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A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography

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ABSTRACT

The privileged location of Santa Maria Island (Azores archipelago) in the middle of the North Atlantic makes the fossiliferous outcrops on this island of utmost importance to gain a better understanding of how coeval living communities relate to the broader evolutionary and biogeographic history of the Atlantic basin during the late Neogene and the Quaternary. Here we focus on this island's MIS 5e fossil record, offering a comprehensive review on the palaeobiodiversity, palaeoecology and palaeobiogeography of the biota living in the mid North Atlantic during this interglacial. Several studies in oceanic islands stress the huge impact of sea level changes on insular communities. Pleistocene sea-level changes occur during the short-time events known as "Terminations" (associated to glacial/interglacial shifts) as well as with the onset of glaciations (associated to interglacial/glacial shifts). Both are responsible for extinctions and local disappearance of species, bottleneck effects and formation of new species, resulting in community structure changes. This work increases the number of fossil marine taxa reported from the Last Interglacial deposits of Santa Maria to 143 species. All the 19 new records are molluscs (13 gastropods and 6 bivalves), thus increasing the number of fossil molluscs to 136 species. Although thermophilic members of the "Senegalese" tropical fauna were found in these deposits, many of the most emblematic species (e.g., *Persististrombus latus* (=*Strombus bubonius*), *Cymbula safiana*, *Harpa doris*, *Cardita senegalensis*, *Barbatia plicata*, *Ctena eburnea* or *Hyotissa hyotis*) are absent, suggesting that they did not reach the Azores. Our results indicate that the main differences between the species composition of the MIS 5e and the present-day shallow-water Azorean communities are probably due to the dropping of sea surface temperature associated with the onset of the last glaciation, which had both direct and indirect effects on species ecology. A group of 21 thermophilic species was directly affected by the lower sea surface temperature, whereas a group of four sand-associated species was indirectly but similarly affected by the lowering of the sea level. Both groups have locally disappeared from the Azores. However, none of the extant endemic species found on the studied MIS 5e outcrops was apparently

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affected by the lowering SST. In contrast to the biogeographical relationships of the recent Azorean shallow marine molluscs, which are predominantly with the Mediterranean Region, Portugal and with the Madeira and Canary Islands archipelagos, the palaeobiogeographical relationships of the MIS 5e Azorean marine molluscs are mainly with Canaries and West Africa. Despite the general low similarity of the biogeographical relationships between the Azores and Cape Verde Archipelago, on both the recent and the MIS 5e analysis, this similarity is nevertheless higher for the MIS 5e mollusc assemblages, emphasizing the role of Cape Verde as an important source of warm-water species during the Last Interglacial.

1. Introduction

Sea-level fluctuations associated with interglacial/glacial transitions have strongly affected both coastal sediment distribution and availability, and marine (and terrestrial) fauna living on reefless volcanic oceanic islands worldwide. Changing sea levels were the direct and indirect cause of extinctions (Valentine and Jablonski, 1991), local disappearances of species (Ávila et al., 2008a, 2008b), bottleneck effects (Ávila, 2013; Ludt and Rocha, 2015) and formation of new species (Ludt and Rocha, 2015), all resulting in changes of community structure (Budd et al., 1996).

