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Body forms of extant lamniform sharks (Elasmobranchii: Lamniformes), and comments on the morphology of the extinct megatooth shark, *Otodus megalodon*, and the evolution of lamniform thermophysiology

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ABSTRACT

The megatooth shark, *Otodus megalodon*, is an iconic Neogene lamniform shark known only from its teeth and vertebrae. Its thermophysiology is previously inferred to have been regionally endothermic, like the extant lamnids that are active predatory lamniforms. By considering the entire Lamnidae as the ecological and physiological analogue to *O. megalodon*, a recent study proposed inferred body dimensions of *O. megalodon* based on morphometric analyses on body forms of extant lamnids. Here, we reassessed the recent study by testing whether a two-dimensional approach used in the study can actually tease out the difference between ectothermic and endothermic fishes in the first place. Morphometric comparisons of the whole body and different body parts (e.g. head, different fins, and precaudal body with and without fins) among the 15 extant species of Lamniformes were conducted using principal component analyses and simple clustering methods. Our study strongly indicates that, two-dimensionally, there is no relationship between thermophysiology and body form in lamniforms. The reality is that there are presently no scientific means to support or refute the accuracy of any of the previously published body forms of *O. megalodon*. We also clarify that regional endothermy likely evolved in multiple clades independently through lamniform phylogeny.

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Introduction

The order Lamniformes (Figure 1) is a relatively small group of sharks but an ecologically diverse monophyletic assemblage, including a number of iconic taxa. They include large planktivorous forms, such as the megamouth (*Megachasma*) and basking (*Cetorhinus*) sharks, small to large 'macrophagous' forms, such as the goblin (*Mitsukurina*), 'sandtiger' (*Carcharias* and *Odontaspis*), crocodile (*Pseudocarcharias*), white (*Carcharodon*), mako (*Isurus*), and porbeagle or salmon (*Lamna*) sharks, as well as the thresher sharks (*Alopias*) that prey on small fishes by stunning them using their elongated caudal fin (Compagno 2002; Figure 1). Furthermore, Lamniformes is unique in that it represents the only shark group that includes endothermic forms (more precisely regional endothermy or mesothermy, that is the conservation of heat through vascular countercurrent heat exchangers, and elevated tissue temperatures in specific internal issues of the body: e.g. Carlson et al. 2004; Bernal et al. 2012; Ferrón 2017; Ferrón et al. 2017; Pimiento et al. 2019; Harding et al. 2021). Whereas extant lamniforms are represented only by 15 species (Figure 1), the shark order is well represented in the fossil record where their origin can be traced back to the Jurassic and underwent a major radiation in the Cretaceous (Maisey et al. 2004; Cappetta 2012; Shimada et al. 2020).

Among the numerous extinct forms within Lamniformes is the well-known megatooth shark, *Otodus megalodon* (Otodontidae), based primarily on its gigantic teeth commonly found in the late Neogene marine deposits nearly worldwide (Cappetta 2012; Shimada 2019). With a possible size at birth of about 2 m TL (Shimada et al. 2021), *O. megalodon* is estimated to have reached at least 15 m in total length (TL) (Shimada 2019), and possibly as much as 18–20 m TL (Pimiento and Balk 2015; Perez et al. 2021). However, the body form of *O. megalodon* remains largely speculative. Recently, Cooper et al. (2020) presented a study inferring body dimensions of *O. megalodon* two-dimensionally in lateral view based on morphometric analyses conducted on body forms of all five living species of the lamniform family Lamnidae: *Carcharodon carcharias* (white shark), *Isurus oxyrinchus* (shortfin mako), *I. paucus* (longfin mako), *Lamna ditropis* (salmon shark), and *L. nasus* (porbeagle shark) (Figure 1). Cooper et al.'s (2020) work was novel in that they used the entire Lamnidae as the ecological and physiological analogue to *O. megalodon* by following the hypothesis that *O. megalodon* was an endothermic, active, macrophagous predator like the extant lamnids (see Ferrón 2017). Whereas endothermic fast-swimming fishes tend to converge evolutionarily in body form (e.g. between lamnids and tunas), their substantiated homoplasious similarities are based primarily on transverse cross-sectional (i.e. three-dimensional) shapes of the body, including well-developed keels at their caudal peduncle, and the organisation and function of their axial body musculature (e.g. Bernal et al. 2001; Donley et al. 2004). However, whether or not Cooper et al.'s (2020) two-dimensional approach can adequately tease out the difference between ectothermic and endothermic fishes has never been examined.

The purpose of this paper is four-fold. First, we test whether the observed body forms of lamniform sharks are indeed influenced by thermophysiology (ectothermic vs. endothermic). Second, we

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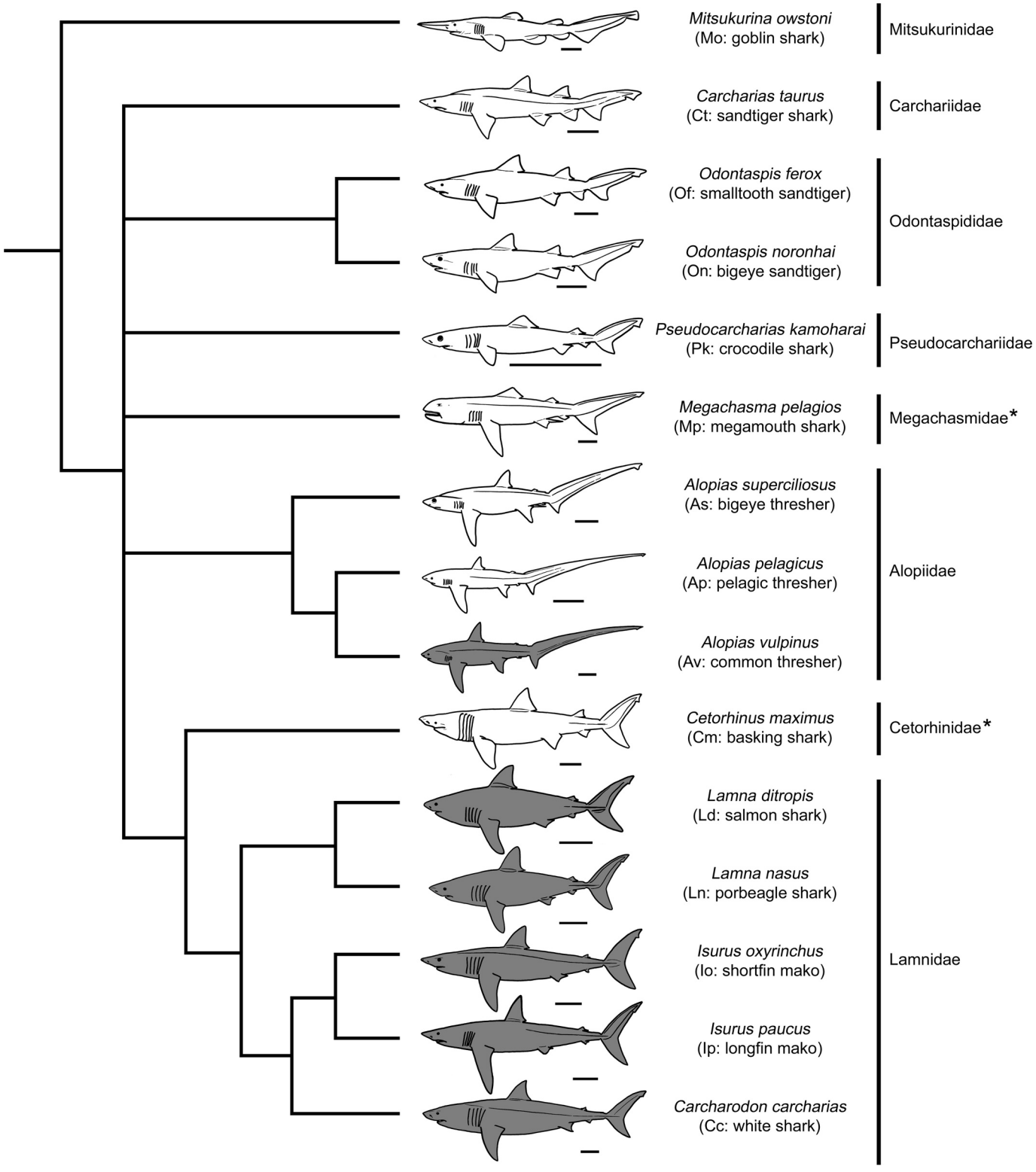

Figure 1. Fifteen extant species of Lamniformes (drawings after Ebert et al. 2013; scale bar = 50 cm) with current understanding of their phylogenetic interrelationships and family-level classification, along with two-letter abbreviation used in this study and vernacular name of each species in parentheses (phylogenetic arrangement reflects general synthesis among previous phylogenetic analyses based on trees complied by Stone and Shimada 2019). Species in grey denote those with regional endothermy; families with asterisk are planktivorous taxa.

provide critical evaluation of Cooper et al.'s (2020) proposed body form of *Otodus megalodon*. Third, we discuss the current understanding of the body form of *O. megalodon*. Fourth, we review the evolution of regional endothermy in Lamniformes. This study is significant because it provides renewed perspective on the biology of *O. megalodon* as well as the evolution of lamniforms.

