenson, N. D., 2015c. Fossil Mysticeti from the Pleistocene of Santa Maria
600 Island, Azores (NE Atlantic Ocean), and the prevalence of fossil cetaceans on
601 oceanic islands. *Palaeontologia Electronica* **18.2.27A**, 1–12.
602 Ávila, S. P., Melo, C., Berning, B., Cordeiro, R., Landau, B. & da Silva, C. M., 2016.
603 *Persististrombus coronatus* (Mollusca: Strombidae) in the early Pliocene of
604 Santa Maria Island (Azores: NE Atlantic): palaeoecology, palaeoclimatology
605 and palaeobiogeographic implications on the NE Atlantic Molluscan
606 Biogeographical Provinces. *Palaeogeography, Palaeoclimatology,*
607 *Palaeoecology* **441**, 912–923.
608 Ávila, S. P., Ramalho, R. S., Habermann, J. M. & Titschack, J., 2018. The marine fossil
609 record at Santa Maria Island (Azores). In: U. Kueppers, and C. Beier (Eds),
610 Volcanoes of the Azores. Revealing the Geological Secrets of the Central
611 Northern Atlantic Islands. Springer, Berlin, pp. 155–196.
612 Ávila, S. P., Melo, C., Sá, N., Quartau, R., Rijsdijk, K., Ramalho, R. S., Berning, B.,
613 Cordeiro, R., de Sá, N. C., Pimentel, A., Baptista, L., Medeiros, A., Gil, A. &
614 Johnson, M. E., 2019. Towards a “Sea-Level Sensitive Marine Island
615 Biogeography” model: the impact of glacio-eustatic oscillations in global
616 marine island biogeographic patterns. *Biological Reviews* **94**, 1116–1142.
617 Baarli, B. G., Santos, A., Mayoral, E. J., Ledesma-Vázques, J., Johnson, M. E., da Silva, C.
618 M. & Cachão, M., 2013. What Darwin did not see: Pleistocene fossil

assemblages on a high-energy coast at Ponta das Bicudas, Santiago, Cape Verde Islands. *Geological Magazine* **150**, 183–189.

Baarli, B. G., Malay, M. C. D., Santos, A., Johnson, M. E., da Silva, C. M., Meco, J., Cachão, M. & Mayoral, E. J., 2017. Miocene to Pleistocene transatlantic dispersal of *Ceratoconcha* coral-dwelling barnacles and North Atlantic island biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* **468**, 520–528.

Bauzá, J., 1948. Nuevas aportaciones al conocimiento de la ictiología del Neógeno catalano-balear. Estudios Geológicos, 8: 221-239.

Bauzá, J. & Plans, J., 1973. Contribución al conocimiento de la fauna ictiológica del Neógeno Catalano Balear. Boletín de la Sociedad de Historia Natural de las Baleares, 28: 72-131.

Bellwood, D. R. & Schultz, O., 1991. A Review of the fossil record of the parrotfishes (Labroidei: Scaridae) with a description of a new *Calotomus* species from the middle Miocene (Badenian) of Austria. *Annalen des Naturhistorischen Museums in Wien* **92**, 55–71.

Bellwood, D. R., Schultz, O., Siqueira, A. C. & Cowman, P. F., 2019. A review of the fossil record of the Labridae. *Annalen des Naturhistorischen Museums in Wien, Serie A* **121**, 125–193.

Bernardi, G., Robertson, D. R., Clifton, K. E. & Azzurro, E., 2000. Molecular systematics, zoogeography, and evolutionary ecology of the Atlantic parrotfish genus *Sparisoma*. *Molecular Phylogenetics and Evolution* **15**, 292–300.

641 Betancort, J. F., Lomoschitz, A. & Meco, J., 2014. Mio-Pliocene crustaceans from the
642 Carany Islands, Spain. *Rivista Italiana di Paleontologia e Stratigrafia* **120**, 337–
643 349.
644 Betancort, J. F., Lomoschitz, A. & Meco, J., 2016. Early Pliocene fishes (Chondrichthyes,
645 Osteichthyes) from Gran Canaria and Fuerteventura (Canary Islands, Spain).
646 *Estudios Geológicos* **72**, e054.
647 Beu, A. G., 2017. Evolution of *Janthina* and *Recluzia* (Mollusca: Gastropoda:
648 Epitoniidae). *Records of the Australian Museum* **69**, 119–222.
649 Blanc, P.-L., 2002. The opening of the Plio-Quaternary Gibraltar Strait: assessing the
650 size of a cataclysm. *Geodinamica Acta* **15**, 303–317.
651 Briggs, J. C., 1974. Marine zoogeography. McGraw-Hill, New York, 475 pp.
652 Briggs, J. C., 1995. Global Biogeography. Elsevier, Amsterdam, 452 pp.
653 Bullock, A. E. & Monod, T., 1997. Myologie céphalique de deux poissons perroquets
654 (Teleostei: Scaridae). *Cybium* **21**, 173–199.
655 Cocchi, I., 1864. Monografia dei Pharyngodopilidae. Nuova famiglia di Pesci Labroidi.
656 *Annali del Museo Imperiale di Fisica e Storia Naturale di Firenze* **1**, 62–152.
657 Cordeiro, R., Borges, J. P., Martins, A. M. F. & Ávila, S. P., 2015. Checklist of the littoral
658 gastropods (Mollusca: Gastropoda) from the Archipelago of the Azores (NE
659 Atlantic). *Biodiversity Journal* **6**, 855–900.
660 Crowley, T. J., 1981. Temperature and circulation changes in the eastern North Atlantic
661 during the last 150,000 years: Evidence from the planktonic foraminiferal
662 record. *Marine Micropaleontology* **6**, 97–129.
663 Cutwa, M. M., & Turingan, R. G., 2000. Intralocality variation in feeding biomechanics
664 and prey use in *Archosargus probatocephalus* (Teleostei, Sparidae), with

665 implications for the ecomorphology of fishes. *Environmental Biology of Fishes*
666 **59**, 191–198.
667 Darwin, C., 1859. On the origin of species by means of natural selection, or the
668 preservation of favoured races in the struggle for life. John Murray, London,
669 502 pp.
670 Day, J. J., 2002. Phylogenetic relationships of the Sparidae (Teleostei: Percoidei) and
671 implications for convergent trophic evolution. *Biological Journal of the*
672 *Linnean Society* **76**, 269–301.
673 Dolomatova, S., Zukowb, W. & Brudnickib, R., 2013. Role of temperature in regulation
674 of the life cycle of temperate fish. *Russian Journal of Marine Biology* **39**, 81–
675 91.
676 Domingues, V. S., Santos, R. S., Brito, A. & Almada, V. C., 2006. Historical population
677 dynamics and demography of the eastern Atlantic pomacentrid *Chromis*
678 *limbata* (Valenciennes, 1833). *Molecular Phylogenetics and Evolution* **40**, 139–
679 147.
680 Domingues, V. S., Alexandrou, M., Almada, V. C., Robertson, D. R., Brito, A., Santos, R.
681 S. & Bernardi, G., 2008. Tropical fishes in a temperate sea: evolution of the
682 wrasse *Thalassoma pavo* and the parrotfish *Sparisoma cretense* in the
683 Mediterranean and the adjacent Macaronesian and Cape Verde Archipelagos.
684 *Marine Biology* **154**, 465–474.
685 Estevens, M. & Ávila, S. P., 2007. Fossil whales from the Azores. *Açoreana* **Suplemento**
686 **5**, 140–161.
687 Fernández-Palacios, J.M., Rijsdijk, K. F., Norder, S. J., Otto, R., de Nascimento, L.,
688 Fernández-Lugo, S., Tjørve, E. & Whittaker, R. J., 2016. Towards a glacial–

689 sensitive model of island biogeography. *Global Ecology and Biogeography* **25**,
690 817–830.
691 Ferreira, O. da V., 1955. A fauna miocénica da ilha de Santa Maria (Açores).
692 *Comunicações dos Serviços Geológicos de Portugal* **36**, 9–44.
693 Froese, R. & Pauly, D. (eds), 2018. FishBase. *Sparisoma cretense*. Available from
694 http://www.fishbase.org, version (06/2018). Accessed on 4 October 2018.
695 Gagnaison, C., 2017. Le site paléontologique du Grand Morier (Pont-Boutard, Indre-et-
696 Loire, France): contexte géologique et détail biostratigraphique des formations
697 cénozoïques à partir des assemblages de vertébrés fossiles. *Geodiversitas* **39**,
698 251–271.
699 Garcia-Castellanos, D., Estrada, F., Jiménez-Munt, I., Gorini, C., Fernàndez, M., Vergés,
700 J. & de Vicente, R., 2009. Catastrophic flood of the Mediterranean after the
701 Messinian salinity crisis. *Nature* **462**, 778–781.
702 Guidetti, P. & Boero, F., 2002. Spatio-temporal variability in abundance of the parrotfish,
703 *Sparisoma cretense*, in SE Apulia (SE Italy, Mediterranean Sea). *Italian Journal*
704 *of Zoology* **69**, 229–232.
705 Harzhauser, M., Piller, W. E. & Steininger, F. F., 2002. Circum-Mediterranean Oligo–
706 Miocene biogeographic evolution – the gastropods' point of view.
707 *Palaeogeography, Palaeoclimatology, Palaeoecology* **183**, 103–133.
708 Janssen, A. W., Kroh, A. & Ávila, S. P., 2008. Early Pliocene heteropods and pteropods
709 (Mollusca, Gastropoda) from Santa Maria (Azores, Portugal): systematics and
710 biostratigraphic implications. *Acta Geologica Polonica* **58**, 355–369.
711 Johnson, M. E., Ramalho, R. S., Baarli, B. G., Cachão, M., da Silva, C. M., Mayoral, E. J. &
712 Santos, A., 2014. Miocene–Pliocene rocky shores on São Nicolau (Cape Verde

