SCALING A GIANT

To date, only the total length of the largest prehistoric shark has been known. Now, **Jack Cooper** reveals the first measurements of the rest of Megalodon's body, including a dorsal fin as large as a human adult

Megalodon. Literally translated, it means "Big Tooth"—and for good reason. At a maximum size of 15 to 18 metres, it is the largest predatory shark known to have ever roamed the oceans. Its teeth have become some of the most iconic fossils in palaeontology and are as big as human hands, reaching sizes of about 160 mm high (Fig. 1). These huge fossil teeth have been found on every continent except Antarctica, suggesting that the species lived worldwide, and are dated to the Miocene and Pliocene epochs (23 to 2.6 million years ago) (Pimiento *et al.*, 2016). As well as its teeth, palaeontologists have found rare vertebrae from this shark which are over 150 mm in diameter, and serrated bite marks on whale bones indicating that whales may have been amongst its prey (Gottfried *et al.*, 1996). The fossil evidence paints a picture of a terrifyingly large shark. But just how big was this animal?

Despite the popularity of this enormous extinct shark, with its huge teeth and its recent starring role in the Hollywood blockbuster The Meg, only its total length has ever been calculated. This was done using the relationship between tooth height and total length in the modern great white shark. But what about the dimensions of the rest of its body? How big was its dorsal fin, slicing through the water as it homed in on prey? What about the tail that powered its swimming, the head that held its enormous jaws, or the gills that allowed it to breathe? Knowing the sizes of these body parts gives a more complete picture of what this huge shark may have looked like, and provides ecological inferences of how it may have lived.

Closest living relatives

Determining Megalodon's size appears daunting at first. Its teeth (Fig. 1) are almost all that remains of the shark, so we have no complete skeletons to start from. This means that scientists have to base their calculations on modern day sharks and, with over 500 species of shark living today, it can seem impossible to know where to start. However, at first glance, Megalodon teeth bear a striking resemblance to those of today's largest ▶

Fig. 1: A Megalodon tooth; the same size as a human hand.

▶ predatory shark—the great white (*Carcharodon carcharias*). Both have large, triangular and serrated teeth; dental traits typical of a shark that feeds on marine mammals (Fig. 2). These teeth have such similar shapes that scientists initially concluded that Megalodon had to be a direct ancestor of the great white shark, leading them to name the giant shark *Carcharodon megalodon*.

A closer examination of the teeth, however, reveals distinct differences. Megalodon's teeth have rounder, finer serrations compared to the triangular, irregular and jagged serrations of the great white. Also, they have a thicker lingual side (the part closest to the tongue) and a dental band that is not present in the teeth of great whites. Further analyses found no overlap in the shape variance of the teeth of both animals and revealed that great white shark teeth are much closer in shape to extinct mako sharks (Nyberg *et al*., 2006). Therefore it has been proposed that the great white did not evolve from Megalodon after all and instead comes from an ancient lineage of mako sharks. Megalodon is now considered part of the extinct Family Otodontidae—also known as the megatoothed clade—and is generally referred to as *Otodus megalodon*.

So where exactly is Megalodon's family


Fig. 2: A Megalodon tooth compared to a great white shark tooth.

on the shark tree of life? That is unclear, but given the similarity in tooth shape to the great white, it is highly likely that Megalodon fits within the order of sharks called Lamniformes, an order more commonly known as mackerel sharks. With 15 living species in this order, including the great white, basking, megamouth and thresher sharks, there are a number of different positions in the family tree that the megatoothed family may be found (Fig. 3). However, there is a way to infer a probable position without the use of fossils, a way that also allows us to deduce which modern sharks could be used to calculate Megalodon's body size. The approach is called extant phylogenetic bracketing (EPB) and it enables the potential phylogenetic positions of extinct taxa to be inferred based on the biological traits that they are known to share with modern taxa.

