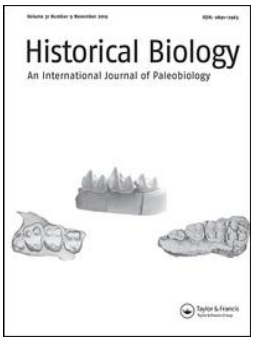

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ARTICLE

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*

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ABSTRACT

Extinct lamniform sharks (Elasmobranchii: Lamniformes) are well represented in the late Mesozoic–Cenozoic fossil record, yet their biology is poorly understood because they are mostly represented only by their teeth. Here, we present measurements taken from specimens of all 13 species of extant macrophagous lamniforms to generate functions that would allow estimations of body, jaw, and dentition lengths of extinct macrophagous lamniforms from their teeth. These quantitative functions enable us to examine the body size distribution of all known macrophagous lamniform genera over geologic time. Our study reveals that small body size is plesiomorphic for Lamniformes. There are four genera that included at least one member that reached >6 m during both the Mesozoic and Cenozoic, most of which are endothermic. The largest form of the genus *Otodus, O. megalodon* ('megatooth shark') that reached at least 14 m, is truly an outlier considering that all other known macrophagous lamniforms have a general size limit of 7 m. Endothermy has previously been proposed to be the evolutionary driver for gigantism in Lamniformes. However, we contend that ovoviviparous reproduction involving intrauterine cannibalism, a possible synapomorphy of Lamniformes, to be another plausible driver for the evolution of endothermy achieved by certain lamniform taxa.

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Chondrichthyes; Elasmobranchii; fossil record; intrauterine cannibalism; tooth

Introduction

Lamniformes (Chondrichthyes: Elasmobranchii) is a monophyletic shark order with only 15 extant species (Figure 1(a)) but well represented by numerous taxa in the late Mesozoic−Cenozoic fossil record (Cappetta 2012; Stone and Shimada 2019). The order includes iconic extant taxa, such as the mako (*Isurus*) and white (*Carcharodon*) sharks, as well as extinct forms like *Otodus megalodon* or the so-called 'megatooth shark' (note: this fossil taxon that was previously classified in genera such as *Carcharocles, Procarcharodon*, and *Megaselachus* is placed in *Otodus* to avoid *Otodus* non-monophyly: Shimada et al. 2017). Besides these large macrophagous taxa, Lamniformes also exhibits wide behavioural and ecological diversity, including small piscivorous (crocodile shark, *Pseudocarcharias*), deep-water (goblin shark, *Mitsukurina*), tail-wipping hunting (thresher sharks, *Alopias*), and suspension-feeding (megamouth and basking sharks, *Megachasma* and *Cetorhinus*, respectively) forms. Likewise, wide behavioural and ecological ranges are represented among extinct taxa, such as benthic (*Palaeocarcharias*) and yet another suspension-feeding form (*Pseudomegachasma*) (e.g. Compagno 2002; Ebert et al. 2013; Shimada et al. 2015; Jambura et al. 2019). Furthermore, Lamniformes is represented by both ectothermic and endothermic forms (e.g. Bernal et al. 2012; Ferrón 2017; Pimiento et al. 2019). It is of particular note that since the Cretaceous when they underwent remarkable adaptive radiation (Maisey et al. 2004; Underwood 2006; Cappetta 2012; Guinot et al. 2012), lamniforms have represented major carnivores in both macrophagous and planktivorous diet regimes. Therefore, it is reasonable to assert that they must have played an important role in the evolution of marine ecosystems through geologic time.

One simple biological parameter that has a profound impact on organisms and their ecosystem is body size. For animals and especially sharks, body size affects the range of travelling distances, predation risks, energy storage capacity, and the extent of heat retention, that may in turn influence their life history and behavioural strategies, tolerance level to extreme environmental conditions, predatory successes, and mortality risks (e.g. Peters 1986; Kram and Taylor 1990; Cohen et al. 1993; Hone and Benton 2005; Speakman 2005; Brown and Sibly 2006; Huston and Wolverton 2011; Healy et al. 2013). In addition to the body size, another size-related variable that impacts the predatory success and food intake in sharks is the size of the mouth or jaws, because it affects the ability to grasp food or to cut off parts of food especially for macrophagous forms (e.g. Springer 1961; Motta and Wilga 2001; Wilga et al. 2007; Tomita 2011; Huber et al. 2019). Therefore, knowledge about the maximum possible body size as well as the size of the mouth or jaw of animals, especially major carnivores like macrophagous lamniform sharks, is critical to understanding the ecology and evolution of their past and present ecosystems.

Where cartilaginous skeletons of extinct sharks are poorly represented in the fossil record, shark teeth, including those of macrophagous lamniforms, are arguably the most commonly collected vertebrate fossils (Hubbell 1996; note that the phrase 'macrophagous,' rather than 'macropredatory' like by Ferrón (2017) and Pimiento et al. (2019), is deliberately used in this paper because predatory behaviour of extinct forms cannot be ascertained without compelling direct evidence: e.g. post-bite bone healing in the fossil record: Shimada (1997d); Kallal et al. (2010)). Thus, the tooth size of sharks (particularly macrophagous lamniforms), such as the height

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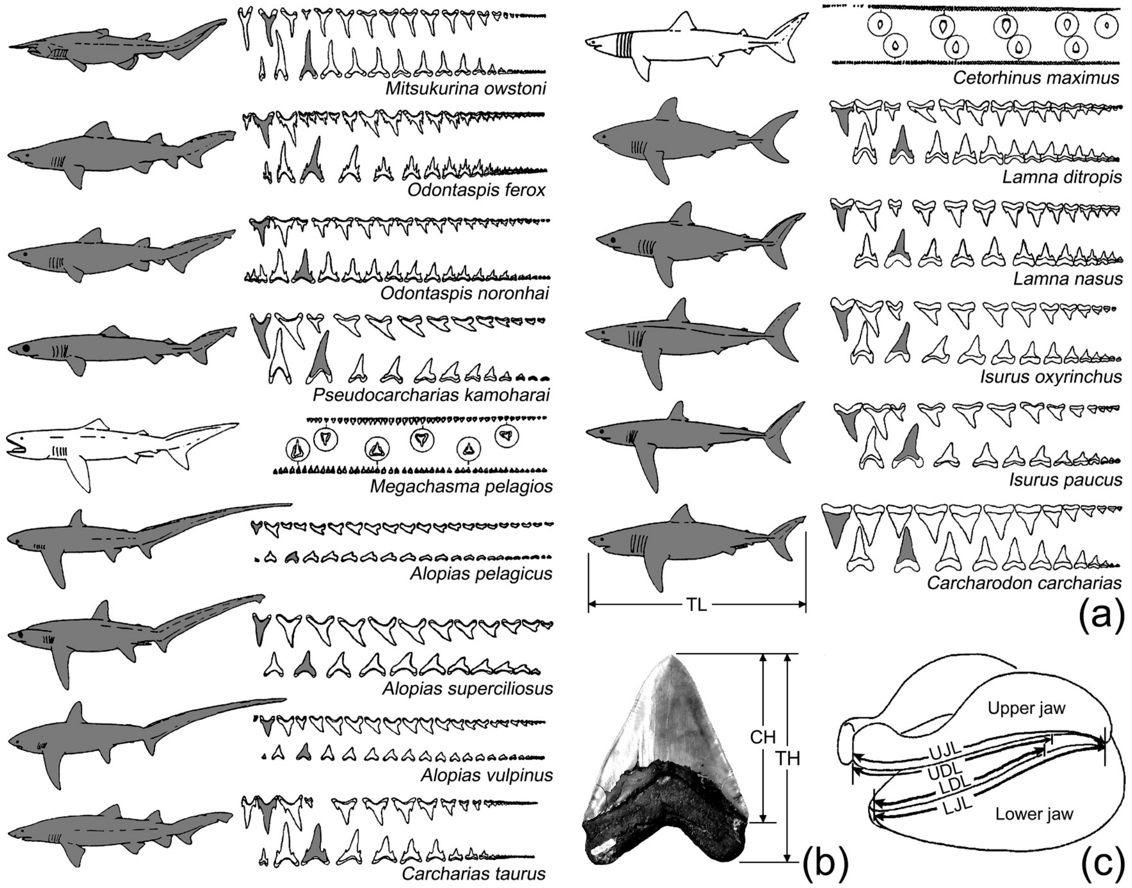

Figure 1. Extant lamniform sharks and measured variables in this study. (a) entire body in left lateral view (grey = macrophagous forms focused in this study) and right dentition in labial view (grey = upper first and lower second anterior teeth focused in this study) of all 15 extant species of the order Lamniformes, along with total length (TL) measurement (images after Shimada 2002, figures 1, 6); (b) photograph of presumed upper anterior tooth of *Otodus megalodon* (Miocene, USA) in labial view as example showing crown height (CH) and tooth height (TH) measurements (NSM PV-19896 in National Museum of Science and Nature, Tsukuba, Ibaraki, Japan: see Shimada 2019, Figure 1(b)); (c) schematic drawing of paired upper and lower jaws showing upper jaw length (UJL) and lower jaw length (LJL) as well as upper dentition length (UDL) and lower dentition length (LDL) measurements (see text for details). All images not to scale.

of their tooth crown (CH), is often used to infer the total body length (TL) because CH generally 'grows' proportionately through tooth replacement as TL increases ontogenetically (Shimada 2019, and references therein). For the purpose of this present study, we surveyed the CH-TL relationships of all 13 species of extant macrophagous lamniforms to generate a single theoretical function that would represent a general quantitative relationship between the CH and TL. We also examined their quantitative relationship with jaw lengths as well as dentition lengths, that together with the CH-TL function, would allow tentative estimations of basic anatomical parameters critical to understanding their ecological and evolutionary histories. In addition, based on our body size estimation function, we: (1) examine the body size distribution of macrophagous lamniform sharks over geologic time, (2) highlight some major evolutionary trends including the uniquenss of *Otodus megalodon*, and (3) provide additional insights into the evolution of gigantism in lamniforms.

Materials and methods

Data from extant macrophagous lamniforms

This study uses the following four sets of variables (Figure 1): (1) the total length (TL) of the body (including the head and caudal fin); (2) the length along the perimeter of the upper (UJL) and lower (LJL) jaws between the symphysis and a jaw joint; (3) the total length of the upper (UDL) and lower (LDL) dentitions measured from the jaw symphysis to the distal end of the distal-most tooth in each dental series; and (4) the vertical maximum crown (enameloid) height (CH) of the upper first anterior tooth (A1) and lower second anterior tooth (a2) (sensu Shimada 2002). The A1 and a2 are chosen because those teeth in 11 of the 13 extant macrophagous lamniforms have the tallest CH in their respective dental series (Shimada 2002) where the use of the tallest anterior teeth would minimise the risk of unnecessary overestimation for fossil taxa (e.g. Shimada 2019, table 1; see below). Although the upper second anterior tooth (A2) and lower first anterior tooth (a1) are also tall, they are not used in this study because only two species have slightly taller CH in their A2 and a1 than their A1 and a2, respectively (Shimada 2002). Table 1 shows all the measurements taken from samples of extant lamniforms with a reliable TL, comprising all 13 extant macrophagous species in the shark order. The two microphagous lamniforms, *Megachasma pelagios* and *Cetorhinus maximus*, are excluded because of uncertainty in their dental homologies due to their reduced homodontous teeth (see Shimada 2002). The examined samples consist of 32 nonembryonic specimens housed in the following institutions: American Museum of Natural History (AMNH), New York, USA; Bernice P. Bishop Museum (BPBM), Honolulu, USA; Field Museum of Natural History (FMNH), Chicago, USA; California Academy of Sciences (CAS), San Francisco, California, USA; Museum of Zoology, Hokkaido

Table 1. Examined specimens of extant macrophagous lamniforms and their specimen data and measurements (asterisk [*] = data from Shimada 2002, appendix 1; measurement in parentheses = estimated value from damaged tooth). Abbreviations: A1, vertical maximum crown (enameloid) height of upper first anterior tooth in millimetres; a2, vertical maximum crown (enameloid) height of lower second anterior tooth in millimetres; F, female; L, left; LDL, dentition length in lower jaw in millimetres; LJL, lower jaw length in millimetres; M, male; R, right; TL, total (body) length in centimetres; UDL, dentition length in upper jaw in millimetres; UJL, upper jaw length in millimetres.

