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# Ontogenetic growth pattern of the extinct megatooth shark *Otodus megalodon*—implications for its reproductive biology, development, and life expectancy

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## 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.

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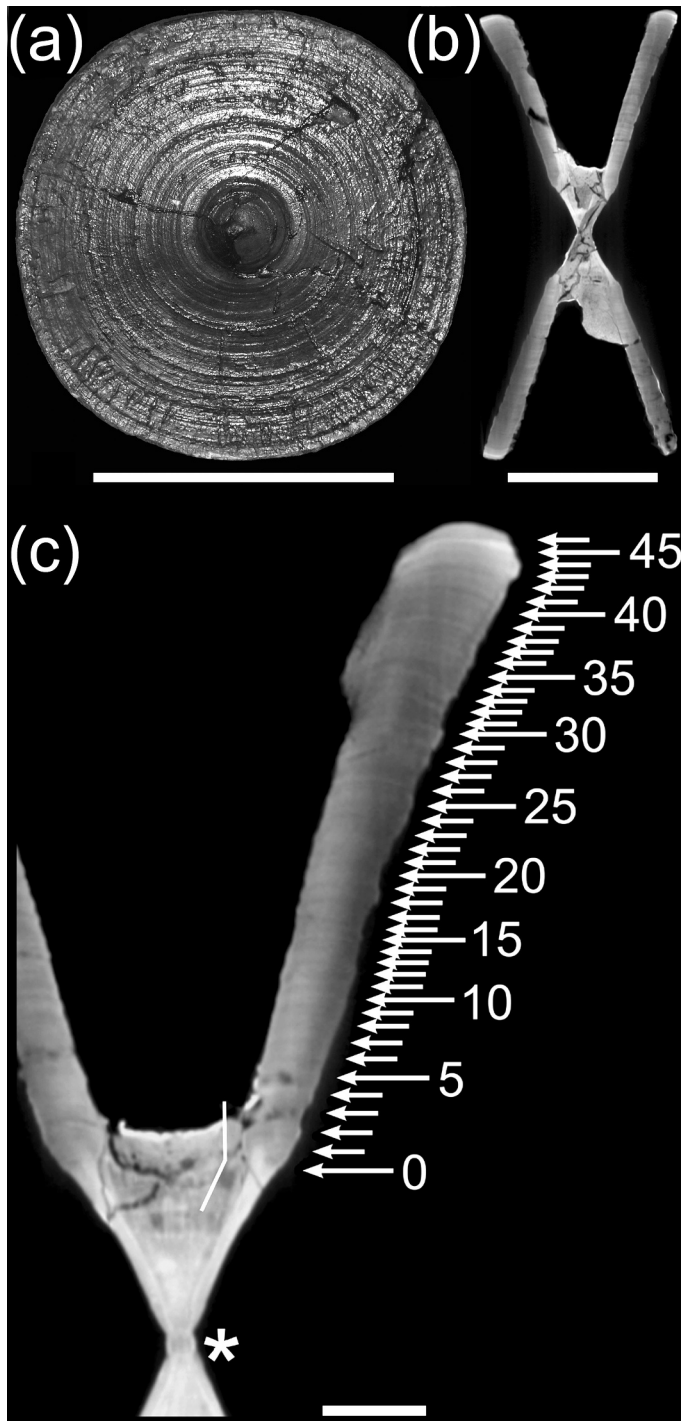
## Introduction

The megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), is an iconic extinct shark known mostly from its gigantic teeth in the late Neogene marine fossil record (e.g. Cappetta 2012; Boessenecker et al. 2019; Perez et al. 2019). The species was previously placed in various genera such as *Carcharocles*, *Procarcharodon*, and *Megaselachus*, as well as the white shark genus *Carcharodon* (Lamnidae), but it is now generally regarded as a species of *Otodus* in order to avoid *Otodus* nonmonophyly (Shimada et al. 2017) and direct phylogenetic linkage to *Carcharodon* or Lamnidae (Ehret et al. 2012). Its most commonly cited estimated maximum size is about 18–20 m in total length (TL) (e.g. Pimiento and Balk 2015; Nelson et al. 2016; Razak and Kocsis 2018; Pimiento et al. 2019; Cooper et al. 2020), but individuals exceeding 14.1–15.3 m TL have not yet been convincingly substantiated in the scientific literature (Shimada 2019; Shimada et al. 2020). The conservative estimates are nonetheless still gigantic especially given that nonplanktivorous sharks have a general size limit of 7 m TL (Pimiento et al. 2019; Shimada et al. 2020). The gigantism of *O. megalodon* is attributed to the evolution of regional endothermy (Ferrón 2017), possibly along with the inferred live-bearing reproductive mode involving intrauterine cannibalism in the form of oophagy (Shimada et al. 2020). Yet, exactly how *O. megalodon* developed throughout its lifetime has remained largely in the realm of speculations (Gottfried et al. 1996; Kent 2018).

