

Original Article

**Cite this article:** Ávila SP, Azevedo JMN, Madeira P, Cordeiro R, Melo CS, Baptista L, Torres P, Johnson ME, and Vullo R. Pliocene and Late Pleistocene actinopterygian fishes from Santa Maria Island, Azores (NE Atlantic Ocean): palaeoecological and palaeobiogeographical implications. *Geological Magazine* <https://doi.org/10.1017/S0016756820000035>

Received: 15 September 2019

Revised: 4 December 2019

Accepted: 6 January 2020

**Keywords:**

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

**Author for correspondence:**

Sérgio P. Ávila, Email: [avila@uac.pt](mailto:avila@uac.pt)

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

Sérgio P. Ávila<sup>1,2,3</sup> , José M.N. Azevedo<sup>2,4</sup>, Patrícia Madeira<sup>1,2,3</sup>, Ricardo Cordeiro<sup>1,2,3</sup>, Carlos S. Melo<sup>1,3,5,6</sup>, Lara Baptista<sup>1,2,3</sup>, Paulo Torres<sup>1,2,3</sup>, Markes E. Johnson<sup>7</sup> and Romain Vullo<sup>8</sup> 

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

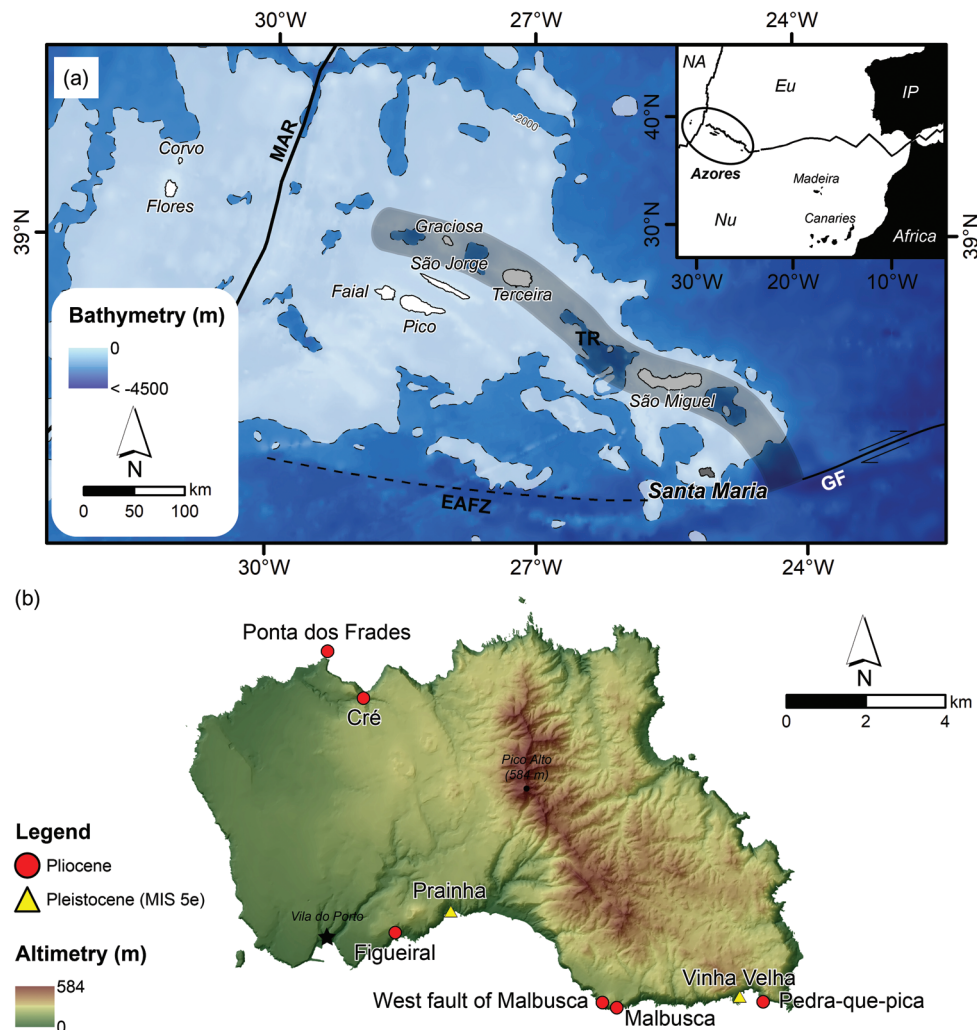
## Abstract

Fossil fishes 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. We report on the fossil fishes, resulting in an increase in the number of Pliocene fishes from the Azores to 11 taxa: seven Chondrichthyes and at least four 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, as a result of the remobilization and sediment transport to abyssal depths, during the Last Glacial episode; these are viewed as post-glacial colonizers or as ‘bottleneck’ survivors from the Last Glaciation.

## 1. 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 with that for vastly larger continents (Ávila *et al.* 2018). However, the dating of an island’s fossil fauna and flora 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). 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, 2015b, c, 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 remains also



**Fig. 1.** (Colour online) (a) Location of the Azores Archipelago in the NE Atlantic, plus location and geotectonic setting of Santa Maria Island within the Azores Archipelago and within the Azores triple junction, respectively. The light blue area represents the Azores plateau (see text). MAR – Mid-Atlantic Ridge; EAFZ – East Azores fault zone; GF – Gloria fault; NA – North American plate; Eu – Eurasian plate; Nu – Nubian (African) plate. (b) Location of the Pliocene (red circles) and Pleistocene fossiliferous outcrops (yellow triangles) of Santa Maria Island. The Pleistocene outcrops are restricted to the warmest interval of the Last Interglacial Period (c. 130–116 ka), which is known as MIS 5e (Marine Isotopic Substage 5e; Ávila *et al.* 2018).

have been studied, most notably cetaceans (Estevens & Ávila, 2007; Ávila *et al.* 2015a) and sharks (Ávila *et al.* 2012). Fossil bony fishes are known from the island, but the last account for Santa Maria fossil Actinopterygii fishes dates from the 1950s and 1960s (Ferreira, 1955; Zbyszewski & Ferreira, 1962). With few exceptions (Ávila *et al.* 2012; Betancort *et al.* 2016), the majority of the published palaeoecological and palaeobiogeographical studies on the marine fauna and flora of the Macaronesian archipelagos targeted sessile or low-motility species, such as the marine molluscs, echinoderms, bryozoans, barnacles, ostracods and algae (Meco, 1977; Meco *et al.* 1997, 2015, 2016; Ávila *et al.* 2008a, b, 2009a, b, 2015b; Winkelmann *et al.* 2010; Madeira *et al.* 2011; Santos *et al.* 2011, 2012a, b; Meireles *et al.* 2012, 2014; Ávila, 2013; Baarli *et al.* 2013, 2017; Betancort *et al.* 2014; Johnson *et al.* 2014; Rebelo *et al.* 2014; Tuya *et al.* 2017). Still largely unresolved, an interesting question is how the evolutionary patterns and processes inferred from these studies relate to the dispersal capabilities of species (Ávila *et al.* 2019). This study therefore aims to: (1) review and update the status of all existing Actinopterygii fossil material from Santa Maria Island; (2) use this new data to test previous statements by several authors (e.g. Briggs, 1974; Santos *et al.*

1995; Domingues *et al.* 2006, 2008) who concluded that the shallow littoral fauna of the Azores was extirpated during the Last Glacial episode; and (3) compare the palaeobiogeographical and palaeoecological patterns known from sessile and low-dispersive species (e.g. non-planktotrophic marine molluscs) with that of highly motile species such as fishes.

## 2. Geographical and geological setting

### 2.a. Azores Archipelago

The nine volcanic oceanic islands that form the Azores Archipelago are located in the NE Atlantic Ocean (Fig. 1) and rise from a bathymetric anomaly (the Azores Plateau) with depths of c. 2000 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

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

Outcrop	Age (Ma)	Reference	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	Ramalho <i>et al.</i> (2017)	Sandstone	?	4		
Figueiral	4.78 ± 0.13 to 4.13 ± 0.19	Ramalho <i>et al.</i> (2017)	Sandstone	?	1		
Ponta dos Frades	4.78 ± 0.13 to 4.13 ± 0.19	Ramalho <i>et al.</i> (2017)	Sandstone	?		6	
Pedra-que-pica	4.78 ± 0.13 to 4.13 ± 0.19	Ramalho <i>et al.</i> (2017)	Coquina	-40	26	1	2
Malbusca	4.32 ± 0.06 to 4.02 ± 0.06	Sibrant <i>et al.</i> (2015)	Sandstone	-60	17		
West fault of Malbusca	4.32 ± 0.06 to 4.02 ± 0.06	Sibrant <i>et al.</i> (2015)	Sandstone	-60	2		
Vinha Velha	Last Interglacial (MIS 5e)	Ávila <i>et al.</i> (2015b)	Sand	+1 to +2		1	

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 NE and east (Searle, 1980; Fig. 1a). This area (i.e. the Azores Plateau, the Azores Triple Junction and the islands that comprise the Azores Archipelago), 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', is referred to as the 'Azores Geosyncline' (Vogt & Jung, 2018).

## 2.b. Santa Maria Island

This island has a complex geological history (for a review, see Ramalho *et al.* 2017). It is the oldest island of the Azores Archipelago and first rose above sea level at *c.* 6 Ma, initially by Surtseyan activity (the Cabrestantes Formation) and then by subaerial, monogenetic volcanism associated with 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 by the present-day insular shelf (Ricchi *et al.* 2018). Although the entire volcanic edifice has likely undergone subsidence since extrusion of the first lavas of the submarine edifice, a prolonged subsidence rate of *c.* 100 m Ma<sup>-1</sup> lasted from 5.3 Ma until 3.5 Ma (Ramalho *et al.* 2017). Volcanic activity associated with the Anjos shield volcano ceased at *c.* 5.3 Ma and was followed by a period of *c.* 1.2 Ma with almost no volcanism, during which the protoisland nearly vanished due to erosion (Ávila *et al.* 2012; Ramalho *et al.* 2017), thus originating a large, flat, shallow seamount. The sediments of this unit (the Touril volcano-sedimentary complex; 5.30–4.13 Ma) are highly fossiliferous and correspond to early Pliocene outcrops (Ávila *et al.* 2018) formerly described in the literature as being of Miocene in age (see Madeira *et al.* 2007 for a review). Volcanic activity initiated again at *c.* 4.1 Ma during the first rejuvenated stage with eruptive foci associated with the Pico Alto volcanic successions, first submarine and later subaerial in nature (Ramalho *et al.* 2017), thus causing the revival of Santa Maria as an island. This stage lasted until 3.5 Ma, when the subsidence trend was reversed and the island's volcanic edifice initiated an uplift trend continuing to the present day. Initially, a rate of 59 m Ma<sup>-1</sup> occurred during 3.50–2.15 Ma, and then a slower rate of 42 m Ma<sup>-1</sup> between 2.15 Ma and the present (Ricchi *et al.* 2018). This uplift trend, coupled with

Pleistocene glacio-eustatic sea-level fluctuations, produced a staircase of ten subaerial and five submerged marine terraces, the former particularly evident across the island's western sector at elevations ranging from 7–11 to 210–230 m (Ramalho *et al.* 2017), and the latter on the shelf all around the island at depths ranging between 40–50 and 120–140 m below sea level (Ricchi *et al.* 2018). A second rejuvenated stage occurred during 3.2–2.8 Ma, associated with monogenetic volcanism of the Feteiras Formation. Uplift has continued until today, but erosion became the dominant agent impacting the island's landscape during the last 2.8 Ma (Ramalho *et al.* 2017).

