

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

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21 **Abstract**

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

37

38 **Keywords**

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

40

41 **1. Introduction**

42

43 The extinct megatooth shark species *Carcharocles megalodon* (Agassiz, 1843) (Elasmobranchii,
44 Lamniformes, Otodontidae) is known by large serrated teeth and vertebrae from Neogene marine
45 and brackish-transitional deposits worldwide, ranging in age from the late early Miocene

46 (Burdigalian) to the late Pliocene (e.g., Cappetta, 2012; Pimiento and Clements, 2014; Carrillo-
47 Briceño et al., 2015, 2016). Reaching an estimated total body length of more than 16 m (Gottfried et
48 al., 1996; Pimiento et al., 2010), *C. megalodon* is widely regarded as an apex predator that likely
49 filled the top trophic levels of the global ocean (e.g., Aguilera et al., 2008; Ehret, 2010). Despite *C.*
50 *megalodon* being interpreted as a whale-eating predator (e.g., Compagno, 1990; Purdy, 1996; Wroe
51 et al., 2008; Ehret, 2010), and its remains being common in Neogene deposits, little direct evidence
52 for the trophic ecology of this giant shark arose from the fossil record to date. This scarce fossil
53 record includes: (1) several large whale bones (mainly vertebrae and forelimb bones) from the
54 Pliocene Yorktown Formation (USA) bearing bite marks made by very large serrated teeth (Purdy,
55 1996); (2) one cetacean vertebra probably from the Burdigalian to ?early Langhian Cantaure
56 Formation (Venezuela) pierced by a tooth of *C. megalodon* (Aguilera et al., 2008; Carrillo-Briceño
57 et al., 2016); and (3) one vertebral centrum of a small-sized (ca. 6 m long) whale from the Miocene
58 Chesapeake group of Maryland (USA) presenting a partially healed compression fracture,
59 tentatively attributed to failed predation by *C. megalodon* (Godfrey and Altman, 2005). In this
60 paper, we describe new shark bite marks attributed to *C. megalodon* and affecting cetacean and
61 pinniped bones from the late Miocene deposits of the Pisco Formation. The latter is a shallow-
62 marine sedimentary unit exposed along the southern coast of Peru which has recently yielded
63 multiple clues of trophic interactions between marine vertebrates (Ehret et al., 2009b; Collareta et
64 al., 2015, in press; Lambert et al., 2015) besides a remarkable fossil record of sharks (Alván de la
65 Cruz et al., 2006; Alván de la Cruz, 2008; Ehret et al., 2009a,b, 2012; Altamirano-Sierra, 2012;
66 Takakuwa, 2014; Landini et al., 2017; Collareta et al., in press). To our knowledge, the trace fossils
67 described herein represent the first record of *C. megalodon* bite marks from the Southern
68 Hemisphere, and the first instance when a prey (or scavenging item) of *C. megalodon* is identified
69 at the species level (as *Piscobalaena nana*, a small-sized cetotheriid baleen whale). This fossil
70 occurrence stimulates various inferences about the trophic habits of *C. megalodon* and its

71 extinction.

72

73 **2. Material and methods**

74

75 **2.1 Geographical, geological, and palaeontological context**

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

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

92 Brand et al. (2011) argued that the sediment package exposed at Hueso Blanco (featuring the LM
93 10 marker bed) is roughly correlative with the El Jahuay (ELJ) vertebrate level of Muizon and
94 DeVries (1985) and Muizon (1988). In turn, Lambert and Muizon (2013) reattributed the LM 10
95 marker bed to the Aguada de Lomas (AGL) vertebrate level, based on faunal and sedimentary

96 similarities (Muizon and DeVries, 1985; Muizon, 1988). Based on K/Ar dating of underlying tuff
97 layers, the AGL vertebrate level is considered younger than 7.93 Ma (about 7.5-7.0 Ma) (Muizon
98 and DeVries, 1985; Muizon and Bellon, 1986; Lambert and Muizon, 2013). Finally, $^{87}\text{Sr}/^{86}\text{Sr}$
99 analyses on marine mollusc shells bracketed the age of the AGL level between 7.46 Ma and 7.30
100 Ma (Ehret et al., 2012).

