



Fossil Mysticeti from the Pleistocene of Santa Maria Island, Azores (Northeast Atlantic Ocean), and the prevalence of fossil cetaceans on oceanic islands

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ABSTRACT

Fossil remains of Cetacea are known globally from nearshore marine sediments along continental coastlines, but they are poorly known from volcanic oceanic island archipelagos. Here we report Pleistocene fossil cetacean material from late Neogene and Quaternary age outcrops on the Santa Maria Island of the Azores island archipelago in the North Atlantic Ocean. These remains consist of an isolated and highly worn fragment from the mandible of a medium- to large-sized baleen-bearing mysticete (i.e., Chaeomysticeti), which was exposed at the marine isotope stage 5 (sub-stage MIS 5e) level at Praia do Calhau, after Hurricane Gordon hit Santa Maria Island in August 2012. While this occurrence represents only the second description of Pleistocene cetaceans from volcanic oceanic islands, we predict that fossil cetaceans are likely under-reported from oceanic islands, given their extant abundance and richness near oceanic island archipelagos today, whose geomorphology and oceanography provide important settings for the migration and life history patterns of living cetaceans.

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INTRODUCTION

Extant cetaceans are found in all of the world's oceans, yet their geographic distributions are constrained by resource availability, which are mostly linked to productivity regimes along continental coasts and shelves (Croll et al., 2005; Kaschner et al., 2011). The ecology and distributions of pelagic cetaceans in the open-ocean remain largely unknown because of the logistical challenges of studying and tracking their patterns across ocean basins (Goldbogen et al., 2013). Volcanic oceanic islands provide one means to sample open-ocean cetacean diversity, either as a stable platform for land- or boat-based observations, or via passive monitoring from the stranding record (Pyenson, 2011). In the oceanic island archipelago of the Azores, in the northeast Atlantic Ocean (Figure 1), 28 living cetacean species have been documented in the surrounding waters (Ávila et al., 2011). This area, with narrow shelves and high slopes of the islands (Quartau et al., 2010, 2012, 2014) and, consequently, high depths at a relatively close distance to the shore, is considered as a mating, breeding, and feeding area for sperm whales (Matthews et al., 2001), and as a resting and feeding area for large migratory cetaceans (Silva et al., 2013) due to the abundance of food (Gordon and Steiner, 1992). Large baleen whales, e.g., sei whales *Balaenoptera borealis* Lesson, 1828, fin whales *B. physalus* (Linnaeus, 1758), Bryde's whale *B. edeni* Anderson, 1878, blue whales *B. musculus* (Linnaeus, 1758), and North Atlantic right whales *Eubalaena glacialis* (Müller, 1776) have also been reported from the Azores Islands (Steiner et al., 2007; Olsen et al., 2009; Silva et al., 2012).

In contrast with the moderately high abundance and richness of cetaceans nearby islands in the present-day — e.g., 21 species reported from Galapagos and 16 species reported from the Hawaii island archipelagos in the Pacific Ocean; Palacios et al. (2004), and Maldini et al. (2005), respectively — the fossil record of cetaceans on islands is almost anecdotal in comparison with that of continental shelves (Fitzgerald, 2011). In fact, exceptional cetacean fossil sites with complete, articulated skeletons are mostly reported from localities along former continental shelves, such as the Eocene lagoonal deposits of Wadi Al-Hitan in Egypt (Gingerich, 1992), the Middle Miocene Sharktooth Hill bonebed from California (Pyenson et al., 2009), the Late Miocene site Cerro Ballena of Chile (Pyenson et al., 2014), and from the Mio-Pliocene Pisco Basin of Peru (Muizon, 1988; Esperante et al., 2002, 2008). Neogene outcrops with cetacean remains listed in the Paleobiology Database are also reported from the eastern Atlantic Ocean and of the Mediterranean Sea, including the Miocene of Belgium (Abel, 1905), the Miocene of Portugal (Esteves and Antunes, 2004; Esteves, 2006), and the Pliocene of Spain (Sendra, 1997; Sendra et al., 1998, 1999; Muñiz et al., 2006; Esperante et al., 2009).