## 2.c. Institutional abbreviations

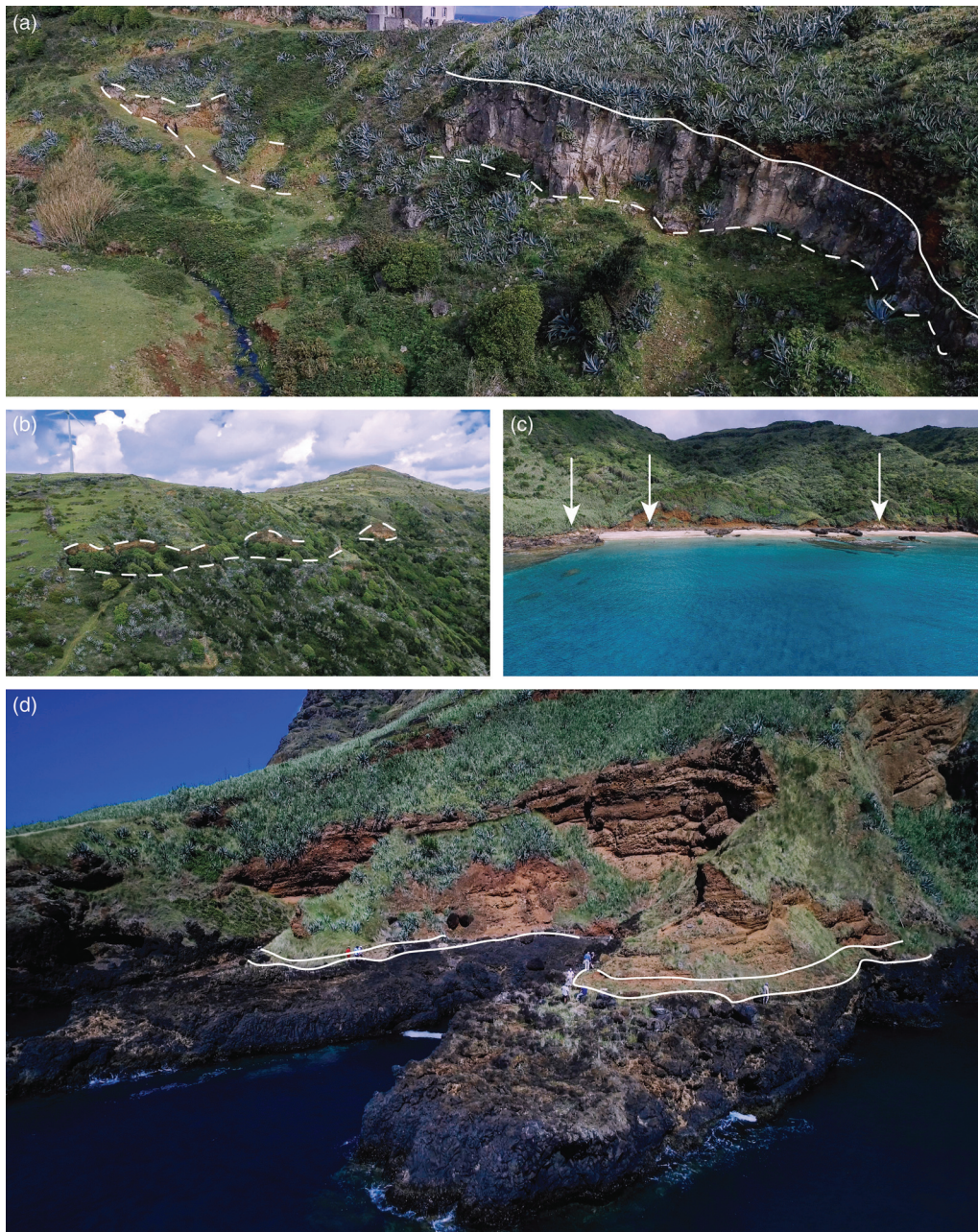
DBUA-F: fossil collection of the Department of Biology of the University of the Azores (Portugal).

LAQ-F: fossil collection of the Liceu Antero de Quental, Ponta Delgada, São Miguel Island (Azores, Portugal).

MGM: fossil collection of the former Museu Geológico e Mineiro, now Museu Geológico, LNEG, Lisbon (Portugal).

## 3. Materials and methods

Most of the 20 known fossiliferous outcrops on Santa Maria Island are early Pliocene in age, but scattered Last Interglacial deposits from the Pleistocene Epoch are also known from the north (Lagoinhas; Ávila *et al.* 2009a, b) and southern shores (Prainha, Praia do Calhau and Vinha Velha outcrops; Ávila *et al.* 2002, 2010, 2015b; Fig. 1b). The fossil fish specimens reported here were found in sedimentary layers from a total of eight outcrops (Table 1). Six of these contain fauna that deposited during early Pliocene time: Cré (Kroh *et al.* 2008; Fig. 2a), Figueiral (Rebelo *et al.* 2016a; Ávila *et al.* 2018; Fig. 2b), Malbusca (Rebelo *et al.* 2016b; Johnson *et al.* 2017; Fig. 3a), West Fault of Malbusca (Uchman *et al.* 2017; Fig. 3b), Pedra-que-pica (Ávila *et al.* 2015c, 2018; Uchman *et al.* 2016; Fig. 3c), and the yet undescribed Ponta dos Frades outcrop. The two remaining outcrops (Prainha, Fig. 2c; Vinha Velha, Fig. 2d) include faunas from the Last Interglacial period (*c.* 130–116 ka), of which the warmest interval is known as MIS 5e (Marine Isotopic Stage 5e) (Ávila *et al.* 2015b). Figure 1b shows the geographical location of each outcrop and Figure 4 displays representative composite sections of the studied outcrops.



**Fig. 2.** (Colour online) Aerial (drone) views of the fossiliferous outcrops from Santa Maria Island. (a, b) Pliocene outcrops and (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); and (d) Vinha Velha.

All specimens described were collected during 14 fieldwork campaigns of the *Palaeontology in Atlantic Islands* workshops, held on Santa Maria Island from 2002 to 2017. In compliance with the legislation that rules the PalaeoPark Santa Maria, all fossil specimens collected were deposited in the fossil collection at the Department of Biology of the University of the Azores (DBUA-F). Over 1300 lots containing fossil specimens collected at Santa Maria Island were screened for fossil Actinopterygii fishes, yielding a total of 42 lots containing oral and pharyngeal tooth plates. As the oral and pharyngeal tooth plates are frequently well preserved in the fossil record and display diagnostic features (Bellwood & Schultz, 1991), direct comparisons of the fossil remains with fossil and recent specimens (whenever available) were used to classify our material. Systematics for Actinopterygii

conform to the World Register of Marine Species (<http://www.marinespecies.org>) and the teeth terminology for Scaridae is in accordance with Day (2002).

All data generated or analysed during this study are included in this published article.

#### 4. Results

Actinopterygian fish taxa were found in the fossiliferous sediments of Santa Maria Island: at least two extinct Sparidae species with a probable Mio-Pliocene temporal range (Fig. 5a–q); *Sparisoma cretense* (Linnaeus, 1758) (Fig. 6), an extant Scaridae reported here for the Pliocene and Pleistocene epochs (Last Interglacial, MIS 5e) of the Azores; and *Labrodon pavimentatum*



**Fig. 3.** (Colour online) 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; and (c) Pedra-que-pica. At West fault of Malbusca, the fossil strata are displaced by a fault slip of c. 20 m. Pedra-que-pica outcrop (c) spreads from the intertidal to about 4 m in elevation, and is probably the largest worldwide multispecific coquina ever described from a volcanic oceanic island with a total estimated area of >23 400 m<sup>2</sup> and a total thickness of sediments of 10–11 m, 7 m of which are presently underwater (Ávila *et al.* 2015c).

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

#### 4.a. Systematic palaeontology

Class Actinopterygii Klein, 1885

Order PERCIFORMES Bleeker 1859

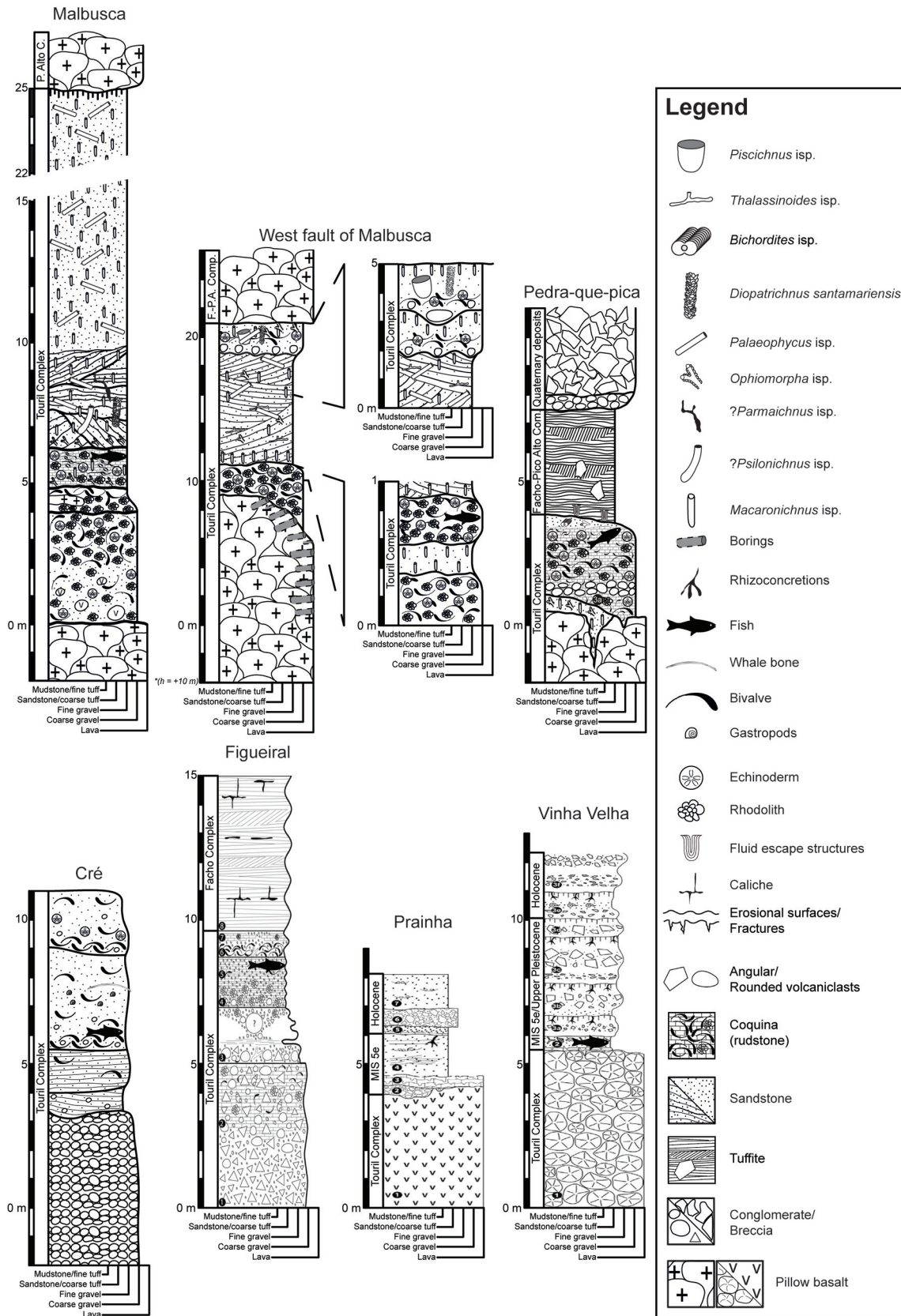
Family Sparidae Rafinesque, 1818

Genera and species indet.

