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

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

4  
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21  
22  
23

24 **Abstract**

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

43

44 **Keywords**

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

47

48 **Introduction**

49 Oceanic islands have long been considered as ideal places to study biogeographical  
50 patterns and processes, and to test evolutionary theories (Darwin, 1859; Wallace,  
51 1880). A detailed knowledge of an island's geological history and evolution is of  
52 paramount importance, influenced by the ontogenic state of the island as determined  
53 by a series of factors [e.g. geological age of the oldest subaerial lavas, terrestrial area,  
54 maximum altitude, latitude; see Whittaker et al. (2010); Fernández-Palacios et al.  
55 (2016)]. Such factors ultimately regulate and explain both the number of species that  
56 live on the island, as well as the functional composition of the biological assemblage  
57 itself. The marine fossil record for volcanic oceanic islands may be considered as rare  
58 or poor, especially when compared to that for vastly larger continents (Ávila et al.,  
59 2018). However, the dating of an island's fossil fauna and flora when coupled with  
60 checklists validated by experts provides valuable insights for a number of disciplines  
61 such as palaeobiogeography, palaeoceanography, phylogenetic and climate-change  
62 studies (Ávila et al., 2019).

63         The remarkable marine fossil record of Santa Maria Island in the Azores  
64 Archipelago has been intensively studied over the last decades (for a review, see Ávila  
65 et al. (2018) and references therein). The result has been 204 Pliocene and 146  
66 Pleistocene (Last Interglacial) species and 15–20 further ichnospecies reported for the  
67 island (Santos et al., 2015; Uchman et al., 2016, 2017; Raposo et al., 2018). The vast  
68 majority of specimens collected are invertebrates: molluscs (Zbyszewski & Ferreira,  
69 1962; Ávila et al., 2002, 2015a, 2015b, 2016; Janssen et al., 2008), brachiopods (Kroh  
70 et al., 2008), crustacean balanids (Winkelmann et al., 2010), echinoderms (Madeira et  
71 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**

## 96 *Azores Archipelago*

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

112

## 113 *Santa Maria Island*

114 This island has a complex geological history (see Ramalho et al. (2017) for a review). It  
115 is the oldest island of the Azores Archipelago, first rising above sea level at about 6 Ma,  
116 initially by Surtseyan activity (the Cabrestantes Formation), and then by subaerial,  
117 monogenetic volcanism associated to the Porto Formation. High rates of magma  
118 production formed a shield volcano (the Anjos volcanic complex, dating from 5.8 to 5.3  
119 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 fossiliferous 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

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

195

196 SYSTEMATIC PALAEOLOGY

197

198 Class ACTINOPTERYGII Klein, 1885

199 Order PERCIFORMES Bleeker 1859

200 Family SPARIDAE Rafinesque, 1818

201 Genus and species indet.

202

203 Figure 5A–Q

204 **Material Examined**—54 teeth in total: Pedra-que-pica (26 teeth), Malbusca (17), Cré (4),  
205 West Fault of Malbusca (2), Figueiral (1): DBUA-F 165-1, 165-2, 204-2, 205-2, 250-1, 260,  
206 286, 313, 344-2, 350, 382, 448, 460-1, 477-2, 508-1, 508-2, 595, 596, 597, 598, 599, 601,  
207 647, 667, 668, 669, 671, 672, 673, 674, 966-2, 991, 1014, 1017, 1073, 1083. Cré, formerly  
208 also known as Pedreira dos Frades (2): MGM 11311, 11312 (one spheroidal and one oval  
209 molariform teeth, respectively); Santa Maria Island (4 teeth), no locality: MGM 11313.

210 **Description**—The 50 teeth examined from the DBUA collection represent three types of  
211 dentition: molariform, conical and incisiform teeth. We have examined a total of 39  
212 molariform teeth, corresponding to the lingual series (36 spheroidal in shape (Fig. 5A-F,  
213 5L), ranging from 2.87 to 17.34 mm in diameter; and 3 oval in shape, 5.89–11.51 mm),  
214 9 conical teeth (Fig. 5G-K), corresponding to the labial series (2.41–7.93 mm in diameter)  
215 and 2 ‘spatulate’ incisiform teeth (1.45–1.53 mm in diameter; DBUA-F 668, 671). Some

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

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

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

226 **Stratigraphic and geographic range**—Extinct *Archosargus* species are reported from the  
227 Miocene and Pliocene of the Mediterranean Sea (Obrador & Mercadal, 1973; Vicens &  
228 Rodríguez-Perea, 2003; Mas & Antunes, 2008) and from the Miocene of France  
229 (Gagnaison, 2017). In the Atlantic, *Archosargus* species are reported from the Miocene  
230 of Portugal (Zbyszewski & Moitinho d’Almeida, 1950; Jonet et al., 1975) and Morocco  
231 (Lecointre, 1952), the Pliocene of Canary Islands (Gran Canaria Island) (Betancort et al.,  
232 2016) and from the Pliocene of the Azores (Santa Maria Island) (Zbyszewski & Moitinho  
233 d’Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962; Ávila et al., 2015b). The  
234 extinct species formerly known as *D. jomnitanus* is reported from the Miocene of France  
235 (Gagnaison, 2017), Portugal (Zbyszewski & Moitinho d’Almeida, 1950; Jonet et al., 1975)  
236 and the Mediterranean Sea (Vicens & Rodríguez-Perea, 2003), and from the Pliocene of  
237 the Azores (Santa Maria Island) (Zbyszewski & Moitinho d’Almeida, 1950; Ferreira, 1955;  
238 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

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

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

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

280 **Stratigraphic and geographic range**—This extant species is presently reported from the  
281 Mediterranean Sea and from the eastern Atlantic shores of Portugal, the Azores,  
282 Madeira, Canary Islands, Cabo Verde and Senegal (Abecasis et al., 2008; Randall, 1990).