Species	Specimen (sex; side)	TL	UJL	LJL	UDL	LDL	A1	a2
Mitsukurina owstoni	CAS 113888 (F; L)	120	120	106	100	88	11.7	15.0
Mitsukurina owstoni	MCZ 1279 (F; R)	110	116	99	99	80	10.0	10.9
Mitsukurina owstoni	NMNH 50972 (F; L)	335	320	266	265	211	21.5	25.0
Odontaspis ferox	BPBM 9335 (M?; L)	297	288	241	230	188	20.7	26.9
Odontaspis ferox	SIO 80-255 (?; L)	214	214	188	189	165	17.9	22.6
Odontaspis noronhai	HUMZ 110959 (M; R)	217	237	225	193	179	(15.0)	18.5
Pseudocarcharias kamoharai	CAS 58069 (F; R)	96	97	81	81	65	9.7	11.5
Pseudocarcharias kamoharai	LACM 45857 (F; R)	92	90	78	72	61	9.0	(11.0)
Alopias pelagicus	FMNH 117473 (F; R)	169	78	66	55	53	1.5	1.5
Alopias pelagicus	LACM 38116-39a (F; L)	179	79	75	56	55	2.2	2.0
Alopias pelagicus	LACM 38116-39b (F; L)	241	123	116	87	85	3.8	3.3
Alopias pelagicus	LACM 38116-40 (M; L)	170	72	70	53	51	2.7	2.3
Alopias superciliosus	CAS 76134 (M; L)	325	190	173	161	138	(14.9)	11.5
Alopias vulpinus	CAS 65976 (F; L)	155	60	58	53	48	2.9	2.1
Alopias vulpinus	LACM 39325-1 (?; L)	356	137	123	107	95	6.4	5.5
Alopias vulpinus	LACM 39342-1 (M; L)	131	59	56	47	40	1.6	1.5
Alopias vulpinus	MCZ 36089 (?; L)	397	167	151	140	126	8.2	(7.1)
Carcharias taurus	AMNH 79962SD (M; L)	241	244	208	199	165	21.0	(26.3)
Carcharias taurus	LACM 39334-2 (F; R)	273	277	245	222	179	(23.3)	28.0
Carcharias taurus	LACM 39335-1 (M; R)	112	110	93	86	71	10.3	12.3
Carcharias taurus	LACM 39336-4 (M; L)	148	158	134	123	101	14.0	13.7
Lamna ditropis	CAS 26683 (M; L)	206	190	166	157	133	11.8	12.3
Lamna ditropis	CAS 112656 (M; L)	92	100	92	80	77	(8.4)	9.3
Lamna nasus	MCZ 36251 (?; R)	165	135	125	108	98	10.1	11.1
Lamna nasus	MCZ 36253 (?; R)	104	93	83	74	65	7.8	8.7
Lamna nasus	MCZ 36257 (?; R)	132	115	105	92	81	8.9	9.6
Lamna nasus	MCZ 36258 (?; R)	152	136	128	109	99	10.4	11.8
Isurus oxyrinchus	LACM 32667-1 (F; R)	351	385	340	295	264	34.4	36.7
Isurus oxyrinchus	LACM 39338-1 (M; L)	121	144	118	118	92	11.7	13.4
Isurus paucus	UF 160174 (M; R)	117	125	109	100	84	11.3	12.1
Carcharodon carcharias	LACM 39474-1 (M; R)	165	172	150	135	114	14.5	(13.7)
Carcharodon carcharias	SIO 55-95g (F; R)	181	178	157	143	122	(16.3)	(15.5)
Carcharodon carcharias	'GH-Car1-13 (M; R)*	379	-	-	-	-	33.0	28.5
Carcharodon carcharias	'GH-Car1-19 (F; R)*	594	-	-	-	-	48.8	39.5

University (HUMZ), Japan; Natural History Museum of Los Angeles (LACM), California, USA; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA; Scripps Institution of Oceanography (SIO), University of California at San Diego, La Jolla, USA; Florida Museum of Natural History, University of Florida (UF), Gainesville, USA; and United States National Museum (NMNH; Smithsonian Institution), Washington, DC, USA. Whereas several species are represented only by one or two samples, no more than four samples for each species are examined in order to minimise potential skewing of quantitative analyses by certain species. When more than four samples were available, the four samples were chosen to reflect a wide size range for each species whenever possible. Whereas the extant white shark, *Carcharodon carcharias*, reaches up to 6–7 m TL (Compagno 2002; McClain et al. 2015), the two samples of the species we examined were both <2 m TL. Because teeth of *C. carcharias* are considered to be the best modern analogue to estimate the gigantic size of the extinct megatooth shark, *Otodus megalodon* (e.g. Gottfried et al. 1996; Shimada 2003; Reolid and Molina 2015; D'Anastasio et al. 2018), we added the TL and essential tooth measurements (CH of A1 and a2) from a 'mid-sized' (ca. 3.8 m TL) individual as well as from the largest (ca. 6 m TL) individual presented by Shimada (2003, appendix 1).

A preliminary scatter plot showing the relationships between CH of A1 and TL was generated to examine the general pattern of data point distribution. Three distinct groups of plots were evident: (1) *Alopias pelagicus* and *A. vulpinus*, (2) *A. superciliosus*, and (3) the remaining macrophagous lamniforms. The separation of *Alopias* spp. from the remaining lamniform taxa was expected due to their unusually elongate caudal fin (e.g. Shimada 2006b; Frumkin and Shimada 2020). However, what was not necessarily expected was the realisation that *A. superciliosus* ($n = 1$) being quite distinct even from the other two *Alopias* species, that warranted the need to treat it as a separate group.

In this study, some analyses examine the quantitative relationships of CH of A1 or a2 with other variables, whereas some other analyses either combine CH data from A1 and a2 altogether ('combined' CH data [cCH]) or do not require any CH data. Therefore, different combinations of the following six datasets were examined in different analyses for the purpose of this study: Dataset 1 with *A. pelagicus* and *A. vulpinus* only; Dataset 2 with *A. superciliosus* only; Dataset 3 with all non-*Alopias* macrophagous lamniforms with A1 and a2 data separate; Dataset 4 with all non-*Alopias* macrophagous lamniforms (with A1 and a2 data combined for cases that involve cCH values); Dataset 5 with all macrophagous lamniforms including *Alopias* spp. with A1 and a2 data separate; and Dataset 6 with all macrophagous lamniforms including *Alopias* spp. (with A1 and a2 data combined for cases that involve cCH values).

Based on the six types of datasets assembled from Table 1, four sets of regression analyses were conducted: (1) CH (A1, a2, and cCH) on TL; (2) CH (A1, a2, and cCH) on the jaw length (UJL and LJL) or dentition length (UDL and LDL); (3) relationships among the jaw and dentition lengths (UJL, LJL, UDL, and LDL); and (4) TL on the upper jaw length (UJL).

Because previous quantitative studies have shown the relationship between tooth measurements and TL in various lamniforms to be adequately linear (e.g. Gottfried et al. 1996; Shimada 2019, and references therein), a linear regression was used on each of the aforementioned combinations of datasets (Table 2). However, we also conducted a regression analysis using a power function that would accompany each linear regression to examine the distribution pattern of regressed data (Table 2). Whereas a linear relationship of data with a high coefficient of determination (r^2) value can be justified further if the power function closely follows its linear regression counterpart also with a high r^2-value, each power function can be used to evaluate whether a given linear function may potentially provide an underestimated or overestimated y-value predicted from an x–value. For example, if the curvature of a power function shows a steeper slope than the slope of its linear function counterpart, the linear equation is considered to provide underestimated (conservative) values.

Application to extinct macrophagous lamniforms

One of the goals of this study is to provide a way to estimate the length of the body, jaw, and dentition of extinct macrophagous lamniform taxa based on their tooth sizes. The dentition of most macrophagous lamniform sharks exhibit heterodonty referred to as the ‘lamnoid tooth pattern’ where teeth with the tallest crown in the mouth are always the so-called ‘anterior teeth’ and are typically represented by two tooth rows located mesially on each jaw quadrant (Shimada 2002). Although the level of tooth differentiation varies from taxon to taxon, tallest teeth are generally found, or easily interpreted to be present, at or near the mesial end of each jaw cartilage in extinct macrophagous lamniforms based on articulated or associated tooth sets (sensu Shimada 2006a: e.g. Shimada 1997a, 2007b; Cook et al. 2011; Vullo et al. 2016; Shimada and Everhart 2019). It is also reasonable to assert that the same condition must have been generally present in other extinct macrophagous lamniforms known only from isolated teeth, especially if their crown is tall and erect. We used this general pattern (i.e. all anterior teeth in the mouth are generally the tallest teeth and of a similar size) as a presumption and further assumed that cCH (i.e. based on A1 and a2 measurements altogether) would be a reasonable robust proxy to estimate the length of the body, jaw, and dentition for all extinct macrophagous lamniforms. In addition, because overestimating sizes of sharks or their parts may potentially lead to unrealistic or erroneous conclusions about their palaeobiology, we utilise quantitative functions that provide conservative estimates rather than those that tend to yield overestimations.

For the purpose of this study, we examined the maximum possible TL (mTL), maximum possible upper dentition length (mUDL), and maximum possible upper jaw length (mUJL) of all known extinct macrophagous lamniform genera based on the tallest tooth reported for each genus, using functions that would give robust, but conservative, estimates (see Results for specific functions that were chosen). To execute the calculations, the CH of the tallest anterior tooth on record needed to be determined for each genus, where the CH was not commonly documented explicitly but the total tooth height (TH: see Figure 1(b)). Thus, an estimated maximum crown height (mCH) was calculated for each genus by first determining the proportion of the CH of an anterior tooth illustrated in literature with respect to its TH, and applying that proportion to the maximum total tooth height (mTH) for that genus documented in the literature. Sources of information for mTH and mCH include: Siverson (1999, figure 9.1), Compagno (2002), Shimada (2008), Underwood and Cumbaa (2010), Bourdon et al. (2011), Cappetta (2012), Guinot et al. (2013), Kriwet et al. (2015), Siversson et al. (2015), Vullo et al. (2016), Amalfitano et al. (2017), Shimada et al. (2017), and Shimada (2019, figure 1(b)). For genera with extant species that constitute the largest forms, their recorded mTL from the literature (specifically Compagno 2002) was directly used (Table 3).

In addition to estimating mTL, mUDL, and mUJL of each genus, we surveyed the distribution of the mTL estimates through geologic time (Table 3). We compiled the recorded stratigraphic range of each macrophagous lamniform genus using the same aforementioned literature sources for mTH and mCH. We also classified the calculated mTL estimates using the following four size categories: ‘small,’ 1–200 cm; ‘medium,’ 201–400 cm; ‘large,’ 401–600 cm; and ‘gigantic,’ >600 cm). Although these categorisations are artificial, they were chosen to encompass the range for ‘small’ to include the extant *Pseudocarcharias* that is often characterised as a small lamniform (e.g. Compagno 2002; Ebert et al. 2013), and the range for

Table 2. Functions of pair of linear- and power-based regression lines (Ln.) shown in Figures (Fig.) 2 and 3, along with type of dataset (Ds.), sample size (n), and coefficient of determination (r^2) of each function or function pair. Variables: A1, crown height (in mm) of upper first anterior tooth; a2, crown height (in mm) of lower second anterior tooth; cCH, crown height (in mm) based on A1 and a2 data combined; LDL, lower dentition length (in mm); LJL, lower jaw length (in mm); TL, total length (in cm) of body; UDL, upper dentition length (in mm); UJL, upper jaw length (in mm) (Figure 1; see text for detail). Datasets (Ds.): 1, *Alopias pelagicus* and *A. vulpinus* only; 2, *Alopias superciliosus*; 3, all non-*Alopias* macrophagous lamniforms with A1 and a2 data separate; 4, all non-*Alopias* macrophagous lamniforms (with A1 and a2 data combined for cases that involve cCH values); 5, all macrophagous lamniforms including *Alopias* spp. with A1 and a2 data separate; 6, all macrophagous lamniforms including *Alopias* spp. (with A1 and a2 data combined for cases that involve cCH values). Functions in bold represent those used or discussed in text extensively.