Materials and methods

Our study uses a combination of analytical methods used by Cooper et al. (2020) and Sternes and Shimada (2020) (see below). However, for our samples, like the classic work on shark body forms by Thomson and Simanek (1977), who based their study using Bigelow and Schroeder's (1948) illustrations, we used Sternes and Shimada's (2020) strategy of applying geometric morphometrics to the body form of lamniform sharks illustrated in *Sharks of the World: A Fully Illustrated Guide* by Ebert et al. (2013). Although our method inherently gives only one 'sample' per species, the use of Ebert et al.'s (2013) standardised guidebook illustrations is interpreted to adequately serve the purpose of this study because they are specifically designed for species identification by depicting generalised characteristics of each species. In fact, using Ebert et al.'s (2013) illustrations is ideal because they include lateral drawings of adult sharks drawn by a single illustrator with a uniform method, including the left pectoral and pelvic fins that are consistently depicted to be ventrally directed in the most planar view possible (Sternes and Shimada 2020). The planar view of those fins is particularly important for morphometric analyses to eliminate potential artificial distortions of their outlines (vs. perceived fin and body outlines based on photographs of sharks taken under a broad range of specimen conditions: e.g., see Cooper et al.'s (2020) 'Data availability' file).

The illustrations of the 15 lamniform species (Figure 1) were scanned directly from Ebert et al.'s (2013) book, and tpsUtil64 (Rohlf 2015) was subsequently used to upload and organise all illustrations into an electronic storage folder. Landmarks were digitised using tpsDig232 (Rohlf 2015). To investigate lamniform body morphology, we conducted two sets of analyses. One set of analyses utilised the same morphometric landmarks used by Cooper et al.'s (2020), here referred to Analysis Set A, where our analyses examined the morphology of the following six attributes: 1) the whole (full) body (70 total landmarks including those along the fins); 2) precaudal body (i.e. head + trunk; 16 total landmarks excluding semilandmarks along the fins); 3) head region (10 homologous landmarks); 4) caudal fin (four homologous landmarks and 21 semilandmarks); 5) first dorsal fin (two homologous landmarks and 18 semilandmarks); and 6) pectoral fin (two homologous landmarks and 13 semilandmarks) (Figure 2(a)). The other set of analyses we conducted here referred to Analysis Set B, overall followed Sternes and Shimada's (2020) landmark scheme but some parts reflecting Cooper et al.'s (2020) scheme (Figure 2(b)). The scheme consists of 25 total homologous landmarks including the position of the eye, mouth, and the first gill slit included in Cooper et al.'s (2020) study, whereas we also added the morphometrics of the second dorsal, pelvic, and anal fins. Whereas our landmarks for the caudal fin (Figure 2(b)) are identical to those of Cooper et al. (2020) (Figure 2(a)), the major difference is that, similar to Sternes and Shimada's (2020), our precaudal body consists of 30 semilandmarks in equidistance delineating the curvature of its dorsal side as well as the curvature of its ventral side between the anterior-most point (homologous landmark 1) and the posterior-most point (homologous landmark 8 and 11, respectively) (Figure 2(b)). Our Analysis Set B consisted of two analyses: 1) the full body analysis that would also include the second dorsal, pelvic, and anal fins in order to capture the entire body form not conducted by Cooper et al. (2020); and 2) the 'modified' precaudal body analysis where the precaudal portion of the body would also include all the non-caudal fins.

Morphometric analyses were conducted using MorphoJ 1.07a (Klingenberg 2011). For each separate analysis, a Procrustes fit was performed to generate a covariance matrix. The Procrustes fit removes any differences in location, orientation and scale of each sample. The covariance matrix was then used to conduct each separate Principal Component Analysis (PCA) as well as each shape change analysis. After each PCA was produced, cluster analyses based on a simple clustering method, Unweighted Pair Group

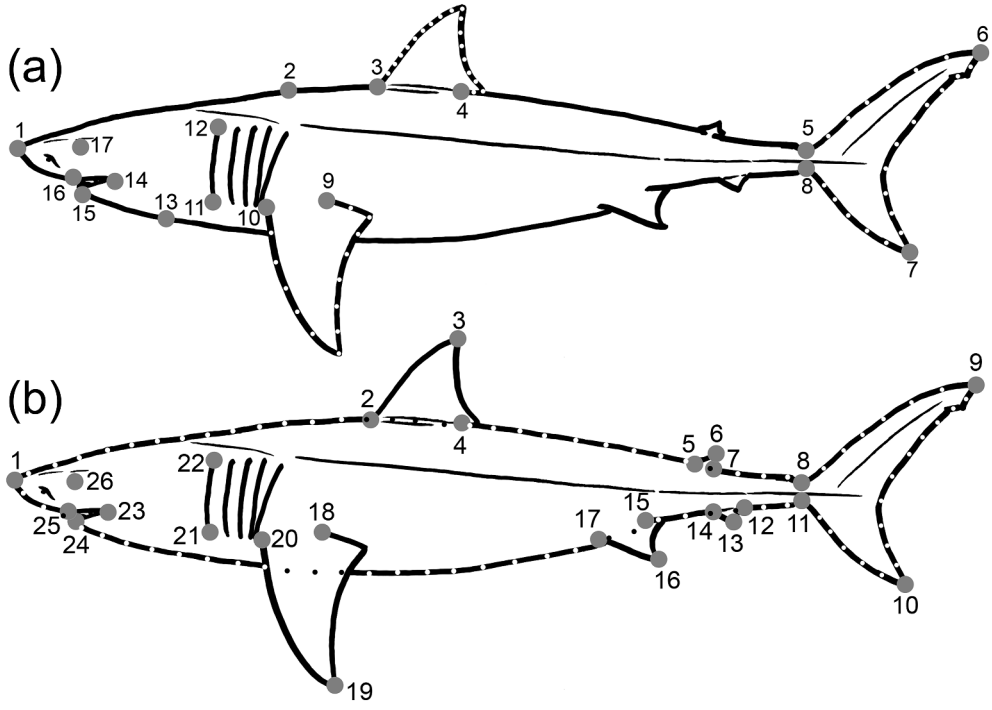

Figure 2. Drawings of extant white shark (*Carcharodon carcharias*) as an example showing homologous landmarks (large grey dots) and semilandmarks (small white or black dots) used in this study. (a) Landmarks based on Cooper et al. (2020) used for Analysis Set A in this study. (b) Landmarks based largely on Sternes and Shimada (2020) used for Analysis Set B in this study (see text for detail).

Table 1. Percent variation of first five principal components (PC1–PC5) from each analysis conducted in this study (A [Analysis Set A] = landmarks based on Cooper et al. 2020 [Figure 2(a)]; B [Analysis Set B] = landmarks based largely on Sternes and Shimada (2020) [Figure 2(b)]): FB = full body analysis; PB = precaudal body analysis; HR = head region analysis; CF = caudal fin analysis; DF = (first) dorsal fin analysis; PF = pectoral fin analysis; mPB = modified precaudal body analysis.

PC	A: FB	A: PB	A: HR	A: CF	A: DF	A: PF	B: FB	B: mPB
PC1	70.28	38.69	45.58	73.09	85.96	66.15	81.37	39.97
PC2	13.11	25.75	22.01	20.01	6.17	19.66	8.19	17.86
PC3	8.97	15.76	15.19	2.39	3.53	7.52	1.93	15.54
PC4	2.61	6.38	7.23	1.48	1.63	1.84	1.50	8.55
PC5	2.01	4.87	3.10	1.19	0.99	1.57	0.90	4.98

Method with Arithmetic Means (UPGMA), were performed based on Procrustes coordinates data from each morphometric analysis. For the cluster analyses, we used PAST (Paleontological Statistics: Hammer et al. 2001) to calculate Euclidian distances and to generate dendrograms of relatedness of each morphological part examined among the 15 lamniform species.

Results

Table 1 lists the percent variation of the first five principal components (PC1–PC5) of each of the eight analyses (six analyses in Analysis Set A and two analyses in Analysis Set B) conducted in this study. Because PC1 and PC2 together explain the majority of variation in all eight analyses (i.e. at least 57%, or at least about two-thirds, of the total variation), the relative contribution of principal components beyond PC2 is considered negligible for the purpose of this study. Thus, our discussion on our PCA focuses on the first two principal components, although it should be noted that the data used for our cluster analyses are independent of our PCA because each cluster tree is based on all landmark coordinates for each analysis.

Figure 3 shows the distribution of the 15 extant lamniform species in morphospace between PC1 and PC2 using Cooper et al.'s (2020) morphometric landmarks (Analysis Set A: Figure 2(a)) applied to: 1) the full body; 2) precaudal body; 3) head region; 4) caudal fin; 5) first dorsal fin; and 6) pectoral fin. Figure 4 shows the cluster trees displaying the relative similarities of taxa in terms of the six respective analyses in Figure 3. Figure 5 shows the distribution of the 15 extant lamniform species in morphospace between PC1 and PC2 using Sternes and Shimada's (2020) landmarks (Analysis Set B: Figure 2(b)) applied to the full body (Figure 5(a)) and 'modified' precaudal body (Figure 5(c)) along with their respective cluster tree (Figure 5(b,d)). Results of each of the eight analyses are described below.