283 A search for fossil *Sparisoma* species on the PaleoBiology Database and on Bellwood et  
284 al. (2019) yielded no occurrences. With the exception of otolithes from the Late Eocene  
285 of France referred to *Sparisoma* [Nolf (1988) but see remarks by Bellwood et al. (2019),  
286 in whose opinion these otoliths are not secure evidence of *Sparisoma*], this genus is  
287 reported herein for the first time from the fossil record based on dental remains. *S.*

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

291

292 Tribe HYP SIGENYINI Günther, 1861

293 Genus *LABRODON* Gervais, 1857

294 † *Labrodon pavimentatum* Gervais, 1857

295 Figure 7

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

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

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

312 1988) and the Azores (Santa Maria Island: Zbyszewski & Moitinho d'Almeida, 1950;  
313 Ferreira, 1955; Zbyszewski & Ferreira, 1962; this work).

314

315

## 316 **Discussion**

317 During the late Miocene, the once continuous and large tropical Miocene European-  
318 West African palaeobiogeographical molluscan province (Ávila et al., 2016) stretched  
319 between about 50° N to the equator and further south to Angola (Baarli et al., 2017),  
320 at about 15° S (Fig. 8A). The waters around the Azores thus exhibited tropical  
321 temperatures during the late Miocene/early Pliocene, with mean annual sea surface  
322 temperatures (SSTs) estimated to be about 3.7–6.3°C higher than the present-day  
323 20.6°C (Ávila et al., 2016). The extinct Pliocene fish species reported from the  
324 fossiliferous sediments of Santa Maria Island in the Azores (two Sparidae indet. and  
325 *Labrodon pavimentatum*) add at least three more taxa to an increasing number of  
326 known thermophilic taxa that went extinct or locally disappeared from this volcanic  
327 oceanic island (as well as from other Atlantic islands/archipelagos) during the  
328 pronounced climatic cooling events that characterized the mid-Piacenzian stage,  
329 towards the end of the Pliocene at about 3.3–3.6 Ma (or sometime prior),  
330 consequence of a global glaciation (the MIS M2; see Lisiecki & Raymo, 2005; Fig 8B).  
331 Several warm-water species are also known to have disappeared from the Canary  
332 Islands at about 4.2–4.1Ma (Meco et al., 2007). As a direct consequence of the MIS M2  
333 glaciation, a southward geographical range contraction of the biogeographical  
334 provinces took place (Ávila et al., 2016; Fig. 8B). Table 3 lists examples of several  
335 extinctions or extirpations of Pliocene species from the marine fauna of Santa Maria

336 Island across a wide spectrum of phyla: molluscs (5 bivalves, 1 benthic  
337 macrogastropod, 1 neustonic gastropod and 4 holoplanktonic gastropods; Janssen et  
338 al., 2008; Beu, 2017; Ávila et al., 2015, 2016, 2018a), 4 echinoderms (Madeira et al.,  
339 2011), 1 brachiopod (Kroh et al., 2008), 1 barnacle (Winkelmann et al., 2010) and 5  
340 sharks (Ávila et al., 2012). This pattern of extinctions/extirpations from volcanic  
341 oceanic islands during the late Pliocene also is reported for other Atlantic archipelagos,  
342 such as Madeira (Santos et al., 2012), Canary Islands (Meco et al., 2007, 2015, 2016;  
343 Baarli et al., 2017) and Cabo Verde (Baarli et al., 2017).

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



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

362           The final closure of the Central American Seaway, caused by re-emergence of  
363 the Panamanian land bridge (Briggs, 1995) at about 2.8 Ma (O’Dea et al., 2016), and  
364 the associated strengthening of the Gulf Stream, altered the north Atlantic system of  
365 sea surface circulation. The effect of a stronger Gulf Stream is testified by the shallow-  
366 water (<50 m depth) marine molluscs of the Azores, which show a gradual increase in  
367 the number of Western-Atlantic related species from 10.0% to 12.3%, when Last  
368 Interglacial (MIS 5e) checklists of fossil marine molluscs from the Azores (Ávila et al.,  
369 2002, 2009a, 2009b, 2015a) are compared to recent checklists available from this  
370 archipelago (Ávila, 2000; Cordeiro et al., 2015; Fig. 8C).