713 Islands): Contrasting windward and leeward biofacies on a volcanically active
714 oceanic island. *Palaeogeography, Palaeoclimatology, Palaeoecology* **395**, 131–
715 143.
716 Johnson, M. E., Uchman, A., Costa, P. J. M., Ramalho, R. S. & Ávila, S.P., 2017. Intense
717 hurricane transport sand onshore: example from the Pliocene Malbusca
718 section on Santa Maria Island (Azores, Portugal). *Marine Geology* **385**, 244–
719 249.
720 Jonet, S., 1968. Notes d'ichthyologie miocène portugaise. IV – Les Labridae. *Boletim da*
721 *Sociedade Geológica de Portugal* **16**, 209–221.
722 Jonet, S., 1975. Notes d'ichthyologie Miocene Portugaise. Boletim da Sociedade
723 Geológica de Portugal, 29(3): 135-173.
724 Jonet, S., Kotchetoff, Y. & Kotchetoff, B., 1975. L'helvétien du Penedo et sa faune
725 ichthyologique. *Comunicações dos Serviços Geológicos de Portugal* **59**, 193–
726 228.
727 van der Kraak, G. & Pankhurst, N. W., 1997. Temperature effects on the reproductive
728 performance of fish; pp. 159–176 in Wood, C. M. & Macdonald D. G. (Eds.),
729 Global warming: implications for freshwater and marine fish. CUP, Cambridge.
730 Kroh, A., Bitner, M. A. & Ávila, S. P., 2008. *Novocrania turbinata* (Brachiopoda) from
731 the Early Pliocene of the Azores (Portugal). *Acta Geologica Polonica* **58**, 473–
732 478.
733 Laughton, A. S., & Whitmarsh, R. B., 1974. The Azores-Gibraltar plate boundary; pp.
734 63–81 in L. Kristjansson (Ed.), Geodynamics of Iceland and the North Atlantic
735 Area. Kufstein, Austria.

Laurito, C. A., Calvo, C., Valerio, A. L., Calvo, A. & Chacón, R., 2014. Ictiofauna del mioceno inferior de la localidad de Pacuare de Tres Equis, formación río Banano, provincia de Cartago, Costa Rica, y descripción de un nuevo género y una nueva especie de Scaridae. *Revista Geológica de América Central* **50**, 153–192.

Lecointre, G., 1952. Recherches sur le Néogène et le Quaternaire marin de la Côte Atlantique du Maroc, Tome 2 – Paléontologie. *Notes et Mémoires du Service Géologique du Maroc* **99**, 1–172.

Lisiecki, L. E. & Raymo, M. E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography* **20**, PA1003.

de Lumley, H., 1988. La stratigraphie du remplissage de la Grotte du Vallonnet. *L'Anthropologie* **92**, 407–428.

Madeira, P., Kroh, A., Martins, A. M. F. & Ávila, S. P., 2007. The marine fossils from Santa Maria Island (Azores, Portugal): an historical overview. *Açoreana* **Suplemento 5**, 59–73.

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

Martín-González, E., Buckeridge, J., Castillo, C. & García-Talavera, F., 2012. First record of a tropical shallow water barnacle *Tetraclita* sp. (Cirripedia: Tetraclitoidea) from the middle Neogene of the Canary Islands. *Vieraea* **40**, 97–106.

Mas, G. & Antunes, M. T., 2008. Presència de *Tomistoma* cf. *lusitanica* (Vianna i Moraes, 1945) (Reptilia: Crocodylia) al Burdigalià inferior de Mallorca (Illes Balears,

760 Mediterrània occidental). Implicacions paleoambientals. *Bolletí de la Societat*
761 *d'Història Natural de les Balears* **51**, 131–146.
762 Meco, J., 1977. Los *Strombus* Neogenos y Cuaternarios del Atlantico Eurafricano.
763 (Taxonomia, Biostratigrafia y Palaeoecologia). *Palaeontologia de Canarias* **1**,
764 1–142.
765 Meco, J., Petit−Maire, N., Fontugne, M., Shimmield, G. & Ramos, A. J., 1997. The
766 Quaternary deposits in Lanzarote and Fuerteventura (Eastern Canary Islands,
767 Spain): an overview; pp. 123–136 in J. Meco, and N. Petit−Maire (Eds.),
768 Climates of the Past−Proceedings of the CLIP meeting 1995. Universidad de
769 Las Palmas de Gran Canaria, Servicio de Publicaciones, Gran Canaria.
770 Meco, J., Scaillet, S., Guillou, H., Lomoschitz, A., Carracedo, J. C., Ballester, J.,
771 Betancort, J.-F. & Cilleros, A., 2007. Evidence for long-term uplift on the
772 Canary Islands from emergent Mio–Pliocene littoral deposits. *Global and*
773 *Planetary Change* **57**, 222–234.
774 Meco, J., Koppers, A. A. P., Miggins, D. P., Lomoschitz, A. & Betancort, J.-F., 2015. The
775 Canary record of the evolution of the North Atlantic Pliocene: New $^{40}Ar/^{39}Ar$
776 ages and some notable palaeontological evidence. *Palaeogeography,*
777 *Palaeoclimatology, Palaeoecology* **435**, 53–69.
778 Meco, J., Lomoschitz, A. & Betancort, J.-F., 2016. Early Pliocene tracer of North Atlantic
779 and South Pacific sea surface currents: *Janthina typica* (Bronn, 1860)
780 (Mollusca: Gastropoda). *Revista Mexicana de Ciencias Geológicas* **33**, 192–
781 197.
782 Meireles, R. P., Faranda, C., Gliozzi, E., Pimentel, A., Zanon, V. & Ávila, S. P., 2012. Late
783 Miocene marine ostracods from Santa Maria Island, Azores (NE Atlantic):

784 Systematics, palaeoecology and palaeobiogeography. *Revue de*
785 *Micropaléontologie* **55**, 133–148.
786 Meireles, R. P., Keyser, D. & Ávila, S. P., 2014. The Holocene to Recent ostracods of the
787 Azores (NE Atlantic): systematics and biogeography. *Marine*
788 *Micropaleontology* **112**, 13–26.
789 Nolf, D., 1988. Les otolithes de téléosténs éocènes d'Aquitaine (sud-ouest de la France)
790 et leur intérêt stratigraphique. Académie Royale de Belgique, Mémoires de la
791 Classe des Sciences, Collection 4, (Serie 2) 19, 1-147. Bruxelles.
792 Obrador, A. & Mercadal, B., 1973. Nuevas localidades con fauna ictiológica para el
793 Neógeno menorquín. *Acta Geológica Hispánica* **8**, 115–119.
794 O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L.,
795 Collins, L. S., de Queiroz, A., Farris, D. W., Norris, R. D., Stallard, R. F.,
796 Woodburne, M. O., Aguilera, O., Aubry, M.-P., Berggren, W. A., Budd, A. F.,
797 Cozzuol, M. A., Coppard, S. E., Duque-Caro, H., Finnegan, S., Gasparini, G. M.,
798 Grossman, E. L., Johnson, K. G., Keigwin, L. D., Knowlton, N., Leigh, E. G.,
799 Leonard-Pingel, J. S., Marko, P. B., Pyenson, N. D., Rachello-Dolmen, P. G.,
800 Soibelzon, E., Soibelzon, L., Todd, J. A., Vermeij, G. J. & Jackson, J. B. C., 2016.
801 Formation of the Isthmus of Panama. *Science Advances* **2**, e1600883.
802 Pankhurst, N. W. & Porter, M. J. R., 2003. Cold and dark or warm and light: variations
803 on the theme of environmental control of reproduction. *Fish Physiology and*
804 *Biochemistry* **28**, 385–389.
805 Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival
806 rates of the pelagic early life history stages of marine fish. *Canadian Journal of*
807 *Fisheries and Aquatic Sciences* **48**, 503–518.

