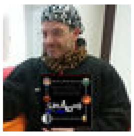
Bibliographic ADDENDA to the Open Question
""Megalodon is hostage to an anthropomorphic interpretation hyper iconic-metaphorical of the fossil remains (strong allometry & heterochrony)??””



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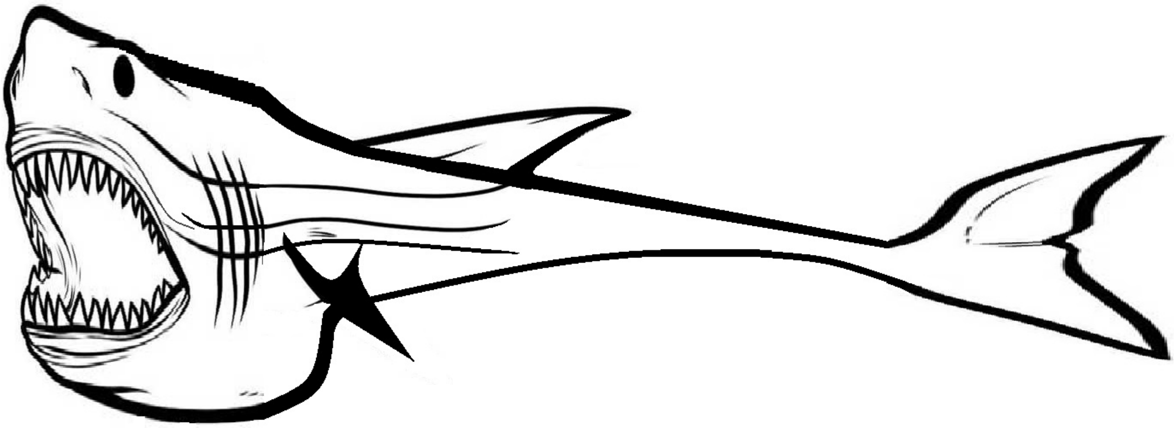

-------Tessellated calcified cartilage and placoid scales of the Neogene megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), offer new insights into its biology and the evolution of regional endothermy and gigantism in the otodontid clade. Historical Biology, International Journal of Paleobiology, June 2023. DOI:10.1080/08912963.2023.2211597.

ABSTRACT.-- The late Neogene megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), is mostly known for its gigantic teeth and vertebrae. Re-examination of the rock matrix surrounding a previously described associated tooth set of O. megalodon from the upper Miocene of Japan resulted in the observation of numerous fragments of tessellated calcified cartilage and placoid scales. The morphology of each tessera and the arrangement of overall tessellated calcified cartilage are practically identical to those of extant chondrichthyans. Many placoid scales possess pronounced, rather broadly-spaced keels. A quantitative relationship between interkeel distances of keeled scales and reported cruising speeds across extant pelagic lamniforms and carcharhiniforms suggests that O. megalodon with a representative interkeel distance of ca. 100 µm was not a fast swimmer. We propose that O. megalodon was generally a slow cruising shark with occasional burst swimming for prey capture, where much of its metabolic heat through regional endothermy was possibly used to facilitate the digestion of large pieces of ingested meat as well as absorbing and processing nutrients. If so, the relative importance of the functional roles of regional endothermy possibly shifted from maintaining high cruising speeds to visceral food processing through the evolution towards gigantism in otodontids.

Conclusions

Because energetics is tightly linked to the fitness of organisms (Gleiss et al. Citation2022), it is not an overstatement that the structure and dynamics of ecosystems are a direct consequence of organisms’ metabolism (Brown et al. Citation2004). Therefore, understanding the biology of gigantic organisms like Otodus megalodon and its phylogenetic relatives is meaningful because they must have played significant roles in the evolution of their ecosystems. This present study has offered new insight into such issues by examining associated tessellated calcified cartilage and placoid scales from an individual O. megalodon estimated to be 11.7 m TL collected from the lower upper Miocene (middle Tortonian) Tsuchishio Formation in central Japan. The morphology of each predominantly hexagonal tessera and the arrangement of overall tessellated calcified cartilage in O. megalodon are practically identical to those of the extant chondrichthyans, suggesting that the same mechanism for the ontogenetic development of cartilage operated in O. megalodon. The collected placoid scales can be classified into three broad categories, where their overall sizes are comparable to many extant pelagic lamniforms and carcharhiniform sharks, indicating that the exceptional gigantism seen in O. megalodon did not necessarily produce exceptionally large placoid scales. Many of the scales possess pronounced parallel keels on the crown surface with a representative IKD of about 100 µm. Our study demonstrates that, albeit somewhat weak, there is a quantitative relationship between IKDs of keeled placoid scales and reported CS values among extant pelagic lamniform and carcharhiniforms, and it suggests that O. megalodon was not a fast-swimming shark. Specifically, our inferred cruising speed for O. megalodon is approximately 2.0 km h−1 with a range of 0.9–3.0 km h−1. This result is in contrast with previous studies (Jacoby et al. Citation2016; Ferrón Citation2017; Cooper et al. Citation2022) that suggested that O. megalodon was a fast-swimming (4.8–5.1 km h−1) shark. Whereas O. megalodon fed on marine mammals based on the fossil record, our interpretation is that O. megalodon was generally a relatively slow cruising shark with occasional burst swimming for prey capture; however, much of its metabolic heat through regional endothermy was possibly used to promote digestion of large pieces of meat it ingested as well as absorbing and processing

nutrients. If our interpretations are correct, then, the relative importance of the functional roles of regional endothermy possibly shifted from maintaining high CSs in the early part of the otodontid history marked by ~3 m TL Cretalamna to visceral food processing through the evolution towards gigantism leading to 15+ m TL O. megalodon that must have swallowed large pieces of food.
https://doi.org/10.1080/08912963.2023.2211597
https://www.researchgate.net/publication/371841325

-------Allometric Growth of the Enigmatic Deep-Sea Megamouth Shark Megachasma pelagios Taylor, Compagno, and Struhsaker, 1983 (Lamniformes, Megachasmidae). Fishes 2023, 8(6) -- DOI:10.3390/fishes8060300.
Abstract.--- Megamouth sharks Megachasma pelagios Taylor, Compagno, and Struhsaker, 1983, are a large-bodied, planktivorous, deep-sea species with peculiar morphology. Since their initial description in the late 20th century, many individuals of different sizes have been reported, but few studies examined ontogenetic changes in body shapes. Here, we assess the growth changes in their heads and fins based on length measurements from nine different-sized individuals (177–544 cm in total length). Bivariate analyses showed that the head becomes larger relative to body length with increasing body size (i.e., positive allometry), whereas the relative size of the caudal fin remains constant (i.e., isometric growth). This trend differs from basking sharks and apparently resembles whale sharks and some baleen whales, although they are all large-bodied filter feeders. Given that relative mouth size is linked to feeding modes, our results suggest that megamouth sharks have different feeding modes from ram-feeding basking sharks and may have some similarity with suction-feeding whale sharks and engulfment-feeding baleen whales.
Discussion.--- We showed that 14 of the 26 measurements taken from megamouth sharks scale positively and 9 of them scale isometrically against total length (Table S2). Although 95% confidence intervals of slopes included 1 for the five variables from the head (Table S2), these results might represent “soft” isometry [34], associated with small sample sizes and wide confidence intervals. Indeed, the estimates of slopes (1.190–1.424) are well above 1. Moreover, we found at least one of these variables (the mouth width) is larger and increases at a faster rate in megamouth sharks than other lamniform species. This result shows that megamouth sharks deviate from the main trend of negative allometry to isometry seen in other lamniform species (Figure 5B). Collectively, our results indicate that head measurements generally scale positively in megamouth sharks, unlike other lamniform species.
Intriguingly, only three variables we examined show negative allometry. One of them (second dorsal fin height) had a low R2 value, suggesting that this result represents individual variations rather than general patterns during growth (Table S2). Collectively, our results showed largely positive allometric growth during the ontogeny of megamouth sharks, especially around the head, as well as isometric scaling in the caudal fin. Such a growth trend differs from that of basking sharks, which show negative allometric growth in the caudal fin and head [15]. It also differs from the growth patterns of white sharks and tiger sharks, in which the caudal fin scales negatively [14,15,19,20,22]. Isometric growth trends in caudal fins, as we observed for megamouth sharks, were reported for a variety of small-bodied sharks, such as nurse sharks Ginglymostoma cirratum Bonnaterre, 1788, and spiny dogfish [14,18]. Given that megamouth sharks are the third largest extant shark species in the world, being only smaller than whale sharks Rhincodon typus Smith, 1828, and basking sharks [11], it is intriguing that the changes in relative length of multiple body regions during the growth of this

species are similar to those of smaller shark species, rather than its distant large relatives. It should be emphasized, however, that the results presented in this work should be considered preliminary due to the relatively small sample size (n = 9). In some cases, we may have failed to detect allometric relationships (“soft” isometry) [34], as discussed earlier. While individuals of both sexes were pooled in our analyses, we feel this is reasonable due to the absence of sex differences in body shapes in this species. Moreover, although our dataset covers an extensive size range (177–544 cm in total length), medium-sized individuals (250–350 cm) are lacking [8], partially limiting our analyses. Note, however, that some studies of fossil organisms used even fewer specimens than this study to successfully detect allometric growth trends [35,36,37]. To advance our understanding of the relative growth of megamouth sharks, detailed length measurements from various parts of the body, rather than just total length and weight, should be reported when new individuals are found in future studies.

The heterocercal caudal fin of megamouth sharks bears a horizontally directed vertebral column with a small curvature (low “Cobb’s angle”) and posteriorly directed hypochordal rays [38]. Such fin morphology is a basal condition for lamniforms, and the caudal fin with a dorsally oriented vertebral column seen in basking sharks and Lamnidae is a derived character [38]. Although our results should be considered somewhat provisional, we suggest several explanations for why megamouth sharks retain isometric growth patterns in the caudal fin instead of the negative allometry seen in white and basking sharks. Megamouth sharks feed primarily on slow-moving zooplankton such as euphausiids, copepods, and jellyfishes [11,26,30]. Although little information is available for the diet of juveniles, tooth morphology does not appear to change during growth [27], suggesting that diets do not change, either. It is possible, therefore, that no change in feeding ecology is reflected by little changes in the shape or proportion of caudal fins. Indeed, isometric growth in the caudal fin was reported for nurse sharks [14], which also prey on slow-moving organisms, including benthic fishes and invertebrates, without showing dramatic changes in diets during growth [20,39]. Of note, basking sharks also prey on small zooplankton and do not exhibit ontogenetic changes in diets, yet this species shows negative allometry in the caudal fin [15]. Basking sharks have a unique caudal fin morphology among lamniforms with a dorsally oriented vertebral column, yet they have posteriorly directed hypochordal rays, unlike ventrally directed hypochordal rays in Lamnidae. Thus, their caudal fin is morphologically intermediate between heterocercal and homocercal morphotypes [15,38]. Such distinct morphology is thought to reflect a unique lifestyle of this species, cruising at a slow speed with the mouth opened to collect foods [15,38,40]. Perhaps the difference in the shape of the caudal fin, or the growth trend, raises the possibility that the foraging mode of megamouth sharks is different from that of basking sharks. Another explanation, perhaps simpler, is that because megamouth sharks are phylogenetically less derived than basking sharks and other lamnid species within Lamniformes (e.g., [11,41,42,43]), they retain their morphologically basal condition throughout their lifespan.

We found that the heads of megamouth sharks show positive allometry during growth, unlike basking sharks which exhibit negative allometry [15]. While eye size shows negative allometry, this trend is common among vertebrates, including large sharks [15,44,45]. Given that head shape in vertebrates, including sharks, is closely linked to their diet and feeding modes [19], our findings raise the possibility that megamouth and basking sharks, both of which are filter feeders, use different feeding modes. Interestingly, the feeding mode of megamouth sharks is controversial. It was initially suggested that megamouth sharks are a ram feeder (i.e., swimming towards prey and catching it without using suction forces generated by the mouth) like basking sharks [1]. However, Compagno [46] raised the possibility of suction feeding (i.e., quickly opening the mouth to generate suction forces to collect prey), as in whale sharks, based on the morphological characteristics of megamouth sharks, including the heavy and anteroposteriorly elongated jaw, restricted internal gill openings, relatively weak body musculature, and relatively soft fins. Further, Nakaya et al. [47] suggested that megamouth sharks are an engulfment feeder (similar to rorqual and humpback whales) in that they approach zooplankton swarms and engulf prey-laden water by expanding the gape laterally and ventrally. Tomita et al. [48] provided support for the ram feeding mode, based on their analyses which showed that the ceratohyal of megamouth sharks is not stiff enough to produce suction forces.

