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A call to address the taxonomic gap in the Pleistocene of Santa Maria Island (Azores Archipelago)

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ABSTRACT:

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Taxonomic impediment and taxonomic gap are two major problems that challenge the advancement of biological and palaeontological sciences such as (palaeo)ecology and (palaeo)biogeography. In an effort to overcome these difficulties, the Last Interglacial fossiliferous deposits from the Island of Santa Maria (Azores Archipelago, Portugal) have been intensively studied during the last two decades. The epitoniid gastropod *Epitonium jani* Segers, Swinnen and De Prins, 2009 is an example, herein, of a new addition to the fossil record worldwide. This finding increases the number of fossil molluscs reported from the warmest period of the Last Interglacial deposits of the Azores (Marine Isotopic Substage 5e; MIS 5e) to 138 taxa (114 Gastropoda and 24 Bivalvia). As in other insular settings, the Phylum Mollusca is the best represented marine group in the Pliocene and Pleistocene (MIS 5e) fossiliferous outcrops and an update on the palaeobiodiversity of the Azores Archipelago is provided, herein.

Key words: Taxonomic impediment; Taxonomic gap; Systematics; MIS 5e; Azores Archipelago; Mollusca; Epitoniidae; *Epitonium jani*.

INTRODUCTION

The taxonomic impediment, *sensu stricto*, is a problem that is intensifying our current taxonomic gap (Carvalho *et al.* 2005; Löbl 2018) due to the current lack of taxonomists with sufficient background to revise old records and biological collections, and thus properly classify marine faunas and floras and to keep up with evaluations that include the discovery of new species. This gap may be defined as the difference between accurate, real biodiversity numbers and the existing knowledge of them (Raposo *et al.* 2020). With the exception of a few phyla such as the algae, the Mollusca, the Echinodermata and the Chordata (bony fishes and selaceans), the present-day shallow-water marine biodiversity of the Azores Archipelago (Portugal) remains largely unknown. A similar situation occurs with the Pliocene and Pleistocene (MIS 5e – Marine Isotopic Substage 5e, i.e., the warmest phase of the Last Interglacial) fossil record of the archipelago (Ávila *et al.* 2018).

In this 'century of extinctions' (Dubois 2003), preserving as many species as possible is mandatory. In the marine realm, the delimitation of marine protected areas and of 'no-take zones (e.g., the Condor and Antialtair seamounts; Morato *et al.* 2010; O'Leary *et al.* 2012; Ressurreição and Giacomello 2013) constitute ocean management tools useful to improve current efforts of biodiversity conservation (Faria *et al.* 2024). Similar strategies must also be prescribed to conserve outcrops and their fossil record (Calado *et al.* 2007). The innovative concept of 'Palaeopark' (Lipps 2009; Ávila *et al.* 2014), first implemented by the Regional Government of the Azores in 2018, is based on a regional law that provides a legal framework targeting conservational aims (Decreto Legislativo Regional 2018). This regional decree-law protects the entire island of Santa Maria in the Azores Archipelago and, consequently, all fossiliferous outcrops that range in age from the Pliocene to the Pleistocene (MIS 5e). At Santa Maria Island, so far no Pleistocene fossils prior to the MIS 5e (129–117 kyr) have been found. The explanation for this is twofold: 1) first, and as showed by Ricchi *et al.* (2018), the submarine and the subaerial erosional terraces resulting from the uplift of the island coupled with sea level variation are all polygenetic in origin; 2) as a result, older interglacial fossil deposits – e.g., corresponding to MIS 9 (337–300 kyr) or MIS 11 (424–374 kyr) – were destroyed by marine erosion, either through the retreat of the coastline and consequent loss of possible deposits, or through the direct action of waves on these same fossiliferous deposits. For a review on the most important palaeosites of Santa Maria Island see Madeira *et al.* (2007) and Ávila *et al.* (2016, 2018, 2022, 2023).

During the last two decades, continuous funding by the Regional Government of the Azores was crucial to establish Santa Maria Island as one of the best studied islands in the world, especially in what concerns its geological evolution and fossil/ichnofossil record. Based on an integrative approach, multidisciplinary teams led by members of the MBP/CIBIO-Açores (Marine Palaeontology and Biogeography Lab) and composed of geologists, palaeontologists and marine biologists who explored the island and its surrounding bottoms during nineteen major workshops entitled 'Palaeontology in Atlantic Islands'. Two of the major issues facing taxonomy were overcome through the enactment of these scientific expeditions: the funding necessary for the collection of samples and proper storage of specimens in curated collections (Britz *et al.* 2020).

