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Phylogeny of lamniform sharks (Chondrichthyes: Elasmobranchii) and the contribution of dental characters to lamniform systematics

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Abstract. Lamniform sharks (Chondrichthyes: Elasmobranchii) are common in the fossil record but are represented mainly by isolated teeth. A phylogenetic analysis of 15 extant lamniform species based on 42 morphological characters using *Scyliorhinus* (Carcharhiniformes) as an outgroup produces a consensus tree with the following generic relationships: [*Mitsukurina* + [*Carcharias* + *Odontaspis* + *Pseudocarcharias* + *Megachasma* + [*Alopias* + [*Cetorhinus* + [[*Isurus* + *Carcharodon*] + *Lamna*]]]]]. When an extinct form, *Cretoxyrhina mantelli*, is added to the analysis, the fossil taxon occurs within the *Alopias* clade. Comparisons among the cladogram based on 29 non-dental characters alone, that based on 19 dental characters, and that based on combined (48) characters, suggest that dental characters provide at least some phylogenetic signal. Mapping of quantitative dental data on the cladogram based on non-dental characters suggests 1) a decrease in the number of tooth rows through lamniform phylogeny, 2) possible relationships between the crown heights and food types or feeding habits, and 3) that narrower crowns are plesiomorphic in lamniforms.

Key words: cartilaginous fish, cladistics, dentition, fossil, morphology, teeth

Introduction

Sharks (Chondrichthyes: Elasmobranchii) exhibit diverse tooth morphologies (e.g., Meng and Zhu, 1984). Their hard teeth have left an excellent fossil record, but that record consists mainly of isolated teeth (Cappetta, 1987). Complete skeletons of fossil sharks are rare because their cartilage-based skeleton is not well mineralized. Consequently, systematics and paleoecology of fossil sharks as well as other paleobiological inferences have mainly been based on isolated teeth.

Maisey (1983, p. 50) stated that "to study the dentition of an individual fossil shark might seem hopeless, in the face of so many formidable possibilities for variation." Where shark dentitions generally exhibit heterodonty (e.g., see Cappetta, 1986), ontogenetic, sexual, individual, and geographic differences in tooth morphology may be present (e.g., Sadowsky, 1970; Taniuchi, 1970; Gruber and Compagno, 1981; Raschi *et al.*, 1982; Lucifora *et al.*, 2003), and various types of dental abnormalities occur sporadically (e.g., Gudger, 1937; Cadenat, 1962; Compagno, 1967). Thus, reconstructing the dentition of extinct sharks is difficult based on isolated teeth, which concomitantly makes any phylogenetic inferences difficult (for criticism, see e.g.: Maisey, 1983; Compagno, 1988; Applegate and Espinosa-Arrubarrena, 1996; Gottfried *et al.*, 1996; Hubbell, 1996). Naylor and Marcus' (1994) study, in which teeth from species of extant *Carcharhinus* were identified on morphometric criteria, was novel. However, they were concerned with the designation of species based on quantitative descriptions (α taxonomy) and not with the phylogeny-based taxonomy (β taxonomy). The fundamental question critical to shark paleontology – i.e., whether or not dental characters can be used to elucidate the phylogenetic relationships of sharks – has been largely neglected.

This paper focuses on the phylogeny of the order Lamniformes. Various extinct lamniforms occur worldwide in many marine deposits, ranging from early Cretaceous to Recent in age. However, like most other fossil sharks, teeth are the only parts of the body known for most fossil lamniforms (e.g., Case, 1985;