Comparing the scaling pattern of the megamouth shark's head and mouth to that of other aquatic animals with known feeding modes may shed some light on this issue. Mobulid rays are large planktivorous elasmobranchs that employ ram feeding [49]. Setyawan et al. [50] showed that the head width of the reef manta ray Mobula alfredi Krefft, 1868, scales negatively against body length, similar to basking sharks. Additionally, we found that in lamniform sharks with a conical head similar to basking sharks, mouth width and head length scale isometrically or negatively (Figure 5). In general, Lamniform sharks with a conical head are fast swimmers, and they ram-feed on their prey by approaching close enough to consume it [48,51]. While one species included in our analyses (goblin sharks Mitsukurina owstoni Jordan, 1898) has a slightly different head morphology compared to typical conical shape in lamniforms (i.e., elongated and flattened), it nevertheless shares a pointed head tip and also performs ram-feeding [48,52]. Given that mouth width is strongly correlated with the perimeter of the upper jaw in sharks [33], isometric to negatively allometric scaling of the mouth width in lamniforms (excluding megamouth sharks) suggest that the shape of the head remains conical or becomes more pointed as the shark grows. Given that conical head shape in sharks reduces drag while swimming [14,19], narrowing or conserving the conical morphology of the head in "typical" lamniform might be advantageous to their ram-feeding behavior, as they have to swim fast enough to approach the prey [51]. While basking sharks cruise at a slower speed during feeding than expected for their size, they nevertheless capture zooplankton by strong forward swimming [53,54,55,56].

In contrast, the lack of conical head morphology [1,11] combined with the apparent positive scaling of the head size suggests that head shape and its growth pattern in megamouth sharks are not optimal for the obligate ram-feeding mode seen in basking sharks and other lamnid species. Our result of positive allometry for the heads of megamouth sharks is similar to that of whale sharks [44,57]. Additionally, the largemouth bass Micropterus salmoides Lacépède, 1802, considered as a behavioral analogue of megamouth sharks by Nakaya et al. [47] in its being a slow-swimming, high-volume suction feeder [51,58], show isometric [59,60] to positive allometry in the heads [61]. In rorqual and humpback whales, considered as another behavioral analogue of megamouth sharks by Nakaya et al. [47] by their engulfment feeding mode, the dimensions of the jaw and skull scale positively [62,63]. These comparisons suggest that the head of megamouth sharks' scales like that of a suction or engulfment feeder. Although Tomita et al. [48] argued against the obligate suction feeding mode in megamouth sharks, these authors noted that the engulfment feeding mode is not inconsistent with their results given that the engulfment feeding is a derived mode of ram feeding. Their suggestion that the ceratohyal of megamouth sharks is not stiff enough to perform obligate suction feeding [48], coupled with the results of this study, might imply that the feeding mode of this species is engulfment, or at least differs from the obligate ram feeding mode of basking sharks. By having a larger head relative to body, larger megamouth sharks may be able to engulf larger amounts of food and water, increasing the efficiency of their feeding activities.

Another potential piece of evidence that megamouth sharks are engulfment feeders comes from their diet; stomach contents analyses showed that megamouth sharks feed primarily on krill (euphausiid) that form dense swarms [30], rather than the dispersed prey of basking sharks [55]. To capture such dense swarms, suction or engulfment feeding modes are more efficient than the ram-feeding mode employed by basking sharks [56]. Nevertheless, as Watanabe and Papastamatiou [11] noted, the feeding behavior of megamouth sharks should be directly observed by biologging technology with animal-borne video cameras [64] in future studies to resolve this debate.

The anterior margin and the height of pectoral fins show isometric scaling. This result is consistent with the studies on other shark species, including other lamniforms [20,21]. In contrast, pectoral fin bases showed positive allometry. This result is different from other lamniform species [21], in which pectoral fin width scales isometrically. Tomita et al. [24] found that the pectoral fins of megamouth sharks are highly flexible and mobile, unlike those of fast-swimming sharks (such as shortfin mako and salmon sharks) which have stiff, relatively immobile fins. Based on this, Tomita et al. [24] suggested that the pectoral fins of megamouth sharks are specialized for maintaining body posture during slow-speed swimming. Given that pectoral fin bases are attachment sites for various pectoral muscles [24], the positive allometric scaling of megamouth sharks in this part may indicate that muscle volumes supporting pectoral fins increase disproportionally as they grow in order to maintain maneuverability in the water.

Conclusions.--- Despite the small sample size, we show that megamouth sharks exhibit positive allometric scaling in the head and isometric growth in the caudal fin. Such trends differ from another planktivorous lamniform species, basking sharks, in which both the head and the caudal fin scale negatively. We also found that the head length and mouth width of megamouth sharks grow faster (relative to body length) compared to other lamniform sharks. Such allometric trends are different from the isometric to negatively allometric growth trends seen in many ram-feeding sharks, but rather similar to those of suction-feeding whale sharks and engulfment-feeding rorqual whales. We suggest that megamouth sharks have different feeding mode from obligate, ram-feeding basking sharks, the species often thought to have a comparable ecology to megamouth sharks. However, the sample size should be expanded and electronic tagging experiments are needed in future studies to draw firm conclusions.

https://doi.org/10.3390/fishes8060300

-------The mystery of Mitchill’s monster: An Otodus megalodon skeleton, or an associated O. megalodon and whale? zenodo, March 2023. DOI:10.5281/zenodo.7903372

Abstract.-- In 1818, Samuel L. Mitchill briefly detailed a fossil vertebral column with teeth found in North Carolina. It was believed to have been a sea serpent or giant shark and it was lost in a museum fire in 1866. Its true identity is difficult to ascertain with the sparse information and absence of illustrations. This specimen, dubbed 'Mitchill's monster', is reevaluated here with modern geological and paleontological knowledge. It probably came from the marine, Mio-Pliocene Eastover or Yorktown Formations. It was most likely baleen whale vertebrae with associated teeth of the megatooth shark Otodus megalodon, yet it is also not impossible that both the vertebrae and teeth were O. megalodon. Regardless of which hypothesis is correct, the monster would have been a major discovery.

CONCLUSIONS.

Had it not perished in flames, Mitchill’s monster would have been an important specimen. If it was the less likely O. megalodon teeth and vertebrae, it was the first megatooth shark skeletal

material ever documented.6 The earliest confirmed otodontid skeletons were published almost 70 years later (Dollo, 1887). If it was the more likely O. megalodon teeth andw hale vertebrae, it was also the first of its kind.Whales with associated O. megalodon teet hwere not published until recently. These includea vertebra with an embedded tooth (Aguilera etal., 2008) and two fractured vertebrae with an adjacent tooth (Godfrey & Beatty, 2022). The vertebra in Mitchill's possession lacked embedded teeth or other pathologies, but it is possible that the vertebrae not collected had them. Bite marks occur on isolated whalevertebrae in the Yorktown Formation (Purdy,1996; Godfrey et al., 2018), so they may have been present on the monster's as well. If it wasthe remains of a predation and/or feedingevent, as opposed to a coincidental association,it represented an uncommon occasion. Largebaleen whales were infrequently encounteredby O. megalodon compared to smaller prey(Cooper et al., 2022). In any case, the monsterdemonstrates the many pitfalls of earlypaleontology — precise locality andstratigraphic data were not recorded, themajority of the specimen was not retrieved, itwas erroneously interpreted as a fantasticalcreature, it was never thoroughly described orfigured, and it was destroyed alongside anentire museum. It likewise demonstrates thatthere is merit to reexamining historical losses, as they may have been more significant thanpreviously thought.
https://zenodo.org/doi/10.5281/zenodo.7903371
https://www.researchgate.net/publication/371121018

-------A Recently Discovered Megalodon Fossil Shark Tooth Artifact from Horse Cave, Hart County, Kentucky. October 2023. Conference: 66 Annual Midwest Archaeological ConferenceAt: Bowling Green, Kentucky.
Abstract.-- Fossil shark teeth from archaeological sites in Kentucky are not commonly reported in the literature. In July 2023, a broken Megalodon (Otodus megalodon) fossil shark tooth was discovered by the landowner in an agricultural drainage ditch in Horse Cave, Hart County, Kentucky. The partial tooth shows clear evidence of tool use. Mineralogic deposits and staining similar to that on flint artifacts found in the vicinity of the tooth as well as in-situ video substantiate the discovery. Otodus megalodon lived during the Miocene and Pliocene Epochs. There are no geologic deposits of this age in Kentucky or natural processes which could have transported the fossil to the site from outside of the area, indicating that the shark tooth artifact was brought to Kentucky through human activity. Additional investigation is ongoing. The reporting of this discovery would not have been possible without the curiosity and collaboration of the land owner.
https://www.researchgate.net/publication/374725536

-------A Look Back at Megalodon Discoveries From The Last 115 Years. Sep 07, 2022. Newsweek.
An Atlantic Shark Institute team was disappointed yesterday when what seemed to be a massive megalodon shark was only a large school of mackerel. The team said on social media they hoped the image they saw on the scanner was the extinct megalodon, but they must remain satisfied with fossil discoveries for now.
Megalodons are prehistoric predatory fish that are believed to be big enough to eat a whale, according to reports. Newsweek reported the megalodon's mouth opened to 11 feet wide and was lined with as many as 276 teeth. That makes megalodon fossil discoveries somewhat common, as the prehistoric predators lost a set of teeth every fortnight, equaling 40,000 teeth in its lifetime.

1992. Although Megalodon teeth are frequently discovered, a full megalodon jaw has never been discovered. Saltwater breaks down cartilage, so all megalodon jaws have likely dissolved.

1909. Paleontologists estimated the size of the monstrous jaw by using the fossilized teeth. Bashford Dean reconstructed the first megalodon jaw at the American Museum of Natural History in 1909 according to Dutch Shark Society, but it is believed Dean overestimated the thickness of the cartilage, making the model taller than reality.

In 1992, the Smithsonian Institute had a set of megalodon jaw replicas constructed by paleontologist John Maisey. The replicas include a nearly complete set of fossilized megalodon teeth found in North Carolina.

2020. A study by the University of Bristol reported that the teeth can be larger than a human hand. The study found the Megalodon could have stretched up to more than 50 feet in length with a dorsal fin that was taller than an adult human.

Paleontologist Jack Cooper and a team of researchers used the isolated teeth fossil discoveries to estimate the true breadth of the megalodon. Their findings were published in Scientific Reports in 2020. The project was supervised by Dr. Catalina Pimiento. The study found the giant prehistoric shark is not a direct ancestor of only the great white shark, as previously believed.

"Megalodon is not a direct ancestor of the great white but is equally related to other macropredatory sharks such as the Makos, Salmon shark and Porbeagle shark, as well as the great white," Pimiento said in the study. "We pooled detailed measurements of all five to make predictions about megalodon."

Fox News reported in 2020 that several megalodon nurseries were discovered in Spain. Reports show that many fossils from young and adult megalodons were unearthed. A study by The Royal Society reported as many as five megalodon nurseries have been found in the Atlantic, Caribbean and Pacific basins. The fossils were from as long as 16 million years ago, with the most recent fossils being from around 3 million years ago when the shark went extinct.

The nurseries were home to fossils from megalodons as young as 1 month old, at approximately 16 feet in length, to adolescent megalodons that stretched over 30 feet in length. Researchers anticipate the megalodon could be twice to three times the size of a great white shark. A great white shark can be more than 20 feet long.