Most of the older literature on the Azorean fossil record is dedicated to the Pliocene marine fossils of Santa Maria Island (Bronn 1861; Bronn in Reiss 1862; Mayer 1864; Berkeley Cotter 1892; Ferreira 1952, 1955; Zbyszewski and Ferreira 1962). However, fossils of Pleistocene age (MIS 5e) are also present (Zbyszewski and Ferreira 1961; García-Talavera 1990). Their study, along with the production of accurate checklists of the recent and past Azorean marine flora and fauna, proved to be crucial for ecological and evolutionary studies in islands (Morton *et al.* 1998; Costa and Ávila 2001; Martins *et al.* 2008; Baptista *et al.* 2019, 2024; Cacabelos *et al.* 2021; Rebelo *et al.* 2021; Melo *et al.* 2022, 2023; Ávila *et al.* 2024) and for the development and testing of new theories in the field of marine island biogeography (Ávila *et al.* 2019).

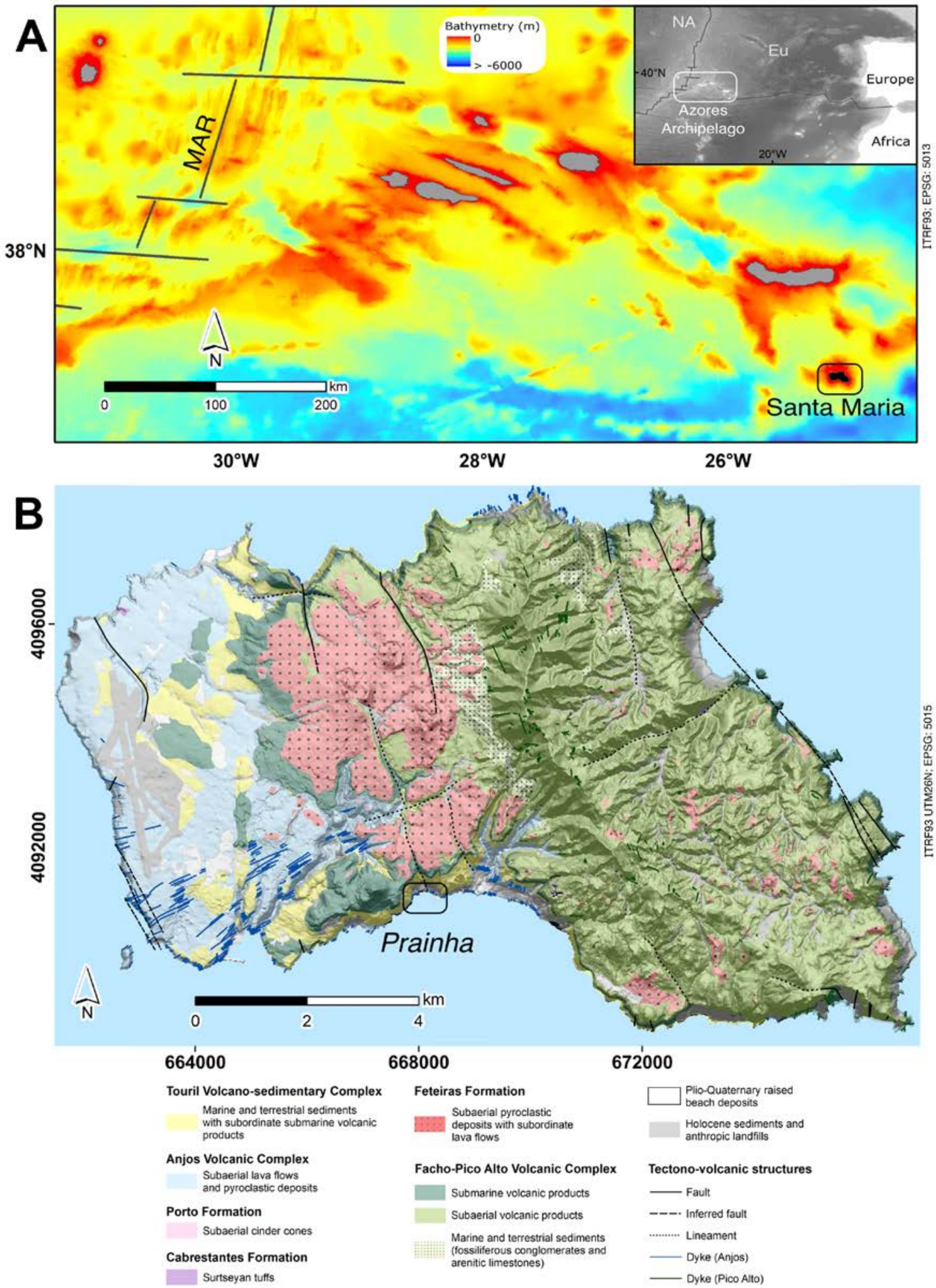
This study draws attention to the taxonomic gap in the Pleistocene record of Santa Maria Island and further contributes to our knowledge about the palaeobiodiversity of the Azores during the MIS 5e.