Fig.	Ln.	Ds.	n	Linear function	r^2	Power function	r^2
2(a)	a	1	8	$\mathrm{TL} = 40.066 \cdot \mathrm{A1} + 78.009$	0.946	$\mathrm{TL} = 21.339(\mathrm{A1} + 3.236)^{1.212}$	0.947
2(a)	b	1	8	$\mathrm{TL} = 47.424 \cdot \mathrm{a2} + 74.772$	0.969	$\mathrm{TL} = 84.225(\mathrm{a2} + 0.462)^{0.779}$	0.971
2(a)	c	2	1	Not applicable due to $n = 1$		Not applicable due to $n = 1$	
2(a)	d	3	25	$\mathrm{TL} = 11.620 \cdot \mathrm{A1} + 9.293$	0.929	$\mathrm{TL} = 16.407(\mathrm{A1} - 0.907)^{0.917}$	0.930
2(a)	e	3	25	$\mathrm{TL} = 12.348 \cdot \mathrm{a2} - 18.682$	0.849	$\mathrm{TL} = 0.00006(\mathrm{a2} + 46.989)^{3.564}$	0.869
2(a)	f	4	50	$\mathbf{TL = 11.784 \cdot cCH - 0.331}$	0.880	$\mathrm{TL} = 3.047(\mathrm{cCH} + 6.335)^{1.319}$	0.883
2(b)	g	5	32	$\mathrm{UJL} = 10.241 \cdot \mathrm{A1} + 36.876$	0.871	$\mathrm{UJL} = 2.694(\mathrm{A1} + 8.960)^{1.336}$	0.878
2(b)	h	5	32	$\mathrm{LJL} = 7.113 \cdot \mathrm{a2} + 46.540$	0.811	$\mathrm{LJL} = 0.002(\mathrm{a2} + 45.108)^{2.795}$	0.833
2(b)	i	5	32	$\mathrm{UDL} = 8.304 \cdot \mathrm{A1} + 28.884$	0.871	$\mathrm{UDL} = 5.315(\mathrm{A1} + 5.243)^{1.115}$	0.870
2(b)	j	5	32	$\mathrm{LDL} = 5.602 \cdot \mathrm{a2} + 36.278$	0.810	$\mathrm{LDL} = 0.035(\mathrm{a2} + 30.213)^{2.125}$	0.825
2(b)	k	6	64	$\mathbf{UJL = 9.118 \cdot cCH + 44.464}$	0.841	$\mathrm{UJL} = 1.205(\mathrm{cCH} + 13.725)^{1.484}$	0.850
2(b)	l	6	64	$\mathbf{UDL = 7.409 \cdot cCH + 34.849}$	0.843	$\mathrm{UDL} = 3.635(\mathrm{cCH} + 7.798)^{1.177}$	0.845
3(a)	m	6	32	$\mathrm{LJL} = 0.845 \cdot \mathrm{UJL} + 6.666$	0.991	$\mathrm{LJL} = 0.603(\mathrm{UJL} + 17.282)^{1.054}$	0.991
3(a)	n	6	32	$\mathrm{LDL} = 0.838 \cdot \mathrm{UDL} + 5.368$	0.928	$\mathrm{LDL} = 1.621(\mathrm{UDL} - 8.590)^{0.890}$	0.929
3(a)	o	6	32	$\mathrm{UDL} = 0.808 \cdot \mathrm{UJL} - 0.609$	0.992	$\mathrm{UDL} = 1.645(\mathrm{UJL} - 19.309)^{0.884}$	0.993
3(a)	p	6	32	$\mathrm{LDL} = 0.769 \cdot \mathrm{LJL} + 3.643$	0.972	$\mathrm{LDL} = 1.011(\mathrm{LJL} - 2.027)^{0.955}$	0.972
3(b)	q	1	8	$\mathrm{UJL} = 0.385 \cdot \mathrm{TL} + 9.980$	0.936	$\mathrm{UJL} = 7.407(\mathrm{TL} - 91.648)^{0.537}$	0.949
3(b)	r	2	1	Not applicable due to $n = 1$		Not applicable due to $n = 1$	
3(b)	s	4	23	$\mathrm{UJL} = 1.020 \cdot \mathrm{TL} - 3.360$	0.969	$\mathrm{UJL} = 0.113(\mathrm{TL} - 59.514)^{1.341}$	0.971

Table 3. List of known macrophagous lamniform genera with their geologic range (GR; follows Cappetta's (2012, figure, p. 30) stratigraphic codes), source of maximum possible tooth height (mTH) measurements and estimated maximum possible crown height (mCH; in mm), estimated maximum possible total body length (mTL; in cm), estimated maximum possible upper dentition length (mUDL; in mm), and estimated maximum possible upper jaw length (mUJL; in mm), and body size category (SC) of each genus (see Materials and Methods for detail; exclude planktivorous *Cetorhinus, Megachasma*, and *Pseudomegachasma*). References (Ref.): A, Cappetta (2012); B, Compagno (2002); C, Kriwet et al. (2015); D, Siversson et al. (2015); E, Shimada et al. (2017); F, Shimada (2019, figure 1(b)); G, Siverson (1999, figure 9.1); H, Shimada (2008); I, Underwood and Cumbaa (2010); J, Amalfitano et al. (2017); K, Guinot et al. (2013); L, Bourdon et al. (2011); M, Vullo et al. (2016). Size category (SC): small (S) = 1–200 cm; medium (M) = 201–400 cm; large (L) = 401–600 cm; gigantic (G) = >600 cm; single asterisk (*) = likely underestimation where it could have been 'large' but not 'gigantic' (see Discussion).

Family									
	Genus	GR	Ref.	mTH (page)	mCH (source)	mTL	mUDL	mUJL	SC
Mitsukurinidae									
	Anomotodon	Apt–Prb	A	25 (p. 184)	20 (fig. 175D)	235	183	227	M
	Mitsukurina	Ypr–Hol	B	–	–	384[a]	313[b]	388[c]	M
	Scapanorhynchus	Apt–Maa	A	70 (p. 186)	54 (fig. 177A)	636	435	537	G
	Striatolamia	Dan–Prb	A	50 (p. 189)	42 (fig. 178A)	495	346	427	L
	Woellsteinia	Lut–Rup	A	26 (p. 190)	22 (fig. 179A)	259	198	245	M
'Odontaspididae' sensu lato									
	Araloselachus	Prb–Lan	A	50 (p. 191)	39 (fig. 180A)	459	324	400	L
	Borealotodus	Prb	A	40 (p. 192)	33 (fig. 181A)	389	279	345	M
	Brachycarcharias	Dan–Lut	A	25[d] (p. 193)	19 (fig. 182A)	224	176	218	M
	Carcharias	Cen–Hol	B	–	–	318	259[b]	321[c]	M
	Cenocarcharias	Cen	A	8 (p. 196)	7 (fig. 184A)	82	87	108	S
	Glueckmanotodus	Dan–Ypr	A	38 (p. 196)	28 (fig. 185A)	330	242	300	M
	Hispidaspis	Hau–Maa	A	60 (p. 198)	51 (fig. 186A)	601	413	509	G
	Hypotodus	Ypr–Brt	A	30 (p. 199)	24[a] (fig. 188A)	282	213	263	M
	Jaekelotodus	Dan–Prb	A	45 (p. 199)	35 (fig. 189B)	412	294	364	L
	Johnlongia	Alb–San	A	7.5 (p. 201)	6[e] (fig. 190E)	70	553	99	S
	Mennerotodus	Lut–Brt	A	40 (p. 202)	33 (fig. 191C)	389	279	345	M
	Odontaspis	Cmp–Hol	A	40 (p. 204)	41 (fig. 192C)	483	339	418	L
	Orpodon	Sel	A	12 (p. 205)	36[e] (fig. 193A)	424	302	373	L
	Palaeohypotodus	Dan–Tha	A	30 (p. 206)	24 (fig. 192G)	282	213	263	M
	Roulletia	Cen	A	10 (p. 207)	7[e] (fig. 194B)	82	87	108	S
	Sylvestrilamia	Ypr	A	20 (p. 208)	17 (fig. 195B)	200	161	199	S
	Turania	Brt	A	–	18[a] (fig. 196B)	212	168	209	M
Pseudocarchariidae									
	Pseudocarcharias	Bur–Hol	A	15 (p. 209)	13 (fig. 197A)	153	131	162	S
Lamnidae									
	Carchariolamna	Miocene	A	20 (p. 210)	16[e] (fig. 198A)	188	153	190	S
	Carcharodon[f]	Bur–Hol	A	70 (p. 216)	55 (fig. 201A)	648	442	546	G
	Carcharoides	Rup–Lan	A	25 (p. 214)	19 (fig. 198B)	224	176	218	M
	Carcharomodus	Tor–Zan	C	50 (p. 869)	41 (fig. 10A_1)	483	339	418	L
	Isurolamna	Dan–Cht	A	40 (p. 217)	32 (fig. 202D)	377	272	336	M
	Isurus	Rup–Hol	A	70 (p. 218)	56 (fig. 303H)	660	450	555	G
	Karaisurus	Brt	A	30 (p. 218)	23[e] (fig. 204A)	270	205	254	M
	Lamna	Zan–Hol	B	–	–	370	302[b]	374[c]	M
	Lethenia	Rup–Cht	A	15 (p. 220)	12[e] (fig. 206A)	141	124	154	S
	Macrorhizodus	Ypr–Rup	A	45 (p. 211)	31 (fig. 207A)	365	265	327	M
Otodontidae									
	Cretalamna[g]	Alb–Prb	D	– (p. 353)	30[a] (fig. 9A_3)	353	257	318	M
	Kenolamna	Cen	D	– (p. 378)	23 (fig. 23B_1)	271	205	254	M
	Megalolamna	Aqt–Bur	E	– (p. 708)	39[a] (fig. 2I)	459	324	400	L
	Otodus	Dan–Zan	F	149[a]	120[a]	1414	923	1139	G
	Parotodus	Ypr–Zan	A	60 (p. 227)	43 (fig. 211A)	506	353	437	L
Xiphodolamiidae									
	Xiphodolamia	Ypr–Prb	A	30 (p. 228)	24 (fig. 212C)	282	213	263	M
Cardabiodontidae									
	Cardabiodon	Alb–Tur	G	35.5	29[a] (fig. 213A)	341	249	309	M*
	Pseudoisurus	Alb–Cen	A	–	29[a] (fig. 214A)	341	249	309	M
Archaeolamnidae[h]									
	Archaeolamna	Alb–Maa	A	25 (p. 233)	19[e] (fig. 215 L)	223	176	218	M
Cretoxyrhinidae[i]									
	Acrolamna	Alb–Cmp	A	25 (p. 231)	20 (fig. 215B)	235	183	227	M
	Cretoxyrhina	Alb–San	H	– (p. 27)	53[e] (fig. 6B)	624	428	528	G
	Dallasiella	Cen–San	A	10 (p. 236)	8 (fig. 217A)	94	94	117	S
	Telodontaspis[i]	Cen–Tur	I	12 (p. 926)	11 (pl. 6, fig. 27)	129	116	145	S
Paraisuridae									
	Paraisurus	Apt–Alb	A	40 (p. 238)	32 (fig. 218A)	377	272	336	M
Pseudoscapanorhynchidae									
	Cretodus[j]	Alb–San	J	–	53[a] (appendix 1)	624	428	528	G
	Eoptolamna[j]	Brm–Cmp	K	5 (p. 47)	4 (fig. 17B)	47	64	81	S
	Leptostyrax	Alb	A	30 (p. 238)	25 (fig. 219A)	294	220	272	M
	Protolamna	Vlg–Maa	A	20 (p. 239)	16 (fig. 220C)	188	153	190	S
	Pseudoscapanorhynchus	Alb–Tur	A	15 (p. 240)	13 (fig. 221A)	153	131	163	S
Alopiidae									
	Alopias	Ypr–Hol	B	–	–	610[a]	181[b]	225[k]	G

(*Continued*)

Table 3. (Continued).

