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Retrieving Palaeoecological Information from Historic Fossil Finds: A Taphonomic Cold Case from Orciano Pisano (Central Italy) Reveals a Distinctive Trophic Interaction in the Pliocene Mediterranean Sea

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Abstract: Evidence of trophic interactions between sharks and cetaceans is rather widespread in the fossil record, consisting as it does of tooth marks on bones and rarer teeth or tooth fragments embedded in (or associated with) skeletal remains. Here, we reappraise a partial mysticete (baleen whale) forelimb that was collected more than a century ago from Pliocene deposits exposed at the celebrated fossil locality of Orciano Pisano (Tuscany, central Italy). This specimen, which is revealed to originate from an early juvenile individual, features shark tooth marks on both the humerus and radius. Whether these traces are due to active predation or to scavenging cannot be ascertained. During the Pliocene, the Mediterranean Basin was inhabited by a diverse elasmobranch fauna, including a number of mammal-eating forms that no longer inhabit the Mediterranean Sea (e.g., *Galeocerdo* and some *Carcharhinus* spp. as well as the extinct *Parotodus*). Early juvenile mysticetes were also likely more common than today in the Pliocene Mediterranean Sea, which may have contained balaenid and balaenopterid calving grounds, thus providing the Mediterranean mammal-eating sharks with vulnerable, energetically valuable potential prey items. Thus, our results evoke a kind of trophic interaction that was likely common and ecologically relevant in the Pliocene Mediterranean Sea.

Keywords: tooth marks; forelimb; mammal-eating sharks; Mysticeti; palaeoecology; taphonomy; Tuscany



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1. Introduction

Several shark species in different orders, including Lamniformes, Carcharhiniformes and Hexanchiformes, are well-known as predators of echolocating toothed whales (Cetacea: Odontoceti) [1–5]. In turn, the literature documenting shark predation on baleen whales (Cetacea: Mysticeti) is comparatively scarce. Most trophic interactions between sharks and mysticetes involve scavenging on carcasses rather than active predation, and it is widely recognized that several shark species include significant amounts of large whale carrion in their diet [2,6–15]. Predation by sharks on mysticetes is known from a limited number of cases, mostly at the expense of abandoned, ill, or entangled calves and early juveniles [16–20], although opportunistic predation on debilitated adults has also been reported [15,17,18,20]. The prevalence of attacks on young mysticetes is due to their being a very valuable food source as well as one that is much more vulnerable to predation

than the larger-sized adults [18]. Indeed, the larger the prey, the higher the probabilities that predation will not succeed and/or that the predator itself will be injured in the making [20–22].

In the fossil record, the evidence of trophic interaction between sharks and cetaceans (including both toothed and baleen whales) conforms to four different typologies: (i) the occurrence of shark tooth marks on cetacean bones; (ii) the observation of shark teeth or tooth fragments embedded into cetacean bones; (iii) the close association between shark teeth and cetacean bones; and (iv) the co-occurrence of shark teeth and cetacean bones within the same stratal package [23]. Although such occurrences—and especially those belonging to the most informative typologies (i) and (ii)—are widely documented [22–33], distinguishing between active predation and scavenging is typically challenging when dealing with fossil remains [34], though some remarkable exceptions exist [22,35,36].

Our aim here is to report on shark tooth marks occurring on a partial mysticete forelimb that was described more than a century ago from the celebrated Italian Pliocene locality of Orciano Pisano. The case is made for this specimen to provide evidence for trophic interactions between a shark and an early juvenile mysticete in the fossil record. By doing so, we further support the notion that significant palaeoecological information can sometimes be retrieved from the taphonomic reappraisal of historic fossil finds, which is in good agreement with recent works on the subject [35,37–39].

