

Article

First Evidence of Lanternfishes from the Last Interglacial (MIS 5e) of Santa Maria Island (Azores Archipelago: NE Atlantic Ocean): Paleoecology and Paleobiodiversity

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Abstract

Fossils provide invaluable data for evolutionary studies in oceanic islands. The paleontological record of the Macaronesian archipelagos has been the target of many researchers for a long time, with a recent surge in interest in scientific research related to their paleontological heritage. In the Macaronesian Azores archipelago, the marine invertebrate fossil record from the warmest period of the Last Interglacial stage (also known as Marine Isotopic Stage 5e—MIS 5e) represents approximately 95.6% of the total species. In contrast, the MIS 5e marine vertebrate fossil record comprises only four reported species (2.2%), with marine algae accounting for the remaining 2.2% (four species). This study reports on—and adds to the paleobiodiversity of the MIS 5e deposits at Santa Maria Island (Azores Archipelago)—two marine mesopelagic lanternfishes, identified from their otoliths: *Diaphus* cf. *holti* Tåning, 1918, and *Symbolophorus veranyi* (Moreau, 1888). Finally, we offer a plausible explanation for the presence of mesopelagic fishes in the MIS 5e fossiliferous deposits of Santa Maria Island.

Keywords: fossil fishes; Myctophidae; lanternfish; otoliths; palaeobiodiversity; storm events



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1. Introduction

The living terrestrial and marine biota of island systems, as well as their fossil record, have long attracted the scientific interest of scholars. For example, Charles Darwin reported Devonian fossils from the Falkland Islands [1], whereas Alfred Russel Wallace noted in his

field notebook that the endemic species from the Galápagos Islands resembled those of the nearest mainland and that older islands had more endemic species than younger ones [2]. Over the past century, high-quality taxonomic checklists have been compiled from islands and archipelagos [3–8], providing a solid ground for important advances in biology and evolutionary thinking [9–17]. Moreover, these databases have been instrumental in testing biogeographic theories for both terrestrial [18–22] and marine organisms [17,23–30], as well as in geoheritage conservation [31,32].

The Macaronesian islands are no exception, with the Azores, Madeira, Selvagens, Canaries, and Cabo Verde archipelagos witnessing a sustained increase in scientific research related to their paleontological heritage [33–37]. In the Azores, as with elsewhere in general, the Mollusca and the Echinodermata are the most abundant and diversified marine phyla reported from fossiliferous sediments today exhumed on these oceanic islands [38–44]. In contrast, the insular vertebrate fossil record is much rarer [45–47]. Despite being the most diverse group of fossil marine vertebrates [48], marine fishes are seldom recorded from the fossil record of oceanic islands. The few known examples are from the Arctic island of Spitsbergen in Svalbard, which contains a massive 249-million-year-old bonebed from a thriving ancient ocean [49]; Gavdos Island (Greece), from where Cretaceous fishes are reported [50]; Jamaica Island, with ancient fishes dating to the Eocene, Miocene and Pliocene [51–53]; Cuba, with fossil fishes dated from the Miocene and Pliocene [54,55]; and the Dominican Republic, with fossil fishes represented in Miocene and Pliocene outcrops [56,57]. Similarly, only a few marine bony fish species have been reported from the Pliocene (4–5 species) and the Pleistocene outcrops (1 species) of the Azores Archipelago [58]. Here, we report the recent discovery of two fossil marine fish taxa identified from otoliths found in coastal marine sediments from the warmest period of the Last Interglacial, i.e., Marine Isotopic Stage (MIS) 5e, at Prainha and Praia do Calhau, on Santa Maria Island. Finally, we offer a plausible explanation for the presence of mesopelagic fishes in the MIS 5e fossiliferous deposits of Santa Maria Island.

2. Materials and Methods

Stratigraphical and Sedimentological Characterization

The Prainha outcrop (Figure 1) was classified as a paleosite of international relevance by Ávila and colleagues [31,59]. The sedimentary sequence at Prainha was first described by Ávila [60] and later complemented by Ávila et al. [38,61–63]. Figure 2A provides an overview of the Prainha paleosite and the location of the strip log, whereas Figure 2B depicts the stratigraphic interpretation of the cross-section. This log was used to construct a stratigraphic section along a representative vertical profile of Prainha (Figure 3). The Praia do Calhau MIS 5e outcrop is located about 500 m east of Prainha, and a stratigraphical log of the MIS 5e fossiliferous sedimentary sequence at that site was also performed (cf. Figure 3). Detailed aspects of the internal structures and contacts between the subunits individualized in the sedimentary deposit are presented. Special attention was given to register changes in facies and fossil content.

Fossil surveys and both qualitative and quantitative collections were performed on the MIS 5e sediments at both outcrops. The best-preserved and conspicuous fossil specimens (e.g., mollusks and echinoderms) were photographed on site. Ten standardized 1 kg bulk samples containing fossiliferous sediments were collected and labeled in the field and later sorted at the MPB lab (University of the Azores) under a NIKON SMZ1000 binocular microscope (maximum magnification used: 50x), by hand-picking all fossil remains from the sediments (including specimens down to a size of 0.1 mm). The samples were analyzed in their original state, bypassing the washing and sieving stages. Photos were shot in the laboratory using a NIKON D850 camera attached to the binocular microscope. The

nomenclature for the fossil taxa follows that adopted in the “WoRMS” database [64], but we follow Near & Thacker [65] for the higher systematic classification adopted for the two fossil fish species herein reported. Ecological information on the bony fishes was obtained from FishBase “<https://www.fishbase.se/search.php> (accessed on 20 December 2025)”. It is also provided a description of the otoliths of the two fish species, as well as information regarding the species ecology, habitat, and stratigraphic and geographic range.

