

Article

The Palaeobiology of the False Mako Shark, *Parotodus benedenii* (Le Hon, 1871): A View from the Pliocene Mediterranean Sea

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Abstract: The extinct “false mako” shark, *Parotodus benedenii* (Lamniformes: Otodontidae), is essentially known from large, robust teeth that are widespread but overall rare in Oligocene to Pliocene deposits worldwide. More than 150 years after its description, this species still represents a palaeontological conundrum, as very little is known about its body aspect and palaeoecology. Here, we describe new specimens of *P. benedenii* from the Pliocene of Tuscany, central Italy. These new finds comprise some of the geologically youngest finds of *P. benedenii* worldwide, witnessing to the survival of false makos until the Late Pliocene at least, which in turn suggests that *P. benedenii* may have been the latest surviving member of the family Otodontidae. Building upon a thorough literature review, we provide an updated synthesis of the palaeobiology of *P. benedenii*. In light of the morphological evidence, and considering previously published suggestions, *P. benedenii* may be reconstructed as a large-sized, carnivorous shark that dwelt in pelagic settings and fed primarily on large, soft prey and scavenging items. Thus, some ecological partitioning did likely exist between *P. benedenii* and other elasmobranch apex predators of the Neogene mid-latitude seas (including, in Pliocene times, the extant species *Carcharodon carcharias*, *Carcharhinus leucas* and *Galeocerdo cuvier*).

Keywords: Lamniformes; mackerel sharks; macrophagy; Otodontidae; palaeoecology; pelagic habitats; Piacenzian; trophic ecology; Tuscany; Valdelsa Basin



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1. Introduction

Teeth assigned to the extinct lamniform genus *Parotodus* are geographically widespread but uncommon in lower Eocene to Pliocene marine deposits [1]. These massive dental specimens are characterised by crowns with smooth cutting edges and a broad base, as well as by roots that bear a strongly developed lingual protuberance and a U-shaped basal edge [2]. Owing to their rarity and highly atypical shape, the remains of *Parotodus* have risen to almost mythical status among fossil collectors [3].

Ranging chronostratigraphically between the Oligocene (Rupelian) and the Pliocene, *Parotodus benedenii* is the geologically youngest representative of *Parotodus* [1,4]. Originally described as one of the many nominal species of Agassiz’s genus *Oxyrhina* [5], the *benedenii* morphology has long been considered to represent a close relative of the extant mako sharks in the genus *Isurus* [6–8]. Eventually, *Oxyrhina benedenii* came to be chosen as the type species of the then-new genus *Parotodus* by Cappetta [9], hence its vernacular name, “false mako” shark [3,10,11]. *Parotodus benedenii* and its congeners are mostly regarded as phylogenetically close to the extinct mega-toothed sharks (*Otodus* and kin), and as such, *Parotodus* is often referred, more or less confidently, to the family Otodontidae [12].

However, alternative attributions to Alopiidae, Cardabiodontidae and Lamnidae have also been proposed [13–15], and some works list *Parotodus* as *incertae sedis* [16].

Teeth of *P. benedenii* have been reported from world regions as disparate as Europe (Belgium, Germany, Hungary, Italy, Malta, the Netherlands, Portugal, Slovakia and Switzerland), Africa (Angola and South Africa), Macaronesia (the Azores and the Canary Islands), North America (USA, along both the eastern and western coasts of the country, and Mexico), South America (Ecuador and Peru), Indonesia (Sumatra) and the western Pacific (South Korea, Japan, New Caledonia; Australia and New Zealand) [3,4,17–21], as well as from the floor of the Indian and Pacific oceans, where this otherwise uncommon taxon appears to be surprisingly abundant [22,23]. As regards the peri-Mediterranean area, finds of *P. benedenii* come from the Miocene of Malta [24], southern Spain [25] and southern Italy [6,26], as well as from the Pliocene of the Balearic Islands [17] and many Italian localities [27]. In particular, the Pliocene marine deposits of Tuscany (central Italy) have yielded teeth of *P. benedenii* for a very long time. For instance, the celebrated 19th century palaeoichthyologist Roberto Lawley (b. 1818–d. 1881) [28] described and figured false mako teeth from the historical localities of Orciano Pisano, Siena and Volterra under five different species-level names (namely, *Otodus sulcatus*, *Oxyrhina quadrans*, *Oxyrhina crassa*, *Oxyrhina gibbosissima* and *Oxyrhina Forestii*) [29] (Figure 1).

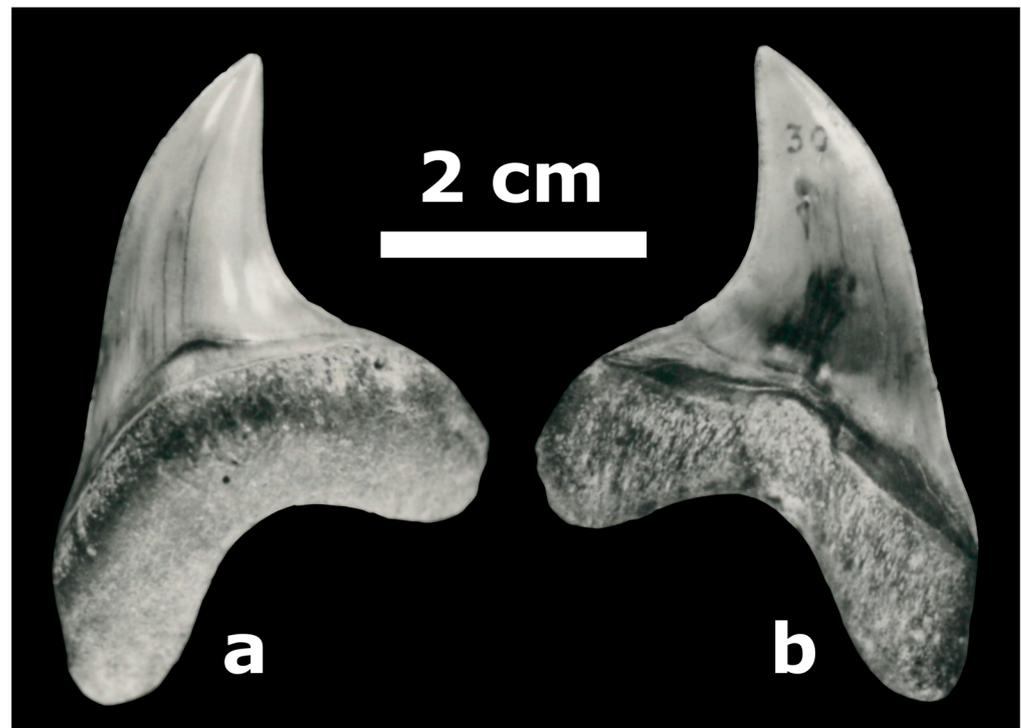


Figure 1. *Parotodus benedenii*, tooth from the historical “Lawley Collection” of Tuscan Pliocene fossils kept in the Museo di Storia Naturale dell’Università di Pisa, in (a) lingual and (b) labial views. Identified by Landini ([30]: pl. XVI[V]: figure 16) with the specimen code M.P.P.1.6.[3], this tooth was reported therein as having been assigned to *Oxyrhina quadrans* by Roberto Lawley. Reproduced from Landini ([31]: pl. III, figure 3).