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

111

112 **2.2 Palaeontological material**

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

121

122 **2.3 Analysis of shark bite marks**

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

126

127 **3. Results**

128

129 **3.1 Identification of the bitten mammalian remains**

130 MUSM 3239 (Figs. 2a-b and S2) is a fragment of a mysticete left mandible belonging to a
131 Cetotheriidae *s.s.*, owing to the presence of an angular process protruding posteriorly beyond the
132 edge of the mandibular condyle, the latter being oriented obliquely with respect to the long axis of
133 the bone (El Adli et al., 2014; Gol'din et al., 2014). The shape and size of MUSM 3239 are
134 strikingly reminiscent of *Piscobalaena nana*, known from upper Miocene deposits of Peru (Pilleri
135 and Siber, 1989; Bouetel and Muizon, 2006), including the AGL vertebrate level (Bouetel and
136 Muizon, 2006; Lambert and Muizon, 2013) and the beds of the Pisco Formation exposed at Hueso
137 Blanco (pers. obs). In particular, the proportions of the groove for the insertion of the internal
138 pterygoid muscle (running medially and posteriorly between the mandibular condyle and the
139 angular process, Fig. S2b) and the moderate extent of posterior projection of the angular process
140 (Figs. 2a-b and S2a-b), which allow to distinguish *P. nana* from other cetotheriids for whom these
141 features are known, strongly support a positive, unambiguous attribution of MUSM 3239 to *P.*
142 *nana*. MUSM 3240a,b,c (Figs. 2d and S3) are three fragments of an horizontal ramus of a ?right
143 mysticete mandible also approaching *P. nana* in size and shape (for its roughly D-shaped cross-
144 section). Since the site of Hueso Blanco is rich in remains of *P. nana*, a tentative attribution to this
145 cetotheriid species is here proposed. MUSM 3241 (Figs. 2e, S4, and S5) is a fragmentary rib

146 belonging to an indeterminate cetacean. MUSM 2392 (Figs. 2c and S6) is a partial right frontal
147 belonging to a small-sized mysticete individual (e.g., a full grown *P. nana* or a juvenile
148 balaenopteroid). Due to poor preservation and absence of diagnostic characters, we refer MUSM
149 2392 to Mysticeti indet. MUSM 2536 (Figs. 2f-g and S7) is a fragmentary right scapula attributable
150 to a relatively large-sized pinniped close in size and overall morphology to the monachine
151 *Piscophoca pacifica*. As in *P. pacifica*, the supraspinous fossa is remarkably wide and anteriorly
152 expanded, whereas the scapular spine is high and posterodorsally-anteroventrally oriented (Muizon,
153 1981). However, the anterior margin of the scapula seems more pointed than observed in the
154 holotype of *P. pacifica*, and a sharper crest is present on the anteriormost portion of the medial
155 surface parallel to the anterior margin of the bone. Therefore, we refer MUSM 2536 to cf.
156 *Piscophoca* sp.

157

158 **3.2 Description of the shark bite marks**

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

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

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

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

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

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

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

202

203 **3.3 Identification of the biting shark**

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

221 (Bianucci et al., 2010a, 2016; Lambert et al., 2010, 2015; Collareta et al., 2015; Gariboldi et al.,
222 2015; Di Celma et al., 2016; Gioncada et al., 2016; Stucchi et al., 2016; Landini et al., 2017).
223 MUSM 2096 is an upper tooth (second anterior to anterolateral), which presents 12-15 serrae per
224 cm; it is 140 mm high, and as such, it belonged to a physically mature individual of *C. megalodon*.
225 Following Pimiento et al. (2010), we applied the equation proposed by Shimada (2003) for
226 *Carcharodon carcharias* in order to estimate the total body length of the *C. megalodon* individual
227 which bore the tooth MUSM 2096, obtaining a value of 12.8 m; a slightly larger estimate (13.2 m)
228 was obtained by applying the linear regression of Gottfried et al. (1996). Although indicative, such
229 values match the range of body sizes typical of adult *C. megalodon* (i.e., total length greater than
230 10.5 m, Pimiento et al., 2010).