2. Geological Background

The historic palaeontological locality of Orciano Pisano (Pisa Province, Tuscany, central Italy) takes its place in the Tora–Fine Basin, which extends between the Livorno hills to the West and the Castellina hills to the East (Figure 1a). The sedimentary fill of this basin ranges chronostratigraphically between the Upper Miocene (Tortonian) and the Lower Pleistocene, with most outcrops being Pliocene in age [40–44]. Such outcrops commonly expose the Pliocene Argille Azzurre Formation [42,45], which in turn includes a lower and an upper stratal package, the former being especially fossiliferous [45–47]. The palaeoenvironmental setting was reconstructed as an open shelf, characterized by a muddy seafloor and punctuated by basement islands [44,46,47].

The surroundings of Orciano Pisano have been renowned since the 18th century for their rich fossil content, which includes abundant and remarkable remains of invertebrates [48–51], fishes [52–57], seabirds [58], reptiles [53,54,59–61] and marine mammals, among which are dolphins, whales, and seals [37,38,45,47,53–55,62–70]. On the basis of a biostratigraphic age of 3.19–2.82 Ma obtained at a fossil-bearing horizon in the vicinity of Orciano Pisano, Dominici et al. [47,70] hypothesized a mid-Piacenzian age for most of the historic finds labelled as coming from this loosely defined locality. However, while few such finds include rather precise provenance metadata (Figure 1b), the exact geographic and stratigraphic context of most specimens remains uncertain [71–73].