371           Intensification of the Pleistocene glacial episodes clearly impacted the Azorean  
372 fish pool in a similar manner to that described for the marine molluscs (Ávila et al.,  
373 2008a, 2008b, 2009a). We here expand on those conclusions, which were based on the  
374 MIS 5e mollusc fossil record from Santa Maria Island, and we postulate that range  
375 expansions of tropical and subtropical fishes with a Cabo Verdean origin probably  
376 occurred during ‘windows of opportunity’ towards the end of glacial Terminations (i.e.  
377 the short periods of time, c. 6 kyr, between the end of a glacial episode and the  
378 inception of a full interglacial episode). During those intervals, some fish species might  
379 have been able to reach, colonize and establish viable populations in the Canaries,  
380 Madeira and, in less numbers, the Azores Archipelago (Fig. 8D). We further  
381 hypothesize that, again in a similar manner to the marine molluscs (Ávila et al., 2008a,  
382 2008b, 2009a), during the subsequent glacial episode, (1) all tropical species with a  
383 Cabo Verdean provenience that became established in the northern archipelagos

384 (Azores, Madeira and Canaries) during the previous interglacial were extirpated (Ávila  
385 et al., 2019; Fig. 8E), and (2) shallow-water fish species associated with fine sediments  
386 were functionally extirpated (i.e. locally disappeared from most volcanic oceanic  
387 islands) or their insular populations passed through a ‘bottleneck’ effect, resulting in a  
388 substantial net decrease in population size. The latter event occurs because the fine-  
389 sand habitat is mostly lost whenever sea level falls below the erosive edge of the  
390 insular shelf during glacial episodes (Ávila et al., 2008b, 2015a; Fig. 8G-I). The trigger  
391 for this outcome resides with the slope of the insular volcanic edifice being so steep  
392 below the erosive shelf edge, that it no longer becomes possible to physically retain  
393 fine sediments around the island, ultimately being lost to the abyssal depths (Fig. 8H).  
394 Either way, be it post-glacial colonizers or ‘bottleneck’ glacial survivors, we predict  
395 lower genetic diversity of the populations of shallow-water insular fish species  
396 associated with sandy bottoms [e.g. the following extant species in the Azores: the  
397 European finless eel *Apterichtus caecus* (Linnaeus, 1758); the wide-eyed flounder  
398 *Bothus podas* (Delaroche, 1809); the striped red mullet *Mullus surmuletus* Linnaeus,  
399 1758; the Atlantic lizard fish *Synodus saurus* (Linnaeus, 1758); the greater weever  
400 *Trachinus draco* Linnaeus, 1758; and the pearly razorfish *Xyrichtys novacula* (Linnaeus,  
401 1758)], when compared with continental populations. This prediction can be tested  
402 using molecular tools.

403         In contrast, fish species associated with algae-covered rocky shores, such as the  
404 omnivorous parrotfish *Sparisoma cretense*, were not affected by the drop in SSTs  
405 associated with the inception of glacial episodes, which was estimated at about 2–3°C  
406 (Crowley, 1981) in the region of the Azores. The lineage that led to the two eastern  
407 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  $4.78 \pm 0.13$  to  $4.13 \pm 0.19$  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

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

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

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

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

477

478 **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

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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**

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536

537

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906



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<sup>2</sup> and a total thickness for the sediments of 10–11 m (Ávila et al., 2015b).

930 [Intended for page width].

931

932 **Figure 4.** Stratigraphic columns of the studied outcrops: Malbusca (Rebelo et al.,  
933 2016a; Uchman et al., 2017), Figueiral (Ávila et al., 2018), Pedra-que-pica (Ávila et al.,  
934 2015b), West fault of Malbusca (Uchman et al., 2017), Cré (Janssen et al., 2008),  
935 Prainha and Vinha Velha (Ávila et al., 2010, 2015a). [Intended for page width].

936

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

947

948 **Figure 6.** Actinopterygian fishes from Early Pliocene (DBUA-F 825, 1069, 1214) and Late  
949 Pleistocene (Last Interglacial, MIS 5e; DBUA-F 1030) deposits of Santa Maria Island  
950 (Azores). **A:** Lower grinding face view of Early Pliocene fragmentary tooth plate (DBUA-  
951 F 1069) of *Sparisoma cretense*. **B–E:** Upper grinding face view of pharyngeal plates of  
952 *Sparisoma cretense*. **B–C, E:** Lower pharyngeal plates. **B** (DBUA-F 1030), **C** (DBUA-F  
953 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].