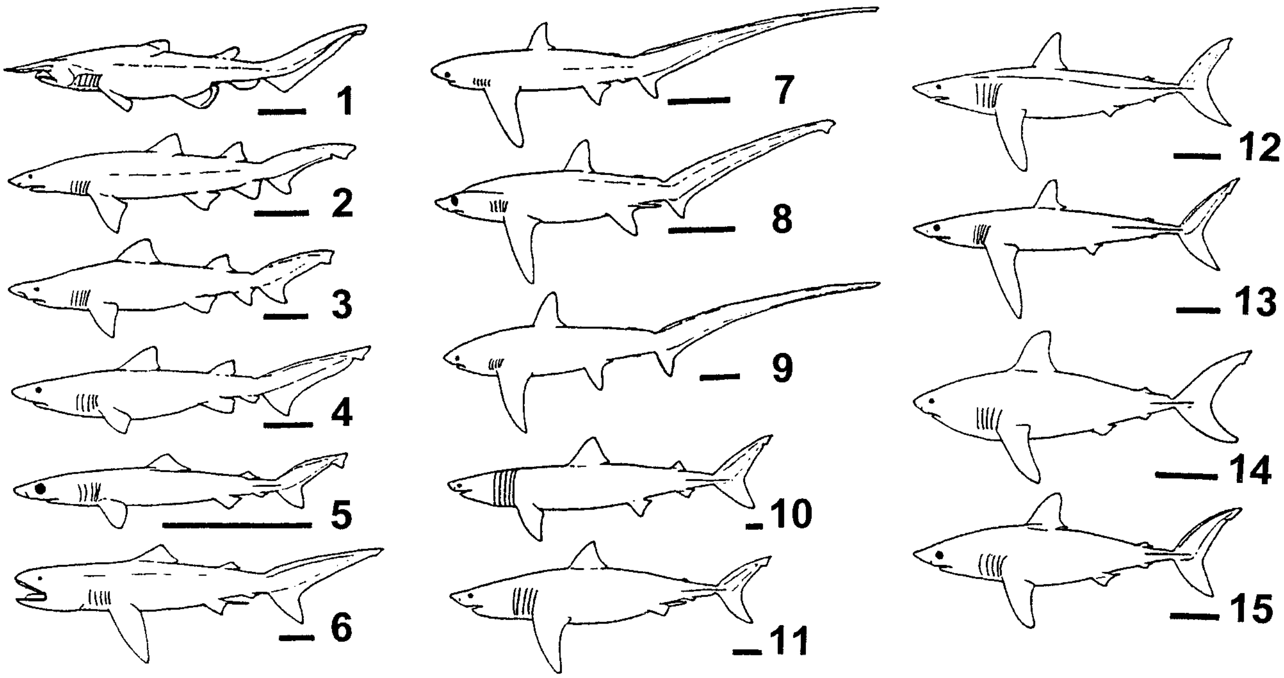

Figure 1. Extant lamniform species (after Shimada, 2002a, figure 1). **1**, *Mitsukurina owstoni*; **2**, *Carcharias taurus*; **3**, *Odontaspis ferox*; **4**, *Odontaspis noronhai*; **5**, *Pseudocarcharias kamoharai*; **6**, *Megachasma pelagios*; **7**, *Alopias pelagicus*; **8**, *Alopias superciliosus*; **9**, *Alopias vulpinus*; **10**, *Cetorhinus maximus*; **11**, *Carcharodon carcharias*; **12**, *Isurus oxyrinchus*; **13**, *Isurus paucus*; **14**, *Lamna ditropis*; **15**, *Lamna nasus*. Bar scale = 50 cm.

Cappetta, 1987; Kemp, 1991; Siverson, 1992, 1996). There are 15 living lamniform species including microphagous (filter-feeding) and macrophagous forms (Figure 1; Table 1; excluding the dubious *Carcharias tricuspidatus* [Day, 1878] [see Compagno, 1990, 1999] and an undescribed species of *Alopias* [see Eitner, 1995]). Modern species live in tropical to temperate oceans worldwide, ranging from intertidal depths to the deep sea (Compagno, 1984). Most extant macrophagous lamniforms possess a unique heterodont dentition called "lamnoid tooth pattern" (Compagno, 1984; Shimada, 2002a), and the pattern is confirmed in at least one extinct species, *Cretoxyrhina mantelli* (Agassiz, 1843) (Shimada, 1997a, 2002a). The goals of this paper are threefold: 1) to elucidate phylogenetic relationships by the cladistic method (Hennig, 1966) among extant lamniform species and *C. mantelli* based on morphology; 2) to investigate the role of dental characters for the elucidation of lamniform phylogeny; and 3) to examine evolutionary trends in lamniform dentitions.

Table 1. Classification of extant lamniform species (based on Compagno, 1984). Asterisk indicates microphagous forms (species without asterisk are macrophagous).

Family	Species
Mitsukurinidae	*Mitsukurina owstoni* Jordan, 1898
Odontaspididae	*Carcharias taurus* (Rafinesque, 1810)
	Odontaspis ferox (Risso, 1810)
	Odontaspis noronhai (Maul, 1955)
Pseudocarchariidae	*Pseudocarcharias kamoharai* (Matsubara, 1936)
Megachasmidae	*Megachasma pelagios** Taylor *et al.*, 1983
Alopiidae	*Alopias pelagicus* Nakamura, 1935
	Alopias superciliosus (Lowe, 1839)
	Alopias vulpinus (Bonnaterre, 1788)
Cetorhinidae	*Cetorhinus maximus** (Gunnerus, 1765)
Lamnidae	*Carcharodon carcharias* (Linnaeus, 1758)
	Isurus oxyrinchus Rafinesque, 1810
	Isurus paucus Guitart-Manday, 1966
	Lamna ditropis Hubbs and Follett, 1947
	Lamna nasus (Bonnaterre, 1788)