From Megalodon's fossils, we know that this giant shark had serrated teeth, fed on marine mammals and was most likely able to physiologically control its internal temperature (Ferrón, 2017). Modern lamniform taxa with all of these traits can be narrowed down not only to the great white shark, but also the two species of mako shark, the salmon shark and the porbeagle shark. As such, given the dental, ecological and physiological similarities these species all have with Megalodon, they represent the best available analogues. And, given that Megalodon is not a direct ancestor of the great white, all of these sharks can be considered equally related to the giant. We can therefore regard all five modern sharks as potential analogues, and their body structures that support the traits shared with Megalodon are our best modern insights into the size and appearance of this huge extinct shark.

Body size calculations

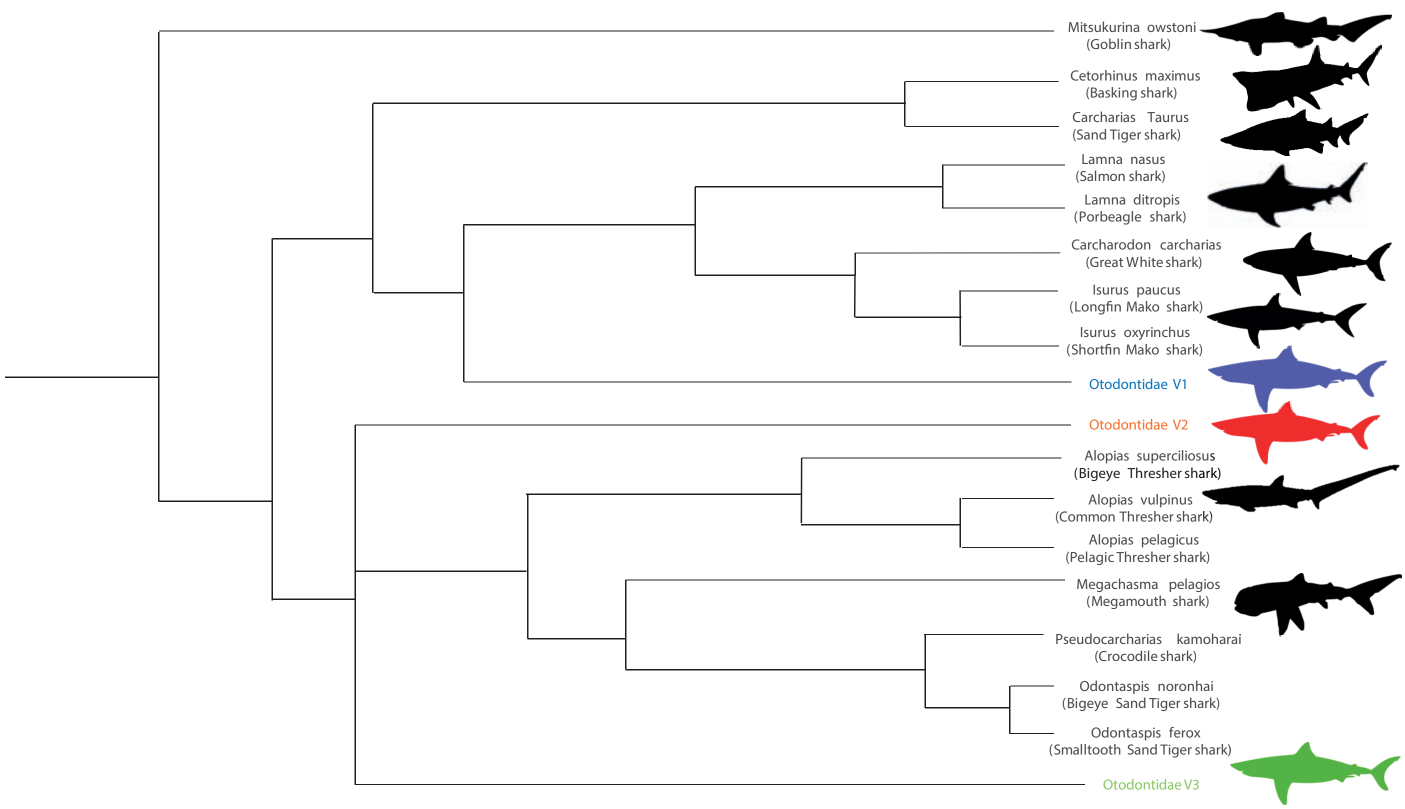
Although the only widely available fossils of Megalodon are their teeth, using these teeth to calculate its total length only requires knowledge of the tooth's position in the jaw and some fairly basic maths. The total length of a shark has a very strong linear relationship with the crown height of its teeth, and is reported as:

$$y = mx + c$$

In this equation, y represents the shark's total length, m is the slope of the relationship between total length and x, the crown height, while c is an intercept that changes depending on the position of the tooth in the jaw (Shimada, 2002).

Such a relationship is found in great whites, shortfin makos and porbeagle sharks among others. To calculate total length from the crown height of Megalodon, we typically extrapolate the same relationship from that of the great white shark. Although the two are not as closely related as originally thought, the great white remains the shark with by far the most similarly shaped tooth to Megalodon. Furthermore, the relationship ▶

Fig. 3: A phylogenetic, or family tree of Order Lamniformes. There are 15 extant species in the Lamniformes order (shown in back). It is unclear where the Otodontidae family, that of Megalodon, sits in relation to these living sharks and 3 separate hypotheses (V1, V2 and V3 – shown in blue, orange and green respectively) are shown as examples. V1 (blue) suggests that the closest living ancestors would be family Lamnidae, the family consisting of the great white, mako, salmon and porbeagle sharks. V2 and V3 suggest that Otodontidae share common ancestors with thresher and sand tiger sharks respectively, theories that have also been proposed. However, given that Megalodon shares numerous traits with the lamnid sharks, including dental and physiological similarities, we suggest that the V1 placement is the most parsimonious. Silhouettes for M. owstoni (by Haplochornis, vectorised by T. Michael Kessey), C. carcharias (by Steven Traver), Isurus species (uncredited), O. megalodon (by Scarlet23, vectorised by T. Michael Kessey) and M. pelagicus (by Jose I. Castro, vectorised by J. Boyle) are found on Phylopic (licence: https://creativecommons.org/licenses/by-sa/3.0/). All other silhouettes created by Jack A. Cooper.



▶ between total length and crown height in these sharks is isometric, meaning that the rate of tooth replacement and growth is near-identical to the rate of body growth. As such, palaeontologists have applied this relationship between crown height and total length to sharks and calculated maximum lengths of 15 to 18 m for Megalodon (Pimiento & Balk, 2015). More recently, it has been found that the middle front teeth of the upper jaw are the teeth that best correlate to total length, and the largest such teeth that are publicly available in museums correspond to lengths of 15 to 16 m. However, there are reports of even larger teeth in private collections that, if confirmed, would represent a maximum (and likely exceptional) length of 18 m (Shimada, 2019).

Although this simple approach is very effective for telling us Megalodon's length, it does not reveal the shark's specific body dimensions, such as the head, gills, tail and individual fins. The next step, therefore, is to apply the same method, but to correlate total length with body parts other than the size of the teeth.

From extant to extinct sharks

While a fully preserved skeleton of Megalodon has never been found, measuring the head, tail or fins of modern sharks and comparing them to total length helps us to understand how long these specific body parts may have been in the giant shark. As stated above, Megalodon shared dental, ecological and physiological traits with the great white shark (Fig. 4), both species of mako shark (shortfin and longfin makos), the salmon shark and the porbeagle shark. Based on EPB, these five species are therefore the five we use to understand the relationship between different body parts and total length. This relationship is the same basic formula as the earlier one, written again as:

$$y = mx + c$$

In this equation, y is a specific body measurement, m is the slope of the relationship, x is total length and c is the intercept.