More than 150 years after its description, *Parotodus benedenii* still represents a palaeontological conundrum, as very little is known about its body aspect and palaeoecology. Herein, we report on the discovery of new specimens of *P. benedenii* from Pliocene deposits of the Valdelsa Basin of Tuscany. We also provide an updated synthesis of the palaeobiology of *P. benedenii* based on a thorough literature review and first-hand observations.

2. Stratigraphic Framework

The Valdelsa Basin is a 25 × 60 km, NW–SE trending extensional basin of central-western Tuscany. Its sedimentary infill accounts for some 1000 m of continental and marine deposits that range chronostratigraphically from the Upper Miocene to the Lower Pleistocene [32]. A detailed sequence stratigraphic framework exists for the Valdelsa Basin, which allows for dividing its sedimentary infill into seven different synthems, namely, S1–S7 from older to younger [32].

Abundant remains of both marine and nonmarine vertebrates have been collected from several localities of the Valdelsa Basin [33–47]. In particular, the specimens discussed herein have been collected by one of us (SC) at two different Pliocene outcrops.

The first such outcrop consists of an abandoned quarry located in the Castelfiorentino municipality (indicative geographic coordinates: 43°35'57" N, 10°58'51" E) (Figure 2). Here, a 30 m thick mudstone succession is exposed, which belongs to the upper part of the upper Zanclean to lower Piacenzian S3 synthem and represents deposition during the normal-polarity Gauss chron [40]. These strata have been interpreted as representing a lower Piacenzian highstand [40].

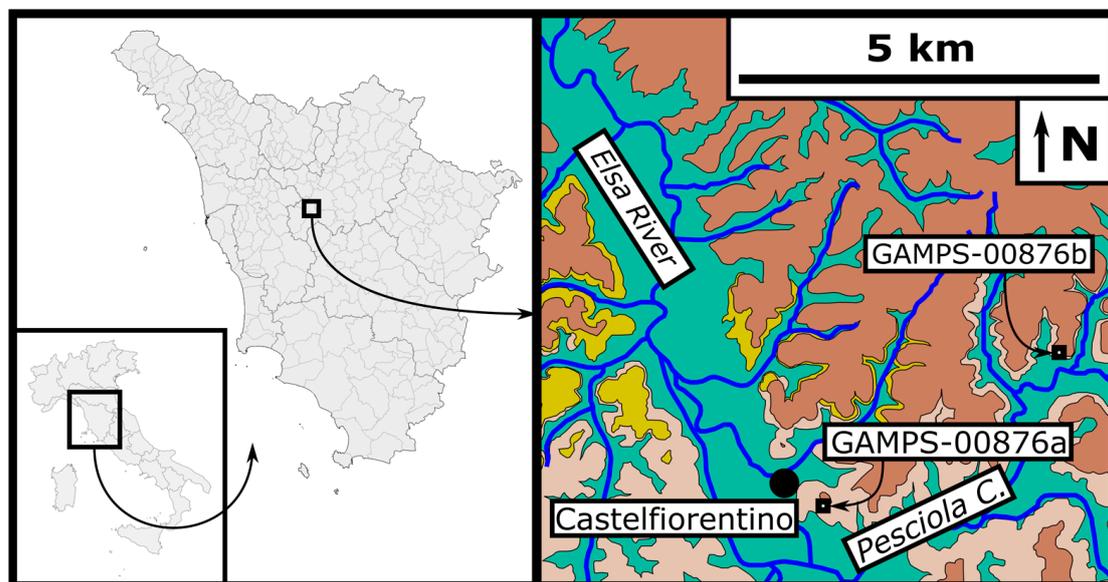


Figure 2. Geographic and stratigraphic location of the new finds of *Parotodus benedenii* documented in the present work (GAMPS-00876a and GAMPS-00876b). Green-coloured areas indicate recent deposits; cream-coloured areas indicate the S3 synthem; yellow-coloured areas indicate the S4 synthem; brown-coloured areas indicate the S5 synthem. Base maps in left panels after wikimedia.org; right panel redrawn and modified from Benvenuti et al. ([32]: figure 1).

Another tooth of *P. benedenii* was collected loose from the ground at a cultivated field in the Montespertoli municipality (indicative geographic coordinates: 43°37'01" N, 11°01'12" E) (Figure 2). According to the schematic geological map provided by Benvenuti et al. ([32]: figure 1), both the S3 synthem and the mid-Piacenzian S5 synthem occur in this area. Thus, the *P. benedenii* tooth from Montespertoli is either roughly coeval or slightly geologically younger than the material from Castelfiorentino.

3. Materials and Methods

3.1. Repository

The specimens discussed herein consist of two teeth that are stored in the Museo Geopaleontologico Scienze della Terra—Gruppo AVIS Mineralogia e Paleontologia Scandicci (=GAMPS; Badia a Settimo, Scandicci, Florence Province) with accession numbers GAMPS-00876a and GAMPS-00876b, respectively.

3.2. Specimen Documentation

Photographs of the studied material were taken with a Nikon D850 camera equipped with a Nikon Micro Nikkor AF-S 60 mm f/2.8 G ED macro lens.

4. Systematics

Otodontidae Glikman, 1964 [48]

Parotodus Cappetta, 1980 [9]

Parotodus benedenii (Le Hon, 1871) [5]

(Figure 3)