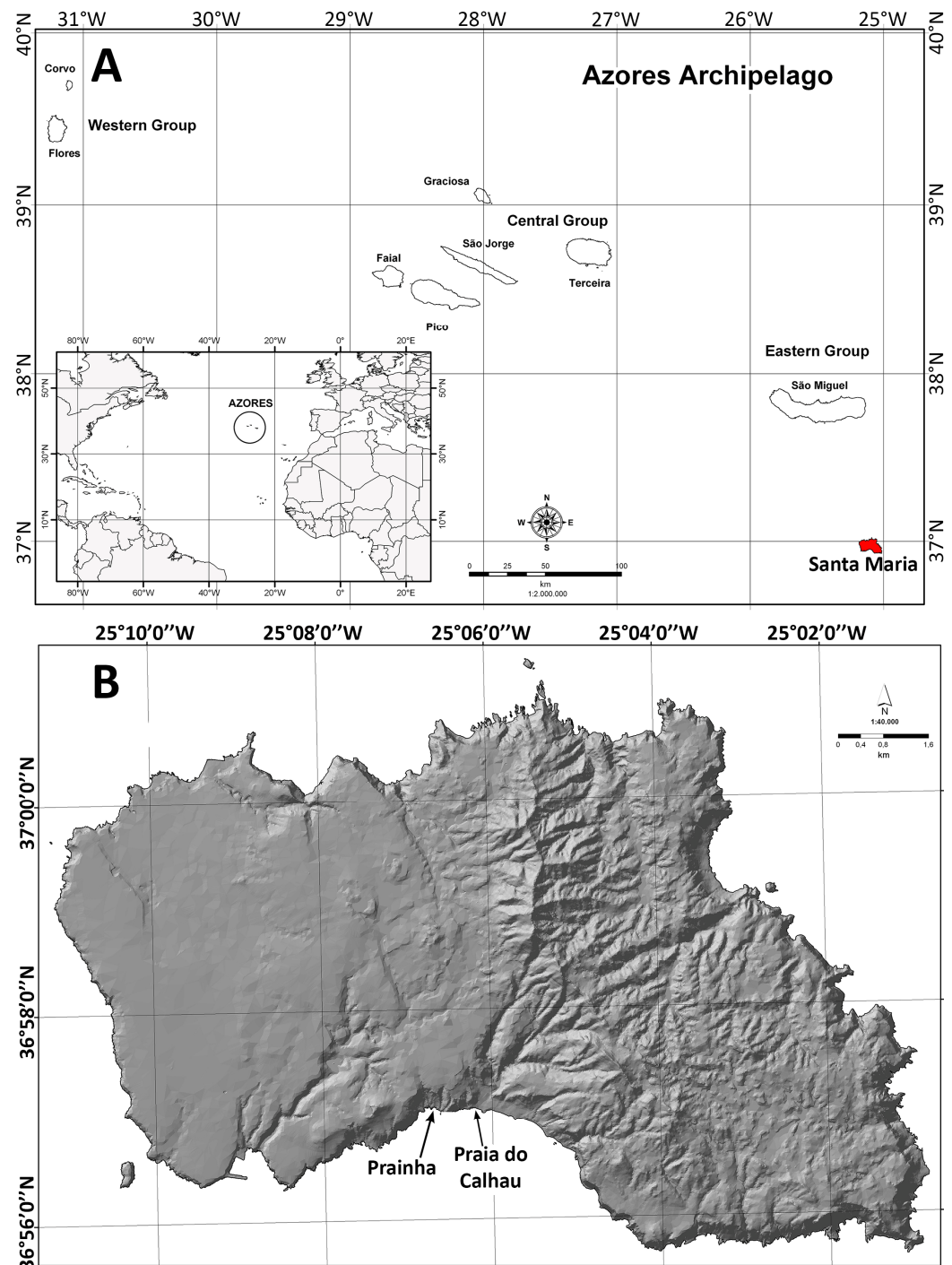


Figure 1. Location maps. (A) Location of the Azores Archipelago within the NE Atlantic (insert) and Santa Maria Island within the Azores Archipelago. Coastline delimitation from the Portuguese Hydrographic Institute free data “<https://www.hidrografico.pt/op/33> accessed 15 November 2025)”. (B) Map of Santa Maria Island (modified from [61]), with the location of the Prainha and Praia do Calhau outcrops. Underlying digital elevation model from the 1:5000-scale digital altimetric database.

