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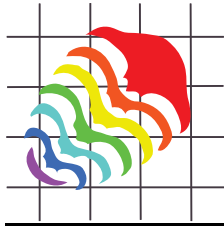
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White shark comparison reveals a slender body for the extinct megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae)

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ABSTRACT

The extinct megatooth shark, †*Otodus megalodon*, which likely reached at least 15 m in total length, is an iconic extinct shark represented primarily by its gigantic teeth in the Neogene fossil record. As one of the largest marine carnivores to ever exist, understanding the biology, evolution, and extinction of †*O. megalodon* is important because it had a significant impact on the ecology and evolution of marine ecosystems that shaped the present-day oceans. Some attempts inferring the body form of †*O. megalodon* have been carried out, but they are all speculative due to the lack of any complete skeleton. Here we highlight the fact that the previous total body length estimated from vertebral diameters of the extant white shark for an †*O. megalodon* individual represented by an incomplete vertebral column is much shorter than the sum of anteroposterior lengths of those fossil vertebrae. This factual evidence indicates that †*O. megalodon* had an elongated body relative to the body of the modern white shark (*Carcharodon carcharias*). Although its exact body form remains unknown, this proposition represents the most parsimonious empirical evidence, which is a significant step towards deciphering the much-debated body form of †*O. megalodon*.

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INTRODUCTION

The extinct megatooth shark, †*Otodus megalodon* (Lamniformes: †Otodontidae), is an iconic prehistoric shark that has captured the attention of both scientists and the public due to its large teeth. Yet, one major challenge palaeontologists have faced is exactly what †*O. megalodon* looked like because no complete skeleton of the fossil species is known to date. Traditionally, the extant white shark (*Carcharodon carcharias*) has been used as a model species to reconstruct the body form of †*O. megalodon* (e.g., Gottfried et al., 1996). The most recent attempts have been the 2D reconstruction work by Cooper et al. (2020), followed by Cooper et al.'s (2022) 3D model of the body of †*O. megalodon*. Cooper et al. (2020, 2022) used the extant white shark as a model representation of †*O. megalodon* because the fossil shark has been inferred to be regionally endothermic like the extant lamnid sharks that include the white shark (Ferrón, 2017). In particular, Cooper et al. (2022) used an extant juvenile white shark specimen to generate a 3D model of †*O. megalodon* first, and then conducted a 'model adjustment' using all the extant lamnids because of the uncertainty in the phylogenetic position of †*O. megalodon* within Lamniformes. Based on their body form reconstruction, they concluded that †*O. megalodon* was a fast-cruising shark much like the extant lamnids. However, using the extant white shark or other lamnids as a template to reconstruct the body form of †*O. megalodon* lacks empirical fossil support (Sternes et al., 2023). Furthermore, it is also tenuous on the phylogenetic basis because †*O. megalodon*, as an otodontid, lies outside of the Lamnidae and may not be closely related to the family at all (Sternes et al., 2023; Figure 1A; but see also Appendix 1).

One key question is: "Did †*O. megalodon* look like a large extant white shark?" It is true that the extant white shark has generally been used to estimate the body size of †*O. megalodon* (Shimada, 2019; Perez et al., 2021), but unlike preserved

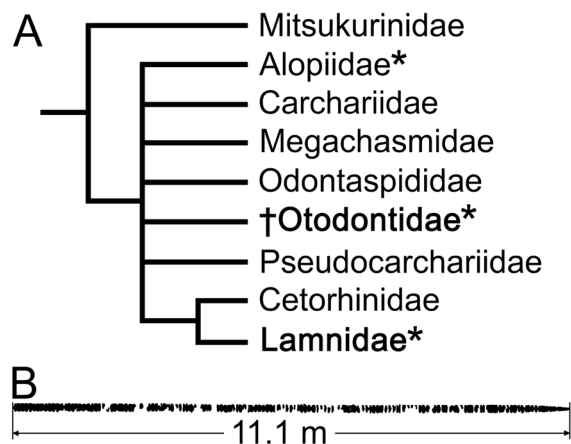


FIGURE 1. Simplified family-level phylogenetic hypothesis of Lamniformes showing all extant clades and †Otodontidae (**A**: dagger [†] indicates extinct), and silhouette depiction of fossil vertebral column of †*Otodus megalodon* (**B**). **A**, Current understanding of lamniform phylogeny demonstrating that a large portion of the phylogenetic tree remains unresolved due to conflicting results based on various molecular and morphological studies (Sternes et al., 2023 and references therein); although the placement of †Otodontidae is tentative and other extinct families are not depicted in this tree, the main point of this illustration is to demonstrate that †Otodontidae lies outside of Lamnidae (both clades highlighted in bold letters) where clades containing one or more species with regional endothermy (indicated by an asterisk [*]) do not share an immediate common ancestry (Sternes et al., 2023). **B**, Reconstructed vertebral column and its total measured length by Cooper et al. (2022) based on an incomplete associated vertebral set from the Miocene of Belgium; this specific specimen was previously estimated to have come from an individual that measured 9.2 m in total length, including the head and caudal fin (Gottfried et al., 1996) based on the modern white shark, not accounted for by Cooper et al. (2022).

teeth that are at least tangibly comparable, the lack of any complete skeleton, or even a complete cranial skeleton or vertebral column, makes any skeletal or body reconstruction speculative. However,

there are three critical pieces of information relevant to addressing the question that have become available since Cooper et al.'s (2022) study. First, on the basis of geochemical evidence, the endothermic physiology in †*O. megalodon* (specifically, likely regional endothermy) is empirically confirmed (Griffiths et al., 2023). Second, the newly described placoid scales of †*O. megalodon*, particularly the scales' interkeel distances that vary independent of body sizes in sharks, indicate that the general cruising speed of †*O. megalodon* was likely slower than the cruising speeds of extant lamnids, including the white shark (Shimada et al., 2023). Third, and more significantly, two other lamniform species, the extant planktivorous basking shark (*Cetorhinus maximus*), which has traditionally been regarded as a sluggish shark, as well as the deep-water, benthopelagic smalltooth sand tiger (*Odontaspis ferox*) have both been reinterpreted to be endothermic (also likely regional endothermy: Dolton et al., 2023a, 2023b; despite at least *O. ferox* is suggested to be ectothermic based on isotopic analyses by Griffiths et al., 2023). Hence, while †*O. megalodon* was indeed 'endothermic' (Griffiths et al., 2023), the new palaeontological (Shimada et al., 2023) and neontological (at least Dolton et al., 2023a, at present) evidence do not corroborate the previous assumption and its rationale that †*O. megalodon* must have physically resembled the extant white shark or lamnids in general (Cooper et al., 2020, 2022). Therefore, the purpose of this paper is two-fold: 1) to re-evaluate the validity of the most recently proposed body form reconstruction of †*O. megalodon*; and 2) to provide a new hypothesis on the body form of †*O. megalodon* based on available evidence.