231

232 **4. Discussion**

233

234 **4.1 Active predation or scavenging?**

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

246 Dicken et al., 2008). During scavenging events, great white sharks generally show an initial
247 preference for foraging on the tail of the baleen whale before proceeding to blubber-rich regions of
248 the body of the cetacean (Fallows et al., 2013). Nevertheless, great white sharks rarely scavenge on
249 significantly smaller targets as seals or diminutive odontocetes, thus exhibiting a preference for
250 huge, fat-rich carcasses; in particular, adult individuals of *C. carcharias* seem to spend a large
251 amount of time looking for large whale carrion (Fallows et al., 2013). The shark that bit the
252 cetotheriid individual represented by the mandible MUSM 3239 was approximately three to four
253 times longer than the bitten baleen whale; this size ratio is similar to that between an adult
254 individual of *C. carcharias* and various of its target prey (e.g., some fur seals), thus suggesting that
255 a predator-prey relationship between *C. megalodon* and *P. nana* is not only overly plausible but also
256 probable. Although scavenging could not be definitively ruled out, for the rest of our discussion we
257 will consider that the bite marks found on the specimens here studied resulted from active predation
258 events.

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

269 Interestingly, the strategies used by modern large sharks to attack small, echolocating toothed
270 whales are believed to have developed to avoid detection by both the lateral visual field and the

271 anteriorly directed biosonar of the prey (Long and Jones, 1996; Bianucci et al., 2010b). Predation
272 patterns of *C. carcharias* on non-echolocating marine mammals (i.e., pinnipeds) inferred from
273 wounded carcasses contrast markedly in the fact that bite marks are more evenly distributed all
274 across the body, and could even concentrate on the head region in the case of true seals, thus
275 possibly suggesting that great white sharks focus on the anterior part of the body when attacking
276 these prey (Long et al., 1996). Noteworthy, Fahlke (2012) proposed that the giant Eocene
277 basilosaurid *Basilosaurus isis* used to prey on the smaller basilosaurid *Dorudon atrox* by attacking
278 the head (note that both *D. atrox* and *B. isis* were non-echolocating archaic cetaceans). Therefore,
279 the possibility that ancient large sharks feeding on mysticetes (which never evolved an echolocation
280 system) attacked the anterior part of the body (thus biting also the head region of the prey) should
281 be taken into account. Nowadays, only the killer whale (*Orcinus orca*) actively forages on baleen
282 whales; although also biting the rear body of mysticetes (Mehta et al., 2007), this predator focuses
283 its attacks on the head region (Jefferson et al., 1991, and references therein). According to Silber
284 and Newcomer (1990), such an attack dynamic could reflect the predator's need for avoiding the
285 danger of being hit by the powerful tail of the mysticete prey. Therefore, a predatory behaviour
286 somewhat similar to that of the great white shark attacking seals may tentatively be proposed for *C.*
287 *megalodon* and other ancient large sharks preying upon small mysticetes (this paper; Deméré and
288 Cerutti, 1982, Ehret et al., 2009b, 2012) (Fig. 3).

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

295

296 **4.2 On the trophic spectrum and dietary preferences of *C. megalodon***

297 The fossil remains reported here suggest that, at least in the late Miocene of southern Peru, adult
298 individuals of *C. megalodon* foraged on small-sized baleen whales (i.e., cetotheriids) and smaller
299 marine mammals in coastal areas where these food items were abundant. During late Miocene
300 times, the area of Aguada de Lomas was most likely inhabited by a high biomass of small-sized
301 marine mammals, which attracted large sharks able to actively prey on them; a similar ecological
302 pattern is currently observed in coastal “hot spots” where great white sharks (*C. carcharias*)
303 aggregate to feed around pinniped colonies (Pimiento et al., 2010). Interestingly, the rather poorly
304 diversified chondrichthyan assemblage reported by Muizon and DeVries (1985) from the AGL
305 vertebrate level is strikingly similar to that recognized in a shark tooth-bearing interval (ST-up1
306 horizon of Landini et al., 2017) of the Pisco Formation exposed at Cerro Colorado; the latter
307 assemblage was recently interpreted as referable to a transient community (or vagrant individuals)
308 of littoral apex-predators closely linked to the local presence of a pinniped colony (Landini et al.,
309 2017).