808 Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S.,
809 Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman,
810 D. S. & Sydeman, W. J., 2016. Responses of Marine Organisms to Climate
811 Change across Oceans. *Frontiers Marine Science* **3**, 62 (2016).
812 Quignard, J.-P. & Pras, A., 1986. Scaridae; Vol. II, pp. 943–944 in Whitehead, P. J. P.,
813 Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E. (Eds), Fishes of the
814 North-eastern Atlantic and the Mediterranean. UNESCO, Paris.
815 Ramalho, R. S., Helffrich, G., Madeira, J., Cosca, M., Thomas, C., Quartau, R., Hipólito,
816 A., Rovere, A., Hearty, P. J. & Ávila, S. P., 2017. The emergence and evolution
817 of Santa Maria Island (Azores) – the conundrum of uplifted islands revisited.
818 *Geological Society of America Bulletin* **129**, 372–390.
819 Randall, J. E., 1990. Scaridae; Vol. II, pp. 883–887 in J. C. Quero, J. C. Hureau, C. Karrer,
820 A. Post, and L. Saldanha (Eds.), Check-list of the fishes of the eastern
821 tropical Atlantic. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.
822 Raposo, V. B., Melo, C. S., Silva, L., Ventura, A., Câmara, R., Pombo, J., Johnson, M. E. &
823 Ávila, S. P., 2018. Comparing methods of evaluation of geosites: the
824 fossiliferous outcrops of Santa Maria Island (Azores, NE Atlantic) as a case
825 study for sustainable island tourism. *Sustainability* **10**, 3596.
826 Rebelo, A. C., Rasser, M. W., Riosmena-Rodríguez, R., Neto, A. I. & Ávila, S. P., 2014.
827 Rhodolith forming coralline algae in the Upper Miocene of Santa Maria Island
828 (Azores, NE Atlantic): a critical evaluation. *Phytotaxa* **190**, 370–382.
829 Rebelo, A. C., Meireles, R. P., Barbin, V., Neto, A. I., Melo, C. & Ávila, S. P., 2016a.
830 Diagenetic history of lower Pliocene rhodoliths of the Azores Archipelago (NE

Atlantic): application of cathodoluminescence techniques. *Micron* **80**, 112–121.

Rebelo, A. C., Rasser, M. W., Kroh, A., Johnson, M. E., Ramalho, R. S., Melo, C., Uchman, A., Berning, B., Silva, L., Zannon, V., Neto, A. I., Cachão, M. & Ávila, S. P., 2016b. Rocking around a volcanic island shelf: Pliocene Rhodolith beds from Malbusca, Santa Maria Island (Azores, NE Atlantic). *Facies* **62**, 22.

Ricchi, A., Quartau, R., Ramalho, R. S., Romagnoli, C., Casalbore, D., da Cruz, J. V., Fradique, C. & Vinhas, A., 2018. Marine terrace development on reefless volcanic islands: New insights from high-resolution marine geophysical data offshore Santa Maria Island (Azores Archipelago). *Marine Geology* **406**, 42–56.

Sacco, F., 1916. Apparati dentali di Labrodon e di Chrysophrys del Pliocene italiano. *Memorie della Reale Accademia delle Scienze di Torino* **60**, 144–149.

Santos, A., Mayoral, E. J., da Silva, C. M., Cachão, M. & Johnson, M. E., 2011. Miocene intertidal zonation on a volcanically active shoreline: Porto Santo in the Madeira Archipelago, Portugal. *Lethaia* **44**, 26–32.

Santos, A., Mayoral, E., Baarli, B. G., da Silva, C. M., Cachão, M. & Johnson, M. E., 2012a. Symbiotic association of a Pyrgomatid barnacle with a coral from the volcanic Middle Miocene shoreline (Porto Santo, Madeira archipelago, Portugal). *Palaeontology* **55**, 173–182.

Santos, A., Mayoral, E., Johnson, M. E., Baarli, B. G., Cachão, M., da Silva, C. M. & Ledesma-Vázques, J., 2012b. Extreme habitat adaptation by boring bivalves on volcanically active paleoshores from North Atlantic Macaronesia. *Facies* **58**, 325–338.

Santos, A., Mayoral, E., Dumont, C. P., da Silva, C. M., Ávila, S. P., Baarli, B. G., Cachão, M., Johnson, M. E. & Ramalho, R. S., 2015. Role of environmental change in rock-boring echinoid trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **432**, 1–14.

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M. & Isidro, E. J., 1995. Marine research, resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**, 311–354.

Sauvage, H.-E., 1875. Note sur le genre *Nummopalatus* et sur les espèces de ce genre trouvés dans les terrains tertiaires de la France. *Bulletin de la Société Géologique de France* **3**, 613–642.

Searle, R., 1980. Tectonic pattern of the Azores spreading centre and triple junction. *Earth and Planetary Science Letters* **51**, 415–434.

Simonelli, V., 1889. Terreni e fossili dell'Isola di Pianosa nel Mar Tirreno. *Bolletino del Reale Comitato Geolologico d'Italia* **10**, 193–237.

Tuya, F., Betancort, J. F., Haroun, R., Espino, F., Lomoschitz, A. & Meco, J., 2017. Seagrass paleo-biogeography: Fossil records reveal the presence of *Halodule* cf. in the Canary Islands (eastern Atlantic). *Aquatic Botany* **143**, 1–7.

Uchman, A., Johnson, M. E., Rebelo, A. C., Melo, C., Cordeiro, R., Ramalho, R. S. & Ávila, S. P., 2016. Vertically-oriented trace fossil *Macaronichnus segregatis* from Neogene of Santa Maria Island (Azores; NE Atlantic) records vertical fluctuations of the coastal groundwater mixing zone on a small oceanic island. *Geobios* **49**, 229–241.

Uchman, A., Quintino, V., Rodrigues, A. M., Johnson, M. E., Melo, C., Cordeiro, R., Ramalho, R. S. & Ávila, S. P., 2017. The trace fossil *Diopatrichnus*

878 *santamariaensis* nov. isp. – a shell armoured tube from Pliocene sediments of
879 Santa Maria Island, Azores (NE Atlantic Ocean). *Geobios* **50**, 459–469.
880 Vicens, D. & Rodríguez-Perea, A., 2003. Vertebrats fòssils (Pisces i Reptilia) del Burdigalià
881 de cala Sant Vicenç (Pollença, Mallorca). *Bolletí de la Societat d'Història Natural*
882 *de les Balears* **46**, 117–130.
883 Vogt, P. R., & Jung, W.-Y., 2018. The "Azores Geosyndrome" and Plate Tectonics:
884 Research History, Synthesis, and Unsolved Puzzles; pp. 27–56 in U. Kueppers,
885 and C. Beier (Eds.), Volcanoes of the Azores. Revealing the Geological Secrets
886 of the Central Northern Atlantic Islands. Springer, Berlin.
887 Wallace, A. R., 1880. Island life, or, the phenomena and causes of insular faunas and
888 floras: including a revision and attempted solution of the problem of
889 geological climates. Macmillan, London, 526 pp.
890 Whittaker, R. J., Triantis, K. A. & Ladle, R. J., 2010. A General Dynamic Theory of
891 Oceanic Island Biogeography: Extending the MacArthur–Wilson Theory
892 to Accommodate the Rise and Fall of Volcanic Islands; pp. 88–115 in J. B.
893 Losos, and R. E. Ricklefs (Eds.), The theory of island biogeography
894 revisited. Princeton University Press, Princeton, New Jersey.
895 Winkelmann, K., Buckeridge, J. S., Costa, A. C., Dionísio, M. A. M., Medeiros, A.,
896 Cachão, M. & Ávila, S. P., 2010. *Zullobalanus santamariaensis* sp. nov., a new
897 late Miocene barnacle species of the family Archeobalanidae (Cirripedia:
898 Thoracica), from the Azores. *Zootaxa* **2680**, 33–44.
899 Worms Editorial Board, 2018. World Register of Marine Species. Available from
900 http://www.marinespecies.org at VLIZ. Accessed on 4 October 2018.

Zbyszewski, G. & Moitinho d'Almeida, F., 1950. Os peixes miocénicos portugueses. *Comunicações dos Serviços Geológicos de Portugal* **31**, 309–423.

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

907 **Figure Legends**

908 **Figure 1**. **A**: Location of the Azores Archipelago in the NE Atlantic, and location and
909 geotectonic setting of Santa Maria Island within the Azores Archipelago and within the
910 Azores triple junction, respectively. The light blue area represents the Azores plateau
911 (see text). MAR: Mid-Atlantic Ridge; EAFZ: East Azores fault zone; GF: Gloria fault; NA:
912 North American plate; Eu: Eurasian plate; Nu: Nubian (African) plate. **B**: location of the
913 Pliocene (red circles) and Pleistocene fossiliferous outcrops (yellow triangles) of Santa
914 Maria Island. The Pleistocene outcrops are restricted to the warmest interval of the
915 Last Interglacial Period (*c*. 116–130 kyr), which is known as MIS 5e (Marine Isotopic
916 Substage 5e). [Intended for page width].

