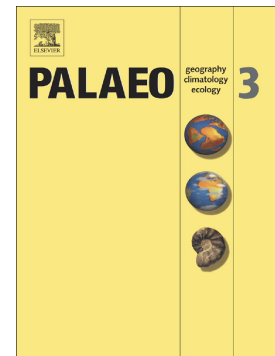


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Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru

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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).

Keywords

Megatooth shark, *Piscobalaena nana*, shark bite marks, predation, scavenging, co-extinction

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,b, 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 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.), crocodylians (*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 Muizon and DeVries (1985) and Muizon (1988). In turn, Lambert and Muizon (2013) reattributed the LM 10 marker bed to the Aguada de Lomas (AGL) vertebrate level, based on faunal and sedimentary

similarities (Muizon and DeVries, 1985; 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) (Muizon and DeVries, 1985; Muizon and Bellon, 1986; Lambert and Muizon, 2013). Finally, $^{87}\text{Sr}/^{86}\text{Sr}$ analyses on marine mollusc shells bracketed the age of the AGL level between 7.46 Ma and 7.30 Ma (Ehret et al., 2012).

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, 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 Muizon and DeVries (1985), whereas they constitute large part of other late Miocene chondrichthyan assemblages of the Pisco Formation (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 mandibular condyle, the latter being oriented obliquely with respect to the long axis of the bone (El Adli et al., 2014; Gol'din et al., 2014). The shape and size of MUSM 3239 are strikingly reminiscent of *Piscobalaena nana*, known from upper Miocene deposits of Peru (Pilleri and Siber, 1989; Bouetel and Muizon, 2006), including the AGL vertebrate level (Bouetel and Muizon, 2006; Lambert and Muizon, 2013) and the beds of the Pisco Formation exposed at Hueso Blanco (pers. obs). In particular, the proportions of the groove for the insertion of the internal pterygoid muscle (running medially and posteriorly between the mandibular condyle and the angular process, Fig. S2b) and the moderate extent of posterior projection of the angular process (Figs. 2a-b and S2a-b), which allow to distinguish *P. nana* from other cetotheriids for whom these features are known, strongly support a positive, unambiguous attribution of MUSM 3239 to *P. nana*. MUSM 3240a,b,c (Figs. 2d and S3) are three fragments of an horizontal ramus of a ?right mysticete mandible also approaching *P. nana* in size and shape (for its roughly D-shaped cross-section). Since the site of Hueso Blanco is rich in remains of *P. nana*, a tentative attribution to this cetotheriid species is here proposed. MUSM 3241 (Figs. 2e, S4, and S5) is a fragmentary rib

belonging to an indeterminate cetacean. MUSM 2392 (Figs. 2c and S6) is a partial right frontal belonging to a small-sized mysticete individual (e.g., a full grown *P. nana* or a juvenile balaenopteroid). Due to poor preservation and absence of diagnostic characters, we refer MUSM 2392 to Mysticeti indet. MUSM 2536 (Figs. 2f-g and S7) is a fragmentary right scapula attributable to a relatively large-sized pinniped close in size and overall morphology to the monachine *Piscophoca pacifica*. As in *P. pacifica*, the supraspinous fossa is remarkably wide and anteriorly expanded, whereas the scapular spine is high and posterodorsally-anteroventrally oriented (Muizon, 1981). However, the anterior margin of the scapula seems more pointed than observed in the holotype of *P. pacifica*, and a sharper crest is present on the anteriormost portion of the medial surface parallel to the anterior margin of the bone. Therefore, we refer MUSM 2536 to cf. *Piscophoca* sp.

3.2 Description of the shark bite marks

A 52-mm-long, clearly serrated mark affects the labial face of the mandible MUSM 3239; it can be classified as due to a type I cutting action. This mark, whose posterior termination cuts the ventrolateral edge of the mandibular condyle, could be composite (i.e., consisting of a pair of aligned and practically adjacent incisions produced by two similarly-directed impacts by the same shark tooth). Dorsal and anterior to this incision, the posteriormost portion of another type I mark is preserved; the two marks form a roughly right angle. On the ventrolateral margin of the mandibular condyle, near and parallel to the posterior termination of the aforementioned type I mark, various short, indistinct gouges can be observed. The ventral portion of MUSM 3239a displays various tooth marks. These marks are short (only one is more than 15 mm long), not clearly denticulated, and in some cases superimposed; they belong to the types I and II. A putative type V mark takes place on the ventral side of the angular process.