Materials

Extant shark specimens (mostly skeletonized jaws) were examined in the following collections (Appendix 1): American Museum of Natural History (AMNH), New York; California Academy of Sciences (CAS), San Francisco; Field Museum of Natural History (FMNH), Chicago, Illinois; Natural History Museum of Los Angeles County (LACM), California; Museum

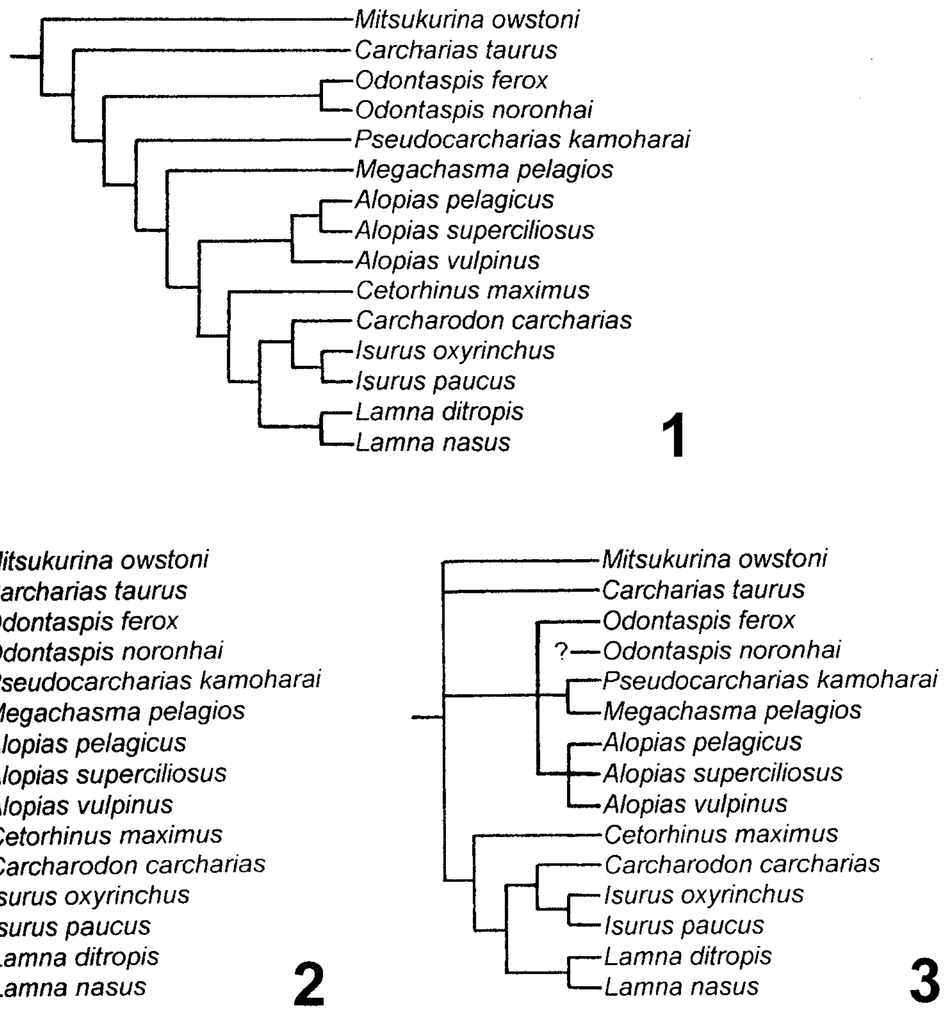

Figure 2. Previously proposed phylogenetic relationships of extant lamniform species. **1**, based on morphological data by Compagno (1990); **2**, based on morphological data by Shirai (1996); **3**, based on molecular data by Naylor *et al.* (1997).

of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; National Museum of Natural History (NMNH), Washington, D.C.; Scripps Institution of Oceanography (SIO), La Jolla, California; Gordon Hubbell collection (GH), JAWS International, Gainesville, Florida, USA; and School of Dental Medicine, Tsurumi University (TU), Yokohama, Japan. Literature records supplemented the enumeration of intraspecific variation of tooth row counts (Appendix 2). Additional morphological data were also taken from the literature (Appendix 3).