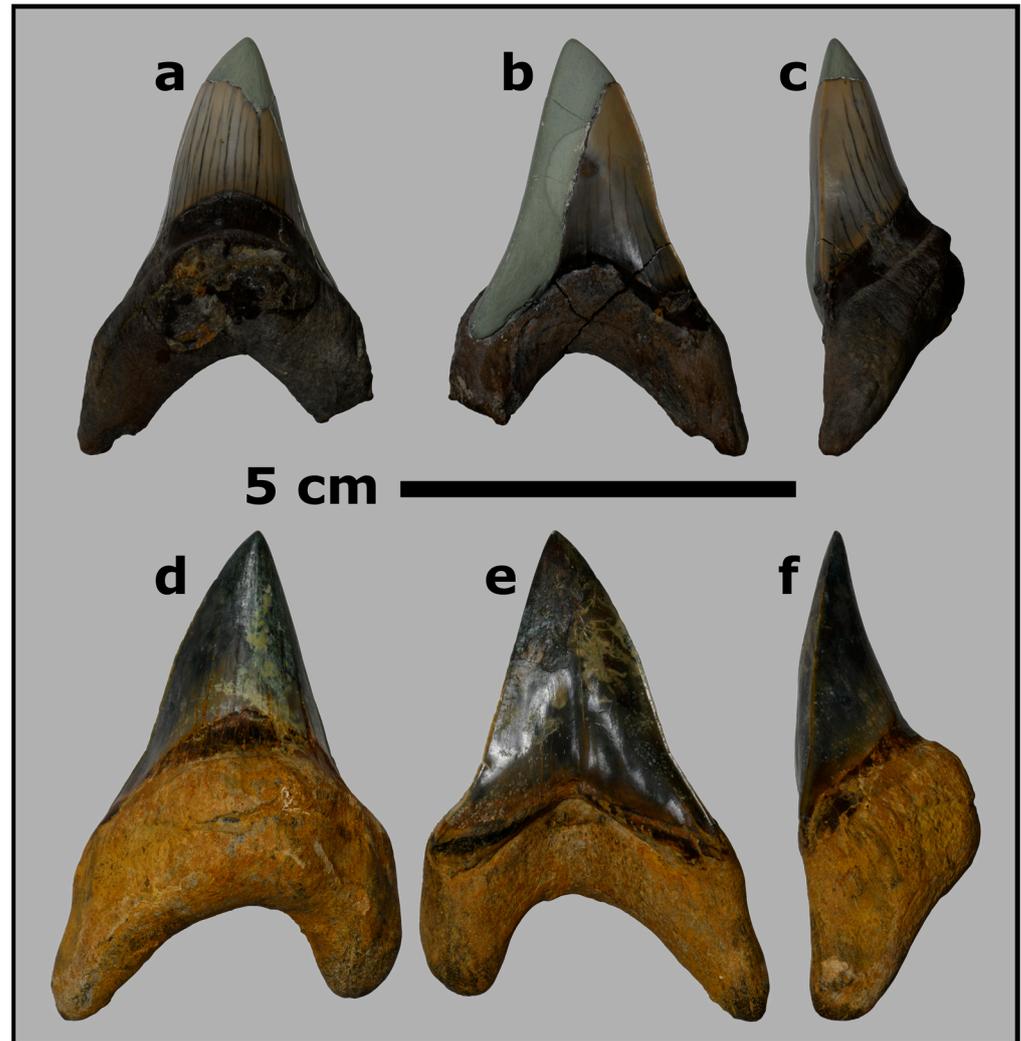


Figure 3. *Parotodus benedenii*, Tuscan Pliocene teeth kept in the Museo Geopaleontologico Scienze della Terra—Gruppo AVIS Mineralogia e Paleontologia Scandicci. (a–c) GAMPS-00876a, a partial tooth from Upper Pliocene deposits cropping out at an abandoned quarry in the vicinity of Castelfiorentino (Florence Province), in (a) lingual, (b) labial and (c) mesial views (note that the crown was partly reconstructed with grey plasticine). (d–f) GAMPS-00876b, an essentially complete tooth from ?Upper Pliocene deposits cropping out at a cultivated field in the vicinity of Montespertoli (Florence Province), in (d) lingual, (e) labial and (f) mesial views.

Synonymy: See Kent ([4]: 96).

Nomenclatural caveat: Le Hon [5] described *Oxyrhina Benedenii* based on a tooth from deposits of the alleged Pliocene age of the Antwerp area ([3]; but see also [49] for a different chronostratigraphic assignment of this and other finds by Le Hon). As the species name

was clearly meant to honour the Belgian zoologist and palaeontologist van Pierre-Joseph Van Beneden [3], a rigorous application of the genitive case would have led to obtaining “[van]benedeni”, rather than “[van]benedenii”, as the correct epithet. It is likely for this reason that several subsequent works have considered either *Isurus benedeni* or *Parotodus benedeni* as the correct binomial name for this species [6,8,17,50]. One of the authors of the present paper (AC) has also taken this position in some earlier papers of his [51]. However, Le Hon’s [5] seemingly erroneous Latinisation must be treated under the ICZN [52] Code’s Article 32.5.1, which means that it cannot be considered as an inadvertent error, and as such cannot be corrected in a later contribution (see also [53,54]). That said, it is also possible that Le Hon [5] derived the epithet “benedenii” from some Latinised version of Van Beneden’s surname such as “Benedenius”, which would make this species name to conform perfectly to the Code’s Article 31.1.1. Circumstantial support for this interpretation may come from Le Hon’s [5] concomitant description of *Anatodus Agassizii*, whose species name was clearly meant to honour the French polymath Louis Agassiz, the latter being sometimes referred to as “Agassizius” in earlier scientific works [55].

Referred material and occurrence: GAMPS-00876a, one partial tooth from Upper Pliocene deposits cropping out at an abandoned quarry in the vicinity of Castelfiorentino, and GAMPS-00876b, one essentially complete tooth from ?Upper Pliocene deposits cropping out at a cultivated field in the vicinity of Montespertoli (Florence Province, Tuscany, Italy).

Description and taxonomic identification: GAMPS-00876a (Figure 3a–c) is an incomplete tooth whose crown was partly reconstructed with grey plasticine. Its maximum height, including the reconstructed crown part, is 55.5 mm. What is preserved of the crown is robust and greatly thickened labiolingually. The cutting edges are smooth. The lingual crown surface is strongly convex and smooth throughout, and features a broad neck at its base. The labial crown surface is concave in its median part above the crown–root junction, being gently convex elsewhere. In the same depressed area, longitudinal enameloid folds are present. The root is very thick, U-shaped, with long, arched root lobes. The mesial root lobe is bluntly pointed, whereas the distal root lobe is incompletely preserved. The lingual protuberance is conspicuous and shaped as a dome-like torus. Here, the root surface is damaged, and no nutrient foramina could be observed.

GAMPS-00876b (Figure 3d–f) is a complete, 60 mm high tooth. In labial/lingual view, the 44 mm high crown is broadly triangular, its tip being only gently bent distally. It is provided with smooth, complete cutting edges as well as with long shoulders that line the proximal portions of both root lobes and display no cusplets. As for GAMPS-00876a, the crown of GAMPS-00876b is robust and greatly thickened labiolingually; in profile view, it is distinctly curved labially. The lingual crown surface is strongly convex and smooth throughout, and features a broad neck at its base. The labial crown surface is strongly concave in its median part above the crown–root junction, being gently convex elsewhere. Longitudinal enameloid folds mark the basal portion of the labial crown surface, being particularly long and salient in the aforementioned depressed area. The labial crown surface distinctly overhangs the U-shaped root, which is very thick, even more so than in GAMPS-00876a. The root lobes are long and arched, and asymmetrically developed. The mesial root lobe is slender and bluntly pointed, whereas the distal root lobe is shorter and stouter. The lingual protuberance is extremely massive and shaped as a bulging torus. No nutrient foramina are clearly observable in this region of the lingual root surface.