The medial surface of the mandible MUSM 3240a presents at least 6 marks. In addition to an

oval tip, five sub-rectilinear marks caused by serrated teeth are present. Not completely preserved, the longest one is more than 60 mm long; it is a type I mark which evolves downwards in a type II mark. The lateral surface of MUSM 3240a does not present bite marks. MUSM 3240b presents four sub-parallel marks affecting the lateral surface of the mandible. The cortical region of the bone is poorly preserved, and the exact terminations of the marks cannot be precisely defined; nevertheless, the marks appear to be denticulated. MUSM 3240c bears four incisions: two of them are short and affect the dorsal edge of the mandible; the remaining two marks, incompletely preserved, are distinctly serrated type I marks.

A distal portion of the rib MUSM 3241 bears more than 20 serrated bite marks distributed on both sides (laterodorsal and medioventral). Two of them are incomplete, slightly S-shaped type I incisions roughly parallel to the edges of the rib, more than 51 mm and more than 46 mm long respectively. The other bite marks are shorter and referable to the types I and II; a distinctly serrated type IV mark is also present.

At least 15 shark bite marks can be observed on the dorsal face of the frontal MUSM 2392; they are oriented roughly parallel to the lateral edge of the bone. Most of them are deep, distinctly denticulated incisions referable to the type I. Partially preserved, the longest of these marks is 54 mm long. A few shallow linear incisions are also present. Some mm-sized chips of bone detached from the dorsal face of MUSM 2392 are most likely due to ubiquitous biting (type V mark). The ventral surface of the supraorbital process of MUSM 2392 bears only a single 48-mm-long eroded mark proceeding from the preorbital process parallel to the lateral edge of the bone.

On the lateral face of the scapula MUSM 2536, about 20 bite marks have been recognized, mostly pertaining to the type I (only two of them are distinctly type II marks). These incisions do not exceed 20 mm in length. They are posteroventrally-anterodorsally oriented and concentrate on convex features such as the prominent scapular spine and, especially, the inflated posterior margin of the blade. As observed also in MUSM 2392, small chips of bone are lacking where tooth

incisions concentrate (type V mark). On the medial face of MUSM 2536, at least 25 bite marks are preserved. Most incisions belong to the type I, although a distinctly serrated type IV scrap has been observed. The bite marks are concentrated on the posterior half of the scapula and do not affect the crest-like eminences located on the anterior portion of the bone; the longest bite mark is 36 mm long. The overall orientation of the bite marks observed on the medial face of MUSM 2536 agrees with orientations observed on the lateral face of the scapula.

3.3 Identification of the biting shark

In our opinion, among the shark taxa represented in the AGL vertebrate level, only *C. megalodon* can be evoked in order to explain the denticulated bite marks found on the mammalian bones here studied. Indeed, other large-sized sharks with serrated teeth have not been detected in the AGL level to date. Among Lamniformes, *Carcharocles chubutensis* is present in the underlying Chilcatay Formation (Alvan de la Cruz et al., 2006), but not in the Pisco Formation; *Carcharodon hubbelli* and *C. carcharias* locally appear in the younger latest Miocene beds of the Sacaco area (Ehret et al., 2012). Large Carcharhiniformes such as *Carcharhinus leucas*, *Galeocerdo* spp., and *Physogaleus contortus* have not been reported from the AGL level to date; moreover, the morphology and size of their teeth could hardly match the geometry and, especially, the length of the longest bite marks observed on the fossil mammal bones described in this paper. Although Neogene teeth of *Cosmopolitodus plicatilis* (= *Carcharodon xiphodon*) occasionally show incipient serration (e.g., Purdy et al., 2001), the size and spatial frequency of denticulation of the best-preserved serrated tooth marks observed on the fossil bones here described are much more compatible with large teeth belonging to adult individuals of *C. megalodon*. For example, both the spatial frequency of denticulation (ca. 7 dots in 5.5 mm) and the shape of the longest mark observed on MUSM 3239a match well those of the tooth of *C. megalodon* MUSM 2096, collected from Cerro Colorado, another locality where late Miocene beds of the Pisco Formation are exposed (Bianucci et al.,