310 Nowadays, the great white shark is a highly generalist predator (reported prey include other
311 sharks, bony fish, various odontocete cetaceans and pinnipeds, sea turtles, seabirds, cephalopods,
312 crustaceans, and molluscs) showing a predilection for small, fat-rich marine mammals (e.g., fur
313 seals) (Compagno, 1984). The feeding habits of *C. carcharias* vary widely with ontogenetic growth
314 in body size and from site to site, whereas scavenging on large mysticete carcasses is believed to
315 contribute to a major portion of the diet of adults (Carey et al., 1982; Dicken, 2008; Fallows et al.,
316 2013). Allowing for the obvious dimensional differences, a similar pattern could be proposed for the
317 larger *C. megalodon*. According to recent works (Carrillo-Briceño et al., 2015; Landini et al., 2017),
318 the trophic spectrum of this extinct megatooth shark may have featured a quite broad diversity of
319 food items, i.e., bony and cartilaginous fish, marine mammals (including sirenians and euryhaline
320 cetaceans besides pinnipeds and salt water cetaceans), seabirds, marine reptiles (including turtles

321 and crocodiles), cephalopods, molluscs, crustaceans, and other invertebrates. Juveniles of *C.*
322 *megalodon* were likely more purely piscivorous than their adult conspecifics (e.g., Landini et al.,
323 2017); nevertheless, the target prey of adult individuals of *C. megalodon* may still have been the
324 highly energetic small- to medium-sized mysticetes (e.g., cetotheriids, typically 2.5 m to 7 m long),
325 as evoked earlier (Lambert et al., 2010). As reported above, the modern great white shark only
326 attacks cetacean individuals that are considerably smaller than him, and never actively preys upon
327 animals from its own size class (Long and Jones, 1996). Applying this simple field observation to
328 *C. megalodon*, it seems overly unlikely that *C. megalodon* preyed on a regular basis upon large
329 baleen whales (e.g., adult balaenopteroids) that would have approached the size of a physically
330 mature individual of *C. megalodon*; nevertheless, large mysticete carcasses were most likely part of
331 the diet of *C. megalodon*.

332

333 **4.3 Mysticetes and megatooth sharks: size-driven co-evolution to co-extinction?**

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

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

366

367 **5. Conclusions**

368

369 Bite marks attributed to the megatooth shark *Carcharocles megalodon* have been described on
370 fossil cetacean and pinniped bones collected from upper Miocene (about 7.5-7 Ma) deposits of the