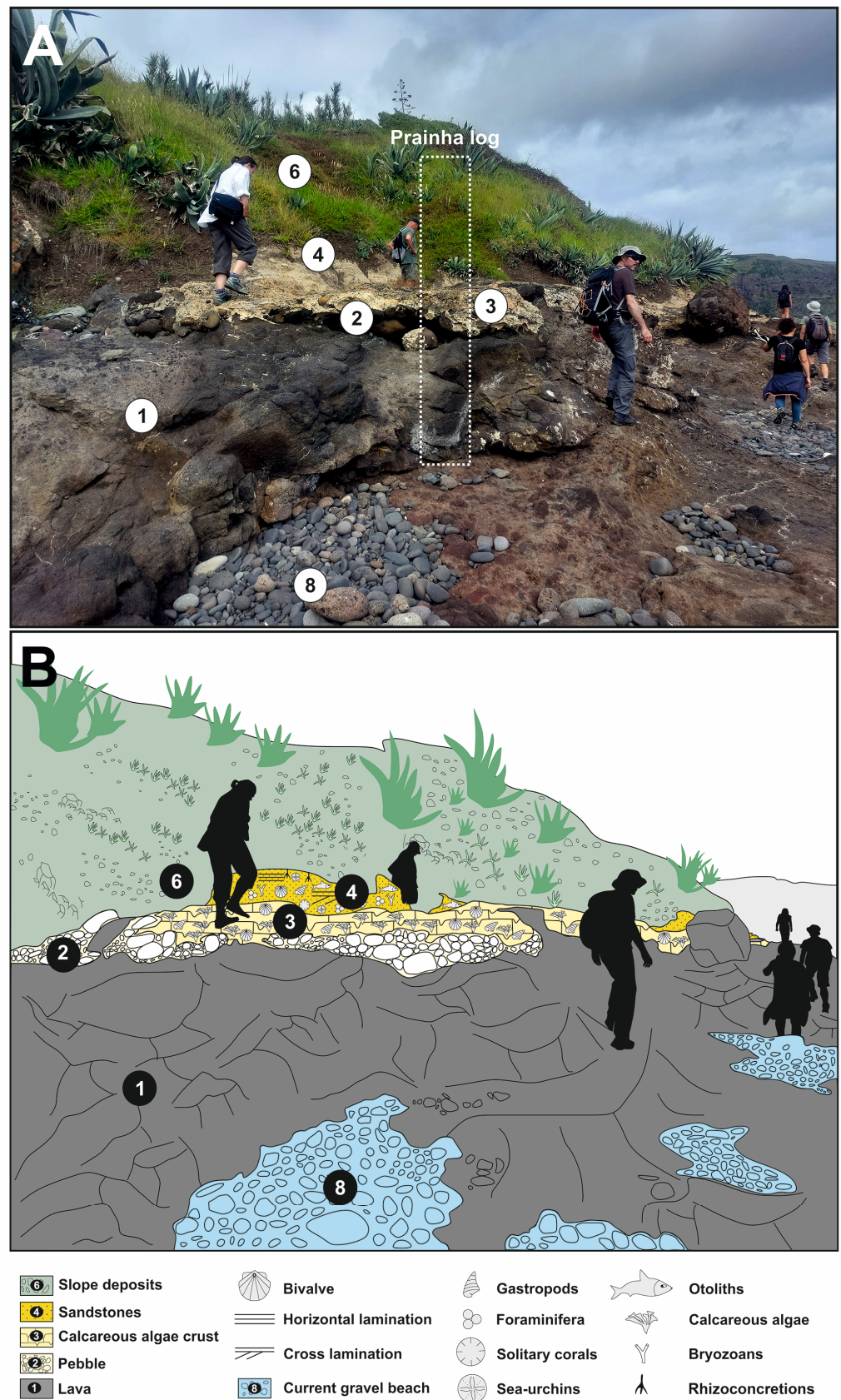


Figure 2. Prainha, on the southern shores of Santa Maria Island. (A) General view of the outcrop, and location of the stratigraphic log. (B) Interpretation of the sedimentary sequence at Prainha. Numbers correspond to the described depositional units (see main text and Figure 3).