Even taking into account that nowadays there are over 20,000 oceanic islands on our planet, to the best of our knowledge, remains of fossil cetaceans have only been reported from the Neogene of Miyako Island (Japan) (Hasegawa and Otsuka, 1973), the Mio-Pliocene of Santa Maria Island (Azores) (Berthois, 1953; Esteves and Ávila, 2007), the Pliocene of the Balearic Islands — Menorca (Mercadal et al., 1985) and Maiorca (Mas, 2004) —, and the Pleistocene of Nauru Island (Fitzgerald, 2011), thus attesting the rarity of

such fossils in volcanic oceanic islands. Fossils of ectoparasitic whale barnacles (*Coronula* spp.), which are mainly found on living humpback whales *Megaptera novaeangliae* (Borowski, 1781) were also reported from the Pliocene-Pleistocene of Espiritu Santo Island, Vanuatu Archipelago (Bianucci et al., 2006) and from the Pleistocene of Isabela Island, Galápagos Archipelago (Zullo, 1986), despite the lack of associated cetacean body fossils.

Here we report the second discovery of a Pleistocene cetacean from a volcanic oceanic island, based on a fragmentary mandible from the Pleistocene (the marine isotope stage 5e [MIS 5e], i.e., last interglacial) of Santa Maria Island (Azores).

MATERIALS AND METHODS

Geographic and Geological Settings

The Azores archipelago comprises nine volcanic oceanic islands located in the northeast Atlantic Ocean (Figure 1). Santa Maria was the first island to have emerged above sea level during the Late Miocene (Ramalho et al., 2014) and the geological evolution of Santa Maria can be summarised as follows: 1) first subaerial volcanic edifices (Cabrestantes and Porto formations) and building of a subaerial shield volcano during the Late Miocene (Anjos Complex); 2) erosion and probable total submersion and thus, disappearance underwater of the first island of Santa Maria during the Late Miocene–Early Pliocene (Touril Complex); 3) intensification of the volcanic activity and gradual change from submarine to subaerial eruptions, with lava deltas forming along coeval coastlines during the Early Pliocene (Facho-Pico Alto Complex); 4) subaerial and littoral erosion followed by low-volume volcanism associated with monogenetic cones during the Late Pliocene (Feteiras Formation); and 5) uplift and erosion of the edifice from Early Pleistocene to the present (Ávila et al., 2012; Ramalho et al., 2014).

The highly fossiliferous Touril Complex has a total height of 130 m (Serralheiro, 2003) and was deposited in submarine conditions, during a period when the first island had most probably completely disappeared under water, thus corresponding to a large seamount with shallow depths. These conditions favoured the incorporation in the marine sediments of abundant remains of marine vertebrates including fishes (Zbyszewski and Ferreira, 1962), cetaceans (Estevens and Ávila, 2007), and sharks (Ávila et al., 2012). There are also abundant inver-

tebrate species, such as molluscs (Janssen et al., 2008), brachiopods (Kroh et al., 2008), crustaceans (Winkelmann et al., 2010), echinoderms (Madeira et al., 2011), ostracods (Meireles et al., 2012), as well as calcareous algae forming rhodoliths (Rebelo et al., 2014), whose fossils are nowadays exposed in 15 Late Miocene–Early Pliocene outcrops scattered in the island (Ávila et al., in press).

Late Pleistocene deposits are also known from Santa Maria and were recently revised (Ávila et al., 2015). Prainha and Praia do Calhau, both located on the southern shores at about 3–4 m above present sea level (Zbyszewski and Ferreira, 1961; García-Talavera, 1990; Ávila et al., 2002, 2009a, 2009b, 2010), are amongst the best studied outcrops of the island. Ávila et al. (2008) suggested that the Prainha fossiliferous sequence was formed during the MIS 5e, based on U/Th ages on shells of *Patella* spp., and on faunal, facies, and geomorphological considerations.

Fossil Material

The primary material for this research was a large fragment of a cetacean mandibular corpus, which was exposed at Praia do Calhau outcrop (36°57'07.11"N, 25°06'18.69" W), after Hurricane Gordon hit Santa Maria Island on the evening of August 19 and the night of August 20, 2012. When the specimen was found, only the more poorly preserved end of the fragment was visible.