Family	Genus	GR	Ref.	mTH (page)	mCH (source)	mTL	mUDL	mUJL	SC
	Anotodus	Bur–Zan	A	45 (p. 242)	37 (fig. 223A)	436	309	381	L
	Usakias	Ypr–Rup	A	25 (p. 242)	21 (fig. 224A)	247	190	236	M
Anacoracidae									
	Nanocorax	Cen–Cmp	A	4 (p. 246)	3[e] (fig. 226A)	35	57	72	S
	Ptychocorax	Con–Cmp	A	20 (p. 246)	15 (fig. 227A)	176	146	181	S
	Scindocorax[l]	San	L	–	6[a,e] (fig. 7C)	70	79	99	S
	Squalicorax	Alb–Maa	A	37 (p. 248)	24 (fig. 228A)	282	213	263	M*
Pseudocoracidae									
	Galeocorax	Tur–Maa	A	10 (p. 249)	9[e] (fig. 229F[m])	106	101	127	S
	Pseudocorax	Tur–Maa	A	15 (p. 250)	11 (fig. 229C)	129	116	145	S
Serratolamnidae									
	Serratolamna	Cmp–Maa	A	30 (p. 252)	25 (fig. 232B)	294	220	272	M
Haimirichiidae									
	Haimirichia	Alb–Cen	M	–	7[a] (fig. 5L1)	82	87	108	S
Lamniformes incert. fam.									
	Dwardius	Alb–Con	A	30 (p. 255)	34 (fig. 235A)	400	287	354	M
	Eostriatolamia	Apt–Maa	A	20 (p. 256)	16 (fig. 236A)	188	153	190	S
	Palaeocarcharias	Tth	A	10 (p. 258)	9 (fig. 237E)	106	102	127	S
	Palaeocarcharodon	Dan–Tha	A	35 (p. 259)	29 (fig. 238A)	341	250	309	M
	Paranomotodon	Cen–Maa	A	20 (p. 260)	16 (fig. 239B)	188	153	190	S
	Priscusurus	Alb	A	15 (p. 261)	12[e] (fig. 240A)	141	124	154	S
	Trigonotodus	Ypr–Prb	A	15 (p. 261)	13 (fig. 241A)	153	131	163	S

[a] Measurement taken directly from photograph, text, or specimen

[b] Used UDL = 0.808·UJL – 0609

[c] Used UJL = 1.020·TL – 3.360

[d] Interpreted to be '25 mm' (not '2.5 mm' as indicated in text)

[e] Height inferred from slightly broken tooth

[f] Include '*Cosmopolitodus*' *hastalis*

[g] See Shimada et al. (2017)

[h] See Underwood and Cumbaa (2010)

[i] Newbrey et al. (2015) and Siversson et al. (2015) considered *Telodontaspis* Underwood and Cumbaa, 2010, to be congeneric with *Cretoxyrhina*, but because of its large tooth size difference with *Cretoxyrhina*, it is treated as a separate genus under the family Cretoxyrhinidae for the purpose of this study; the Turonian occurrence of *Telodontaspis* is based on McIntosh et al. (2016)

[j] See Shimada and Everhart (2019)

[k] Used UJL = 0.385·TL + 9.980

[l] See Cappetta et al. (2014)

[m] Likely based on a lateral tooth

'gigantic' to consist of sharks referred to as 'giants' by Pimiento et al. (2019). It should be noted that mTL values used assume the general body form of extinct forms to conform to that of non-*Alopias* macrophagous lamniform taxa for the purpose of this study.

Results

Quantitative relationships among measured variables in extant macrophagous lamniforms

Table 2 summarises 19 sets of regression analyses (= total of 38 separate analyses) that were conducted, although two sets were not possible for computation due to sample availability (i.e. n = 1 for *Alopias superciliosus*). Each set of linear and power functions in Table 2 are illustrated in Figures 2 and 3.

Relationships between CH and TL

Figure 2(a) depicts the relationships of CH (A1, a2, and cCH) on TL. Both linear functions for A1 and a2 of *Alopias pelagicus* and *A. vulpinus* ('solid' Lines a and b) exhibit a steep slope resulted from their relatively small teeth with respect to their TL that includes an elongate caudal fin as long as the precaudal body length (see Figure 1(a)). Their power functions ('broken' Lines a and b) closely follow the linear functions, all of which have the highest coefficient of determination values (r^2 of ≥0.946) among all the functions depicted in Figure 1. Therefore, the linear functions ('solid' Lines a and b) are considered to be reasonable proxies to predict TL from CH using A1 or a2 for highly derived alopiids characterised by an exceptionally elongate caudal fin. On the other hand, *A. superciliosus* differs from *A. pelagicus* and *A. vulpinus* by its comparably larger teeth despite its elongate caudal fin. Its CH-TL relationships (plots 'c' for A1 and a2 in Figure 1(a)) fall almost exactly between the lines for *A. pelagicus* and *A. vulpinus* (Lines a and b) and those for the remaining non-*Alopias* macrophagous lamniforms (Lines d–f).

The linear functions using A1 and a2 to predict TL in non-*Alopias* macrophagous lamniforms ('solid' Lines d and e) have similar low-angle slopes relative to those of *A. pelagicus* and *A. vulpinus* (Lines a and b) (Figure 2(a)). Whereas the power function for A1 ('broken' Line d) is similar to its linear function counterpart ('solid' Line d), the power function for a2 ('broken' Line e) significantly deviates from its linear function counterpart ('solid' Line e) with a significant upward curved slope. The unrealistically upward curvature was found to be caused largely by the inclusion of the only sample from a shark measuring >400 cm TL in our dataset – i.e. the largest (594 cm TL) white shark *Carcharodon carcharias* (Table 1; x-mark plot in Figure 2(a)). Because an experimental removal of that specific sample from the dataset would result in a power function [TL = $23.302(\text{a2} - 2.857)^{0.792}$; r^2 = 0.8375; not shown in Figure 2(a)] with a curvature that slopes even more gently than any other lines in Figure 2(a), the predictability of TL from a2 is determined to be less reliable than from A1, that is also suggested by the slightly lower r^2-values for a2 (0.849 and 0.869) compared to those for A1 (0.929 and 0.930).

An additional linear function ('solid' Line f) and its power function counterpart ('broken' Line f) were generated by combining the

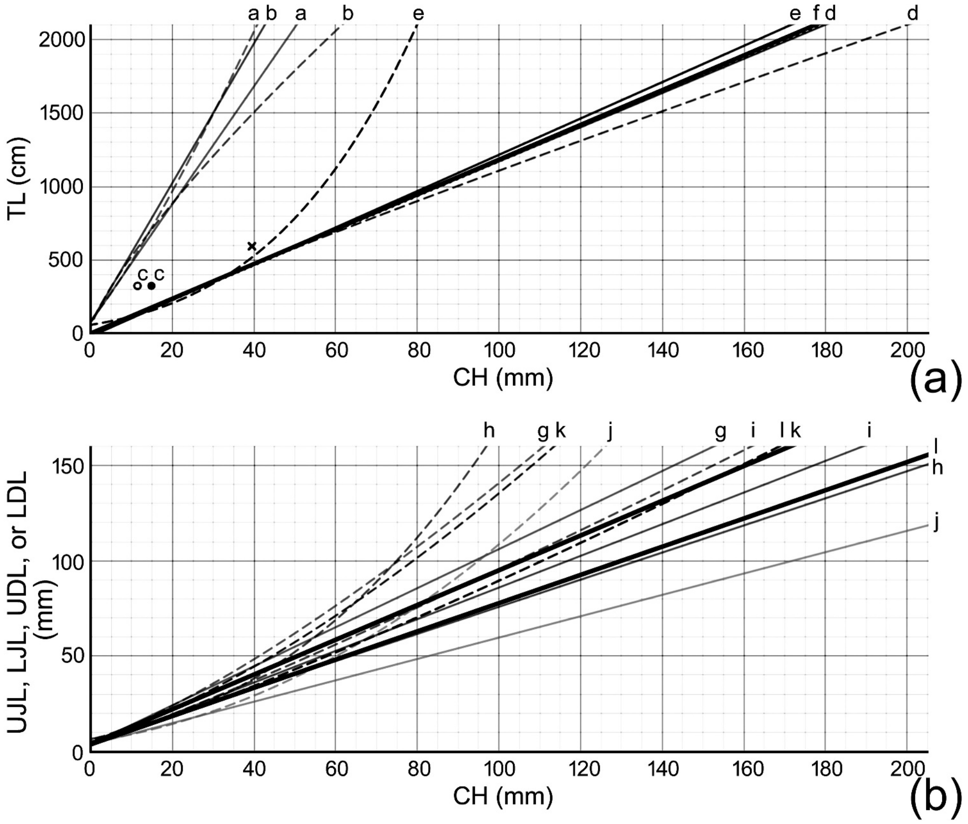

Figure 2. Linear- (solid line) and power-based (broken line) regression analyses relating crown heights of upper first anterior teeth, lower second anterior teeth, or A1 and a2 combined data (a) with total body lengths (TL), or (b) with upper jaw length (UJL), lower jaw length (LJL), upper dentition length (UDL), or lower dentition length (LDL) in 13 extant species of macrophagous lamniform sharks (see Figure 1 for included species and measured variables). Lines or plots: a and b = *Alopias pelagicus* and *A. vulpinus* only; c = *A. superciliosus* (*n*= 1); d and e = all non-*Alopias* macrophagous lamniforms with A1 and a2 data separate; f = all non-*Alopias* macrophagous lamniforms (with A1 and a2 data combined for cases that involve cCH values); g–j = all macrophagous lamniforms including *Alopias* spp. with A1 and a2 data separate; k and l = all macrophagous lamniforms including *Alopias* spp. (with A1 and a2 data combined for cases that involve cCH values); x-mark = plot of largest (594 cm TL) individual of *Carcharodon carcharias* that significantly affects curvature of Line e power function (see text for details; see Table 1 for examined specimens and raw measurements; see Table 2 for statistics of each function or function pair).

A1 and a2 data altogether (cCH; see Line f in Table 2). Our results show that, whereas the power function would produce an overestimated TL for a given CH as the line shows an upward curvature (not shown in Figure 2(a)) again primarily due to the largest sample of *Carcharodon carcharias* (x-mark plot in Figure 2(a)), the linear function ('solid' Line f) remains nearly identical to the linear functions for A1 and a2 ('solid' Lines e and d). Both the linear function ('solid' Line f) and power function ('broken' Line f) have similar coefficient of determination values, r^2 = 0.880 and 0.883, respectively.

Relationships between CH and jaw or dentition length

Figure 2(b) depicts the relationships of CH (A1, a2, or cCH) on either the jaw length (UJL or LJL) or dentition length (UDL or LDL) among all macrophagous lamniforms including *Alopias* spp. *Alopias* spp. are included in these instances by considering the analysed dental and jaw measurements to be independent of the TL or body form that could be influenced by the length of the caudal fin. Lines g–j show the quantitative relationships of A1 and a2 with their jaw length (UJL and LJL, respectively) or dentition length (UDL and LDL, respectively). In all cases, the curvature of each power function consistently shows steeper slopes than the angle of each respective linear function, suggesting that power functions would consistently give overestimations of CH to jaw or dentition length relative to their linear function counterparts. However, the coefficient of determination of the jaw length or dentition length from the CH is found to be higher for A1 on UJL (Line g: r^2 = 0.871 or 0.878) or UDL (Line i: r^2 = 0.871 or 0.870) than a2 on LJL (Line h: r^2 = 0.811 or 0.833) or LDL (Line j: r^2 = 0.810 or 0.825) for both linear and power functions. Therefore, whereas the overall total range of r^2 = 0.810–0.878 can be regarded as small, measurements from the upper jaw have slightly stronger correlation than measurements from the lower jaw.