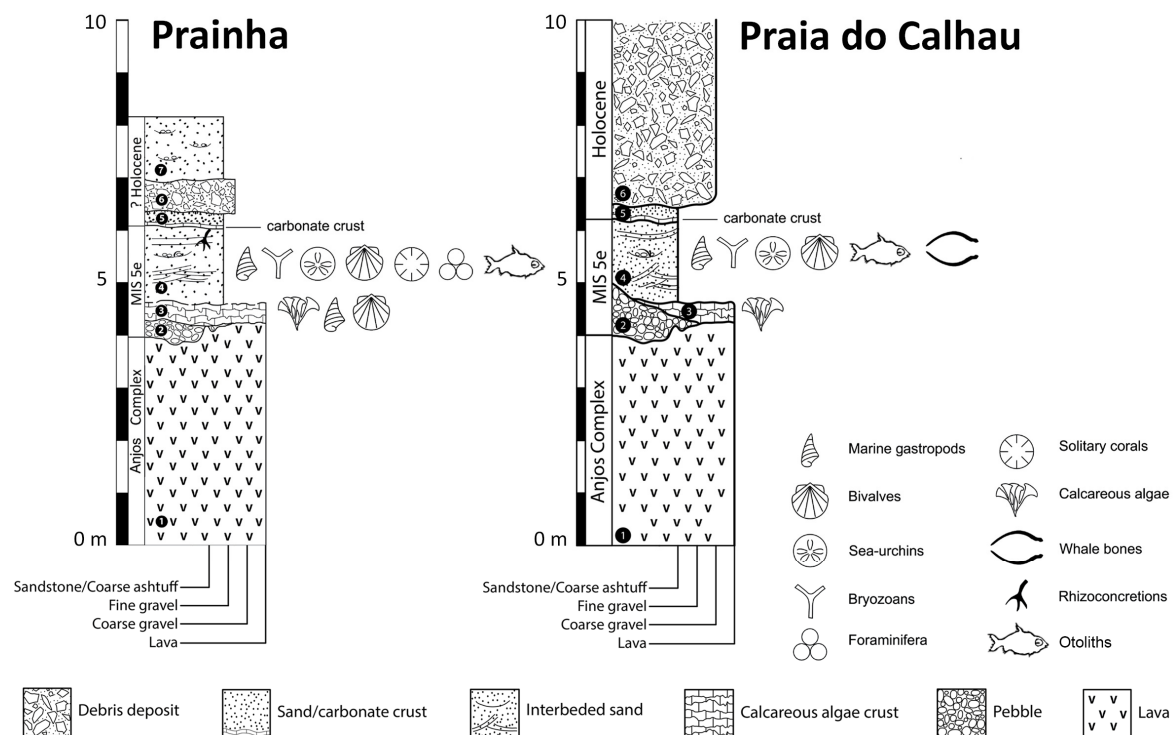


Figure 3. Simplified strip logs of the studied outcrops, representing main lithologies, sedimentary structures, contacts and fossiliferous content. Numbers correspond to the described depositional units.

3. Results

Stratigraphical and Sedimentological Characterization

The sedimentary sequence at both Prainha and Praia do Calhau outcrops is deposited on top of basalts from the Anjos Volcanic Complex that were carved during the Last Interglacial period, forming an erosional shore platform (unit 1, Figure 3). This sequence begins with a beach conglomerate (unit 2, Figure 3), composed of well-sorted clast-support cobbles, that contains a reduced number of species and few fossils, the most abundant being shells of *Patella aspera* Röding, 1798. This beach conglomerate presents normal gradation (Figure 4D); it has a maximum thickness of 1.00–1.10 m at Praia do Calhau, being less developed at Prainha, where it reaches only about 40–50 cm in thickness (Figure 3). It follows unit 3, a calcite cemented biostrome of calcareous coralline algae (Figure 4E) with a similar thickness (about 50–60 cm) in both Prainha and Praia do Calhau outcrops. This biostrome covers unit 2, involving cobbles and filling accommodation spaces, and is composed of four species of algae [66]. Unit 4 consists of up to 1.5–1.7 m thick volcano-bioclastic, unconsolidated, highly fossiliferous sands (Figure 4G), which display sedimentary structures with horizontal and cross-lamination (Figure 3). In both outcrops, two or more layers of sand, separated by a carbonate crust, are visible. Some mixed and well-sorted fine-grained sand layers are rich in macro- and microfossils—condensed shell layers—including a few fossil fish otoliths. Three fossil otoliths were collected, two at Prainha outcrop (DBUA-F 84 and DBUA-F 1171 samples) and another at Praia do Calhau (DBUA-F 1177), both belonging to unit 4. Holocene (?) slope deposits cover the MIS 5e sedimentary sequence (unit 6).