Analysis set A

Full body analysis – PC1 and PC2 together capture 83.39% of the total variation (Table 1). PC1 explains 70.28% of the variation that is largely affected by the overall shape and aspect ratio of the caudal fin. Sharks with a highly symmetrical (= high aspect ratio) caudal fin have lower PC1 values compared to those with a more asymmetrical (= low aspect ratio) caudal fin. PC2 explains 13.11% of the variation that is greatly affected by the overall shape of the dorsal fins and the aspect ratio of the pectoral fin. Higher PC2 values are the result of tall, erect dorsal fins and a high aspect ratio of the pectoral fins, whereas lower PC2 values indicate shorter, rounded dorsal fins and a low aspect ratio of the pectoral fins. Both our full body analysis plotting the relationship between PC1 and PC2 (Figure 3(a)) and the cluster analysis (Figure 4(a)) show that there are three types of body forms among the lamniform sharks: 1) a cluster consisting of Lamnidae (*Lamna, Isurus*, and *Carcharodon*) and Cetorhinidae (*Cetorhinus*); 2) that containing *Mitsukurina, Carcharias, Odontaspis, Pseudocarcharias*, and *Megachasma*; and 3) that represented exclusively by Alopiidae (*Alopias*). Both the PCA and cluster tree show that ectothermic *Cetorhinus* closely occur with regionally endothermic lamnids, whereas regionally endothermic *Alopias vulpinus* closely occurs with the other two *Alopias* species that are ectothermic.

Precaudal body analysis – PC1 and PC2 together capture 64.44% of the total variation (Table 1). PC1 explains 38.69% of the total variation, and it is mainly affected by the depth of the head region. Sharks with a deeper head scored lower values compared to sharks with a shorter shallower head. PC2 explains 25.75% of the total variation. PC2 is loaded heavily on the rostral region of the shark, where sharks with an elongate rostrum scored low PC2 values compared to sharks with a short rostrum. In our PCA between PC1 and PC2 (Figure 3(b)), all taxa within Lamnidae (*Lamna, Isurus*, and *Carcharodon*) are clustered in one region of the morphospace, but no decisive clustering of taxa at the higher taxonomic levels (e.g. family) is discernible, including the fact that the two species of *Odontaspis* and *Alopias vulpinus* closely occur with lamnid species. Our cluster tree (Figure 4(b)) also shows ectothermic *Odontaspis* spp. and regionally endothermic *A. vulpinus* being nested among regionally endothermic lamnid species. It is also noteworthy that all three species of *Alopias* occur in separate clusters within the tree, that *Cetorhinus* is not clustered closely with lamnids but rather with *Pseudocarcharias* and *A. pelagicus*, and that *Mitsukurina* and *Megachasma* appear as outliers relative to other species.

Head region analysis – PC1 and PC2 together capture 67.59% of the total variation (Table 1). PC1 explains 45.58% of the variation. It mainly focuses on the rostrum of the sharks, where sharks with a short rostrum scored lower PC1 values relative to sharks with an elongated rostrum. PC2 explains 22.01% of the total variation observed, and it focuses on the location of the first gill slit of the sharks. Sharks with more anteriorly placed first gill slits scored lower PC2 values compared to sharks with more posteriorly placed first gill slits. In our PCA between PC1 and PC2 (Figure 3(c)), all taxa of Lamnidae (*Lamna, Isurus*, and *Carcharodon*) are clustered closely with *Carcharias taurus, Odontaspis* spp., *Alopias superciliosus*, and *A. vulpinus* without any obvious taxonomic pattern, whereas *Mitsukurina* and *Megachasma* appear as separate outliers. Our cluster tree (Figure 4(c)) also shows that *Mitsukurina* and *Megachasma* are quite different from each other as well as from the remaining lamniform taxa, which, more significantly, show no taxonomic patterns. For example, practically all species of all multispecies families (Odontaspididae, Alopiidae, and Lamnidae) occur in separate taxonomically heterogeneous clusters in the trees mixed with species of monospecific families other than Cetorhinidae, Mitsukurinidae, and Megachasmidae. A rather widely scattered arrangement of lamnid species also means that decisive clustering of species with regional endothermy is absent in the tree.

Caudal fin analysis – PC1 and PC2 together capture 93.1% of the total variation (Table 1). PC1 explains 73.09% of the variation and is heavily loaded on both the overall symmetry and aspect ratio of the caudal fin. Sharks with a highly asymmetrical (= low aspect ratio) caudal fin scored lower PC1 values, whereas sharks with a highly symmetrical (= high aspect ratio) caudal fin scored higher values. PC2 explains 20.01% of the total variation, and it primarily focuses on the depth of the upper lobe of the caudal fin. Sharks with a narrower upper lobe scored higher PC2 values compared to sharks with a deeper upper lobe. Like the full body analysis (Figures 3(a), 4(a)), both the PCA and cluster tree of our caudal

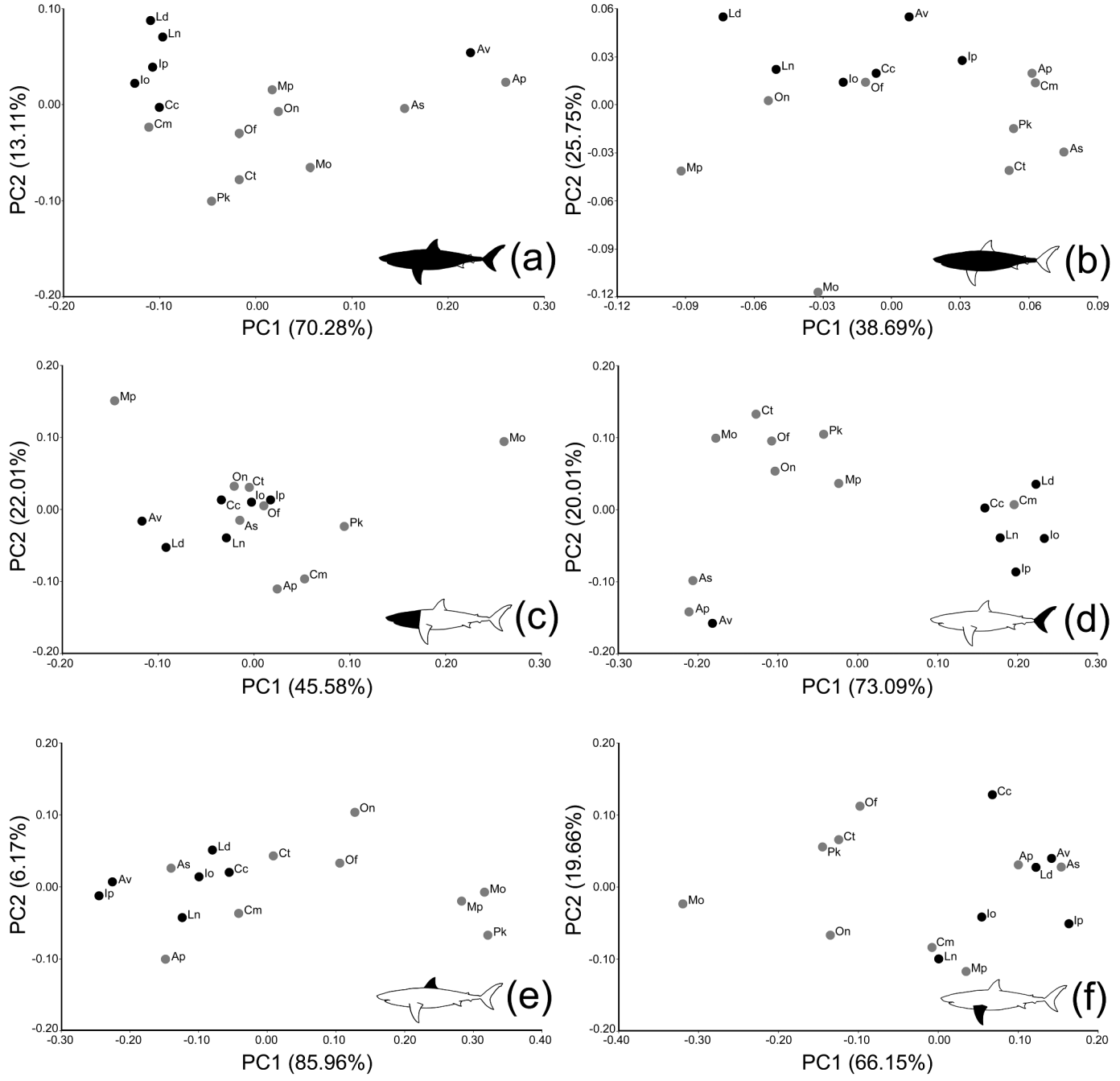

Figure 3. Principal component analyses showing morphological distributions of 15 extant species of Lamniformes (for abbreviations of taxa, see Figure 1) by body parts based on Cooper et al.'s (2020) landmark scheme (Figure 2(a)). (a) Full body analysis. (b) Precaudal body analysis. (c) Head only analysis. (d) Caudal fin analysis. (e) First dorsal fin analysis. (f) Pectoral fin analysis. Percentage in parentheses in each axis denotes percent variation explained by that principal component (PC1 or PC2). Grey plots denote ectothermic species, and black plots denote species with regional endothermy.

fin analysis (Figures 3(d), 4(d)), three types of caudal fin forms are found among the lamniform sharks: 1) a cluster consisting of Lamnidae (*Lamna, Isurus*, and *Carcharodon*) and Cetorhinidae (*Cetorhinus*); 2) that containing *Mitsukurina, Carcharias, Odontaspis, Pseudocarcharias*, and *Megachasma*; and 3) that represented exclusively by Alopiidae (*Alopias*). These taxonomic arrangements mean that regionally endothermic lamnids occur closely with ectothermic *Cetorhinus*, but not with regionally endothermic *Alopias vulpinus*.