917

918 **Figure 2**. Aerial (drone) views of the fossiliferous outcrops from Santa Maria Island. **A**–
919 **B**: Pliocene outcrops; **C**–**D**: Pleistocene (MIS 5e) outcrops. The white line delimits the
920 outcrops. **A**: Cré. **B**: Figueiral. **C**: Prainha (the white arrows point to the areas where
921 fossiliferous sediments are better preserved). **D**: Vinha Velha. [Intended for page
922 width].

923

924 **Figure 3**. Aerial (drone) views of the Pliocene fossiliferous outcrops from Santa Maria
925 Island. The white line delimits the outcrops. **A**: Malbusca. **B**: West fault of Malbusca. **C**:
926 Pedra-que-pica. At West fault of Malbusca (**B**), the fossil strata are displaced by a fault
927 slip of about 20 m. Pedra-que-pica (**C**) is probably the largest worldwide multispecific
928 coquina ever described from a volcanic oceanic island, with a total estimated area of
929 >23,400 m^2 and a total thickness for the sediments of 10–11 m (Ávila et al., 2015b).
930 [Intended for page width].

Figure 4. Stratigraphic columns of the studied outcrops: Malbusca (Rebelo et al., 2016a; Uchman et al., 2017), Figueiral (Ávila et al., 2018), Pedra-que-pica (Ávila et al., 2015b), West fault of Malbusca (Uchman et al., 2017), Cré (Janssen et al., 2008), Prainha and Vinha Velha (Ávila et al., 2010, 2015a). [Intended for page width].

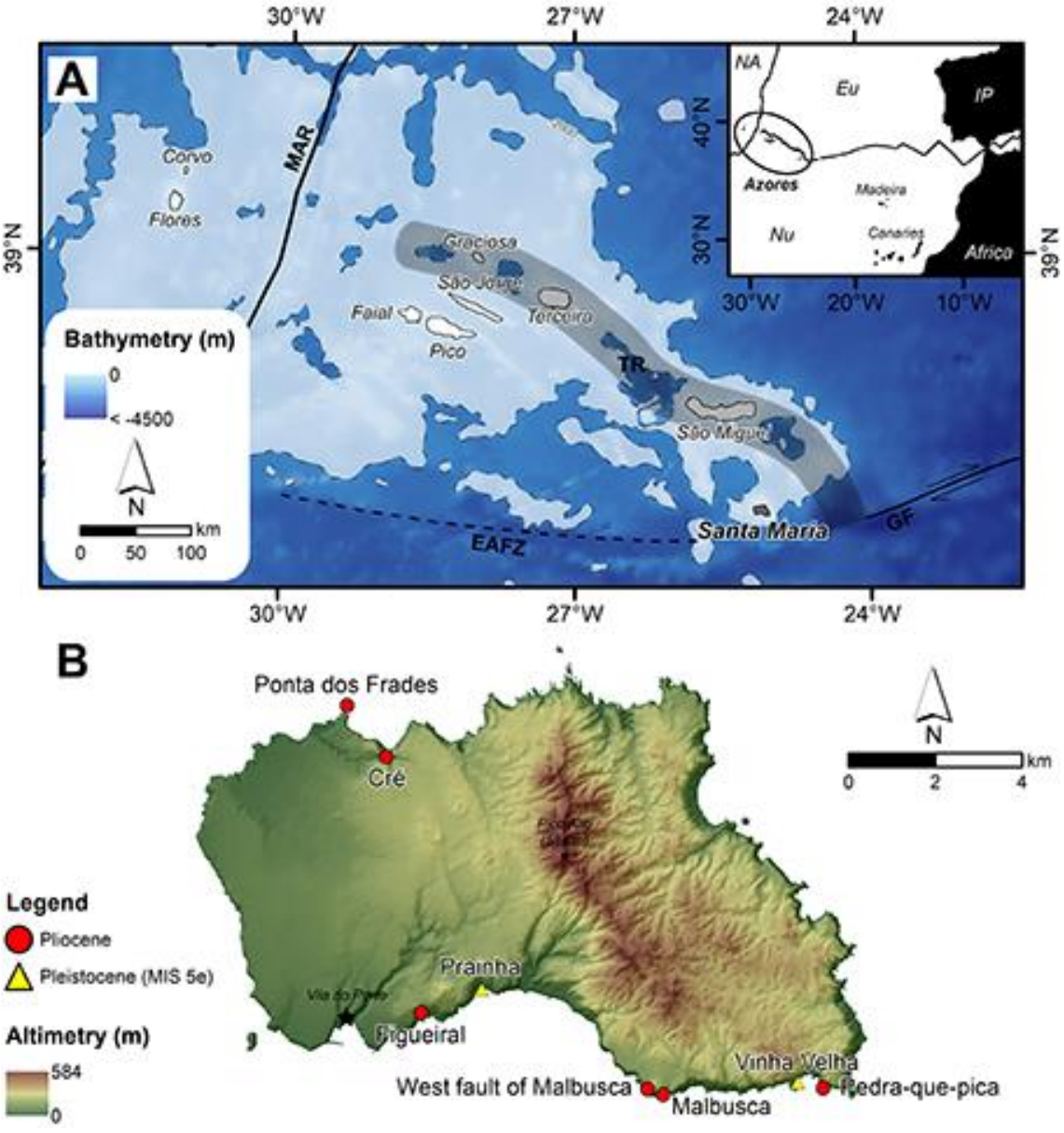
Figure 5. Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island (Azores). **A**–**L**: Teeth of Sparidae indet. **A**–**F**, **L**: Upper lingual hemispheroidal molariform. Note the central depression in teeth photographed in **A–C** and **F**. **A**–**C** (DBUA-F 165-1); **D**–**E** (LAQ, not numbered); **F** (DBUA-F 674). **G**–**K**: anterior teeth. **G**–**H** (DBUA-F 667); **I** (DBUA-F 599); **J**–**K** (DBUA-F 477-2); **L** (MGM 11321). **M**–**Q**: Teeth of Sparidae indet.; these specimens were collected by Georges Zbyszewski at Santa Maria Island (no information for locality) and originally referred to *Diplodus jomnitanus*. Original label by the former Serviços Geológicos de Portugal (presently housed at the Museu Geológico e Mineiro, Lisbon: MGM 11313). M, P: Apical view of the teeth; N–O, Q: Lateral view. [Intended for page width].

Figure 6. Actinopterygian fishes from Early Pliocene (DBUA-F 825, 1069, 1214) and Late Pleistocene (Last Interglacial, MIS 5e; DBUA-F 1030) deposits of Santa Maria Island (Azores). **A**: Lower grinding face view of Early Pliocene fragmentary tooth plate (DBUA-F 1069) of *Sparisoma cretense*. **B**–**E**: Upper grinding face view of pharyngeal plates of *Sparisoma cretense.* **B**–**C**, **E**: Lower pharyngeal plates. **B** (DBUA-F 1030), **C** (DBUA-F 1214-1), **E** (DBUA-F 825). **D**: Upper pharyngeal plate (DBUA-F 1214-2). **F**–**G**: Upper

954 grinding face view of recent pharyngeal plates from a dissected *S. cretense*. **F**: Upper
955 pharyngeal plate. **G**: Lower pharyngeal plate. [Intended for page width].
956
957 **Figure 7**. Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island
958 (Azores). **A–G**: *Labrodon pavimentatum* Gervais, 1857. **A–E**: Fragmentary pharyngeal
959 plates collected at Pedra-que-pica outcrop (**B**, **D**: DBUA-F 678; **C**, **E**: DBUA-F 386); **F–G**:
960 Fragmentary pharyngeal plate collected at Santa Maria (no locality; MGM 11318). **C**, **D**,
961 **F**: Upper grinding face view of lower pharyngeal plate. **E**, **G**: Lower grinding face view
962 of lower pharyngeal plate. [Intended for page width].
963
964 **Figure 8**. **A–C**: NE Atlantic Biogeographic Molluscan Provinces from late Miocene to
965 Pliocene (**A**, 6.0–5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm
966 Period (**B**, 5.33–2.95 Ma) and the present (**C**) (Ávila et al., 2016). **D–F**: Comparison of
967 large-scale evolutionary and biogeographical patterns, as a result of long-distance
968 dispersal of marine species between oceanic islands located at different climate
969 settings (subtropical versus temperate latitudes) for the last 150 kyr, encompassing the
970 Last Interglacial (MIS 5e), the Last Glacial episode, and the present interglacial[6]. **D**:
971 During the final phase of Termination 2 and/or the beginning of the Last Interglacial, a
972 subset of marine subtropical species expands their geographical ranges towards higher
973 latitudes (red arrow), reaching temperate archipelagos and establishing viable
974 populations in those islands (e.g. small red star in **D**). In a similar way, a subset of
975 marine temperate species expands their geographical ranges towards higher latitudes,
976 reaching boreal/arctic archipelagos and establishing viable populations as well (blue
977 arrow). **E**: During the course of the Last Glacial episode, the thermophilic species that