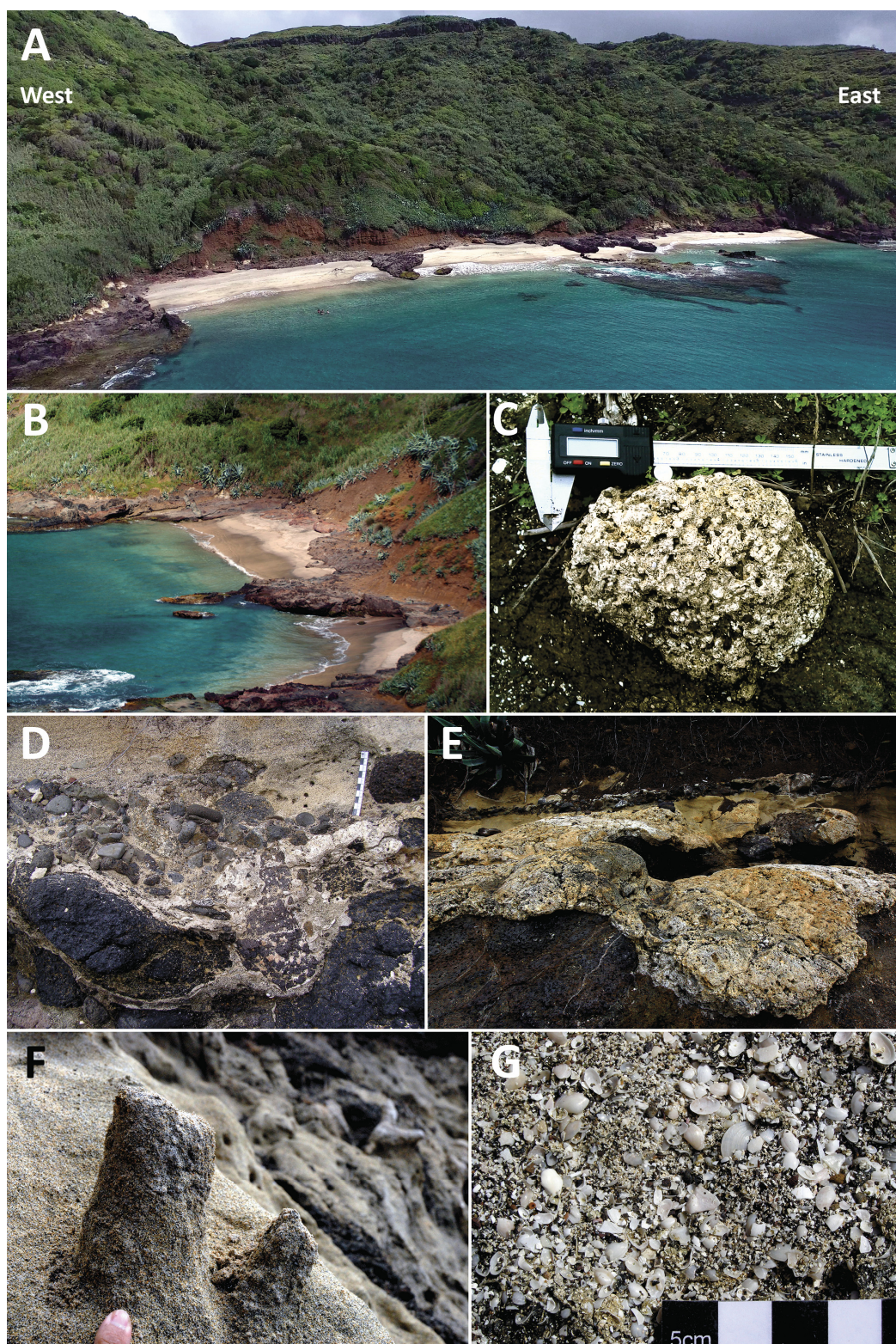


Figure 4. Prainha. (A,B) Aerial, drone view. (C) Calcareous algal crust at the western end of Prainha beach. (D) Conglomerate beach deposit filling in the paleotopography of the shore platform carved on top of the basalts of the Anjos Volcanic Complex. (E) Crustose algal framework. (F) Rhizoconcretions. (G) Surface of unit 4 (cf. Figure 3), with very abundant disarticulated valves of the bivalve *Ervilia castanea* (Montagu, 1803).

Systematic Paleontology
Phylum Chordata Haeckel, 1874

Class Teleostei Müller, 1848
 Order Myctophiformes
 Family Myctophidae Gill, 1893
 Genus *Diaphus* Eigenmann & Eigenmann, 1890
Diaphus cf. *holti* Tåning, 1918
 (Figure 5A,B and Figure 6A,B)

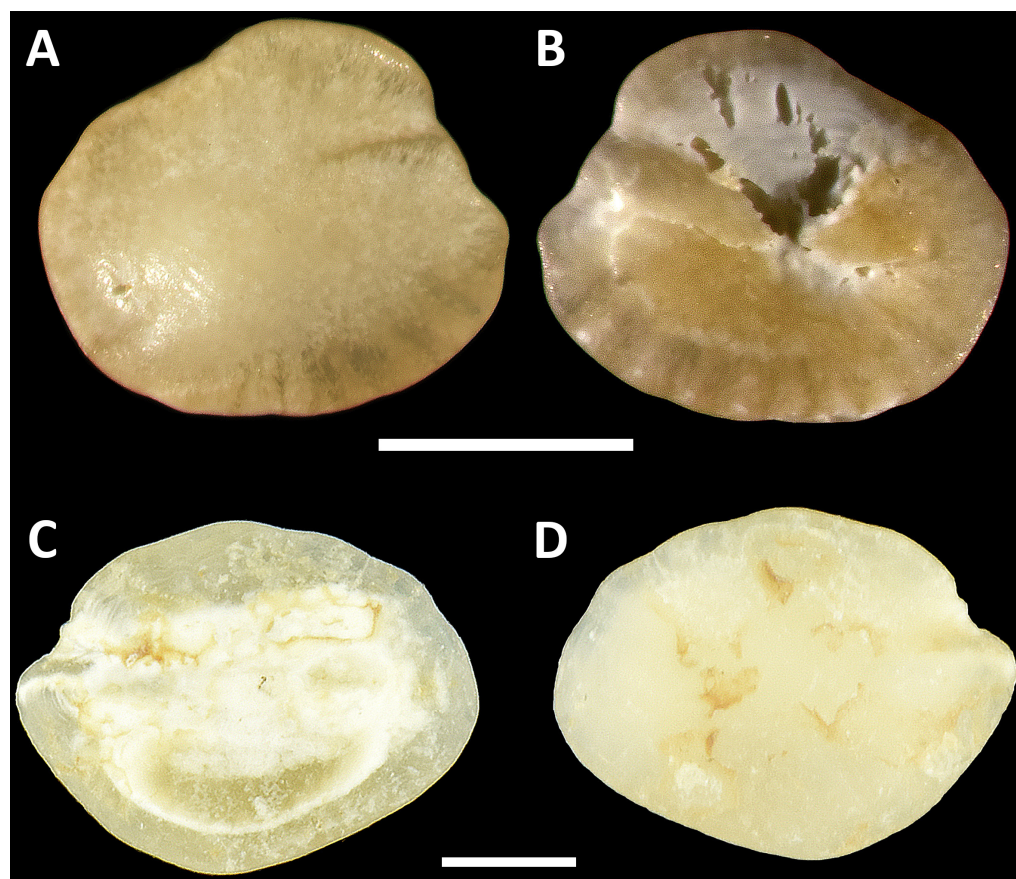


Figure 5. (A,B) *Diaphus* cf. *holti* Tåning, 1918. Otolith in dorsal (A) and ventral (B) view, DBUA-F 1177. (C,D) *Symbolophorus veranyi* (Moreau, 1888). Otolith in ventral (C) and dorsal (D) view, DBUA-F 1171. Scale bar: 1 mm.