First dorsal fin analysis – PC1 and PC2 together capture 92.13% of the total variation (Table 1). PC1 explains 85.96% of the total variation, where sharks with short, rounded dorsal fins scored higher PC1 values than those with a tall, erect dorsal fin. PC2 explains 6.17% of the total variation, and it mainly focused on the apex of the dorsal fin. Sharks with a sharp, pointed dorsal fin scored lower PC2 values relative to sharks with a more rounded dorsal fin apex. Both the PCA and cluster tree of our first dorsal fin analysis (Figures 3(e), 4(e)) show two major clusters: 1) one cluster consisting of Alopiidae, Carchariidae, Cetorhinidae, Lamnidae, where ectothermic species are mixed with regionally endothermic species with no specific pattern; and 2) that consisting of the remaining taxa (Mitsukurinidae, Megachasmidae, Odontaspididae, and Pseudocarchariidae) that are exclusively of ectothermic taxa.

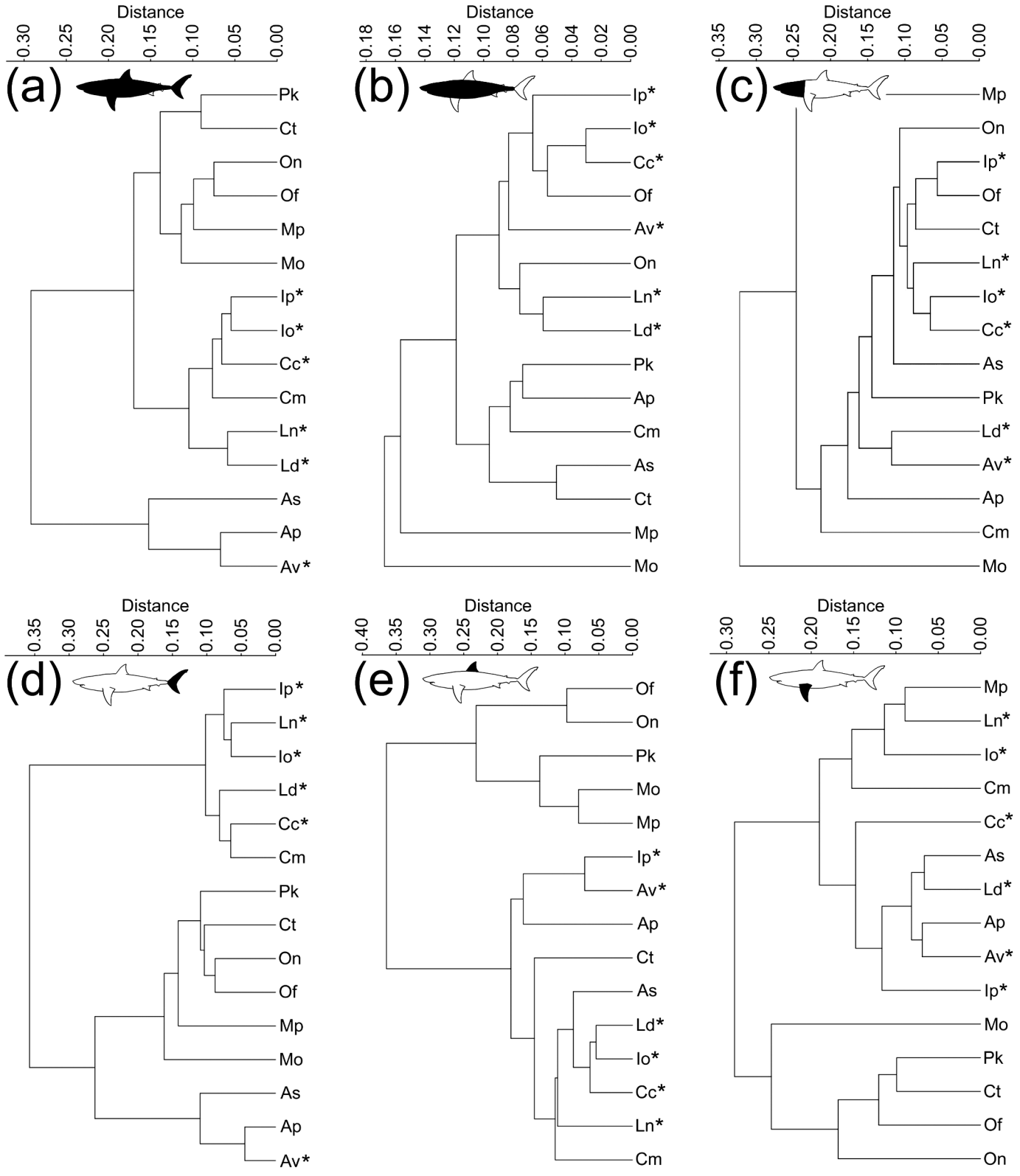

Figure 4. Cluster trees showing relative morphological similarities among 15 extant species of Lamniformes (for abbreviations of taxa, see Figure 1) by body parts using morphometric coordinates based on Cooper et al.'s (2020) landmark scheme (Analysis Set A: Figure 2(a)). (a) Full body analysis. (b) Precaudal body analysis. (c) Head region analysis. (d) Caudal fin analysis. (e) First dorsal fin analysis. (f) Pectoral fin analysis. Species denoted by asterisk are those with regional endothermy.

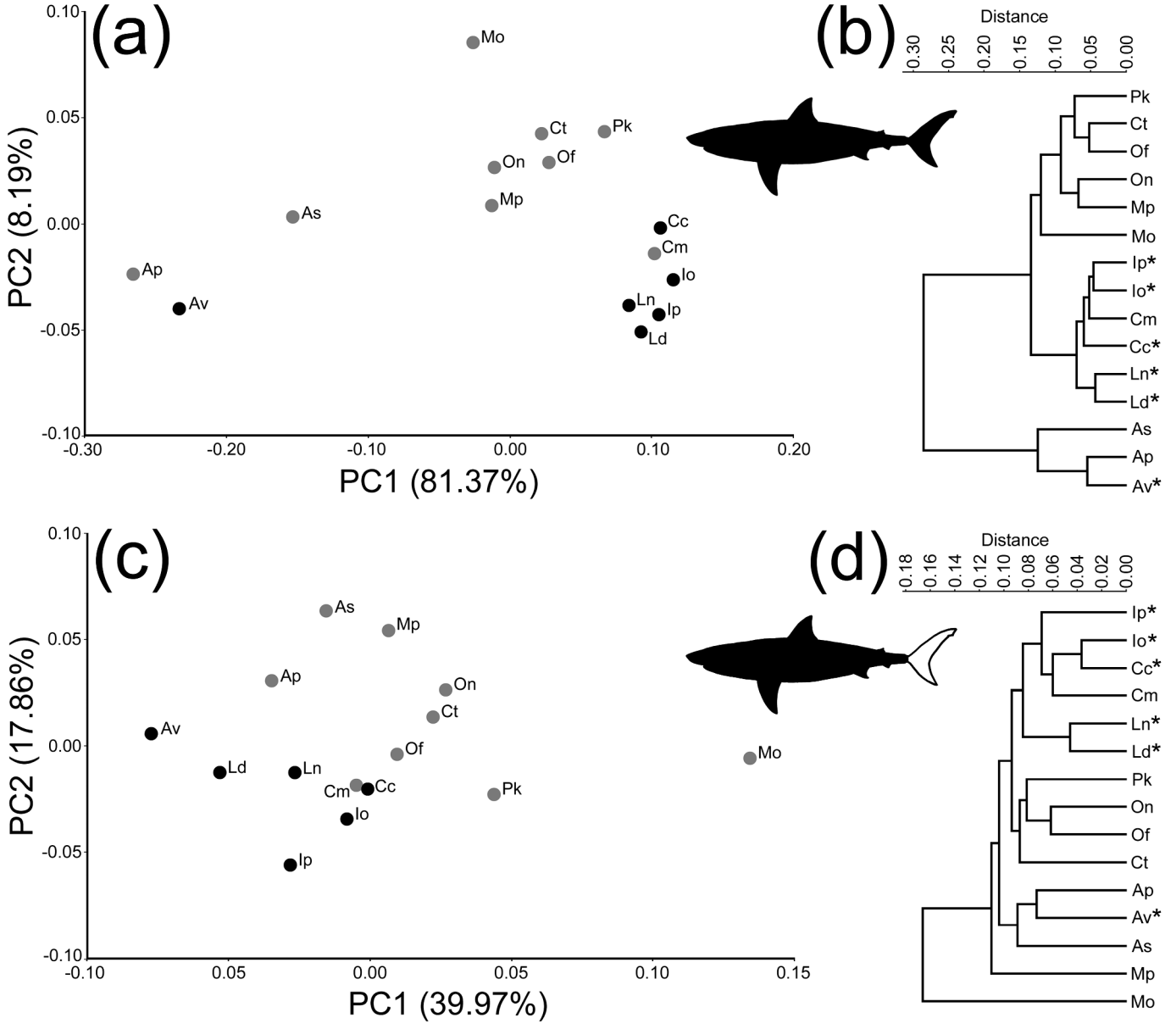

Figure 5. Scatter plot diagrams and cluster trees showing morphological distribution and similarities of 15 extant species of Lamniformes (for abbreviations of taxa, see Figure 1) using landmarks in terms of full body ((a) and (b)) and modified precaudal body ((c) and (d)) based largely on Sternes and Shimada's (2020) landmark scheme (Analysis Set B: Figure 2(b)). Percentage in parentheses in each axis of scatter plot diagrams denotes percent variation explained by that principal component (PC1 or PC2). In scatter plot diagrams, grey plots denote ectothermic species, and black plots denote species with regional endothermy, whereas species with regional endothermy in cluster trees are indicated by asterisks.