Lines k and l (Figure 2(b)) show the quantitative relationships of combined A1 and a2 data (cCH) with either UJL or UDL among all macrophagous lamniforms, including *Alopias* spp., examined. Similar to the functions that treat each anterior tooth separately (Lines g–j), the curvature of both nearly linear power functions shows steeper slopes than the slope of both respective linear functions, indicating that power functions would yield overestimated values of CH to jaw or dentition length relative to their linear function counterparts. Although the coefficient of determination is slightly higher for power functions than linear functions, the differences are negligible with the overall total range of r^2 = 0.841–0.850.

Relationships among the jaw and dentition lengths

Figure 3(a) shows the linear and power functions to predict: (1) LJL from UJL (Line m), (2) LDL from UDL (Line n), (3) UDL from UJL (Line o), and (4) LDL from LJL (Line p). Each power function closely follows its linear function counterpart. The fact that all eight lines in Figure 3(a) cluster closely with high coefficient of determination values (r^2 = 0.928–0.993) suggest that not only is the increase in the jaw and dentition lengths of the upper jaw proportional to the increase in those lengths of the lower jaws, but the

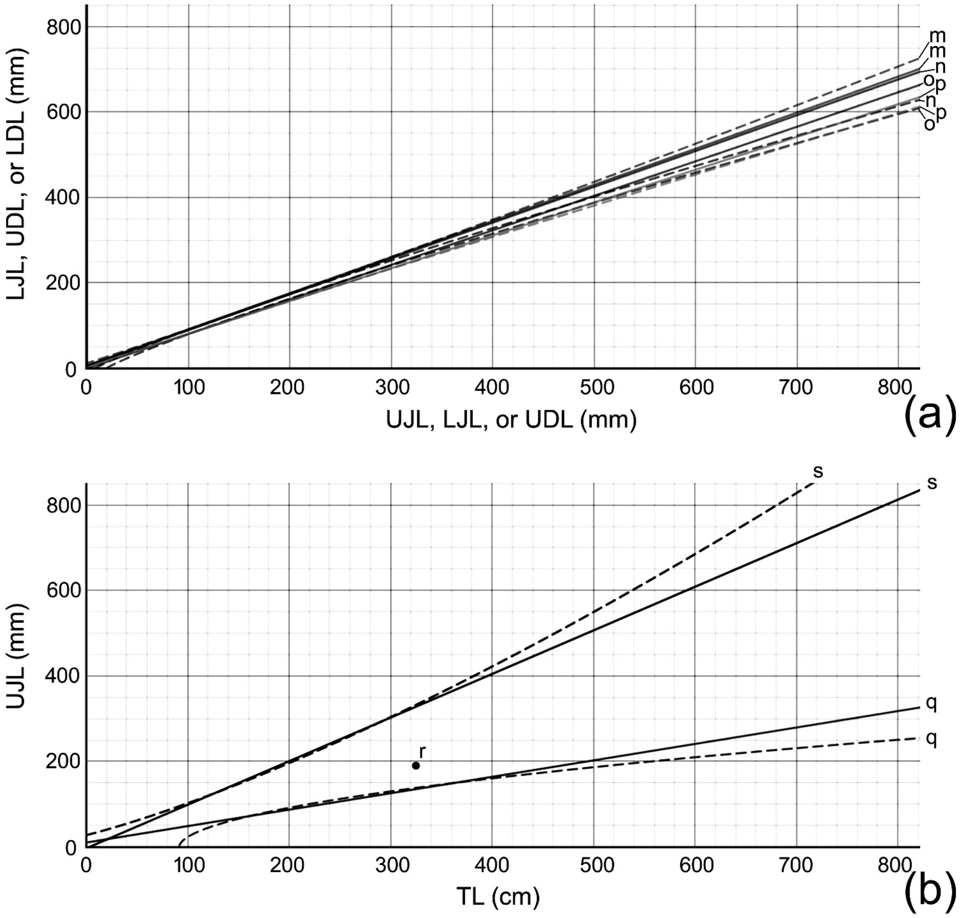

Figure 3. Linear- (solid line) and power-based (broken line) regression analyses (a) between jaw lengths and jaw lengths, dentition lengths and dentition lengths, or jaw lengths and dentition lengths, or between total body lengths and upper jaw length in 13 extant species of macrophagous lamniform sharks (see Figure 1 for included species and measured variables). Lines or plot: m–p = all macrophagous lamniforms including *Alopias* spp. (with A1 and a2 data combined for cases that involve cCH values); q = *Alopias pelagicus* and *A. vulpinus* only; r = *Alopias superciliosus* (*n* = 1); s = all non-*Alopias* macrophagous lamniforms (with A1 and a2 data combined for cases that involve cCH values) (see Table 1 for examined specimens and their raw measurements; see Table 2 for statistics of each function or function pair).

increase in each jaw length is also proportional to the increase of its respective dentition length.

Relationships between TL and upper jaw length

Figure 3(b) shows the linear and power functions between the TL and UJL in: (1) *Alopias pelagicus* and *A. vulpinus* (Line q); (2) *A. superciliosus* (Plot r); and (3) all non-*Alopias* macrophagous lamniforms (Line s). Although with similar coefficient of determination values, the power function ('broken' Line q; r^2 = 0.949) is found to yield underestimated values relative to its linear counterpart ('solid' Line q; r^2 = 0.936) in *Alopias pelagicus* and *A. vulpinus*. An exactly opposite trend is found between the linear and power functions for all non-*Alopias* macrophagous lamniforms where the power function ('broken' Line s; r^2 = 0.971) would yield over-estimated values relative to its linear counterpart ('solid' Line s; r^2 = 0.969). One plot based on a single specimen of *A. superciliosus* (Plot r) is found to occur between the two pairs of aforementioned lines.

Estimated body, jaw, and dentition lengths in extinct macrophagous lamniforms

To extrapolate the maximum length of the body (mTL), jaw (mUJL), and dentition (mUDL) of extinct macrophagous lamniform sharks, we specifically chose cCH-based functions in Table 2 that would provide more robust, but conservative, mTL, mUJL, and mUDL estimates rather than functions that use a specific tooth type (e.g. A1 or a2) or yield overestimated values: i.e. mTL = 11.784·mCH − 0.331 (Line f with r^2 = 0.880) for body length estimations; mUJL = 9.118·mCH + 44.464 (Line k with r^2 = 0.841) for jaw length estimations; and mUDL = 7.409·mCH + 34.849 (Line l with r^2 = 0.843) for dentition length estimations (note that cCH is replaced by mCH for the purpose of this portion of the present study).

Table 3 gives a list of measurements from 70 known lamniform genera under at least 16 known families, excluding planktivorous *Cetorhinus* (Cetorhinidae), *Megachasma* (Megachasmidae), and *Pseudomegachasma* ('Odontaspididae' sensu lato) (Compagno 2002; Shimada et al. 2015). Stratigraphically, they range from the Tithonian (Late Jurassic) through the Holocene, where the oldest known lamniform genus is *Palaeocarcharias* (Lamniformes incert. fam.). The obtained mTH and mCH values range from 4–149 mm and 3–120 mm, respectively, with the smallest values are from *Nanocorax* (Anacoracidae) and the largest values from *Otodus* (Otodontidae). However, it is worth noting that the second largest anterior teeth in the literature measure 70 mm in mTH with mCH ranging 54–56 mm and occur in three genera: *Scapanorhynchus* (Mitsukurinidae), *Carcharodon* (Lamnidae), and *Isurus*

(Lamnidae). Because mTL, mUJL, and mUDL are dependent on mCH, taxa with smallest, second largest, and largest mTL, mUJL, and mUDL values are also represented by the aforementioned taxa: i.e. *Nanocorax* with 35 cm in mTL, 72 mm in mUJL, and 57 mm in mUDL; *Scapanorhynchus, Carcharodon*, and *Isurus* with 636–660 cm in mTL, 537–555 mm in mUJL, and 435–450 in mUDL (*Isurus* being the largest among the three); and *Otodus* with 1,414 cm in mTL, 1,139 mm in mUJL, and 923 mm in mUDL. Among the 70 macrophagous lamniform genera, the calculated mTL values yield 23 genera consisting exclusively of ‘small’ forms, 30 genera with at least one species classified as ‘medium,’ nine genera with at least one species classified as ‘large,’ and eight genera with at least one species classified as ‘gigantic,’ based on our body size categorisation scheme (see Materials and Methods).

Discussion

Adequacy of body, jaw, and dentition length estimations from tooth crown height

Table 2 demonstrates strong quantitative relationships among the CH, TL, jaw lengths, and dentition lengths, where linear functions represented by non-*Alopias* macrophagous lamniforms generally tend to yield underestimated values compared to their power function counterparts. In particular, we regard our linear function Line f, TL = 11.784·CH − 0.331 (Table 2), to offer a reasonable conservative TL estimate from a CH of any anterior tooth in any given non-*Alopias* macrophagous lamniform taxon. This contention can be supported by a few extinct macrophagous lamniform taxa known from one or more complete or nearly complete skeletons in the fossil record. For instance, the monospecific genus *Palaeocarcharias* is known to reach up to about 1 m TL based on multiple complete and nearly complete skeletons (Kriwet and Klug 2004; Cappetta 2012), and our linear function calculation suggests that *Palaeocarcharias* is estimated to be 106 cm TL (Table 3). Based on a large partial skeleton of *Cretodus* sp., Amalfitano et al. (2017) estimated its total length to be about 6.5 m, and our calculated linear function suggests the genus to be up to about 624 cm TL.

Cretoxyrhina mantelli is known from a nearly complete skeleton that measures 5 or 5.5 m TL (Shimada 1997b, 2008; Newbrey et al. 2015). The mCH in the specimen is 40 mm, and if that CH value is applied to our linear function Line f, TL = 11.784·CH − 0.331, the estimated mTL for the specimen is 471 cm. In addition, whereas the vertebra-based theoretical growth model proposed for *C. mantelli* suggested that the species could have attained as much as about 6.9 m TL (Shimada 2008), our present study based on the largest known tooth suggests that *C. mantelli* reached at least 624 cm TL (Table 3). These results illustrate that our linear function (Line f) indeed provides conservative TL estimates for this species. However, the likelihood of underestimating its mTL by more than, for example, 1 m is highly unlikely.

Another example of macrophagous lamniforms known from a nearly complete, articulated skeleton is represented by *Squalicorax* cf. *S. falcatus*, measuring about 200 cm TL with the mCH of 11 mm (Shimada and Cicimurri 2005, figure 2(a), appendix 3). The application of the mCH to our linear function Line f, TL = 11.784·CH − 0.331, yields a considerably underestimated mTL, 129 cm, and this is almost certainly due to its *Galeocerdo*-like, low crown teeth. However, if its UDL of about 20 cm (based on Shimada and Cicimurri 2006, figure 4) is applied to UDL = 0.808·UJL − 0.609 (linear function Line o: Table 2) to solve for UJL, followed by using UJL = 1.020·TL − 3.360 (linear function Line s: Table 2) to solve for TL, our calculations yield a slightly overestimated 243 cm TL. These results further demonstrate that our linear function TL = 11.784·CH − 0.331 consistently yields a conservative TL estimates whereas the use of jaw and dentition lengths may give overestimated TL at least for *Squalicorax*. In addition, it is worth noting that Shimada and Cicimurri (2005) described a set of 10 associated shark vertebrae from the mid-Campanian that could belong to *S. pristodontus*. The largest vertebra in the vertebral set was about 2.5 times larger than the average maximum vertebral diameter of the aforementioned complete skeleton of *Squalicorax* cf. *S. falcatus*, suggesting that the possible *S. pristodontus* individual could have measured approximately 4.8 m TL (see also Becker et al. 2008). If so, *Squalicorax* could have reached up to the range of our ‘large’ size category, instead of ‘medium’ as categorised in Table 3.