Institutional abbreviations

DBUA-F, fossil reference collection of the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island, Azores);
NMR, Natural History Museum Rotterdam, the Netherlands.

GEOLOGICAL SETTING

Located in the Northeast Central Atlantic, the Azorean volcanic oceanic islands form a relatively isolated Portuguese archipelago of nine islands and several islets, lying about half way between continental Europe and North America (Text-fig. 1A). A complex geodynamic setting characterises the area as it corresponds to the western segment of the Eurasia-Nubia Plate boundary, here ending in a



Text-fig. 1. Location maps. A – Location of the Azores Archipelago within the NE Atlantic (insert) and Santa Maria within the Azores Archipelago. NA – North American plate; Eu – Eurasian plate; Nu – Nubian (African) plate; MAR – Mid-Atlantic Ridge. Bathymetry extracted from GEBCO 2019 (https://www.gebco.net/data_and_products/gridded_bathymetry_data/); coastline delimitation from the Portuguese Hydrographic Institute free data (https://www.hidrografico.pt/op/33). B – Geological map of Santa Maria Island modified from Serralheiro *et al.* (1987) and Ramalho *et al.* (2017), with the location of the Prainha outcrop. Underlying digital elevation model from the 1:5000 scale digital altimetric database.

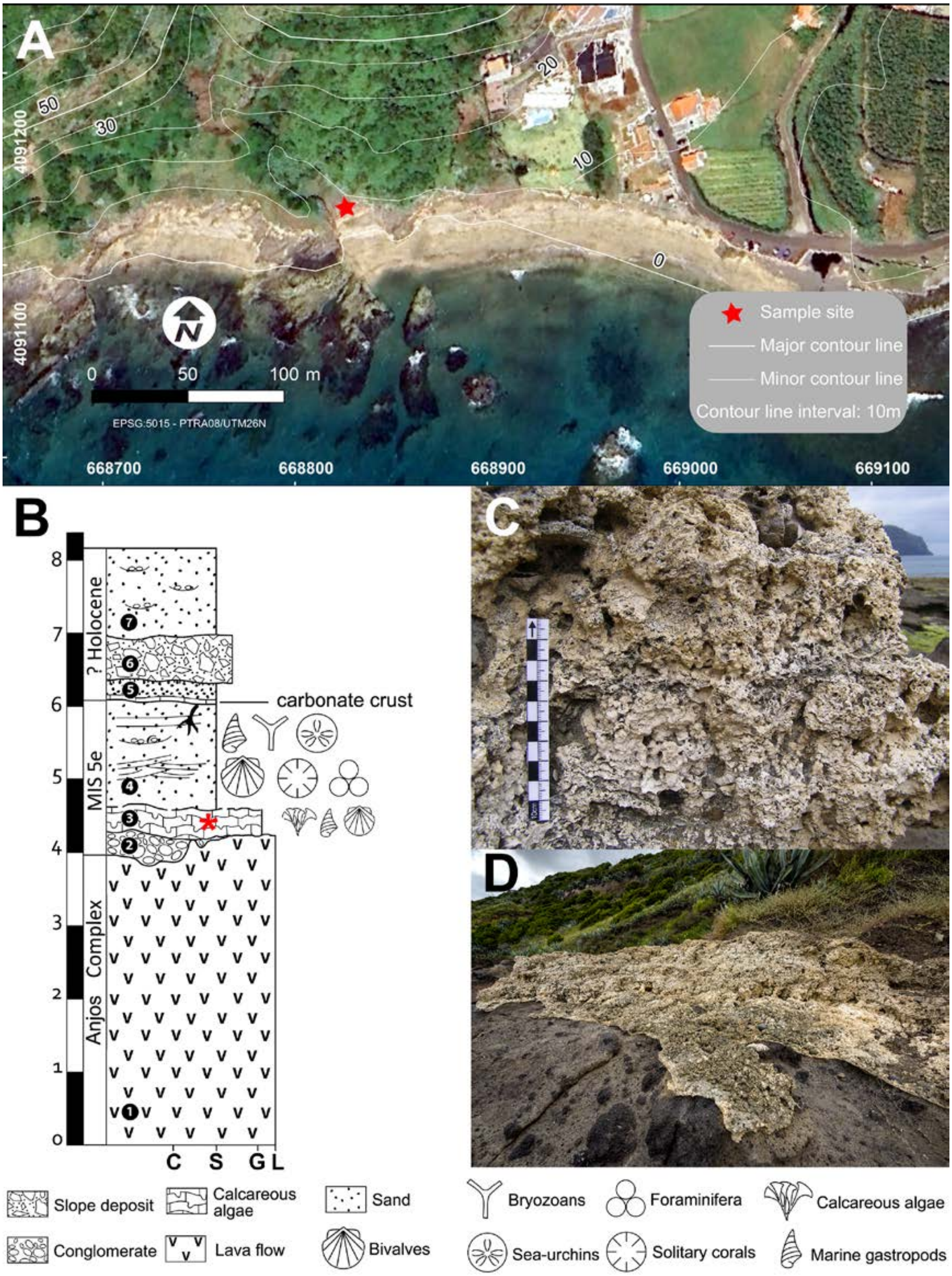
triple junction. The Mid-Atlantic Ridge separates the North American Plate from the Eurasian and Nubian plates. To the west, a diffuse plate boundary, where ultra-slow spreading occurs together with right lateral shear (accommodating the differential motion between the Eurasian and Nubian plates) forms the Azorean segment of the Eurasia-Nubia plate boundary (e.g., Lourenço *et al.* 1998; Dias *et al.* 2007; Hipólito *et al.* 2013). Spreading is distributed along a non-conventional geometry defined by a relatively young (<3 Ma, Miranda *et al.* 2014, 2018) rift and off-ridge volcanism expressed by several linear volcanic ridges. Although there is still controversy regarding a magmatic or 'melting' anomaly (e.g., Vogt and Jung 2018) underlying the Azores attributed to a mantle plume or plume head, a recent review work by O'Neill and Sigloch (2018) points to the existence of a mantle plume with origin in the core-mantle boundary beneath west Africa, as the source for the volcanism in the Azores region. Santa Maria is the oldest island, with an age of 6.03 Ma (Ramalho *et al.