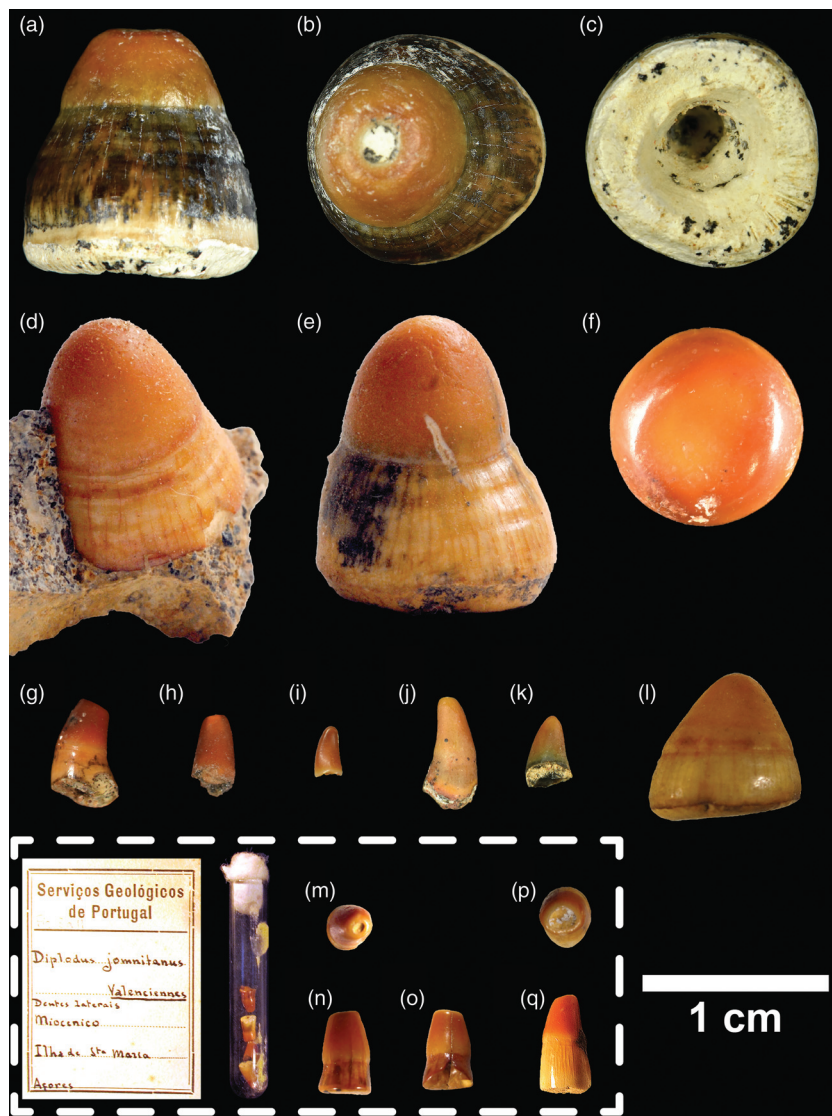
Figure 5a–q

*Material examined.* Fifty-six 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 incisi-form teeth. We have examined a total of 39 molariform teeth corresponding to the lingual series (36 spheroidal in shape,



**Fig. 4.** Stratigraphic columns of the studied outcrops: Malbusca (Rebello *et al.* 2016a; Uchman *et al.* 2017), West fault of Malbusca (Uchman *et al.* 2017), Pedra-que-pica (Ávila *et al.* 2015c), Cré (Janssen *et al.* 2008), Figueiral (Ávila *et al.* 2018), Prainha and Vinha Velha (Ávila *et al.* 2010, 2015b).



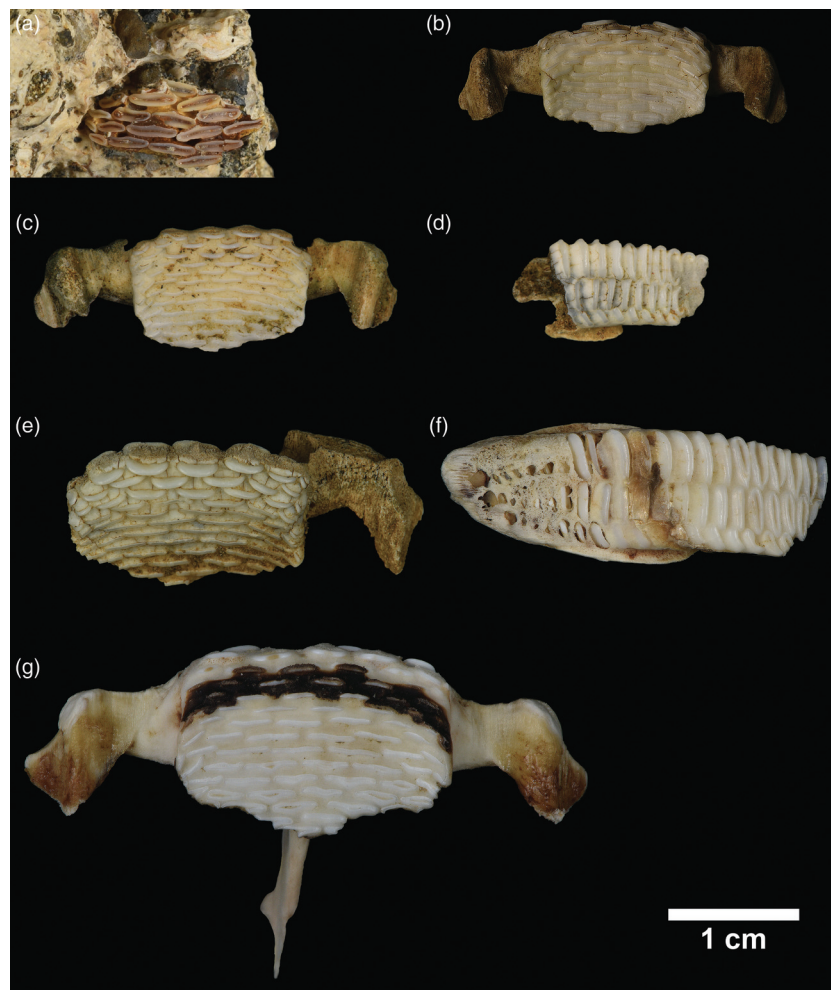
**Fig. 5.** (Colour online) Actinopterygian fishes from Early Pliocene deposits of Santa Maria Island (Azores). (a–l) Teeth of Sparidae indet. (a–f, l) Upper lingual hemispheroidal molariform. Note the central depression in teeth photographed in (a–c) and (f). (a–c) (DBUA-F 165-1); (d, e) (LAQ, not numbered); (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 11312). (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; and (n, o, q) lateral view.

2.87–17.34 mm in diameter; Fig. 5a–f, l; 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, f). 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 sediments of the Mediterranean Sea (Obrador & Mercadal, 1973; Vicens & Rodríguez-Perea, 2003; Mas & Antunes, 2008) and from the Miocene strata of France (Gagnaison, 2017). In the Atlantic, *Archosargus* species are reported from the Miocene sediments of Portugal (Zbyszewski & d’Almeida, 1950; Jonet *et al.* 1975) and Morocco (Lecointre, 1952), the Pliocene strata of the Canary Islands (Gran Canaria Island) (Betancort *et al.* 2016) and from the Pliocene Series of the Azores (Santa Maria Island) (Zbyszewski & d’Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962; Ávila *et al.* 2015c). The extinct species formerly known as *D. jomnitanus* is reported from the Miocene strata of France (Gagnaison, 2017), Portugal (Zbyszewski & d’Almeida, 1950; Jonet *et al.* 1975) and the Mediterranean Sea (Vicens & Rodríguez-Perea, 2003), and from the Pliocene sediments of the Azores (Santa Maria Island) (Zbyszewski & d’Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962). Extinct *Pagrus* species



**Figure 6.** (Colour online) Actinopterygian fishes from lower Pliocene (DBUA-F 825, 1069, 1214-1, 1214-2) and upper Pleistocene (Last Interglacial, MIS 5e; DBUA-F 1030) deposits of Santa Maria Island (Azores). (a) Lower grinding face view of lower Pliocene fragmentary tooth plate (DBUA-F 1069) of *Sparisoma cretense*. (b–e) Upper grinding face view of Last Interglacial pharyngeal plates of *Sparisoma cretense*. (b, c, e) Lower pharyngeal plates: (b) (DBUA-F 1030), (c) (DBUA-F 1214-1) and (e) (DBUA-F 825). (d) Upper pharyngeal plate (DBUA-F 1214-2). (f, g) Upper grinding face view of recent pharyngeal plates from a dissected *S. cretense*: (f) upper pharyngeal plate and (g) lower pharyngeal plate.

are reported from Mio-Pliocene sediments from the Mediterranean Sea and from Europe (Arambourg, 1927; Bauzá, 1948; Menesini, 1969; Bauzá & Plans, 1973; Jonet, 1975; Antunes *et al.* 1981).

Family LABRIDAE Cuvier, 1816

Tribe SCARINI Rafinesque, 1810

Genus *Sparisoma* Swainson, 1839

*Sparisoma cretense* (Linnaeus, 1758)

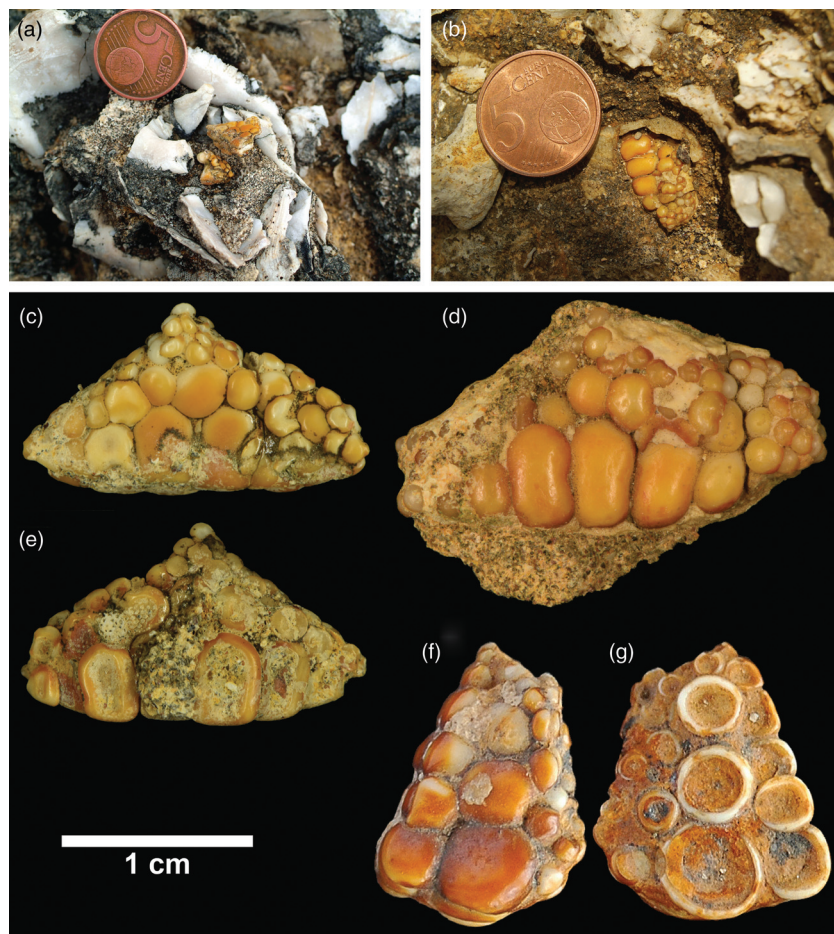
Figure 6

**Material examined.** Seven pharyngeal plates (four lower and three upper) plus one fragmentary tooth plate: Ponta dos Frades (three lower and three upper pharyngeal plates), Vinha Velha (one lower pharyngeal plate) and Pedra-que-pica (one fragmentary tooth plate): DBUA-F 825, 1030, 1069, 1214-1 to 1214-5.