Vertebrae, if well calcified, are often used to examine the growth pattern in modern elasmobranchs (sharks and rays) (Goldman et al. 2012, and references therein). Although taxon-specific exceptions do exist (e.g. Harry 2017; Natanson et al. 2018; Natanson and Deacy 2019), their circular vertebral centra deposit annual bands in many

elasmobranch taxa, including lamniform sharks (e.g. Cailliet and Goldman 2004; Goldman et al. 2012; Harry 2017). Some studies have suggested that growth bands may not necessarily record age or time but rather simply growth or vertebral size leading to systemic age underestimation (Passerotti et al. 2014; Harry 2017; Natanson et al. 2018; Natanson and Deacy 2019). The situation may be particularly problematic for older individuals because not all growth bands may be deposited in vertebrae past a certain age (Francis et al. 2007; Passerotti et al. 2014; Harry 2017). Nevertheless, where well-demonstrated cases of annual band deposition are known (Goldman et al. 2012, and references therein; Ong et al. 2020), the relationship of growth bands to time or age can still be broadly correlated (Natanson and Deacy 2019), and remains a widely used life-history assessment technique for diverse modern elasmobranchs (e.g. Ong et al. 2020; Rolim et al. 2020). Furthermore, vertebral growth bands are especially important in the fossil record because they are practically the only source that offers insights into the life history of extinct elasmobranchs (Shimada 2008; Newbrey et al. 2015; Amalfitano et al. 2017; Sternes and Shimada 2018; Shimada and Everhart 2019; Jambura and Kriwet 2020).

Growth bands are also observed on the articular faces of vertebrae of *Otodus megalodon* (Gottfried et al. 1996; Kent 2018; Bendix-Almgreen 1983; Uyeno and Sakamoto 1984; Figure 1(a)). In this paper, we examine the only reasonably preserved vertebral column of the species in the entire world in order to determine the growth pattern and longevity of *O. megalodon*. As one of the largest carnivores that ever existed on Earth (Shimada 2019), the evolution and extinction of *O. megalodon* must have contributed to shaping the present-day marine ecosystem. Hence, deciphering such growth parameters of *O. megalodon* is critical to understand the role large carnivores play in the context of ecology and evolution.



**Figure 1.** Examples of examined vertebrae of *Otodus megalodon* (IRSNB P 9893). (a) One of the largest vertebrae ('centrum #1') in IRSNB P 9893 (scale bar = 10 cm; photograph courtesy of IRSNB). (b) Computed tomographic image showing sagittal cross-sectional view of vertebra depicted in (a) (scale bar = 5 cm). (c) Computed tomographic image of sagittal cross-sectional view the largest vertebrae ('centrum #4') in IRSNB P 9893 showing incremental grown bands presumably formed annually (\* = centre of vertebra; scale bar = 1 cm).

## Materials and methods

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  $\mu$ A at a spatial resolution of 0.184 mm with an RX EasyTom  $\mu$ CT 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 mid-sagittal 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% (Table 1). In addition, an

estimated growth length (eGL) gains from one band to the next was determined from the eTL data and tabulated (Table 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](http://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  $L_{\infty}$  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  $L_{\infty}$ : 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).