* 2017), and its development was contemporaneous of the first rifting phases in the Eurasian-Nubian plate boundary in the Azores region (Miranda *et al.* 2018). It is also the only Azorean Island that has experienced extreme uplift, at a rate of about 60 m/Ma for the last 3.5 Ma (Ramalho *et al.* 2017), attributed to magmatic underplating beneath the island (Ramalho *et al.* 2017). Vertical land motions experienced by Santa Maria Island added to a complex geological history. The island initially breached sea level at about 6 Ma. However, the end of this first volcanic phase at about 5.5 Ma, combined with the effect of subsidence and marine and aerial erosion, destroyed the first island, resulting in a large, shallow guyot (Ávila *et al.* 2012, 2018). For about 0.5 to 1 Ma, life thrived on these shoals and the remains of many marine organisms were preserved by sediments that added to the fossil record. This is the origin of the abundant and diversified Pliocene marine fossils from Santa Maria Island that includes algae (Rebelo *et al.* 2014, 2016) and vertebrate remains (Estevens and Ávila 2007; Uchman *et al.* 2018; Ávila *et al.* 2020) as well as invertebrate fossils and ichnofossils (Janssen *et al.* 2008; Kroh *et al.* 2008; Winkelmann *et al*. 2010; Madeira *et al.* 2011; Meireles *et al.* 2012; Uchman *et al.* 2017, 2020; Dávid *et al.* 2021; Hyžný *et al.* 2021; Sacchetti *et al.* 2023). A renewed phase of volcanic activity, coupled with the reversal from a subsidence trend of the island to an uplift trend, initiated at about 3.5 Ma, provoked the re-emergence of the island (Ramalho *et al.* 2017). Though fewer in number, fossiliferous shoreline-marine deposits from the warmest phase of the Last Interglacial (MIS 5e) also outcrop in Santa Maria (Ávila *et al.* 2002, 2015a, b; Rebelo *et al.* 2021). Despite being a somewhat restricted in environmental representation where rocky shoreline deposits prevailed (Madeira *et al.* 2011), the abundance and diversity of these well-preserved fossil assemblages favours a remarkably high species-richness in the MIS 5e deposits from Santa Maria.