Both GAMPS-00876a and GAMPS-00876b are referred to *Parotodus benedenii* because they are readily distinguished from other lamniform sharks by the following combination of characteristics: large size, crown and root robust and labiolingually thickened, absence of serrated cutting edges, absence of lateral cusplets, presence of a broad neck, basal edge of the root U-shaped, and development of a conspicuous lingual protuberance of the root [1–3,15,27,56].

Given the observation of a crown apex that is only slightly bent distally, a very prominent torus, and a mesial root lobe that is longer than the distal root lobe, GAMPS-00876b

can be identified as a right lower anterior tooth [15,56]. The incomplete nature of GAMPS-00876a prevents from drawing definitive conclusions on its position in the dentition.

GAMPS-00876b is larger than many other Italian Pliocene false mako teeth and matches the figure reported by Cappetta [1] for the largest dental specimens of *P. benedenii* (though larger teeth do exist; [57]). Therefore, it is here interpreted as originating from a remarkably large-sized adult individual of *P. benedenii*.

Stratigraphic remarks: Marsili [27,58] regarded *Parotodus benedenii* as occurring in both the Lower and Upper Pliocene of the Mediterranean region. Conversely, Cappetta [1], Kent [4] and Everaert [59] listed this extinct lamniform species as making its last global appearance in Early Pliocene times. Our discovery of GAMPS-00876a in lower Upper Pliocene deposits confirms that the chronostratigraphic range of *P. benedenii* extends into the Piacenzian. Other Upper Pliocene records of *P. benedenii* appear to exist elsewhere, e.g., in Japan [2].

If the otodontid affinities of the false mako are accepted, then the extinction of *P. benedenii* not earlier than the Late Pliocene could also mean that this species represents the latest surviving member of the family Otodontidae. In fact, the extinction of *Carcharocles megalodon* (which at present is often regarded as a member of the genus *Otodus*) is now believed to have occurred around the Zanclean–Piacenzian transition ([60]; but see also [61] for an alternative extinction age of about 2.6 Ma). As for the Mediterranean region in particular, the disappearance of *C. megalodon* appears to have occurred during the Zanclean [27].

5. The Palaeobiology of *Parotodus benedenii*: An Updated Review

5.1. Body Size

Information about *Parotodus benedenii* is essentially limited to its dental remains, though some dermal denticles have also been mentioned in the literature [62]. Such a paucity of fossil materials leaves tooth sets as the sole source of data for reconstructing the body size of this impressive extinct lamniform species.

Kent and Powell [56] described an associated tooth set of *P. benedenii* from the Lower Pliocene of the Yorktown Formation in the Lee Creek Mine, Aurora, North Carolina, USA. Consisting of 114 teeth, the largest of which is slightly shorter than 60 mm (viz the height of GAMPS-00876b), this tooth set allowed Kent and Powell [56] to reconstruct the dentition of *P. benedenii* with 14 upper files (including a reduced intermediate) and 13 lower files. Emendations to this scheme focusing on the identification of symphyseal and intermediate teeth have been proposed by Purdy et al. [15], Ward and Bonavia [24] and Kent [4]. The same North Carolinian tooth set was used by Kent [57] to extrapolate a total body length of 7.6 m based on the reconstructed upper jaw perimeter. Considering the largest size values of isolated teeth of *P. benedenii*, some of which reach 72 mm in height, Kent [57] estimated that this extinct shark species may have grown up to 20% longer, that is, about 9.2 m total body length. Even if false makos did not exceed the more conservative 7.6 m total length estimate, this figure would make the largest individuals of *P. benedenii* much larger than any modern or fossil specimen of white shark (*Carcharodon carcharias*) for which a total body length has been reliably measured/estimated (up to ca. 7 m or slightly more; [63,64]).

Interestingly, *P. benedenii* may have reached its maximum size values during the Pliocene [4]. Thus, for some time, *C. carcharias* and *P. benedenii* persisted side-by-side as two of the largest macrophagous sharks of at least some quarters of the global ocean, including the Mediterranean Sea, though the latter—and larger—taxon appears to have been consistently rarer than the former.

5.2. Body Shape

Inferring the body shape of an extinct animal whose taxonomically informative remains are essentially limited to overall rare fossil teeth may look as a wild-goose chase. Nonetheless, some insightful guesses on the body aspect of false makos were provided by Kent [57] based on Otodontidae and Lamnidae being regarded as the most derived lineages of Lamniformes as well as being sister groups to each other. *Parotodus benedenii* was thus

reconstructed as characterized by a stiff and fusiform body, with a restricted jaw protrusion, long pectoral fins, an elevated first dorsal fin, reduced second dorsal and anal fins with pivoting bases, a slightly depressed caudal peduncle, caudal keels and a lunate tail, as well as by gigantothermy. Furthermore, considering the alleged open-sea palaeoenvironmental preferences of *P. benedenii* (see Section 5.3 below), Kent [57] hypothesised that false makos may have displayed long, wing-like pectoral fins like those of extant pelagic sharks such as *Alopias superciliosus*, *Isurus paucus*, *Carcharhinus longimanus* and *Prionace glauca*.

Kent's [57] painstaking reconstruction of the body shape of *P. benedenii* is partly dependent on what is currently known as the "Lamnoidea hypothesis", that is, the existence of a sister group relationship between otodontids and lamnids [65]. Such a hypothesis, however, is hotly debated [66,67], which suggests that alternative body shapes should also be considered. Among the aspects of Kent's [57] reconstruction that may merit some rethinking is thermoregulation, whose role in *P. benedenii* could be reappraised in light of the recent discovery that regionally endothermic traits are commoner than hitherto known across Lamniformes ([68]; but see also [69] for an assessment of *P. benedenii* as an ectothermic species).

5.3. Habitat Preferences

That the false mako was a pelagic shark with a predilection for open-sea settings is widely recognised in the literature. Based on the common occurrence of teeth of *Parotodus benedenii* in nodules of the Central Pacific seafloor [22,23,70] hypothesised an offshore lifestyle for this extinct mackerel shark species. Cappetta [1] pointed out that the members of the genus *Parotodus* were essentially pelagic forms whose presence in neritic fossil-bearing localities should be regarded as exceptional. Ward et al. [2] also noted that teeth of *Parotodus* spp. occur most typically in mid- and outer shelf settings. Canevet [3] and Everaert [59] followed on the same lines, supporting a preference for pelagic, farshore habitats for *P. benedenii*.