**Description.** This species has a jaw formed from modified hindmost gill-arch, with tooth-bearing bones above, denominated upper pharyngeal plates and a large, single bone below, the lower pharyngeal plate. Our fossil specimens' pharyngeal plates are very similar to those of Recent specimens of *Sparisoma cretense*. The

tooth rows of the lower pharyngeal plate range from 11 to 12 in the fossil material, and from 10 (in smaller specimens) to 14 (in larger animals) in the recent material. We detected some intra-specific variation on the pharyngeal jaw elements in both fossil and recent specimens (i.e. the increasing number of tooth rows with the total length of the specimen, as well as the slightly different angles of the lateral bony articulation in smaller fossil and recent specimens), which we attribute to ontogeny. For example, a fresh specimen of *S. cretense* was weighted and measured (1.585 kg; 45.50 cm in total length; 40.50 cm standard length). Its lower pharyngeal plate was 4.11 cm wide, which compares with those from fossil material that 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 three 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



**Figure 7.** (Colour online) Actinopterygian fishes from lower 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.

African shores; Rocha *et al.* 2012; and *S. frondosum* (Agassiz, 1831), endemic to Cabo Verde; Clements *et al.* 2016); and the eurythermic *S. cretense*, with a wider geographical distribution, occurring in all the Macaronesian archipelagos, the Mediterranean Sea, Iberian shores and Senegal (Randall, 1990; Abecasis *et al.* 2008). The upper pharyngeal bones of *S. frondosum* are different from the Azorean fossil specimens; both species have three teeth on each row, but, and for the same row, the lateral tooth of *S. cretense* is consistently about half the size of the medium tooth, in contrast to about two-thirds the size of the medium tooth in the case of *S. frondosum*. We therefore identify the actinopterygian fossils of Santa Maria Island as *S. cretense*. No data were available in the literature to compare the fossil material with *S. choati*.

**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 (Randall, 1990; Abecasis *et al.* 2008). A search for fossil *Sparisoma* species on the PaleoBiology Database (<https://paleobiodb.org/#/>) and on Bellwood *et al.* (2019) yielded no occurrences. With the exception of otoliths from the upper Eocene strata 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 here for the first time from the fossil record based on dental remains. *S. cretense* is reported here from the Pliocene (Pedra-que-pica and Ponta dos Frades outcrops) and Pleistocene (Vinha Velha outcrop; Last Interglacial, MIS 5e) sediments of Santa Maria Island, Azores.

Tribe HYPISIGENYINI 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.

**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 Finiserra 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 NW Africa, from the Straits of Gibraltar south to Senegal; ASC – Ascension Island; STH – Saint Helena Island; SWA – SW 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
<i>S. choati</i>	0	0	0	0	1	1	0	0	1	0	0	0	0	0
<i>S. cretense</i>	1	1	1	1	1	0	1	1	1	1	0	0	0	0
<i>S. frondosum</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>S. amplum</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>S. atomarium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. auofrenatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. axillare</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>S. chrysopterum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. griseorubrum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. radians</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>S. rocha</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>S. rubripinne</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. strigatum</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>S. tuiupiranga</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>S. viride</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1

**Description.** The dentition of Labridae is characterized by subtriangular pharyngeal plates composed of 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 multidentis* (Sacco, 1916) and to *L. pavimentatum* (Simonelli, 1889).

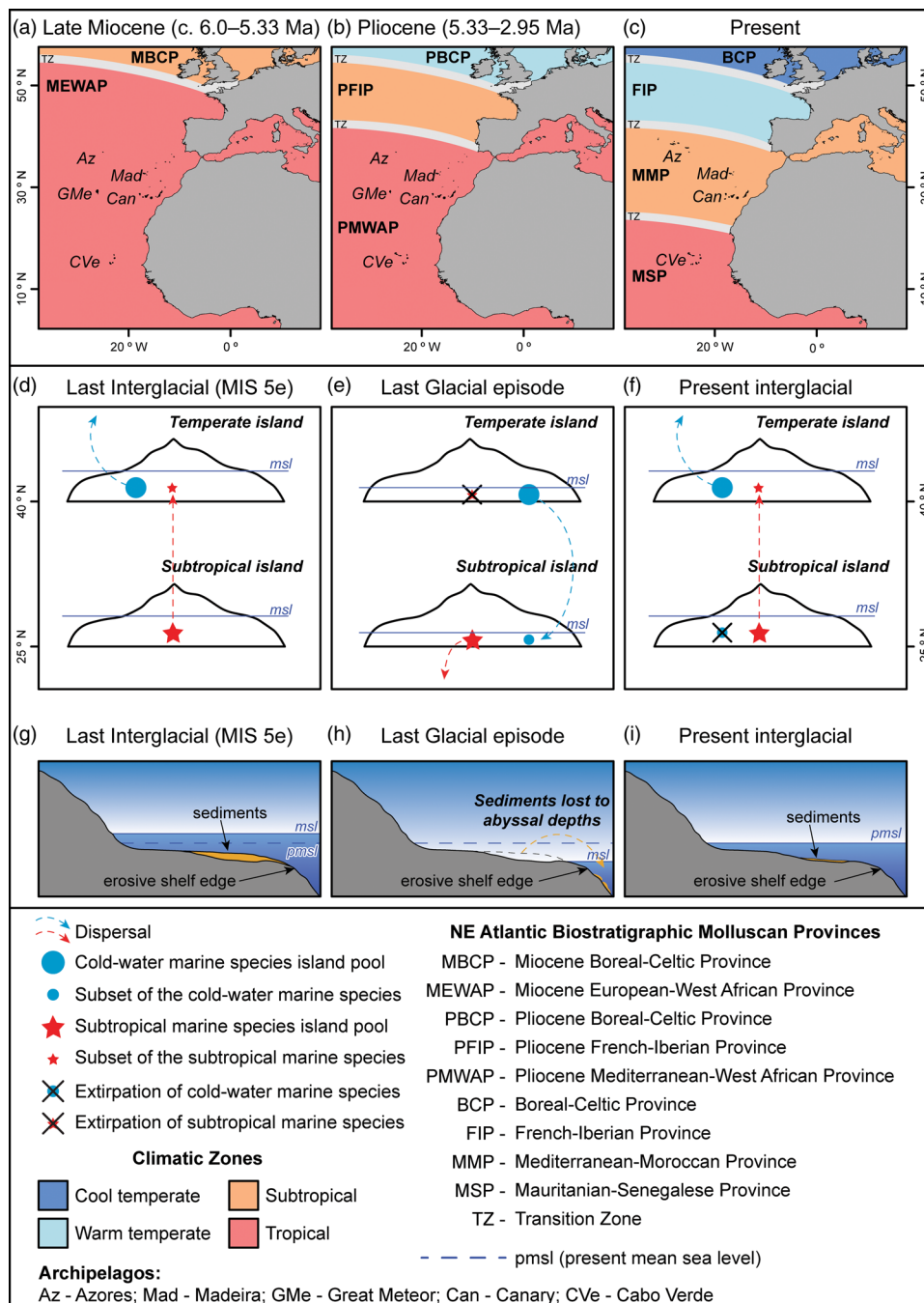
**Stratigraphic and geographic range.** This extinct species is reported from the Miocene sediments of France (Sauvage, 1875; Gagnaison, 2017), Portugal (Jonet *et al.* 1975), Poland (Bellwood *et al.* 2019) and the Mediterranean (Cocchi, 1864; Landini, 1977; Mas & Antunes, 2008). It is also reported from the western Atlantic, from the Miocene strata of Costa Rica (Laurito *et al.* 2014) and also from the Pliocene strata of Morocco (Lecointre, 1952), France (de Lumley, 1988) and the Azores (Santa Maria Island: Zbyszewski & d'Almeida, 1950; Ferreira, 1955; Zbyszewski & Ferreira, 1962; this work).

## 5. Discussion

This contribution expands the number of Pliocene fishes reported from the Azores to at least 11 taxa: 7 taxa of Chondrichthyes (Ávila *et al.* 2012): *Carcharias acutissima* (Agassiz, 1833–1843), *Carcharhinus cf. leucas* (Valenciennes, 1839 in Müller & Henle, 1839), *Cosmopolitodus hastalis* (Agassiz, 1833–1843), *Isurus oxyrinchus* Rafinesque, 1810, *Otodus (Megaselachus) megalodon* (Agassiz in Charlesworth, 1837), *Notorynchus primigenius* (Agassiz, 1833–1843) and *Paratodus benedenii* (Le Hon, 1871); and 4 of Actinopterygii (this work): at least two Sparidae indet. taxa, *Labrodon pavimentatum* and *Sparisoma cretense*. Most of these

are also reported from the Pliocene sediments of Canaries (Betancort *et al.* 2016), the exceptions being *Carcharhinus cf. priscus* (Agassiz, 1833–1843), *Diodon scillae* Agassiz, 1833–1843 and *Galeocerdo cf. aduncus* Agassiz, 1833–1843, which are only reported for the Canary Islands.

During late Miocene time, the once continuous and large tropical Miocene European-West African palaeobiogeographical molluscan province (MEWAP; Ávila *et al.* 2016) stretched between c. 50° N to the equator and further south to Angola (Baarli *et al.* 2017) at c. 15° S (Fig. 8a). The waters around the Azores exhibited tropical temperatures during late Miocene – early Pliocene time, with mean annual sea surface temperatures (SSTs) estimated to be c. 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 the increasing number of known thermophilic taxa that either 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 middle Piacenzian Stage (towards the end of the Pliocene Epoch at c. 3.3–3.6 Ma, or sometime prior), a 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 c. 4.2–4.1 Ma (Meco *et al.* 2007). As a direct consequence of the MIS M2 glaciation, a S-directed geographical range contraction of the biogeographical provinces took place, with the appearance of the subtropical Pliocene French-Iberian Province (PFIP) located on the former northern range of the tropical MEWAP (cf. Fig. 8b; Ávila *et al.* 2016). 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 (five bivalves, one benthic



**Figure 8.** (Colour online) (a–c) NE Atlantic Biogeographic Molluscan Provinces from (a) late Miocene – Pliocene time (6.0–5.33 Ma); (b) early Pliocene time to the end of the middle Piacenzian Warm Period (5.33–2.95 Ma); and (c) the present (adapted from Ávila *et al.* 2016; see ‘Discussion’ section for further explanation). (d–f) Comparison of large-scale evolutionary and biogeographical patterns as a result of long-distance dispersal of marine species between oceanic islands located at different climate settings (subtropical v. temperate latitudes) for the last 150 ka, encompassing the Last Interglacial (MIS 5e), the Last Glacial episode, and the present interglacial (adapted from Ávila *et al.* 2019). (d) During the final phase of Termination 2 and/or the beginning of the Last Interglacial, a subset of marine subtropical species expanded their geographical ranges towards higher latitudes (red arrow), reaching temperate archipelagos and establishing viable populations in those islands (e.g. small red star). In a similar way, a subset of marine temperate species expanded their geographical ranges towards higher latitudes, reaching boreal/arctic archipelagos and also establishing viable populations (blue arrow). (e) During the course of the Last Glacial episode, the thermophilic species that established on temperate islands are extirpated; it is expected that a subset of marine temperate species (small blue circles) adapted to cool temperatures may have expanded their geographical ranges towards lower latitudes, reaching subtropical archipelagos and establishing viable populations. (f) The subsequent episode of global warming that led to the present interglacial extirpates the cold-adapted species that reached subtropical islands during the previous glacial episode, and the range expansion of species towards higher latitudes is documented. (g–i) Mobile sediment response to glacio-eustatic sea-level fluctuations (adapted from Ávila *et al.* 2008a, 2010). (g) During the Last interglacial (MIS 5e), as a result of marine and fluvial erosion sediments are transported to the island shelf where they accumulate in the distal parts of the shore platform, with clinoforms ending at the erosive shelf edge. (h) The inception of sea-level lowstands during the Last Glacial episode promotes the remobilization and transport downslope of sediments from the island shelf, when relative mean sea level falls below the erosive shelf edge and sediments are lost to the abyssal depths that surround the insular edifice. (i) Sediments accumulate again on the island shelf as a result of marine and fluvial erosion during the present sea-level highstand.