MATERIALS AND METHODS

The main specimen used for the re-evaluation of the recently proposed body form of †*O. megalodon* and further discussion in this study is IRSNB P 9893, which is housed in the Royal Belgian Institute of Natural Sciences (IRSNB) in Brussels. This fossil specimen, formerly referred to as 'IRSNB 3121' (Gottfried et al., 1996), consists of 141 associated, but disarticulated, vertebral centra from an individual collected from the Miocene of Belgium (Shimada et al., 2021b; Cooper et al., 2022) (Figure 1B). Although it was not associated with any teeth, the specimen is broadly accepted to have come from †*O. megalodon* due to the large size and structure of the centra, which are consistent with non-cetorhinid lamniform vertebrae (Gottfried et al., 1996; Shimada et al., 2021b; Cooper et al.,

2022). Based on the maximum width of the largest centrum in the specimen ('vertebra #4' measuring 155 mm in width), the †*O. megalodon* individual was estimated to be 9.2 m TL in life based on a linear regression function describing the quantitative relationship between the maximum vertebral width and TL measurements from 16 extant white sharks (Gottfried et al., 1996). Cooper et al. (2022, data S1) also took measurements of each vertebra of IRSNB P 9893 and presented the sum of antero-posterior lengths of all centra to be approximately 11.1 m (Figure 1B). Our study compared that measurement (11.1 m) with an estimated total length (9.2 m) for that specific †*O. megalodon* individual based on the extant white shark (Gottfried et al., 1996).

For comparisons, some preserved extant specimens housed in the following repository institutions were examined radiographically: Field Museum of Natural History (FMNH), Chicago, Illinois, USA; Natural History Museum of Los Angeles County (LACM), California, USA; and Florida Museum of Natural History, University of Florida (UF), Gainesville, USA. We used a Siemens Medical Systems' SOMATOM Sensation 64-slice computed tomography (CT) scanner at the Children's Memorial Hospital, Chicago, Illinois, USA, with the following settings: 120 kVp, effective mAs 200 with automatic exposure control activated, rotation time 0.33 sec, 0.75 pitch, 32 detectors using z-flying focal spot technique, 0.625-mm slice thickness and 0.4 mm overlapping slice reconstruction. Multiple CT images showing the skeletal elements of the specimens were generated using Siemens' InSpace software.

We acknowledge that different types of intra-specific variation may occur in sharks, including sexual dimorphism where, in many lamniform taxa, females tend to reach sexual maturity at larger body sizes or attain larger maximum body sizes (Compagno, 2002). However, for the purpose of re-evaluating the validity of Cooper et al.'s (2022) reconstructed vertebral column of †*O. megalodon*, we examined in detail the CT scans of a juvenile *Carcharodon carcharias* specimen (LACM 43805-1), which are available on the MorphoSource database (<https://www.morphosource.org/concern/media/000545335>). Vertebral diameters were measured from this specimen by using the open-source web program postDICOM (Herten, The Netherlands; www.postdicom.com, last accessed July 25, 2023). Each measurement was taken three times to minimize possible measurement errors and to calculate a mean value that was subsequently

used. A total of 163 vertebral centra were measured across the entire body of the specimen (see Appendix 2).

RESULTS AND DISCUSSION

Re-evaluation of the Validity of the Recently Reconstructed Body Form of †*O. megalodon*

Cooper et al. (2022) proposed the most recent 3D model of †*O. megalodon* and used it to make various inferences on the ecology of the extinct shark. We re-evaluated their assumptions and propositions by considering available evidence and other recent discoveries. Our re-evaluation result is that there are at least four major concerns with their body reconstruction that are worthy of discussion.

The first issue is the questionable accuracy of their reconstructed vertebral column of †*O. megalodon*. Cooper et al. (2022) used 141 associated vertebrae from an †*O. megalodon* individual (IRSNB P 9893) collected from a Miocene deposit in Belgium. Despite being the best-preserved vertebral column of †*O. megalodon*, there are several major concerns that must be taken into consideration about using this fossil specimen. As Cooper et al. (2022, p. 8) also pointed out, this set of vertebrae is most certainly incomplete. For instance, Cooper et al. (2022) followed the sequence of curatorially assigned vertebral numbers that do not represent the vertebral sequence in life and noted that “centra 30, 35 to 37, 45, 105, 131, 136, 141, 146, 147, 149 are missing from the column”. Although Cooper et al. (2022) accounted for those vertebrae with artificially and likely arbitrarily (Gottfried et al., 1996) assigned numbers that are interpreted to be missing, exactly how many more vertebrae were present in the vertebral column in life remains uncertain. In fact, vertebral counts are known to vary widely even among lamniform sharks (Springer and Garrick, 1964). It is therefore impossible to even decisively determine the total number of vertebra, yet alone the total number of precaudal and caudal vertebrae, originally present in †*O. megalodon*. However, not only did Cooper et al. (2022) choose to assume that all preserved centra in the specimen represent precaudal vertebrae in their 3D model of †*O. megalodon*, they put the largest vertebrae near the neurocranium of their model (Figure 2). We point out that, in previous studies of both extinct (Conte et al., 2019) and extant (Natanson et al., 2018) lamniform sharks, the largest vertebrae are found in the girthiest portion of their trunk (mid-body), and this condition is