978 established on temperate islands are extirpated and it is expected that a subset of
979 marine temperate species (small blue circles), adapted to cool temperatures may
980 expand their geographical ranges towards lower latitudes, reaching subtropical
981 archipelagos and establishing viable populations. **F**: the subsequent episode of global
982 warming that led to the present interglacial, extirpates the cold-adapted species that
983 reached subtropical islands during the previous glacial episode, and range expansion of
984 species towards higher latitudes is documented. **G–I**: Mobile sediment response to
985 glacio-eustatic sea level fluctuations (Ávila et al., 2008b, 2010). **G**: During the Last
986 interglacial (MIS 5e), as a result of marine and fluvial erosion, sediments are
987 transported to the island shelf where they accumulate between the shoreline angle
988 (i.e., the angle between the cliff of the island and the shore platform) and the erosive
989 shelf edge. **H**: The inception of sea-level lowstands during the Last Glacial episode,
990 promotes the remobilization and transport downslope of sediments from the island
991 shelf, when relative mean sea level falls below the erosive shelf edge. Whenever this
992 happens, sediments are lost to the abyssal depths that surround the insular edifice. **I**:
993 Sediments accumulate again on the island shelf, as a result of marine and fluvial
994 erosion, during the present sea-level highstand. [Intended for page width].
995
996
997

998 **Figures**



999

1000 **Figure 1**. **A**: Location of the Azores Archipelago in the NE Atlantic, and location and
1001 geotectonic setting of Santa Maria Island within the Azores Archipelago and within the
1002 Azores triple junction, respectively. The light blue area represents the Azores plateau
1003 (see text). MAR: Mid-Atlantic Ridge; EAFZ: East Azores fault zone; GF: Gloria fault; NA:
1004 North American plate; Eu: Eurasian plate; Nu: Nubian (African) plate. **B**: location of the
1005 Pliocene (red circles) and Pleistocene fossiliferous outcrops (yellow triangles) of Santa
1006 Maria Island. The Pleistocene outcrops are restricted to the warmest interval of the

Last Interglacial Period (*c*. 116–130 kyr), which is known as MIS 5e (Marine Isotopic Substage 5e). [Intended for page width].

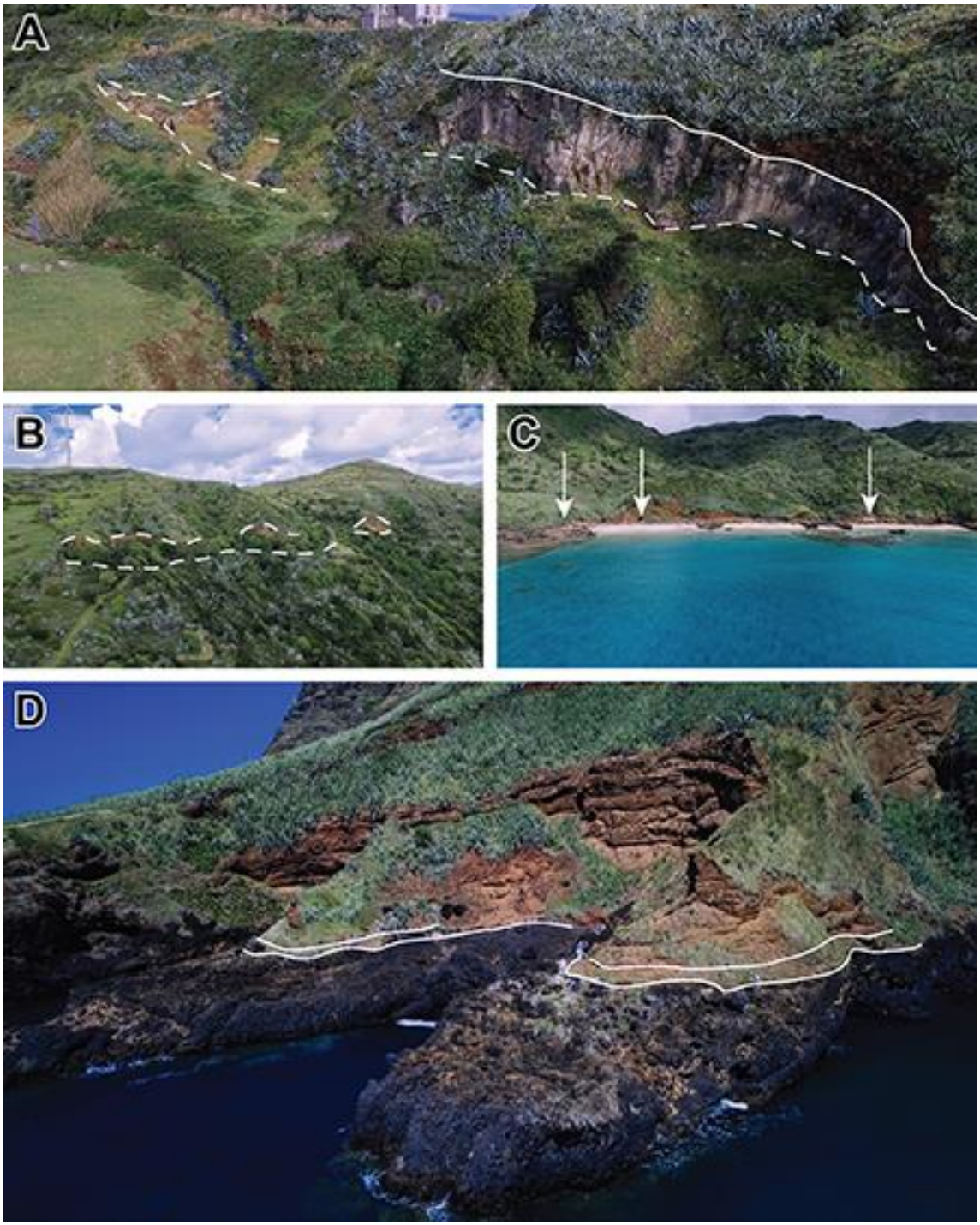


Figure 2. Aerial (drone) views of the fossiliferous outcrops from Santa Maria Island. **A**–**B**: Pliocene outcrops; **C**–**D**: Pleistocene (MIS 5e) outcrops. The white line delimits the outcrops. **A**: Cré. **B**: Figueiral. **C**: Prainha (the white arrows point to the areas where fossiliferous sediments are better preserved). **D**: Vinha Velha. [Intended for page width].

Figure 3. Aerial (drone) views of the Pliocene fossiliferous outcrops from Santa Maria Island. The white line delimits the outcrops. **A**: Malbusca. **B**: West fault of Malbusca. **C**:

1020 Pedra-que-pica. At West fault of Malbusca (**B**), the fossil strata are displaced by a fault
1021 slip of about 20 m. Pedra-que-pica (**C**) is probably the largest worldwide multispecific
1022 coquina ever described from a volcanic oceanic island, with a total estimated area of
1023 >23,400 m^2 and a total thickness for the sediments of 10–11 m (Ávila et al., 2015b).
1024 [Intended for page width].
1025
1026