**Table 3.** Taxa/species reported from the Pliocene sediments of Santa Maria Island that are presently extinct or were extirpated (local disappearances) from the marine fauna of the island during the global climate deterioration that characterizes late Pliocene time. L. dis – local disappearance.

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
Echinodermata	<i>Clypeaster altus</i> (Leske, 1778)	Extinct
	<i>Eucidaris tribuloides</i> (Lamarck, 1816)	L. dis
	<i>Echinoneus</i> cf. <i>cyclostomus</i> Leske, 1778	L. dis
	<i>Schizobrissus</i> sp.	Extinct
Brachiopoda	<i>Novocrania turbinata</i> (Poli, 1795)	Extinct
Arthropoda (Crustacea)	<i>Zullobalanus santamariaensis</i> Buckeridge & Winkelmann, 2010	Extinct
Chordata (Elasmobranchii)	<i>Notorynchus primigenius</i> (Agassiz, 1833–1843)	Extinct
	<i>Carcharias acutissima</i> (Agassiz, 1833–1843)	Extinct
	<i>Cosmopolitodus hastalis</i> (Agassiz, 1833–1843)	Extinct
	<i>Paratodus benedenii</i> (Le Hon, 1871)	Extinct
	<i>Megaelachus megalodon</i> (Agassiz in Charlesworth, 1837)	Extinct
Chordata (Actinopterygii)	Sparidae indet.	Extinct
	<i>Labrodon pavementatum</i> Gervais, 1857	Extinct

macrogastropod, one neustonic gastropod and four holoplanktonic gastropods; Janssen *et al.* 2008; Ávila *et al.* 2015c, 2016, 2018; Beu, 2017), four echinoderms (Madeira *et al.* 2011), one brachiopod (Kroh *et al.* 2008), one barnacle (Winkelmann *et al.* 2010) and five sharks (Ávila *et al.* 2012). This pattern of extinctions/extirpations from volcanic oceanic islands during late Pliocene time is also reported for other Atlantic archipelagos, such as Madeira (Santos *et al.* 2012), the Canary Islands (Meco *et al.* 2007, 2015, 2016; Martín-González *et al.* 2012; Baarli *et al.* 2017) and Cabo Verde (Baarli *et al.* 2017).

Between 5.3 and 4.13 Ma, the protoisland of Santa Maria was probably entirely destroyed, originating a large seamount where marine sediments rich in organic debris were deposited (Ávila *et al.* 2012; Ramalho *et al.* 2017). 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 (O’Dea *et al.* 2016) and

the Gibraltar Seaway had just reopened at 5.33 Ma in an event known as the Zanclean or post-Messinian flood (Blanc, 2002; Garcia-Castellanos *et al.* 2009). As attested by the fossil record of their geographical distribution, most of the Actinopterygii (this work) and Chondrichthyes (Ávila *et al.* 2012) fishes reported from the Pliocene sediments of the Azores are also reported from Pliocene deposits in the NE Atlantic and the Mediterranean Sea, with some species also being reported from Pliocene sediments along the NW shores of Africa; no western Atlantic species have been 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). Additionally, the high number of shared species on archipelagos over 1100 km apart such as the Azores and Cabo Verde is understandable when it is considered that all these archipelagos (i.e. the Azores, Madeira, Selvagens, Canaries and Cabo Verde) were part of the same Atlantic biostratigraphic molluscan province (the Pliocene Mediterranean-West African Province (PMWAP) of Ávila *et al.* (2016); see Fig. 8b), sharing similar tropical palaeoclimatic conditions, during the Pliocene Epoch.

The final closure of the Central American Seaway, caused by re-emergence of the Panamanian land bridge (Briggs, 1995) at c. 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. Moreover, the climatic deterioration that characterized the entire Pleistocene Epoch was responsible for a further equatorial shift of the Atlantic biogeographic provinces, as depicted in Figure 8c (Ávila *et al.* 2016). The effect of a stronger Gulf Stream is testified by the shallow-water (< 50 m depth) marine molluscs of the Azores, which show an 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, b, 2015b) are compared with recent checklists available from this archipelago (Ávila, 2000; Cordeiro *et al.* 2015).

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, b, 2009a). We 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 ka, 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, b, 2009a), that during the subsequent glacial episode (1) all tropical species with a Cabo Verdean provenance 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 experience 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.* 2008a, 2015b; Fig. 8g–i). The trigger for this outcome is when the slope of the insular volcanic edifice becomes so steep below the erosive shelf edge that it is no longer physically possible to retain fine sediments around the island, which are ultimately lost to the abyssal depths (Fig. 8h). Either way, whether post-glacial colonizers or ‘bottleneck’ glacial survivors, we predict a lower genetic diversity of the populations of shallow-water insular fish species associated with sandy bottoms – for example, 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 conspecific 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 as *c.* 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 the eastern Atlantic shores of mainland Portugal, the Azores, Madeira, Canaries, Cabo Verde and Senegal; cf. Table 2) and *S. strigatum* (Günther, 1862) (endemic to Saint Helena and Ascension islands; Table 2), originated at *c.* 10 Ma from a west Atlantic ancestor (Bernardi *et al.* 2000). The oldest known fossil specimens of *S. cretense* were collected in two Pliocene outcrops from Santa Maria Island (Pedra-que-pica and Ponta dos Frades) and dated as  $4.78 \pm 0.13$  to  $4.13 \pm 0.19$  Ma in age (Table 1); our data are therefore in agreement with the estimates of Bernardi *et al.* (2000).

Last Interglacial (MIS 5e) fossils of *S. cretense* were also collected from a Pleistocene outcrop (Vinha Velha; cf. Table 1). Today, *S. cretense* lives as far north as the eastern Atlantic shores of mainland Portugal, where it breeds during the summer from July to September (Abecasis *et al.* 2008; <http://www.fishbase.org>), with mean SSTs varying from 17 to 19°C. The present average SSTs range in the Azores is from 15°C in the winter to *c.* 23–24°C in the summer (Ávila *et al.* 2008c). The gonadosomatic index of *S. cretense* (which is closely associated with mean temperature) increases in the Azores from June to August and then drops to a minimum in November (Afonso *et al.* 2008). Although it mainly breeds from mid-July to mid-September, it is therefore possible that this species extends its reproductive activity through October (Afonso *et al.* 2008). In our opinion, neither temperature nor habitat shift were therefore an impediment for the survival of this species in the Azores throughout the last glacial episode. Our view differs from that of previous authors, who suggested that ‘the drop of sea temperatures . . . that occurred during the Pleistocene probably resulted in mass extinctions’ (of fishes) and so ‘most of the organisms now present would have reached the Azores in the last 17,000 years’ (Santos *et al.* 1995). Our reasoning also 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 preclude 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 into consideration the facts that: (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, b, 2009b, 2015b); (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 previously published theories (Ávila *et al.* 2008a, 2009b, 2015b), 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; and (3) if *S. cretense* was a post-glacial colonizer of the Azores, the genetic diversity of the Azorean populations should be low in comparison to southern Madeiran populations (postulated to have been unaffected by the drop of SSTs); that is not the case, however, as pointed out by Domingues *et al.* (2008). 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 therefore 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, as long as their ecological traits were not constrained to sandy habitats.

## 6. Conclusions

The genus *Sparisoma* Swainson, 1839 is reported here for the first time in the fossil record. The discovery of several pharyngeal plates of *S. cretense* in Pliocene and MIS 5e sediments (Last Interglacial) of Santa Maria Island challenges former authors (Briggs, 1974; Santos *et al.* 1995; Domingues *et al.* 2006, 2008) who argued that mass extinctions affected the shallow-water marine fauna of the Azores during the course of the Last Glaciation and that, as a consequence, most of the present Azorean marine species colonized the area during the last 17–18 ka. A multidisciplinary approach, merging our palaeontological data with ecological and genetic data, offers an alternative, more plausible explanation, suggesting that most (if not all) of the Azorean shallow-water subtropical and temperate marine species living in the archipelago during the Last Interglacial (and probably also in previous interglacials) and associated with non-mobile sediments (e.g. rocky shores, covered or not by algae) were not affected by the drop in the SSTs during the Last Glacial episode.

Finally, we also predict that the only marine fish species that were extirpated from the Azores during the course of the Last Glaciation were those associated with fine sand (Fig. 8g–i) and the thermophilic species that colonized the archipelago during the Last Interglacial/Termination 2 ‘window of opportunity’ (Fig. 8d–f). Whether fish species ecologically associated with fine sediments and presently living in the Azores are post-glacial colonizers or ‘bottleneck’ survivors from the Last Glaciation should be assessed by genetic tools, and we anticipate a low genetic

diversity of the Azorean populations when compared with continental counterparts.

**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 photographs. We thank M Ramalho and J Anacleto (Museu Geológico, LNEG, Lisbon) for 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 benefits from 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 the fish fossil collection at the Museum für Naturkunde, Berlin (DE-TAF-1071). This work was also 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 from the Regional Government of the Azores (15%) through Programa Operacional Açores 2020 under the project “AZORESBIOPORTAL – PORBIOTA”: Acores-01-0145-FEDER-000072.

**Declaration of interest.** SPA and RV designed the research plan. SPA, PM, RC and RV collected the fossil material. CSM constructed all figures. SPA, MEJ and RV wrote the manuscript with input from all authors, who discussed and commented on the manuscript. All authors approved the final version and they declare no competing interests.