If isometry is found in these relationships in all species, we can extrapolate them to Megalodon—as was done in the relationship between crown height and total length in the great white shark. Isometry in these new relationships would suggest to us that the specific body part being measured is growing at the around same rate as the total length of the shark in question. Indeed we do see this when we chart each body dimension against total length. We see it when we plot each individual modern shark species, and we even see it when plotting all five species together. As such, these linear body parts do not change in their proportions to total length and thus we can calculate those proportions and apply them to Megalodon to determine how large those body parts would have been in relation to the shark's length.

A more complete profile

When we convert our measurements of body parts into proportions of total length, we find that if we combine our modern day sharks as equal counterparts to Megalodon, head length is ~29% of total length, each of the five gills are ~9% of total length, dorsal fin height and width are ~10% and ~12% of total length respectively, and tail height is ~24% of total length. As we measured 41 total sharks across those five species, we naturally found some variation and thus those percentages represent the mean proportion. To account for this in our results, we also calculated the standard deviation of each measurement. These deviations proved to be very small indeed, suggesting that while there was likely some variation in the size of body parts between individual Megalodon, our results can be considered accurate and reliable.

We also found that isometry held true when we used landmark-based morphometric analyses—an approach that allows the quantification of shapes and shape variation. This approach gave us an indication as to how shape in the head and fins of our sharks change as total length increases. For example, we found that the caudal, or tail fins, were identical between our analogues—supporting previous work that had found four distinct types of caudal fin in Order Lamniformes (Kim *et al*., 2013). Pectoral fins, those on the side, also became proportionately longer and dorsal fins along the back were found to become taller and slightly narrower with increased total length.

So how big were the head, fins and tail of a 16-metre-long Megalodon—a size typically considered amongst its largest? When we apply our proportional findings to the body dimensions, we uncover some extraordinary sizes along Megalodon's body. We find that the head of a 16-metre-long shark would have been approximately 4.65 metres—larger than the average size of an entire great white shark! The dorsal fin,

Fig. 4: A great white shark (Carcharodon carcharias), by far the most commonly used analogue of Megalodon.

the famous icon of a shark stalking its prey from beneath the waves, was at least 1.6 metres tall, the same height as many adult humans. And the tail that powered its swimming through the ancient oceans was around 3.85 metres high. On top of these remarkable numbers, we found gills were about 1.41 metres tall, pectoral fins more than 3 metres long, and a distance of more than 4.5 metres from the tip of the dorsal fin to the bottom of the stomach.

The knowledge of these sizes, combined with our morphometric results of how fins are shaped in larger sharks, allowed us to produce a full 2D reconstruction, providing a complete profile of Megalodon. This reconstruction was finalised in a piece of gorgeous artwork put together by the incredibly talented palaeo-artist Oliver Demuth (Fig. 5). Palaeo-artists provide a key, and often underappreciated, way to engage the public and capture imaginations with illustrations of prehistoric worlds and creatures. There is no better way to express the grand beauty and scale of the Megalodon.

Ecological insights

Now that we have a complete profile of the largest predatory shark to ever exist (Cooper *et al*., 2020), it will inform future model reconstructions of this animal, which are often displayed in museums worldwide. We can also potentially connect some dots about its ecology. For example, how heavy was Megalodon? Estimates exist, but these are mostly based on extrapolations from the great white shark. Megalodon's size may have varied between different habitats (Pimiento & Balk, 2015), perhaps affecting what prey it targeted. Its diet of marine mammals is well documented in the fossil record and suggests that it may have gone after relatively small-bodied whales (Collareta *et al*., 2017). Furthermore, knowledge of Megalodon's full body form could provide insight on how its swimming may have supported such a lifestyle and, by extension, how its lifestyle may have contributed to the shark's eventual extinction in the Pliocene (Boessenecker *et al*., 2019).