-------Body forms of extant lamniform sharks (Elasmobranchii: Lamniformes), and comments on the morphology of the extinct megatooth shark, Otodus megalodon , and the evolution of lamniform thermophysiology. Historical Biology VOL.35(2), Feb.2022. DOI: 10.1080/08912963.2021.2025228

ABSTRACT.-- The megatooth shark, Otodus megalodon, is an iconic Neogene lamniform shark known only from its teeth and vertebrae. Its thermophysiology is previously inferred to have been regionally endothermic, like the extant lamnids that are active predatory lamniforms. By considering the entire Lamnidae as the ecological and physiological analogue to O. megalodon, a recent study proposed inferred body dimensions of O. megalodon based on morphometric analyses on body forms of extant lamnids. Here, we reassessed the recent study by testing whether a two-dimensional approach used in the study can actually tease out the difference between ectothermic and endothermic fishes in the first place. Morphometric comparisons of the whole body and different body parts (e.g. head, different fins, and precaudal body with and without fins) among the 15 extant species of Lamniformes were

conducted using principal component analyses and simple clustering methods. Our study strongly indicates that, two-dimensionally, there is no relationship between thermophysiology and body form in lamniforms. The reality is that there are presently no scientific means to support or refute the accuracy of any of the previously published body forms of O. megalodon. We also clarify that regional endothermy likely evolved in multiple clades independently through lamniform phylogeny.
https://web.archive.org/web/20220222200526id_/https://www.tandfonline.com/doi/pdf/10.1080/08912963.2021.2025228
https://doi.org/10.1080/08912963.2021.2025228

-------The extinct shark Otodus megalodon was a transoceanic superpredator: Inferences from 3D modeling. SCIENCE ADVANCES, Aug.2022, Vol.8. DOI:10.1126/sciadv.abm9424.
Abstract.-- Although shark teeth are abundant in the fossil record, their bodies are rarely preserved. Thus, our understanding of the anatomy of the extinct Otodus megalodon remains rudimentary. We used an exceptionally well-preserved fossil to create the first three-dimensional model of the body of this giant shark and used it to infer its movement and feeding ecology. We estimate that an adult O. megalodon could cruise at faster absolute speeds than any shark species today and fully consume prey the size of modern apex predators. A dietary preference for large prey potentially enabled O. megalodon to minimize competition and provided a constant source of energy to fuel prolonged migrations without further feeding. Together, our results suggest that O. megalodon played an important ecological role as a transoceanic superpredator. Hence, its extinction likely had large impacts on global nutrient transfer and trophic food webs.
INTRODUCTION.-- Computer modeling has given paleontologists the unprecedented ability to use exceptionally well-preserved fossils to reconstruct the entire body of extinct animals, which in turn allows estimations of biological traits from the resulting geometry (1–4). For example, complete skeletons of Tyrannosaurus rex have been used to estimate an adult mass of ~5000 to 10,000 kg (1, 3, 4). This task is, however, considerably harder for extinct sharks, whose cartilaginous skeletons have poor preservation potential in the fossil record and usually only leave behind teeth and occasionally vertebrae (5). Therefore, biological traits of extinct sharks are typically inferred on the basis of extrapolations from close relatives and ecological analogs.
Otodus megalodon, a member of the extinct family Otodontidae (order: Lamniformes), was the largest known macropredatory shark (6). Fossil remains of this extinct giant consist mainly of teeth. On the basis of the age, morphology, and worldwide distribution of these teeth, it has been proposed that this species was a cosmopolitan predator that lived from the Miocene to the Pliocene [23 to 2.6 million years (Ma) ago; (6–10)]. Its extinction has been attributed to a reduction of productive coastal habitats in the late Pliocene, which likely caused the loss of other marine megafaunal species, many of which could have been O. megalodon prey, and the appearance of potential competitors (9, 11).
The body length of the iconic O. megalodon has been inferred on the basis of tooth measurements and comparisons with the extant great white shark (Carcharodon carcharias: order Lamniformes, family Lamnidae), which is regarded as the best available ecological analog despite belonging to a different family (12, 13). For instance, extrapolations of the relationship between tooth crown height and total length (i.e., length from the snout to the tip of the tail; herein TL) in C. carcharias (12) have suggested a maximum TL of 14 to 18 m for O. megalodon (6, 7, 13). More recently, however, a maximum TL of 20 m has been calculated on

the basis of the tooth crown width of associated dentitions of other lamniform sharks (14). The dimensions of O. megalodon body parts have also been estimated using multiple lamniform analogs, suggesting that an adult ~16-m O. megalodon would have had a head 4.7 m long, a dorsal fin 1.6 m tall, and a tail about 4 m high (15).

The body mass of O. megalodon at different life stages (e.g., ~48,000 kg for a ~16-m individual) has also been estimated on the basis of vertebral centra and extrapolations from C. carcharias (7). Vertebral columns hardly ever preserve, with only two specimens to our knowledge reported from Miocene deposits of Belgium and Denmark (7, 16). The column from Belgium consists of 141 centra (IRSNB P 9893; formerly labeled IRSNB 3121) and was previously examined by Gottfried et al. (7), who concluded that it belonged to a single individual, undoubtedly an exceptional fossil due to the sheer number of centra preserved. Although a recent study examined the growth bands of three of the centra and concluded that IRSNB P 9893 died at age 46 (17), no study, prior or since, has attempted to reconstruct this specimen in detail based on its vertebral column.

Fossil evidence of bite marks on bones has shed some light on the autoecology of O. megalodon (18–21). For instance, it has been hypothesized that O. megalodon preferentially preyed on small- to medium-size cetaceans [e.g., 2.5 to 7 m; (19, 20)] such as the extinct Piscobalaena nana (19) and Xiphiacetus bossi (20). Larger prey includes taxa related to the modern humpback (Megaptera novaeangliae) or blue whales [Balaenoptera musculus; (18)]. Evidence from calcium isotopes has further suggested that O. megalodon occupied a higher trophic level than did C. carcharias (22), which typically consumes comparatively small prey in their entirety [e.g., sharks, Carcharhinus obscurus and Prionace glauca, and dolphins, Tursiops truncatus and Delphinus delphis; (23, 24)], and travels great distances across oceans (25). Last, it has been proposed that an adult O. megalodon could reach cruising speeds of 1.3 to 1.4 m/s (26, 27) and burst speeds of 10.3 m/s (26), and that such an ability was enhanced by mesothermy (26), a thermoregulatory adaptation that elevates the temperature of locomotory muscles (28). The purported mesothermic physiology of O. megalodon has been supported by multiple lines of evidence, including comparative analyses, stable isotopes, and species distribution models (9, 26, 29).

Notwithstanding these advances in the understanding of O. megalodon, its full-body anatomy and critical aspects of its ecology remain unclear or outdated. For instance, its body mass, a key trait to infer other ecophysiological properties, was last estimated in the early 1990s based on the assumption that C. carcharias is a direct descendant of O. megalodon (7), which has since been disfavored (30). Given the most recent advances in computer modeling, it is now possible to make a more comprehensive and up-to-date reconstruction of O. megalodon to estimate various biological traits of this extinct shark.

Here, we create the first three-dimensional (3D) model of the body of O. megalodon and use it to infer its movement and feeding ecology. We first reconstructed the axial skeleton using 3D scans of the exceptional vertebral column IRSNB P 9893 from Belgium, an associated dentition from the United States, and a C. carcharias chondrocranium (Fig. 1 and figs. S1 and S2). We completed the model by adding “flesh” around the skeleton using a full-body scan of C. carcharias (Fig. 1) and adjusted it based on a 2D reconstruction of O. megalodon that accounts for other analogs [i.e., Isurus and Lamna spp.; see Materials and Methods; (15)]. We quantified TL, volume, and gape size from the complete 3D model. Volume was then used to calculate body mass. Last, we estimated the model’s swimming speed, stomach volume, daily energetic demands, and prey encounter rates based on their mathematical relationships with mass in extant sharks. Our results reveal the potentially distinctive ecological role that O. megalodon played in the global oceans, advancing our knowledge of the impacts of megafaunal species on marine ecosystems in deep time and the potential ecological consequences of their extinctions.

.... Feeding ecology.-- Our prey size and intake results suggest that a ~16-m O. megalodon could completely ingest, and in as few as five bites, prey as large as O. orca (i.e., 8 m), a top consumer in modern marine food webs (63). The macroraptorial sperm whale Zygophyseter varolei occupied a similar ecological niche to modern orcas in the Miocene and likely overlapped with O. megalodon (64, 65). Z. varolei is only known from a holotype specimen from Italy and has been estimated to reach 7 m of length (64, 65). Accordingly, O. megalodon could potentially have fully consumed this large predator. Such a predatory behavior would be similar to that of large extant predators such as C. carcharias, which can fully consume dolphins in two pieces (24). The potential ability of O. megalodon to fully consume large predators has two main ecological implications. First, it supports previous findings of O. megalodon sitting at a higher trophic level than apex predators today based on calcium isotopes (22), further implying an important ecological function as an apex superpredator. Second, when also considering the potential competitive interactions from our swimming speed analyses, it further suggests the possibility of a dietary preference for large prey. Although it has been previously hypothesized that O. megalodon preferred prey of 2 to 7 m (19, 20), empirical studies have shown that large sharks prey upon a broader range of sizes than their smaller counterparts (66). Moreover, one of the benefits of gigantism in macropredatory marine taxa is the ability to exploit less competitive niches by consuming large prey (29, 35, 67). For example, while toothed whales tend to feed on large patches of small prey, the largest sperm whales can acquire similar amounts of energy from eating just a few large, high-energy items (67). Similar energetic gains from frequent but small prey relative to less frequent but large prey were also found in our O. megalodon prey encounter analysis (Fig. 3). Hence, it is possible that large O. megalodon individuals may have minimized competition by targeting large prey.

Our results further suggest that large prey would have provided O. megalodon calories well beyond its energetic demands and would have been found frequently enough to support adult populations (Fig. 3 and table S1). Although frequent predation on smaller prey such as X. bossi or Metaxytherium (Table 2) would have also sufficed O. megalodon's caloric needs (Fig. 3 and table S1), it is common for large macropredatory sharks to consume far more than their required daily energy intake at a time, particularly ram-ventilating mesotherms that need to swim continuously to acquire oxygen and power metabolism (32, 33, 57). For example, adult C. carcharias can consume more than 30 kg of blubber from scavenging a large cetacean carcass without filling their stomachs, which is hypothesized to sustain them for up to 1.5 months, assuming continuous cruising speed (38). Moreover, they have been observed eating entire dolphins (24), which would provide up to 60 times their daily energy requirement [44 kg of blubber in a 200-kg dolphin = ~293,000 kcal (41)]. Prey intake beyond daily energetic demands is also common in other aquatic top predators, like polar bears (Ursus maritimus), which can obtain enough calories to live for up to 60 days from fully consuming an adult seal (68). In sharks, like C. carcharias, excess energy from consuming calories beyond their daily requirements is stored in liver lipids, sustaining them during prolonged migrations (57). This fits an established hypothesis that large mesothermic taxa have higher mass-specific metabolic limits [e.g., (29)], which notably lowers the cost of transport and enhances fasting capabilities (69). The hypothetical full consumption of a cetacean of the size of a modern O. orca (8 m) might have sustained a ~16-m O. megalodon for 63 days without jeopardizing population survival, which would have allowed it to travel over 7500 km, assuming a continuous cruising speed of 1.4 m/s. Although this suggestion is inherently inferential, it fits observations of extant species, specifically its ecological analog C. carcharias (25, 37). Together, our results indicate that a preference for, and the full consumption of, large prey would have not only allowed O. megalodon to exploit less competitive niches but also potentially enabled transoceanic movements. The extinction of O. megalodon therefore may have released large cetaceans from a strong predatory pressure (8), likely affecting global trophic webs [e.g., (59)].

The exceptionally preserved vertebral column of the extinct giant shark O. megalodon from Belgium (IRSNB P 9893; Fig. 1, A and B, and fig. S1) provided a unique opportunity to reconstruct its entire body using 3D computer modeling, which in turn enabled previously unknown inferences on its movement and feeding ecology. It is important to acknowledge, however, that there are inherent uncertainties associated with any estimations of biological properties in extinct animals, which magnify when they are used as the basis for further inferences. Our conservative estimates and cautious interpretations suggest that O. megalodon was likely able to swim great distances and to feed on prey as large as modern apex predators, implying an ecological function as a transoceanic superpredator. A potential preference for large prey would have allowed adult individuals not only to obtain enough calories to undertake prolonged migrations, much like its modern ecological analogs (25, 57), but also to exploit less competitive niches. The extinction of this purported highly migratory superpredator likely had large-scale impacts, from releasing large cetaceans from a strong predatory pressure, thus affecting global food webs (8), to altering global nutrient transport, ocean productivity, and ecosystem stability (58).

https://doi.org/10.1126/sciadv.abm9424

https://www.science.org/cms/10.1126/sciadv.abm9424/asset/e7a2be1f-ec48-4429-86de-427ac51e080e/assets/images/large/sciadv.abm9424-f1.jpg

https://www.science.org/doi/pdf/10.1126/sciadv.abm9424

-------What Is The Biggest Megalodon Tooth Ever Found?. July 26, 2022. Dutch Shark Society.

The megalodon (Otodus megalodon) was the largest shark ever to have lived, so it might not surprise you to hear that this predator also had the biggest teeth of any shark species.

When the monster sharks finally became extinct more than 3.6 million years ago, it left behind the largest shark tooth fossils ever as an astonishing record of its existence.

The biggest megalodon tooth ever found has a slant height of 7.48 inches (19 centimeters). It was discovered in Peru and is the largest megalodon tooth ever unearthed.