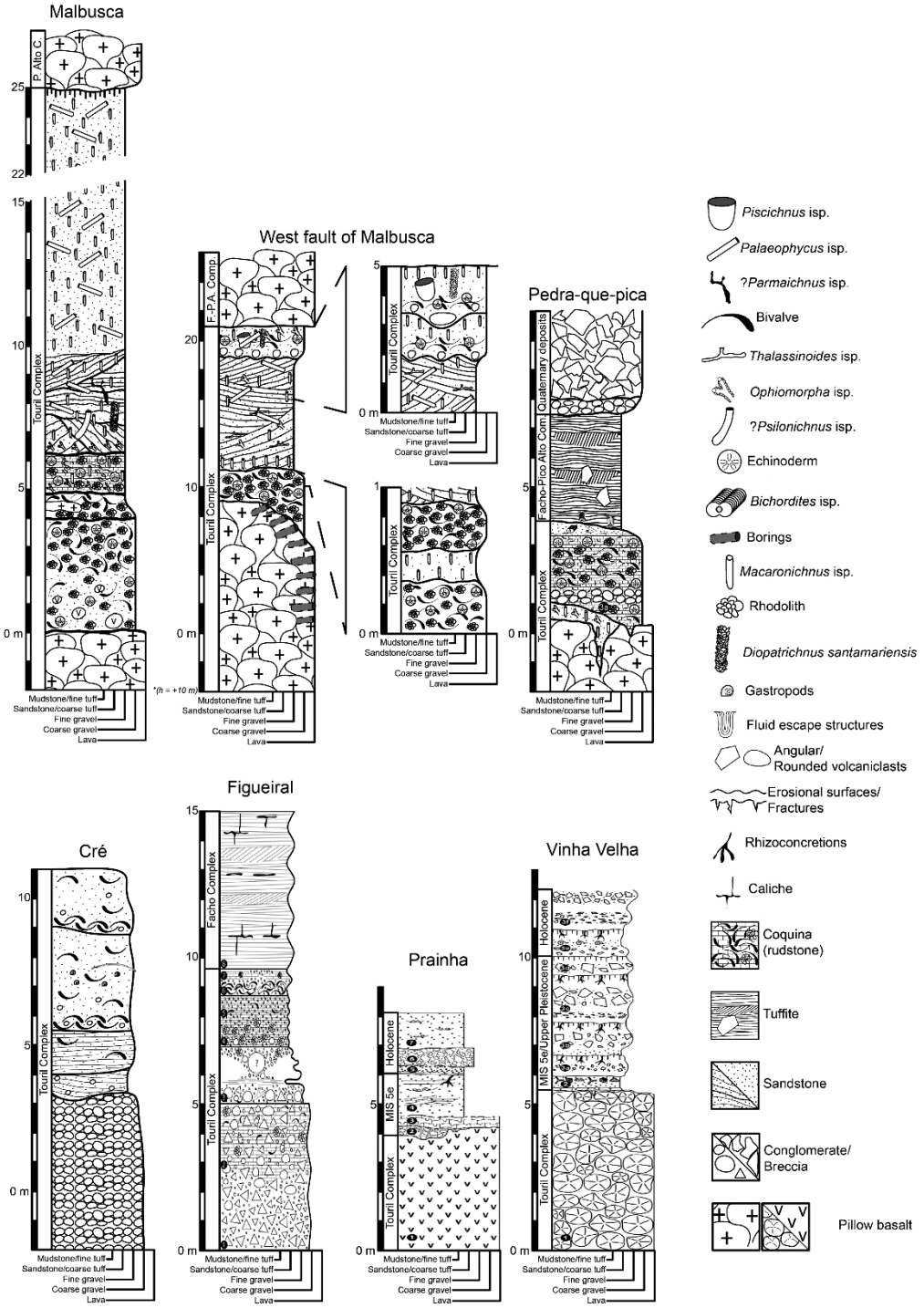
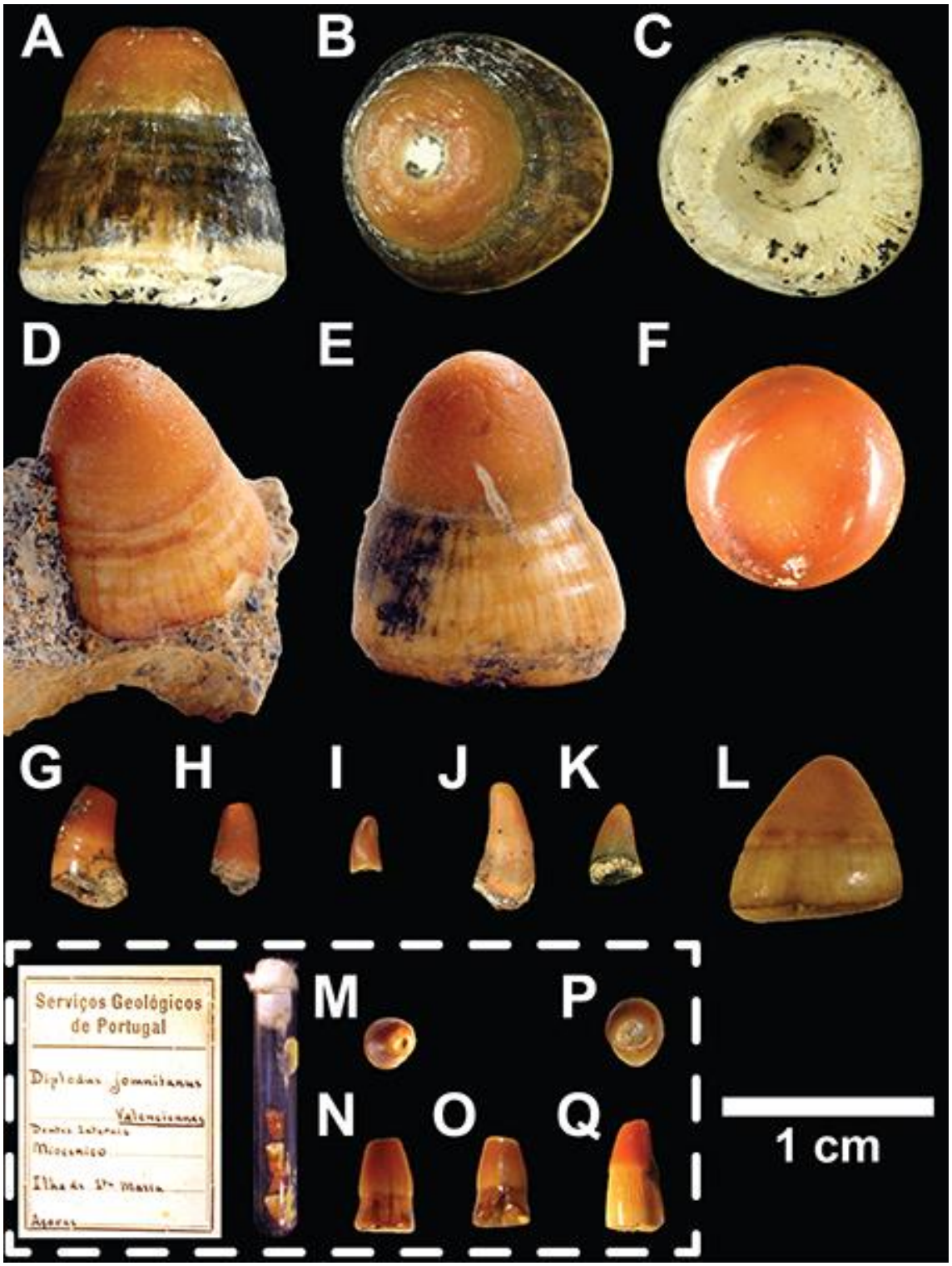


Figure 4. Stratigraphic columns of the studied outcrops: Malbusca (Rebelo et al., 2016a; Uchman et al., 2017), Figueiral (Ávila et al., 2018), Pedra-que-pica (Ávila et al., 2015b), West fault of Malbusca (Uchman et al., 2017), Cré (Janssen et al., 2008), Prainha and Vinha Velha (Ávila et al., 2010, 2015a). [Intended for page width].



1033

1034 **Figure** 5. Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island

1035 (Azores). **A**–**L**: Teeth of Sparidae indet. **A**–**F**, **L**: Upper lingual hemispheroidal

1036 molariform. Note the central depression in teeth photographed in **A**–**C** and **F**. **A**–**C**

1037 (DBUA-F 165-1); **D**–**E** (LAQ, not numbered); **F** (DBUA-F 674). **G**–**K**: anterior teeth. **G**–**H**

(DBUA-F 667); **I** (DBUA-F 599); **J–K** (DBUA-F 477-2); **L** (MGM 11321). **M–Q**: Teeth of Sparidae indet.; these specimens were collected by Georges Zbyszewski at Santa Maria Island (no information for locality) and originally referred to *Diplodus jomnitanus*. Original label by the former Serviços Geológicos de Portugal (presently housed at the Museu Geológico e Mineiro, Lisbon: MGM 11313). **M**, **P**: Apical view of the teeth; **N–O**, **Q**: Lateral view. [Intended for page width].