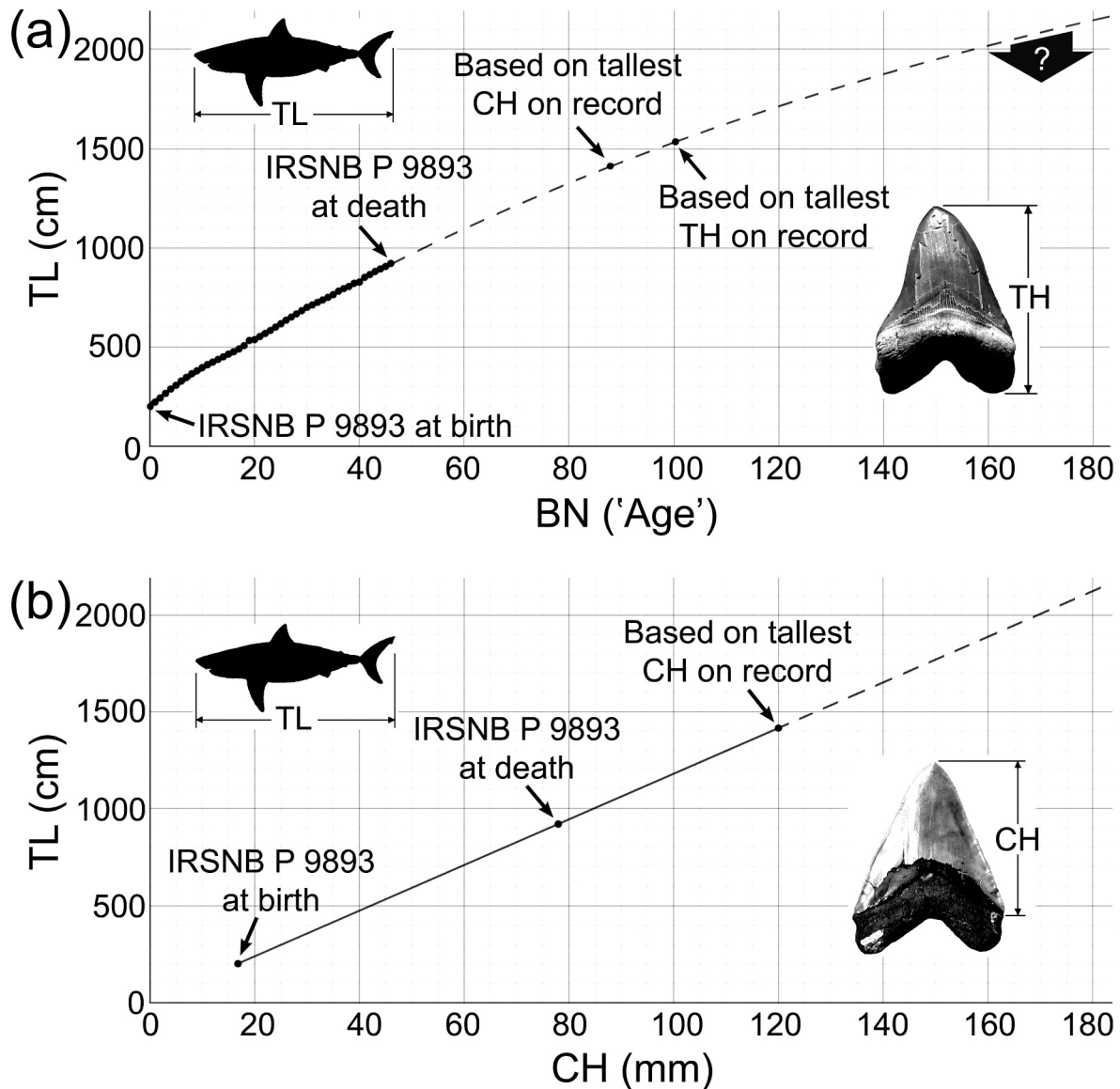
## Discussion

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

**Table 1.** Raw measurements (BN, CR, and BI) and derived measurements (pCR, eTL, and eGL) based on the sectioned vertebra of *Otodus megalodon* (IRSNB P 9893, 'centrum #4'; Figure 1(c)). Abbreviations: BN, band number; CR, centrum radius; BI, band interval from the previous band; pCR, percent centrum radius from centre of the vertebra; eTL, extrapolated total length of entire shark; eGL, estimated growth length gain from the previous year.