Let’s look at some of the most enormous megalodon teeth ever found to truly appreciate just how massive these sharks were.

The slant height is the diagonal length measured from the pointed tip of the tooth to the corner of its root. Whichever of the two sides is longest is stated as the tooth’s length.

When looking at the biggest megalodon tooth ever found, anything with a slant height of over 6 inches (15.24 cm) is considered significant.

Most adult megalodon teeth fossils that have been found measure between 4 and 5 inches. Only about 1% of the many megalodon teeth discovered have a slant height of over 6 inches. So, not only did they come from the largest shark, but they’re also pretty rare teeth.

The world of fossil hunting can be filled with secrecy.

Many colossal shark teeth are stored in natural history museums.

However, several of the largest megalodon teeth are in private collections and have not been widely seen or evaluated.

Let’s look at the huge shark teeth that have been verified, starting with the biggest known.

7.48 Inches (19 cm) – Ocucaje Desert, Peru
The current world's largest measured megalodon tooth was found in the Peruvian Ocucaje desert.
.... Has a Megalodon Jaw Ever Been Found?
No, a megalodon jaw has never been found because, like the rest of its skeleton, the jaw was made from cartilage rather than bone.
-- https://www.dutchsharksociety.org/biggest-megalodon-tooth-ever-found/

-------The extinct shark Otodus megalodon was a transoceanic superpredator: Inferences from 3D modeling. SCIENCE ADVANCES, 17 Aug 2022, Vol.8. DOI:10.1126/sciadv.abm9424.
Abstract.-- Although shark teeth are abundant in the fossil record, their bodies are rarely preserved. Thus, our understanding of the anatomy of the extinct Otodus megalodon remains rudimentary. We used an exceptionally well-preserved fossil to create the first three-dimensional model of the body of this giant shark and used it to infer its movement and feeding ecology. We estimate that an adult O. megalodon could cruise at faster absolute speeds than any shark species today and fully consume prey the size of modern apex predators. A dietary preference for large prey potentially enabled O. megalodon to minimize competition and provided a constant source of energy to fuel prolonged migrations without further feeding. Together, our results suggest that O. megalodon played an important ecological role as a transoceanic superpredator. Hence, its extinction likely had large impacts on global nutrient transfer and trophic food webs.

DISCUSSION

Body size

The calculated TL (15.9 m) for the IRSNB P 9893–based 3D model is markedly longer than previously estimated for this specimen [9.2 m; (7)]. When scaled to real size in Blender (155 mm diameter in centrum 4; see Materials and Methods), the complete column alone was 11.1 m. Size differences likely stem from the fact that the previous estimation was based on the relationship between the largest centrum diameter and TL in C. carcharias and, thus, based only on centrum 4 (7). Nevertheless, there are some problems with the latter approach. First, it implicitly assumed that O. megalodon was a direct ancestor of C. carcharias, which is now disfavored (30). Second, it assumed that both species have similar vertebrae numbers and column structure (i.e., similar proportions of caudal and precaudal centra); however, the number of vertebrae varies even within members of the same family (47). Last, although the centrum used to estimate TL comes from an exceptionally well-preserved fossil, it is still not an entirely complete specimen (7); hence, it is unknown whether that was in fact the largest centrum. Larger O. megalodon centra have been reported elsewhere, with the largest measuring 230 mm in diameter (16). Our O. megalodon 3D reconstruction is also larger than a maximum size of 14.2 to 15.3 m previously proposed based on upper anterior teeth (13). The model's large size combined with the existence of known vertebral centra ~50% larger than those of IRSNB P 9893 (16) supports a more recent suggestion that O. megalodon may have reached a maximum TL of 20 m (14).
Our estimated body mass (61,560 kg; Table 1) was also ~23% higher than that previously inferred for a 16-m O. megalodon based on the relationship between TL and mass in C. carcharias [47,690 kg; (7)]. This mass difference could be due to the reliance on C. carcharias in previous estimates, whereas we adjusted our model to account for multiple analogs, namely, all members of the family Lamnidae (order Lamniformes; see Materials and Methods). It has been shown that incorporating multiple lamnids results in stockier O. megalodon body

reconstructions (15). The use of multiple analogs to reconstruct the body of O. megalodon has recently been questioned based on a supposed lack of a relationship between body form and thermophysiology in lamniforms when analyzing drawings of all 15 extant species (48). Nevertheless, justification for the use of multiple analogs to reconstruct the body of O. megalodon is based on the combination of ecology with thermophysiology, as both ultimately determine swimming strategy and, consequently, body form in sharks (29, 49). Accordingly, the analogs used to inform the reconstruction of O. megalodon encompass only the lamniforms that share similar diet, feeding strategy, and thermoregulatory physiologies (15). These include the family Lamnidae (49–52) but exclude ectothermic filter feeders (families Cetorhinidae and Megachasmidae) and the family Alopiidae, which includes a mesothermic species but displays anatomical adaptations (i.e., enlarged caudal fins) for a specialized hunting behavior (53) unlikely to be analogous to O. megalodon (18–21). Hence, the purported lack of a relationship between body form and thermophysiology in extant lamniforms based on the inclusion of species not analogous to O. megalodon (48) is not only irrelevant to the reconstruction of the extinct species as proposed in (15) but also at odds with previous studies demonstrating body form convergence among mesothermic taxa, including lamnid sharks, tunas (49, 50), and ichthyosaurs (54, 55). We therefore contend that, although C. carcharias is the best available ecological analog of O. megalodon, the use of multiple lamnids to inform our 3D reconstruction is appropriate given the uncertainties regarding the interrelationships between extinct and extant Lamniformes (see Materials and Methods). Given that our best-case validity test suggests that our volumetric approach does not result in overestimations (see Materials and Methods), we consider a mass of 61,560 kg to be conservative to infer ecological parameters based on extant sharks. Together, our body size results suggest that the IRSNB P 9893 specimen is bigger than hitherto proposed and larger than the maximum size estimated for O. megalodon based on anterior teeth only (13). These results highlight the importance of using body parts other than anterior teeth and multiple analogs to infer the size of this extinct shark.

Movement ecology

Absolute cruising speed (m/s) estimations and species-level comparisons (Fig. 2A) suggest that the reconstructed ~16-m individual was able to cruise faster than all extant species analyzed (33), including its closest mesothermic, macropredatory, extant relatives. Notably, the model was also much faster than the largest extant shark species, which is the filter-feeding, ectothermic whale shark (R. typus; maximum size, ~18 m; Fig. 2A) (35). A faster cruising speed than R. typus was also found when considering relative speed (BL/s), a metric inversely correlated with body size (fig. S3A). It is well supported that mesothermy allows all mackerel sharks [family Lamnidae: C. carcharias, Isurus spp., and Lamna spp.; (49, 50)] and the common thresher [Alopias vulpinus; (56)] to reach faster speeds than their ectothermic counterparts (51, 52). Different lines of evidence have suggested that O. megalodon also had this thermoregulatory adaptation (26, 35). Given that our estimated cruising speed for O. megalodon was based mostly on ectothermic, hence slower, species [see Materials and Methods; (51, 52)], we consider it to be conservative.

The potential ability of O. megalodon to cruise at faster absolute speeds than other species (Fig. 2A) would enable it to move greater distances, thus increasing prey encounter rates (51). Fossils of marine mammals with multiple bites from the Miocene Pisco Formation of Peru have been used to hypothesize that O. megalodon may have exploited pinniped colonies for foraging (19). Hence, the ecological benefits of a faster cruising speed likely allowed O. megalodon to move between distant feeding sites, a predation tactic also used by C. carcharias to find abundant, calorie-rich prey (57). Overall, our species-level comparisons of absolute cruising speed suggest that O. megalodon was, in general, an adept swimmer capable of undertaking long migrations, perhaps even farther than extant species. In modern oceans, a C. carcharias swimming at a mean cruising speed of 1.3 m/s (0.1 m/s slower than O. megalodon) can travel as far as 11,110 km across the entire Indian Ocean (25). Considering that large, highly mobile animals disproportionately drive nutrient movement between marine regions today (58), we propose that O. megalodon likely played an important ecological role transporting nutrients across oceans. Hence, the extinction of this species may have negatively affected global nutrient transfer, potentially compromising ecosystem diversity, productivity, and stability [e.g., (58, 59)].

Individual-level comparisons between O. megalodon absolute (m/s) cruising speed with that of the 391 sharks analyzed, combined with relative cruising estimations (BL/s), provide additional clues about the biotic interactions of this extinct species. A few smaller macropredatory individuals can exceed the absolute cruising speed of a ~16-m O. megalodon [i.e., two adult (Fig. 2B, nos. 5 and 6) and one subadult (Fig. 2B, #4) C. carcharias and a juvenile I. oxyrinchus (Fig. 2B, no 7, and data S1)]. Similarly, the relative cruising speed (BL/s) of the O. megalodon model (Table 1) was found to be slower than almost all other macropredatory sharks (fig. S3). This finding is expected given the size of the model (Fig. 1) relative to extant species. Nevertheless, when taken together, these results suggest that despite O. megalodon’s potential ability to move greater distances than any other species today, its gigantic size likely imposed constraints on its swimming abilities when compared to smaller macropredatory individuals. For instance, the fact that the absolute speed of a 16-m O. megalodon could hypothetically be exceeded by an adult C. carcharias, which would share a similar diet (60), suggests that ancient white sharks [e.g., Carcharodon hubbelli, a 5-m species (14) that overlaps with O. megalodon in the Pisco Formation (30)] could also cruise faster, potentially outcompeting it. Although this is highly speculative given that we only estimated cruising speed and not burst speed, which is directly related with prey capture (61, 62), it has been observed that small C. carcharias outcompete larger individuals using swift burst speeds when ambushing prey (61). Moreover, it has been previously proposed that an 18-m O. megalodon could reach burst speeds of 10 m/s (26), whereas a 3.4-m C. carcharias can reach at least 12 m/s (62). Given that body mass is curvilinearly correlated with absolute burst speed across both terrestrial and marine taxa (34), O. megalodon’s burst speed was most likely limited by the drag produced by its gigantic size (32). Therefore, O. megalodon’s maximum speed would have been attained by younger individuals, while those approaching 16 m [which is close to maximum size (6, 14)] would have been less agile hunters. The appearance of potential competitors in the late Miocene has already been proposed to have contributed to the extinction of O. megalodon in the Pliocene, in addition to habitat loss driven by sea-level oscillations and the decline of potential prey (9–11). Although our absolute cruising speed comparisons do not provide enough evidence to propose that ancient white sharks were able to reach faster burst speeds for swifter and more effective predatory attacks, they do imply that if O. megalodon faced competition, it would have been with smaller, yet adult homeothermic macropredators. Future studies considering burst speeds could shed more light on the competitive interactions between O. megalodon and other sharks.

Feeding ecology

Our prey size and intake results suggest that a ~16-m O. megalodon could completely ingest, and in as few as five bites, prey as large as O. orca (i.e., 8 m), a top consumer in modern marine food webs (63). The macroraptorial sperm whale Zygophyseter varolei occupied a similar ecological niche to modern orcas in the Miocene and likely overlapped with O. megalodon (64, 65). Z. varolei is only known from a holotype specimen from Italy and has been estimated to reach 7 m of length (64, 65). Accordingly, O. megalodon could potentially have fully consumed this large predator. Such a predatory behavior would be similar to that of large extant predators such as C. carcharias, which can fully consume dolphins in two pieces (24).

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Together, our results indicate that a preference for, and the full consumption of, large prey would have not only allowed O. megalodon to exploit less competitive niches but also potentially enabled transoceanic movements. The extinction of O. megalodon therefore may have released large cetaceans from a strong predatory pressure (8), likely affecting global trophic webs [e.g., (59)].