## References

- Abecasis, D, Bentes L, Ribeiro J, Machado D, Oliveira F, Veiga P, Gonçalves JMS and Erzini K (2008) First record of the Mediterranean parrotfish, *Sparisoma crenense* in Ria Formosa (south Portugal). *Marine Biodiversity Records* 1, e27. <https://doi.org/10.1017/S175526720600248X>.
- Afonso P, Morato T and Santos RS (2008) Spatial patterns in reproductive traits of the temperate parrotfish *Sparisoma crenense*. *Fisheries Research* 90, 92–9. <https://doi.org/10.1016/j.fishres.2007.09.029>.
- Agassiz L (1831) *Recherche sur les Poissons Fossils*. Imprimerie de Petitpierre, Neuchâtel. Tome 1, 188 pp.
- Agassiz L (1833–1843) *Recherches sur les Poissons Fossiles (Contenant l’Histoire des Cycloïdes)*. Imprimerie de Petitpierre, Neuchâtel, 1420 pp.
- Antunes MT, Jonet S and Nascimento A (1981) Vertébrés (crocodiliens, poissons) du Miocène marin de l’Algarve occidentale. *Ciências da Terra* 6, 9–38.
- Arambourg C (1927) Les poissons fossiles d’Oran. *Matériaux pour la carte géologique de l’Algérie, Paléontologie, Alger* 6, 1–293.
- Ávila SP (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago Life and Marine Sciences Supplement* 2 (Part A), 99–131.
- Ávila SP (2013) Unravelling the patterns and processes of evolution of marine life in oceanic islands: a global framework. In *Climate Change Perspectives from the Atlantic: Past, Present and Future* (eds JM Fernández-Palacios, L de Nascimento, JC Hernández, S Clemente, A González and JP Díaz-González), pp. 95–125. Tenerife: Universidad de La Laguna.
- Ávila SP, Amen R, Azevedo JMN, Cachão M and García-Talavera F (2002) Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). *Açoreana* 9, 343–370.
- Ávila SP, Cordeiro R, Rodrigues AR, Rebelo AC, Melo C, Madeira P and Pyenson ND (2015a) Fossil Mysticeti from the Pleistocene of Santa Maria Island, Azores (NE Atlantic Ocean), and the prevalence of fossil cetaceans on oceanic islands. *Palaeontologia Electronica* 18.2.27A, 1–12. <https://doi.org/10.26879/548>.
- Ávila SP, da Silva CM, Cachão M, Landau B, Quartau R and Martins AMF (2008a) Local disappearance of bivalves in the Azores during the last glaciation. *Journal of Quaternary Science* 23, 777–85. <https://doi.org/10.1002/jqs.1165>.
- Ávila SP, da Silva CM, Schiebel R, Cecca F, Backeljau T and Martins AMF (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. <https://doi.org/10.2113/gssgfbull.180.4.295>.
- Ávila SP, Madeira P, Mendes N, Rebelo AC, Medeiros A, Gomes C, García-Talavera F, da Silva CM, Cachão M, Hillaire-Marcel C and Martins AMF (2008b) Mass extinctions in the Azores during the last glaciation: fact or myth? *Journal of Biogeography* 35, 1123–9. <https://doi.org/10.1111/j.1365-2699.2008.01881.x>.
- Ávila SP, Madeira P, Zazo C, Kroh A, Kirby M, da Silva CM, Cachão M and Martins AMF (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. <https://doi.org/10.1016/j.palaeo.2008.12.014>.
- Ávila SP, Melo C, Berning B, Cordeiro R, Landau B and da Silva CM (2016) Persististrombus coronatus (Mollusca: Strombidae) in the early Pliocene of Santa Maria Island (Azores: NE Atlantic): palaeoecology, palaeoclimatology and palaeobiogeographic implications on the NE Atlantic Molluscan Biogeographical Provinces. *Palaeogeography, Palaeoclimatology, Palaeoecology* 441, 912–23. <https://doi.org/10.1016/j.palaeo.2015.10.043>.
- Ávila SP, Melo PJ, Lima A, Amaral A, Martins AMF and Rodrigues A (2008c) The reproductive cycle of the rissoid *Alvania mediolittoralis* Gofas, 1989 (Mollusca, Gastropoda) at São Miguel Island (Azores, Portugal). *Journal of Invertebrate Reproduction and Development* 52, 31–40. <https://doi.org/10.1080/07924259.2008.9652269>.
- Ávila SP, Melo C, Sá N, Quartau R, Rijdsdijk K, Ramalho RS, Berning B, Cordeiro R, de Sá NC, Pimentel A, Baptista L, Medeiros A, Gil A and Johnson ME (2019) Towards a “Sea-Level Sensitive Marine Island Biogeography” model: the impact of glacio-eustatic oscillations in global marine island biogeographic patterns. *Biological Reviews* 94, 1116–42. <https://doi.org/10.1111/brv.12492>.
- Ávila SP, Melo C, Silva L, Ramalho RS, Quartau R, Hipólito A, Cordeiro R, Rebelo AC, Madeira P, Rovere A, Hearty PJ, Henriques D, da Silva CM, Martins AMF and Zazo C (2015b) A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews* 114, 126–48. <https://doi.org/10.1016/j.quascirev.2015.02.012>.
- Ávila SP, Ramalho RS, Habermann JM, Quartau R, Kroh A, Berning B, Johnson ME, Kirby MX, Zanon V, Titschack J, Goss A, Rebelo AC, Melo C, Madeira P, Cordeiro R, Meireles R, Bagaço L, Hipólito A, Uchman A, da Silva CM, Cachão M and Madeira J (2015c) Palaeoecology, taphonomy, and preservation of a lower Pliocene shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores, NE Atlantic Ocean). *Palaeogeography, Palaeoclimatology, Palaeoecology* 430, 57–73. <https://doi.org/10.1016/j.palaeo.2015.04.015>.
- Ávila SP, Ramalho RS, Habermann JM and Titschack J (2018) The marine fossil record at Santa Maria Island (Azores). In *Volcanoes of the Azores. Revealing the Geological Secrets of the Central Northern Atlantic Islands* (eds U Kueppers and C Beier), pp. 155–96. Berlin: Springer.
- Ávila SP, Ramalho RS and Vullo R (2012) Systematics, palaeoecology and palaeobiogeography of the Neogene fossil sharks from the Azores (Northeast Atlantic). *Annales de Paléontologie* 98, 167–89. <https://doi.org/10.1016/j.annpal.2012.04.001>.
- Ávila SP, Rebelo AC, Medeiros A, Melo C, Gomes C, Bagaço L, Madeira P, Borges PA, Monteiro P, Cordeiro R, Meireles R and Ramalho RS (2010) *Os Fósseis de Santa Maria (Açores). 1. A Jazida da Prainha*. Lagoa: OVGA – Observatório Vulcanológico e Geotérmico dos Açores, 103 p.
- Baarli BG, Malay MCD, Santos A, Johnson ME, da Silva CM, Meco J, Cachão M and Mayoral EJ (2017) Miocene to Pleistocene transatlantic dispersal of Ceratoconcha coral-dwelling barnacles and North Atlantic island biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 468, 520–28. <https://doi.org/10.1016/j.palaeo.2016.12.046>.

- Baarli BG, Santos A, Mayoral EJ, Ledesma-Vázquez J, Johnson ME, da Silva CM and 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**, 183–9. <https://doi.org/10.1017/S001675681200074X>.
- Bauzá J** (1948) Nuevas aportaciones al conocimiento de la ictiología del Neógeno catalano-balear. *Estudios Geológicos* **8**, 221–239.
- Bauzá J and 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.
- Bellardi L** (1873) *I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte I. Cephalopoda, Pteropoda, Heteropoda. Gasteropoda (Muricidae et Tritonidae)*. Stamperia Reale, Torino, 264 pp., 15 pl.
- Bellwood DR and Schultz O** (1991) A Review of the fossil record of the parrotfishes (Labroidae: 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 DR, Schultz O, Siqueira AC and Cowman PF** (2019) A review of the fossil record of the Labridae. *Annalen des Naturhistorischen Museums in Wien, Serie A* **121**, 125–93.
- Bernardi G, Robertson DR, Clifton KE and Azzurro E** (2000) Molecular systematics, zoogeography, and evolutionary ecology of the Atlantic parrotfish genus *Sparisoma*. *Molecular Phylogenetics and Evolution* **15**, 292–300. <https://doi.org/10.1006/mpev.1999.0745>.
- Betancort JF, Lomoschitz A and Meco J** (2014) Mio-Pliocene crustaceans from the Canary Islands, Spain. *Rivista Italiana di Paleontologia e Stratigrafia* **120**, 337–49. <https://doi.org/10.13130/2039-4942/6076>.
- Betancort JF, Lomoschitz A and Meco J** (2016) Early Pliocene fishes (Chondrichthyes, Osteichthyes) from Gran Canaria and Fuerteventura (Canary Islands, Spain). *Estudios Geológicos* **72**, e054.
- Beu AG** (2017) Evolution of *Janthina* and *Recluzia* (Mollusca: Gastropoda: Epitoniidae). *Records of the Australian Museum* **69**, 119–222.
- Blanc P-L** (2002) The opening of the Plio-Quaternary Gibraltar Strait: assessing the size of a cataclysm. *Geodinamica Acta* **15**, 303–17. <https://doi.org/10.1080/09853111.2002.10510763>.
- Bleeker P** (1859) Enumeratio specierum piscium hucusque in Archipelago indico observatarum. *Acta Societatis Scientiarum Indo-Neerlandae* **6**, 1–276.
- Briggs JC** (1974) *Marine Zoogeography*. New York: McGraw-Hill, 475 p.
- Briggs JC** (1995) *Global Biogeography*. Amsterdam: Elsevier, 452 p.
- Brocchi GB** (1814) *Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente*. Dalla Stamperia Reale, Milano. Vol. 1: i–lxxx, 1–56, 1–240; vol. 2: 241–712, 16 pls.
- Brönn HG** (1861) *Die Klassen und Ordnungen der Weichtiere (Malacozoa)*. CF Winter'sche Verlagshandlung, Leipzig und Heidelberg, 1861, 3(2): 103–223.
- Brönn HG** (1862) *Die Klassen und Ordnungen der Weichthiere (Malacozoa). Kopflose Weichthiere (Malacozoa Acephala)*. CF Winter'sche Verlagshandlung, Leipzig pp. 1306 + 118 pl.
- Buckeridge JS and Winkelmann K** (2010) *Zullobalanus santamariaensis* sp. nov., a new late Miocene barnacle species of the family Archeobalanidae (Cirripedia: Thoracica), from the Azores. *Zootaxa* **2680**, 33–44.
- Bullock AE and Monod T** (1997) Myologie céphalique de deux poissons perroquets (Teleostei: Scaridae). *Cybiurn* **21**, 173–199.
- Charlesworth E** (1837) A notice of the remains of vertebrate animals occurring in the Tertiary beds of Norfolk and Suffolk. *The Magazine of Natural History* **2**, 40–43.
- Clements KD, German DP, Piché J, Tribollet A and Choat JH** (2016) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society* **120**, 729–751. <https://doi.org/10.1111/bij.12914>.
- Cocchi I** (1864) Monografia dei Pharyngodopilidae. Nuova famiglia di Pesci Labroidi. *Annali del Museo Imperiale di Fisica e Storia Naturale di Firenze* **1**, 62–152.
- Collins RL** (1934) A monograph of the American Tertiary pteropod mollusks. *Johns Hopkins University Studies in Geology* **11**, 137–234.
- Cordeiro R, Borges JP, Martins AMF and Ávila SP** (2015) Checklist of the littoral gastropods (Mollusca: Gastropoda) from the Archipelago of the Azores (NE Atlantic). *Biodiversity Journal* **6**, 855–900.
- Crowley TJ** (1981) Temperature and circulation changes in the eastern North Atlantic during the last 150,000 years: Evidence from the planktonic foraminiferal record. *Marine Micropaleontology* **6**, 97–129.
- Cutwa MM and Turingan RG** (2000) Intralocality variation in feeding biomechanics and prey use in *Archosargus probatocephalus* (Teleostei, Sparidae), with implications for the ecomorphology of fishes. *Environmental Biology of Fishes* **59**, 191–98. <https://doi.org/10.1023/A:1007679428331>.
- Cuvier GLCED** (1816) *Le Règne Animal Distribué D'après son Organisation Pour Servir de Base à L'histoire Naturelle des Animaux et D'introduction à L'anatomie Comparée. T. II, Les reptiles, les Poissons, les Mollusques et les Annélides*. Deterville, Paris, 532 pp.
- Darwin C** (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray, 502 p.
- Day JJ** (2002) Phylogenetic relationships of the Sparidae (Teleostei: Percoidei) and implications for convergent trophic evolution. *Biological Journal of the Linnean Society* **76**, 269–301. <https://doi.org/10.1111/j.1095-8312.2002.tb02088.x>.
- de Lumley H** (1988) La stratigraphie du remplissage de la Grotte du Vallonnet. *L'Anthropologie* **92**, 407–28.
- Defrance JLM** (1827) *Dictionnaire des Sciences Naturelles*. FG Levrault, Strasbourg.
- Delaroche F-É** (1809) Suite du mémoire sur les espèces de poissons observées à Iviça. Tableau des espèces de poissons que j'ai observées à Iviça pendant les mois de décembre, janvier et février. Tableau des poissons que j'ai observés à Maiorque et à Barcelonne, mais que je n'ai point vus à Iviça. Observations sur quelques-uns des poissons indiqués dans le précédent tableau, et descriptions des espèces nouvelles ou peu connues. *Annales du Muséum d'Histoire Naturelle, Paris* **13**, 313–61, plates 20–25.
- Dolomatova S, Zukowb W and Brudnickib R** (2013) Role of temperature in regulation of the life cycle of temperate fish. *Russian Journal of Marine Biology* **39**, 81–91. <https://doi.org/10.1134/S1063074013020041>.
- Domingues VS, Alexandrou M, Almada VC, Robertson DR, Brito A, Santos RS and Bernardi G** (2008) Tropical fishes in a temperate sea: evolution of the wrasse *Thalassoma pavo* and the parrotfish *Sparisoma cretense* in the Mediterranean and the adjacent Macaronesian and Cape Verde Archipelagos. *Marine Biology* **154**, 465–74. <https://doi.org/10.1007/s00227-008-0941-z>.
- Domingues VS, Santos RS, Brito A and Almada VC** (2006) Historical population dynamics and demography of the eastern Atlantic pomacentrid *Chromis limbata* (Valenciennes, 1833). *Molecular Phylogenetics and Evolution* **40**, 139–47. <https://doi.org/10.1016/j.ympev.2006.02.009>.
- Estevens M and Ávila SP** (2007) Fossil whales from the Azores. *Açoreana Suplemento* **5**, 140–61.
- Fernández-Palacios JM, Rijsdijk KF, Norder SJ, Otto R, de Nascimento L, Fernández-Lugo S, Tjørve E and Whittaker RJ** (2016) Towards a glacial-sensitive model of island biogeography. *Global Ecology and Biogeography* **25**, 817–30. <https://doi.org/10.1111/geb.12320>.
- Ferreira O da V** (1955) A fauna miocénica da ilha de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal* **36**, 9–44.
- Gagnaison C** (2017) Le site paléontologique du Grand Morier (Pont-Boutard, Indre-et-Loire, France): contexte géologique et détail biostratigraphique des formations cénozoïques à partir des assemblages de vertébrés fossiles. *Geodiversitas* **39**, 251–71. <https://doi.org/10.5252/g2017n2a5>.
- García-Castellanos D, Estrada F, Jiménez-Munt I, Gorini C, Fernández M, Vergés J and de Vicente R** (2009) Catastrophic flood of the Mediterranean after the Messinian salinity crisis. *Nature* **462**, 778–81. <https://doi.org/10.1038/nature08555>.
- Gervais FLP** (1857) Sur un poisson labroïde fossile dans les sables marins de Montpellier (*Labrodon pavementatum*). *Mémoires de la Académie des Sciences de Montpellier* **3**, 515 pp.
- Guidetti P and Boero F** (2002) Spatio-temporal variability in abundance of the parrotfish, *Sparisoma cretense*, in SE Apulia (SE Italy, Mediterranean Sea). *Italian Journal of Zoology* **69**, 229–32. <https://doi.org/10.1080/11250000209356464>.
- Günther ACLG** (1861) A preliminary synopsis of the labroid genera. *The Annals and Magazine of Natural History, Zoology, Botany, and Geology* **8**, 382–89.