BN	CR (mm)	BI (mm)	pCR (%)	eTL (cm)	eGL (cm)
0	16.8	-	21.7	200	-
1	18.7	1.9	24.1	222	22
2	20.5	1.8	26.4	243	21
3	22.4	1.9	28.9	266	23
4	24.2	1.8	31.2	288	22
5	25.8	1.7	33.3	307	19
6	27.6	1.8	35.6	328	21
7	29.2	1.6	37.7	347	19
8	30.7	1.5	39.6	365	18
9	32.0	1.3	41.3	380	15
10	33.3	1.3	43.0	396	16
11	34.6	1.3	44.6	411	15
12	35.7	1.1	46.0	424	13
13	36.8	1.1	47.4	437	13
14	37.9	1.1	48.9	450	13
15	39.1	1.2	50.4	464	14
16	40.0	1.0	51.7	476	12
17	41.2	1.2	53.2	490	14
18	42.6	1.4	55.0	507	17
19	43.9	1.3	56.7	522	16
20	45.2	1.3	58.3	537	15
21	46.5	1.3	60.0	553	16
22	47.8	1.2	61.7	568	15
23	49.1	1.3	63.3	583	15
24	50.0	1.4	65.2	600	17
25	51.9	1.4	67.0	617	17
26	53.4	1.5	68.9	635	18
27	54.8	1.4	70.7	651	16
28	56.1	1.3	72.4	667	16
29	57.5	1.4	74.2	683	16
30	58.9	1.4	76.0	700	17
31	59.9	1.0	77.3	712	12
32	61.0	1.1	78.7	725	13
33	62.0	1.0	80.0	737	12
34	63.1	1.0	81.4	750	13
35	64.3	1.2	83.0	764	14
36	65.7	1.4	84.8	781	17
37	66.8	1.0	86.2	794	13
38	67.8	1.0	87.4	805	11
39	69.1	1.3	89.2	821	16
40	70.4	1.3	90.8	837	16
41	71.6	1.2	92.4	851	14
42	72.8	1.2	94.0	865	14
43	74.0	1.2	95.5	880	15
44	75.1	1.1	96.9	893	13
45	76.3	1.1	98.4	906	13
46	77.5	1.2	100.0	921	15





**Figure 2.** Growth models of *Otodus megalodon* based on IRSNB P 9893 (Figure 1). (a) von Bertalanffy growth function (VBGF) fitted to data points (Table 1) that show relationship of number of vertebral growth bands (BN, or 'age' of individual in years) with total length (TL; see left inset using hypothetical body silhouette) and some key information discussed in text along with photograph of tallest known upper anterior tooth of *O. megalodon* in scientific literature (Shimada 2019) in lingual view (right inset) housed in Field Museum of Natural History (FMNH PF 11306), Chicago, Illinois, USA, depicting total tooth height (TH). (b) Linear function showing relationship of crown height (CH) of upper anterior teeth with TL ( $TL = 11.788 \cdot CH + 2.143$ ) (Shimada 2019) and some key reference points discussed in text along with photograph of upper anterior tooth of *O. megalodon* with tallest CH in scientific literature (Shimada 2019) in lingual view (right inset) housed in National Museum of Nature and Science (NSM PV-19896), Tsukuba, Ibaraki Prefecture, Japan, depicting CH.

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  $L_{\infty}$  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  $L_{\infty}$  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  $L_{\infty}$  would have been much lower than 3,172.740 cm TL calculated here. The  $L_{\infty}$  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  $L_{\infty}$  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  $0.00588 \text{ yr}^{-1}$  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  $L_{\infty}$  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  $L_{\infty}$  (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 (Capetta 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.

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## Disclosure statement

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## References

- Amalfitano J, Giusberti L, DallaVecchia FM, Kriwet J. 2017. First skeletal remains of the giant sawfish *Onchosaurus* (Neoselachii, Sclerorhynchiformes) from the Upper Cretaceous of northeastern Italy. *Cret Res.* 69:124–135. doi:10.1016/j.cretres.2016.09.005.
- Bendix-Almgreen SE. 1983. *Carcharodon megalodon* from the Upper Miocene of Denmark, with comments on elasmobranch tooth enameloid: coronoid n. *Bull Geol Soc Denmark.* 32:1–32.
- Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum Biol.* 10:181–213.
- Boessenecker RW, Ehret DJ, Long DJ, Churchill M, Martin E, Boessenecker SJ. 2019. The early Pliocene extinction of the mega-toothed shark *Otodus megalodon*: a view from the eastern North Pacific. *PeerJ.* 7:e6088. doi:10.7717/peerj.6088
- Cailliet GM, Goldman KJ. 2004. Age determination and validation in chondrichthyan fishes. In: Carrier JC, Musick JA, Heithaus MR, editors. *The biology of sharks and their relatives*. Boca Raton (Florida): CRC Press; p. 339–447.

