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Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru

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ABSTRACT

We report on bite marks incising fossil mammal bones collected from upper Miocene deposits of the Pisco Formation exposed at Aguada de Lomas (southern Peru) and attributed to the giant megatooth shark *Carcharocles megalodon*. The bitten material includes skull remains referred to small-sized baleen whales as well as fragmentary cetacean and pinniped postcrania. These occurrences, the first in their kind from the Southern Hemisphere, significantly expand the still scarce record of bite marks for *C. megalodon*; moreover, for the first time a prey (or scavenging item) of *C. megalodon* is identified at the species level (as *Piscobalaena nana*, a diminutive member of the extinct mysticete family Cetotheriidae). Due to the fragmentary nature of the studied material, the exact origin of the detected marks (i.e., by scavenging or by active predation) cannot be ascertained. Nevertheless, relying on actualistic observations and size-based considerations, we propose that diminutive mysticetes (e.g., cetotheriids) were some of the target prey of adult *C. megalodon*, at least along the coast of present-day Peru. *C. megalodon* is thus here interpreted as an apex predator whose trophic spectrum was focused on relatively small-sized prey. Lastly, we propose a link between the recent collapse of various lineages of diminutive mysticetes (observed around 3 Ma) and the extinction of *C. megalodon* (occurring around the end of the Pliocene).

1. Introduction

The extinct megatooth shark species *Carcharocles megalodon* (Agassiz, 1843) (Elasmobranchii, Lamniformes, Otodontidae) is known by large serrated teeth and vertebrae from Neogene marine and brackish-transitional deposits worldwide, ranging in age from the late early Miocene (Burdigalian) to the late Pliocene (e.g., Cappetta, 2012; Pimiento and Clements, 2014; Carrillo-Briceño et al., 2015, 2016). Reaching an estimated total body length of more than 16 m (Gottfried et al., 1996; Pimiento et al., 2010), *C. megalodon* is widely regarded as an apex predator that likely filled the top trophic levels of the global ocean (e.g., Aguilera et al., 2008; Ehret, 2010). Despite *C. megalodon* being interpreted as a whale-eating predator (e.g., Compagno, 1990; Purdy, 1996; Wroe et al., 2008; Ehret, 2010), and its remains being common in Neogene deposits, little direct evidence for the trophic ecology of this giant shark arose from the fossil record to date. This scarce fossil record includes: (1) several large whale bones (mainly vertebrae and forelimb bones) from the Pliocene Yorktown Formation (USA) bearing bite marks made by very large serrated teeth (Purdy, 1996); (2) one cetacean vertebra probably from the Burdigalian to ?early Langhian Cantaure Formation (Venezuela) pierced by a tooth of *C. megalodon* (Aguilera et al., 2008; Carrillo-Briceño et al., 2016); and (3) one vertebral centrum of a small-sized (ca. 6 m long) whale from the Miocene Chesapeake group of Maryland (USA) presenting a partially healed compression fracture, tentatively attributed to failed predation by *C. megalodon* (Godfrey and Altman, 2005). In this paper, we describe new shark bite marks attributed to *C. megalodon* and affecting cetacean and pinniped bones from the late Miocene deposits of the Pisco Formation. The latter is a shallow-marine sedimentary unit exposed along the southern coast of Peru which has recently yielded multiple clues of trophic interactions between marine vertebrates (Ehret et al., 2009b; Collareta et al., 2015, in press; Lambert et al., 2015) besides a remarkable fossil record of sharks (Alván de la Cruz et al., 2006; Alván de la Cruz, 2008; Ehret et al., 2009a, 2009b, 2012; Altamirano-Sierra, 2012; Takakuwa, 2014; Landini et al., 2017; Collareta et al., in press). To our knowledge, the trace fossils described herein represent the first record

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of *C. megalodon* bite marks from the Southern Hemisphere, and the first instance when a prey (or scavenging item) of *C. megalodon* is identified at the species level (as *Piscobalaena nana*, a small-sized cetotheriid baleen whale). This fossil occurrence stimulates various inferences about the trophic habits of *C. megalodon* and its extinction.

2. Material and methods

2.1. Geographical, geological, and palaeontological context

The Hueso Blanco study area is located in the valley of Aguada de Lomas (indicative geographic coordinates: S 15°28′50″; W 74°48′17″), Lomas area of the Sacaco Basin, where a 287-m-thick succession of upper Miocene beds of the Pisco Formation is exposed (Brand et al., 2011) (Fig. 1). The sediment package exposed at Hueso Blanco (bed LM 10 in Brand et al., 2011) is about 15 m thick and consists mainly of sparsely to moderately bioturbated, well-sorted, fine- to medium-grained sandstones (Electronic supplementary material; Fig. S1).

At Hueso Blanco, marine vertebrate fossil remains are common (pers. obs.), consisting of small-sized mysticetes around 3–4 m in estimated total body length (Cetotheriidae: *Piscobalaena nana*), large-sized mysticetes (Balaenopteroidea indet.), odontocetes (*Phocoenidae*: cf. *Lomacetus* sp.), pinnipeds (*Acrophoca longirostris*, *Piscophoca* sp.), seabirds (*Sula magna*, *Spheniscus* sp.), crocodilians (*Piscogavialis jugaliperforatus*), and aquatic sloths (*Thalassocnus* sp.); remains of bony fish (including cycloid scales attributed to the Pacific pilchard *Sardinops*) are also present. The mammalian fossils generally consist in fragmentary and isolated cranial and postcranial elements, occasionally displaying shark bite marks as tooth scrapes and gouges. Most of these remains, including those here described, lack a precise stratigraphic position; they rolled down from the easily erodible knolls of Hueso Blanco to accumulate at their base.