- Günther ACLG** (1862) *Catalogue of the fishes in the British Museum*. Printed by order of the trustees, London. Vol. 4, 534 pp.
- Harzhauser M, Piller WE and Steininger FF** (2002) Circum-Mediterranean Oligo–Miocene biogeographic evolution – the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology* **183**, 103–33. [https://doi.org/10.1016/S0031-0182\(01\)00464-3](https://doi.org/10.1016/S0031-0182(01)00464-3).
- Janssen AW, Kroh A and Ávila SP** (2008) Early Pliocene heteropods and pteropods (Mollusca, Gastropoda) from Santa Maria (Azores, Portugal): systematics and biostratigraphic implications. *Acta Geologica Polonica* **58**, 355–69.
- Johnson ME, Ramalho RS, Baarli BG, Cachão M, da Silva CM, Mayoral EJ and Santos A** (2014) Miocene–Pliocene rocky shores on São Nicolau (Cape Verde Islands): contrasting windward and leeward biofacies on a volcanically active oceanic island. *Palaeogeography, Palaeoclimatology, Palaeoecology* **395**, 131–43. <https://doi.org/10.1016/j.palaeo.2013.12.028>.
- Johnson ME, Uchman A, Costa PJM, Ramalho RS and Ávila SP** (2017) Intense hurricane transport sand onshore: example from the Pliocene Malbusca section on Santa Maria Island (Azores, Portugal). *Marine Geology* **385**, 244–49. <https://doi.org/10.1016/j.margeo.2017.02.002>.
- Jonet S** (1968) Notes d'ichthyologie miocène portugaise. IV – Les Labridae. *Boletim da Sociedade Geológica de Portugal* **16**, 209–21.
- Jonet S** (1975) Notes d'ichthyologie Miocene Portugaise. *Boletim da Sociedade Geológica de Portugal* **29**, 135–73.
- Jonet S, Kotchetoff Y and Kotchetoff B** (1975) L'helvétien du Penedo et sa faune ichthyologique. *Comunicações dos Serviços Geológicos de Portugal* **59**, 193–228.
- Klein EF** (1885) Beiträge zur Bildung des Schädels der Knochenfische. *Jahreshefte Vereins Vaterländischer Naturkunde in Württemberg* **42**, 205–300.
- Kroh A, Bitner MA and Ávila SP** (2008) Novocrania turbinata (Brachiopoda) from the Early Pliocene of the Azores (Portugal). *Acta Geologica Polonica* **58**, 473–78.
- Lamarck J-BM de** (1816) *Histoire Naturelle des Animaux sans Vertèbres*. Tome second. Verdrière, Paris, 568 pp.
- Landini W** (1977) Osservazioni sulle placche faringee di alcuni labridi del Pliocene della Toscana. *Atti de la Società Toscana di Scienze Naturali, Serie A* **83**, 230–50.
- Laughton AS and Whitmarsh RB** (1974) The Azores-Gibraltar plate boundary. In *Geodynamics of Iceland and the North Atlantic Area* (ed. L Kristjansson), pp. 63–81. Austria: Kufstein.
- Laurito CA, Calvo C, Valerio AL, Calvo A and 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**, 153–92. <https://doi.org/10.15517/rgac.v0i50.15121>.
- Le Hon H** (1871) *Préliminaires d'une Mémoire sur les Poissons Tertiaires de Belgique*. H Merzbach, Bruxelles, 15 pp.
- Lecoindre 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.
- Leske NG** (1778) Jacobi Theodori Klein naturalis dispositio echinodermatum et lucubratiunculam de aculeis echinorum marinorum. Ex Officina Gleditschiana, Leipzig, xx + 214 pp.
- Linnaeus C** (1758) *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Holmiae, Impensis Direct, Laurentii Salvii. Vol 1, 10th ed., 824 pp.
- Lisiecki LE and Raymo ME** (2005) A Pliocene–Pleistocene stack of 57 globally distributed benthic  $\delta^{18}O$  records. *Paleoceanography* **20**, PA1003. <https://doi.org/10.1029/2004PA001071>.
- Madeira P, Kroh A, Cordeiro R, Meireles R and Ávila SP** (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica* **61**, 243–64.
- Madeira P, Kroh A, Martins AMF and Ávila SP** (2007) The marine fossils from Santa Maria Island (Azores, Portugal): an historical overview. *Açoreana Suplemento* **5**, 59–73.
- Martín-González E, Buckeridge J, Castillo C and 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 and Antunes MT** (2008) Presència de Tomistoma cf. lusitanica (Vianna i Moraes, 1945) (Reptilia: Crocodylia) al Burdigalià inferior de Mallorca (Illes Balears, Mediterrània occidental). Implicacions paleoambientals. *Bolletí de la Societat d'Història Natural de les Balears* **51**, 131–46.
- Mayer C** (1864) Description de coquilles fossiles des terrains tertiaires supérieurs (suite). *Journal de Conchyliologie* **12**(2), 160–68, 168–81, pls 8–9 (20 April); **12**(4), 350–61, pl. 14 (17 October).
- Meco J** (1977) Los Strombus Neogenos y Cuaternarios del Atlantico Eurafricano. (Taxonomia, Biostratigrafia y Palaeoecologia). *Palaeontologia de Canarias* **1**, 1–142.
- Meco J, Koppers AAP, Miggins DP, Lomoschitz A and Betancort J-F** (2015) The Canary record of the evolution of the North Atlantic Pliocene: New 40Ar/39Ar ages and some notable palaeontological evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **435**, 53–69. <https://doi.org/10.1016/j.palaeo.2015.05.027>.
- Meco J, Lomoschitz A and Betancort J-F** (2016) Early Pliocene tracer of North Atlantic and South Pacific sea surface currents: Janthina typica (Bronn, 1860) (Mollusca: Gastropoda). *Revista Mexicana de Ciencias Geológicas* **33**, 192–7.
- Meco J, Petit-Maire N, Fontugne M, Shimmield G and Ramos AJ** (1997) The Quaternary deposits in Lanzarote and Fuerteventura (Eastern Canary Islands, Spain): an overview. In *Climates of the Past: Proceedings of the CLIP Meeting 1995* (eds J Meco and N Petit-Maire), pp. 123–36. Gran Canaria: Universidad de Las Palmas de Gran Canaria, Servicio de Publicaciones.
- Meco J, Scaillet S, Guillou H, Lomoschitz A, Carracedo JC, Ballester J, Betancort J-F and Cilleros A** (2007) Evidence for long-term uplift on the Canary Islands from emergent Mio–Pliocene littoral deposits. *Global and Planetary Change* **57**, 222–34. <https://doi.org/10.1016/j.gloplacha.2006.11.040>.
- Meireles RP, Faranda C, Gliozzi E, Pimentel A, Zanon V and Ávila SP** (2012) Late Miocene marine ostracods from Santa Maria Island, Azores (NE Atlantic): Systematics, palaeoecology and palaeobiogeography. *Revue de Micropaléontologie* **55**, 133–48. <https://doi.org/10.1016/j.revmic.2012.06.003>.
- Meireles RP, Keyser D and Ávila SP** (2014) The Holocene to Recent ostracods of the Azores (NE Atlantic): systematics and biogeography. *Marine Micropaleontology* **112**, 13–26. <https://doi.org/10.1016/j.marmicro.2014.08.002>.
- Menesini E** (1969) Ittiodontoliti Miocenici di Terra d'Otranto (Puglia). *Palaeontographia Italica* **65**, 1–61.
- Müller J and Henle FGJ** (1839) *Systematische Beschreibung der Plagiostomen*. Veit & Co., Berlin, vol. 2, 73 pp.
- Nolf D** (1988) Les otolithes de téléostéens éocènes d'Aquitaine (sud-ouest de la France) et leur intérêt stratigraphique. *Académie Royale de Belgique, Mémoires de la Classe des Sciences Collection* **4**, (Serie 2) **19**, 1–147. Bruxelles.
- Obrador A and Mercadal B** (1973) Nuevas localidades con fauna ictiológica para el Neógeno menorquín. *Acta Geológica Hispánica* **8**, 115–19.
- O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, Collins LS, de Queiroz A, Farris DW, Norris RD, Stallard RF, Woodburne MO, Aguilera O, Aubry M-P, Berggren WA, Budd AF, Cozzuol MA, Coppard SE, Duke-Caro H, Finnegan S, Gasparini GM, Grossman EL, Johnson KG, Keigwin LD, Knowlton N, Leigh EG, Leonard-Pingel JS, Marko PB, Pyenson ND, Rachello-Dolmen PG, Soibelzon E, Soibelzon L, Todd JA, Vermeij GJ and Jackson JBC** (2016) Formation of the Isthmus of Panama. *Science Advances* **2**, e1600883. <https://doi.org/10.1126/sciadv.1600883>.
- Pankhurst NW and Porter MJR** (2003) Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry* **28**, 385–9. <https://doi.org/10.1023/B:FISH.0000030602.51939.50>.
- Pepin P** (1991) Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 503–18. <https://doi.org/10.1139/f91-065>.
- Poli JX** (1795) Testacea utriusque Siciliae eorumque historia et anatomicae tabulis aeneis illustrata. *Ex Regio Typographeio, Parmae* **2**, pp. i–xlx, [1–2], 75–264, pls 19–39.
- Poloczanska ES, Burrows MT, Brown CJ, García Molinos J, Halpern BS, Hoegh-Guldberg O, Kappel CV, Moore PJ, Richardson AJ, Schoeman DS and Sydeman WJ** (2016) Responses of marine organisms to climate change across oceans. *Frontiers Marine Science* **3**, 62. <https://doi.org/10.3389/fmars.2016.00062>.