The Last Interglacial period, of which the warmest interval is known as MIS 5e (Marine Isotopic Stage 5e, ~130 ka to ~116 ka; Oppo et al., 2006; Bauch and Erlenkeuser, 2008), was warmer than the present one (Hillaire-Marcel et al., 1996; Muhs et al., 2002; Shackleton et al., 2003; CAPE – Last Interglacial, Project Members, 2006; Hearty et al., 2007). During MIS 5e, sea level was higher than today and global eustatic estimates vary between +2/+4 to +6/+9 m (Kopp et al., 2009; Dutton and Lambeck, 2012). Several studies have addressed field evidence of MIS 5e sea levels (Hillaire-Marcel et al., 1996; Muhs et al., 2002; Murray-Wallace, 2002; Zazo et al., 2003, 2007; O'Leary et al., 2013), and a number of debates are fuelling the discussion on this interglacial about the timing, eustatic sea level, and existence of pulses within MIS5e (and their causes). For example, in Western Mediterranean, several authors postulated the existence of at least two highstands during MIS 5e (e.g. Hearty et al., 2007; Dorale et al., 2010; Dabrio et al., 2011). However, Ferranti et al. (2006) compiled the MIS 5e highstand sites spanning the coastline of Italy and from the 246 listed sites, less than 50 have evidences of two highstands, while three highstands separated by lowstand phases have been described by Zazo et al. (2003) and Bardají et al. (2009). Therefore, the chronology of these sea-level highstands and their related climatic changes remain controversial. For instance, Rohling et al. (2008), based on marine cores, indicated a +6 m sea-level highstand at 123 ka, followed by a sea-level drop. After this period, sea-level rose to a +9 m highstand at 121.5 ka, with another sea-level drop that was followed by a smaller highstand at 119.5 ka (Rijsdijk et al., 2014). In the Atlantic islands of the Macaronesia, at least two highstands have been described during MIS 5e, at +2/+4 m and +1/+1.5 m (Zazo et al., 2002, 2007, 2010). These higher sea-levels imprinted worldwide depositional and geomorphological benchmarks in the shores of continents and islands in the form of beach conglomerates, beach fossiliferous deposits, fossil algae biostromic reefs, palaeocoral reefs, and morphological elements such as raised shore platforms and wave-cut notches. All these geological and palaeontological features contain important information that, if analysed in light of tectonics, glacial isostatic adjustments and ice models, can be employed to use the Last Interglacial as a proxy for future sea level changes and ice sheet collapses.

Santa Maria is the oldest and the southeastern-most island in the Azores (Fig. 1A) and one of the best oceanic islands to study the late Neogene and Quaternary marine fossil record in the North Atlantic framework. This volcanic island is unusually rich in exposed marine fossiliferous sediments (Ferreira, 1952, 1955; Zbyszewski and Ferreira, 1962; Estevens and Ávila, 2007; Kirby et al., 2007; Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 2010; Habermann, 2011; Madeira et al., 2011; Ávila et al., 2012; Meireles et al., 2012, 2013) and submarine volcanic sequences (Serralheiro and Madeira, 1990; Madeira et al., 2007), due to a combination of a peculiar geological history with a noticeable uplift trend and erosion during the Quaternary. From the late Pliocene to the Holocene, erosion and a slow uplift trend were the dominant processes, with a series of well-preserved staircase shore platforms' in the western portion of the island at various altitudes, ranging from +3/+9 m up to +200/+230 m (Ávila et al., 2012). It is due to this recent uplift trend, together with marine and, in a lesser extent, fluvial erosion that such diverse and rich submarine volcanic and sedimentary sequences are nowadays observable.

Thus, the fossiliferous outcrops on Santa Maria are crucial to understand how coeval communities relate to the broader evolutionary and biogeographic history of the Atlantic basin during the late Neogene and Quaternary. Within this framework, we revised the most important MIS 5e fossiliferous sequences of Santa Maria Island, encompassing a comprehensive characterisation of the recently-found Vinha Velha deposit from a sedimentological and palaeontological point of view. This work is part of a broad line of research aimed at understanding the community structure evolution from MIS 5e to recent marine ecosystems and grounds on former studies by Zbyszewski and Ferreira (1961), García-Talavera (1990), Callapez and Soares (2000) and Ávila et al. (2002, 2007b, 2009a, 2009b, 2010). The main goals of this study are to: 1) reconstruct the palaeoenvironment of the sedimentary facies of the recently found MIS 5e outcrop of Vinha Velha; 2) characterise and compare the mollusc fossil assemblages of the various MIS 5e highstand deposits known from Santa Maria Island; 3) produce a palaeoenvironmental reconstruction for these sequences; and finally, 4) to determine the palaeobiodiversity of the MIS 5e faunas and to establish the associated palaeobiogeography, within this mid-Atlantic context.

2. Geological setting and previous studies on MIS 5e deposits

Santa Maria Island emerged sometime during the late Miocene (Serralheiro et al., 1987; Serralheiro, 2003). Scattered late Pleistocene deposits assigned to MIS 5e are known from Santa Maria, outcropping on the shores around the island at slightly different heights (Fig. 1B). The most studied outcrops are Prainha and Praia do Calhau, both located on the southern shores at +3 to +4 m (Zbyszewski and Ferreira, 1961; García-Talavera, 1990; Ávila et al., 2002, 2007b, 2009a, 2009b, 2010; Amen et al., 2005) and Lagoinhas, on the northern shores, at +7.4 m (Callapez and Soares, 2000; Ávila et al., 2002, 2009a). As the shore platforms where these outcrops occur are covered by talus deposits, and since the