Pectoral fin analysis – PC1 and PC2 together capture 85.81% of the total variation (Table 1). PC1 explains 66.15% of the variation, and it mainly focuses on the aspect ratio of the pectoral fin. Sharks with a high aspect ratio of the pectoral fin scored higher PC1 values compared to sharks with a low aspect ratio of the pectoral fin. PC2 explains 19.66% of the total variation, and it mainly focuses on the posterior margin of the pectoral fin. Sharks possessing pectoral fins with a relatively shorter posterior margin scored higher PC2 values compared to sharks having pectoral fins with a longer posterior margin. Similar to our first dorsal fin analysis (Figures 3(e), 4(e)), the PCA and cluster tree of our pectoral fin analysis (Figure 3(f), 4(f)) show two major clusters: 1) one cluster consisting of Alopiidae, Cetorhinidae, Megachasmidae, Lamnidae, where ectothermic species are mixed with regionally endothermic species without any particular pattern; and 2) that consisting of the remaining taxa (Carchariidae, Mitsukurinidae, Odontaspididae, and Pseudocarchariidae) that are exclusively of ectothermic taxa.

Analysis set B

Full body analysis – PC1 and PC2 together capture 89.56% of the total variation (Table 1). PC1 explains 81.37% of the variation, and it heavily focuses on the symmetry and aspect ratio of the caudal fin. Sharks with a more symmetrical (= high aspect ratio) caudal fin scored higher PC1 values, whereas sharks with an asymmetrical (= low aspect ratio) caudal fin scored lower PC1 values. PC2 explains 8.19% of the variation, and it primarily focuses on both the first dorsal and pectoral fins. Sharks with longer dorsal and pectoral fins

scored lower PC2 values compared to sharks with shorter, more rounded dorsal and pectoral fins. Consistent with the full body analysis of Analysis Set A (Figure 3(a), 4(a)), the PCA and cluster trees based on the full body analysis of our Analysis Set B (Figure 5 (a,b)) yield three types of body forms among the lamniform sharks: 1) that consisting of Cetorhinidae and Lamnidae; 2) that comprising Carchariidae, Mitsukurinidae, Megachasmidae, Odontaspididae, and Pseudocarchariidae; and 3) that represented exclusively by Alopiidae. Both the PCA and cluster tree show that regionally endothermic lamnids are closely clustered with ectothermic *Cetorhinus* but not with regionally endothermic *Alopias vulpinus*.

Modified precaudal body analysis – PC1 and PC2 together capture 57.83% of the total variation (Table 1). PC1 explains 39.97% of the total variation. It focuses on both the first dorsal and pectoral fins as sharks with more elongate first dorsal and pectoral fins scored lower PC1 values compared to sharks with shorter first dorsal and pectoral fins. PC2 explains 17.86% of the variation, and it is mainly dependent on the location of the first dorsal fin. Sharks with a more anteriorly placed first dorsal fin scored lower PC2 values compared to sharks with a more posteriorly placed first dorsal fin. Our PCA between PC1 and PC2 (Figure 5(c)) shows the following three plot distributions: 1) all alopiids occur in the top left area of the morphospace; 2) Cetorhinidae is clustered closely with all the lamnid species in the bottom left area of the morphospace; and 3) all other lamniform taxa occur in the morphospace to the right side of the area occupied by alopiid, cetorhinid, and lamnid taxa, while *Mitsukurina* is placed far to the right as an outlier. In addition, all species with regional endothermy (*Alopias vulpinus* and all lamnids) are clustered towards the bottom left corner of the morphospace. Our cluster analysis (Figure 5(d)) reveals that the modified precaudal body shapes take on three different forms besides *Mitsukurina* and *Megachasma* being outliers: 1) a group consisting of Cetorhinidae and Lamnidae; 2) that comprising Carchariidae, Megachasmidae, Odontaspididae, and Pseudocarchariidae; and 3) that represented only by Alopiidae. The groupings based on our cluster analysis reveal that regionally endothermic lamnids are not closely clustered with regionally endothermic *A. vulpinus*, where ectothermic *Cetorhinus* is nested deeply among the lamnids.

Discussion

Is thermophysiology an evolutionary driver for the lamniform body plan?

Previous studies that demonstrated the similarity in body form across phylogenetically distant groups of endothermic fast-swimming fishes (e.g. between lamnids and tunas) primarily focused on the examination of transverse cross-sectional (i.e. three-dimensional) shapes of their body and body muscle organisation and function (e.g. Bernal et al. 2001; Donley et al. 2004). To reconstruct the body form of *Otodus megalodon* that is interpreted to be endothermic, Cooper et al. (2020), on the other hand, used a two-dimensional approach without testing whether such a method can differentiate endothermic lamniforms from ectothermic lamniforms in the first place. If endothermic lamniforms have a similar body plan that is fundamentally different from ectothermic lamniform sharks, the following two conditions should be expected from our analyses. First, all endothermic taxa (i.e. *Alopias vulpinus* and all five extant lamnid species) should be clustered closer together in our PCAs and cluster trees. Second, those endothermic taxa should be clearly separated from any of the ectothermic taxa.

In our study, specific PCAs that show all six endothermic lamniform species clustered closely together are on the precaudal body, head only, dorsal fin, and pectoral fin (Figures 3(b,c,e,f), 5(c)). Those PCAs that do not cluster the six are the full body and caudal fin analyses, where *Alopias vulpinus* occur closely with the other two *Alopias* species, that are far apart from the five lamnid plots (Figure 3(a,d), 5(a)). Although this result is not necessarily surprising because of the highly elongated caudal fin in *Alopias* spp., it is important to point out that none of our PCAs show any clear separation of the endothermic taxa from ectothermic taxa. Specifically, at least one of the following ectothermic species always occur together with the endothermic taxa in our PCAs: *Odontaspis* spp., *Carcharias taurus, A. pelagicus*, and/or *A. superciliosus* (Figures 3(b,c,e,f),5(c)). It is particularly noteworthy that when the five lamnid species cluster together without *A. vulpinus*, the ectothermic *Cetorhinus maximus* always occurs closely with the five lamnids (Figures 3(a,d),5(a)).

The lack of any relationship between thermophysiology and body form in lamniforms is even more evident in our cluster analyses. For example, none of our cluster analyses places the six endothermic species into an exclusive branch (Figures 4,5(b,d)). Even for cluster trees with the five lamnid species closely gathered together, *Cetorhinus maximus* also always occurs with them (Figures 4(a,d),5(b,d)).

It is important to note that *Cetorhinus maximus* is phylogenetically sister to Lamnidae (Figure 1) – a well-established systematic relationship based on multiple molecular and morphological studies (see Stone and Shimada 2019, and references therein). Therefore, along with a separate clustering of the three *Alopias* spp., the close clustering of *C. maximus* with the five lamnid species in some of our analyses (Figures 3(a,d), 4(a,d),5(a,b,d)) likely represents a signal from their phylogenetic history, rather than a thermophysiological signal.

Table 2 summarises our interpretations about the relative contribution between thermophysiology and phylogeny on body form in extant lamniforms based on each morphometric analysis conducted in this study. The most important finding is the fact that none of our analyses shows any thermophysiological signal. On the other hand, strong phylogenetic influence was detected in both the full body and caudal fin data of Analysis Set A as well as the full body and modified precaudal body data of Analysis Set B. However, the cluster analysis on modified precaudal body data where all three *Alopias* species are clustered together and are well separated from all the lamnids (Figure 5 (d)) suggests that the removal of the caudal fin from *Alopias* spp. apparently does not make the precaudal body any similar to lamnids or any other lamniforms. This observation indicates

Table 2. Interpretations about relative contribution between thermophysiology and phylogeny on body form in extant lamniforms based on each morphometric analysis conducted in this study (A [Analysis Set A] = landmarks based on Cooper et al. 2020 [Figure 2(a)]; B [Analysis Set B] = landmarks based largely on Sternes and Shimada (2020) [Figure 2(b)]): FB = full body analysis; PB = precaudal body analysis; HR = head region analysis; CF = caudal fin analysis; DF = (first) dorsal fin analysis; PF = pectoral fin analysis; mPB = modified precaudal body analysis.

Signal type	A: FB	A: PB	A: HR	A: CF	A: DF	A: PF	B: FB	B: mPB
Thermophysiological	No	No	No	No	No	No	No	No
Phylogenetic	Yes	No	No	Yes	No	No	Yes	Yes

that the elongation of the caudal fin has fundamentally modified the precaudal body properties of *Alopias* spp., including the endothermic *A. vulpinus*.