The exceptionally preserved vertebral column of the extinct giant shark O. megalodon from Belgium (IRSNB P 9893; Fig. 1, A and B, and fig. S1) provided a unique opportunity to

reconstruct its entire body using 3D computer modeling, which in turn enabled previously unknown inferences on its movement and feeding ecology. It is important to acknowledge, however, that there are inherent uncertainties associated with any estimations of biological properties in extinct animals, which magnify when they are used as the basis for further inferences. Our conservative estimates and cautious interpretations suggest that O. megalodon was likely able to swim great distances and to feed on prey as large as modern apex predators, implying an ecological function as a transoceanic superpredator. A potential preference for large prey would have allowed adult individuals not only to obtain enough calories to undertake prolonged migrations, much like its modern ecological analogs (25, 57), but also to exploit less competitive niches. The extinction of this purported highly migratory superpredator likely had large-scale impacts, from releasing large cetaceans from a strong predatory pressure, thus affecting global food webs (8), to altering global nutrient transport, ocean productivity, and ecosystem stability (58).
https://doi.org/10.1126/sciadv.abm9424
https://www.researchgate.net/publication/362751360

-------Revisiting body size trends and nursery areas of the Neogene megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), reveals Bergmann's rule possibly enhanced its gigantism in cooler waters. Historical Biology, 35(2022). DOI:10.1080/08912963.2022.2032024.
ABSTRACT.-- The late Neogene megatooth shark, Otodus megalodon, is known mainly from its gigantic teeth and possibly reached 18–20 m in total length (TL). We re-examine the previously proposed body size trends and nursery areas of O. megalodon by confining the previously used samples to upper anterior teeth offering more reliable TL estimates, and by taking paleolatitudes and sea-surface temperatures into consideration. We demonstrate that individuals of O. megalodon are on average larger in cooler water than those in warmer water – a pattern attributable to Bergmann's rule showing a latitudinal body size gradient at least for the eastern Pacific late Miocene and the western Atlantic early Pliocene assemblages. While it is still possible that neonatal O. megalodon could have utilised nursery areas, the previously identified paleo-nursery areas based on body size may reflect temperature-dependent trends rather than the inferred reproductive strategy. Thus, the gigantism of O. megalodon in cooler waters was possibly further enhanced by its cooler environment. If so, the corollary of this study is that not all populations of O. megalodon likely grew to gigantic sizes equally, where the common notion that the species reached 18–20 m TL should be applied primarily to populations in cooler environments.
https://doi.org/10.1080/08912963.2022.2032024

-------Body forms of extant lamniform sharks (Elasmobranchii: Lamniformes), and comments on the morphology of the extinct megatooth shark, Otodus megalodon , and the evolution of lamniform thermophysiology. Feb.2022 - Historical Biology 35(2).
DOI:10.1080/08912963.2021.2025228
Abstract.-- The megatooth shark, Otodus megalodon, is an iconic Neogene lamniform shark known only from its teeth and vertebrae. Its thermophysiology is previously inferred to have been regionally endothermic, like the extant lamnids that are active predatory lamniforms. By considering the entire Lamnidae as the ecological and physiological analogue to O. megalodon, a recent study proposed inferred body dimensions of O. megalodon based on morphometric analyses on body forms of extant lamnids. Here, we reassessed the recent

study by testing whether a two-dimensional approach used in the study can actually tease out the difference between ectothermic and endothermic fishes in the first place. Morphometric comparisons of the whole body and different body parts (e.g. head, different fins, and precaudal body with and without fins) among the 15 extant species of Lamniformes were conducted using principal component analyses and simple clustering methods. Our study strongly indicates that, two-dimensionally, there is no relationship between thermophysiology and body form in lamniforms. The reality is that there are presently no scientific means to support or refute the accuracy of any of the previously published body forms of O. megalodon. We also clarify that regional endothermy likely evolved in multiple clades independently through lamniform phylogeny.
https://dx.doi.org/10.1080/08912963.2021.2025228
https://web.archive.org/web/20220222205455id_/https://www.tandfonline.com/doi/pdf/10.1080/08912963.2021.2025228?needAccess=true
https://www.researchgate.net/publication/358409107

-------Ontogenetic growth pattern of the extinct megatooth shark Otodus megalodon—implications for its reproductive biology, development, and life expectancy. Historical Biology, Intern.J.Paleobiol., Vol.33, 2021 - DOI:10.1080/08912963.2020.1861608.
ABSTRACT.-- The extinct megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), is known primarily from its gigantic teeth in the late Neogene marine fossil record. It is known to reach at least 14.1–15.3 m in length, but its reproductive biology and ontogenetic growth pattern have remained largely in the realm of speculation. Here, we examined incremental growth bands in fossil vertebrae of a 9.2-m-long individual O. megalodon, revealing that the shark was born large, 2 m in length, and died at age 46. This large size at birth is characteristic of lamniform sharks and is indicative of live-bearing reproduction along with embryos' intrauterine cannibalism behaviour in the form of oophagy. The trajectory of the generated growth curve beyond the age of death and the maximum length (about 15 m) calibrated from the largest known teeth of O. megalodon suggest that the species had a lifespan of at least 88–100 years with an average growth rate of about 16 cm/yr at least for the first 46 years. As one of the largest carnivores that ever existed on Earth, deciphering such growth parameters of O. megalodon is critical to understand the role large carnivores play in the context of the evolution of marine ecosystems.
Our study is based on IRSNB P 9893 housed in the Royal Belgian Institute of Natural Sciences (IRSNB) in Brussels. This specimen previously referred to as 'IRSNB 3121′ (Gottfried et al. 1996), consists of approximately 150 associated, but disarticulated, vertebrae from an individual collected from the Miocene of Belgium (Figure 1(a)). Although it was not associated with any teeth, the specimen is broadly accepted to have come from Otodus megalodon due to their large sizes and structure consistent with lamniform vertebrae (Gottfried et al. 1996, who also morphologically dismissed the specimen to be from the only other gigantic lamniform alternative, the basking shark; Kent 2018). Based on the maximum width of the largest vertebra in the specimen ('vertebra #4′ measuring 155 mm in width), the individual is estimated to be 921 cm TL in life based on a linear regression function describing the quantitative relationship between the maximum vertebral width and TL from 16 extant white sharks, Carcharodon carcharias (Gottfried et al. 1996). It should be noted that all other known vertebral specimens attributed to O. megalodon (Bendix-Almgreen 1983; Uyeno and Sakamoto 1984; Gottfried et al. 1996; Kent 2018) are too incomplete to determine their anatomical positions or TL.
We first examined archival photographs of 15 vertebrae made available to us by IRSNB, each

with a specific ‘centrum number’ that has no bearing in terms of its anatomical position (#1, 4, 5, 6, 7, 8, 9, 14, 14, 17, 18, 19, 20, 21 and 26). Where each vertebra largely consists of a circular amphicoelous centrum like conventional shark centra, these photographs allowed us to confirm the universal presence of the same concentric pattern on their articular faces. We then used micro-computed tomography (micro-CT: see below for specific settings) to image the band pattern along the sagittal section of three specific vertebrae, #1 (Figure 1(a), (b)), 4 (Figure 1(c)) and 18, that have a maximum width, or an estimated maximum width of 152, 155 and 148 mm, respectively. Vertebra #4 is incomplete, but it was deliberately included because it represents the largest vertebra in the specimen (Gottfried et al. 1996), whereas the other two are selected because their preservation was excellent and their slight width differences indicate that they must have come from slightly different pre-caudal positions.

Each vertebra was scanned at 150 kV and 490 µA at a spatial resolution of 0.184 mm with an RX EasyTom µCT scanner (RX Solutions, Chavanod, France; http://www.rxsolutions.fr), reconstructed with X-Act software (RX Solutions) and segmented using Dragonfly software for Windows (Object Research Systems (ORS) Inc., Montreal, Canada). The resulting TIFF slices consisting of anteroposterior transverse sections were imported into FIJI (https://fiji.sc/; http://imagej.nih.gov/ij) and were oriented such that the regions of the neural and haemal plates were vertical using the transform rotate command. Auto brightness and contrast adjustments in FIJI were used to enhance the images. Next, sagittal sections of each vertebra were obtained using the orthogonal view command in FIJI. For each vertebra, the mid-sagittal section was determined by dividing the total number of sagittal sections by two.

Additionally, one sagittal section medial and lateral to the midsagittal plane was also captured to check for variation in growth bands around the mid-sagittal section. The selected sagittal sections were then exported as TIFF files which were cropped and rotated in Adobe Photoshop before being analysed.

In the well-calcified body (corpus calcareum) of elasmobranch vertebrae, the concentric patterns generally comprise annually formed ‘band pairs’, each pair consisting of a narrow ‘opaque’ band and a wide ‘translucent’ band in cross-sectional view representing two contrasting seasons (e.g. Cailliet and Goldman 2004).

A band that forms at birth (or age 0) is often identified based on an ‘angle change’ typically recognised along the inner rim (and possibly outer rim) of the corpus calcareum (e.g. Goldman et al. 2012).

Our cross-sectional micro-CT images of the three vertebrae in IRSNB P 9893 also showed the same band pattern that appeared as alternating bright and dark bands (two examples in Figure 1(b), (c)). The band at birth was determined from the position of the angle change seen in both the inner and outer rims of the angle change (e.g. the inner one marked by a bent line and the outer one pointed by the arrow ‘0′ in Figure 1(c)). Subsequent narrow, bright (in micro-CT images) bands towards the periphery of each vertebra were counted with the assumption that they formed annually as do commonly in living sharks with calcified vertebrae (Cailliet and Goldman 2004; Goldman et al. 2012). Each band was sequentially assigned a band number (BN) with the assumption that it represents an annual ‘ontogenetic age’.

For the purpose of our analysis, we have focussed on the largest vertebra (centrum #4) in IRSNB P 9893 that has the centrum radius (CR) of 77.5 mm. We then measured each band interval (BI) from one band to its successive band starting from BN of 0, calculated the percent centrum radius (pCR) at each BN by treating the last BN as 100% and computed each extrapolated TL (eTL) from each pCR at each BN by considering the estimated TL of 921 cm for the individual (Gottfried et al. 1996) as 100% (Tab.1). In addition, an estimated growth length (eGL) gains from one band to the next was determined from the eTL data and tabulated (Tab.1).

The original and derived measurements, specifically BN and eTL (Table 1) formed the basis of our primary analysis using the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938). The VBGF is a common quantitative method used to describe the growth of modern fishes, especially sharks and rays, based on growth bands on calcified structures such as vertebral centra (Cailliet and Goldman 2004; Goldman et al. 2012). Conventional VBGF studies on modern elasmobranchs use independent measurements taken from a large number of random samples from a population. However, because our study is constrained by the fossil record to a single but best-preserved specimen, the VBGF was used simply as an exploratory tool to fit the BN-TL data using the least-squares method, because measurements taken from one specimen are considered dependent measurements. In other words, the statistical operation was conducted under a hypothetical supposition that each BN-TL pair (including BN 0) was obtained from a randomly sampled individual of a population. Where nondental skeletal remains of cartilaginous fishes are exceptionally rare in the fossil record, this method has proven to be a viable approach to elucidate the growth pattern and life-history strategy of extinct sharks and rays (Shimada 2008; Sternes and Shimada 2018; Shimada and Everhart 2019).

The VBGF parameters for Otodus megalodon (or specifically IRSNB P 9893; Table 1) were calculated using the Desmos Inc. graphing software (www.desmos.com) based on the following form of VBGF that describes the length (L) as a function of the age of the animal (t): $L(t) = L_{\infty} (1 - e^{-k(t - t_0)}$, where L_{∞} is the estimate of asymptotic (= maximum) length, k the rate constant with units of reciprocal time (i.e. the time it takes for a fish in a population to reach near its mean maximum length), and t_0 the theoretical time at zero length. Based on the obtained VBGF curve, we also determined the length at birth (L_0) represented by its y-intercept. This also enabled us to estimate the longevity of the shark using a published equation (Natanson et al. 2006) for the estimated age at 95% of the L_{∞}: i.e. Longevity = $(1/k)\ln\{(L_{\infty} - L_0)/[L_{\infty}(1 - x)]\}$ with $x = L(t)/L_{\infty} = 0.95$. Results All three vertebrae in IRSNB P 9893 showed 46 bands (47 if the band at birth is included: Figure 1(c)) where the outer-most band (band number [BN] 46) marked their periphery, representing when the shark died. In the absence of compelling evidence to the contrary, and given that all three vertebrae we sampled had the same number of regularly spaced bands, we assumed that these bands represent annual growth markers in Otodus megalodon. It should be noted that, while many of these bands are also expressed as concentric ridges and grooves on the articular surfaces of the vertebral centra, not all of the 47 radiographically identified bands are physically expressed externally. Based on the 47 pairs of BN-TL values, Figure 2(a) shows the VBGF fitted to correlate BN values with TL values. The nonlinear regression line ($r^2 = 99.9\%$; $p < 0.001$) has the following VBGF parameters: $L_0 = 199.817$ cm TL, $L_{\infty} = 3{,}172.740$ cm TL, and $k = 0.00588$ yr^{-1}. The longevity of the shark is calculated to be about 498.415 years based on these VBGF parameters (see Materials and Methods).