After obtaining the necessary legal authorization of the "Parque de Ilha de Santa Maria," the skeletal remains were excavated during September 2012 by careful digging with shovels, trowels, knives, and small chisels. The position of the bone was mapped using a grid. Smaller fragments were collected as well and their positions also noted. A stratigraphic section was assembled along a representative vertical profile of the studied MIS 5e outcrop of Praia do Calhau displaying the internal structures and contacts of the sedimentary deposits. All bone fragments were photographed in situ before being removed from the outcrop wrapped in polyurethane foam, to protect them during handling, and subsequently transported to the laboratory, where the material was unpacked and cleaned with brushes, trowels, and small tweezers. No liquids were used during this operation. After cleaning, all bones were again photographed under different orientations. The fossils collected in this study are housed in the "Centro de Interpretação Ambiental Dalberto Pombo," Vila do Porto, Santa Maria Island (Azores, Portugal).

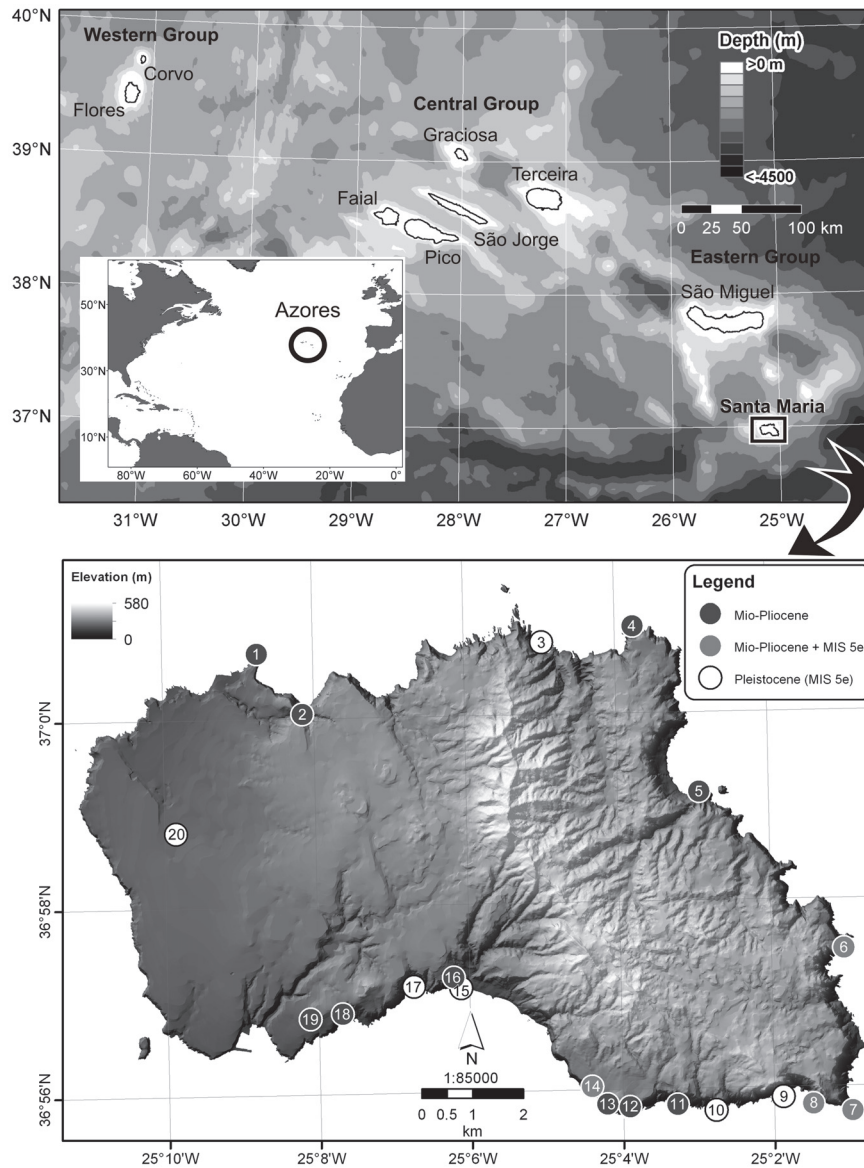


FIGURE 1. Top: location maps. Insert: location of the Azores archipelago in the Northeast Atlantic and location of Santa Maria Island, within the Azores Archipelago. Bottom: map of Santa Maria with the location of the most important Mio-Pliocene and Pleistocene (MIS 5e) outcrops— 1, Ponta dos Frades; 2, Cré; 3, Lagoinhas; 4, Ponta do Norte; 5, Ponta Negra; 6, Ponta do Cedro; 7, Ponta do Castelo; 8, Pedra-que-pica; 9, Vinha Velha; 10, Pedrinha da Cré; 11, Baía de Nossa Senhora; 12, Malbusca; 13, West fault of Malbusca; 14, Ichnofossil's cave; 15, Praia do Calhau; 16, Macela; 17, Prainha; 18, Figueiral; 19, Pedreira do Campo; 20, Airport.