- Cappetta H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: teeth. In: Schultze H-P, editor. Handbook of paleoichthyology (Vol. 3E). Munich: Verlag Dr. Friedrich Pfeil; p. 1-512.
- Carrier JC, Pratt HL, Castro JJ. 2004. Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of sharks and their relatives. Boca Raton (Florida): CRC Press; p. 269-286.
- Conrath CL, Musick JA. 2012. Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of sharks and their relatives. 2nd ed. Boca Raton (Florida): CRC Press; p. 291-311.
- Cooper JA, Pimiento C, Ferrón HG, Benton MJ. 2020. Body dimensions of the extinct giant shark *Otodus megalodon*: a 2D reconstruction. Sci Rep. 10:14596. doi:10.1038/s41598-020-71387-y
- Ebert D, Fowler S, Compagno L, Dando M. 2013. Sharks of the world: a fully illustrated guide. Plymouth (New Hampshire): Wild Nature Press; p. 528.
- Ehret DJ, MacFadden BJ, Jones DS, Devries TJ, Foster DA, Salas-Gismondi R. 2012. Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. Palaeontology. 55:1139-1153.
- Ferrón H. 2017. Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. PLoS ONE. 12:e0185185. doi:10.1371/journal.pone.0185185
- Francis MP, Campana SE, Jones CM. 2007. Age under-estimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae? Mar Fresh Res. 58:10-23. doi:10.1071/MF06069.
- Gilmore RG, Putz O, Dodrill JW. 2005. Oophagy, intrauterine cannibalism and reproductive strategy in lamnoid sharks. In: Hamlett WC, editor. Reproductive biology and phylogeny of Chondrichthyes. Enfield (New Hampshire): Science Publishers; p. 435-462.
- Goldman KJ, Cailliet GM, Andrews AH, Natanson LJ. 2012. Assessing the age and growth of chondrichthyan fishes. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of sharks and their relatives. 2nd ed. Boca Raton (Florida): CRC Press; p. 31-57.
- Gottfried MD, Compagno LJV, Bowman SC. 1996. Size and skeletal anatomy of the giant "megatooth" shark *Carcharodon megalodon*. In: Klimley AP, Ainley DG, editors. Great white sharks: the biology of *Carcharodon carcharias*. San Diego: Academic Press; p. 55-66.
- Harry AV. 2017. Evidence for systemic age underestimation in shark and ray ageing studies. Fish Fisher. 116. doi:10.1111/faf.12243.
- Herráiz JL, Ribé J, Botella H, Martínez-Pérez C, Ferrón HG. 2020. Use of nursery areas by the extinct megatooth shark *Otodus megalodon* (Chondrichthyes: Lamniformes). Biol Lett. 16:20200746. doi:10.1098/rsbl.2020.0746
- Hsu HH, Joung SJ, Hueter RE, Liu KM. 2014. Age and growth of the whale shark (*Rhincodon typus*) in the north-western Pacific. Mar Fresh Res. 65:1145-1154. doi:10.1071/MF13330.
- Jambura PL, Kriwet J. 2020. Articulated remains of the extinct shark *Ptychodus* (Elasmobranchii, Ptychodontidae) from the Upper Cretaceous of Spain provide insights into gigantism, growth rate and life history of ptychodontid sharks. PLoS ONE. 15(4):e0231544.
- Kent BW. 2018. The cartilaginous fishes (chimaeras, sharks, and rays) of Calvert Cliffs, Maryland, USA. In: Godfrey SJ, editor. The geology and vertebrate paleontology of Calvert Cliffs, Maryland. Washington D.C.: Smithsonian Scholarly Press; p. 45-157.
- Natanson LJ, Deacy BM. 2019. Using oxytetracycline validation for confirmation of changes in vertebral band-pair deposition rates with ontogeny in sandbar sharks (*Carcharhinus plumbeus*) in the western North Atlantic Ocean. Fish Bull. 117:50-58. doi:10.7755/FB.117.1.6.
- Natanson LJ, Kohler NE, Ardizzone D, Cailliet GM, Wintner SP, Mollet HF. 2006. Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ Biol Fish. 77:367-383. doi:10.1007/s10641-006-9127-z.
- Natanson LJ, Skomal GB, Hoffmann SL, Porter ME, Goldman KJ, Serra D. 2018. Age and growth of sharks: do vertebral band pairs record age? Mar Fresh Res. 69:1440-1452.
- Nelson JS, Grande TC, Wilson MVH. 2016. Fishes of the World. Hoboken (New Jersey): Wiley and Sons; p. 752.