With regard to the new Tuscan Pliocene records, the one with the best stratigraphic control (i.e., GAMPS-00876a) also originates from open shelf deposits [40]. We may be content to suggest that *P. benedenii* was an open-sea shark that frequented the marginal-marine waters much less commonly than the eurytrophic littoral forms (*sensu* [71]) such as the bull shark (*Carcharhinus leucas*) and tiger shark (*Galeocerdo cuvier*), which were also present in the Mediterranean Basin in Pliocene times [27]. In all likelihood, *P. benedenii* was also less coastal than *C. carcharias*, which nonetheless has recently been demonstrated to be more pelagic than was previously thought [72]. All things considered, significant differences in habitat preferences suggest that some degree of ecological partitioning existed between *P. benedenii* and other elasmobranch apex predators of the Pliocene mid-latitude seas, including *C. carcharias*, *C. leucas* and *G. cuvier*.

5.4. Trophic Ecology

In order to propose a comprehensive reconstruction of the palaeobiology of *P. benedenii*, its feeding habits should also be discussed. Given the highly unusual shape of its teeth, as well as the little that is positively known about its anatomy beyond the dentition, the trophic ecology of *Parotodus benedenii* remains quite a conundrum, though most authors agree that *P. benedenii* was a formidable carnivore [2,27,56]. Kent and Powell [56] astutely noted that the "*P. benedenii* [sic] teeth are adapted for piercing and rending fibrous, compliant tissues [...] such as the skin and muscles of vertebrate prey [...]. Functionally, the teeth and dentition of *P. benedenii* more closely resemble those of the extinct mosasaurs and the extant killer whales [*Orcinus orca*], than those of other sharks. With a piercing-lacerating dentition of large, robust teeth attached to equally robust jaws, *P. benedenii* could have produced gaping wounds and massive soft tissue trauma in their prey". Compagno (in [15]) suggested that *P. benedenii* "fed by grabbing prey, such as seabirds, porpoises, and seals, with its teeth and swallowing it whole". Ward et al. [2] further observed that all the nominal species of *Parotodus* display relatively little damage to the apex of their tooth crowns, particularly

compression fractures caused by impacts on bone, which in turn may suggest that this predator used to eat relatively soft-bodied prey such as sharks. All things considered, the sturdy, smooth-edged teeth of *P. benedenii* appear to be less fit than the strongly compressed, serrated teeth of, e.g., *Carcharodon carcharias* for slicing flesh [56], as well as for dealing with somewhat coriaceous food items such as sea turtles (especially the hard-shelled cheloniids).

In our opinion, comparisons between the dental design of the false mako and those of the living taxa of Lamniformes are of somewhat limited usefulness for the purposes of clarifying the trophic ecology of *P. benedenii*. Though similarities with the extant species *Isurus oxyrinchus* (aka the shortfin mako, a member of Lamnidae) and *Alopias vulpinus* (aka the common thresher shark, a member of Alopiidae) have long been highlighted [4], differences are so considerable that whether functional and dietary convergence exist between *P. benedenii* and the aforementioned mackerel shark species remains uncertain at best. Teeth of *P. benedenii* are also similar to those of some Cretaceous lamniforms such as *Cardabiodon* [14], whose feeding habits are similarly uncertain.

Further considerations on the trophic ecology of *P. benedenii* may be made by considering the alleged habitat preferences of this extinct taxon. Unlike what is known for *C. carcharias*, a predilection for farshore, essentially pelagic settings would have made coastal animals such as seals only rarely available as potential prey items for *P. benedenii* [73]. In turn, it is reasonable to hypothesise that large vertebrate carcasses drifting in the open sea would have provided the piercing-lacerating dentition of the essentially pelagic *P. benedenii* with relatively soft carrion to dismember and forage on, especially in the cetacean-rich Pliocene Mediterranean palaeobiotopes [64,74]. All things considered, significant differences in tooth design and dentition, which we interpret as witnessing to an only partial overlap of dietary spectra, suggest that a certain degree of trophic partitioning existed between *P. benedenii* and other elasmobranch apex predators of the Mediterranean Basin and other Neogene mid-latitude seas, including, in Pliocene times, the extant species *C. carcharias*, *Carcharhinus leucas* and *Galeocerdo cuvier*.

However well-reasoned these arguments may be, it should be noted that no taphonomic evidence exists of the trophic ecology of *Parotodus benedenii*. As a possible reflection of its farshore habitats, as well as of the alleged “overrepresentation” of shelfal palaeoenvironments in the Cenozoic fossil record of marine vertebrates such as whales [75], no fossil skeletons appear to exist at present preserving associated teeth or even bite marks that would compare favourably with the false mako. That said, the possibility that some of the widespread unserrated bite marks that are often assigned to commoner shark species such as *Cosmopolitodus* spp. [76–78] do rather belong to *P. benedenii* should also be taken into account.

6. Conclusions

We reported on the discovery of new specimens of *Parotodus benedenii* from Pliocene deposits of the Valdelsa Basin (Tuscany, central Italy). These new records comprise some of the geologically youngest finds of *P. benedenii* worldwide, witnessing to the survival of false makos until the Late Pliocene at least. Thus, for some time, the white shark and *P. benedenii* persisted side by side as two of the largest macrophagous sharks of at least some quarters of the global ocean, including the Mediterranean Sea.

Building upon a thorough literature review, an updated synthesis of the palaeobiology of *P. benedenii* was also provided herein. In light of the morphological evidence, and considering previously published suggestions, *P. benedenii* may be reconstructed as a large-sized (up to more than 7 m total body length), carnivorous shark that dwelt in pelagic settings and fed primarily on large, soft prey and scavenging items. Open-sea habits and a trophic spectrum that was likely poor in coriaceous prey items suggest that some ecological partitioning existed between *P. benedenii* and other elasmobranch apex predators of the Neogene mid-latitude seas (including, in Pliocene times, the extant species *C. carcharias*, *Carcharhinus leucas* and *Galeocerdo cuvier*).