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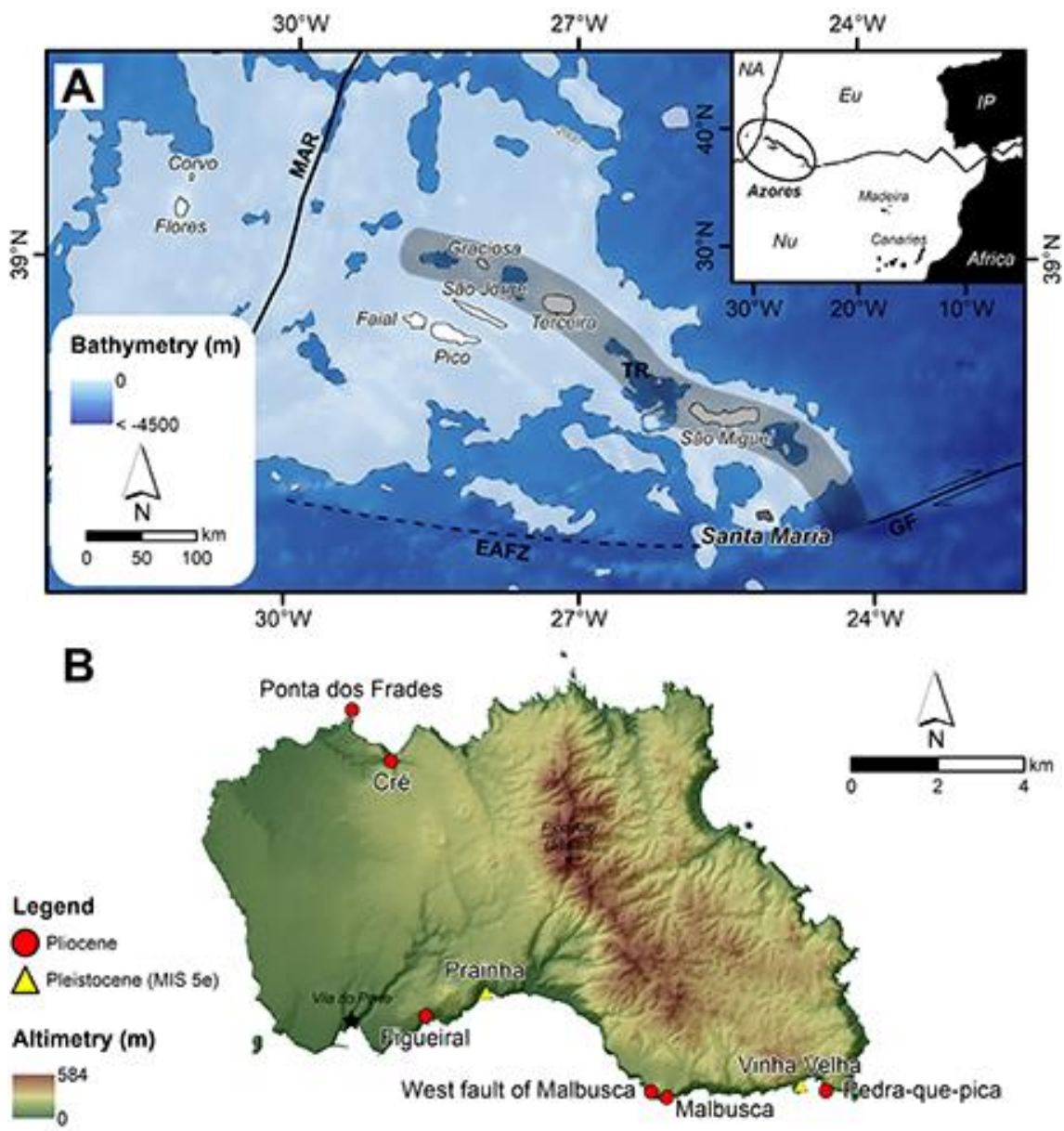
964 **Figure 8.** **A–C**: NE Atlantic Biogeographic Molluscan Provinces from late Miocene to  
965 Pliocene (**A**, 6.0–5.33 Ma), early Pliocene to the end of the mid-Piacenzian Warm  
966 Period (**B**, 5.33–2.95 Ma) and the present (**C**) (Ávila et al., 2016). **D–F**: Comparison of  
967 large-scale 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<sup>6</sup>. **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].

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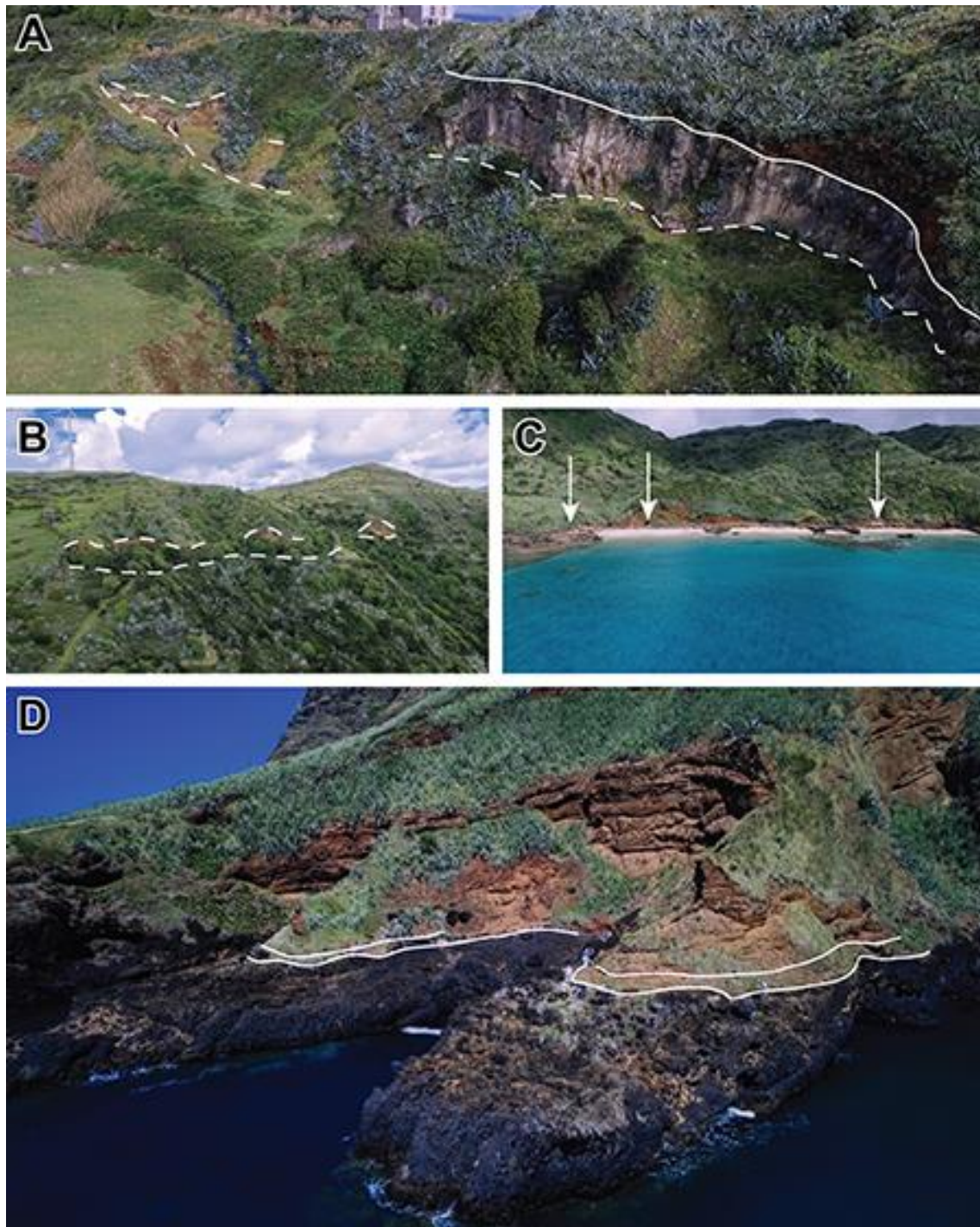
1000 **Figure 1. A:** Location of the Azores Archipelago in the NE Atlantic, and location and  
 1001 geotectonic setting of Santa Maria Island within the Azores Archipelago and within the  
 1002 Azores triple junction, respectively. The light blue area represents the Azores plateau  
 1003 (see text). 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