MATERIAL AND METHODS

Nineteen *Palaeontology in Atlantic Islands* expeditions were conducted at Santa Maria Island in the Azores during the last two decades. In February 2000, fossiliferous sediments and qualitative samples were collected from the algal crust layer at Prainha Pleistocene outcrop (MIS 5e; Text-fig. 2A) by one of the authors (SPA). A total of 8 bulk samples, each of ~1 kg of fossiliferous sand, were collected for quantitative studies (facies 4 in Text-fig. 2B). Additionally, several broken pieces of the algal crust layer (Text-fig. 2C, D) were acquired. The calcareous coralline algal biostrome (facies 3 in Text-fig. 2B) of the entire Prainha outcrop, having a lateral extension of about 800 m, was thoroughly investigated and all the fossils found were hand-picked. Strip logs for stratigraphic sections were assembled along a representative vertical profile for this MIS 5e outcrop (Text-fig. 2B), displaying the internal structures and contacts of the sedimentary deposits. Care was taken to register changes in facies and fossil content. These sediments were sorted at the MPB lab under a binocular microscope, and photographed with a Nikon SMZ100 binocular microscope. Scanning Electronic Microscope photographs were taken at CIBIO-Açores research centre, with a Phenom ProX. All samples were given a sequential code number and deposited at the Department of Biology of the University of the Azores (Ponta Delgada, São Miguel Island). We compared our material with the original description of *Epitonium jani* provided by Segers *et al.* (2009).

SYSTEMATIC PALAEONTOLOGY

The classification adopted in this study is according to WoRMS (2024). We also provide a description of *Epitonium jani*, as well as information regarding its ecology, habitat, stratigraphic and geographic range.



Text-fig. 2. The Prainha section log and views. A – Aerial view of Prainha (southern coast of Santa Maria Island, 36º57'07.1" N, 25º06'13.7" W) with indication of the sampling site (red mark). B – Stratigraphic sections representing the main lithologies, sedimentary structures, contacts and fossiliferous content present in the Last Interglacial (MIS 5e) Pleistocene sedimentary succession at Prainha (modified from Ávila *et al.* 2015a, 2018). Numbers correspond to the depositional units as described in Ávila *et al.* (2002, 2015a, 2018): 1 –irregular shore platform carved in the basalts of the Anjos Complex; 2 – beach conglomerates; 3 – calcareous coralline algal biostrome; 4 – fossiliferous bioclastic sands with a thin carbonate crust of pedogenic origin on top; 5 – aeolian dunes; 6 and 7 – colluvial-alluvial deposits; C – clay; S – sand; G – gravel; L – lava. Scale is in meters. C, D – Cross-section photographs of the calcareous algae layer at Prainha.

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda L.R. Cox, 1960
Order Caenogastropoda *incertae sedis*
Family Epitoniidae S.S. Berry, 1910 (1812)

Genus *Epitonium* Röding, 1798

TYPE SPECIES: *Turbo scalaris* Linnæus, 1758 accepted as *Epitonium scalare* (Linnæus, 1758) (type by subsequent designation).

Epitonium jani Segers, Swinnen and De Prins, 2009
(Text-fig. 3)

2009. *Epitonium jani* Segers, Swinnen and De Prins, 2009, pp. 100, 101.

TYPE LOCALITY: Seixal, Madeira Island, 12 m depth.