Institutional Abbreviations: DBUA-F, fossil collection of the Department of Biology of the University of the Azores.

SYSTEMATIC PALAEONTOLOGY

Order CETACEA Brisson, 1762
Suborder MYSTICETI Flower, 1864

Infraorder CHAEOMYSTICETI Mitchell, 1989
Chaemysticeti incertae sedis

Material examined. DBUA-F 1079 consists of a fragmentary mandibular corpus (Figure 2).

Provenance. The specimen was collected September 17, 2012, at about 0.2 m above the contact between a basal conglomerate (facies 2, Figure 3) and the overlying 2.6 m thick, yellowish, partly cross-laminated, volcanoclastic to bioclastic, unce-

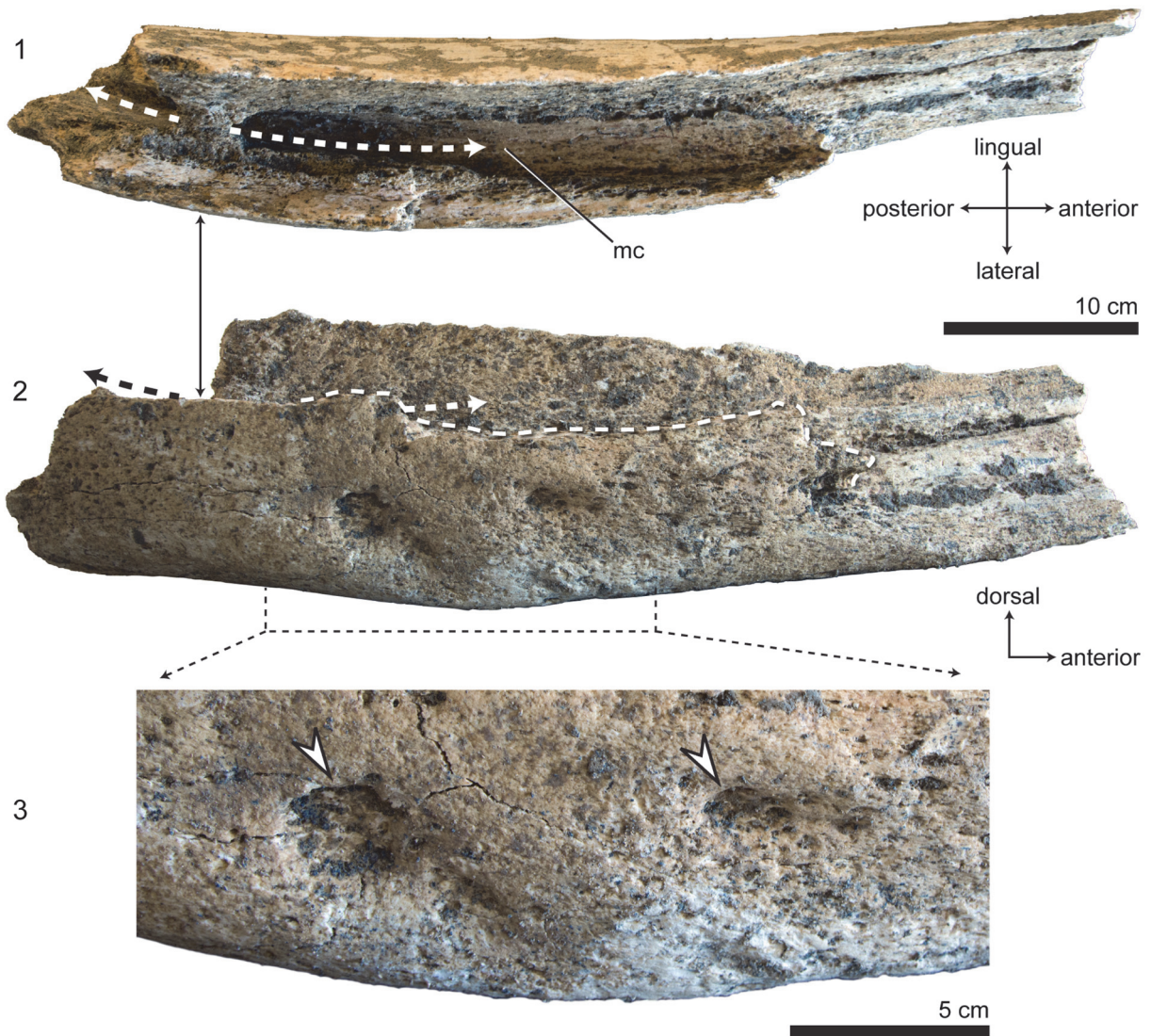


FIGURE 2. Right mandibular corpus (DBUA-F 1079) belonging to a medium-large size Mysticeti. **1**, dorsal view; **2**, lateral view; and **3**, inset magnification of unknown bone modification to the lateral surface (denoted by arrows). Abbreviation “mc” indicates the mandibular canal. Thick broken arrows show passages of the mandibular canal through the fragment.

mented sands (facies 4, Figure 3). These sediments correspond to a beach foreshore (intertidal) facies (Ávila et al., 2015), and they are covered by aeolian dunes and colluvial–alluvial deposits (Figure 3). The specimen was deposited in a north-south direction, perpendicular to the present shoreline, in a subvertical position, and making a gentle slope of $\sim 23^\circ$ with the horizontal.

Description. As preserved, the fragment measures approximately 1.0 m in greatest length and approximately 0.2 m in greatest width. It is broadly cylindrical in presentation, dominated by one major surface that is convex and curved along the length

of the major axis of the fragment; another surface, opposite of the latter one, is more planar, with a more gentle curve, largely paralleling the direction of the former one (Figure 2). The best-preserved end of the fragment shows how both of these surfaces communicate enclosing a canal that extends similarly parallel to the major axis of the fragment. This inner surface of the bone forming this canal is notably smooth and maintains a consistent diameter (~ 3 cm) throughout its length. A small fragment at this best-preserved end, which roofs over this canal, suggests that in life the canal was likely completely enclosed conduit. The more poorly pre-