1007 Last Interglacial Period (c. 116–130 kyr), which is known as MIS 5e (Marine Isotopic

1008 Substage 5e). [Intended for page width].

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1011

1012 **Figure 2.** Aerial (drone) views of the fossiliferous outcrops from Santa Maria Island. **A–**  
 1013 **B:** Pliocene outcrops; **C–D:** Pleistocene (MIS 5e) outcrops. The white line delimits the  
 1014 outcrops. **A:** Cré. **B:** Figueiral. **C:** Prainha (the white arrows point to the areas where  
 1015 fossiliferous sediments are better preserved). **D:** Vinha Velha. [Intended for page  
 1016 width].





1017

1018 **Figure 3.** Aerial (drone) views of the Pliocene fossiliferous outcrops from Santa Maria

1019 Island. The white line delimits the outcrops. **A:** Malbusca. **B:** West fault of Malbusca. **C:**

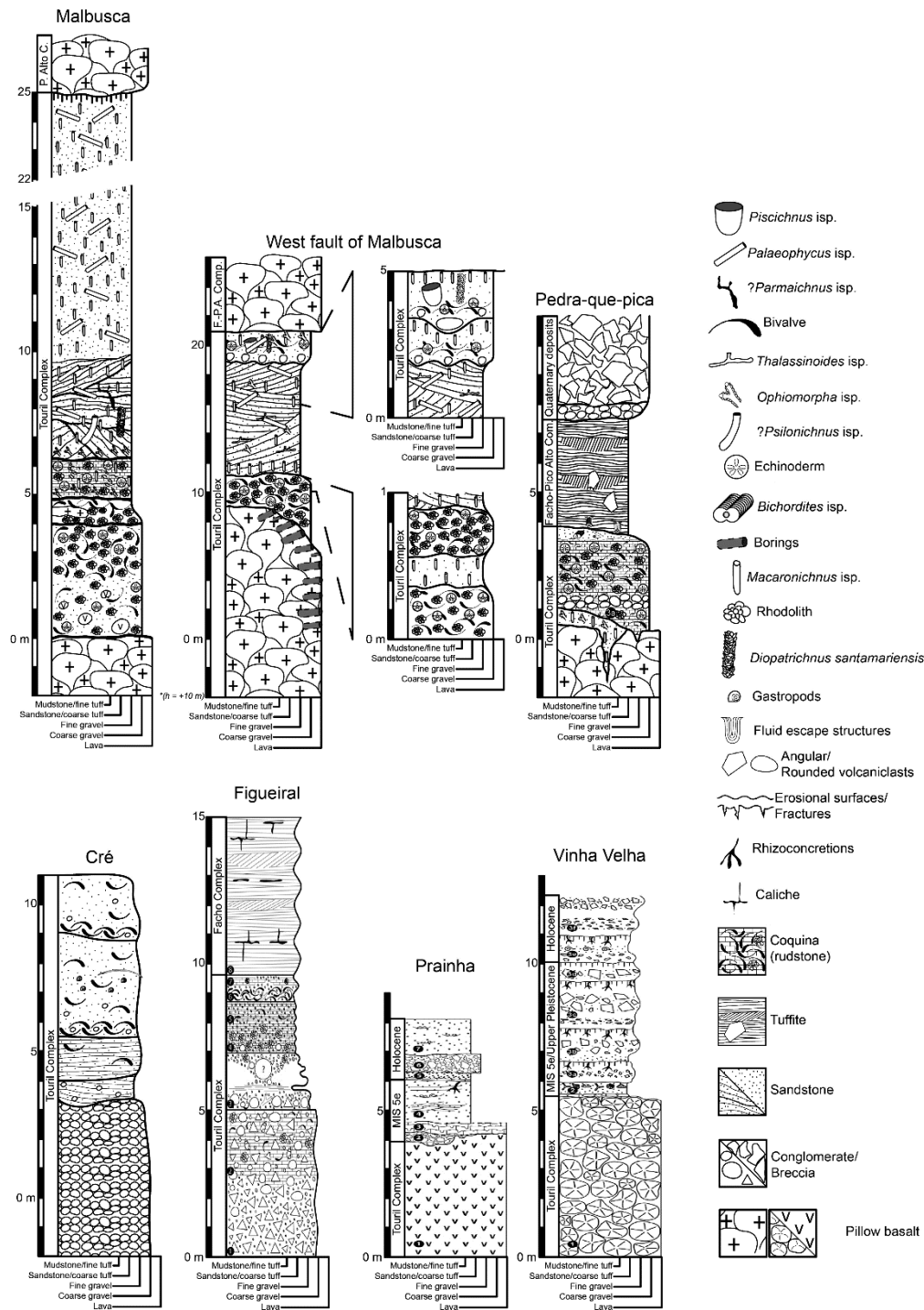


1020 Pedra-que-pica. At West fault of Malbusca (**B**), the fossil strata are displaced by a fault  
1021 slip of about 20 m. Pedra-que-pica (**C**) is probably the largest worldwide multispecific  