Newbrey et al. (2015) estimated the TL of *Cardabiodon ricki* to be 5.5 m TL by determining its ‘lower jaw bite circumference’ (i.e. equivalent to LDL x 2) based on an associated dentition. Our mTL-estimate for *Cardabiodon* from the mCH is 341 cm TL (Table 3) where our smaller value than Newbrey et al.’s (2015) estimation could be due to the robust root in *Cardabiodon* possibly dwarfing the CH relative to the entire TH. In addition, it is plausible that the specific tooth of *Cardabiodon* that we measured is not the one with the tallest CH due to our constraint relying only on literature for the genus. In fact, *Cardabiodon* could have reached at least about 5.3 m TL if we use their ‘bite circumference’ with a LDL of 373 mm (Newbrey et al. 2015, figure 4) using LDL = 0.838·UDL + 5.368 (linear function Line n, Table 2; giving 438.702 mm UDL) to solve for UDL, followed by solving for UJL using UDL = 0.808·UJL − 0.609 (linear function Line o, Table 2; giving 542.948 mm UJL), and then by solving for TL using UJL = 1.020·TL − 3.360 (linear function Line s, Table 2; giving 532.302 cm TL). If so, the TL of *Cardabiodon* could have reached our ‘large’ size category, rather than ‘medium’ as shown in Table 3.

There are several other macrophagous lamniforms represented by associated skeletal remains in the fossil record (e.g. Cappetta 1980; Shimada 2007b; Cook et al. 2011; Kriwet et al. 2015; Vullo et al. 2016; Collareta et al. 2017; Shimada and Everhart 2019). However, they are rather incomplete, or their exact tooth sizes are not well documented, where those remains do not offer meaningful insights to further evaluate the reliability of our linear function Line f, TL = 11.784·CH − 0.331. Nevertheless, aforementioned examples are sufficient enough to strongly suggest that this linear function is adequate to capture the general TL of any given macrophagous lamniform not known from complete specimens, where a presumption can be made that the linear function tends to provide underestimate TL values.

Some examples of the utility of functions involving jaw and dentition lengths are included in the discussion above. We note additionally that those jaw- and dentition-based functions may also be useful for reconstructing the dentition of the vast majority of extinct macrophagous lamniforms known only from isolated teeth or incomplete specimens. For example, knowing the UDL or LDL (or UJL or LJL) from a given anterior tooth of a macrophagous lamniforms taxon would allow an estimate about the possible total number of teeth needed to fit the given length when reconstructing a dentition. As a confirmatory example, possibly the most complete dentition of extinct macrophagous lamniforms based on an articulated dentition is represented by *Haimirichia amonensis* (Haimirichiidae) with the UDL of about 88 mm (see Vullo et al. 2016, figure 5; but considering less gaps between adjacent teeth in their line drawing based on their photograph of the dentition, figure 4) where our calculation using the function, UDL = 7.409·cCH + 34.849 (Line l), yielded the UDL of approximately 87 mm (Table 3). However, we should also note that, like the example above from *Squalicorax* using UJL and UDL functions that gave an overestimated TL, our CH-based functions for jaw and dentition lengths may also provide tenuous estimations. For instance, a partial skeleton of *Cretalamna* (Otodontidae) preserves nearly complete upper jaws with the UJL of about 208 mm (Shimada 2007b, figure 1), and if the CH of the tallest anterior tooth, 16 mm (Shimada 2007b, appendix 1), is applied to the function, UJL = 9.118·CH + 44.464 (Line k), an underestimated UJL of 190 mm is attained. These results likely indicate that species-specific quantitative relationships exist among the examined variables, where our functions are based on a limited number of extant specimens consisting of multiple species that may not have any direct phylogenetic affinities to certain extinct lamniform taxa. Hence, with the general presumption that our linear functions provide conservative estimates, the functions in Table 2 should be used only as first approximations until complete skeletons with articulated dentitions become available for any given extinct macrophagous lamniform taxon.

Body size distribution of macrophagous lamniforms through geologic time

Figure 4 summarises the stratigraphic range and maximum possible body length category of each macrophagous lamniform genus based on Table 3. The excluded lamniforms are the following four planktivorous genera: *Cetorhinus* (Cetorhinidae; Burdigalian–Holocene; up to 9.8 m TL: Compagno 2002; Welton 2014, 2015); *Keasius* (Cetorhinidae; Bartonian(?)–Langhian(?); up to 5(?) m TL: Hovestadt and Hovestadt-Euler (2012); Welton 2013, Welton (2015)); *Megachasma* (Megachasmidae; mid-Priabonian–Holocene; up to 8.1(?) m TL: Shimada et al. (2014); Shimada and Ward (2016)); and *Pseudomegachasma* ('Odontaspididae' sensu lato; Cenomanian–early Turonian; up to 3.3(?) m TL: Shimada (2007a); Shimada et al. (2015)). It must be noted that each line may be represented by a single species or multiple species within the genus. In addition, the body size category for each genus indicated by a specific shade (e.g. light grey, medium grey, dark grey, or black) simply means that at least one member of the genus attained that body size category where the specific 'maximum body size representation' may be restricted to only a specific time frame within the total stratigraphic range of that genus. For example, extant *Isurus* spp. are known to reach slightly over 4 m TL (Compagno 2002), but our mTL estimate for the genus is calculated to be 6.6 m (Table 3), implying that the largest species in the genus is most certainly represented by a fossil form (species unspecified in Cappetta 2012). As another example, the genus *Cretoxyrhina* is known from three species: *C. denticulata*, *C. mantelli*, and *C. vraconensis* (note: see Table 3 for our treatment of '*C. agassizensis*'). However, *C. mantelli* is likely the only species of the genus that attained the 'gigantic' size category, and even though *C. mantelli* is known from the Cenomanian–Santonian (or possibly the Lower Campanian) deposits, only the post-Turonian members within the species likely attained the 'gigantic' body size as teeth of the genus show increasing sizes over time within the lineage (e.g. see Shimada 1997c). Similar but not identical cases are also found in *Otodus* that represents a lineage with different chronospecies that successively increased in body size (see below for further discussion) as well as in *Squalicorax* with many species that are not necessarily chronospecies where the geologically youngest species (*S. pristodontus*) marks the largest species within the genus (Shimada and Cicimurri 2005, 2006; see also discussion on *Squalicorax* above). Whereas the presumption is made that our calculations may provide underestimated TL values (see above), the genera coded as 'medium' may contain species that are 'small,' those coded as 'large' may include species that are 'small' and/or 'medium,' and those coded as 'gigantic' may include species that are 'small,' 'medium' and/or 'large.' The scale of our genus-level analysis is appreciably coarse where it does not elucidate the species-level patterns. In addition, Figure 4 does not show exactly when the largest form for each genus was specifically represented in its total geologic range, although the general rule is that the geologically oldest member of each genus that included at least one 'gigantic' form was likely not a gigantic form but smaller (e.g. see example from *Cretoxyrhina* above). Nevertheless, there are a number of robust observations that can be made from Figure 4.

The geologically oldest known lamniform, *Palaeocarcharias* from the Tithonian (latest Late Jurassic) (Jambura et al. 2019), is a small shark (up to ca. 1 m TL) based on complete skeletons (Kriwet and Klug 2004; Cappetta 2012) as well as our calculations (Table 3; Figure 4). The evolution of early lamniforms is complicated by the fact that the earliest Cretaceous fossil record of elasmobranchs is generally poorly documented (Kriwet et al. 2008). In fact, there is no fossil record of lamniforms documented from the Berriasian, and the Valanginian that followed is represented by only one lamniform genus, *Protolamna* (Figure 4). Nevertheless, the fact that both *Palaeocarcharias* and *Protolamna* were 'small' sharks (Figure 4) suggests that 'small' body size is a plesiomorphic condition within the order Lamniformes.

Besides the basal taxa (*Palaeocarcharias* and *Protolamna*), the small body size as a lamniform plesiomorphy is also reflected in the overall body size distribution in Figure 4. For example, not counting the genera that crossed the Cretaceous-Palaeogene (K-Pg; or Mesozoic-Cenozoic) boundary, 18 (56%) out of 32 genera consist entirely of 'small' forms during the Mesozoic, whereas only five (15%) of 34 such genera are represented during the Cenozoic. There are only 10 (31%) out of 32 genera categorised as 'medium' and none (0%) at all as 'large' during the Mesozoic, whereas 16 (47%) and nine (26%) of 34 Cenozoic genera are 'medium' and 'large' body sizes, respectively. Although any body size category larger than 'small' assigned to a genus can also include small or smaller forms, the fact that more than half (56%) of the known Mesozoic genera are exclusively of 'small' forms (vs. 15% for Cenozoic genera) and that more sharks reached 'medium' or 'large' sizes during the Cenozoic than the Mesozoic does not contradict the small body size to be plesiomorphic for the shark order.

Belben et al. (2017) conducted an ecological study based on tooth morphometry and demonstrated a significant body size reduction in macrophagous lamniforms immediately after the K-Pg extinction event. Our rather coarse body size distribution analysis does not allow elucidation of the exact body size changes across the K-Pg boundary. Nevertheless, there were four genera that included at least one member that reached 'gigantic' (*Cretodus, Cretoxyrhina, Hispidaspis*, and *Scapanorhynchus*), but none of them crossed the K-Pg boundary. The genera that crossed the K-Pg boundary (*Anomotodon, Carcharias*, and *Odontaspis*) were groups categorised as either 'medium' or 'large' that could have included one or more species with smaller body sizes. However, what is more intriguing is the fact that there were also four genera with at least one 'gigantic' form that evolved during the Cenozoic (*Alopias, Carcharodon, Isurus*, and *Otodus*). Whether or not *Alopias* (specifically *A. vulpinus* that is said to reach at least about 610 cm TL: Compagno 2002) merits its categorisation into 'gigantic' may be arguable because its precaudal body length is only about half of the TL due to its exceptionally elongate caudal fin (see Figure 1(a)). However, it is noteworthy that *A. vulpinus* as well as *Carcharodon, Isurus*, and *Otodus* are all endothermic or inferred to be endothermic (e.g. Bernal et al. 2012; Ferrón 2017). Although the thermophysiology of *Cretodus* has never been investigated, *Scapanorhynchus* (Mitsukurinidae) and *Hispidaspis* ('Odontaspididae') are considered ectothermic based on the fact that extant mitsukurinid (*Mitsukurina*) and 'odontaspidid'