also true for the extant white shark (vertebrae 54–64: Appendix 2; Figure 2). For example, when plotting Cooper et al.’s (2022) reconstructed vertebral column, a gradual decline in vertebral diameter starting from the first vertebra is observed whereas the extant white shark shows a gradual increase in vertebral diameter and then a decline, which is the same pattern observed in other extant lamniform sharks (Natanson et al., 2018) (Figure 2). Furthermore, our reexamination of IRSNB P 9893 based on measurements provided by Cooper et al. (2022) suggests that not all centra in the specimen are precaudal vertebrae based on comparisons with a complete vertebral column in the extant white shark (Appendix 2). For example, in Cooper et al.’s (2022) computer model, the largest vertebra in IRSNB P 9893 (centrum 4) was 155 mm in diameter whereas the smallest vertebra (centrum 150) was 57 mm in diameter. When comparing the largest vertebra to the smallest in Cooper et al.’s (2022) model, this generates a ratio of 2.7. This same ratio (2.7) is present when comparing the largest vertebra found in the mid-body of the extant white shark to that of a vertebra found in its caudal fin, specifically, vertebrae #61 and #132 measuring 19.75 mm and 7.27 mm in diameter, respectively (Appendix 2). This fact strongly indicates that the reconstructed precaudal portion of the vertebral column of Cooper et al. (2022) indeed includes caudal vertebrae. Taking all the information into account, the model of the vertebral column created by Cooper et al. (2022) is most certainly incomplete and inaccurate.

The second issue is the discrepancy in jaw size. The ratio of the anteroposterior upper jaw length to the largest vertebral diameter in two specimens of the extant white sharks we measured from CT images (Figure 3) is about 8.3. On the other hand, Cooper et al.’s (2022) 3D †*O. megalodon* skeletal model has a ratio of 10.6. This means that the jaw size in the 3D skeletal model is oversized relative to its vertebrae if the extant white shark is used. Such a discrepancy may indicate that there is a flaw in Cooper et al.’s (2022) skeletal reconstruction, the extant white shark may not necessarily be an appropriate body form analog for the extinct species (i.e., †*O. megalodon* could have had a different body form), or both. In addition, Cooper et al. (2022) noted that their reconstruction of the †*O. megalodon* head is slightly ‘undersized’ (p. 9), but we would argue that, while the overall length of the cranial region relative to its TL may be on par with that of the extant white shark (see above), at least their jaw reconstruction may actu-

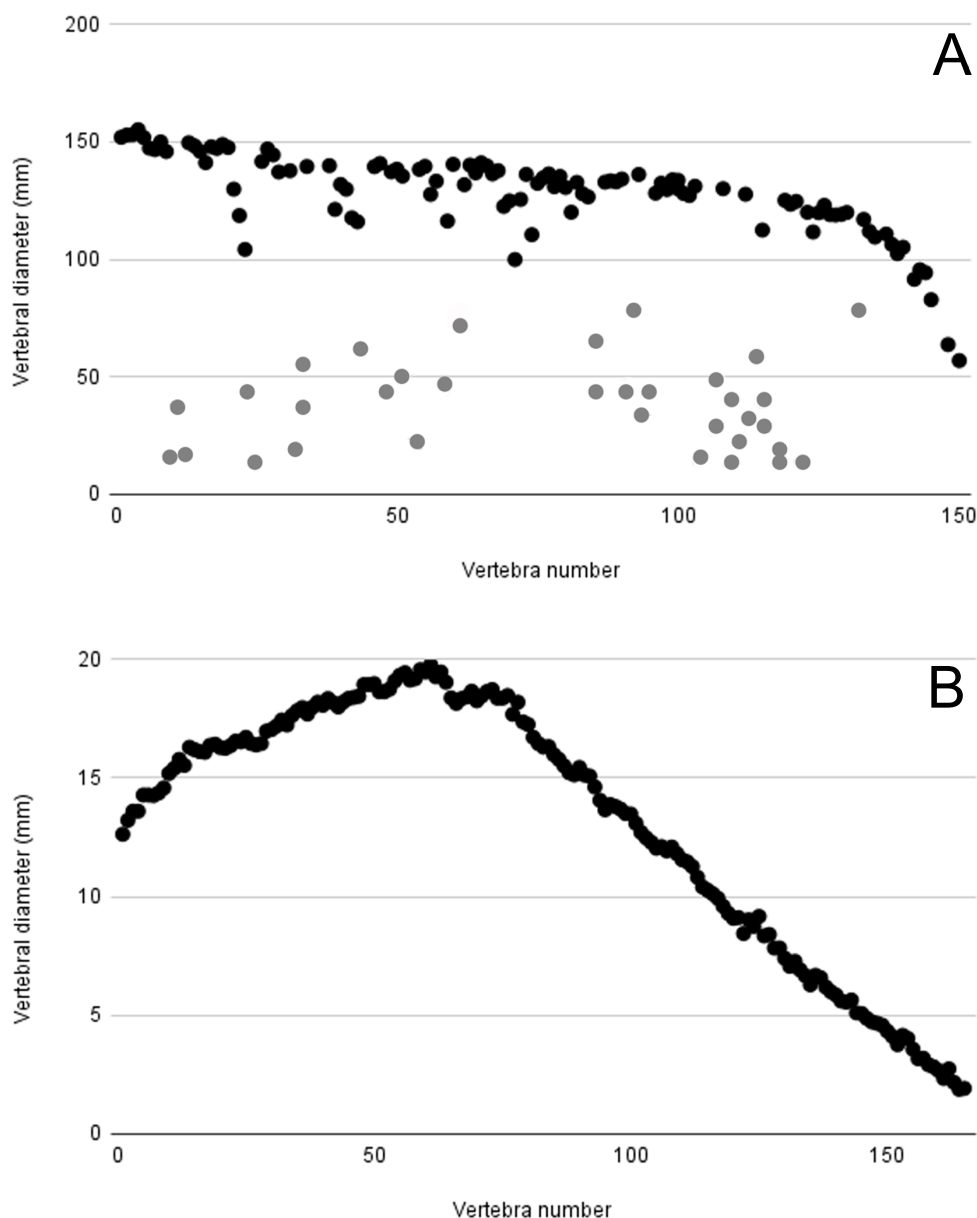


FIGURE 2. The distribution of vertebral diameters throughout each vertebral column, where vertebral number ‘1’ represents the anterior-most centrum in each specimen. **A**, Graph based on Cooper et al.’s (2022) Data S1 for the vertebral column of †*Otodus megalodon* from the Miocene of Belgium (IRSNB P 9893), where the vertebral column is most certainly incomplete and the vertebral numbers do not necessarily reflect the original anatomical sequence (grey plots represent significantly damaged vertebrae). **B**, Graph based on CT-scanned data of an extant white shark (*Carcharodon carcharias*) specimen (LACM 43805-1), where the vertebral column is complete and the vertebral numbers reflect the anatomical sequence.

ally be oversized relative to its body if the overall skeletal organization of the extant white shark (Figure 3), which Cooper et al. (2022) did not account for, is used as a model at face value.