Lamnids do have a similar body plan as demonstrated by Cooper et al. (2020), and our study certainly does not imply *Alopias* or *Cetorhinus* to be a suitable body form analogue for *Otodus megalodon*. It should also be noted that our study relies on the quality of illustrations used (Ebert et al. 2013), where individual variation in body form should be explored further, including ontogenetic changes (see below). However, the lack of a unique body plan among endothermic lamniforms that is essentially different from ectothermic lamniforms in our study indicates the underlying premise of Cooper et al.'s (2020) study – that their two-dimensional approach would decisively allow the elucidation of an endothermic body plan to reconstruct the body dimensions of *O. megalodon* – to be fundamentally flawed.

Previously proposed body form of Otodus megalodon

The body form of *Otodus megalodon* remains speculative because of the lack of any complete skeleton of the species in the fossil record, although the extant *Carcharodon carcharias* has traditionally been envisioned to be a reasonable model for *O. megalodon* (Gottfried et al. 1996). For this reason, Cooper et al.'s (2020) study was novel in that 1) they considered the entire Lamnidae as a model taxon for *O. megalodon*, and 2) attempted to reconstruct the body form of the extinct shark quantitatively. However, besides the fact that there are no decisive body forms unique to endothermic lamniform sharks based on our analyses (see above), there are additional shortcomings in Cooper et al.'s (2020) studies, which make their body form restoration for *O. megalodon* questionable.

Traditionally, extant *Carcharodon carcharias* has been used as a logical comparative model to infer the biology and size of *Otodus megalodon* because *C. carcharias* is the largest extant macrophagous lamniform and is the only extant lamniform with large serrated teeth indicative of a similar diet as *O. megalodon* (e.g. Randall 1973; Gottfried et al. 1996; Razak and Kocsis 2018; Shimada 2019). Cooper et al. (2020), who used the entire family Lamnidae instead as the ecological and physiological analogue to *O. megalodon*, noted that the reliance on *C. carcharias* as the only analogue for *O. megalodon* is potentially problematic because the two species

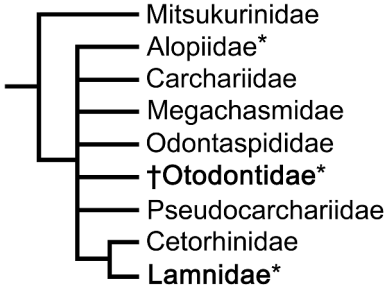

Figure 6. Simplified family-level lamniform phylogeny showing all extant clades (cf. Figure 1) and likely systematic position of Otodontidae that includes *Otodus megalodon* (dagger [†] indicates extinct). A large portion of the phylogenetic tree remains unresolved due to conflicting results based on various molecular and morphological studies (see Stone and Shimada 2019). Although the placement of Otodontidae is tentative and other extinct families are not depicted in this tree, the main points of this illustration are to demonstrate that: 1) Otodontidae lies outside of Lamnidae (both clades highlighted in bold letters); and 2) clades containing one or more species with regional endothermy (indicated by asterisk [*]) do not share an immediate common ancestry where all other depicted clades are ectothermic (Note: It is important to highlight the fact that only one of the three extant species in Alopiidae, *Alopias vulpinus*, exhibits regional endothermy).

likely belong to different families where the phylogenetic position of *Otodus* within Lamniformes remains uncertain (Figure 6). Yet, it is important to point out that their use of Lamnidae as a modern analogue does not necessarily solve this matter. They attempted to justify their approach by noting that 'the five chosen analogue taxa possess tooth morphologies similar to various otodontids, suggesting similar diet and ecology' (p. 6) and went on stating that '*L. nasus* is considered the best dental analogue for both *Cretalamna* and *Megalolamna*, mako sharks (*Isurus* spp.) have similar dental morphology to *Otodus*, and *C. carcharias* has similar dentition to *Otodus* (*Carcharocles*) and *Otodus* (*Megaselachus* [including *O. megalodon*: Cappetta 2012])' (p. 6). If their rationale is used especially where lamnid species are invariably regionally endothermic, however, it is arguably more logical to consider *Lamna* spp. as the best modern analogue for *Cretalamna* and *Megalolamna, Isurus* spp. for *Otodus* with unserrated teeth, and like in the past (Gottfried et al. 1996; Razak and Kocsis 2018; Shimada 2019), *C. carcharias* for *Otodus* with serrated teeth. In fact, their proposed body form for *O. megalodon* based on the combined morphometric information from the five extant lamnids should be regarded as the generalised 'lamnid body plan' where their logic of its applicability to *O. megalodon* is not necessarily any better than the logic of using extant *C. carcharias* as a modern analogue for the fossil species (e.g. Gottfried et al. 1996).

At least on the basis of a two-dimensional morphometric approach, the direct application of the lamnid body plan to *Otodus megalodon* is particularly questionable considering the strong influence of phylogeny determining the body forms of lamniforms based on our study (Table 2), where *O. megalodon* indeed does not share an immediate common ancestry with Lamnidae (Figure 6). Although Cooper et al. (2020) correctly recognised that *O. megalodon* does not belong to Lamnidae but rather to Otodontidae, their phylogenetic framework used is also uncertain based on their statement that both Lamnidae and Otodontidae are 'believed to have evolved from the family Cretoxyrhinidae' (p. 6). This is an unsubstantiated or outdated claim, where the stratigraphic ranges of these taxa do not corroborate it. For example, the oldest fossil record for both Otodontidae and Cretoxyrhinidae are in the Early Cretaceous (Albian) (Cappetta 2012; Shimada et al. 2017), so stating that Otodontidae was derived from Cretoxyrhinidae is dubious, especially because a sister relationship between the two extinct families has not even been determined yet. Furthermore, Cretoxyrhinidae is a Cretaceous taxon, and Lamnidae is a Cenozoic taxon, and because the present fossil record suggests that Cretoxyrhinidae became extinct before the end of the Cretaceous (mid-Campanian: e.g. Ikejiri et al. 2020), Lamnidae could not have evolved from Cretoxyrhinidae.

Cooper et al. (2020) stated that they utilised the extant phylogenetic bracketing technique, a phylogenetic approach using a monophyletic group of fossil and extant taxa to infer unfossilised features in a fossil taxon from anatomical correlates universally present in extant taxa represented in the cladogram (Witmer 1995). For this approach to work, the fossil taxon in question must be nested within extant clades without any exclusion or omission of certain taxa. Although much of the systematic relationships among lamniform taxa is still in debate due to conflicting results (see Stone and Shimada 2019), Cooper et al.'s (2020) study involved only two clades, *Otodus megalodon* (or Otodontidae) and extant Lamnidae, where the fossil taxon lies outside of Lamnidae (Figure 6). In short, Cooper et al. (2020) could not have bracketed *O. megalodon* (or Otodontidae) with the extant lamnids if the technique was used properly. If the bracketing process also involved all other extant lamniform clades dominated by ectotherms, they then could not have constrained

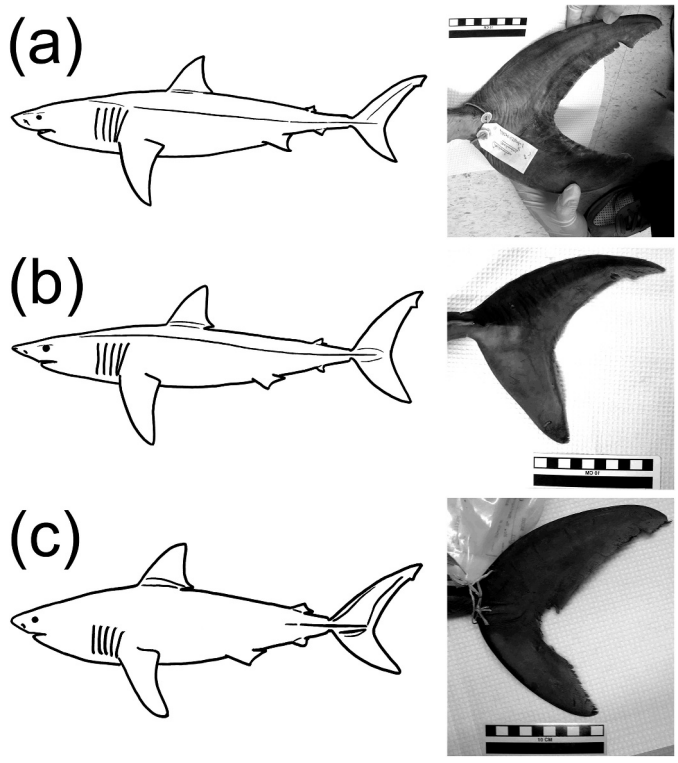

Figure 7. Three representative extant members of Lamnidae showing body outline of adults (after Ebert et al. 2013) (left; not to scale) along with caudal fin of neonates (right; scale = 10 cm). (a) *Carcharodon carcharias* (white shark) with photograph of caudal fin of 126-cm male (LACM 43805–1, Natural History Museum of Los Angeles, California, USA; image reversed). (b) *Isurus oxyrinchus* (shortfin mako) with photograph of caudal fin of 89-cm female (UMMZ 177116, Museum of Zoology, University of Michigan, Ann Arbor, USA; image reversed). (c) *Lamna ditropis* with photograph of caudal fin of 79-cm female (USNM 201731, United States National Museum of Natural History, Washington, D.C., USA). Note rounded upper caudal fin lobe that is directed posteriorly in neonates compared to adults with less curved upper lobe directed dorsoposteriorly.