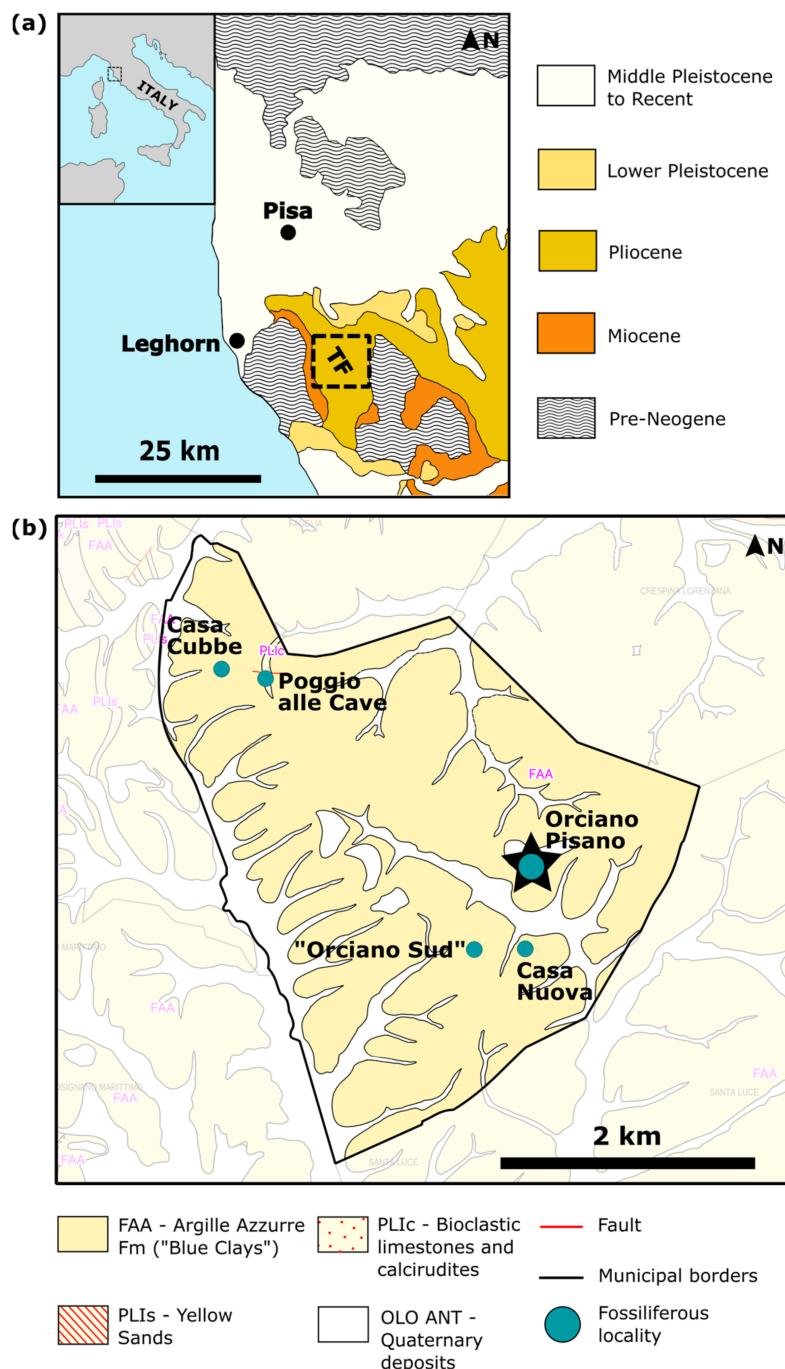


Figure 1. Geographic and geological setting. (a) Schematic geological map of central–western Tuscany (central Italy), redrawn and modified from Benvenuti et al. [74]. TF: Tora–Fine Basin. (b) Schematic geological map of the Orciano Pisano area that yielded the cetacean specimen MSNUP I-12559 (modified from Regione Toscana [75]). The location of some discoveries of fossil vertebrates for which precise geographic whereabouts are known has been reconstructed after Bianucci and Landini [45]. Note that the exact finding site of the fossil specimen dealt with herein is unknown.

3. Material and Methods

The studied materials consist of a partial right forelimb, including the humerus, radius, and fragmentary ulna, stored at the Museo di Storia Naturale dell’Università di Pisa (=MSNUP; Calci, Pisa Province, Italy) under accession number MSNUP I12559 (Figures 2 and 3). Out of these three bones, the humerus and radius are on display in the “Gallery of Geological Eras” [76].