2010a, 2016; Lambert et al., 2010, 2015; Collareta et al., 2015; Gariboldi et al., 2015; Di Celma et al., 2016; Gioncada et al., 2016; Stucchi et al., 2016; Landini et al., 2017). MUSM 2096 is an upper tooth (second anterior to anterolateral), which presents 12-15 serrae per cm; it is 140 mm high, and as such, it belonged to a physically mature individual of *C. megalodon*. Following Pimiento et al. (2010), we applied the equation proposed by Shimada (2003) for *Carcharodon carcharias* in order to estimate the total body length of the *C. megalodon* individual which bore the tooth MUSM 2096, obtaining a value of 12.8 m; a slightly larger estimate (13.2 m) was obtained by applying the linear regression of Gottfried et al. (1996). Although indicative, such values match the range of body sizes typical of adult *C. megalodon* (i.e., total length greater than 10.5 m, Pimiento et al., 2010).

4. Discussion

4.1 Active predation or scavenging?

Except for a few cases in which a shark attack interpretation is favoured due to bite marks preserved on almost complete prey skeletons (Cigala Fulgosi, 1990; Bianucci et al., 2010b; Bianucci and Gingerich, 2011) or to bone healing around a tooth-related wound (Kallal et al., 2012), it is virtually impossible to discriminate between active predation and scavenging when dealing with fossil specimens. Considered a modern analogous of *C. megalodon* (Purdy, 1996; Ehret, 2010; Pimiento et al., 2010), the smaller Recent great white shark *Carcharodon carcharias* commonly preys on various pinniped targets but never attacks healthy, fully adult baleen whales: except for the pygmy right whale *Caperea marginata*, adult individuals of all extant mysticete taxa largely surpass in size adult great white sharks; consequently, adult baleen whales are not suitable for predation by *C. carcharias* (Long and Jones, 1996). In turn, Recent great white sharks are known to ordinarily scavenge on large mysticete carcasses (Carey et al., 1982; Long and Jones, 1996; Curtis et al., 2006; Dicken et al., 2008). During scavenging events, great white sharks generally show an initial

preference for foraging on the tail of the baleen whale before proceeding to blubber-rich regions of the body of the cetacean (Fallows et al., 2013). Nevertheless, great white sharks rarely scavenge on significantly smaller targets as seals or diminutive odontocetes, thus exhibiting a preference for huge, fat-rich carcasses; in particular, adult individuals of *C. carcharias* seem to spend a large amount of time looking for large whale carrion (Fallows et al., 2013). The shark that bit the cetotheriid individual represented by the mandible MUSM 3239 was approximately three to four times longer than the bitten baleen whale; this size ratio is similar to that between an adult individual of *C. carcharias* and various of its target prey (e.g., some fur seals), thus suggesting that a predator-prey relationship between *C. megalodon* and *P. nana* is not only overly plausible but also probable. Although scavenging could not be definitively ruled out, for the rest of our discussion we will consider that the bite marks found on the specimens here studied resulted from active predation events.

Since no extant shark taxon is known as a predator of baleen whales, the possibility that *C. megalodon* actively preyed on *P. nana* deserves further consideration. Nowadays, *C. carcharias* hunts a number of small toothed whale species, although such predation events seem infrequent (Long and Jones, 1996). In these cases, the shark generally attacks the dolphin from above, below, or behind, thus biting the rear part or the dorsum of the prey, without affecting the cranial region (Long and Jones, 1996); after one or a few deadly bites, the shark waits for the death of the prey prior to eating its carcass (Tricas and McCosker, 1984; Long et al., 1996). The bite marks observed on MUSM 2392 (a partial frontal), MUSM 3239, and MUSM 3240 (both fragmentary mandibles) suggest another dynamic of attack, with the predator targeting also (or predominantly) the anterior part of the body of the prey.