The third concern is the lack of ontogenetic consideration. The specific extant white shark specimen scanned for Cooper et al.’s (2022) †*O.*

megalodon body reconstruction may not be ideal. Setting aside a slight upward bend of the head that is a rather unconventional posture compared to an otherwise fusiform body that typically characterizes the white shark and sharks in general (Sternes and Shimada, 2020; Paig-Tran et al., 2022; Sternes et al., 2023), the white shark specimen they used rep-

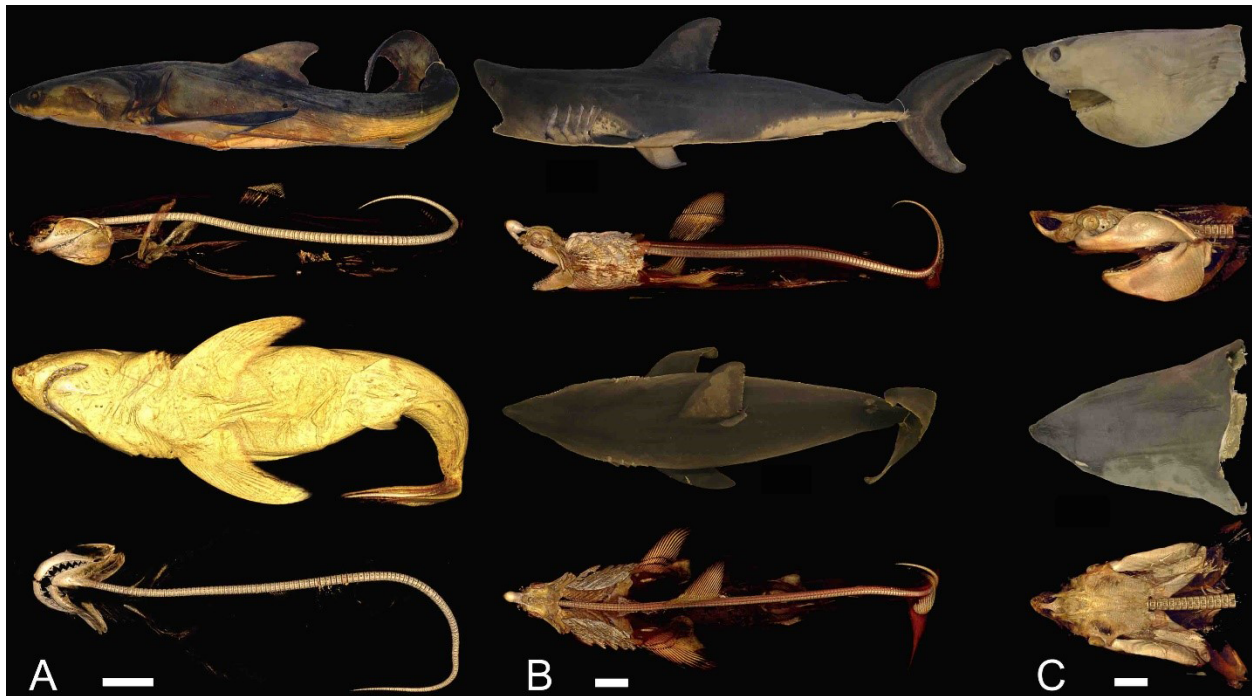


FIGURE 3. Photographic (*) and CT images (**) of preserved specimens of extant white shark (*Carcharodon carcharias*) and salmon shark (*Lamna ditropis*). **A.** Complete specimen of 126-cm-TL male *C. carcharias* caught off central California, USA (LACM 43805-1): from top to bottom, external body* and skeleton** in left lateral view and external body** and skeleton** in ventral view. **B.** Complete specimen of 151 cm TL male *L. ditropis* caught off central California (FMNH 117475): from top to bottom, external body* and skeleton** in left lateral view and external body* and skeleton** in dorsal view. **C.** Head specimen of estimated 271-cm-TL male *C. carcharias* caught off southern Florida, USA (FMNH 38335): from top to bottom, external head* and cranial skeleton** in left lateral view and external head* and cranial skeleton** in dorsal view. All scale bars equal 10 cm.

resents a 2.56-m-TL juvenile individual. Importantly, allometric changes in girth and the caudal fin morphology at various developmental stages are known for the white shark and other lamnids (Casey and Pratt, 1985; Lingham-Soliar, 2005; Tomita et al., 2018; Sternes et al., 2023). However, Cooper et al. (2022) did not address the possible effects of ontogenetic morphological differences in reconstructing the body form of †*O. megalodon*. Therefore, we question whether the use of a 2.6-m-TL juvenile white shark is appropriate for the extinct shark that likely reached at least 15 m TL (Shimada, 2019; Perez et al., 2021).

The fourth and perhaps the most critical issue is their method of body form reconstruction. Cooper et al. (2022) used a computer tomographic (CT) scan of an extant white shark cranial skeleton as a hypothetical substitute for that of †*O. megalodon* where they superimposed their artificially reconstructed dentition based on an incomplete associated tooth set of an †*O. megalodon* individual from the Pliocene of North Carolina, USA, esti-

mated to be 17.3 m in total length (TL) (Perez et al., 2021) onto the digital image of the white shark jaws. Even though the exact size of the cranial skeleton relative to the vertebral column remains uncertain based on the present fossil record, Cooper et al. (2022) then attached their cranial reconstruction to their reconstructed vertebral column based on an incomplete associated set of vertebrae of another †*O. megalodon* individual from the Miocene of Belgium (Figure 1B). To reconstruct the body, they scaled the full-body scan of an extant white shark so that their reconstructed vertebral column “ended at the base of the caudal fin” (Cooper et al., 2022, p. 9). Effectively, their †*O. megalodon* skeletal reconstruction based on the two fossil specimens served practically no purpose in inferring the body shape of †*O. megalodon* because the entire head and body were based on the extant white shark. Therefore, by taking this methodological assessment along with the other three aforementioned concerns into account, the

validity of their 3D model of †*O. megalodon* is highly questionable.