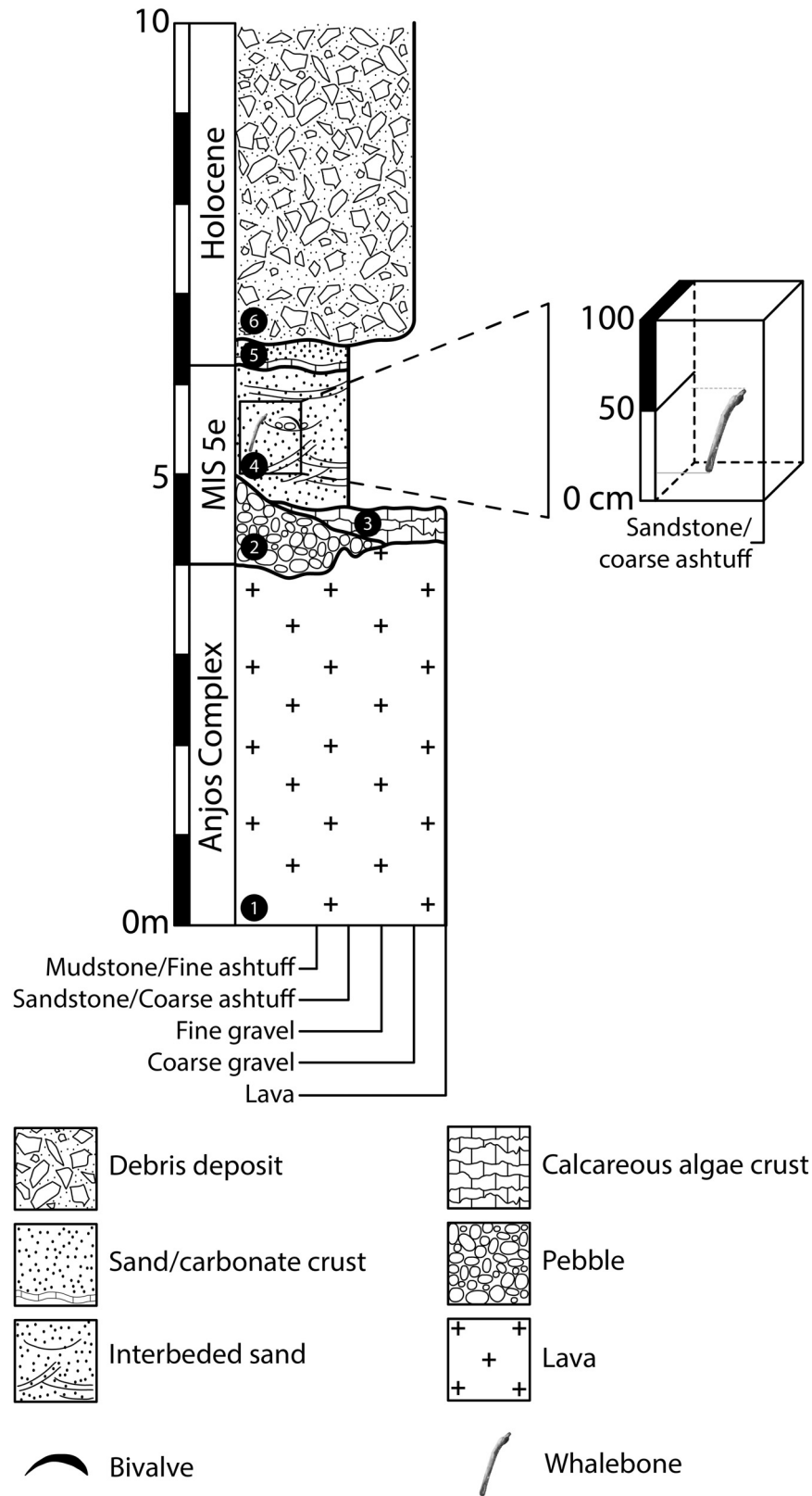


FIGURE 3. Detailed composite stratigraphic column at Praia do Calhau. The numbers depicted in filled circles correspond to facies 1–7, which are described in Ávila et al. (2015).

served end mostly consists of highly eroded fragments that belong to the planar surface. There are two, small notable pit-like depressions on the convex surface.

Remarks. Although DBUA-F 1079 merely consists of a mandibular corpus, some taxonomic precision can be inferred from its preserved morphology and provenance. First, the general complexity and texture of the preserved cortical bone surface and the exposed cancellous bone indicate that it belongs to Mammalia. Its morphology is inconsistent with rib or any other appendicular or axial postcranial material; moreover, both its consistently sub-cylindrical shape and the inclusion of a large canal preclude it from belonging to the rostrum or another part of the cranium. Its preservation in marine deposits on an oceanic island points strongly to it being a marine mammal; its absolute size (~1.0 m in its largest dimension) excludes it belonging to any lineage except for baleen whales (Mysticeti). Thus, on the whole, we argue that DBUA-F 1079 represents a fragment from the mandible of a mysticete.