O. megalodon (or Otodontidae) to be a regional endotherm or having their proposed body dimensions. Hence, their claim of the use of the extant phylogenetic bracketing technique is also questionable.

Using the extant lamnids as collectively a reasonable analogue of *Otodus megalodon*, Cooper et al. (2020) conducted morphometric analyses of their body parts and found no evidence of allometry in lamnids. It should be pointed out that this finding is at odds with a previous morphometric study on the caudal fin of *Carcharodon carcharias*, showing negative allometry (Lingham-Soliar 2005). In addition, significant morphological changes through ontogeny are also well documented in yet another study on the caudal fin morphology of *C. carcharias* starting in the embryonic stage and into the neonate stage where it is quite different from non-neonate juveniles and adults (Tomita et al. 2018) (Figure 7(a)). Although formal review and analyses await, substantial differences in caudal fin morphology between neonates and adults are also evident in *Isurus* and *Lamna* where their neonates have a more rounded, dorsoventrally shallower caudal fin than adults (Figure 7(b,c)). Therefore, whether Cooper et al.'s (2020) reconstructed body form of *O. megalodon* can also be applicable to neonates needs additional support.

Current understanding of body form of Otodus megalodon

Multiple studies based on teeth have indicated that *Otodus megalodon* reached at least 15 m in total length (Pimiento and Balk 2015; Shimada 2019; Perez et al. 2021). Besides its gigantic teeth, *O. megalodon* is known from some isolated and associated vertebral specimens that are also indicative of its large body size (e.g. Uyeno and Sakamoto 1984; Gottfried et al. 1996; Kent 2018). The best-preserved vertebral specimen in particular consists of approximately 150 centra from an individual collected from the Miocene of Belgium (Gottfried et al. 1996; Shimada et al. 2021). However, it is difficult to interpret the body form from the specimen because not all centra from the original vertebral column are represented and no teeth were associated with them that would offer the proportional relationship of its dentition with the body. Therefore, the body form of *O. megalodon* can only be speculated at the present time.

Building on Thomson and Simanek's (1977) pioneer work on the body forms of sharks, Sternes and Shimada (2020) investigated the diversity of body forms in nearly all the known (ca. 470) extant shark species using landmark-based geometric morphometric analyses. Their study, that is nearly equivalent to the full body analysis of Analysis Set A here, revealed that there are two major body forms in sharks, one characterised as a 'shallow-bodied' form (Group A) and another a 'deep-bodied' form (Group B) (Figure 8), which are generally correlated with different swimming modes. Specifically, Group A sharks are predominantly anguilliform swimmers, many of which are benthic, whereas Group B sharks are represented by pelagic carangiform and thunniform swimmers. All lamniform species belong to Group B, where the three species of *Alopias* including *A. vulpinus*, are uniquely situated within the morphospace because of their exceptionally elongate caudal fin (Figure 8). Although all five lamnid species are closely clustered together, it is important to note that *Cetorhinus maximus* and some ectothermic non-lamniform shark species (i.e. plots adjacent to *Lamna ditropis* as well as *Isurus* spp. and *Carcharodon carcharias*) occupy the same

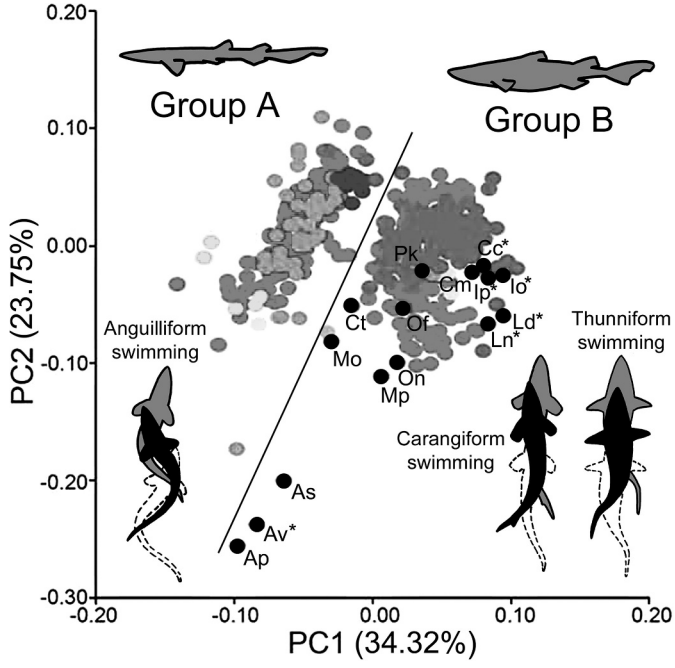

Figure 8. Scatter plot diagram of Sternes and Shimada's (2020, figures 3(b), 5) full body analysis showing division (line) between Group A and Group B sharks discussed in their paper as well as in this paper (solid black plots = lamniforms [see Figure 1 for species codes; asterisks indicate species with regional endothermy]; plots in different shades of grey = non-lamniform sharks by different taxonomic orders [for detail, see Sternes and Shimada 2020). Top two silhouette images of sharks in lateral view represent respective generalised body form of taxa located at approximate centre of each of the two main clusters of plots. Bottom three silhouette images of sharks illustrate three swimming modes in dorsal view and their general distribution by body form group (see Sternes and Shimada 2020).

region as the lamnid morphospace. It is also important to point out that there are many non-lamniform species that share the morphospace with non-alopiid lamniforms. Given the plot distribution, results of this present study, and the fact that *Otodus megalodon* does not belong to Lamnidae or Alopiidae, it is tempting to consider the possibility that the body form of *O. megalodon* could have been situated somewhere within the total morphospace defined by all these 15 extant lamniform taxa. However, it is also possible that *O. megalodon* could have occupied a unique position not represented by any of the extant shark species (e.g. a scenario exemplified by the recent discovery of a putative planktivorous lamniform with a remarkably peculiar body morphology for sharks: Vullo et al. 2021). This is plausible given that *O. megalodon* had a uniquely large body size for macrophagous lamniforms with exceptionally gigantic serrated teeth (Shimada et al. 2020).

Cooper et al.'s (2020) intent and effort are commendable, where their logic of considering the entire Lamnidae as the ecological and physiological analogue to *O. megalodon* is as reasonable as the traditional approach of using the extant *Carcharodon carcharias* as a living analogue for *O. megalodon* (e.g. Gottfried et al. 1996). Although it is still entirely possible that *O. megalodon* could have indeed resembled the extant *C. carcharias* or lamnids, however, all previously proposed body forms for *O. megalodon* should be regarded as speculations (Figure 9) because there are no scientific means to decisively support or refute the accuracy of any of them. Any meaningful discussion on this specific topic would require the discovery of much better-preserved fossil specimens than what are presently known in the fossil record of *O. megalodon*.

Comments on the evolution of lamniform endothermy

The centre of this present study concerns the thermophysiology in lamniform sharks, where the evolution of regional endothermy in certain lamniform taxa, including *Otodus megalodon*, has received considerable attention in recent years (Ferrón 2017; Shimada et al. 2020). Cooper et al. (2020) also made comments about the origin of regional endothermy within Lamniformes. However, their interpretation is not parsimonious and needs clarification.

Cooper et al. (2020) stated that the endothermy in Lamniformes 'had likely evolved once in the Cretaceous' (p. 6) by citing a previous work by Pimiento et al. (2019). However, this proposition must be viewed as highly tentative especially because Pimiento et al. (2019) also found its analysis to be sensitive to inclusion or exclusion of fossil taxa used especially regarding the origin of regional endothermy. In particular, the dataset used in their study contained only seven fossil lamniform genera where the geologically oldest taxon (*Cretalamna* in the Cretaceous) among the seven genera coded as 'mesothermic' (= regionally endothermic) is likely responsible for the sensitivity and possible deceptive appearance of regional endothermy as an ancestral state for the clade that included the vast majority of lamniforms dominated by ectothermic taxa. Besides the five lamnid species and *Alopias vulpinus* (Figure 1), the Late Cretaceous *Cretoxyrhina mantelli* (Cretoxyrhinidae) and Otodontidae including *Otodus megalodon* are also thought to have exhibited regional endothermy (Ferrón 2017). The phylogenetic position of neither Cretoxyrhinidae nor Otodontidae is resolved, but the evolution of regional endothermy in *A. vulpinus* and Lamnidae is generally regarded as convergent (Dickson and Graham 2004; Sepulveda et al. 2005) because these two clades do not share an immediate common ancestry (Stone and Shimada 2019, and references therein; Figure 1). Independent acquisitions of such a complex thermophysiological trait in multiple lamniform clades seem less parsimonious. However, it must be pointed out that the 'regional endothermy single-origin hypothesis' for Lamniformes actually involves more evolutionary steps than the 'regional endothermy multiple-origin hypothesis' because it would imply independent losses of regional endothermy (evolutionary reversals to become ectothermic) in more clades than clades represented by regional endotherms even if only the 15 extant lamniform species are considered (Figure 1). Where the evolution of warm-bloodedness is apparently quite plastic with many examples of convergence among diverse vertebrates even beyond Lamniformes (Legendre and Davesne 2019), it is therefore more parsimonious to consider regional endothermy to have arisen in multiple clades independently through lamniform phylogeny.