A New Interpretation of †*O. megalodon* Body Form

So, what did †*O. megalodon* actually look like? Despite their questionable reconstructions, we point out that Cooper et al.'s (2022) study is significant because it left an important clue about the body form of †*O. megalodon*. Their reconstructed vertebral column based on **an associated vertebral set from the Miocene of Belgium** was 11.1 m in length (Figure 1B) with the total length of their complete model measuring 15.9 m. The specimen is most certainly incomplete (Gottfried et al., 1996), missing an unknown number of vertebrae (see above). Yet, this specific †*O. megalodon* specimen was previously estimated to have come from an individual that measured 9.2 m TL (i.e., including the head and caudal fin) based on the quantitative relationship between the maximum vertebral width and TL measured from 16 extant white sharks that ranged 1.9–3.7 m TL (Gottfried et al., 1996; Shimada et al., 2021b). The vertebral centra of †*O. megalodon* are short, well mineralized and equipped with densely spaced radial lamellae (Leriche, 1926). This vertebral morphotype, which functionally adds architectural strength, is common within Lamniformes and characterizes both the extant white shark (Newbrey et al., 2015) and many other extinct apex predatory lamniform species (Shimada, 1997; Siverson, 1999; Amalfitano et al., 2022). Yet, the much longer vertebral column length measured by Cooper et al. (2022) (11.1 m)

than the estimate based on the vertebral diameter sizes of the extant white shark (9.2 m TL) indicates that †*O. megalodon* had a more elongated body relative to the extant white shark (Figure 4).

Cooper et al. (2022) did also recognize that their reconstructed 3D model based on the Belgian fossil is “markedly longer than previously estimated for this specimen” (p. 4 of main text) and that their “initial [computer-generated] model [of †*O. megalodon*] appeared rather thin” (p. 16 of their Supplementary Methods). However, constrained by the underlying premise of their study using the extant white shark or Lamnidae as the modern analog for †*O. megalodon*, they did not consider the possibility that †*O. megalodon* could have had an elongated body form compared to the extant white shark. Instead, Cooper et al. (2022) attributed the discrepancy to 1) the distant phylogenetic relationship between †*O. megalodon* and the white shark, 2) the unknown total vertebral count and column structure in †*O. megalodon*, and 3) the uncertainty in whether the Miocene specimen from Belgium preserves the largest vertebral centrum from the individual. However, not only do these additional explanations make their proposition less parsimonious, their phylogenetic justification to explain the discrepancy is contradictory to their very premise of using the extant white shark as a model for †*O. megalodon* in the first place. Furthermore, whereas the likelihood of significantly larger vertebrae missing from the Belgian fossil specimen is rather low because diameter differences across the largest preserved centra are subtle and in a tight range (e.g., nearly 42% of the 141 preserved vertebrae measure 130–155 mm: Figure 2), the possibility

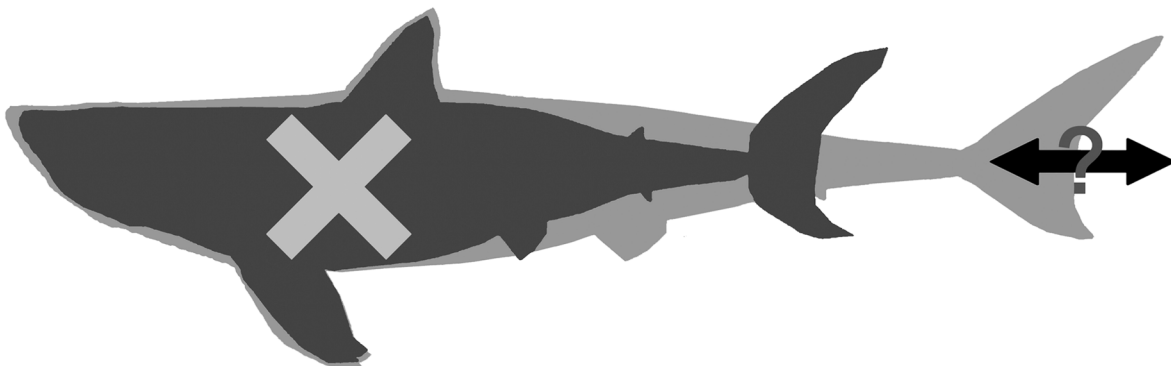


FIGURE 4. Previous and new schematic interpretations of †*Otodus megalodon* body form. A dark grey silhouette depicting the previously reconstructed †*O. megalodon* body form by Cooper et al. (2022) based on the extant white shark, superimposing a light grey outline showing the newly interpreted body form of †*O. megalodon* which is more elongated than the extant white shark. Note: it must be emphasized that this illustration should be strictly regarded as schematic as the exact extent of body elongation, the shape of the head, and the morphology and positions of the fins remain unknown based on the present fossil record.

that more vertebrae could be missing from the specimen would mean that their 11.1 m measurement must be regarded as the minimum possible length of the vertebral column. Alternatively, our proposition is based on evidence that is most parsimonious and empirical: i.e., 11.1 m [= minimum possible actual measured vertebral column length] > 9.2 m [total length of the same fossil individual estimated from the extant white shark].