Lamniform phylogeny

Previous studies

Compagno (1990) proposed the first hypothesis of phylogenetic interrelationships of extant lamniform species (Figure 2-1). His study was based on "a first approximation that uses the simple Hennigian non-computer method of clustering derived taxa, the schema of cladistic argument, and the rationale for determination of character polarities of Compagno (1988)" (Compagno, 1990: 369–370). Despite this statement, the criteria used for polarity decisions were not clearly described in either his 1988 or 1990 paper. Nevertheless, subsequent phylogenetic hypotheses of lamniforms agree with Compagno's (1990) hypothesis that *Mitsukurina* is sister to all other lamniforms (Shirai, 1996; Martin and Naylor, 1997, figure 5; Naylor *et al.*, 1997, only in text [cf. figure 7]; Figure 2-2). Molecular studies (Martin and Naylor, 1997, based on cytochrome b mitochondrial gene; Naylor *et al.*, 1997, based on NADH-2 and cytochrome b mitochondrial genes; Figure 2-3) also support Compagno's (1990) hypothesis of relationships [*Cetorhinus* + [*Lamna* + [*Isurus* + *Carcharodon*]]]. Shirai's (1996) morphology-based cladogram also depicts a close relationship between *Cetorhinus* and the lamnid taxa (*Lamna*, *Isurus*, and *Carcharodon*) (Figure 2-2).

Based on dental characters, Long and Waggoner (1996, figure 1-A) obtained a cladogram with the generic arrangement of [*Mitsukurina* + [[*Megachasma* + *Cetorhinus*] + [[*Carcharias* + *Odontaspis*] + [*Pseudocarcharias* + [*Alopias* + [*Isurus* + [*Carcharodon* +*Lamna*]]]]]]]. All other published cladograms do not contain all extant lamniform genera. Topologies based on morphological data include: [*Odontaspis* + [[*Megachasma* + *Cetorhinus*] + [Alopiidae + Lamnidae]]] by Maisey (1985); and [*Mitsukurina* + [*Alopias* + [*Pseudocarcharias* + *Lamna*]]] by Goto (1996). Those based on molecular data include: [*Megachasma* + [*Lamna* + *Isurus* + *Carcharodon*]] by Boyes and Stepien (1995, based on cytochrome b mitochondrial gene); [*Mitsukurina* + [*Cetorhinus* + [*Lamna* + [*Carcharodon* + *Isurus*]]]] by Kitamura (1996, based on cytochrome b mitochondrial gene); [*Lamna* + [*Carcharodon* + *Isurus*]] by Martin (1995, 1996, based on cytochrome b mitochondrial gene); [*Megachasma* + [*Alopias* + [*Odontaspis* + [*Cetorhinus* + [*Lamna* + [*Isurus* + *Carcharodon*]]]]]] by Morrissey *et al.* (1997, based on 12S rRNA mitochondrial gene); and [*Mitsukurina* + [*Carcharias* + "*Cetorhinus*/lamnids"] + [*Alopias* + [*Pseudocarcharias* + [*Megachasma*]]]] by Maisey *et al.* (2004, fig. 5A, based on RAG-1 nuclear gene).

Maisey's (1985) suggestion of the sister relationship between *Megachasma* and *Cetorhinus* implies that filter-feeding evolved only once in lamniform phylogeny. Long and Waggoner (1996) also found this sister relationship based solely on dental characters (but see below for a critique). Asahida's molecular study (1996, based on 16S rRNA mitochondrial gene) also showed this sister relationship, but Asahida's result is an artifact because lamniforms in his analysis included only those two taxa. However, more comprehensive studies based on both molecular and morphological data strongly refute such a sister relationship indicating that filter-feeding evolved twice in lamniforms (Compagno, 1990; Shirai, 1996; Martin and Naylor, 1997; Morrissey *et al.*, 1997; Naylor *et al.*, 1997; Maisey *et al.*, 2004; Figure 2). The molecular studies by Martin and Naylor (1997), Naylor *et al.* (1997), and Maisey *et al.* (2004) suggest that *Pseudocarcharias* is sister to *Megachasma* (Figure 2-3).

Molecular-based cladograms tend to refute *Alopias* monophyly, where *A. superciliosus* usually "falls off" the clade (Martin and Naylor, 1997; Naylor *et al.*, 1997). However, because of the low cost of invoking *Alopias* monophyly, and because of strong morphological evidence supporting *Alopias* monophyly, Naylor *et al.* (1997, p. 212) noted that "it is likely that the molecular-based inference suggesting a non-monophyletic Alopiidae is erroneous."

The most notable difference between the molecular-based and morphology-based cladograms is perhaps the position of Alopiidae. In molecular-based cladograms, *Alopias* is clustered with *Odontaspis*, *Pseudocarcharias*, and *Megachasma* (Martin and Naylor, 1997; Naylor *et al.*, 1997; Maisey *et al.*, 2004 [note: *Odontaspis* not included]; Figure 2-3). Naylor *et al.* (1997, p. 214) called this group "an ancient monophyletic assemblage." On the other hand, *Alopias* is sister to the clade uniting *Cetorhinus* and Lamnidae in cladograms based on morphology (Maisey, 1985; Compagno, 1990; Shirai, 1996; Figures 2-1, 2-2).