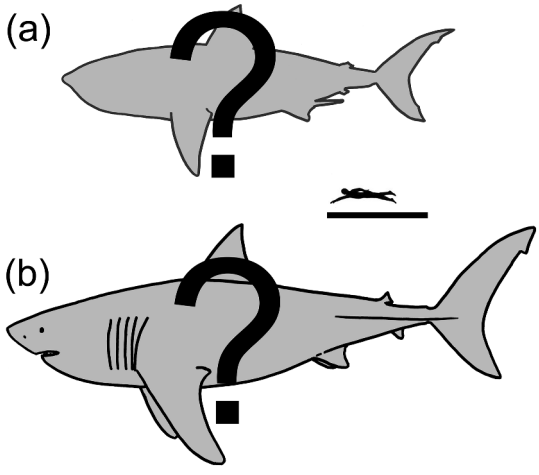

Figure 9. Examples of previously proposed body form of *Otodus megalodon* where question-marks denote uncertainty of morphological accuracy. (a) Body outline of 11-m-long male individual proposed by Gottfried et al. (1996, figure 7). (b) Body form of 16-m-long female(?) individual proposed by Cooper et al. (2020, figure 2 (d)). Scale bar = 3 m; swimmer = size of typical adult human for comparison.

Conclusions

We examined whether a two-dimensional approach employed by Cooper et al. (2020) can adequately tease out the difference between ectothermic and endothermic fishes. Although the five endothermic lamnid species closely gathered together in many of our analyses, the three *Alopias* spp. that include both endothermic and ectothermic taxa occurred as a separate cluster and the ectothermic *Cetorhinus maximus* always occurred with the lamnids. Because *C. maximus* is phylogenetically sister to Lamnidae, our study strongly suggests that one must not neglect the contribution of phylogeny on the evolution of body forms in sharks. In summary, our study demonstrates that two-dimensional geometric morphometrics cannot decisively tease out the endothermic lamniforms from ectothermic lamniforms, implying that the underlying premise of Cooper et al.'s (2020) analysis is invalid.

There are additional shortcomings in Cooper et al.'s (2020) study. They include their uncertain phylogenetic framework used, dubious application of the extant phylogenetic bracketing technique, and questionable finding about the lack of allometry in lamnids. Although their proposed body form can be viewed as a generalised, non-neonate lamnid body plan, these shortcomings make the accuracy of their proposed body dimensions for *O. megalodon* doubtful.

Otodus megalodon most certainly reached at least 15 m in total length based on its gigantic teeth (Shimada 2019; Perez et al. 2021). Besides teeth, *O. megalodon* is also known from some isolated and associated vertebral specimens. It is entirely possible that *O. megalodon* could have indeed resembled the extant

C. carcharias (e.g. Gottfried et al. 1996) or lamnids (Cooper et al. 2020). However, the body form of *O. megalodon* can only be speculated based on the present fossil record, where there are no scientific means to decisively support or refute the accuracy of any of the previously published body forms of the fossil species (Figure 9). The discovery of much better-preserved fossil specimens of *O. megalodon* than what are presently known in the fossil record is needed for any meaningful discussion on its body form.

Cooper et al. (2020) noted that the regional endothermy had likely evolved in Lamniformes only once in the Cretaceous by referring to a previous work by Pimiento et al. (2019). However, this view must be considered highly tentative. Besides the sensitivity and a small number of examined fossil taxa involved in Pimiento et al.'s (2019) study, the currently understood lamniform phylogeny suggests that multiple independent acquisitions of regional endothermy in separate lamniform clades are a more parsimonious interpretation.

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References

Bernal D, Carlson JK, Goldman KJ, Lowe CG. 2012. Energetics, metabolism, and endothermy in sharks and rays. In: Carrier JC, Musick JA, Heithaus MC, editors. Biology of sharks and their relatives. 2nd ed. Boca Raton (Florida): CRC Press; p. 211–237.

Bernal D, Dickson KA, Shadwick RE, Graham JB. 2001. Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. Comp Biochem Physiol. 129A:695–726. doi:10.1016/S1095-6433(01)00333-6.

Bigelow HB, Schroeder WC. 1948. The fishes of the western North Atlantic. No. 1, Part 1. lancelets, cyclostomes and sharks. New Haven: Sears Foundation Press.

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. 512.

Carlson JK, Goldman KJ, Lowe CG. 2004. Metabolism, energetic demand, and endothermy. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of sharks and their relatives. Boca Raton (Florida): CRC Press; p. 203–224.

Compagno LJV. 2002. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2: bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Sp Cat Fish Purp. 1(2):1–269.

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

Dickson KA, Graham JB. 2004. Evolution and consequences of endothermy in fishes. Physiol Biochem Zool. 77:998–1018. doi:10.1086/423743.

Donley JM, Sepulveda CA, Konstantinidis P, Gemballa S, Shadwick RE. 2004. Convergent evolution in mechanical design of lamnid sharks and tunas. Nature. 429:61–65. doi:10.1038/nature02435.

Ebert D, Fowler S, Compagno L, Dando M. 2013. Sharks of the world: a fully illustrated guide. Plymouth (NH): Wild Nature Press.

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

Ferrón HG, Martínez-Perez C, Botella H. 2017. The evolution of gigantism in active marine predators. Hist Biol. 30:712–716. doi:10.1080/08912963.2017.1319829.

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.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: paleontological statistical software package for education and data analysis. Palaeontol Electron. 4 (1):1–9.

Harding L, Jackson A, Barnett A, Donohue I, Halsey L, Huveneers C, Meyer C, Papastamatiou Y, Semmens JM, Spencer E, et al. 2021. Endothermy makes fishes faster but does not expand their thermal niche. Funct Ecol. 1–9. doi:10.1111/1365-2435.13869

Ikejiri T, Lu Y, Zhang B. 2020. Two-step extinction of Late Cretaceous marine vertebrates in northern Gulf Of Mexico prolonged biodiversity loss prior to the Chicxulub impact. Sci Rep. 10:4169. doi:10.1038/s41598-020-61089-w

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.

Klingenberg CP. 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol Ecol Resour. 11:353–357. doi:10.1111/j.1755-0998.2010.02924.x.

Legendre LJ, Davesne D. 2019. The evolution of mechanisms involved in vertebrate endothermy. Phil Trans R Soc B. 375:20190136. doi:10.1098/rstb.2019.0136

Lingham-Soliar T. 2005. Caudal fin allometry in the white shark Carcharodon carcharias: implications for locomotory performance and ecology. Naturwiss. 92:231–236. doi:10.1007/s00114-005-0614-4.

Maisey JG, Naylor GJP, Ward DJ. 2004. Mesozoic elasmobranchs, neoselachian phylogeny, and the rise of modern neoselachian diversity. In: Arratia G, Tintori A, editors. Mesozoic fishes III. systematics, paleoenvironments and biodiversity. Munich: Verlag Pfeil; p. 17–56.

Perez VJ, Leder RM, Badaut T. 2021. Body length estimation of Neogene macrophagous lamniform sharks (Carcharodon and Otodus) derived from associated fossil dentitions. Palaeontol Electron. 24:a09. doi:10.26879/1140

Pimiento C, Balk MA. 2015. Body-size trends of the extinct giant shark *Carcharocles megalodon*: a deep-time perspective on marine apex predators. Paleobiology. 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.

Randall JE. 1973. Size of the great white shark (*Carcharodon*). Science. 181:169–170. doi:10.1126/science.181.4095.169.

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.

Rohlf FJ. 2015. The tps series of software. Hystrix. 26:9–12.

Sepulveda CA, Wegner NC, Bernal D, Graham JB. 2005. The red muscle morphology of the thresher sharks (family Alopiidae). J Exp Biol. 208:4255–4261. doi:10.1242/jeb.01898.

Shimada K. 2019. The size of the megatooth shark, *Otodus megalodon* (Lamniformes: otodontidae), revisited. Hist Biol. 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, Bonnan MF, Becker MA, Griffiths ML. 2021. Ontogenetic growth pattern of the extinct megatooth shark *Otodus megalodon*—implications for its reproductive biology, development, and life expectancy. Hist Biol. doi:10.1080/08912963.2020.1861608

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 'mega-toothed' clade. Hist Biol. 29:704–714. doi:10.1080/08912963.2016.1236795.

Sternes PC, Shimada K. 2020. Body forms in sharks (Chondrichthyes: elasmobranchii), and their functional, ecological, and evolutionary implications. Zoology. 140:125799. doi:10.1016/j.zool.2020.125799

Stone NR, Shimada K. 2019. Skeletal anatomy of the bigeye sand tiger shark, *Odontaspis noronhai* (Lamniformes: odontaspididae), and its implications to lamniform phylogeny, taxonomy, and conservation biology. Copeia. 107:632–652. doi:10.1643/CG-18-160.

Thomson KS, Simanek DE. 1977. Body form and locomotion in sharks. Am Zool. 17:343–354. doi:10.1093/icb/17.2.343.

Tomita T, Toda M, Miyamoto K, Oka S, Ueda K, Sato K. 2018. Development of the lunate-shaped caudal fin in white shark embryos. Anat Rec. 301:1068–1073. doi:10.1002/ar.23776.

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.

Vullo R, Frey E, Ifrim C, González González MA, Stinnesbeck ES, Stinnesbeck W. 2021. Manta-like planktivorous shark in Late Cretaceous oceans. Science. 371:1253−1256. doi:10.1126/science.abc1490.

Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Tomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press; p. 19–33.