Discussion

Our calculated VBGF parameters offer many new insights into the biology of Otodus megalodon. For example, the L_0 value of approximately 2 m TL (see also Figure 2(a)) marks the largest neonate size for sharks on record (e.g. Ebert et al. 2013), exceeding the putative size at birth of approximately 1.7 m TL for the extant megamouth (Megachasma pelagios) and basking (Cetorhinus maximus) sharks (Shimada et al. 2020, table 4).

Furthermore, the large neonate size strongly indicates that O. megalodon gave live birth like all other lamniforms (e.g. Ebert et al. 2013). Moreover, the development of such a large neonate strongly suggests that these species had an ovoviviparous (or aplacental viviparity) reproductive mode with an intrauterine cannibalism behaviour in the form of oophagy by ‘early hatched' embryos (Shimada et al. 2020). This reproductive strategy, that must have evolved by the Late Cretaceous (Shimada and Everhart 2019), is universally present in all extant lamniforms that produce relatively large, well-developed newborns offset by low fecundity (Carrier et al. 2004; Gilmore et al. 2005; Conrath and Musick 2012).

Our L_∞ value indicates that Otodus megalodon could have theoretically reached up to nearly 32 m TL. However, such a large individual would have had anterior teeth with an unrealistic crown height (CH) of 27 cm, where the maximum CH reported for O. megalodon in scientific literature to date is 12 cm (Figure 2(b)).

One likely explanation for our unrealistic L_∞ value is that the specimen we examined, IRSNB P 9893, is a mid-sized individual, which also implies it to represent a 'middle-age' individual for O. megalodon. The curvature of our VBGF (Figure 2(a)) is dictated by only the first 46 years of the individual's life history (Figure 1(c)).

Therefore, it is quite possible that the curvature beyond the BN of 46 could have shown steeper slopes (e.g. see the large arrow with a question mark in Figure 2(a)) if this shark individual lived to the maximum possible life expectancy for the species (see below). If so, the actual position of L_∞ would have been much lower than 3,172.740 cm TL calculated here. The L_∞ would have likely been at least slightly larger than the range of 14.1–15.3 m TL (Shimada 2019; Shimada et al. 2020) and well below 32 m TL, but the likely actual L_∞ value remains unknown at present.

Our k value is exceptionally low, indicating that it takes a very long time for Otodus megalodon to attain the mean maximum theoretical length. As a point of reference, lamnid sharks, that include the white shark, shortfin mako (Isurus oxyrinchus) and porbeagle shark (Lamna nasus), tend to show the lowest k values (as low as 0.05–0.06) among modern lamniforms (Shimada 2008), but they are still 10-fold greater than the value obtained for O. megalodon. However, because the VBGF curve beyond the BN of 46 could have had steeper slopes (see above), the k value could have been somewhat greater than 0.00588 yr–1 calculated here.

Our calculation based on IRSNB P 9893 suggests that Otodus megalodon had a theoretical lifespan of about 498.415 years or roughly 500 years. Although at least the living Greenland shark (Somniosus microcephalus) is known to potentially live up to about 500 years old (Nielsen et al. 2016), our calculated longevity of nearly 500 years is likely an overestimation. This is because our L_∞ and k values used to calculate the longevity are likely inaccurate due to the uncertainty in the exact curvature of the VBGF beyond the BN of 46 (see above). However, if we use our attained VBGF curve (Figure 2(a)) at face value, the scientifically justifiable longevity for O. megalodon is minimally 88 years old if the most conservatively estimated maximum TL of 14.1 m from a tooth with the tallest known CH in scientific literature is used (i.e. a tooth with CH of 120 mm illustrated in Figure 2(b); Shimada 2019). If the tallest known tooth in scientific literature calculated to have come from a 15.3-m-TL individual is used (i.e. 162-mm-tall tooth illustrated in Figure 2(a); Shimada 2019), O. megalodon could have lived up to at least 100 years old. However, it is quite possible that the maximum longevity for O. megalodon was greater than 88–100 years old if indeed the VBGF curved more steeply beyond the BN of 46 with the depressed L_∞ (see above; e.g. the large arrow with a question mark in Figure 2(a)). Nevertheless, just as individuals exceeding 15 m TL must have been exceptionally rare (Shimada 2019), individuals of O. megalodon exceeding 100 years old were likely also quite rare.

IRSNB P 9893 does not preserve any teeth, but the 921-cm-TL individual is calculated to have possessed anterior teeth (tallest teeth in the mouth) with a CH of 16.9 mm at birth and 77.9 mm at death (Shimada 2019) (Figure 2(b)). Another noteworthy observation is its rather slow growth rate, at least for the 46 years it lived. Although Otodus megalodon represented by

IRSNB P 9893 had a slightly higher growth rate during the first 7 years (19–23 cm/yr) compared to the remaining life (11–18 cm/yr), it can hardly be characterised as a ‘growth spurt’ because the range of total annual growth rates throughout its lifetime is quite small (11–23 cm/yr) with an average of 15.7 cm/yr (Table 1). The lack of a substantial ‘growth spurt’ may indicate that the size at birth of 2 m TL was sufficiently large enough that neonates already had a high competitive advantage and a low predation risk.

We contend that the likelihood of age underestimation from the counting of BN (see above; Passerotti et al. 2014; Harry 2017; Natanson et al. 2018) in our study is low. This is because:1) the band intervals are relatively uniform in vertebrae of IRSNB P 9893 especially past age 7 (1.0–1.5 mm: Table 1); and 2) IRSNB P 9893 was not an exceptionally old individual based on its estimated TL of about 9 m. Furthermore, our interpretations about the growth of Otodus megalodon are robust, considering that the estimated longevity for both the modern white shark that grows to about 6 m TL and the whale shark (Rhincodon typus, the largest living fish) that exceeds 15 m TL (Ebert et al. 2013), is at least 50 years old and potentially up to 70–80 years old (Hsu et al. 2014; Harry 2017; Ong et al. 2020).

Understanding the life-history traits of large marine carnivores, including growth patterns, is important to elucidate the effect of these predators on their ecosystems and population dynamics of organisms (Cailliet and Goldman 2004; Goldman et al. 2012). Yet, deciphering the life-history strategy of prehistoric sharks is often challenging because the vast majority of species are represented by teeth as their poorly mineralised cartilaginous skeleton usually does not fossilise (Cappetta 2012). In this regard, our vertebra-based study is a rare exception, where the life-history traits for Otodus megalodon proposed here have a significant bearing on various hypotheses and biological issues, such as its potential use of nursery grounds (Pimiento et al. 2010; Herraiz et al. 2020), its proposed competition with Carcharodon carcharias during the early Pliocene (Boessenecker et al. 2019), and ontogenetic effects on its thermophysiology (Ferrón 2017). However, addressing these issues is beyond the scope of this paper primarily because our study rests on multiple assumptions, such as growth bands in IRSNB P 9893 representing annual cycles and the unconventional application of VBGF to a single individual (see Materials and Methods). In addition, the 9.21-m-TL estimate for IRSNB P 9893 (Gottfried et al. 1996) and tooth-based TL estimates (Gottfried et al. 1996; Shimada 2019) used in this study assume that the modern white shark is the most reasonable analogue of O. megalodon among modern sharks (Randall 1973; Gottfried et al. 1996; Reolid and Molina 2015; Razak and Kocsis 2018; Shimada 2019). Nonetheless, our study is the first of its kind for the iconic species, taking the science of O. megalodon one step further.

https://doi.org/10.1080/08912963.2020.1861608
https://par.nsf.gov/servlets/purl/10293771

-------Estimating lamniform body size. Body length estimation of Neogene macrophagous lamniform sharks (Carcharodon and Otodus) derived from associated fossil dentitions. Paleontological Society, Mar.2021. Submission: 12 Nov.2020. Acceptance: 1 Mar.2021. Article number: 24.1.a09. - DOI:10.26879/1140.

ABSTRACT.-- The megatooth shark, Otodus megalodon, is widely accepted as the largest macrophagous shark that ever lived; and yet, despite over a century of research, its size is still debated. The great white shark, Carcharodon carcharias, is regarded as the best living ecological analog to the extinct megatooth shark and has been the basis for all body length estimates to date. The most widely accepted and applied method for estimating body size of O. megalodon was based upon a linear relationship between tooth crown height and total body length in C. carcharias. However, when applying this method to an associated dentition of O. megalodon (UF-VP-311000), the estimates for this single individual ranged from 11.4 to 41.1 m. These widely variable estimates showed a distinct pattern, in which anterior teeth resulted in lower estimates than posterior teeth. Consequently, previous paleoecological analyses based on body size estimates of O. megalodon may be subject to misinterpretation. Herein, we describe a novel method based on the summed crown width of associated fossil dentitions, which mitigates the variability associated with different tooth positions. The method assumes direct proportionality between the ratio of summed crown width to body length in ecologically and taxonomically related fossil and modern species. Total body lengths were estimated from 11 individuals, representing five lamniform species: Otodus megalodon, Otodus chubutensis, Carcharodon carcharias, Carcharodon hubbelli, and Carcharodon hastalis. The method was extrapolated for the largest known isolated upper tooth of O. megalodon, resulting in a maximum body length estimate of 20 m.

Body Length Estimation using Jaw Width

Methods for estimating body length based on TH, CH, and CW all follow a similar rationalization that teeth grow proportionately with total body length. Reolid and Molina (2015; figure 4) compared the linear relationship between different crown measurements in the second upper anterior tooth position (A2) and total body length (TL) in Carcharodon carcharias, reporting a greater correlation for CH than CW (r=0.92 for CH and r=0.53 for CW). However, after re-calculating the Pearson coefficient of correlation (r) from the Reolid and Molina (2015) dataset, the correlation should be r=0.77 for CW (n=58) and r=0.93 for CH (n=85). While this still indicates that CH is a better predictor of body length than CW, it does not consider other tooth positions or summed crown width (SCW) of associated teeth as a proxy for body length. In addition, there has been inconsistency in the literature regarding tooth position nomenclature. Hubbell (1996) referred to the first two anterior teeth of C. carcharias as A2 and A3, due to a hypothesis from Applegate and Espinosa-Arrubarrena (1996) that C. carcharias had lost an anterior tooth row during its evolution. Consequently, Reolid and Molina (2015) included data from Hubbell (1996) that actually refers to tooth position A1 and combined this with data from other studies for tooth position A2.

Lowry et al. (2009) studied the relationship between jaw circumference and total body length in 14 shark species, as a means of estimating body size from shark bite marks. This forensic method allows researchers to estimate the body size of individuals involved in shark attacks. Lowry et al. (2009) used a metric referred to as the interdental distance (IDD), which is measured as the distance between the crown apex of two neighboring teeth, as a proxy for jaw circumference. A linear regression of IDD versus TL for C. carcharias resulted in an R2 =0.98 for the upper jaw and R2 =0.97 for the lower jaw. Siversson (2012) first emphasized the potential of applying this method to estimate body size in fossil taxa, specifically the extinct Cretaceous lamniform Cardabiodon ricki. Newbrey et al. (2015) applied the jaw circumference method to a partially articulated, associated dentition of C. ricki, resulting in a body length estimate of 5.5 m. This method has a strong foundational premise but does not offer a way to account for missing teeth in fossil dentitions and requires assumptions regarding interdental spacing.