1022 coquina ever described from a volcanic oceanic island, with a total estimated area of  
1023 >23,400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

1024 [Intended for page width].

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1027

1028 **Figure 4.** Stratigraphic columns of the studied outcrops: Malbusca (Rebello et al.,  
 1029 2016a; Uchman et al., 2017), Figueiral (Ávila et al., 2018), Pedra-que-pica (Ávila et al.,  
 1030 2015b), West fault of Malbusca (Uchman et al., 2017), Cré (Janssen et al., 2008),  
 1031 Prainha and Vinha Velha (Ávila et al., 2010, 2015a). [Intended for page width].

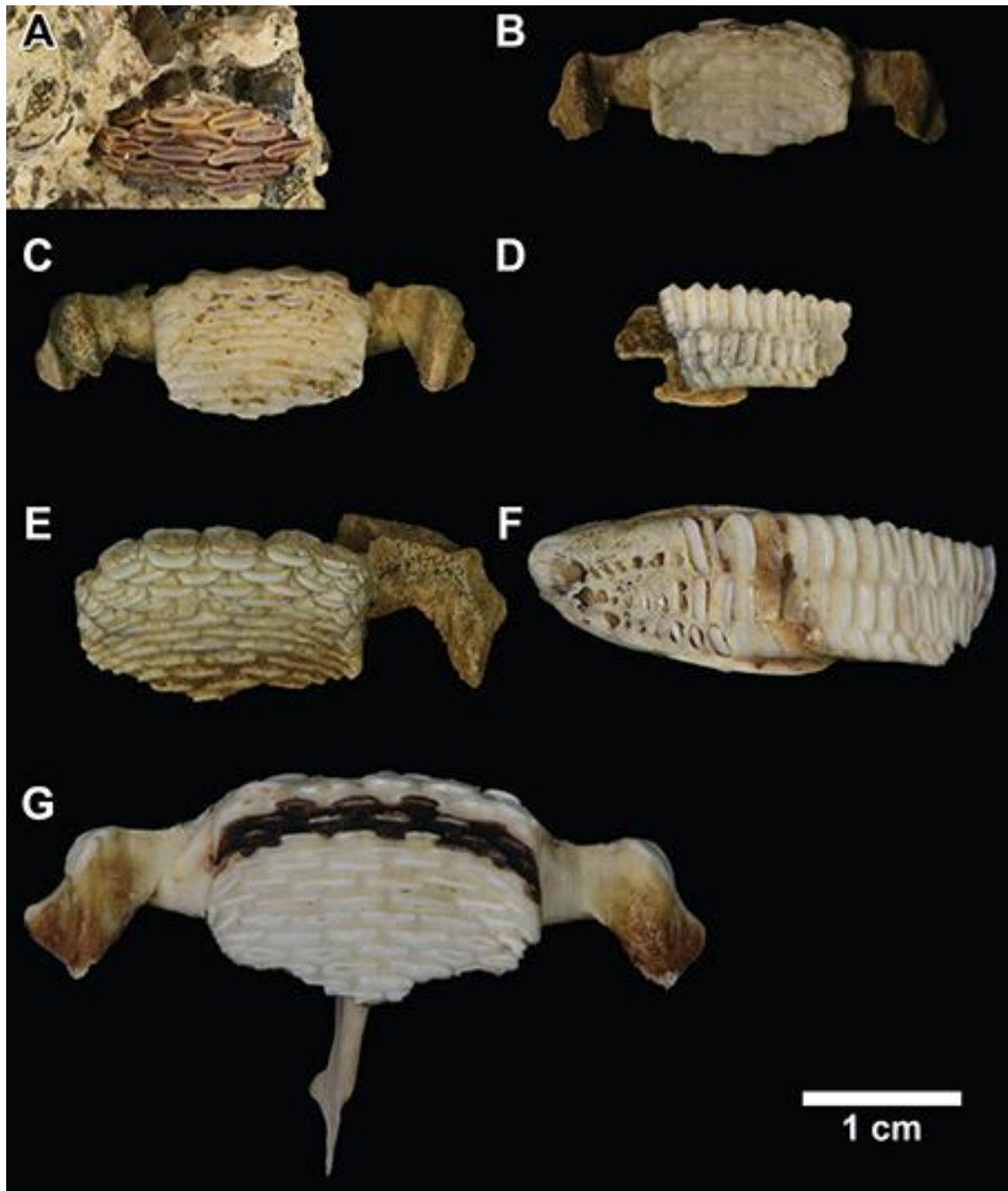
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1034 **Figure 5.** Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island  
 1035 (Azores). **A–L:** Teeth of Sparidae indet. **A–F, L:** Upper lingual hemispheroidal  
 1036 molariform. Note the central depression in teeth photographed 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**