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Cappetta, H. *Handbook of Paleichthyology, Vol. 3E. Chondrichthyes: Mesozoic and Cenozoic Elasmobranchii: Teeth*; Dr. Friedrich Pfeil: Munich, Germany, 2012; pp. 1–512.
2. Ward, D.J.; Nakatani, D.; Bernard, E.L. A new species of *Parotodus* (Lamniformes: Otodontidae) from the Oligocene of Japan. In Proceedings of the 61st PalAss Annual Meeting, London, UK, 17–18 December 2017.
3. Canevet, J.-M. Des dents de requins fossiles! 9. Le genre *Parotodus*: Le faux requin-mako. *Fossiles-Rev. Fr. Paléontol.* **2019**, *37*, 39–50.
4. Kent, B.W. The cartilaginous fishes (chimaeras, sharks, and Rays) of Calvert Cliffs, Maryland, USA. In *The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland*; Godfrey, S.J., Ed.; Smithsonian Institution Scholarly Press: Washington, DC, USA, 2018; pp. 45–156.
5. Le Hon, H. *Préliminaire d'un Mémoire sur les Poissons Fossiles Tertiaires de Belgique*; Muquardt: Bruxelles, Belgium, 1871; pp. 1–15.
6. Menesini, E. Ittiodontoliti miocenici di Terra d'Otranto. *Palaeontogr. Ital.* **1969**, *65*, 1–61.
7. De Ceuster, J. Stratigrafische interpretatie van jongcenozoische afzettingen bij Rumst (België, provincie Antwerpen) en beschrijving van de in een post-mioceen basisgrond aangetroffen vissenfauna, II. Systematische beschrijvingen en conclusies. *Meded. Werkgr. Tert. Kwart. Geol.* **1976**, *13*, 119–172.
8. Applegate, S.P.; Espinosa-Arrubarrena, L. The Fossil History of *Carcharodon* and Its Possible Ancestor, *Cretolamna*. A Study in Tooth Identification. In *Great White Sharks. The Biology of Carcharodon carcharias*; Klimley, A.P., Ainley, D., Eds.; Academic Press: San Diego, CA, USA, 1996; pp. 19–36. [[CrossRef](#)]
9. Cappetta, H. Modification du statut générique de quelques espèces de séliaciens crétacés et tertiaires. *Palaeovertebrata* **1980**, *10*, 29–42.
10. Heinzl, L. Collecting fossil shark teeth in the Lee Creek Mine, Aurora, Nc. *M.A.P.S. Dig.* **2000**, *23*, 110–117.
11. Fitzgerald, E.; Schmidt, R. *Fossils of Beaumaris*; Museum of Victoria: Melbourne, Australia, 2015; pp. 1–15.
12. Shimada, K.; Chandler, R.E.; Lam, O.L.T.; Tanaka, T.; Ward, D.J. A new elusive otodontid shark (Lamniformes: Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the 'megatoothed' clade. *Hist. Biol.* **2017**, *29*, 704–714. [[CrossRef](#)]
13. Herman, J. Réflexions sur la systématique des Galeoidei et sur les affinités du genre *Cetorhinus*, à l'occasion de la découverte d'éléments de la denture d'un exemplaire fossile dans le sables du Kattendijk à Kallo (Pliocène inférieur, Belgique). *Ann. Soc. Géol. Belg.* **1979**, *102*, 357–377.
14. Siverson, M. A New Large Lamniform Shark from the Uppermost Gearle Sandstone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh. Earth Sci.* **1999**, *90*, 49–65. [[CrossRef](#)]
15. Purdy, R.; Schneider, V.; Applegate, S.; McLellan, J.; Meyer, R.; Slaughter, R. The Neogene Sharks, Rays, and Bony Fishes from Lee Creek Mine, Aurora, North Carolina. In *Geology and Paleontology of the Lee Creek Mine, North Carolina*, 3rd ed.; Smithsonian Contributions to Paleobiology; Ray, C.E., Bohaska, D.J., Eds.; Smithsonian Institution Press: Washington, DC, USA, 2001; Volume 90, pp. 71–202.
16. Iserbyt, A.; De Schutter, P.J. Quantitative analysis of elasmobranch assemblages from two successive Ypresian (early Eocene) facies at Marke, western Belgium. *Geol. Belg.* **2012**, *15*, 146–153.
17. Mas, G. Presència de *Parotodus benedeni* (Le Hon, 1871) (Pisces: Chondrichthyes: Otodontidae) al Neogen de Mallorca i Menorca (Illes Balears, Mediterrània occidental). Consideracions taxonòmiques i paleoambientals. *Boll. Soc. Hist. Nat. Balears* **2003**, *46*, 85–90.