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

388

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399

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585 **Table caption**

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

588 **Figure captions**

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

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

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

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

609 Fig. 1.

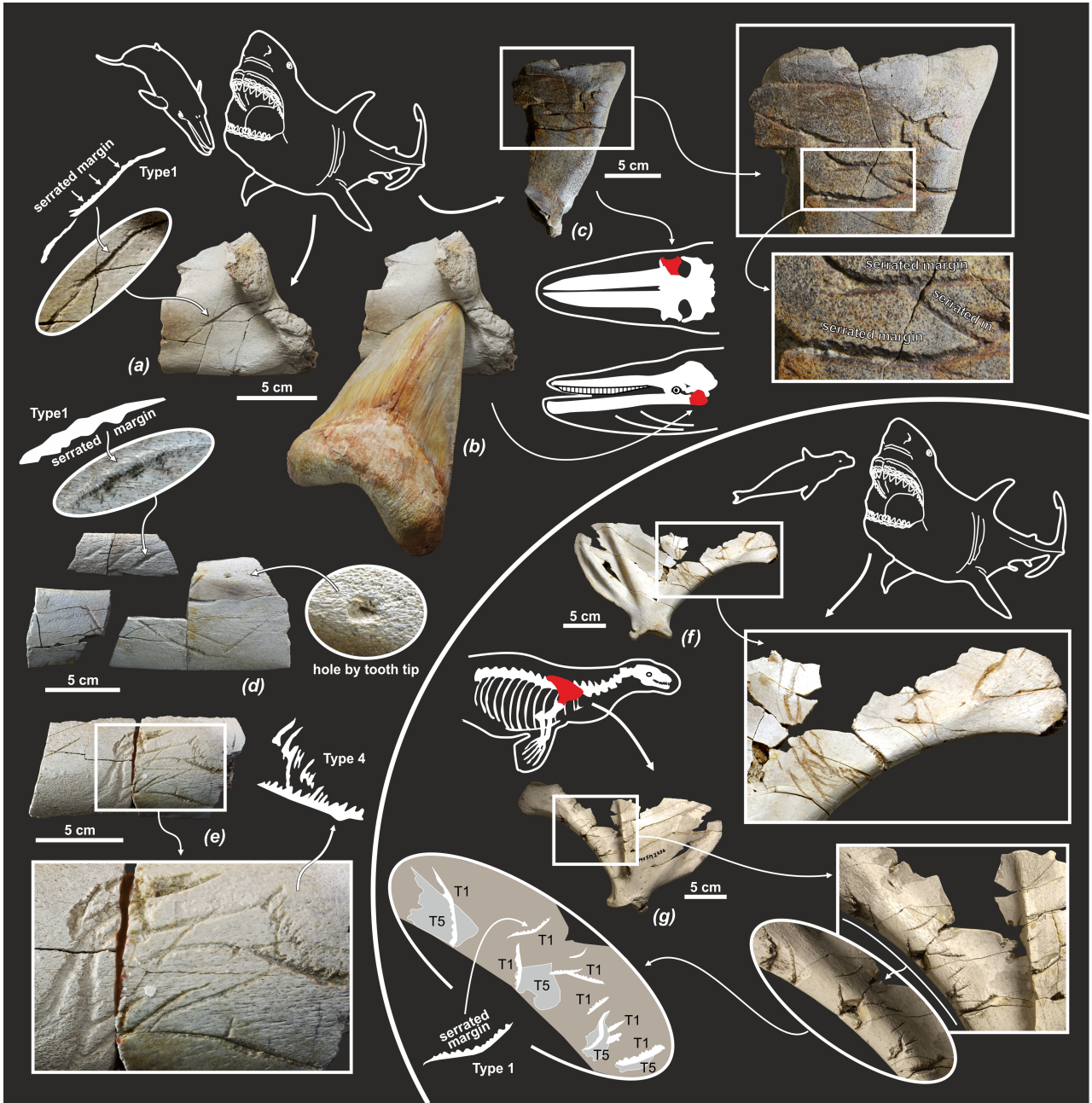
610



612 Fig. 2.

613

614



615 **Fig. 3.**

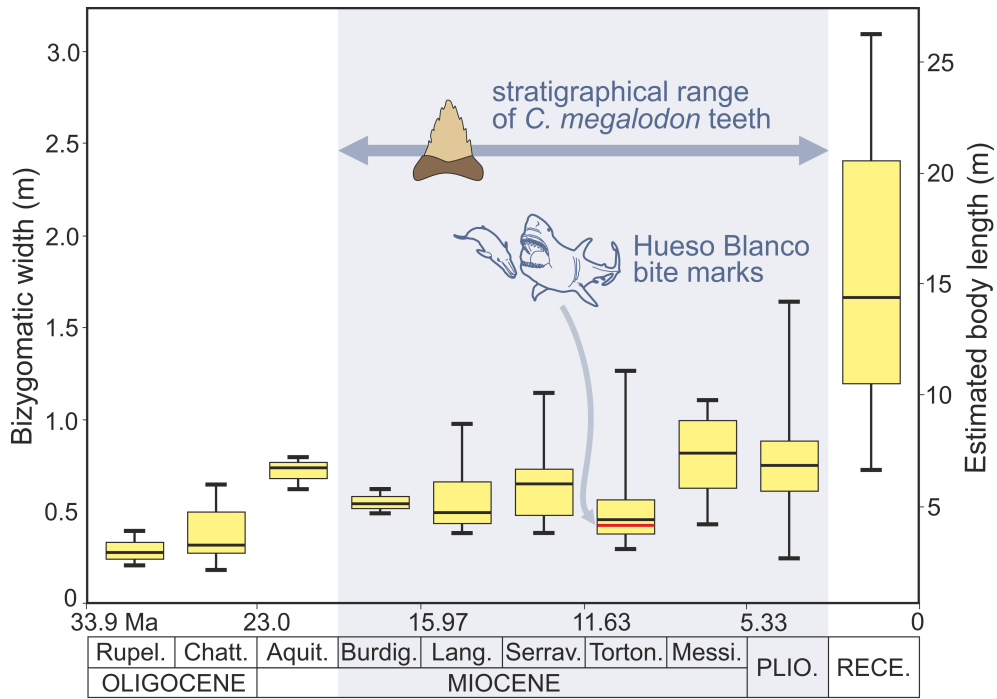
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617



618 Fig. 4.

619



621 **Table 1.**

622

<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

623

624

625 Highlights for

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

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636 **Highlights:**

637 1) We report on shark bite marks affecting late Miocene marine mammal bones of Peru

638 2) The bite marks are referred to the extinct giant shark species *Carcharocles megalodon*

639 3) The bitten items include small mysticetes (e.g., *Piscobalaena nana*) and pinnipeds

640 4) The trophic spectrum of *C. megalodon* could have been focused on relatively small prey

641 5) We support a new ecological hypothesis about the extinction of *C. megalodon*