1038 (DBUA-F 667); **I** (DBUA-F 599); **J–K** (DBUA-F 477-2); **L** (MGM 11321). **M–Q**: Teeth of  
1039 Sparidae indet.; these specimens were collected by Georges Zbyszewski at Santa Maria  
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1041 Original label by the former Serviços Geológicos de Portugal (presently housed at the  
1042 Museu Geológico e Mineiro, Lisbon: MGM 11313). **M, P**: Apical view of the teeth; **N–O**,  
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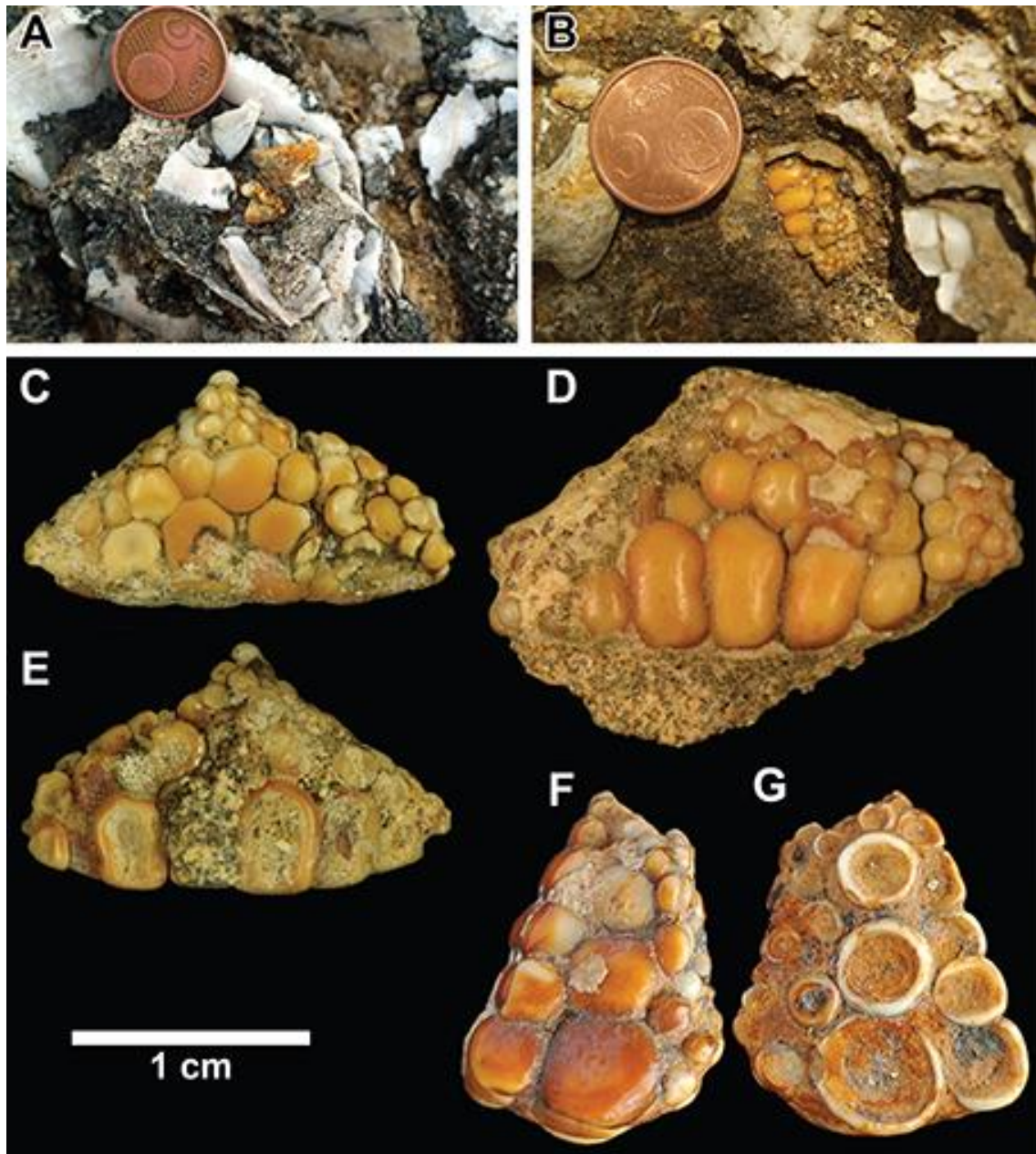


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1047 **Figure 6.** Actinopterygian fishes from Early Pliocene (DBUA-F 825, 1069, 1214) and Late  
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 1052 1214-1), **E** (DBUA-F 825). **D:** Upper pharyngeal plate (DBUA-F 1214-2). **F–G:** Upper