Brand et al. (2011) argued that the sediment package exposed at Hueso Blanco (featuring the LM 10 marker bed) is roughly correlative with the El Jahuay (ELJ) vertebrate level of de Muizon and DeVries (1985) and de Muizon (1988). In turn, Lambert and de Muizon (2013) reattributed the LM 10 marker bed to the Aguada de Lomas (AGL) vertebrate level, based on faunal and sedimentary similarities (de Muizon and DeVries, 1985; de Muizon, 1988). Based on K/Ar dating of underlying tuff layers, the AGL vertebrate level is considered younger than 7.93 Ma (about 7.5–7.0 Ma) (de Muizon and DeVries, 1985; de Muizon and Bellon, 1986; Lambert and de Muizon, 2013). Finally, $^{87}Sr/^{86}Sr$ analyses on marine mollusc shells bracketed the age of the AGL level between 7.46 Ma and 7.30 Ma (Ehret et al., 2012).

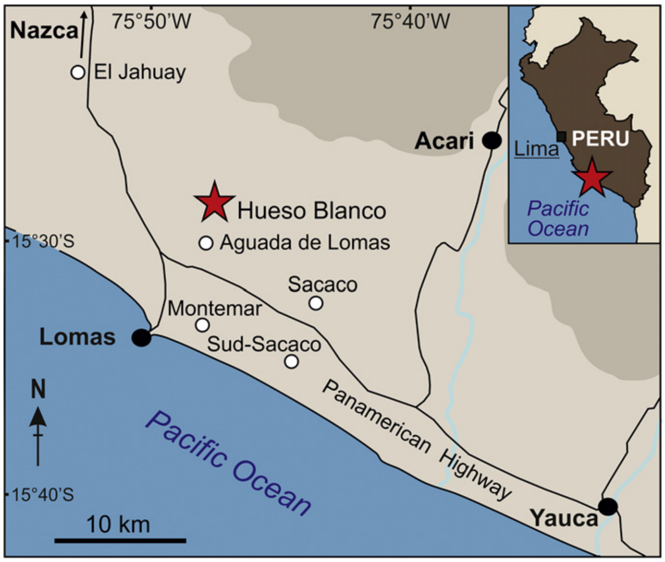

Fig. 1. Geographical position (star) of the site of Hueso Blanco (Aguada de Lomas valley, Sacaco Basin, southern coast of Peru).

Unfortunately, the deposits of the Pisco Formation exposed in the Sacaco Basin suffered decades of heavy exploitation by illegal collectors of fossil shark teeth, so that establishing a pristine fossil elasmobranch assemblage from Hueso Blanco would prove a vexed enterprise. With respect to the AGL vertebrate level, de Muizon and DeVries (1985) recognized a rather scant elasmobranch assemblage consisting of the following taxa: *Carcharocles megalodon*, "*Isurus*" *hastalis* sensu lato (i.e., embracing both *Cosmopolitodus hastalis* and the broad-toothed form *C. plicatilis*), *Isurus* sp. cf. *I. oxyrinchus*, and *Myliobatis* sp. Interestingly, taxa belonging to Carcharhiniformes were not recorded from the AGL vertebrate level by de Muizon and DeVries (1985), whereas they constitute large part of other late Miocene chondrichthyan assemblages of the Pisco Formation (de Muizon and DeVries, 1985; Bianucci et al., 2016; Landini et al., 2017).

2.2. Palaeontological material

In March 2015, we collected various cetacean bones at Hueso Blanco and deposited them in the collection of the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), in Lima. Three of them (MUSM 3239, MUSM 3240, and MUSM 3241) display long serrated bite marks (i.e., grooves in which one margin is 'dotted' by regularly spaced incisions and/or exhibit an inner undulation due to the impact of a denticulated shark tooth). Careful examination of other fossil material from Hueso Blanco kept at the MUSM revealed the presence of two other fossil bones (MUSM 2392 and MUSM 2536) displaying similar bite marks. These five specimens are described in the Results section of this paper.

2.3. Analysis of shark bite marks

We characterized the observed shark bite marks based on a morphological-genetic approach distinguishing five different types of bite marks (all, except the fifth, from Cigala Fulgosi, 1990), each of them deriving from a different type of impact (see list in Table 1).

3. Results

3.1. Identification of the bitten mammalian remains

MUSM 3239 (Figs. 2a–b and S2) is a fragment of a mysticete left mandible belonging to a Cetotheriidae *s.s.*, owing to the presence of an angular process protruding posteriorly beyond the edge of the

Table 1
The five types of shark bite mark recognized in this study, with a synthetic description of the hypothesized producing impact dynamics.

Type of bite mark	Description of the producing impact(s)
Type I	The cutting edge of the tooth impacted the surface of the bone from above downward, thus producing a sub-rectilinear or weakly curved mark.
Type II	The tooth edge dragged in parallel with the dental axis, thus producing a more or less elongated incision.
Type III	The tooth edge dragged, with rectilinear movement, perpendicularly to the dental axis, thus producing a scrape showing several parallel, more or less rectilinear incisions.
Type IV	The tooth edge dragged, with undulatory movement, perpendicularly to the dental axis, thus producing a scrape showing several parallel, distinctly undulate incisions.
Type V	Removal of one or more mm-sized, roughly prismatic or wedge-shaped chips of bone, due to ubiquitous biting or as a result of a single type III or type IV cutting action directed deep into the bone.