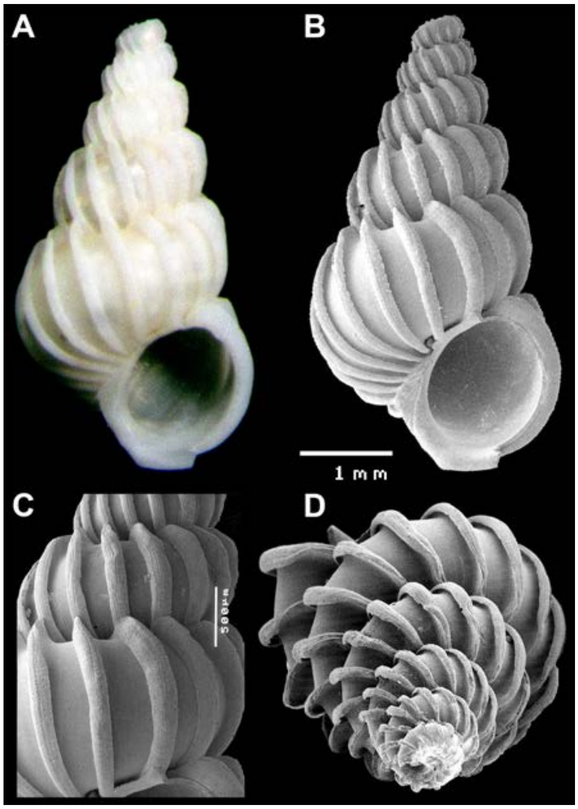
RECENT MATERIAL EXAMINED: NMR 32294.

FOSSIL MATERIAL EXAMINED: DBUA-F 19 Sup 83-2.

DESCRIPTION: Shell small, 4.9×2.9 cm, solid. Protoconch not preserved. Teleoconch of five convex whorls separated by deep suture (Text-fig. 3A, B). Sculpture consisting of 18 relatively high, prosocline, reflected lamellar ribs that extend between and are fused at sutures (Text-fig. 3C), aligned axially in anticlockwise spiral. No spiral sculpture. Last whorl about 55% of total height, strongly convex, without basal angulation or disc, ribs continuous over whorl, fusing with peristome. Aperture ovate, peristome complete, weakly angled abapically. No colour pattern preserved.

ECOLOGY AND HABITAT: This species belongs to a family of carnivorous gastropods with slow-moving locomotion, its life habit being semi-infaunal. A few specimens are reported from under rocks, gravel or pebbles, or attached by its byssus to floating bodies, to shells of the genus *Pecten* O.F. Müller, 1776 and in the middle of rhizomes of large algae (Lucas 1975). The reported depth range is 0–12 m (Segers *et al.* 2009).

STRATIGRAPHIC AND GEOGRAPHIC RANGE: Pleistocene (MIS 5e) of Santa Maria Island (Azores) herein reported is the only specimen known from the fossil record; extant in the Azores, Madeira, and Canaries archipelagos.



Text-fig. 3. Shell of *Epitonium jani* Segers, Swinnen and De Prins, 2009, 4.9×2.9 mm; A, B – Frontal view; C – Detail of the ribs and their ornamentation; D – Apical view highlighting the characteristically reflected and quite high prosocline ribs.

REMARKS: A single specimen of *Epitonium jani* (Text-fig. 3), 4.9×2.9 mm, was collected on the 17th of February, 2000 by one of the authors (SPA), from Prainha outcrop (36°57'07.1" N, 25°06'13.7" W). This specimen was recovered within the calcareous algal layer (unit A_2 of Ávila *et al.* 2002; MIS 5e, facies 3 in Text-fig. 2B) and labelled as DBUA-F 19 Sup 83-2 (Text-fig. 3A–D). The thickness of the calcareous algal layer at the site of collecting the *E. jani* specimen was about 0.4 m. The maximum length reported is 10.0 mm; the largest Azorean recent specimen is 5.2 mm in height (Segers *et al.* 2009).