Interestingly, the strategies used by modern large sharks to attack small, echolocating toothed whales are believed to have developed to avoid detection by both the lateral visual field and the anteriorly directed biosonar of the prey (Long and Jones, 1996; Bianucci et al., 2010b). Predation

patterns of *C. carcharias* on non-echolocating marine mammals (i.e., pinnipeds) inferred from wounded carcasses contrast markedly in the fact that bite marks are more evenly distributed all across the body, and could even concentrate on the head region in the case of true seals, thus possibly suggesting that great white sharks focus on the anterior part of the body when attacking these prey (Long et al., 1996). Noteworthy, Fahlke (2012) proposed that the giant Eocene basilosaurid *Basilosaurus isis* used to prey on the smaller basilosaurid *Dorudon atrox* by attacking the head (note that both *D. atrox* and *B. isis* were non-echolocating archaic cetaceans). Therefore, the possibility that ancient large sharks feeding on mysticetes (which never evolved an echolocation system) attacked the anterior part of the body (thus biting also the head region of the prey) should be taken into account. Nowadays, only the killer whale (*Orcinus orca*) actively forages on baleen whales; although also biting the rear body of mysticetes (Mehta et al., 2007), this predator focuses its attacks on the head region (Jefferson et al., 1991, and references therein). According to Silber and Newcomer (1990), such an attack dynamic could reflect the predator's need for avoiding the danger of being hit by the powerful tail of the mysticete prey. Therefore, a predatory behaviour somewhat similar to that of the great white shark attacking seals may tentatively be proposed for *C. megalodon* and other ancient large sharks preying upon small mysticetes (this paper; Deméré and Cerutti, 1982, Ehret et al., 2009b, 2012) (Fig. 3).

The presence of tooth marks attributed to *C. megalodon* on the pinniped scapula MUSM 2536 strongly evokes the modern predatory behaviour of the great white shark attacking seals. Based on the body length estimate for *Piscophoca pacifica* (Valenzuela-Toro et al., 2015), the seal individual represented by MUSM 2536 should have been relatively large (presumably approaching the size of the Steller sea lion *Eumetopias jubatus*), but still shorter than mature individuals of *P. nana*. As such, it represented a potential prey for both adults and subadults of *C. megalodon*.

4.2 On the trophic spectrum and dietary preferences of *C. megalodon*

The fossil remains reported here suggest that, at least in the late Miocene of southern Peru, adult individuals of *C. megalodon* foraged on small-sized baleen whales (i.e., cetotheriids) and smaller marine mammals in coastal areas where these food items were abundant. During late Miocene times, the area of Aguada de Lomas was most likely inhabited by a high biomass of small-sized marine mammals, which attracted large sharks able to actively prey on them; a similar ecological pattern is currently observed in coastal “hot spots” where great white sharks (*C. carcharias*) aggregate to feed around pinniped colonies (Pimiento et al., 2010). Interestingly, the rather poorly diversified chondrichthyan assemblage reported by Muizon and DeVries (1985) from the AGL vertebrate level is strikingly similar to that recognized in a shark tooth-bearing interval (ST-up1 horizon of Landini et al., 2017) of the Pisco Formation exposed at Cerro Colorado; the latter assemblage was recently interpreted as referable to a transient community (or vagrant individuals) of littoral apex-predators closely linked to the local presence of a pinniped colony (Landini et al., 2017).

Nowadays, the great white shark is a highly generalist predator (reported prey include other sharks, bony fish, various odontocete cetaceans and pinnipeds, sea turtles, seabirds, cephalopods, crustaceans, and molluscs) showing a predilection for small, fat-rich marine mammals (e.g., fur seals) (Compagno, 1984). The feeding habits of *C. carcharias* vary widely with ontogenetic growth in body size and from site to site, whereas scavenging on large mysticete carcasses is believed to contribute to a major portion of the diet of adults (Carey et al., 1982; Dicken, 2008; Fallows et al., 2013). Allowing for the obvious dimensional differences, a similar pattern could be proposed for the larger *C. megalodon*. According to recent works (Carrillo-Briceño et al., 2015; Landini et al., 2017), the trophic spectrum of this extinct megatooth shark may have featured a quite broad diversity of food items, i.e., bony and cartilaginous fish, marine mammals (including sirenians and euryhaline cetaceans besides pinnipeds and salt water cetaceans), seabirds, marine reptiles (including turtles and crocodiles), cephalopods, molluscs, crustaceans, and other invertebrates. Juveniles of *C.*