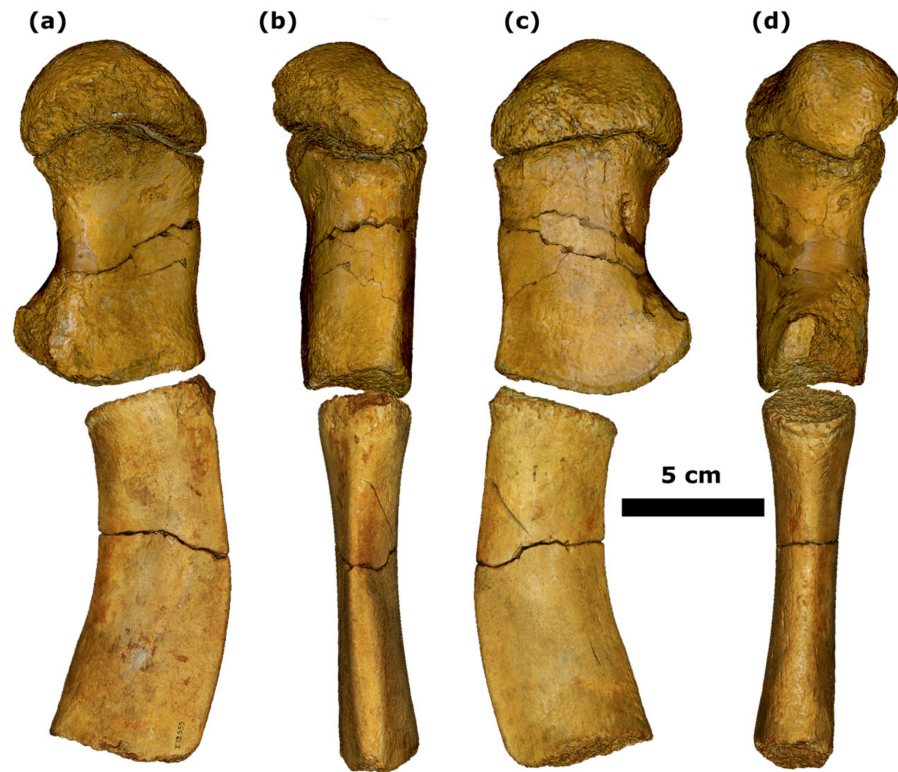


Figure 2. MSNUP I-12559, partial right forelimb of Mysticeti indet. from the Pliocene of Orciano Pisano; humerus and radius in (a) lateral, (b) anterior, (c) medial, and (d) posterior views. All views are digital renderings of the textured 3D models.



Figure 3. MSNUP I-12559, partial forelimb of Mysticeti indet from the Pliocene of Orciano Pisano; distal fragment of the ulna, with its historical supporting tablet and associated label (photograph).

MSNUP I12559 was discovered by Antonio di Paco at an unspecified outcrop in the vicinity of the Orciano Pisano village [66]. As its discovery dates back to more than a century ago, this specimen is among the oldest existing items in the cetological collection of the MSNUP [77].

Textured 3D models of the humerus and radius were obtained with an Artec Space Spider structured-light 3D Scanner (Luxembourg). Digital renderings of the aforementioned models were realized in Meshlab v2023.12 (Supplementary Files S1 and S2), and then assembled in Inkscape 1.3.1 to elaborate the anatomical plates.

4. Results

4.1. Description of the Mysticete Forelimb MSNUP I12559

The overall shape of the humerus (Figure 2) is generally reminiscent of that of other mysticetes (Supplementary File S3). The humeral shaft is relatively slender and moderately compressed mediolaterally, with a sub-straight anterior edge and a broadly concave posterior edge. The greater tubercle is hardly identifiable. The proximal epiphysis is weakly fused to the diaphysis and somewhat porous in texture. The sub-complete caput humeri represents less than one-third of the total length of the bone. It projects posterodorsolaterally and slightly protrudes beyond the humeral shaft, but not as much as in other mysticetes (note, however, that this character may have been partly obliterated by erosion). The radial and ulnar facets are oriented at an obtuse angle. The ulnar face is partially damaged, and the distal epiphysis for the articulation with the radius and ulna is missing. The humerus measures 24.3 cm in total length (HL) and 10.4 cm in anteroposterior width at mid-length, whereas the width of the caput humeri is 13.2 cm.

The radius (Figure 2) is short and robust and lacks both epiphyses. It is gently bent anteriorly and widens toward its distal end. The radius measures 25.5 cm in total length (RL), and its proximal and distal widths are 9.0 cm and 10.2 cm, respectively. The RL/HL ratio is thus very close to 1.

The ulna (Figure 3) is only represented by a fragment of the distal end of the diaphysis, with no indication of the corresponding epiphysis.

The metaphyseal surfaces of all the aforementioned bones display a billowed texture.

4.2. Description of the Tooth Marks

Although the occurrence of shark tooth marks on MSNUP I12559 was noticed by Bianucci and Sorbini [78], these traces have not been described, nor properly figured, to date.

The radius features an elongated tooth mark (Figure 4a,d,e) that runs obliquely across the medial surface of the bone, starting from a point close to the anterior edge. This groove-like incision displays a maximum length of about 5.7 cm and a maximum width of 2.4 mm. The latter is observed at the anterior end of the tooth mark as the trace width decreases to a minimum of 0.4 mm at the opposite end. The tooth mark features a V-shaped cross section, and a variable depth that is maximal at the anterior end and averages 1 mm. No clear serration marks could be detected. By consisting of a straight, elongate, V-shaped groove, the trace in question conforms to the ichnogenus *Linichnus* [79]. At present, *Linichnus* includes two ichnospecies, namely the serrated *Linichnus serratus* [79] and the unserrated *Linichnus bromleyi* [80]. That no serrations are observed on the groove dealt with herein suggests a referral to the latter ichnospecies.