18. González-Barba, G. Descripción de la Asociación Faunística de Elasmobranchios Fósiles del Conglomerado Basal en las Formaciones San Gregorio y el Cien (Oligoceno Temprano) de Baja California Sur, México. Ph.D. Thesis, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico, 2008.
19. Betancort, J.F.; Lomoschitz, A.; Meco, J. Early Pliocene fishes (Chondrichthyes, Osteichthyes) from Gran Canaria and Fuerteventura (Canary Islands, Spain). *Estud. Geol.* **2016**, *72*, e054. [[CrossRef](#)]
20. Carrillo-Briceño, J.D.; Villafaña, J.A.; De Gracia, C.; Flores-Alcívar, F.F.; Kindlimann, R.; Abella, J. Diversity and paleoenvironmental implications of an elasmobranch assemblage from the Oligocene–Miocene boundary of Ecuador. *PeerJ* **2020**, *8*, e9051. [[CrossRef](#)] [[PubMed](#)]
21. Malyshkina, T.P.; Ward, D.J.; Nazarkin, M.V.; Nam, G.S.; Kwon, S.H.; Lee, J.H.; Kim, T.W.; Kim, D.K.; Baek, D.S. Miocene Elasmobranchii from the Duho Formation, South Korea. *Hist. Biol.* **2023**, *35*, 1726–1741. [[CrossRef](#)]
22. Belyaev, G.M.; Glikman, L.S. The teeth of sharks on the floor of the Pacific Ocean. *Trudy Inst. Okaenol. Akad. Nauk. SSSR* **1970**, *88*, 236–251. (In Russian)
23. Roux, C.; Geistdoerfer, P. Dents de requins et bulles tympaniques de cétacés: Noyaux de nodules polymétalliques récoltés dans l’océan Indien. *Cybium* **1988**, *12*, 129–137.
24. Ward, D.J.; Bonavia, C.G. Additions to, and a review of, the Miocene shark and ray fauna of Malta. *Cent. Medit. Nat.* **2001**, *3*, 131–146.
25. Vera-Peláez, J.L.; Lozano-Francisco, M.C.; Pascual-Alayón, P.; Báez, J.C. Primera cita de *Paratodus benedeni* (Le Hon, 1871) (Chondrichthyes, Lamnidae) en los depósitos del Mioceno superior (Tortonense) de Antequera (Málaga) y del Plioceno inferior (Zancliense) del Puerto de Santa María (Cádiz), sur de España. *Rev. Bras. Paleontol.* **2016**, *19*, 341–346. [[CrossRef](#)]
26. Marsili, S.; Carnevale, G.; Danese, E.; Bianucci, G.; Landini, W. Early Miocene vertebrates from Montagna della Maiella, Italy. *Ann. Paléontol.* **2007**, *93*, 27–66. [[CrossRef](#)]
27. Marsili, S. Analisi Sistematica, Paleocologica e Paleobiogeografica della Selociofauna Plio-Pleistocenica del Mediterraneo. Ph.D. Thesis, Università di Pisa, Pisa, Italy, 2007.
28. Manganelli, G.; Benocci, A.; Spadini, V. The scientific bibliography of Roberto Lawley (1818–1881) and his contribution to the study of fossil sharks. *Arch. Nat. Hist.* **2003**, *33*, 267–281. [[CrossRef](#)]
29. Lawley, R. *Nuovi Studi Sopra i Pesci ed Altri Vertebrati Fossili delle Colline Toscane*; Tipografia dell’arte della Stampa: Firenze, Italy, 1876; pp. 1–122.
30. Landini, W. Revisione degli «ittiodontoliti pliocenici» della Collezione Lawley. *Palaeontogr. Ital.* **1977**, *70*, 92–134.
31. Landini, W. Nuovi Studi Sugli Ittiodontoliti della Collezione Lawley. Master’s Thesis, Università di Pisa, Pisa, Italy, 1972.
32. Benvenuti, M.; Del Conte, S.; Scarselli, N.; Dominici, S. Hinterland basin development and infilling through tectonic and eustatic processes: Latest Messinian–Gelasian Valdelsa Basin, Northern Apennines, Italy. *Basin Res.* **2014**, *26*, 387–402. [[CrossRef](#)]
33. Capellini, G. Balene fossili toscane. III *Idiocetus Guicciardini*. *Mem. R. Accad. Sci. Ist. Bologna* **1905**, *6*, 71–80.
34. Azzaroli, A. The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany. *Palaeontogr. Ital.* **1992**, *79*, 1–41.
35. Borselli, V.; Cozzini, F. Il recupero di un cetaceo fossile in località Ponte a Elsa (Pisa). *Museol. Sci.* **1991**, *8*, 9–22.
36. Bianucci, G. A new record of baleen whale from the Pliocene of Tuscany (Italy). *Atti Soc. Tosc. Sci. Nat. Mem. Ser. A* **1995**, *102*, 101–104.
37. Rustioni, M.; Mazza, P. *Taphonomic analysis* of *Tapirus arvernensis* remains from the lower Valdarno (Tuscany, Central Italy). *Geobios* **2001**, *34*, 469–474. [[CrossRef](#)]
38. Abbazzi, L.; Benvenuti, M.; Ceci, M.E.; Esu, D.; Faranda, C.; Rook, L.; Tangocci, F. The end of the Lago-Mare time in the SE Valdelsa Basin (central Italy): Interference between local tectonism and regional sea-level rise. *Geodiversitas* **2008**, *30*, 611–639.
39. Dominici, S.; Rook, L.; Benvenuti, M.; Abbazzi, L. Tapir remains in paralic deposits of Pliocene age in Lower Valdarno (Tuscany, Italy): Facies analysis and taphonomy. *Geobios* **1995**, *28*, 131–135. [[CrossRef](#)]
40. Dominici, S.; Danise, S.; Benvenuti, M. Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna. *Earth-Sci. Rev.* **2018**, *176*, 277–310. [[CrossRef](#)]
41. Collareta, A.; Bosselaers, M.; Bianucci, G. Jumping from turtles to whales: A Pliocene fossil record depicts an ancient dispersal of Chelonibia on mysticetes. *Riv. Ital. Paleontol. Strat.* **2016**, *122*, 35–44. [[CrossRef](#)]
42. Collareta, A.; Casati, S.; Catanzariti, R.; Di Cencio, A. First record of the knifetooth sawfish *Anoxypristis* (Elasmobranchii: Rhinopristiformes) from the Pliocene of Tuscany (central Italy). *Neues Jahrb. Geol. Paläontol. Abh.* **2017**, *284*, 289–297. [[CrossRef](#)]
43. Collareta, A.; Casati, S.; Zuffi, M.A.L.; Di Cencio, A. First authentic record of the freshwater turtle *Mauremys* from the upper Pliocene of Italy, with a new occurrence of the rarely reported ichnotaxon *Thatchtelithichnus holmani*. *Carnets Geol.* **2020**, *20*, 301–313. [[CrossRef](#)]
44. Collareta, A.; Merella, M.; Casati, S.; Di Cencio, A. Did titanic stingrays wander the Pliocene Mediterranean Sea? Some notes on a giant-sized myliobatoid stinger from the Piacenzian of Italy. *Neues Jahrb. Geol. Paläontol. Abh.* **2020**, *298*, 155–164. [[CrossRef](#)]
45. Collareta, A.; Merella, M.; Casati, S.; Coletti, G.; Di Cencio, A. Another thermophilic “Miocene survivor” from the Italian Pliocene: A geologically young occurrence of the pelagic eagle ray *Aetobatus* in the Euro-Mediterranean region. *Carnets Geol.* **2021**, *21*, 203–214. [[CrossRef](#)]
46. Collareta, A.; Mollen, F.H.; Merella, M.; Casati, S.; Di Cencio, A. Remarkable multicuspid teeth in a new elusive skate (Chondrichthyes, Rajiformes) from the Mediterranean Pliocene. *PalZ* **2021**, *95*, 117–128. [[CrossRef](#)]