megalodon were likely more purely piscivorous than their adult conspecifics (e.g., Landini et al., 2017); nevertheless, the target prey of adult individuals of *C. megalodon* may still have been the highly energetic small- to medium-sized mysticetes (e.g., cetotheriids, typically 2.5 m to 7 m long), as evoked earlier (Lambert et al., 2010). As reported above, the modern great white shark only attacks cetacean individuals that are considerably smaller than him, and never actively preys upon animals from its own size class (Long and Jones, 1996). Applying this simple field observation to *C. megalodon*, it seems overly unlikely that *C. megalodon* preyed on a regular basis upon large baleen whales (e.g., adult balaenopteroids) that would have approached the size of a physically mature individual of *C. megalodon*; nevertheless, large mysticete carcasses were most likely part of the diet of *C. megalodon*.

4.3 Mysticetes and megatooth sharks: size-driven co-evolution to co-extinction?

For a long time, the evolution of the megatooth shark lineage and the timing and mode of its extinction have been discussed in relation to global changes in the oceanographic system and/or in the marine mammal biota (e.g., Purdy, 1996; Ehret, 2010; Pimiento and Clements, 2014; Pimiento et al., 2016). Ehret (2010) provided evidence that the species included in the genus *Charcharocles*, which embraces the so-called megatooth sharks (except for *Otodus obliquus* and, possibly, the newly described *Megalolamna paradoxodon* Shimada et al., in press), are characterized by a trend of body size increase through geologic time, peaking in the most recent and largest species of the lineage, *C. megalodon*. Such a trend was interpreted by Ehret (2010) as related to the diversity increase of modern cetaceans (Neoceti), the putative target prey of adult individuals of *Charcharocles* spp. Gigantism appeared in the mysticete lineage during the middle or late Miocene (Lambert et al., 2010) and became the dominant baleen whale size habit at the end of the Pliocene (around 3 Ma), coinciding with the onset of the Northern Hemisphere glaciation (Marx and Fordyce, 2015). The final establishment of modern mysticete gigantism is also contemporaneous

with the decline or disappearance of many forms of small-sized mysticetes (e.g., most cetotheriids and several small balaenids and balaenopterids): this event was possibly due to repeated and rapid changes of shelf environments (likely impacting smaller neritic species more than larger pelagic forms) and to the setup of high-productivity conditions at high latitudes (causing an increased need for long-distance migrations between the breeding and feeding grounds) (Marx and Fordyce, 2015). By analysing the modifications of the geographical distribution and global abundance of *C. megalodon* during the Neogene, Pimiento et al. (2016) argued that the range of this shark species suffered a strong reduction in the Pliocene; such a decline roughly coincides with the above reported drop in the diversity of baleen whales and the rise of new competitors (e.g., large raptorial odontocetes), thus suggesting that the main driver of the extinction of *C. megalodon* could be searched among these biotic factors rather than in direct thermal limitations (as supported instead by Gottfried et al. (1996) and Purdy (1996) among others). Interestingly, the fossil record from Hueso Blanco reported here suggests that small-sized mysticetes made a significant part of the trophic spectrum of adult *C. megalodon*. Therefore, since *C. megalodon* is believed to have gone extinct at the end of the Pliocene (ca. 2.6 Ma; Pimiento and Clements, 2014; Pimiento et al., 2016), the disappearance of the last giant-toothed shark could have been triggered by the decline and fall of several lineages of small- to medium-sized mysticetes (mostly inhabiting coastal upwelling-influenced waters of warm to temperate oceans) in favour of modern, gigantic baleen whales (mostly seasonally migrating to higher latitude cold waters) (Fig. 4).

5. Conclusions

Bite marks attributed to the megatooth shark *Carcharocles megalodon* have been described on fossil cetacean and pinniped bones collected from upper Miocene (about 7.5-7 Ma) deposits of the Pisco Formation exposed at Hueso Blanco (Aguada de Lomas valley, Sacaco basin, southern Peru).