- Newbrey MG, Siversson M, Cook TD, Fotheringham AM, Sanchez RL. 2015. Vertebral morphology, dentition, age, growth, and ecology of the large lamniform shark *Cardabiodon ricki*. Acta Palaeont Pol. 60:877-897.
- Nielsen J, Hedeholm RB, Heinemeier J, Bushnell PG, Christiansen JS, Olsen J, Ramsey CB, Brill RW, Simon M, Steffensen KF, et al. 2016. Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). Science. 353:702-704. doi:10.1126/science.aaf1703
- Ong JLL, Meekan MG, Hsu HH, Fanning LP, Campana SE. 2020. Annual bands in vertebrae validated by bomb radiocarbon assays provide estimates of age and growth of whale sharks. Front Mar Sci. 7:188. doi:10.3389/fmars.2020.00188
- Passerotti MS, Andrews AH, Carlson JK, Wintner SP, Goldman KJ, Natanson LJ. 2014. Maximum age and missing time in the vertebrae of sand tiger shark (*Carcharias taurus*): validated lifespan from bomb radiocarbon dating in the western North Atlantic and southwestern Indian Oceans. Mar Fresh Res. 65:674-687. doi:10.1071/MF13214.
- Perez V, Godfrey SJ, Kent B, Weems R, Nance J. 2019. The transition between *Carcharocles chubutensis* and *Carcharocles megalodon* (Otodontidae, Chondrichthyes): lateral cusplet loss through time. J Vert Paleont. e1546732. doi:10.1080/02724634.2018.1546732
- Pimiento C, Balk MA. 2015. Body-size trends of the extinct giant shark *Carcharocles megalodon*: a deep-time perspective on marine apex predators. Paleobiol. 41:479-490. doi:10.1017/pab.2015.16.
- Pimiento C, Cantalapiedra JL, Shimada K, Field DJ, Smaers JB. 2019. Evolutionary pathways towards shark gigantism. Evolution. 73:588-599. doi:10.1111/evo.13680.
- Pimiento C, Ehret DJ, MacFadden BJ, Hubbell G. 2010. Ancient nursery area for the extinct giant shark *Megalodon* from the Miocene of Panama. PLoS ONE. 5:e10552. doi:10.1371/journal.pone.0010552
- Randall JE. 1973. Size of the great white shark (*Carcharodon*). Science. 181:169-170.
- Razak H, Kocsis L. 2018. Late Miocene *Otodus* (*Megaselachus*) *megalodon* from Brunei Darussalam: body length estimation and habitat reconstruction. Neues Jahrb Geol Palaontol Abh. 288:299-306. doi:10.1127/njgpa/2018/0743.
- Reolid M, Molina JM. 2015. Record of *Carcharocles megalodon* in the eastern Guadalquivir Basin (Upper Miocene, South Spain). Estudios Geol. 71(2): e032. doi:10.3989/egol.41828.342.
- Rolim FA, Siders ZA, Caltabellotta FP, Rotundo MM, Vaske-Júnior T. 2020. Growth and derived life-history characteristics of the Brazilian electric ray *Narcine brasiliensis*. J Fish Biol. 97:396-408. doi:10.1111/jfb.14378
- Shimada K. 2008. Ontogenetic parameters and life history strategies of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, based on vertebral growth increments. J Vert Paleont. 28:21-33.
- Shimada K. 2019. The size of the megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), revisited. Hist Biol. 1-8. doi:10.1080/08912963.2019.1666840
- Shimada K, Becker MA, Griffiths ML. 2020. Body, jaw, and dentition lengths of macrophagous lamniform sharks, and body size evolution in Lamniformes with special reference to 'off-the-scale' gigantism of the megatooth shark, *Otodus megalodon*. Hist Biol. doi:10.1080/08912963.2020.1812598
- Shimada K, Chandler RE, Lam OLT, Tanaka T, Ward DJ. 2017. A new elusive otodontid shark (Lamniformes: Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the 'megatoothed' clade. Hist Biol. 29:704-714. doi:10.1080/08912963.2016.1236795.
- Shimada K, Everhart MJ. 2019. A new gigantic Late Cretaceous lamniform shark from North America with comments on the taxonomy, paleoecology, and evolution of the genus *Cretodus*. J Vert Paleont. 39:e1673399. doi:10.1080/02724634.2019.1673399.
- Sternes PC, Shimada K. 2018. Paleobiology of the Late Cretaceous sclerorhynchid sawfish, *Ischyrochima mira* (Elasmobranchii: Rajiformes), from North America based on new anatomical data. Hist Biol. 31:1323-1340.
- Uyeno T, Sakamoto O. 1984. Lamnoid shark *Carcharodon* from Miocene beds of Chichibu Basin, Saitama Prefecture, Japan. Bull Saitama Mus Nat Hist. 2:47-65.