This is not the only tooth mark that occurs on the studied specimen: a series of shorter traces that only shallowly incise the bone cortex ornament the lateral surface of the radius, close to the posterodorsal corner of the bone, and several such marks are also found on the medial surface of the humerus, departing from the anterior edge thereof (Figure 4a–c).

All these traces are simple, groove-like incisions with an unserrated morphology, ranging between ca. 1 and 3 cm in length. Occasionally, two different incisions are observed to cross each other. These clusters of grooves resemble the ichnogenus *Machichnus*, which, however, typically comprises serial, parallel to subparallel scratches [81,82].

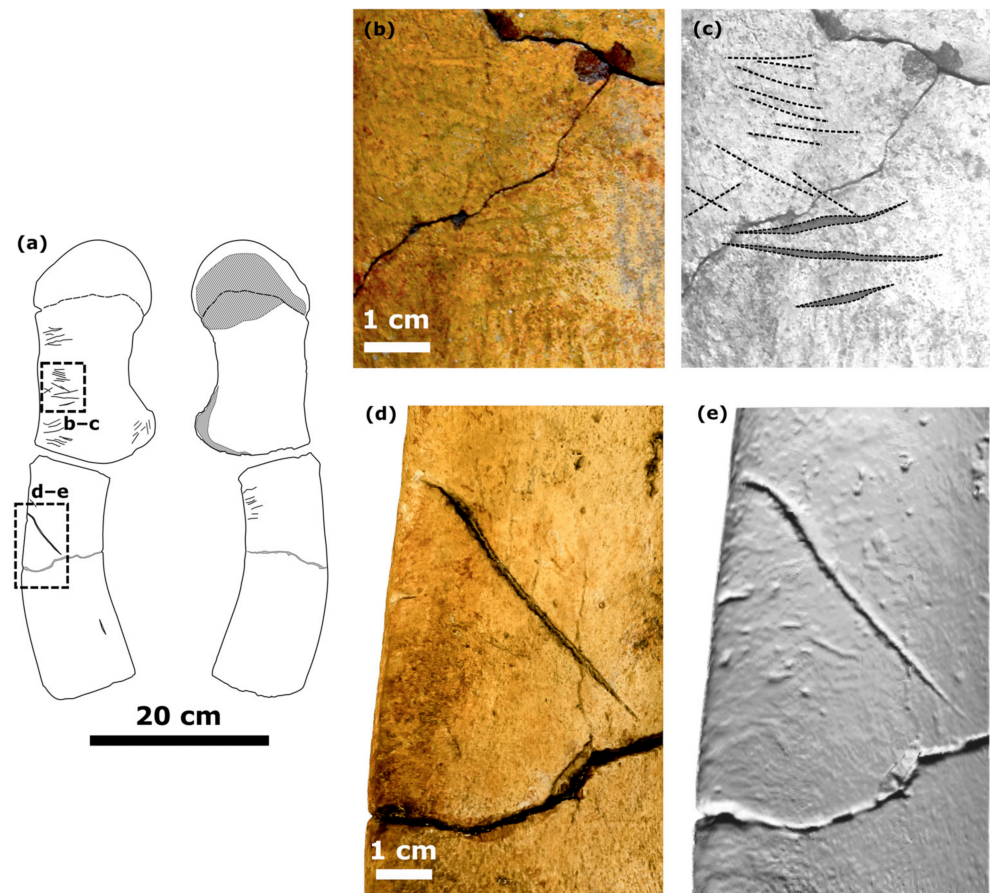


Figure 4. MSNUP I-12559, partial forelimb of Mysticeti indet. from the Pliocene of Orciano Pisano; humerus and radius, close-ups of the tooth marks; grey-shaded areas correspond to damaged bone surfaces. (a) Distribution of the tooth marks over the humerus and radius. (b,c) Short, groove-like tooth marks occurring on the humerus in (b) colour and (c) greyscale photographs. (d,e) Long, groove-like tooth mark occurring on the radius as visible in digital renderings of the textured (d) and (e) untextured 3D model.