Exactly how elongated †*O. megalodon*'s body was relative to the extant white shark is uncertain at the present time (Figure 4) because the extent of missing vertebrae in the associated vertebral set (Figure 1B) is unknown (Cooper et al., 2022; this study). However, besides the aforementioned new palaeontological (Shimada et al., 2023) and neontological (at least Dolton et al., 2023a, at present) evidence, our interpretation is further supported by additional anatomical evidence. In modern lamnids, centrum growth correlates with girth rather than body length (Natanson et al., 2018). White sharks have a thicker vertebral column than shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*) sharks at a comparable body length (Gottfried et al., 1996; Natanson et al., 2002; Doño et al., 2015) but with a similar mass (Kohler et al., 1995). More compression-resistant vertebrae may compensate for the structural issues associated with the thinner columns in shortfin makos and porbeagles (Ingle et al., 2018). The maximum diameter of the †*O. megalodon* vertebrae from Belgium along with the original vertebral column length of 11.1+ m indicates a vertebral column not only much thinner in relative terms than that of a white shark but also more gracile than those of smaller-bodied lamnids with known vertebral size data (Gottfried et al., 1996; Natanson et al., 2002; Doño et al., 2015). If anything, the data from living lamnids indicate a robust vertebral column in a hypothetical lamnid-like shark the size of an †*O. megalodon*. Therefore, the remarkably slender vertebral column of the Belgian †*O. megalodon* specimen raises concerns about the accuracy of girthy, lamnid-like reconstructions of this species suggested by Cooper et al. (2020, 2022). We also note that the body cross-sectional geometry in Cooper et al.'s (2022) 3D body reconstruction of †*O. megalodon* is rather rectangular and distorted, but it is generally elliptical in extant sharks (Tomita et al., 2021), suggesting that it is more parsimonious to consider †*O. megalodon* to also have had an elliptical body cross-section.

The exact body form of †*O. megalodon* (or any other otodontids: see Appendix 1) cannot be

elucidated decisively based on the present fossil record (Sternes et al., 2023). Nevertheless, our new interpretation—that †*O. megalodon* had an elongated body relative to the extant white shark—has significant implications for the biology of the fossil shark, most notably because it would mean that its pleuroperitoneal cavity was likely elongated as well. †*Otodus megalodon* and its predecessors such as †*O. chubutensis* apparently occupied a trophic position similar to (McCormack et al., 2022), or possibly higher than (Kast et al., 2022), the extant white shark based on geochemical evidence, where its diet included marine mammals based on bite marks in fossil pinniped and cetacean bones (Aguilera et al., 2008; Collareta et al., 2017; Godfrey et al., 2018). The morphology of placoid scales suggests that the cruising speed of †*O. megalodon* was probably slower than that of the extant lamnids including the white shark, and its endothermic metabolism is thought to have been used largely to facilitate digesting large, ingested food items and enhancing nutrient absorption and processing (Shimada et al., 2023). Where digestion of food and absorption of nutrients are essential for every vertebrate (Tomita et al., 2023), endothermic fishes possess visceral countercurrent heat exchangers and retain an elevated metabolic rate from food processing (Dickson and Graham, 2004). Sharks have a spiral intestine with complex intestinal muscular activity (Tomita et al., 2023), that is thought to have evolved to increase the absorptive surface area and to reduce the unidirectional flow speed of digesta for prolonging absorptive time (Holmgren and Nilsson, 1999; Leigh et al., 2021). In fact, the spiral intestine is the warmest visceral organ in extant lamnids, along with their warm, large, lipid-rich liver associated with the suprahepatic rete (Carey et al., 1985; Bernal et al., 2001). The elongated body of †*O. megalodon* would imply that its liver as well as its alimentary canal, including the spiral intestine, within the body cavity may have also been long, which would have concomitantly provided more absorptive area and time with heat-induced nutrient processing efficiency. Furthermore, at least some endothermic fishes can exploit cool waters because of a warm viscera that further elevates the body core temperature (Dickson and Graham, 2004). It is conceivable that the worldwide occurrences of †*O. megalodon* fossils (Razak and Kocsis, 2018), including cool areas, may, at least in part, be attributed to this physiological condition.

CONCLUSIONS

Cooper et al.'s (2022) 3D reconstruction work is novel, but because the fundamental assumptions and accuracy of their 3D skeletal and body reconstructions are questionable in the first place, their entire conclusions about the lifestyle of †*O. megalodon* based on their 3D reconstruction must also be considered questionable. In fact, their conclusion that †*O. megalodon* was a fast or long-distance swimmer like the extant white shark is logically circular because their body reconstruction of the fossil shark was based on the fast-swimming, regionally endothermic lamnids including the white shark with known long-distance travel records (Weng et al., 2007; Jorgensen et al., 2010; Watanabe et al., 2015; Harding et al., 2021). The reality is that there is currently no scientific support for Cooper et al.'s (2022) or any of the previously published body forms of †*O. megalodon* (Gottfried et al., 1996; Cooper et al., 2020). Furthermore, our results indicate that the previously published †*O. megalodon*'s possible maximum body size estimates of 15–20 m TL (Shimada, 2019; Perez et al., 2021) as well as its ontogenetic growth model (Shimada et al., 2021b) based on the extant white shark are likely underestimated. We must acknowledge that, without direct fossil evidence such as a complete skeleton, extrapolation over 100 million years of otodontid or lamniform evolution and uniquely 'off-the-scale' gigantism of †*O. megalodon* among macrophagous lamniform sharks (Shimada et al., 2021a) makes the direct compari-

son of body forms even within Lamniformes extremely challenging.

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APPENDIX 1.

Phylogenetic relationships between †Otodontidae and Lamnidae proposed by Greenfield (2022a, 2022b).

Greenfield (2022a, 2022b) made new propositions regarding the close phylogenetic affinity between †Otodontidae and Lamnidae and presented a body restoration of another otodontid taxon. Although they are not central to the scope of this present paper, Greenfield's (2022a, 2022b) propositions are relevant to the context of either Cooper et al.'s (2022) phylogenetic assertion in relation to †*O. megalodon* or considering the body form of †*O. megalodon* and otodontids in general. Therefore, we briefly comment on Greenfield's (2022a, 2022b) propositions here.