One of these bitten bones has been determined as a partial mandible of a small-sized cetotheriid (*Piscobalaena nana*) which was consumed by a mature individual of *C. megalodon*; the other bitten mammal bones here described consist of a fragmentary mysticete mandible, a partial mysticete frontal, an indeterminate cetacean rib, and a pinniped scapula. These occurrences, the first in their kind from the Southern Hemisphere, significantly expand the fossil record of bite marks of *C. megalodon* worldwide and permits for the first time the identification at the specific level of a prey of this megatooth shark. Based on the preserved material, it was not possible to ascertain if the studied bite marks were due to scavenging or to active predation. Nevertheless, based on actualistic observations and size-based considerations, we proposed that small-sized mysticetes (e.g., cetotheriids) could have been one of the target prey of adult *C. megalodon*. A predatory behaviour somewhat similar to that of the great white shark attacking seals may be hypothesized for *C. megalodon* preying upon small mysticetes. We proposed that *C. megalodon* was an apex predator whose trophic spectrum was still focused on small-sized baleen whales. It is therefore noteworthy to observe that the extinction of *C. megalodon* (occurring around the Pliocene-Pleistocene transition) roughly coincides with the collapse of various lineages of small-sized mysticetes, thus possibly evoking a process of co-extinction of prey and predator.

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Table captions

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

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Figure captions

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

Fig. 2. Fossil mammalian bones displaying large serrated shark bite marks found at Hueso Blanco, with explanatory line drawings. (a) MUSM 3239 in lateral view. (b) Correspondence between the longest bite marks observed on MUSM 3239 and the large tooth of *Carcharocles megalodon* MUSM 2096. (c) MUSM 2392. (d) MUSM 3240. (e) MUSM 3241. (f, g) MUSM 2536. Note that bite marks affecting the same bone (e.g., those portrayed in (c), (e), and (g)) are often subparallel and display the same orientation of the serrated margin; this fact possibly suggests that the observed marks originated from few, similarly-directed bites.

Fig. 3. Life reconstruction of an adult of *Carcharocles megalodon* preying on an individual of *Piscobalaena nana* occupied in foraging on a school of pilchards (*Sardinops* sp. cf. *S. sagax*) along the coast of present-day Peru during the late Miocene (illustration by Alberto Gennari).

Fig. 4. Box-and-whiskers plots showing the size of mysticete taxa (expressed both as bizygomatic width, and total body length calculated according to Lambert et al., 2010) for each stage against time (expressed in million years ago). The minimal stratigraphical range of *Carcharocles megalodon* (late early Miocene to Pliocene) is reported. The red line corresponds to the estimated size of the early late Miocene (Tortonian) bitten specimen of *Piscobalaena nana* MUSM 3239. Pliocene and Quaternary (Recent) are considered as single time intervals. Abbreviations: Rupel., Rupelian; Chatt., Chattian; Aquit., Aquitanian; Burdig., Burdigalian; Lang., Langhian; Serrav., Serravallian; Torton., Tortonian; Messi., Messinian; Plio., Pliocene; Rece., Quaternary (Recent).