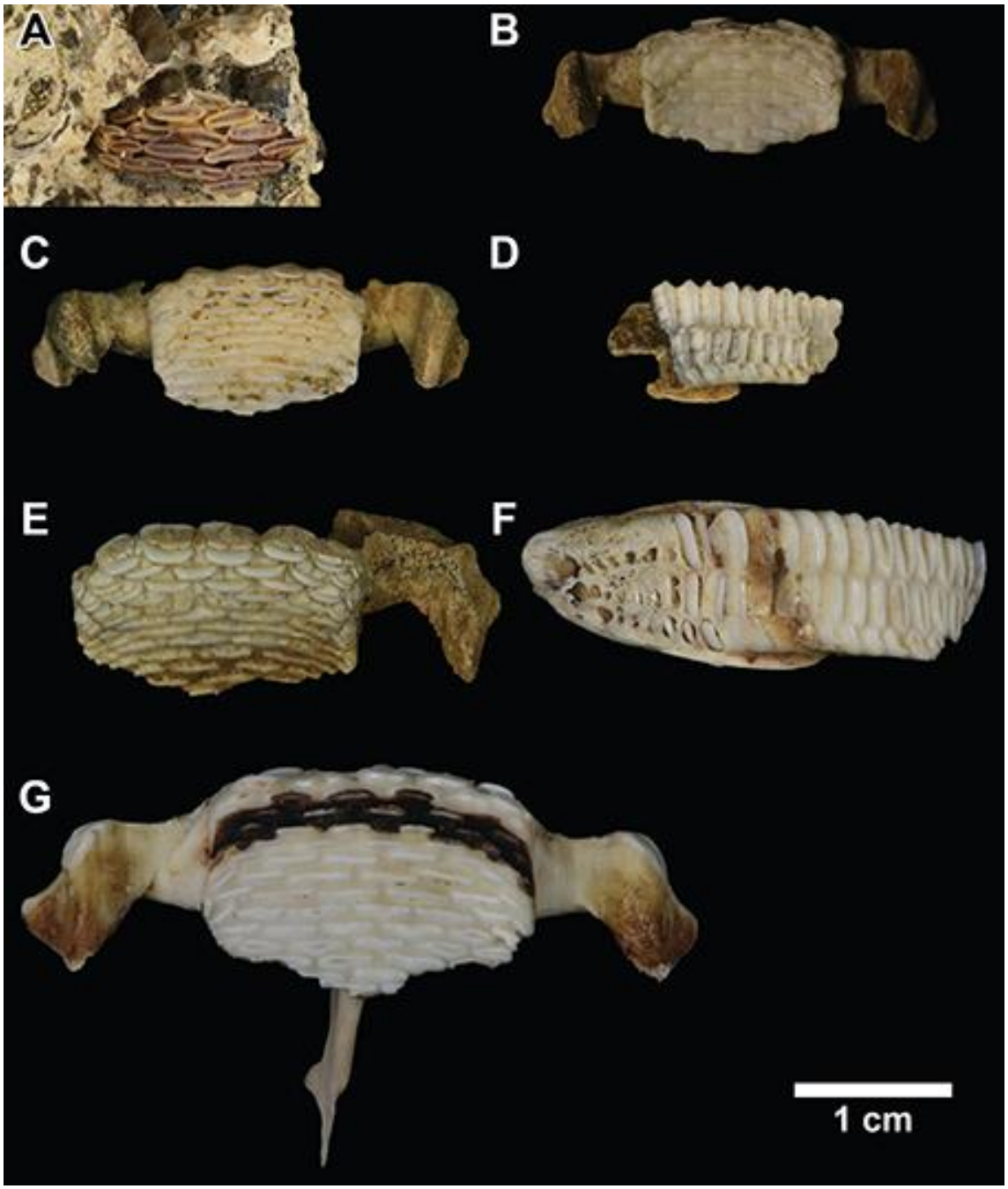


Figure 6. Actinopterygian fishes from Early Pliocene (DBUA-F 825, 1069, 1214) and Late Pleistocene (Last Interglacial, MIS 5e; DBUA-F 1030) deposits of Santa Maria Island (Azores). **A**: Lower grinding face view of Early Pliocene fragmentary tooth plate (DBUA-F 1069) of *Sparisoma cretense*. **B–E**: Upper grinding face view of pharyngeal plates of *Sparisoma cretense.* **B–C**, **E**: Lower pharyngeal plates. **B** (DBUA-F 1030), **C** (DBUA-F 1214-1), **E** (DBUA-F 825). **D**: Upper pharyngeal plate (DBUA-F 1214-2). **F–G**: Upper

1053 grinding face view of recent pharyngeal plates from a dissected *S. cretense*. **F**: Upper

1054 pharyngeal plate. **G**: Lower pharyngeal plate. [Intended for page width].

1055

1056

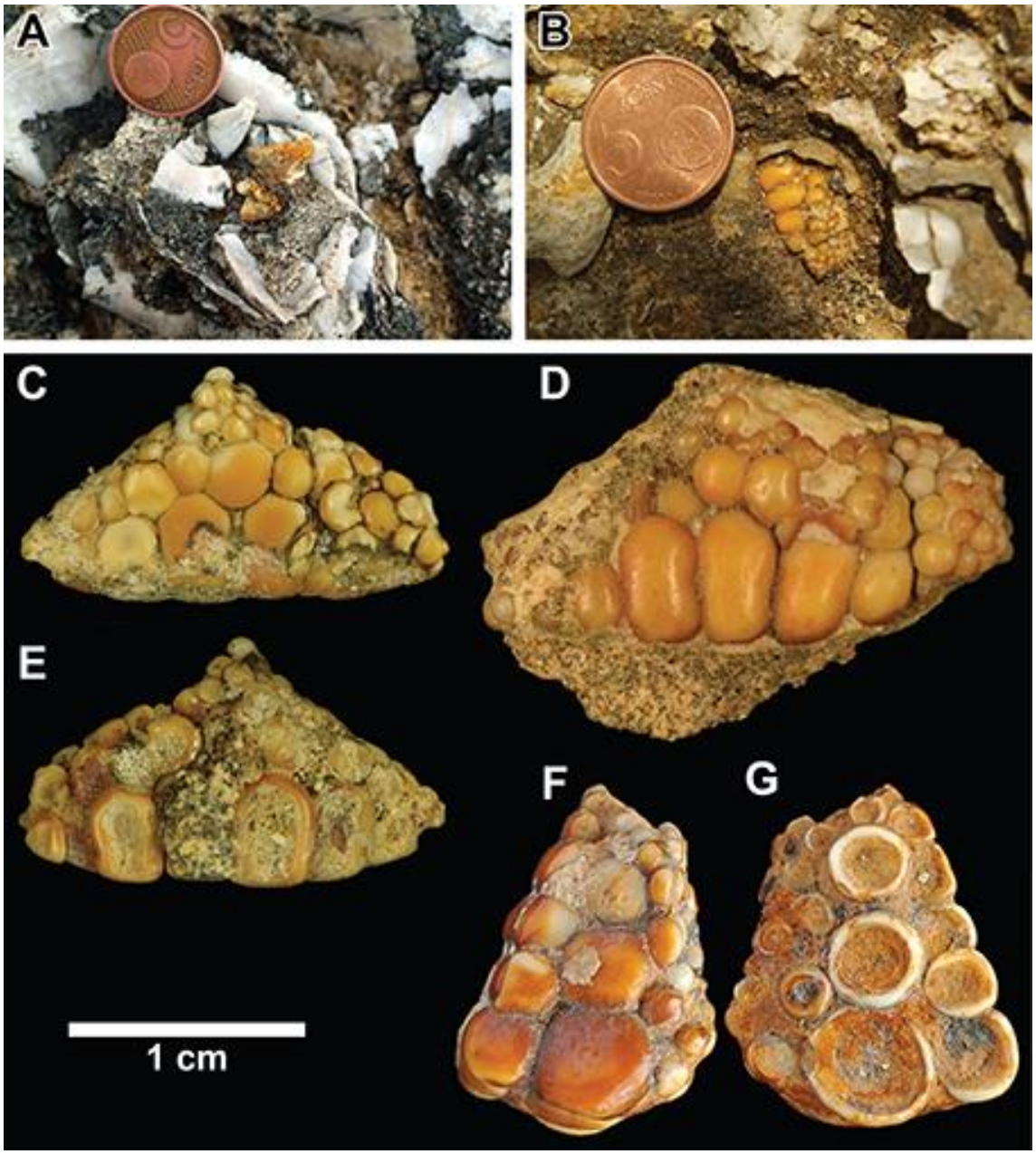


Figure 7. Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island (Azores). **A**–**G**: *Labrodon pavimentatum* Gervais, 1857. **A**–**E**: Fragmentary pharyngeal plates collected at Pedra-que-pica outcrop (**B**, **D**: DBUA-F 678; **C**, **E**: DBUA-F 386); **F**–**G**: Fragmentary pharyngeal plate collected at Santa Maria (no locality; MGM 11318). **C**, **D**, **F**: Upper grinding face view of lower pharyngeal plate. **E**, **G**: Lower grinding face view of lower pharyngeal plate. [Intended for page width].