Phylogenetic Position of †*O. megalodon*

Cooper et al. (2022) noted that “there are uncertainties regarding the interrelationships between extinct and extant Lamniformes, and therefore, †*O. megalodon* could be as closely related to *C. carcharias* as to any other lamniform” (p. 9). Subsequently, Greenfield (2022a, 2022b) contended that †Otodontidae is a sister to the family Lamnidae and even erected a new superfamily Lamnoidea that represents a clade consisting of †Otodontidae and Lamnidae. Greenfield (2022a, 2022b) argued that the following two characters phylogenetically unite †Otodontidae and Lamnidae: 1) robust, calcified rostral cartilages with circular transverse cross-section and without fenestrae and appendices; and 2) regional endothermy. It is important to point out that the taxonomic identity of the isolated fossil rostral cartilages used for Greenfield's (2022a, 2022b) basis remains inferential and requires testing by the discovery of rostral specimens associated with taxonomically diagnostic teeth from the same individual shark. We also note that rostral hypercalcification is not confined to Lamnidae (more specifically *Lamna*: Figure 3) within Lamniformes but also occurs in the extant bigeye thresher (*Alopias superciliosus*: Figure A1) and possibly at least in one member of the Cretaceous taxon, †Anacoracidae (Shimada, 2013). In addition, the assertion that regional endothermy can be used as a synapomorphy to unite †Otodontidae and Lamnidae within Lamniformes is now questionable based on the recent papers suggesting that regional endothermy may be present broadly within Lamniformes (Dolton et al., 2023a, 2023b, and references therein; but see also Griffiths et al., 2023). Greenfield (2022b) noted whether †Otodontidae lies outside of the ‘Cetorhinidae+Lamnidae’ clade has never been tested. However, it should be pointed out that there has been no test conducted on or supporting the ‘†Otodontidae+Lamnidae’ clade either, unlike the existing strong support of the sister relationship between Cetorhinidae and Lamnidae both morphologically and molecularly (Stone and Shimada, 2019; Vella and Vella, 2020; Kousteni et al., 2021; Silva et al., 2023). Even if Cetorhinidae and Lamnidae are not sisters hypothetically (vs. Figure 1A), it will not automatically place †Otodontidae as a sister to Lamnidae simply because there is so far not even one decisive synapomorphy that supports Greenfield's (2022a, 2022b) ‘Lamnoidea hypothesis.’ We stress that the practice of erecting higher taxonomic categories should be conducted carefully, especially for a phylogenetically complex group like Lamniformes (Stone and Shimada, 2019; Shimada, 2022).

Another Problematic Otodontid Body Restoration

Greenfield (2022b) presented a body restoration of another otodontid, †*Cretalamna* sp., based on previously published photographs of multiple partial or nearly complete skeletal specimens from the Upper Cretaceous (Cenomanian Stage) of Lebanon (Pfeil, 2021). Greenfield (2022b) used his restoration to further support his ‘Lamnoidea hypothesis’ on the basis of its putative body form that is vaguely reminiscent of extant lamnids, particularly *Lamna*. Such a restoration of another otodontid may appear significantly relevant to the context of restoring the body form of †*O. megalodon*. However, Greenfield's (2022b) †*Cretalamna* body restoration must be viewed with skepticism. This is because, while the degree of taphonomic distortion or flattening of the body through the fossilization of the specimens was not assessed, the authenticity of the specimens or anatomical parts of the specimens can only be speculated from the photographs. More critically, the †*Cretalamna* skeletons (Pfeil, 2021) are ‘unnumbered’ specimens with uncertain catalog status. Effectively, this condition does not allow the reproducibility of Greenfield's (2022b) propositions, and thus, they cannot be viewed as scientifically valid.



FIGURE A1. Photographic (*) and CT (**) images of cranial region of 187-cm-TL male extant bigeye thresher (*Alopias superciliosus*: UF 160188) caught off Florida, USA, demonstrating hypercalcified rostral cartilage in the species. Top, ventral view*; middle, ventral view**; bottom, left lateral view **. Note that the same hypercalcification is also present in another specimen of *A. superciliosus* (UF 178509: 201-cm-TL male caught off Florida). Scale bar = 10 cm.

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APPENDIX 2.

Measurements of the *Carcharodon carcharias* specimen LACM 43805-1.

Vertebra	∅ #1 (mm)	∅ #2 (mm)	∅ #3 (mm)	∅ mean (mm)
#1	12.73	12.45	12.67	12.62
#2	13.41	13.08	13.15	13.21
#3	13.81	13.44	13.51	13.59
#4	13.77	13.45	13.56	13.59
#5	14.54	13.88	14.39	14.27
#6	14.73	13.58	14.52	14.27
#7	14.65	14.05	14.06	14.25
#8	14.90	14.15	14.02	14.36
#9	14.56	14.67	14.48	14.57
#10	15.17	15.15	15.22	15.18
#11	15.41	15.24	15.53	15.39
#12	16.23	15.34	15.75	15.77
#13	15.65	15.04	15.86	15.52
#14	16.42	16.21	16.22	16.28
#15	16.52	15.92	16.1	16.18
#16	15.99	16.1	16.2	16.10
#17	16.09	16.19	15.92	16.07
#18	16.26	16.79	16.04	16.36
#19	16.38	16.66	16.20	16.41
#20	16.27	16.42	16.13	16.27
#21	16.23	16.36	16.12	16.24
#22	16.38	16.38	16.30	16.35
#23	16.48	16.43	16.71	16.54
#24	16.65	16.38	16.5	16.51
#25	16.91	16.19	16.99	16.70
#26	16.77	16.38	16.17	16.44
#27	16.71	16.02	16.4	16.38
#28	16.83	16.38	16.1	16.44
#29	17.24	17.09	16.54	16.96
#30	17.17	16.9	17.02	17.03
#31	17.08	17.18	17.27	17.18
#32	17.24	17.63	17.43	17.43
#33	17.36	16.78	17.52	17.22
#34	17.9	17.22	17.73	17.62
#35	17.92	17.82	17.71	17.82
#36	18.16	17.89	17.82	17.95
#37	17.95	17.37	17.73	17.68
#38	18.33	17.75	17.83	17.97
#39	18.44	18.17	17.92	18.18
#40	18.38	17.91	17.85	18.05
#41	18.79	18.08	18.13	18.33
#42	18.29	17.97	18.22	18.16