Fig. 1

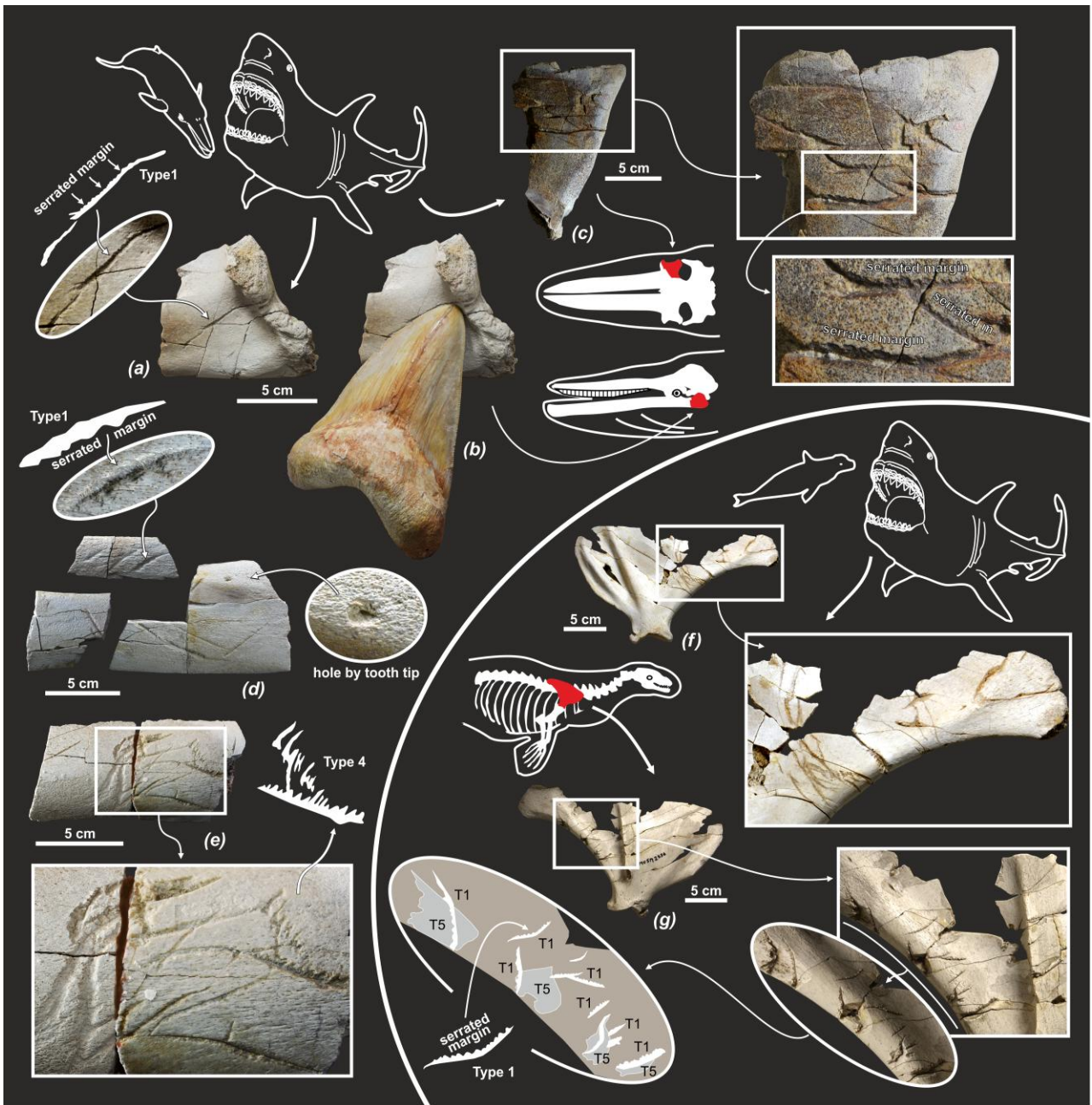


Fig. 2



Fig. 3

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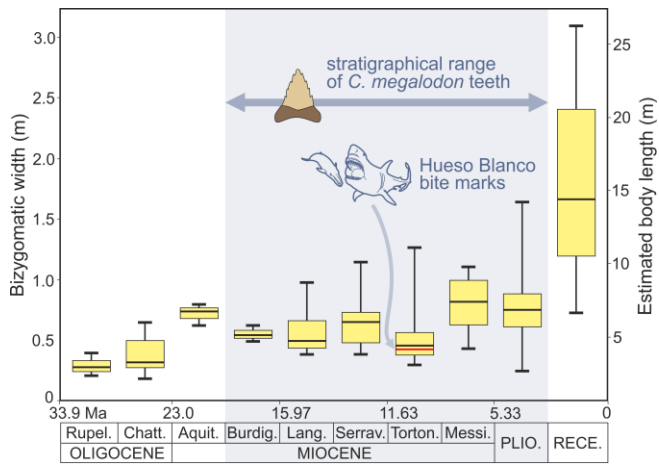


Fig. 4

<i>Type of bite mark</i>	<i>Description of the producing impact(s)</i>
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

Table 1

Graphical abstract



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Highlights

- 1) We report on shark bite marks affecting late Miocene marine mammal bones of Peru
- 2) The bite marks are referred to the extinct giant shark species *Carcharocles megalodon*
- 3) The bitten items include small mysticetes (e.g., *Piscobalaena nana*) and pinnipeds
- 4) The trophic spectrum of *C. megalodon* could have been focused on relatively small prey
- 5) We support a new ecological hypothesis about the extinction of *C. megalodon*

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