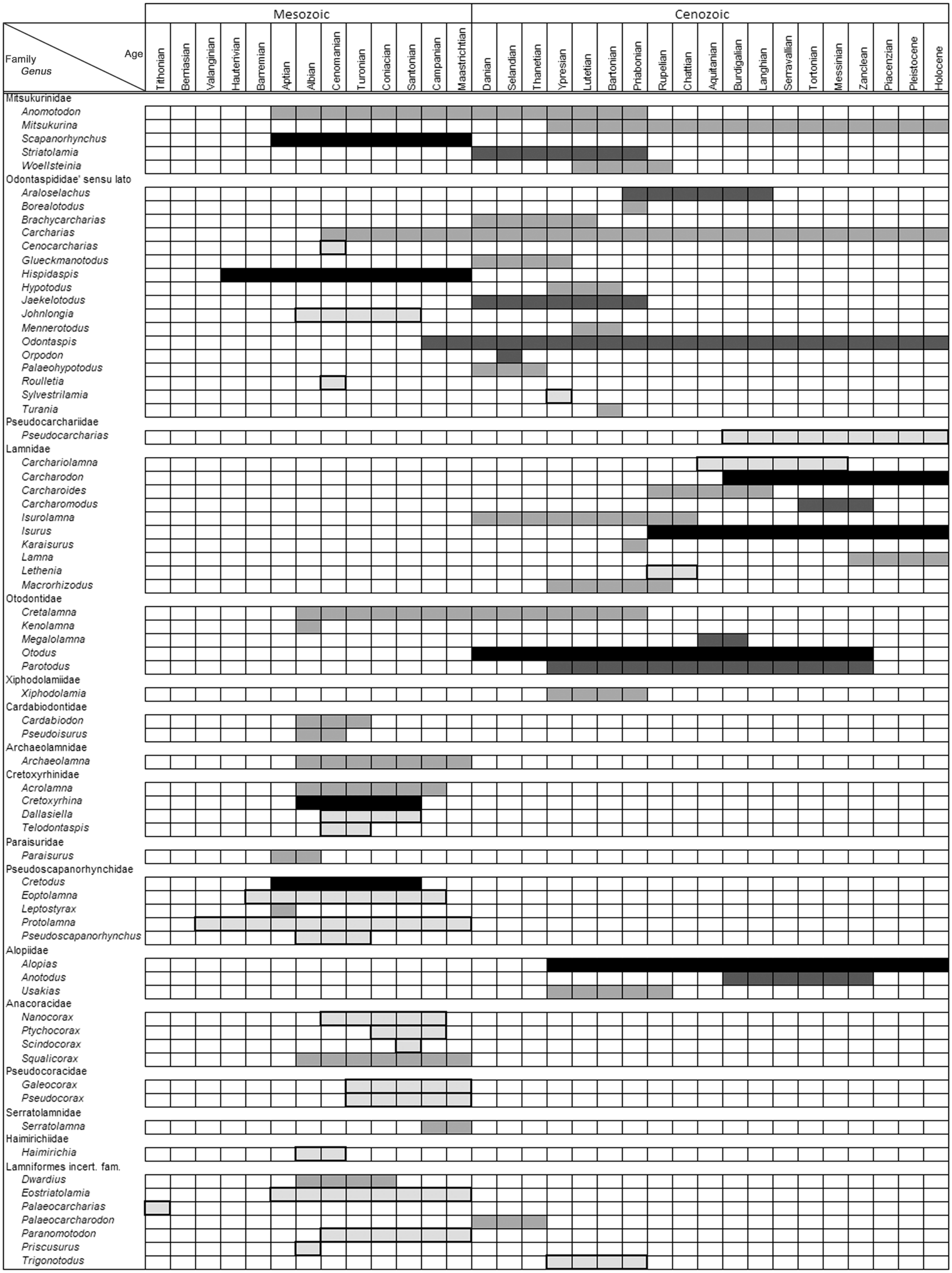

Figure 4. Stratigraphic range of each of 70 macrophagous lamniform genera where specific shade indicates specific maximum possible size category represented in each genus: light grey with thick borders = small (1–200 cm TL); medium grey = medium (201–400 cm TL); dark grey = large (401–600 cm TL); solid black = gigantic (>600 cm TL) (see Table 3).

(*Carcharias* and *Odontaspis*) taxa are ectothermic (Pimiento et al. 2019), whereas *Cretoxyrhina* has been inferred to be endothermic (Ferrón 2017).

Pimiento et al. (2019) found that there are two major evolutionary pathways for elasmobranchs to be 'gigantic,' either becoming a filter-feeder or endothermic, along with a small number of ectothermic macrophagous giants that lack such specialisations. They also found larger (2–6 m) ancestral sizes for elasmobranch clades (3.5 m TL for Lamniformes) that include filter-feeders or endotherms. However, where they found their analysis to be sensitive to inclusion or exclusion of fossil taxa, their larger ancestral sizes may represent overestimations given the fact that their dataset contained only ten fossil taxa that included only seven lamniform genera, all of which were coded to have a maximum body size of ≥3.5 m TL (Pimiento et al. 2019, table S2). Whereas it should also be pointed out that not all filter-feeding and endothermic elasmobranchs are gigantic (e.g. *Lamna* and *Pseudomegachasma*), our analysis is too coarse to examine body size changes within each genus. Nonetheless, our present study, including Figure 4, further demonstrates the uniqueness of Lamniformes as the only chondrichthyan order with all three cases of gigantic forms with at least certain members of: 1) *Cetorhinus* and *Megachasma* as gigantic filter-feeders; 2) *Alopias, Carcharodon, Isurus*, and *Otodus* as gigantic endotherms; and 3) *Scapanorhynchus* and *Hispidaspis* as gigantic unspecialised forms. However, one important observation is that the only forms that exceed 7 m TL are the filter-feeders (*Cetorhinus* and *Megachasma*) and presumably endothermic *O. megalodon* (Table 3; see also below). This is also true even if one considers non-lamniform elasmobranchs, where the only giant that exceeds 7 m TL is the largest extant fish, *Rhincodon typus* (whale shark), that is a filter-feeder reaching up to about 18.8 m TL (Compagno 2002; McClain et al. 2015). Other extant sharks that exceed 6 m TL exist, but their largest confirmed record does not exceed 7 m TL: e.g. up to 6.4 m TL for the Greenland shark, *Somniosus microcephalus*; and up to 6.1 m TL for the great hammerhead shark, *Sphyrna mokarran* (Compagno 1984). It has been suggested that at least some members of the Late Cretaceous durophagous shark genus, *Ptychodus*, possibly reached at least 10 m TL (Shimada et al. 2010; Jambura and Kriwet 2020), and if so, durophagy may be another specialisation pathway that has the potential for elasmobranchs to attain gigantism (Pimiento et al. 2019). In addition, some isolated, over-sized lamniform vertebrae are known from Albian (Lower Cretaceous) deposits, and whereas the largest specimen is estimated to have come from an individual that possibly measured 8.3–9.8 m TL, their taxonomic identity remains uncertain (Shimada 1997e; Frederickson et al. 2015). Regardless, 7 m TL can be regarded as the general size limit for non-durophagous macrophagous elasmobranchs with the genus *Otodus* representing the only known decisive exception (see further discussion below).

It must be highlighted that the largest form of *Otodus, O. megalodon* that reached at least 14 m TL, is unique because the estimated mTL is truly an anomalous outlier – i.e. twice as long as the general size limit of 7 m TL for all other known macrophagous lamniforms (Table 3; see also above), and quite possibly even among all macrophagous elasmobranchs that ever existed (e.g. see Pimiento et al. 2019). Therefore, our body size category 'gigantic' that lumps all taxa measuring >6 m TL is rather deceptive as it does not highlight the remarkable size difference between *O. megalodon* and all other gigantic macrophagous lamniforms. It should be noted that our linear function tends to provide underestimated TL values (see above); however, this presumption applies not only to *O. megalodon*, but also to all macrophagous lamniforms examined (Table 3). Even if any notable underestimation (or overestimation) is present for certain taxa (possibly even including *O. megalodon*) as exemplified by a few examples above (e.g. *Cardabiodon* and *Squalicorax*), the calculated size gap of 7 m between *O. megalodon* and all other macrophagous lamniforms is so great that it is highly improbable that any macrophagous lamniforms, even those already classified as 'gigantic,' would have reached the size of the largest *O. megalodon*.

Evolution of gigantism in lamniforms

Whereas the oldest *Otodus* is known from the Danian (lower Palaeocene), one species, *O. obliquus*, began to attain anterior teeth as large as 9 cm TH by the Ypresian (early Eocene: Cappetta 2012). Based on the method used in this study, 9-cm-tall teeth would have had the CH of approximately 68 mm (Cappetta 2012, figure 208A), and our linear function Line f, TL = 11.784·CH − 0.331, (Table 2) suggests that the individual would have measured 801 cm TL, or about 8 m TL. It is known that *O. obliquus* in the early Eocene constitutes the base of a lineage of multiple chronospecies that followed along with the gradual increase in their overall tooth size, development of serrations, and reduction in lateral cusplets. In chronological order, they are: *O. auriculatus* in the late Eocene; *O. angustidens* in the early Oligocene; *O. chubutensis* in the early to mid-Miocene; and *O. megalodon* in the mid-Miocene through early Pliocene (Pimiento and Balk 2015; Trif et al. 2016; Perez et al. 2019). The tooth of *O. megalodon* illustrated in Figure 1(b) has the tallest known CH in scientific literature for the species, and based on the CH-TL relationship in extant *Carcharodon carcharias*, that specific individual of *O. megalodon* is conservatively estimated to be about 14.5 m TL, although the species could have reached at least slightly over 15 m TL (Shimada 2019). Our present study gives an even more conservative estimate for the individual, about 14.1 m TL (Table 3), but at least it is reasonable to assert that the mTL of chronospecies between *O. obliquus* and *O. megalodon* (i.e. *O. auriculatus, O. angustidens*, and *O. chubtensis*) must have ranged between 8 and 15 m TL.

The mTL of 801 cm TL for *Otodus obliquus* is coincidentally intriguing because another size category, 'super gigantic,' may be created to separate taxa that attain >800 cm TL from those reaching the range of 601–800 cm TL (i.e. alternative size category criterion for the 'gigantic') that would encompass the general size limit (ca. 7 m TL) for non-durophagous macrophagous elasmobranchs (see above). If so, elasmobranch taxa that reach or likely reached the 'super gigantic' range include: the otodontid linage consisting of *O. obliquus, O. auriculatus, O. angustidens, O. chubutensis*, and *O. megalodon*; filter-feeding *Rhincodon, Cetorhinus*, and *Megachasma*; and possibly some members of durophagous *Ptychodus*. This also supports Pimiento et al.'s (2019) proposition that filter-feeding and endothermy as two major pathways to achieve gigantism, with the possibility of yet another pathway, durophagy (see above).

Ferrón (2017) proposed endothermy (more precisely regional endothermy or mesothermy) to be one of the evolutionary drivers for gigantism in Lamniformes (see also Ferrón et al. 2018). Pimiento et al. (2019) illustrated that the occurrences of endothermy are unique to Lamniformes among all elasmobranchs. The evolution of endothermy is regarded to be quite plastic because it is found in many different vertebrate clades (Legendre and Davesne 2019), and it is likely that endothermy arose multiple times through lamniform phylogeny (e.g. *Alopias vulpinus, Cretoxyrhina mantelli*, Lamnidae, and Otodontidae including *O. megalodon*: Bernal et al. 2012; Ferrón 2017; but see also Pimiento et al. 2019). Endothermy involves complex physiological demands associated with elevated metabolic rates and high energetic costs (e.g. Bernal et al. 2012; Ferrón 2017; Ferrón et al. 2018), and it is assumed to be particularly demanding for sharks like lamnids (*Lamna*, *Isurus*, and *Carcharodon*) that require continuous swimming as obligate ram ventilators (Carlson et al. 2004). However, endothermy is said to provide two main advantages in sharks by being more active, eating more food, and growing more rapidly: 1) thermal niche expansion (i.e. tolerance to a broader range of water temperatures), and 2) increased cruising speeds (i.e. elevating prey encounter rates and travel distances) (Watanabe et al. 2015, 2019). While much of the explanation for the evolution of endothermy in certain lamniforms has been attributed to their 'active macropredatory lifestyle' (e.g. Watanabe et al. 2015, 2019; Ferrón 2017; Ferrón et al. 2018), what could have triggered such frequent endothermy only in lamniforms has never been questioned. To address this question, one possible consideration is to identify any physiologically demanding attribute uniquely and universally present within the order Lamniformes, and there is indeed one such candidate – ovoviviparous reproduction (or aplacental viviparity) involving intrauterine cannibalism. Bioenergetics reflects each species' capacity for growth and maintenance as well as reproduction (Pattersen et al. 2018; Lawson et al. 2019); yet, very little attention has been given to this peculiar reproductive biology of lamniforms in the context of the evolution of their bioenergetics and body size.