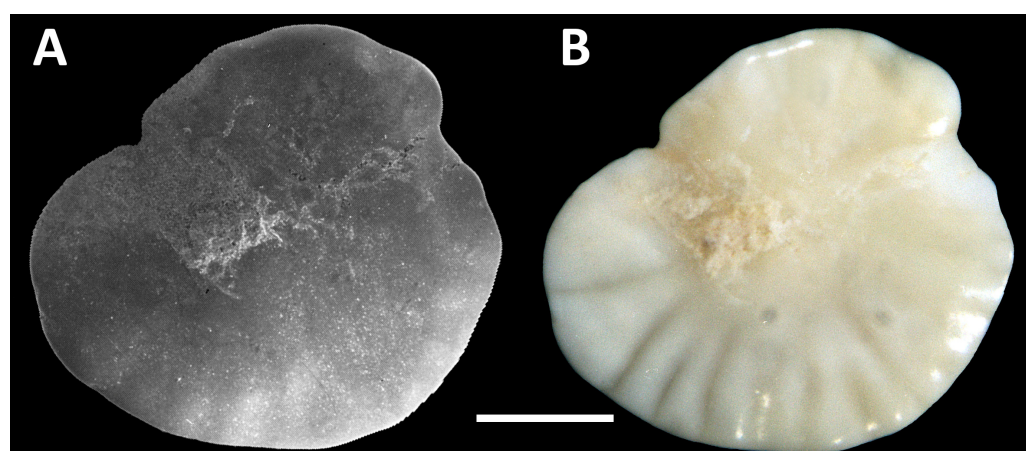


Figure 6. (A,B) *Diaphus* cf. *holti* Tåning, 1918. Otolith in ventral view, DBUA-F 84, Sup. 140-3. Scale bar 1 mm. (A) SEM image. (B) Image obtained from NIKON SMZ1000 binocular microscope with a NIKON D850 body attached.

Diaphus holti Tåning, 1918

Fossil material examined: two otoliths (DBUA-F 84, Sup. 140-3, and DBUA-F 1177).

Localities: Prainha and Praia do Calhau.

Description: The shape of the adult otolith (DBUA-F 84; Figure 6) is slightly elongated along the anterior–posterior axis, with a ratio of 1.05–1.19 between ostial length and ostial height. The rostrum is prominent. The dorsal area is large, and the dorsal rim is slightly pointed at its mid-point. The posterodorsal angle is located posteriorly, at about two thirds of the overall anterior–posterior length.

Ecology and habitat: The small lanternfish, *Diaphus holti*, is an actively mobile fish with a nektonic life habit and a carnivore diet [67]. This oceanodromous species [68] has a maximum length of 70 mm [69] and performs daily vertical migrations, occurring between 0 and –275 m at night, and between –225 and –799 m during the day [69–71].

Stratigraphic and geographic range: This includes the Miocene, Pliocene, and Pleistocene of Greece [72–76] and Italy [74,77–82] and the Pleistocene (MIS 5e) of the Azores (this work). It is reported today from the eastern Atlantic (from the Bay of Biscay south to South Africa) and from the Indian Ocean (eastern shores of Africa) [69]. It also presently occurs in the Mediterranean Sea and the southwest and central North Pacific but is not present in the Benguela Upwelling Region [71] and is also reported from the Condor Seamount, located at about 17 km WSW of Faial Island, within the Azores Exclusive Economic Zone [83].

Remarks: As shown by Nolf & Martinell [84], the morphology of *Diaphus* otoliths changes noticeably over the course of the fish's growth. As a result of these ontogenetic modifications, clear, diagnostic features are only expressed in adult otoliths (>2 mm), as is the case of the specimen illustrated in our Figure 6. Nolf & Martinell [84] and Nolf & Cappetta [85] illustrate otoliths from recent individuals of *Diaphus holti*. Both otoliths are quite eroded, but the DBUA-F 1177 otolith from the Praia do Calhau outcrop is more eroded than the DBUA-F 84 otolith from Prainha. Along the ventral rim, about nine remnants of some former denticles are visible, a typical characteristic for *Diaphus*. There are six species of this genus currently reported from the Azores [71]: the very common *Diaphus holti* and *D. rafinesquii* (Cocco, 1838); the common *D. effulgens* (Goode & Bean, 1896) and *D. metopoclampus* (Cocco, 1829); the rare *D. mollis* Tåning, 1928; and the very rare *D. bertelseni* Nafpaktitis, 1966. Following an actualistic approach and considering the recent geographic distribution of *Diaphus* species, we tentatively identify our samples as *Diaphus* cf. *holti*.

Genus *Symbolophorus* Bolin & Wisner, 1959

Symbolophorus veranyi (Moreau, 1888)

(Figure 5C,D)

Symbolophorus veranyi (Moreau, 1888)

Fossil material examined: one otolith (DBUA-F 1171).

Locality: Prainha.

Description: Elongate otolith with a bent inner face, with a ratio of 1.3 between ostial length (OL = 3.5 mm) and ostial height (OH = 2.7 mm). The dorsal rim exhibits no denticles. Very long and narrow ostium and slender cauda, which are characteristic of this genus. No postdorsal angle is visible. No postdorsal depression is visible.

Ecology and habitat: The largescale lanternfish, *Symbolophorus veranyi*, is an actively mobile fish with a nektonic life habit and a carnivore diet [67]; it feeds on crustaceans [86]. This oceanodromous species [68] has a maximum length of 130 mm [87] and performs daily vertical migrations, occurring at the surface at night, and at –550 to –2308 m during the day [69,71]. At night, small sub-adults usually occur at deeper levels than large sub-adults and adults [88].