4.3. Identity of the Bitten Whale

MSNUP I12559 was first described by Ugolini (1906) and identified therein as a left forelimb of the balaenopterid “*Cetotherium (Cetotheriophanes?) cfr. Capellini*” [sic] based primarily on the observation of a comparatively short radius. Ugolini’s [66] species of choice, which is now recombined as *Cetotheriophanes capellini* [83], is known from an incomplete skeleton from the Pliocene of San Lorenzo in Collina (Bologna Province, Emilia-Romagna, northern Italy [84]). The forelimb of *C. capellini*, which is recognized at present as a basal member of the rorqual family Balaenopteridae [83], is represented by a fragmentary humerus that was collected at the same locality as the type specimen at a later date [85]. Compared to MSNUP I12559, the humerus assigned by Capellini [85] to *C. capellini* displays a distinctly straighter posterior edge.

Ninety years later, Bianucci [86] observed that MSNUP I12559 differs from most balaenopterids from the Italian Pliocene while resembling *Heterocetus* from the Belgian Pliocene based on the combination of small overall dimensions and a comparatively short radius. Bianucci [86] was referring to *Heterocetus affinis*, for which both the humerus and

the radius were figured by Van Beneden [87]. Indeed, *H. affinis* resembles MSNUP I12559 in terms of the overall size of the forelimb bones, but its radius is still distinctly longer than the humerus, with the latter displaying a straighter posterior edge (Supplementary File S3). We do not expand here on Bianucci's [86] tentative assignment of MSNUP I12559 to the family Cetotheriidae, which, until the mid-2000s, was used as a wastebasket taxon for a heterogeneous stock of Neogene mysticetes outside the living families [88,89].

MSNUP I12559 is indeed an idiosyncratic specimen. Our assessment of its systematic affinities takes the steps from Benke's [90] morphometric characterization of the forelimb bones of extant cetaceans and specifically from the often-informative RL/HL ratio. Based on the observation of an RL/HL ratio close to 1.0 in the specimen in question, an assignment of this partial forelimb to the families Balaenopteridae and Eschrichtiidae (=Eschrichtiinae sensu Marx and Fordyce [91]) (Supplementary File S3), both of which are known from the Italian Pliocene [39,92–96], is discarded herein. Indeed, all members of this family are characterized by a greatly elongated radius, where $RL/HL \gg 1.0$ ([90]; but see also Zazzera et al. [97]). Similar considerations may also allow for discarding the largely fossil family Cetotheriidae (s.s.) and the extant putative cetotheriid *Caperea* (Supplementary File S3), the latter being likely present in the Italian Pleistocene [98], as possible matches for MSNUP I12559. In turn, an RL/HL ratio close to 1 is observed in the extant balaenids, including the right whale genus *Eubalaena* (RL/HL ratio about 0.9) and the bowhead genus *Balaena* (RL/HL ratio about 1.1), both of which are known from the Italian Pliocene, along with other extinct members of the family Balaenidae [99,100]. Actually, some similarities exist between MSNUP I12559 and the forelimbs of the Pliocene North Atlantic species *Balaena ricei* [101] and *Antwerpibalaena liberatlas* [102], including a relatively slender outline of the humerus in lateral view; a relatively small, shortly protruding caput humeri; a broadly concave posterior edge of the humeral shaft; and a radius that moderately expands toward its distal end (Supplementary File S3). That said, balaenids typically display a stockier humerus with a more conspicuous caput humeri that protrudes far posteriorly beyond the humeral shaft [90]. All things considered, morphological similarities between MSNUP I12559 and some Pliocene members of Balaenidae are flattering but not conclusive.