47. Merella, M.; Collareta, A.; Casati, S.; Di Cencio, A.; Bianucci, G. Pliocene Geotourism: Innovative Projects for Valorizing the Paleontological Heritage of Three Different-Staged Quarries of Tuscany (Central Italy). *Geoheritage* **2023**, *15*, 82. [[CrossRef](#)]
48. Glikman, L.S. *Paleogene Sharks and Their Stratigraphic Importance*; Akad. Nauk S.S.S.R.: Moscow, Russia, 1964; pp. 1–228. (In Russian)
49. Leriche, M. Les poissons tertiaires de Belgique. IV. Les poissons néogènes. *Mém. Mus. Roy. Hist. Nat. Belg.* **1926**, *32*, 367–472.
50. Reinecke, T.; Louwyw, S.; Havekost, U.; Moths, H. The Elasmobranch Fauna of the Late Burdigalian, Miocene, at Werder-Uesen, Lower Saxony, Germany, and Its Relationships with Early Miocene Faunas in the North Atlantic, Central Paratethys and Mediterranean. *Palaeontos* **2011**, *20*, 1–207.
51. Collareta, A.; Kindlimann, R.; Baglioni, A.; Landini, W.; Sarti, G.; Altamirano, A.; Urbina, M.; Bianucci, G. Dental Morphology, Palaeoecology and Palaeobiogeographic Significance of a New Species of Requiem Shark (Genus *Carcharhinus*) from the Lower Miocene of Peru (East Pisco Basin, Chilcatay Formation). *J. Mar. Sci. Eng.* **2022**, *10*, 1466. [[CrossRef](#)]
52. ICZN [International Commission on Zoological Nomenclature]. *International Code of Zoological Nomenclature*, 4th ed.; International Trust for Zoological Nomenclature: London, UK, 1999; pp. 1–106.
53. Dubois, A. Genitives of species and subspecies nomina derived from personal names should not be emended. *Zootaxa* **2007**, *1550*, 49–68. [[CrossRef](#)]
54. Diesel Abegg, A.; Malta-Borges, L.; Tavares de Carvalho, J.D.; Mario-Da-Rosa, C.; Di Mare, R.A. Cases of unjustified emendations of scientific names dedicated to people in tarantulas (Mygalomorphae: Theraphosidae). *Rev. Colomb. Entomol.* **2016**, *42*, 201–202. [[CrossRef](#)]
55. Ranzani, C. *De Naturali Historia Dissertationes*; Novis Commentariis Accademie Instituti Scientiarum Bononiensis: Bologna, Italia, 1844; pp. 1–41.
56. Kent, B.W.; Powell, G.W., Jr. Reconstructed Dentition of the Rare Lamnoid Shark, *Parotodus benedeni* (Le Hon) from the Yorktown Formation (Early Pliocene) at Lee Creek Mine, North Carolina. *Mosasaur* **1999**, *6*, 1–10.
57. Kent, B.W. Speculations on the Size and Morphology of the Extinct Lamnoid Shark, *Parotodus benedeni* (Le Hon). *Mosasaur* **1999**, *6*, 11–15.
58. Marsili, S. Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediterranean elasmobranch fauna. *Atti Soc. Tosc. Sci. Nat. Mem. Ser. A* **2008**, *113*, 81–88.
59. Everaert, S. *Parotodus benedenii* (Le Hon, 1871) uit het Zand van Antwerpen (Midden Mioceen) te Berchem (Antwerpen, België). *Afzett. Werkgr. Tert. Kwart. Geol.* **2020**, *41*, 36–40.
60. Boessenecker, R.W.; Ehret, D.J.; Long, D.J.; Churchill, M.; Martin, E.; Boessenecker, S.J. The Early Pliocene extinction of the mega-toothed shark *Otodus megalodon*: A view from the eastern North Pacific. *PeerJ* **2019**, *7*, e6088. [[CrossRef](#)]
61. Pimiento, C.; Clements, C.F. When did *Carcharocles megalodon* become extinct? A new analysis of the fossil record. *PLoS ONE* **2014**, *9*, e111086. [[CrossRef](#)]
62. Goto, M.; Kobayashi, F.; Osawa, S. On the teeth of the genus *Isurus* from Tomioka City, Gumma Prefecture, Japan (preliminary report). *J. Geol. Soc. Jpn.* **1978**, *84*, 271–272. [[CrossRef](#)]
63. Adnet, S.; Balbino, A.C.; Antunes, M.T.; Marín-Ferrer, J.M. New fossil teeth of the White Shark (*Carcharodon carcharias*) from the Early Pliocene of Spain. Implication for its paleoecology in the Mediterranean. *Neues Jahrb. Geol. Palaontol. Abh.* **2010**, *256*, 7–16. [[CrossRef](#)]
64. Collareta, A.; Casati, S.; Di Cencio, A.; Bianucci, G. The deep past of the white shark, *Carcharodon carcharias*, in the Mediterranean Sea: A synthesis of its palaeobiology and palaeoecology. *Life* **2023**, *13*, 2085. [[CrossRef](#)]
65. Greenfield, T. List of skeletal material from megatooth sharks (Lamniformes, Otodontidae). *Paleoichthys* **2022**, *4*, 1–9.
66. Greenfield, T. Additions to “List of skeletal material from megatooth sharks”, with a response to Shimada (2022). *Paleoichthys* **2022**, *6*, 6–11.
67. Shimada, K. Phylogenetic affinity of the extinct shark family Otodontidae within Lamniformes remains uncertain—Comments on “List of skeletal material from megatooth sharks (Lamniformes, Otodontidae)” by Greenfield. *Paleoichthys* **2022**, *6*, 1–5.
68. Dolton, H.R.; Jackson, A.L.; Deaville, R.; Hall, J.; Hall, G.; McManus, G.; Perkins, M.W.; Rolfe, R.A.; Snelling, E.P.; Houghton, J.D.R.; et al. Regionally endothermic traits in planktivorous basking sharks *Cetorhinus maximus*. *Endanger. Species Res.* **2023**, *51*, 227–232. [[CrossRef](#)]
69. Griffiths, L.M.; Eagle, R.A.; Kim, S.L.; Flores, R.; Becker, M.A.; Maisch, H.M., IV; Trayler, R.B.; Chan, R.L.; McCormack, J.; Akhtara, A.A.; et al. Endothermic physiology of extinct megatooth sharks. *Proc. Natl. Acad. Sci. USA* **2023**, *120*, e221815312. [[CrossRef](#)]
70. Kuga, N. Revision of the Neogene Mackerel Shark Genus *Isurus* from Japan. *Mem. Fac. Sci. Kyoto Univ. Ser. Geol. Miner.* **1985**, *51*, 1–20.
71. Compagno, L.J.V. Alternative life-history styles of cartilaginous fishes in time and space. *Environ. Biol. Fishes* **1990**, *28*, 33–75. [[CrossRef](#)]
72. Boustany, A.M.; Davis, S.F.; Pyle, P.; Anderson, S.D.; Le Boeuf, B.J.; Block, B.A. Expanded niche for white sharks. *Nature* **2002**, *415*, 35–36. [[CrossRef](#)]
73. Compagno, L.J.V. FAO species catalogue. Sharks of the world. In *An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes*; FAO: Rome, Italy, 1984; Volume 4, pp. 1–258.

74. Collareta, A.; Merella, M.; Casati, S.; Di Cencio, A.; Bianucci, G. Smoking guns for cold cases: The find of a *Carcharhinus* tooth piercing a fossil cetacean rib, with notes on the feeding ecology of some Mediterranean Pliocene requiem sharks. *Neues Jahrb. Geol. Paläontol. Abh.* **2022**, *305*, 145–152. [[CrossRef](#)]
75. Dominici, S.; Danise, S.; Cau, S.; Freschi, A. The awkward record of fossil whales. *Earth-Sci. Rev.* **2020**, *205*, 103057. [[CrossRef](#)]
76. Noriega, J.I.; Cione, A.L.; Aceñolaza, F.G. Shark tooth marks on Miocene balaenopterid cetacean bones from Argentina. *Neues Jahrb. Geol. Paläontol. Abh.* **2007**, *245*, 185–192. [[CrossRef](#)]
77. Collareta, A.; Cigala Fulgosi, F.; Bianucci, G. A new kogiid sperm whale from northern Italy supports psychrospheric conditions in the early Pliocene Mediterranean Sea. *Acta Palaeontol. Polon.* **2019**, *64*, 609–626. [[CrossRef](#)]
78. Godfrey, S.J.; Lowry, A.J. The ichnospecies *Linichnus bromleyi* on a Miocene baleen whale radius preserving multiple shark bite-shake traces suggests scavenging. *Carnets Geol.* **2021**, *21*, 391–398. [[CrossRef](#)]

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