Vertebra	Ø #1 (mm)	Ø #2 (mm)	Ø #3 (mm)	Ø mean (mm)
#43	18.07	17.79	18.09	17.98
#44	18.38	18.03	18.17	18.19
#45	18.73	18.10	18.2	18.34
#46	18.46	18.25	18.44	18.38
#47	18.86	18.13	18.29	18.43
#48	18.97	18.69	19.09	18.92
#49	19.31	18.93	18.52	18.92
#50	19.19	18.97	18.71	18.96
#51	18.73	18.41	18.71	18.62
#52	19.03	18.51	18.32	18.62
#53	18.98	18.63	18.57	18.73
#54	19.46	18.71	19.05	19.07
#55	19.53	19.08	19.33	19.31
#56	19.6	19.43	19.23	19.42
#57	19.53	18.43	19.38	19.11
#58	19.31	19.14	19.06	19.17
#59	19.24	19.65	19.75	19.55
#60	19.19	19.61	19.56	19.45
#61	19.47	19.94	19.85	19.75
#62	18.79	18.91	20.05	19.25
#63	19.2	19.54	19.61	19.45
#64	18.57	19.18	19.31	19.02
#65	17.9	18.45	18.73	18.36
#66	17.94	18.14	18.3	18.13
#67	18.87	17.83	18.28	18.33
#68	18.48	18.55	18.18	18.40
#69	18.93	18.55	18.44	18.64
#70	18.59	18.1	18.04	18.24
#71	18.51	18.44	18.41	18.45
#72	18.93	18.67	18.28	18.63
#73	18.96	18.65	18.53	18.71
#74	18.36	18.26	18.44	18.35
#75	19.28	17.65	18.12	18.35
#76	17.77	18.79	18.82	18.46
#77	17.18	17.46	18.36	17.67
#78	18.21	18.12	18.22	18.18
#79	17.09	17.29	17.67	17.35
#80	17.15	17.18	17.38	17.24
#81	16.39	16.88	16.84	16.70
#82	16.08	16.66	16.58	16.44
#83	15.99	16.47	16.4	16.29
#84	16.1	16.38	16.44	16.31
#85	15.67	16.23	16.02	15.97
#86	15.45	15.66	16.21	15.77
#87	15.2	15.48	15.81	15.50

Vertebra	∅ #1 (mm)	∅ #2 (mm)	∅ #3 (mm)	∅ mean (mm)
#88	15.16	15.28	15.2	15.21
#89	14.87	15.04	15.45	15.12
#90	15.38	15.37	15.53	15.43
#91	14.39	15.32	15.61	15.11
#92	14.62	15.54	15.05	15.07
#93	14.28	14.87	14.69	14.61
#94	13.71	14.15	14.3	14.05
#95	13.63	13.77	13.56	13.65
#96	13.79	13.77	14.06	13.87
#97	13.98	13.63	13.77	13.79
#98	13.79	13.6	13.66	13.68
#99	13.45	13.55	13.46	13.49
#100	13.36	13.51	13.53	13.47
#101	13.1	13.11	13.02	13.08
#102	12.81	12.33	12.97	12.70
#103	12.49	12.12	12.81	12.47
#104	12.52	12.02	12.31	12.28
#105	12.23	11.82	12.05	12.03
#106	12.36	11.82	12.12	12.10
#107	12.24	11.82	11.71	11.92
#108	11.97	12.12	12.14	12.08
#109	12.21	11.44	11.75	11.80
#110	11.77	11.18	11.71	11.55
#111	11.78	11.18	11.41	11.46
#112	11.47	10.94	11.38	11.26
#113	10.93	10.62	10.88	10.81
#114	10.33	10.41	10.45	10.40
#115	10.36	9.98	10.45	10.26
#116	10.11	10.05	10.16	10.11
#117	9.79	10.09	9.87	9.92
#118	9.55	9.91	9.32	9.59
#119	9.46	9.74	8.66	9.29
#120	8.99	9.26	8.99	9.08
#121	8.84	9.66	8.83	9.11
#122	8.5	8.78	8.05	8.44
#123	8.93	9.06	9.08	9.02
#124	8.51	8.91	8.80	8.74
#125	8.49	9.39	9.61	9.16
#126	7.88	8.61	8.54	8.34
#127	7.93	8.83	8.43	8.40
#128	7.34	7.96	8.18	7.83
#129	7.73	7.97	7.78	7.83
#130	7.2	7.85	7.16	7.40
#131	7.08	7.19	6.92	7.06
#132	7.2	7.73	6.87	7.27

Vertebra	Ø #1 (mm)	Ø #2 (mm)	Ø #3 (mm)	Ø mean (mm)
#133	6.8	7.11	6.82	6.91
#134	6.41	7.03	6.58	6.67
#135	6.4	6.37	6.07	6.28
#136	6.49	7.11	6.44	6.68
#137	6.58	7.02	6.14	6.58
#138	6.4	6.35	5.81	6.19
#139	6.08	6.07	5.82	5.99
#140	5.78	5.96	5.82	5.85
#141	5.62	5.87	5.32	5.60
#142	5.76	5.63	5.26	5.55
#143	5.78	5.76	5.38	5.64
#144	5	5.32	4.97	5.10
#145	5.18	5.34	4.68	5.07
#146	4.86	5.05	4.69	4.87
#147	4.72	4.87	4.58	4.72
#148	4.42	5.03	4.52	4.66
#149	4.23	5.16	4.34	4.58
#150	4.23	4.65	4.12	4.33
#151	4.37	4.12	3.85	4.11
#152	3.64	3.84	3.79	3.76
#153	3.84	4.35	4.27	4.15
#154	3.72	4.34	4	4.02
#155	3.2	3.97	3.54	3.57
#156	2.83	3.41	3.26	3.17
#157	2.86	3.49	3.22	3.19
#158	2.44	3.26	3.07	2.92
#159	2.56	2.94	2.99	2.83
#160	2.21	2.82	2.99	2.67
#161	2.21	2.21	2.61	2.34
#162	2.56	2.81	2.84	2.74
#163	2	2.33	2.17	2.17
#164	1.74	2.05	1.86	1.88
#165	1.89	1.92	1.95	1.92
#166	?	?	?	?
#167	?	?	?	?
#168	?	?	?	?
#169	?	?	?	?
#170	?	?	?	?
#171	?	?	?	?