I hope to answer some of these questions by combining my results with analyses of Megalodon's vertebrae fossils to construct a 3D model of the shark. As part of a 4-year PhD project, working with Dr Catalina Pimiento at Swansea University, I will examine the functional diversity of sharks through time, to understand which ecological traits of sharks were most affected by past extinctions, which sharks became more favoured as a result, and what might become of today's sharks in the ongoing extinction crisis.

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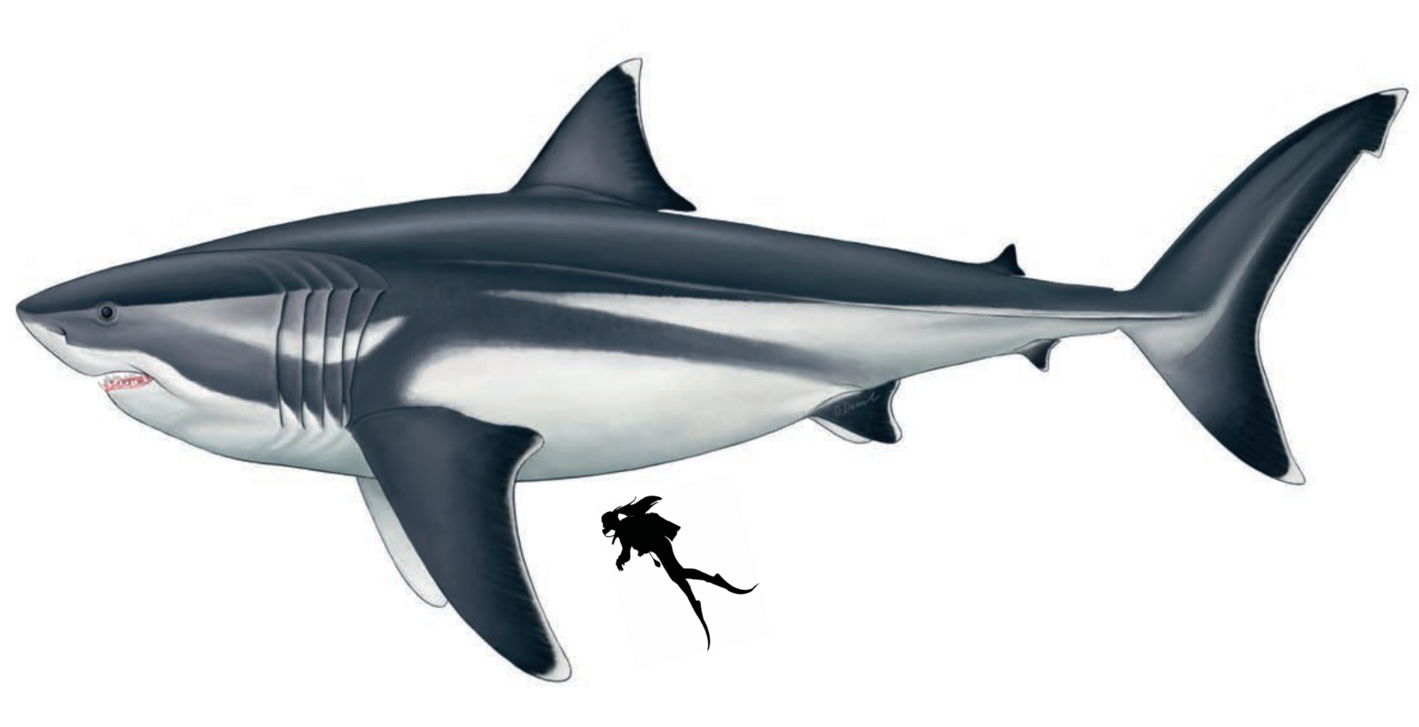

Fig. 5: The final full-body reconstruction of a 16 metre Megalodon created from our work, compared against a 1.6 m diver. Reconstruction by Oliver E. Demuth. Figure from Cooper et al., Sci. Rep. 10, 1-9 (2020). Copyright © 2020, Springer Nature. Creative Commons CC BY license.