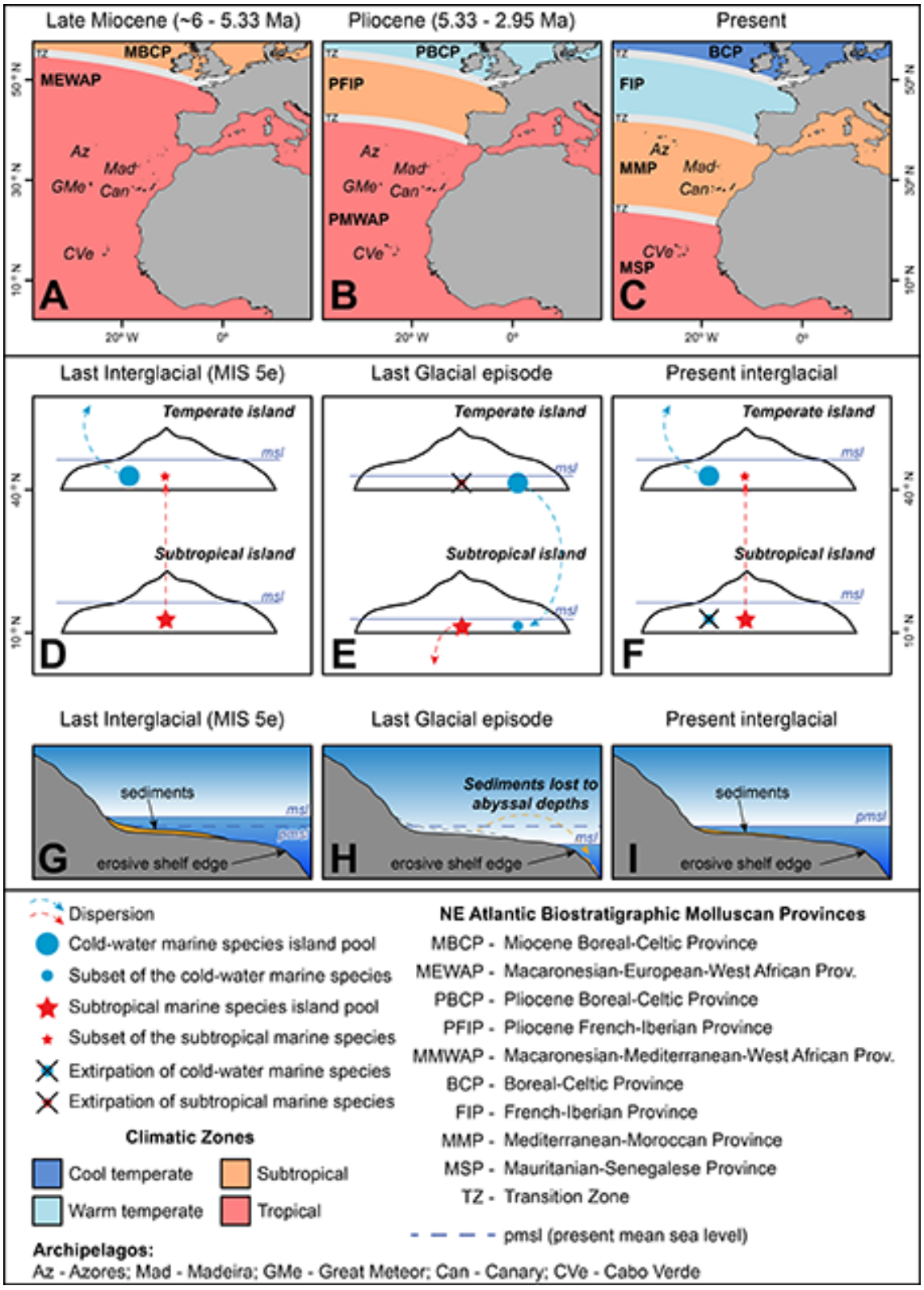


Figure 8. **A**–**C**: NE Atlantic Biogeographic Molluscan Provinces from late Miocene to Pliocene (**A**, 6.0–5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm Period (**B**, 5.33–2.95 Ma) and the present (**C**) (Ávila et al., 2016). **D**–**F**: Comparison of

1069 large-scale evolutionary and biogeographical patterns, as a result of long-distance
1070 dispersal of marine species between oceanic islands located at different climate
1071 settings (subtropical versus temperate latitudes) for the last 150 kyr, encompassing the
1072 Last Interglacial (MIS 5e), the Last Glacial episode, and the present interglacial (Ávila et
1073 al., 2019). **D**: During the final phase of Termination 2 and/or the beginning of the Last
1074 Interglacial, a subset of marine subtropical species expands their geographical ranges
1075 towards higher latitudes (red arrow), reaching temperate archipelagos and
1076 establishing viable populations in those islands (e.g. small red star in **D**). In a similar
1077 way, a subset of marine temperate species expands their geographical ranges towards
1078 higher latitudes, reaching boreal/arctic archipelagos and establishing viable
1079 populations as well (blue arrow). **E**: During the course of the Last Glacial episode, the
1080 thermophilic species that established on temperate islands are extirpated and it is
1081 expected that a subset of marine temperate species (small blue circles), adapted to
1082 cool temperatures may expand their geographical ranges towards lower latitudes,
1083 reaching subtropical archipelagos and establishing viable populations. **F**: the
1084 subsequent episode of global warming that led to the present interglacial, extirpates
1085 the cold-adapted species that reached subtropical islands during the previous glacial
1086 episode, and range expansion of species towards higher latitudes is documented. **G–I**:
1087 Mobile sediment response to glacio-eustatic sea level fluctuations (Ávila et al., 2008b,
1088 2010). **G**: During the Last interglacial (MIS 5e), as a result of marine and fluvial erosion,
1089 sediments are transported to the island shelf where they accumulate between the
1090 shoreline angle (i.e., the angle between the cliff of the island and the shore platform)
1091 and the erosive shelf edge. **H**: The inception of sea-level lowstands during the Last
1092 Glacial episode, promotes the remobilization and transport downslope of sediments

1093 from the island shelf, when relative mean sea level falls below the erosive shelf edge.
1094 Whenever this happens, sediments are lost to the abyssal depths that surround the
1095 insular edifice. **I**: Sediments accumulate again on the island shelf, as a result of marine
1096 and fluvial erosion, during the present sea-level highstand. [Intended for page width].
1097

1098 **Table 1**. Relative age of the outcrops (in millions of years) from Santa Maria Island (Azores) containing fossil remains of Actinopterygii fishes.

Outcrop	Age (Ma)	Bed	Inferred depth of deposition (m)	Number of teeth/pharyngeal plates per species		
				Sparidae	*Sparisoma cretense*	*Labrodon pavimentatum*
Cré	4.78 ± 0.13 to 4.13 ± 0.19	Sandstone	?	4		
Figueiral	4.78 ± 0.13 to 4.13 ± 0.19	Sandstone	?	1		
Ponta dos Frades	4.78 ± 0.13 to 4.13 ± 0.19	Sandstone	?		6	
Pedra-que-pica	4.78 ± 0.13 to 4.13 ± 0.19	Coquina	-40	26	1	2
Malbusca	4.32 ± 0.06 to 4.02 ± 0.06	Sandstone	-60	17		
West fault of Malbusca	4.32 ± 0.06 to 4.02 ± 0.06	Sandstone	-60	2		
Vinha Velha	Last Interglacial (MIS 5e)	Sand	+1 to +2		1	

1099

1100

Table 2. Present geographical distribution of the genus *Sparisoma* in the Atlantic Ocean and the Mediterranean Sea. AZO – Azores Archipelago; MAD – Madeira Archipelago; SEL – Selvagens Archipelago; CAN – Canaries Archipelago; CAB – Cabo Verde Archipelago; STP – São Tomé and Príncipe Archipelago; IBE – Atlantic Iberian shores from Finisterra south to the Straits of Gibraltar; MED – Mediterranean Sea; TWAF – Tropical west African shores, from Cape Blanc (Senegal) south to Angola; NWA – Atlantic coast of Northwest Africa, from the Straits of Gibraltar south to Senegal; ASC – Ascension Island; STH – Saint Helena Island; SWA – Southwest Atlantic, including Brazil and its oceanic islands; WAT – Western Atlantic, including the Caribbean Sea.

Species	AZO	MAD	SEL	CAN	CAB	STP	IBE	MED	TWAF	NWA	ASC	STH	SWA	WAT
Sparisoma choati	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Sparisoma cretense	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Sparisoma frondosum	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sparisoma amplum	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sparisoma atomarium	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparisoma aurofrenatum	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparisoma axillare	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sparisoma chrysopterum	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparisoma griseorubrum	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparisoma radians	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Sparisoma rocha	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sparisoma rubripinne	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sparisoma strigatum	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Sparisoma tuiupiranga	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sparisoma viride	0	0	0	0	0	0	0	0	0	0	0	0	1	1

1107

1108 **Table 3**. Taxa/species reported from the Pliocene sediments of Santa Maria Island and
1109 that are presently extinct or were extirpated (local disappearances) from the marine
1110 fauna of the island during the global climate deterioration that characterizes the late
1111 Pliocene.

Phylum	Taxa	Status
Mollusca	*Aequipecten macrotis* (Sowerby, 1847)	extinct
	Gigantopecten latissimus (Brocchi, 1814	extinct
	Chlamys hartungi (Mayer, 1864)	extinct
	Lopha plicatuloides (Mayer, 1864)	extinct
	Pecten dunkeri Mayer, 1864	extinct
	Persististrombus coronatus (Defrance, 1827)	extinct
	Janthina typica (Brönn, 1861)	extinct
	Cavolinia grandis (Bellardi, 1873)	extinct
	Cavolinia marginata (Brönn, 1862)	extinct
	Cuvierina intermedia (Bellardi, 1873)	extinct
	Bowdenatheca jamaicensis Collins, 1934	extinct
Echinodermata	*Clypeaster altus* (Leske, 1778)	extinct
	Eucidaris tribuloides (Lamarck, 1816)	local disappearance
	Echinoneus cf. *cyclostomus* Leske, 1778	local disappearance
	Schizobrissus sp.	extinct
Brachiopoda	*Novocrania turbinata* (Poli, 1795)	extinct

Table 3. (Continued)

Arthropoda (Crustacea)	*Zullobalanus santamariaensis* Buckeridge & Winkelmann, 2010	extinct
Chordata (Elasmobranchii)	*Notorynchus primigenius* (Agassiz, 1833)	extinct
	Carcharias acutissima (Agassiz, 1833),	extinct
	Cosmopolitodus hastalis (Agassiz, 1833),	extinct
	Paratodus benedenii (Le Hon, 1871),	extinct
	Megaselachus megalodon (Agassiz in Charlesworth, 1837)	extinct
Chordata (Actinopterygii)	Sparidae indet.	extinct
	Labrodon pavimentatum Gervais, 1857	extinct

1112

1113