- 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].  
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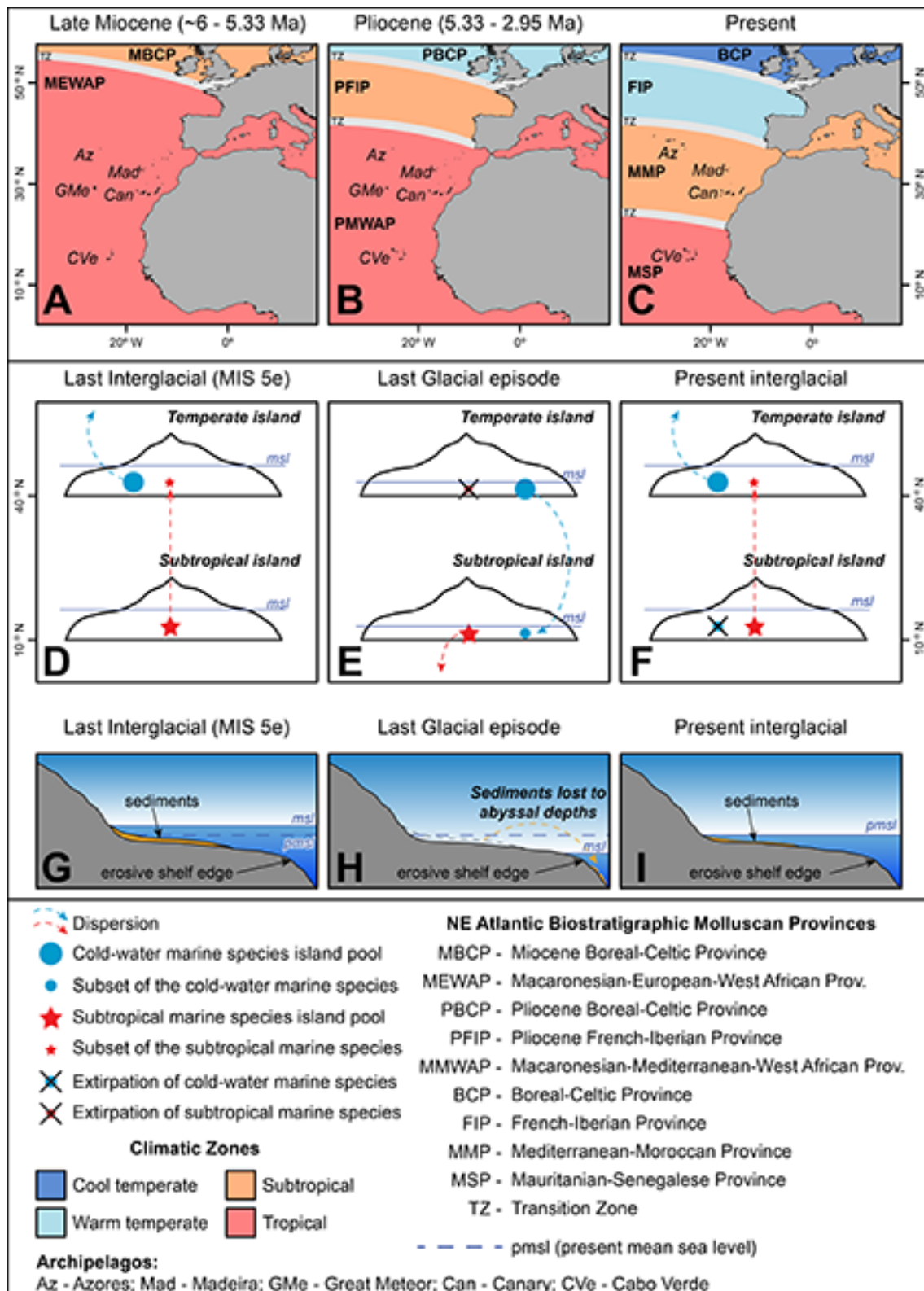




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Period (B, 5.33–2.95 Ma) and the present (C) (Ávila et al., 2016). D–F: Comparison of



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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  
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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  
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1096 and fluvial erosion, during the present sea-level highstand. [Intended for page width].  
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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	<i>Sparisoma cretense</i>	<i>Labrodon pavimentatum</i>
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	

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1101 **Table 2.** Present geographical distribution of the genus *Sparisoma* in the Atlantic Ocean and the Mediterranean Sea. AZO – Azores Archipelago;  
 1102 MAD – Madeira Archipelago; SEL – Selvagens Archipelago; CAN – Canaries Archipelago; CAB – Cabo Verde Archipelago; STP – São Tomé and  
 1103 Príncipe Archipelago; IBE – Atlantic Iberian shores from Finisterra south to the Straits of Gibraltar; MED – Mediterranean Sea; TWAF – Tropical  
 1104 west African shores, from Cape Blanc (Senegal) south to Angola; NWA – Atlantic coast of Northwest Africa, from the Straits of Gibraltar south  
 1105 to Senegal; ASC – Ascension Island; STH – Saint Helena Island; SWA – Southwest Atlantic, including Brazil and its oceanic islands; WAT –  
 1106 Western Atlantic, including the Caribbean Sea.

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



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

**Table 3.** (Continued)

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

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