Any further discussion of the systematic affinities of MSNUP I12559 should take into account its ontogenetic age, which—to the best of our knowledge—has not been addressed before in the literature. Although the degree of maturity indicated by the fusion of long bone epiphyses is a somewhat unexplored issue with respect to mysticetes, the observations by Perrin [103] on spotted and striped dolphins as well as those by Flower [104] and Omura [105] on balaenopterids provide valuable insights in this regard. In extant balaenopterids, the proximal humeral epiphysis fuses earlier than the distal one, such that its incipient fusion and the lack of all other epiphyses indicate that MSNUP I12559 is far from being physically mature [104,106–108]. Along with the spongy texture of the humeral head, these observations indicate that the specimen in question is a very young individual, consistent with the ossification stage I, as defined by Flower [104]. That its metaphyseal surfaces display a billowed aspect further conforms to the osteological traits of early juveniles, as reported by Flower [104] and Scheuer and Black [109]. Interpreting these data in terms of absolute ontogenetic age (i.e., months or years at death) is not straightforward, but MSNUP I12559 certainly died well before attaining sexual and physical maturity [110].

It is worth noting that the role of differential allometric growth in controlling the forelimb bone shape and proportions in mysticete juveniles is still unclear [111]. Although there are no indications that this may invalidate the taxonomic value of the RL/HL ratio in the case of early juveniles, given that MSNUP I12559 displays various characters that are

regarded as indicative of a very young ontogenetic age, we cautiously assign this specimen to Mysticeti indet.

4.4. Identity of the Biting Shark

Several selachian taxa have been reported from the Orciano Pisano locality, including large-bodied, mammal-eating shark species such as *Carcharodon carcharias*, *Cosmopolitodus plicatilis* (= *Isurus xiphodon* Auctt.), *Isurus oxyrinchus*, *Parotodus benedenii*, *Carcharhinus leucas*, *Carcharhinus longimanus*, *Galeocerdo cuvier* and *Hexanchus griseus* [43,45,52–54,71]. Of all these species, only the extant *I. oxyrinchus* and the extinct *C. plicatilis* and *P. benedenii* have teeth provided with unserrated cutting edges. As the main tooth mark observed on MSNUP I12559 is seemingly unserrated, the tracemaker should be searched for among these taxa.

The shortfin mako, *I. oxyrinchus*, has a broad trophic spectrum encompassing marine tetrapods such as seabirds, cetaceans and turtles; nonetheless, *I. oxyrinchus* displays a marked preference for taking fishes and cephalopods, and the contribution of marine mammals (mostly dolphins) to its diet is low overall [112–114]. In turn, both *Cosmopolitodus* and *Parotodus* are currently reconstructed as formidable high-trophic level predators—some that would have regularly eaten marine mammals [13,32,35,115–119]. Since *Cosmopolitodus* was seemingly much commoner than *Parotodus*, the former is left as the most likely tracemaker—though certainly not as the only possible one (see also [78]).

Regardless of the systematic affinities of the biting shark, the very fragmentary nature of MSNUP I12559 frustrates any speculation on whether the observed tooth marks are the product of active predation or scavenging [34]. We may just notice that both white and tiger sharks have been reported to avoid feeding on flippers when scavenging on whale carrion [15], although the former have been observed taking large bites out of the flippers of a floating humpback whale carcass in at least one occasion [8].

5. Broader Palaeoecological Outcome

Evidence for sharks feeding on baleen whales in the present-day Mediterranean Sea is scanty and circumstantial overall ([120], and references therein). This goes hand in hand with a depletion of large-bodied predatory sharks [121] as well as with a highly simplified mysticete fauna that includes a single resident species, namely, the balaenopterid *Balaenoptera physalus*, with other forms such as *Megaptera novaeangliae* being only sighted occasionally in Mediterranean waters [122].