Stratigraphic and geographic range: This includes the Pliocene of Jamaica [52], Pleistocene of Greece [75] and Italy [80], and Pleistocene (MIS 5e) of the Azores (this work). It is currently reported from the eastern, central, and western Atlantic, ranging from north of the British Isles south to Angola [69]. According to Porteiro et al. [71], it also occurs in the Mediterranean Sea, off Brazil at 35°S, and off South Africa, but it is not present in the Namibia Upwelling Region.

Remarks: The otolith from sample DBUA-F 1171 (Prairinha outcrop) is complete regarding the rim but worn on the medial face.

4. Discussion

4.1. The Paleobiodiversity of the MIS 5e Deposits at Santa Maria Island

The MIS 5e fossil record of Santa Maria Island is one of the most extensively studied in oceanic island systems, particularly over the last 20 years [41,89,90]. Nonetheless, the subject is clearly far from being exhausted, and we take this opportunity to provide an updated list of the marine species reported from the MIS 5e deposits on this island. The total number of MIS 5e species is now 182 specific taxa (cf. Table 1). The phylum Mollusca is the best represented, with 162 specific taxa, including four pelagic taxa [*Cavolinia* sp., *Creseis virgula* (Rang, 1828), *Limacina helicina* (Phipps, 1774), and *Limacina lesueurii* (A. d’Orbigny, 1836)], 130 gastropods, and 28 bivalve species. The Cnidaria (Anthozoa) and the cetaceans (Mammalia) are each represented by a single species (Table 1). This work increases the Azorean MIS 5e record of bony fishes to three species: one coastal species—the parrotfish *Sparisoma cretense* (Linnaeus, 1758), based on isolated dentitions—and two mesopelagic lanternfish species, *Diaphus* cf. *holti* Tåning, 1918, and *Symbolophorus veranyi* (Moreau, 1888), both based on otoliths. When the number of MIS 5e species is compared with that presently reported for the Azores by marine group, the coralline algae forming rhodoliths (100%), mollusk gastropods (56.5%), mollusk bivalves (19.6%), and crustacean decapods (11.1%) display a high-to-medium potential for fossilization (cf. Table 2).

Table 1. Total number of taxa per marine group reported for the Pleistocene (MIS 5e) outcrops of Santa Maria Island (Azores Archipelago). PCt—Ponta do Castelo. PCr—Pedrinha da Cré. PCe—Ponta do Cedro. Pqp—Pedra-que-pica. Pra—Prairinha. PCa—Praia do Calhau. Lag—Lagoinhas. VVe—Vinha Velha.

Marine Group	PCt	PCr	PCe	Pqp	Pra	PCa	Lag	VVe	Total Number of Species
Coralline algae forming rhodoliths					4	4	4		4
Cnidaria Anthozoa				1					1
Echinodermata					4	2	3	2	4
Mollusca Gastropoda	2	1	80	47	100	65	48	62	130
Pelagic Mollusca Gastropoda (Heteropoda + Pteropoda)			4						4
Mollusca Bivalvia			15	6	20	16	3	8	28
Crustacea Decapoda					4			5	7
Coastal fishes								1	1
Myctophidae (mesopelagic lanternfishes)					2				2
Cetaceans					0	1			1
Total number of species	2	1	99	54	134	88	58	78	182

Table 2. Comparison of the number of MIS 5e species with the present number of species reported from the Azores Archipelago, by marine group. [‡] The number of marine mammal species that are regularly seen in the Azores is 24, with four additional species that were sighted only once: *Steno bredanensis* (G. Cuvier in Lesson, 1828), *Eubalaena glacialis* (Müller, 1776), *Lagenodelphis hosei* Fraser, 1956, and *Phocoena phocoena* (Linnaeus, 1758).

Marine Group	MIS 5e Species	Recent Species	Ratio (%) MIS 5e/MIS 1
Coralline algae forming rhodoliths	4	4	100.0
Cnidaria Anthozoa	1	31	3.2
Echinodermata	4	64	6.3
Mollusca Gastropoda	130	230	56.5
Mollusca Bivalvia	28	143	19.6
Crustacea Decapoda	7	63	11.1
Myctophidae (lanternfishes)	2	44	4.5
Coastal fishes	1	165	0.6
Cetaceans	1	28 [‡]	3.6
Total number of species	178	772	23.1

4.2. Paleocology and the Lanternfish Fossil Record

The lanternfishes, also known as myctophids (from the Greek μυκτήρ *myktēr*, “nose” and *ophis*, “serpent”), are small mesopelagic fishes of the family Myctophidae that inhabit depths between 200 and 1000 m and are found in oceans worldwide [91]. The Myctophidae is generally considered one of the most diverse families of fishes [92], and this has been so at least since the Miocene [93]. According to the WoRMS database (last consulted 3 December 2025), 35 genera and 261 species are presently accepted as valid within this family. Although, during the middle Eocene, lanternfish were common over shelf and upper-slope regions, today, they mostly occur as mesopelagic inhabitants of the high, open ocean [94]. These species usually stay in deeper waters during the day and ascend to the surface to feed at night [95]. Such diel vertical migrations of hundreds of meters characterize many lanternfish species [96], a pattern that also applies to the two myctophids herein reported from the MIS 5e record of Santa Maria Island. Thus, a question arises: how to reconcile MIS 5e deposits, where 175 out of the 182 fossil-specific taxa (96.2%) are coastal, shallow-water species, with the presence of two mesopelagic fish indicator species, four pelagic mollusk species, and one undetermined cetacean species?