- Quignard J-P and Pras A** (1986) Scaridae. In *Fishes of the North-eastern Atlantic and the Mediterranean* (eds PJP Whitehead, M-L Bauchot, J-C Hureau, J Nielsen and E Tortonese), pp. 943–44. UNESCO, Paris 2.
- Rafinesque CS** (1810). *Caratteri di alcuni nuovi generi e nuove spece di animali e piante della Sicilia*. Parte 1. Stampe di Sanfilippo, Palermo, 105 pp.
- Rafinesque CS** (1818) Discoveries in natural history, made during a journey through the western region of the United States. *The American Monthly Magazine and Critical Review* 3(5), 354–56.
- Ramalho RS, Helffrich G, Madeira J, Cosca M, Thomas C, Quartau R, Hipólito A, Rovere A, Hearty PJ and Ávila SP** (2017) The emergence and evolution of Santa Maria Island (Azores) – the conundrum of uplifted islands revisited. *Geological Society of America Bulletin* 129, 372–90. <https://doi.org/10.1130/B31538.1>.
- Randall JE** (1990) Scaridae. In *Check-List of the Fishes of the Eastern Tropical Atlantic* (eds JC Quero, JC Hureau, C Karrer, A Post and L Saldanha), pp. 883–7. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris 2.
- Raposo VB, Melo CS, Silva L, Ventura A, Câmara R, Pombo J, Johnson ME and Ávila SP** (2018) Comparing methods of evaluation of geosites: the fossiliferous outcrops of Santa Maria Island (Azores, NE Atlantic) as a case study for sustainable island tourism. *Sustainability* 10, 3596. <https://doi.org/10.3390/su10103596>.
- Rebelo AC, Meireles RP, Barbin V, Neto AI, Melo C and Ávila SP** (2016a) Diagenetic history of lower Pliocene rhodoliths of the Azores Archipelago (NE Atlantic): application of cathodoluminescence techniques. *Micron* 80, 112–21. <https://doi.org/10.1016/j.micron.2015.10.004>.
- Rebelo AC, Rasser MW, Kroh A, Johnson ME, Ramalho RS, Melo C, Uchman A, Berning B, Silva L, Zannon V, Neto AI, Cachão M and Ávila SP** (2016b) Rocking around a volcanic island shelf: Pliocene Rhodolith beds from Malbusca, Santa Maria Island (Azores, NE Atlantic). *Facies* 62, 22. <https://doi.org/10.1007/s10347-016-0473-9>.
- Rebelo AC, Rasser MW, Riosmena-Rodríguez R, Neto AI and Ávila SP** (2014) Rhodolith forming coralline algae in the Upper Miocene of Santa Maria Island (Azores, NE Atlantic): a critical evaluation. *Phytotaxa* 190, 370–82. <http://dx.doi.org/10.11646/phytotaxa.190.1.22>.
- Ricchi A, Quartau R, Ramalho RS, Romagnoli C, Casalbone D, da Cruz JV, Fradique C and 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. <https://doi.org/10.1016/j.margeo.2018.09.002>.
- Rocha LA, Brito A and Robertson DR** (2012) Sparisoma choati, a new species of Parrotfish (Labridae: Scarinae) from the tropical eastern Atlantic. *Zootaxa* 3152, 61–67. <http://dx.doi.org/10.11646/zootaxa.3152.1.3>.
- Sacco F** (1916) Apparatı dentali di Labrodon e di Chrysophrys del Pliocene italiano. *Memorie della Reale Accademia delle Scienze di Torino* 60, 144–9.
- Santos RS, Hawkins S, Monteiro LR, Alves M and Isidro EJ** (1995) Marine research, resources and conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5, 311–54. <https://doi.org/10.1002/aqc.3270050406>.
- Santos A, Mayoral E, Baarli BG, da Silva CM, Cachão M and Johnson ME** (2012a) Symbiotic association of a Pyrgomatid barnacle with a coral from the volcanic Middle Miocene shoreline (Porto Santo, Madeira archipelago, Portugal). *Palaeontology* 55, 173–82. <https://doi.org/10.1111/j.1475-4983.2011.01105.x>.
- Santos A, Mayoral EJ, da Silva CM, Cachão M and Johnson ME** (2011) Miocene intertidal zonation on a volcanically active shoreline: Porto Santo in the Madeira Archipelago, Portugal. *Lethaia* 44, 26–32. <https://doi.org/10.1111/j.1502-3931.2010.00222.x>.
- Santos A, Mayoral E, Dumont CP, da Silva CM, Ávila SP, Baarli BG, Cachão M, Johnson ME and Ramalho RS** (2015) Role of environmental change in rock-boring echinoid trace fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 432, 1–14. <https://doi.org/10.1016/j.palaeo.2015.04.029>.
- Santos A, Mayoral E, Johnson ME, Baarli BG, Cachão M, da Silva CM and Ledesma-Vázquez J** (2012b) Extreme habitat adaptation by boring bivalves on volcanically active paleoshores from North Atlantic Macaronesia. *Facies* 58, 325–38. <https://doi.org/10.1007/s10347-011-0283-z>.
- 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, 613–42.
- Searle R** (1980) Tectonic pattern of the Azores spreading centre and triple junction. *Earth and Planetary Science Letters* 51, 415–34.
- Sibrant ALR, Hildenbrand A, Marques FO and Costa ACG** (2015) Volcano-tectonic evolution of the Santa Maria Island (Azores): Implications for paleo-stress evolution at the western Eurasia-Nubia plate boundary. *Journal of Volcanology and Geothermal Research* 291, 49–62.
- Simonelli V** (1889) Terreni e fossili dell'Isola di Pianosa nel Mar Tirreno. *Bolletino del Reale Comitato Geologico d'Italia* 10, 193–237.
- Sowerby GB** (1847) *Thesaurus conchyliorum, or Monographs of genera of shells*. Sowerby, 70 Great Russel Street, Bloomsbury, London.
- Swainson W** (1839) *The Natural History of Fishes, Amphibians, & Reptiles, or Monocardian Animals. Vol. II. Lardner's Cabinet Cyclopædia*. London: Longman, Orme, Brown, Green & Longmans; and John Taylor, 452 pp.
- Tuya F, Betancort JF, Haroun R, Espino F, Lomoschitz A and 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. <https://doi.org/10.1016/j.aquabot.2017.08.002>.
- Uchman A, Johnson ME, Rebelo AC, Melo C, Cordeiro R, Ramalho RS and Ávila SP** (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, 229–41. <https://doi.org/10.1016/j.geobios.2016.01.016>.
- Uchman A, Quintino V, Rodrigues AM, Johnson ME, Melo C, Cordeiro R, Ramalho RS and Ávila SP** (2017) The trace fossil Diopatrachus santamariaensis nov. isp. – a shell armoured tube from Pliocene sediments of Santa Maria Island, Azores (NE Atlantic Ocean). *Geobios* 50, 459–69. <https://doi.org/10.1016/j.geobios.2017.09.002>.
- Valenciennes M** (1839) *Histoire Naturelle des Poissons*. FG Levrault, Paris, Tome 1, 573 pp.
- van der Kraak G and Pankhurst NW** (1997) Temperature effects on the reproductive performance of fish. In *Global Warming: Implications for Freshwater and Marine Fish* (eds CM Wood and DG Macdonald), pp. 159–76. Cambridge: Cambridge University Press.
- Vicens D and Rodríguez-Perea A** (2003) Vertebrats fòssils (Pisces i Reptilia) del Burdigalià de cala Sant Vicenç (Pollença, Mallorca). *Bollet de la Societat d'Història Natural de les Balears* 46, 117–30.
- Vogt PR and Jung W-Y** (2018) The “Azores Geosyncline” and plate tectonics: research history, synthesis, and unsolved puzzles. In *Volcanoes of the Azores. Revealing the Geological Secrets of the Central Northern Atlantic Islands* (eds U Kueppers and C Beier), pp. 27–56. Berlin: Springer.
- Wallace AR** (1880) *Island Life, or, the Phenomena and Causes of Insular Faunas and Floras: Including a Revision and Attempted Solution of the Problem of Geological Climates*. London: Macmillan, 526 p.
- Whittaker RJ, Triantis KA and Ladle RJ** (2010) A general dynamic theory of oceanic island biogeography: extending the MacArthur–Wilson theory to accommodate the rise and fall of volcanic islands. In *The Theory of Island Biogeography Revisited* (eds JB Losos and RE Ricklefs), pp. 88–115. Princeton, New Jersey: Princeton University Press.
- Winkelmann K, Buckeridge JS, Costa AC, Dionísio MAM, Medeiros A, Cachão M and Ávila SP** (2010) Zullobalanus santamariaensis sp. nov., a new late Miocene barnacle species of the family Archeobalanidae (Cirripedia: Thoracica), from the Azores. *Zootaxa* 2680, 33–44. <http://dx.doi.org/10.11646/zootaxa.2680.1.3>.
- Zbyszewski G and d'Almeida FM** (1950) Os peixes miocénicos portugueses. *Comunicações dos Serviços Geológicos de Portugal* 31, 309–423.
- Zbyszewski G and Ferreira O da V** (1962) La faune miocène de l'île de Santa Maria (Açores). *Comunicações dos Serviços Geológicos de Portugal* 46, 247–89.