The situation would have been very different in Pliocene times. At that time, the Mediterranean marine mammal fauna included representatives of the currently extra-Mediterranean cetacean families Balaenidae (including small-sized forms such as *Balaenula* [68]) and Eschrichtiidae (=Eschrichtiinae sensu Marx and Fordyce [91]), besides several members of Balaenopteridae (among which were also small-sized forms such as *Marzanoptera* [39,95]) [92–94,96,99,100,123–126]. Some of these groups were represented by morphotypes that have survived elsewhere, while others, including forms of small-sized mysticetes such as *Balaenula*, have subsequently gone extinct worldwide [23,91,119,127]. Judging from the mere abundance of mysticete skeletons that are preserved in the marine Pliocene deposits of Italy, baleen whales would have been a common presence off the Apennine Peninsula in Zanclean and Piacenzian times. Also, early juvenile mysticetes were likely more common than they are today in the Pliocene Mediterranean Sea, which appears to have been home to breeding/calving grounds of different baleen whale taxa in the families Balaenidae and Balaenopteridae, as also shown by the occurrence of a newborn balaenid in the Pliocene of Orciatice (a locality some 20 km ESE of Orciano Pisano [128]) as well as by the record of whale barnacles from Orciano Pisano itself ([129]; see discussion in Bianucci et al. [130] and Collareta et al. [131]).

The Pliocene elasmobranch fauna of the Mediterranean Sea was also more diverse than the modern one, at least regarding the mammal-eating forms, among which were extant carcharhiniform species that currently inhabit extra-Mediterranean settings, such as *Carcharhinus leucas*, *Carcharhinus longimanus*, and *Galeocerdo cuvier*, and extinct taxa of large-bodied lamniforms such as *Cosmopolitodus plicatilis* and *Parotodus benedenii*, in addition to, e.g., *Carcharodon carcharias*, *Hexanchus griseus*, and *Isurus oxyrinchus* [30,43,45,52–54,71,119,127]. It is highly plausible that the significant presence of mammal-eating sharks in the Pliocene Mediterranean Sea was largely sustained by a more conspicuous and diverse baleen whale fauna than we observe today—one that also featured a relatively high abundance of nutrient-rich prey such as diminutive forms (e.g., *Balaenula* and *Marzanoptera*) and early juveniles, which would have been more easily attainable than large adults, not to mention the high availability of carrion from mysticete individuals of all age classes [30,119,127]. In this context, it is worth noting that over fifty teeth of *C. leucas* have been found in close association with the small-sized holotype of *Marzanoptera tersillae* and that indeterminate tooth fragments are still embedded within some of the whale bones, which also feature shark tooth marks [39,95].

Summarizing, the shark tooth marks detected on the early juvenile mysticete forelimb MSNUP I12559 from the historic locality of Orciano Pisano evoke a type of trophic interaction that was likely common and ecologically relevant in the Mediterranean Sea during the Pliocene, but for which, to date, direct taphonomic evidence was limited. Furthermore, as a token of shark predation or scavenging on an early juvenile mysticete in the fossil record, this find is noteworthy in a way that transcends the Mediterranean context.

6. Concluding Remarks

We re-examined a partial forelimb of a juvenile mysticete from the Italian Pliocene locality of Orciano Pisano that preserves shark tooth marks on the humerus and radius. The origin of these traces—whether from predation or scavenging—remains unclear due to the fragmentary nature of the remains. Nonetheless, this find sheds light on the Pliocene vertebrate palaeoecology of the Mediterranean Sea, which at that time was home to a diverse, conspicuous stock of baleen whales as well as of mammal-eating sharks. Early juvenile mysticetes were likely commoner than today, thus serving as a valuable food source for the sharks in question, as also evoked by the tooth marks observed on our specimen. The latter holds historic as well as scientific value, and its reappraisal highlights the importance of museum collections for palaeontological and palaeoecological research.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/jmse13030508/s1>, File S1: Textured 3D model of the humerus of MSNUP I-12559; File S2: Textured 3D model of the radius of MSNUP I-12559; File S3: Schematic comparison between the humeral and radial morphologies of extant and extinct mysticete species.

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