The mandibular corpus represents a section comprising the approximate mid-length of the element. The maximum width of the fragment is approximately 17 cm; the maximum (and likely sub-complete) dorsoventral height is approximately 18 cm (Figure 2.1-2). The large canal is thus the mandibular canal, which in life would house the nerves and vasculature that pass anteriorly from the mandibular fossa and exit laterally along mental foramina and, in extant mysticetes, also exit dorsally and anteriorly at relictual alveolar foramina (Pyenson et al., 2012, 2013). Given the overall curvature and orientation of the inferred anatomical planes of the specimen, this fragment appears to represent a right mandible: the more planar surface is medial; and the more convex and curved surface is lateral; the best preserved end thus represents the posterior part of the fragment.

The small depressions on the lateral side of the mandible are too large, diffuse, irregular in shape, and too different in size (with respect to one another) to represent mental foramina, which have a clean, pinched aperture (Figure 2.3). The bone modification in DBUA-F 1079 is unknown among other fossil cetaceans. The overall surface geometry does not match any of the categories of bone modification in marine vertebrate fossils (see Boessenecker and Perry, 2011, table 1), including known patterns generated from bites (e.g., punctures, tooth scrapes) or bioerosion (e.g., boring, bioencrustation). We suspect that they represent

some unknown type of bone trauma, parasite or post mortem alteration of the bone surface.