This study introduces a novel method for estimating body size in fossil lamniform sharks that builds on the concept that jaw circumference is proportional to total body length. Such that, the summed crown width (SCW) in the functional series is constrained by jaw size. Based on a simple mathematical concept referred to as the rule of three, this method assumes direct proportionality between the ratio of SCW to TL in related modern and fossil taxa (Figure 1C). Herein, we apply this method to fossil associated dentitions from five macrophagous

lamniform species within the families Otodontidae and Lamnidae: Otodus megalodon, Otodus chubutensis, Carcharodon carcharias, Carcharodon hubbelli, and Carcharodon hastalis.
https://doi.org/10.26879/1140

-------The size of the megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), revisited. Historical Biology, 33 - 2021 - DOI:10.1080/08912963.2019.1666840
ABSTRACT.-- Otodus megalodon (Lamniformes: Otodontidae) is a gigantic late Neogene shark that lived nearly worldwide in tropical-temperate regions. Its gigantic teeth have captivated imaginations of the scientific community and general public alike, where the most commonly cited maximum size range of O. megalodon in scientific literature is 18–20 m in total length (TL). In this study, I reexamined the ontogenetic development of teeth and the quantitative relationships between TL and the crown height of anterior teeth in the extant white shark, Carcharodon carcharias, with an ultimate goal to clarify the current state of the scientific understanding of the body size of O. megalodon. My study suggests that the use of upper anterior teeth is much preferred over lower anterior teeth when estimating TL. This study combined with previous studies suggests that the presently verifiable maximum TL estimates of O. megalodon (i.e. scientifically justifiable account based on museum specimens) are 14.2–15.3 m TL, where individuals of O. megalodon exceeding 15 m TL must have been exceptionally rare. Nevertheless, O. megalodon can still be regarded as one of the largest carnivores, if not superpredators, that have ever lived on Earth.
https://doi.org/10.1080/08912963.2019.1666840

-------Use of nursery areas by the extinct megatooth shark Otodus megalodon (Chondrichthyes: Lamniformes). Biol. Lett. Vol.16, 2020, DOI:10.1098/rsbl.2020.0746.
Abstract.-- Nursery areas are fundamental for the success of many marine species, particularly for large, slow-growing taxa with low fecundity and high age of maturity. Here, we examine the population size-class structure of the extinct gigantic shark Otodus megalodon in a newly described middle Miocene locality from Northeastern Spain, as well as in eight previously known formations (Temblor, Calvert, Pisco, Gatún, Chucunaque, Bahía Inglesa, Yorktown and Bone Valley). In all cases, body lengths of all individuals were inferred from dental parameters and the size-class structure was estimated from kernel probability density functions and Gaussian mixture models. Our analyses support the presence of five potential nurseries ranging from the Langhian (middle Miocene) to the Zanclean (Pliocene), with higher densities of individuals with estimated body lengths within the typical range of neonates and young juveniles. These results reveal, for the first time, that nursery areas were commonly used by O. megalodon over large temporal and spatial scales, reducing early mortality and playing a key role in maintaining viable adult populations. Ultimately, the presumed reliance of O. megalodon on the presence of suitable nursery grounds might have also been determinant in the demise of this iconic top predatory shark.
https://doi.org/10.1098/rsbl.2020.0746

-------Body dimensions of the extinct giant shark Otodus megalodon: a 2D reconstruction. Scientific Reports volume 10 - 2020 - DOI:10.1038/s41598-020-71387-y.
Abstract.--Inferring the size of extinct animals is fraught with danger, especially when they were much larger than their modern relatives. Such extrapolations are particularly risky when

allometry is present. The extinct giant shark †Otodus megalodon is known almost exclusively from fossilised teeth. Estimates of †O. megalodon body size have been made from its teeth, using the great white shark (Carcharodon carcharias) as the only modern analogue. This can be problematic as the two species likely belong to different families, and the position of the †Otodus lineage within Lamniformes is unclear. Here, we infer †O. megalodon body dimensions based on anatomical measurements of five ecologically and physiologically similar extant lamniforms: Carcharodon carcharias, Isurus oxyrinchus, Isurus paucus, Lamna ditropis and Lamna nasus. We first assessed for allometry in all analogues using linear regressions and geometric morphometric analyses. Finding no evidence of allometry, we made morphological extrapolations to infer body dimensions of †O. megalodon at different sizes. Our results suggest that a 16 m †O. megalodon likely had a head~4.65 m long, a dorsal fin~ 1.62 m tall and a tail~3.85 m high. Morphometric analyses further suggest that its dorsal and caudal fins were adapted for swift predatory locomotion and long-swimming periods.
This study marks the first quantitative estimate of †O. megalodon specific body-part dimensions, beyond its overall body size. Our model based on a selection of modern analogues outperforms those using individual species (e.g. C. carcharias) and accounts for variability around body dimension averages. Our results reveal that body dimensions of our analogues isometrically correlate to TL. This finding agrees with previous discoveries of similar relationships in linear body dimensions of several other extant shark species26, 27. Although the exact phylogenetic relatedness of †O. megalodon and its family to the order Lamniformes remains poorly understood21, 22, 25, our chosen analogue taxa are the most ecologically and physiologically similar living species to †O. megalodon. As such, our ecological inferences for †O. megalodon are similar to those of our analogues, but also line up with what has been inferred from its fossil record3, 8, 9, 23,24,25, 37, 39. The knowledge of specific body dimensions beyond TL will therefore enhance further anatomical and ecological reconstructions of this giant marine apex-predator.
DOI: https://doi.org/10.1038/s41598-020-71387-y

-------The size of the megatooth shark, Otodus megalodon (Lamniformes: Otodontidae), revisited. Historical Biology, 33(2019). DOI:10.1080/08912963.2019.1666840.
ABSTRACT.-- Otodus megalodon (Lamniformes: Otodontidae) is a gigantic late Neogene shark that lived nearly worldwide in tropical-temperate regions. Its gigantic teeth have captivated imaginations of the scientific community and general public alike, where the most commonly cited maximum size range of O. megalodon in scientific literature is 18–20 m in total length (TL). In this study, I reexamined the ontogenetic development of teeth and the quantitative relationships between TL and the crown height of anterior teeth in the extant white shark, Carcharodon carcharias, with an ultimate goal to clarify the current state of the scientific understanding of the body size of O. megalodon. My study suggests that the use of upper anterior teeth is much preferred over lower anterior teeth when estimating TL. This study combined with previous studies suggests that the presently verifiable maximum TL estimates of O. megalodon (i.e. scientifically justifiable account based on museum specimens) are 14.2–15.3 m TL, where individuals of O. megalodon exceeding 15 m TL must have been exceptionally rare. Nevertheless, O. megalodon can still be regarded as one of the largest carnivores, if not superpredators, that have ever lived on Earth.
https://doi.org/10.1080/08912963.2019.1666840

-------In Switzerland, they will gather the most complete skeleton of megalodon. APRIL 19, 2018 - Earth-Chronicles.
The exhibition “Sharks of prehistoric times” opens in the Museum of Dinosaurs in the city of Aatal (Switzerland) in the canton of Zurich. As reported by the newspaper Lucerne Zeitung, the exposition presents the most complete of all existing skeletons of megalodone in the world – a giant extinct shark of the Miocene and Pliocene epoch.
According to the founder and director of the museum, Hans-Jacob Sieber, fossil remains of sharks are very rare. The reason is that these animals belong to the class of cartilaginous fish, and the cartilage after the death of the organism is very quickly destroyed. Therefore, the skeletons of these fish rarely turn into fossils.
A fragment of the megalodon skeleton about 4.5 m long was specially delivered to Switzerland from Peru and is a real sensation, Sieber said. “We wanted to organize a better exhibition about fossil sharks, and I think we succeeded,” he said. The exhibition is also formed about two dozen rarities, revealing the evolutionary path of sharks.
Megalodon, extinct about 2 million years ago, is considered the largest shark ever inhabiting the world’s oceans. He reached 15-18 meters in length, and in his mouth could fit a car “Smart”. The largest of the existing marine creatures in modern nature – white sharks – reach a length of 6-8 m.
https://earth-chronicles.com/science/in-switzerland-they-will-gather-the-most-complete-skeleton-of-megalodon.html

-------A new elusive otodontid shark (Lamniformes: Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the ‘megatoothed’ clade. Historical Biology, 29(2016). DOI:10.1080/08912963.2016.1236795.
Abstract.-- We describe a new large otodontid lamniform shark, Megalolamna paradoxodon gen. nov. et sp. nov., chronostratigraphically restricted to the early Miocene (Aquitanian–Burdigalian). This new species is based on isolated teeth found from five globally distributed localities: the Jewett Sand in southern California, USA; the Pungo River Formation of North Carolina, USA; the Chilcatay Formation of Peru; the Oi Formation in Mie Prefecture, Japan; and the O’oshimojo Formation in Nagano Prefecture, Japan. Extrapolations based on available published data on modern macrophagous lamniforms suggest that the largest specimen of M. paradoxodon gen. nov. et sp. nov. possibly came from an individual that measured at least 3.7 m in total length. All specimens came from deposits in the mid-latitudinal zones representing shallow-water, shelf-type, coastal environments. Its dentition likely exhibited monognathic heterodonty suited for capturing and cutting relatively large prey (e.g. medium-sized fishes). We recommend the genus Otodus to include sharks of the ‘megatoothed’ (e.g. megalodon) lineage in order to avoid Otodus paraphyly. We also propose the following phylogenetic hypothesis: [Kenolamna+[Cretalamna+[Megalolamna + Otodus]]].
https://doi.org/10.1080/08912963.2016.1236795

-------SIMPLIFYING THE METHODS - BODY LENGTH ESTIMATES FOR CARCHAROCLES MEGALODON USING ASSOCIATED TOOTH SETS AND JAW WIDTH RELATED DATA FROM GREAT WHITE SHARKS AND MAKOS. January 2016 - DOI:10.1130/abs/2016AM-285189. Conference: GSA Annual Meeting in Denver, Colorado, USA - 2016 Poster.
Abstract.-- Since the first time a Megalodon shark tooth was found and identified as such, the question of the actual size of one of the Neogene top predators was the subject of imaginative

speculation and scientific investigation. Both the results and the methods that are used to determine the size led to enormous dimensions in each case but are still quite diverse and bear a high potential for uncertainty. The problem with the recently most used estimation methods like those from Gottfried (1996) and Shimada (2002) is that they make body length estimates based on isolated teeth rather than entire dentitions. After testing the validity of the body length estimates from Shimada, which is the most accepted at the moment, by using several associated dentitions from C. megalodon, we noticed an extreme variability of the body length estimates depending on the tooth position in the jaw (Perez et al, 2016). In fact, especially estimates from lateral teeth were extremely variable and estimates from posterior teeth also varied significantly. The circumstance that we have this huge range in estimates makes it obvious that the teeth proportions of Megalodon don't correlate with that of the living Great White Shark. Subject of the studies presented in this poster is the use of the sum of the crown width of teeth from associated tooth sets as a measure for the related width of the entire jaw. Then we use this relation for a body length estimate based on the jaw proportions derived from appropriate data from modern Great White sharks and Makos. Moreover, t his study is a positive example of successful collaboration between professional and amateur paleontologists, one of the priorities of the NSF funded FOSSIL project.
https://dx.doi.org/10.1130/abs/2016AM-285189
https://www.researchgate.net/publication/309331648
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-------Body-size trends of the extinct giant shark Carcharocles megalodon: a deep-time perspective on marine apex predators. Paleobiology. 2015 Jun; Vol.41. DOI:10.1017/pab.2015.16. PMCID:PMC4541548. PMID:26321775.
Abstract.-- The extinct shark Carcharocles megalodon is one of the largest marine apex predators ever to exist. Nonetheless, little is known about its body-size variations through time and space. Here, we studied the body-size trends of C. megalodon through its temporal and geographic range to better understand its ecology and evolution. Given that this species was the last of the megatooth lineage, a group of species that shows a purported size increase through time, we hypothesized that C. megalodon also displayed this trend, increasing in size over time and reaching its largest size prior to extinction. We found that C. megalodon body-size distribution was left-skewed (suggesting a long-term selective pressure favoring larger individuals), and presented significant geographic variation (possibly as a result of the heterogeneous ecological constraints of this cosmopolitan species) over geologic time. Finally, we found that stasis was the general mode of size evolution of C. megalodon (i.e., no net changes over time), contrasting with the trends of the megatooth lineage and our hypothesis. Given that C. megalodon is a relatively long-lived species with a widely distributed fossil record, we further used this study system to provide a deep-time perspective to the understanding of the body-size trends of marine apex predators. For instance, our results suggest that (1) a selective pressure in predatory sharks for consuming a broader range of prey may favor larger individuals and produce left-skewed distributions on a geologic time scale; (2) body-size variations in cosmopolitan apex marine predators may depend on their interactions with geographically discrete communities; and (3) the inherent characteristics of shark species can produce stable sizes over geologic time, regardless of the size trends of their lineages.
Broader Implications
To our knowledge, body-size trends of large predatory sharks have never been studied before

over geologic time. Our results have three broader implications that provide a deep-time perspective to the understanding of the body-size trends of marine apex predators:

1. The left-skewed distribution of C. megalodon body size, both in the total temporal range and throughout the different periods studied, suggests a selective pressure favoring larger individuals. At ecological scales, and despite body-form similarities between large and small predatory sharks (Irschick and Hammerschlag 2014), larger individuals tend to prey upon larger animals (Lucifora et al. 2009). This trend is related to an ontogenetic dietary shift whereby smaller individuals avoid large (possibly dangerous) prey, whereas larger individuals consume a broader range of prey sizes (Lucifora et al. 2009; Estrada et al. 2006). This pattern has also been observed across different species of terrestrial predators (Peters 1983; Carbone et al. 1999). The left-skewed distribution of C. megalodon body size may therefore be the result of a long-term selective pressure on marine predatory sharks that favors consumption of a broader range of prey, increasing their impact in the structure of food webs (e.g., Steneck 2013).
2. Given the widespread distribution of a large cosmopolitan apex predator such as C. megalodon, the body-size variations found across oceans and hemispheres may be a result of the heterogeneous ecological conditions that they faced. Currently, sympatric populations of cosmopolitan predatory marine mammals such as the killer whale (Orcinus orca) are genetically distinguishable. This might be a result of assortative mating, which eventually produces morphological (e.g., body size) and behavioral differences between populations through generations (Hoelzel and Dover 1961). Similarly, the great white shark (Carcharodon carcharias) has demographically isolated populations due to their high degree of site fidelity (Jorgensen et al. 2009). Our study of C. megalodon body-size trends through space and geologic time suggests that the ecological distinctiveness of geographically discrete populations of large cosmopolitan marine apex predators may shape their body-size trends in deep time.
3. Finally, the lack of size change in C. megalodon throughout geologic time contrasts with the size increase trend observed not only in the megatooth lineage but also in other lineages of marine predators such as toothed whales (Odontoceti) (Pyenson and Sponberg 2011). Given that sharks have slower evolutionary rates than mammals (Martin et al. 1992), the lack of body-size change in C. megalodon may be the result of the inherent characteristics of shark species, which potentially make them particularly resilient to environmental changes (Martin et al. 1992; Pimiento et al. 2013a). A disconnection between micro- and macroevolutionary body-size patterns (i.e., stasis in the species vs. size increase in the lineage) could be an evolutionary consequence of such characteristics. The macroevolutionary mechanisms that produce the body-size increase in lineages of large marine predators are the subject of a future investigation.