DISCUSSION

One of the key factors for the detection of marine biogeographic processes and patterns is the existence of updated checklists validated by experts. This task is time consuming, albeit fundamental to understand the past and present (palaeo)biogeographic and (palaeo) ecological processes and to infer and interpret their patterns. The last account on the fossil molluscs from the MIS 5e deposits of Santa Maria Island was made by Melo *et al.* (2023) who, based on bibliographic data obtained from previous authors (Callapez and Soares 2000; Ávila *et al.* 2002, 2007, 2009, 2010, 2015a), published a checklist reporting the occurrence of 137 taxa in the Azores Archipelago (113 gastropods and 24 bivalves). Our study increases the number of MIS 5e gastropods to 114, but these figures are expected to substantially rise due to ongoing work on another MIS 5e fossiliferous outcrop (Ponta do Cedro), located on the east shore of Santa Maria Island. Additionally, using the Chao estimator in three MIS 5e deposits from Santa Maria, Ávila *et al.* (2015a) concluded that 23 species are probably present at Prainha and were missed by the quantitative methodology employed (eight replicates sorted, each with 1 kg of fossiliferous sand), whereas six species are expected to be found at Lagoinhas in the north coast of Santa Maria (ten 1 kg replicates sorted), and another six species are expected to be present at Vinha Velha in the south coast of Santa Maria (six 1 kg replicates sorted), but were missed due to undersampling. Therefore, there are strong data to support expectations of a MIS 5e total number of marine molluscs in excess of 150–160 species to be found in the Pleistocene fossil record at Santa Maria Island.

We also take this opportunity to update the Pliocene to Recent marine biodiversity of the Azores archipelago (Table 1), as this is useful information currently scattered in several publications. Table 1 depicts a total of 234 Pliocene species, 156 Pleistocene (MIS 5e) species and 1,558 extant species. The Phylum Mollusca (in this work represented by gastropods and bivalves) is by far the best represented marine group in both the Pliocene (57.3% of the total Pliocene species reported from Santa Maria Island) and the Pleistocene (MIS 5e; 88.5%). Regarding the extant marine species, algae (26.0%), molluscs (23.9%), Polychaeta annelids (10.8%), and coastal fishes (10.6%) are the best represented marine groups (Table 1).

The importance of checklists validated by experts is exemplified by two recent works: Sacchetti *et al.* (2023) reviewed the Pliocene gastropods reported from Santa Maria Island and, besides correcting several misidentifications, increased the number of taxa from 61 to 77; in a similar way, Berning and Wisshak (2024) increased the number of recent native Azorean bryozoans from 19 (Tempera *et al.* 2010) to 221. Whereas the Pliocene fossil record from Santa Maria might be considered to be well known (novelties are however expected in the near future as the Pliocene bivalves are now under revision), some groups still await to be studied in the Pleistocene fossil record (MIS 5e), such as the Bryozoa and the Ostracoda (Crustacea).

Table 1. Total number of taxa reported for the Pliocene and Pleistocene (MIS 5e) outcrops of Santa Maria Island (Azores Archipelago), and for the Recent of the Azores Archipelago. The ratio (in %) of the Pleistocene versus Recent taxa provides a measure of the potential of preservation in the fossil record, by marine group; ‡ data according to Berning and Wisshak (2024); § data according to Ávila *et al.* (in press); þ data according to Sacchetti *et al.* (2023); n.i.a.: no information available.

Marine group	Pliocene	Pleistocene (MIS 5e)	Recent	Pleistocene/ Recent (%)
Algae	7	4	405	1.0
Annelida/Polychaeta	2	0	169	0.0
Brachiopoda	3	0	n.i.a.	n.i.a.
Bryozoa	38‡	0	221‡	0.0
Cnidaria/Anthozoa	11	1	31	3.2
Crustacea/Cirripedia	2	0	7	0.0
Crustacea/Decapoda	3	7	63	11.1
Crustacea/Ostracoda	13	0	20	0.0
Echinodermata	8	4	64	6.3
Coastal fish (bony fish)	3	1	165	0.6
Fish/Sharks	7	0	12	0.0
Mollusca/Bivalvia	57	24	143§	16.8
Mollusca/Gastropoda	77þ	114	230	49.6
Cetaceans	3	1	28	3.6

CONCLUSIONS

The Santa Maria Island MIS 5e fossil record features a somewhat restricted environmental picture, in which rocky-shore dwellers are best represented (Madeira *et al.* 2011). Nonetheless, it presents a rich fauna as demonstrated by palaeontological studies targeting the most common group in the island fossil record, the molluscs. Taxonomic biases remain endemic in the estimations of biodiversity changes through time and space. Despite the overall lack of interest in taxonomic issues, seen as an old-fashioned dull discipline, systematic examination of the building blocks (i.e., 'species') in any biodiversity study is not only necessary but mandatory. The work developed in the last 20 years on the island Santa Maria fossil record, of which the present study is part, demonstrates that taxonomic studies should be seen as a centrepiece in any avenue of research, aiming to understand biota evolution.

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