All extant lamniforms give live birth (ovoviviparity) to relatively large, well-developed newborns where the large size of embryos retained in a gravid female is offset by low fecundity as a result of intrauterine cannibalism generally in the form of oophagy but also adelphophagy in at least one species (*Carcharias taurus*) (Compagno 2002; Carrier et al. 2004; Conrath and Musick 2012; Table 4). Whereas ovoviviparity is common in elasmobranchs (e.g. Compagno 1984, 1990b, 2002), intrauterine cannibalism is a unique behaviour observed, or inferred to be present, only in lamniforms among all known elasmobranchs, and quite possibly among all vertebrates. In fact, Compagno (1990a) specifically considered the intrauterine cannibalism to be a possible synapomorphy for the order Lamniformes (see also Musick and Ellis 2005). Ovoviviparity of lamniforms in the fossil record is substantiated by a partial skeleton of gravid *Carcharias gustrowensis* with eight embryos from the Oligocene of Germany (Hovestadt and Hovestadt-Euler 2010), and ovoviviparity with intrauterine cannibalism behaviour in lamniforms is thought to have already evolved by the Late Cretaceous based on the relatively large estimated size at birth (ca. 120 cm TL) of *Cretodus* and *Cretoxyrhina* (Shimada 2008; Shimada and Everhart 2019).

Table 4. Summary of body size at birth, common and maximum litter sizes per female, and body size of smallest mature individual on record by sex in all 15 species of extant lamniforms (see Figure 1(a); unless otherwise indicated, all data come from Compagno (2002); asterisk [*] = species with confirmed oophagy or confirmed large egg count likely for oophagy; double asterisks [**] = species with confirmed adelphophagy besides oophagy).

Species	Size at birth (cm TL)	Litter size: Common; Maximum	Maturity (cm TL): Female; Male
Mitsukurina owstoni	? [82[a]]	?: ?	335; 264
_Odontaspis ferox_*	>105	?: ?	364; 275
Odontaspis noronhai	?	?: ?	326; 326
_Pseudocarcharias kamoharai_*	41	4; 4	89; 74
_Megachasma pelagios_*	? [177[b]]	?; ?	500; 446
_Alopias pelagicus_*	130–160	2; ?	273; 267
_Alopias superciliosus_*	100–140	2–4; 4	294; 279
_Alopias vulpinus_*	114–160	2–4; 7	315; 300
Carcharias taurus**	95–105	2; 2	220; 190
_Cetorhinus maximus_*	150–170	?; 6	800; 400
_Lamna ditropis_*	40–50	2–4; 5	221; 182
_Lamna nasus_*	60–80	4; 5	200; 150
_Isurus oxyrinchus_*	60–70	10–18; 25	275; 203
_Isurus paucus_*	97–120	2–8; 8	245; 245
_Carcharodon carcharias_*	109–160	2–?; 14?	400; 350

[a] Smallest free-swimming individual reported by Yano et al. (2007)
[b] Smallest free-swimming individual reported by White et al. (2004)

Ovoviviparity in lamniforms takes place in paired uteri aplacentally. Numerous eggs are first formed in the paired ovaries. For example, *Cetorhinus maximus* is reported to produce at least six million follicles and ova in each ovary, where eggs range from 0.5 to 5.0 mm in diameter and already contain a considerable amount of yolk (Matthews 1950). Those eggs are transferred to the oviducts and may become fertilised. Embryos first possess a yolk sac that soon becomes reabsorbed, marking the onset of their intrauterine cannibalism behaviour in the uteri (Gilmore et al. 1983). Early hatched embryos begin to devour surrounding unfertilised eggs (oophagy), and at least for *Carcharias taurus*, may kill and feed on other embryos (Gilmore 1993; Compagno 2002; Gilmore et al. 2005). In fact, this mode of development relies on the continuous supply of yolk in ovulated eggs (Hamlett and Koob 1999). Furthermore, developing embryos may also receive lipid-rich uterine secretions (lipid histotrophy) from their mother as additional nutrition (Sato et al. 2016). The consequences are the low fecundity and large body size at birth where only a few individuals (generally one or two foetuses per uterus) that may be about 20–45% of the size of their mother survive and are born (Table 4; e.g. note the size at birth of 41 cm TL and the onset of females' sexual maturity at 89 cm TL in *Pseudocarcharias kamoharai*). Some species may exhibit a comparably small size at birth, but it may be to compensate a relatively large litter size (e.g. size at birth of 60–70 cm TL with up to 25 pups in *Isurus oxyrinchus*) although not necessarily always (e.g. size at birth of 40–50 cm TL with up to five pups in *Lamna ditropis*) (Table 4). It is worth pointing out that the size at birth for many extant lamniform species is >1 m TL, and the onset of females' sexual maturity for all extant lamniforms begins at ≥2 m TL (i.e. in the 'medium' body size category or larger) with the exception of *P. kamoharai* (Table 4) that reaches only up to about 1.5 m TL (Table 3). Therefore, it is reasonable to assert that ovoviviparity involving intrauterine cannibalism with the need to produce a large quantity of yolk-rich eggs and lipid-rich uterine fluid to nourish developing embryos that can grow to large sizes must be energetically costly to their mother – a unique physiological challenge evolved only in Lamniformes.

Yet, ovoviviparity with intrauterine cannibalism apparently does not necessarily lead to endothermy or gigantism as exemplified by the fact that the vast majority of lamniforms are 'small-large' ectothermic sharks, and even those that do attain 'gigantic' sizes were likely not necessarily endothermic (e.g. *Scapanorhynchus* and *Hispidaspis*). These differences in thermophysiology could be due to different levels of physiological demands imposed by species-specific differences in a multitude of biological and environmental factors, such as the variation in body size at birth, litter size, onset of sexual maturity, gestation period, habitat, diet, and types of predators. Embryos that grow to sizeable lengths before their birth would press higher physiological demands on their mother, which may in turn require the mother to feed more actively – i.e. another possible driving mechanism for the evolution of endothermy achieved by certain lamniform clades that became energetic carnivores allowing them to expand and exploit their diet range. Furthermore, where pups having a larger body size at birth would reduce their predation risk upon their birth, it is also conceivable that endothermic taxa would have also had endothermic embryos that would require more nourishments, that could have exacerbated the physiological demands on their mother to be even more energetic 'super carnivores' possibly contributing to gigantism.

One may question as to why male sharks also merit gigantism that do not face high physiological demands as females do. In fact, although females are generally larger than males in most sharks, including lamniforms (e.g. Compagno 1984, 2002; Table 4), extreme dwarfism of males relative to the female size of the same species is rare. This observation could be the reflection of the need for mature males to stay close to the size of mature females to enable internal fertilisation through the use of their claspers while grasping females' pectoral fins with their toothy mouth during their courtship (e.g. see Carrier et al. 2004; Conrath and Musick 2012) – i.e. to avoid the sexual size dimorphism to become a reproductive isolating barrier. In addition, the need for the use of their teeth during courtship, even for filter feeders, may explain why edentulous elasmobranchs are not known (vs. edentulous filter-feeding bony fishes and cetaceans: e.g. Friedman et al. 2010; Schumacher et al. 2016). Although the reason for the retention of teeth in female filter-feeding sharks is unclear, the fact that lamniforms tended to achieve large body sizes (= larger tooth sizes) possibly due to ovoviviparity with intrauterine cannibalism, along with the need of teeth for courtship, may also be partly responsible for the overall commonness of shark teeth in the fossil record.

Conclusion

The order Lamniformes is well represented in the late Mesozoic–Cenozoic fossil record, and shows remarkable diversity and specialisations, including small to large forms, planktivorous to macrophagous forms, benthic to pelagic forms, and ectothermic to endothermic forms. As many of them represent major carnivores, it is reasonable to assert that lamniforms collectively must have played an important role in the evolution of marine ecosystems through geologic time. However, the vast majority of lamniforms are represented only by their teeth. In this study, we presented tooth, jaw, and dentition measurements taken from 32 non-embryonic specimens of all 13 species of extant macrophagous lamniforms (Figure 1; Table 1) to generate linear functions that would allow estimations of tooth, jaw, and dentition lengths of extinct macrophagous lamniforms from tooth crown height (Table 2; Figure 2, 3).

We regard the linear function, TL = 11.784·CH − 0.331 (Table 2), to offer an adequate conservative TL estimate from a CH of any anterior tooth in any given non-*Alopias* macrophagous lamniform taxon, although an assumption was made that this linear function tends to provide underestimated TL values. Among the 70 macrophagous lamniform genera surveyed, the calculated mTL values yielded 23 genera consisting exclusively of 'small' (1–200 cm TL), 30 genera with at least one species classified as 'medium' (201–400 cm TL), nine genera with at least one species classified as 'large' (401–600 cm TL), and eight genera with at least one species classified as 'gigantic' (>600 cm TL) based on our body size categorisation scheme. Where the geologically oldest known lamniform is *Palaeocarcharias* from the Tithonian (latest Late Jurassic) that is a small shark (up to about 1 m TL), 'small' body size is considered plesiomorphic for Lamniformes. In fact, more sharks reached 'medium' or 'large' sizes during the Cenozoic than the Mesozoic.

There were three genera that crossed the K-Pg boundary (*Anomotodon, Carcharias*, and *Odontaspis*) categorised as either 'medium' or 'large.' There were four genera that included at least one member that reached 'gigantic' (*Cretodus, Cretoxyrhina, Hispidaspis*, and *Scapanorhynchus*), but none of them crossed the K-Pg boundary. Interestingly, there were also four genera with at least one 'gigantic' form in the Cenozoic (*Alopias, Carcharodon, Isurus*, and *Otodus*). In fact, our study demonstrates the uniqueness of Lamniformes as the only chondrichthyan order with all three previously proposed pathways for gigantism (Pimiento et al. 2019) with at least certain members of: (1) *Cetorhinus* and *Megachasma* as gigantic filter-feeders; (2) *Alopias, Carcharodon, Isurus*, and *Otodus* as gigantic endotherms; and (3) *Scapanorhynchus* and *Hispidaspis* as gigantic unspecialised forms. However, the only forms that exceed 7 m TL are the filter-feeders (*Cetorhinus* and *Megachasma*) and presumably endothermic *O. megalodon*; thus, 7 m TL is regarded as the general size limit for macrophagous lamniforms, except for the genus *Otodus*. In fact, the largest form of *Otodus, O. megalodon* that reached at least 14 m TL, is truly off the scale considering the general size limit of 7 m TL for all other known macrophagous lamniforms (Table 3).

Otodus obliquus calculated to be 8 m TL from the early Eocene *Otodus* constitutes the base of a lineage of multiple chronospecies that eventually led to *O. megalodon* with the estimated mTL of 14 or 15 m TL. Ferrón (2017) proposed endothermy to be one of the evolutionary drivers for gigantism in Lamniformes. Endothermy involves complex physiological demands associated with elevated metabolic rates and high energetic costs, where we contend that ovoviviparous reproduction involving intrauterine cannibalism in Lamniformes to be another possible driver for the evolution of endothermy. The increased physiological demands by embryos that grew to be sizeable lengths would have required the mother to feed more actively and possibly triggered certain species to evolve endothermy. Furthermore, endothermic taxa would have also had endothermic embryos that could have exacerbated the physiological demands on their mother to give rise to even more energetic 'super carnivores' possibly also contributing to gigantism. In addition, mature males needed to stay close to the size of mature females to ensure internal fertilisation through the use of their claspers while grasping females' pectoral fins with their toothy mouth during their courtship. Ovoviviparity with intrauterine cannibalism in lamniforms, along with the evolution of elevated bioenergetics (endothermy) in certain species that could have led to larger body sizes (hence larger tooth sizes), combined with their polyphyodont dentition (e.g. Reif et al. 1978) and the fact that toothless sharks are not known, may have contributed to the overall abundance of shark teeth in the fossil record.

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Notes added at proof

After this present manuscript went into production, a new paper written by Cooper et al. (2020) hypothesizing the body form in lateral view and lifestyle of *Otodus megalodon* appeared. In their paper, 16 m TL was given as a 'conservative maximum body size' by citing Shimada's (2019) paper. However, for the sake of scientific accuracy, we must emphasize that the range of 14.1–15.3 m TL is the scientifically justifiable maximum TL estimates for *O. megalodon* at the present time based on voucher specimens in museum collections under public trust (Shimada, 2019; this present paper). This does not mean that individuals of *O. megalodon* exceeding the size range did not exist (Shimada, 2019), but unnecessarily inflated size estimates without justifiable evidence must be avoided in scientific literature.

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