Conclusions

We found that Carcharocles megalodon body size had a left-skewed distribution and was significantly different between hemispheres and ocean basins through geologic time. In addition, we found stasis as the mode of size evolution of C. megalodon, and thus reject our hypothesis of body-size increase over geologic time. Given that C. megalodon is a long-lived giant predator with a fossil record of ~14 Myr, it represents an excellent study system to provide a deep-time perspective to the understanding of body-size trends of marine apex predators. For instance, this study suggests that (1) a selective pressure in predatory sharks for consuming a broader range of prey may favor larger individuals and produce left-skewed distributions over geologic time, (2) body-size variations in cosmopolitan large apex predators may depend on the predators’ interactions within geographically discrete communities, and (3)

the inherent characteristics of shark species can produce a lack of net size changes over geologic time, even though the species' lineage shows size increase. Future research on body-size patterns of additional large apex predators (e.g., other megatooth sharks, toothed whales, plesiosaurs, mosasaurs, archaeocetes) would allow a more complete understanding of the macroevolutionary mechanisms that produce body-size increases, the evolution of gigantism, and the role of body size in extinction risk.
https://doi.org/10.1017/pab.2015.16

-------Fossil of mega-toothed killer whale found in Peru. Reuters, July 1, 2010.
LIMA (Reuters) - The fossil of a giant whale called Leviathan for having teeth bigger than a grown man's forearms has been found in Peru by paleontologists who on Thursday said it may have been the largest predator to ever roam the seas.
Leviathan Melvillei, which was named after the sea monster in the Bible and the author of "Moby Dick" Herman Melville, is an ancestor of the modern day sperm whale, said Rodolfo Salas, a paleontologist at Peru's Natural History Museum who took part in the study.
"This is an enormous tooth, more or less 14 inches long," Salas told Reuters. "The features of the teeth lead us to believe that the Leviathan was a big predator. It has the largest teeth on record."
The fossil of Leviathan was found two years ago and a team of scientists only unveiled the results of their find this week. Leviathan lived roughly 12 million years ago and its teeth were about twice as long as those of the great dinosaur Tyrannosaurus Rex.
"The Leviathan could have fed on other whales, which were very abundant and diverse in that period," said Salas.
As well as ten well-preserved teeth, the team of European and Peruvian paleontologists also found the whale's skull and its lower jaw. The findings were published in the journal Nature and the fossil will soon go on exhibit in Lima, Peru's capital.
The discovery was made in 2008 in the Ocucaje desert in southern Peru, which millions of years ago was the bed of a sea, and an area that has yielded dozens of big discoveries.
"In terms of (ancient) vertebrate sea life, Peru has the privilege of having the most important site in the world, the Ocucaje desert, which is where we've made this find," said Salas.
He said the Leviathan may have been bigger than one of its contemporaries, the Carcharocles Megalodon, widely regarded as the largest shark that ever lived, at some 65.5 feet in length.
"The Leviathan could have been the biggest predator that has ever lived in the sea," said Salas.
-- https://www.reuters.com/article/us-peru-whale-teeth-idUSTRE6603EQ20100701

-------Increase of body size in sixgill sharks with change in diet as a possible background of their evolution.
Historical Biology, 19(2007). DOI:10.1080/08912960701194461.
Abstract.-- Body size variation of a predator is a simple way to follow the main changes in its food source during its life history or along its evolution in ecology and paleoecology, respectively. Here, we present possible first evidence of such predator-prey co-evolution through the study of the body size evolution among sixgill sharks (genus Hexanchus) inferred from their fossil record and by comparison to the life history of its two recent species. As for the observed ontogenic diet change of the living bluntnose sixgill shark (H. griseus), its ancestors appear to have developed a similar penchant for dining on marine mammals at the

end of the Paleogene with a remarkably well-correlated timing.
https://doi.org/10.1080/08912960701194461

------- .....There’s still a lot we don’t know about megalodon.
So far we’ve only found teeth and vertebrae of megalodons. Like other sharks, most of their skeleton is made from cartilage which doesn’t preserve well in the fossil record. There’s still lively debate in the scientific community about the modern species of sharks to which megalodon is most closely related. Scientists who have been studying modern sharks are working with paleontologists to study megalodon and other long-extinct shark species. By asking questions about shark evolution, comparing fossils and modern specimens, and their environments, we can hopefully understand more about these amazing animals.
https://www.floridamuseum.ufl.edu/science/five-facts-megalodon/

-------Megalodon: the truth about the largest shark that ever lived. NHM.
...... Estimates suggest megalodon actually grew to between 15 and 18 metres in length, three times longer than the largest recorded great white shark. It may have been comparable in length to today's biggest whale sharks, the largest of which has measured in at 18.8 metres. Without a complete megalodon skeleton to measure, these figures are based on tooth size. Megalodon teeth can reach 18 centimetres long. In fact, the word megalodon simply means 'large tooth'. These teeth can tell us a lot, such as what these massive animals ate.
What did megalodon eat?
Emma explains, 'With its large serrated teeth megalodon would have eaten meat - most likely whales and large fish, and probably other sharks. If you are that big you need to eat a lot of food, so large prey is required.'
This would have included animals as small as dolphins and as large as humpback whales.
We have other evidence of megalodon's feeding habits in the form of fossilised whale bones. Some of these have been found with the cut marks of megalodon teeth etched in the surface. Others even include the tips of teeth broken off in the bone during a feeding frenzy that occurred millions of years ago.
Megalodon jaws
In order to tackle prey as large as whales, megalodon had to be able to open its mouth wide. It is estimated that its jaw would span 2.7 by 3.4 metres wide, easily big enough to swallow two adult people side-by-side.
These jaws were lined with 276 teeth, and studies reconstructing the shark's bite force suggest that it may have been one of the most powerful predators ever to have existed.
Humans have been measured with a bite force of around 1,317 Newtons (N), while great white sharks have been predicted to be able to bite down with a force of 18,216N. Researchers have estimated that megalodon had a bite of between 108,514 and 182,201N.
What did megalodon look like?
Most reconstructions show megalodon looking like an enormous great white shark, Carcharodon carcharias. This is now believed to be incorrect.
O. megalodon likely had a much shorter nose, or rostrum, when compared with the great white, with a flatter, almost squashed jaw. Like the blue shark, it also had extra-long pectoral fins to support its weight and size.
'A lot of reconstructions have megalodon looking like a bigger version of the great white shark because for a long time people thought they were related,' explains Emma. 'We now know that

this is not the case, and megalodon is actually from a different lineage of shark of which megalodon was the last member.'

The oldest definitive ancestor of megalodon is a 55-million-year-old shark known as Otodus obliquus, which grew to around 10 metres in length. But the evolutionary history of this shark is thought to stretch back to Cretalamna appendiculata, dating to 105 million years old - making the lineage of megalodon over 100 million years old.

'As we've found more and more fossils, we've realised that the ancestor to the great white shark lived alongside megalodon. Some scientists think they might even have been in competition with each other,' says Emma.

Where did the megalodon live?

O. megalodon was adapted to warm tropical and subtropical locations around the globe. The species was so widely spread that megalodon teeth have been found on every continent except Antarctica.

'We can find lots of their teeth off the east coast of North America, along the coasts and at the bottom of saltwater creeks and rivers of North Carolina, South Carolina and Florida,' explains Emma. This is likely due in part to the age of the rocks, but also because they can easily be found on the sea floor allowing collectors to go diving for them.

'They are also quite common off the coast of Morocco and parts of Australia. They can even be found in the UK near Walton-on-the-Naze, Essex,' says Emma, although they are extremely rare in the UK and tend to be of poor quality.

https://www.nhm.ac.uk/discover/megalodon--the-truth-about-the-largest-shark-that-ever-lived.html

-------Megalodon: 5 Interesting Facts About The World's Biggest Shark

An Atlantic Shark Institute team was disappointed yesterday when what seemed to be a massive megalodon shark was only a large school of mackerel. The team said on social media they hoped the image they saw on the scanner was the extinct megalodon, but they must remain satisfied with fossil discoveries for now. Megalodons are prehistoric predatory fish that are believed to be big enough to eat a whale, according to reports. Newsweek reported the megalodon's mouth opened to 11 feet wide and was lined with as many as 276 teeth. That makes megalodon fossil discoveries somewhat common, as the prehistoric predators lost a set of teeth every fortnight, equaling 40,000 teeth in its lifetime. Although Megalodon teeth are frequently discovered, a full megalodon jaw has never been discovered. Saltwater breaks down cartilage, so all megalodon jaws have likely dissolved.

1909. Paleontologists estimated the size of the monstrous jaw by using the fossilized teeth. Bashford Dean reconstructed the first megalodon jaw at the American Museum of Natural History in 1909 according to Dutch Shark Society, but it is believed Dean overestimated the thickness of the cartilage, making the model taller than reality.

1992. In 1992, the Smithsonian Institute had a set of megalodon jaw replicas constructed by paleontologist John Maisey. The replicas include a nearly complete set of fossilized megalodon teeth found in North Carolina.

2020. A study by the University of Bristol reported that the teeth can be larger than a human hand. The study found the Megalodon could have stretched up to more than 50 feet in length with a dorsal fin that was taller than an adult human.

Paleontologist Jack Cooper and a team of researchers used the isolated teeth fossil discoveries to estimate the true breadth of the megalodon. Their findings were published in Scientific Reports in 2020. The project was supervised by Dr. Catalina Pimiento. The study found the giant prehistoric shark is not a direct ancestor of only the great white shark, as previously believed.

"Megalodon is not a direct ancestor of the great white but is equally related to other macropredatory sharks such as the Makos, Salmon shark and Porbeagle shark, as well as the great white," Pimiento said in the study. "We pooled detailed measurements of all five to make predictions about megalodon."

Fox News reported in 2020 that several megalodon nurseries were discovered in Spain. Reports show that many fossils from young and adult megalodons were unearthed. A study by The Royal Society reported as many as five megalodon nurseries have been found in the Atlantic, Caribbean and Pacific basins. The fossils were from as long as 16 million years ago, with the most recent fossils being from around 3 million years ago when the shark went extinct.

The nurseries were home to fossils from megalodons as young as 1 month old, at approximately 16 feet in length, to adolescent megalodons that stretched over 30 feet in length. Researchers anticipate the megalodon could be twice to three times the size of a great white shark. A great white shark can be more than 20 feet long.

2022. Just last month, Newsweek reported a North Carolina fossil hunter found several teeth from the megalodon. The teeth were 5.5 inches and 6 inches long. Megalodon teeth can be up to 7 inches in length, but many fossil finds range from 3 to 5 inches long, according to the Florida Museum of Natural History. Dutch Shark Society reports the largest megalodon tooth discovered was nearly 7.5 inches in length and was found in Peru. Only 1 percent of megalodon fossilized teeth are more than 6 inches long.

The megalodon could have gone extinct for a variety of reasons and experts disagree on what eliminated the species, Newsweek reported earlier this year. One theory is the species was succeeded by the great white shark. Other theories are that sea level changes could have reduced the shark's habitat.

https://www.newsweek.com/look-back-megaladon-discoveries-115-years-1740721

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