Although DBUA-F 1079 lacks other major morphological features (e.g., coronoid process) that would permit easy and direct identification, based on the general curvature of the mandible, we propose that it does not belong to Eschrichtiidae, which generally exhibits mandibular rami that are straight and not bowed (Noakes et al., 2013); also, the lateral breadth of the fragment is greater than all adult specimens *Eschrichtius robustus* (Pyenson and Goldbogen, unpublished data). Similarly, we exclude Neobalaenidae because the lateral breadth of the fragment far exceeds that for extant *Caperea* (which ranges between 3–4 cm, Pyenson and Goldbogen, unpublished data), and there are no extant or fossil Neobalaenidae from the North Atlantic Ocean (Tsai and Fordyce, 2015). Given the size range and remaining taxonomic groups, we cannot discriminate among the latter possibilities: a medium-large species of Balaenopteridae; Balaenidae; or an extinct lineage of Mysticeti, possibly belonging to a very large member of Cetotheriidae sensu lato (Marx, 2011). We thus conservatively argue for its taxonomic identification as a baleen-bearing mysticete (Chaeomysticeti sensu Marx, 2011), likely within the crown of Mysticeti, but cannot exclude it belonging to an unknown stem lineage. Although both Balaenopteridae and Balaenidae have stratigraphic ranges through MIS 5e, this latter timeframe is younger than the youngest known fossil Cetotheriidae sensu stricto, a Middle Pleistocene occurrence of *Herpetocetus* from California (Boessenecker, 2013). It is not clear if large “cetotheriids” in the same body size as mid-size *Balaenoptera* sp., such as *Pelocetus* (Pyenson and Sponberg, 2011) were alive during the time that this specimen was buried.

DISCUSSION

Large baleen whales are seasonally reported from the Azores in the course of their annual long-distance migrations between high-latitude summer feeding areas and low-latitude oligotrophic wintering grounds (Silva et al., 2014). Sei, fin, and blue whales are commonly seen in early spring and summer in the waters around the Azores, whereas they are rarely seen in late autumn and winter (Silva et al., 2013); the two latter species are reported to feed in the area surrounding the islands (Visser et al., 2011), namely at the Azores Front and at seamounts, where high phytoplankton and zooplankton biomasses have been reported (Fasham et al., 1985; Huskin et al., 2001; Santos

et al., 2013). *Balaenoptera physalus* and *B. borealis* are the most common baleen whales on the waters surrounding the Azores archipelago. In a study that examined the movements and migratory behavior of these baleen whales, Silva et al. (2013) found evidence that most individuals paused their spring migratory journey and stayed around the Azores for a residence time of up to two months.

Although baleen whale strandings are rare events (López et al., 2002; Pyenson et al., 2014), these phenomena have been reported for the Azores. Gonçalves et al. (1992) reported strandings of a newborn calf of a humpback whale (*Megaptera novaeangliae*) in São Miguel Island and of an adult sei whale in the same island. Gonçalves et al. (1996) reviewed the cetaceans stranded in the Azores during a period of 5 years (from 1992 to 1996). From a total of 49 strandings, only four (8.2%) corresponded to baleen whales: two in São Miguel Island, including a common minke whale (*Balaenoptera acutorostrata* de Lacépède, 1804) and a sei whale; a fin whale at Terceira Island; and an unidentified whale at Santa Maria Island (*Balaenoptera* sp.). Necropsis and chemical analyses performed on the carcasses of 12 of the stranded cetaceans concluded natural causes of death (Gonçalves et al., 1996). In March 2013, a 12 m long fin whale stranding was also reported from Pico Island.

Adverse sea conditions in the Azores are common throughout the year and various authors have reported an increase of strandings during storms (Duguay and Wisdorff, 1988; López et al., 1996). Similar conditions existed in the area of the Azores during the last interglacial, as testified by the presence of this mandible of a baleen whale in the Pleistocene (MIS 5e) fossil record of Santa Maria Island. Numerical model experiments implemented by Kaspar et al. (2007) suggested that the North Atlantic storm track was stronger during MIS 5e and Ávila et al. (2015) suggested that the occurrence of tropical cyclones during the last interglacial would be expected to be higher than today, thus increasing the possibilities of cetaceans being stranded on the Azores archipelago. Although it is difficult to evaluate whether the fragmentary mandible can be attributed to a stranding event, the taxonomic scope, geographic provenance, and climate conditions around an oceanic island are all consistent with this hypothesis as a potential source for the cetacean material at the MIS 5e outcrop of Praia do Calhau.

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