A direct comparison between modern and Pleistocene (MIS 5e) coastal boulder beach deposits at Santa Maria Island by Ávila et al. [97] concluded that it was not possible to determine whether storminess during the Last Interglacial was higher compared to the present day, as suggested by previous authors [98,99]; for a contrasting opinion, see Rovere et al. [100]. Although the historical meteorological archives record the main onshore wind and wave regimes in the region of the Azores as coming from the WSW-NNW quadrants [101,102], the largest winter storms and the few recorded hurricanes usually hit the Azorean islands from the SW-SE quadrants [97]. Moreover, a direct relationship has been established between adverse weather conditions and an increase in the number of stranded animals along the coasts of islands and continents [103–106].

The shore stranding of myctophids is a rare event in the Azores: in the 1990s, a few lanternfish individuals were found ashore at Praia das Milícias in São Miguel Island (José Azevedo, University of the Azores, personal communication 3 December 2025); in 2021, one lanternfish specimen was found ashore at Praia de Santa Bárbara, São Miguel Island

(João Brum, University of the Azores, personal communication 3 December 2025); and in April/May 2005, some Myctophidae specimens were found ashore at Praia da Vitória in Terceira Island, among Scyphozoa cnidarians (João Pedro Barreiros, University of the Azores, personal communication 4 December 2025). However, in a very protected, enclosed, and shallow bay, Porto Pim, at Faial Island (Azores), this phenomenon happens about 3–4 times/year and is attributed to the bathymetric and oceanographic local conditions that trap these organisms within the bay, preventing them from making the diurnal migration to higher depths, resulting in the shore stranding of several individuals on the sandy beach at Porto Pim (Pedro Afonso, University of the Azores, personal communication 4 December 2025). In the Strait of Messina (Central Mediterranean Sea), shore stranding of mesopelagic fishes also occurs regularly, caused by the local hydrographic system and upwelling currents, coupled with shoreward winds [107]. Moreover, it has been suggested that when strong upwelling occurs, the swim-bladder of myctophids is not able to cope with the sudden pressure changes, resulting in the transport of many individuals towards the shore [108,109]. Finally, a recent study also performed in the Strait of Messina records the highest number of stranding events during the new moon and in the winter season [110]. Thus, we hypothesize that, similarly to the present-day shore stranding events, most probably during the night, when myctophids are closer to the surface of the ocean, and as a result of oceanographic settings associated with adverse meteorological conditions, landward storm winds and waves transported the lanternfish specimens closer to the shore, where these were ultimately shored, stranding at Prainha and Ponta do Calhau, on the southern shores of Santa Maria Island. The organic decay of the soft tissues and the subsequent drop in sea level associated with the last glacial episode allowed for the preservation of their otoliths, which were entrained in the MIS 5e fossiliferous sediments at Prainha.

5. Conclusions

This work highlights the relevance of the paleontological record of Santa Maria Island. The two lanternfish species reported here for the Azores Archipelago increase the total number of MIS 5e taxa to 182 species. Although the vast majority of these MIS 5e records correspond to invertebrates (97.8%), the marine fossil record of vertebrates now comprises four taxa: three fish species and one undetermined cetacean.

The three myctophid otoliths recovered from MIS 5e fossiliferous sediments at Prainha and Praia do Calhau, on the southern coast of Santa Maria Island, are thus interpreted as resulting from high-energy meteorological events. Storm-induced winds and wave action likely transported lanternfish specimens toward the shoreline, promoting the concentration of biogenic remains within condensed, storm-generated layers landward of the storm berm and atop coeval aeolian dunes. These organisms were subsequently buried by sediments, leading to their fossilization, and were only recently exhumed, after being preserved for about 120 kyr.

Finally, the recovery of Myctophidae otoliths in the MIS 5e deposits of the Azores is of particular scientific significance, as there is currently no published record of lanternfish fossil specimens from Last Interglacial oceanic island deposits. While myctophids are well-documented in deep-sea cores and continental Neogene basins (e.g., Italy [111], Japan [93]), their presence in shallow-water, high-energy littoral sediments of the Late Pleistocene is exceptionally rare. In the context of Macaronesia and other oceanic archipelagos, the fossil record for this period is overwhelmingly dominated by marine invertebrates and calcareous algae [38,63]. Our discovery, therefore, represents a novel occurrence that highlights the unique taphonomic conditions of these outcrops and underscores the necessity of high-resolution sampling. The absence of similar reports in the literature further justifies

our rigorous screening of 38 kg of fossiliferous sediment from Last Interglacial deposits at Santa Maria Island, without which these rare meso-pelagic indicators would have remained undetected.

Author Contributions: S.P.Á. and W.S. conceived the ideas; funding acquisition: S.P.Á.; S.P.Á., P.M., A.H. and G.C.Á. collected the samples during fieldwork at Santa Maria Island; S.P.Á. sorted the otoliths; W.S. identified the fossil fishes from the otoliths; the writing was led by S.P.Á. and all co-authors equally contributed to its final design. Figures were structured by S.P.Á. and A.H. Figure 2 was drafted by M.A.D. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

DBUA-F Fossil collection of the Department of Biology, University of the Azores

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