Odontaspididae traditionally consists of *Carcharias* and *Odontaspis* (e.g., Compagno, 1984, 1999). The anatomy of *O. noronhai* remains poorly known. However, recent morphological and molecular studies suggest that *Carcharias* and *Odontaspis* are paraphyletic (Compagno, 1990; Naylor *et al.*, 1997; Figures 2-1, 2-3).

Within Lamnidae, *Carcharodon* is monotypic, and both *Lamna* and *Isurus* contain two sister species. Based only on dental characters, Long and Waggoner (1996) proposed the following lamnid interrelationships: [*Isurus* + [*Carcharodon* + *Lamna*]]. However, molecular data strongly suggest the interrelationships, [*Lamna* + [*Carcharodon* + *Isurus*]] (Kitamura, 1996; Martin, 1995, 1996; Martin and Naylor, 1997; Naylor *et al.*, 1997; Figure 2-3). Compagno (1990) also supported this arrangement based on morphology (Figure 2-1).

Phylogenetic analysis

Method.—The phylogenetic analysis presented here includes one extinct (*Cretoxyrhina mantelli*: Cretoxyrhinidae) and 15 extant lamniform species, and is based on 42 morphological characters (37 binary and five multistate; Characters 1–42 in Appendix 3). The polarity of character states was determined by outgroup comparisons (Maddison *et al.*, 1984), and all character states were recorded as unordered. *Scyliorhinus* (Carcharhiniformes: Scyliorhinidae) is used here as an outgroup because recent phylogenetic studies have suggested that Carcharhiniformes is sister to Lamniformes (Carvalho, 1996; Shirai, 1996), and Scyliorhinidae is one of the closest relatives of lamniforms among carcharhiniforms (Shirai, 1996; Musick *et al.*, 2004, p. 49). The character states of each char-

Table 2. Data matrix showing the distribution of the states of 61 morphological characters in 15 extant lamniform species, their outgroup, and *Cretoxyrhina mantelli*. The definition of each character is given in Appendix 3. Taxon: OG = outgroup (*Scyliorhinus*); FT = fossil taxon (*C. mantelli*); abbreviations for other taxa (all extant), as for Appendix 2.

	Character
	1111111111222222222233333333334444444444555555555566
Taxon	1234567890123456789012345678901234567890123456789012345678901
OG	00000000000000000000000000000000000000000--------------------
Mo	1000100101001001100100101010000010010000000000000000000000000
Ct	100020000010111100010110101001001001000000000?0100001000000010
Of	1000200101101011010101101010010010011010000?01010000000000010
On	1000???1??1??11?0???????10100100100110100 0?0001000000000001010
Pk	1000210100111110011101101110011010011010001 1?11?1011011000010
Mp	00001000001010010001011?111001000101101001--------------------
Ap	100110000010011012100111111111000111202100???01?1001111211111
As	100111010110111002000111111111000111202100 1?0111100101122111 1
Av	100120000010011011100111101101000111202100???01?1000001211111
Cm	01001011001011111201111011110110111121 2011--------------------
Cc	1110100001111011001112101111011011111212010110111010010022011 0
Io	1110100101111011001112101111011011111212010110 11?1111011000110
Ip	111010010111101100111210111101101111121201011011?1111001100110
Ld	11101011101110110111112 1?111101111111212010 1?0110010100010011 0
Ln	1110101110111011011111210111101111111212010110110010100010011 0
FT	1?????00?01?1110??10??11?????????????????00?1?1?1101001???11?

acter for each examined species and their outgroup are listed in Table 2 (the first 42 characters on the table). Uncertain homology, polymorphic condition, and uncertain states are coded as "?". Autapomorphies unique to each species are not included in the analysis.

The parsimony analysis with a heuristic search was undertaken using the computer program Hennig86 (version 1.5, J.S. Farris, Port Jefferson Station, New York, 1988, unpublished). A strict consensus tree with tree statistics was constructed using the computer program CLADOS (version 1.1, K.C. Nixon, Cornell University, Ithaca, New York, 1992, unpublished).

Cretoxyrhina mantelli is a Late Cretaceous shark representing an extinct lamniform arguably with the most accurately reconstructed dentition (i.e., based on articulated teeth on jaws: Shimada, 1997a). Teeth of *C. mantelli* occur in marine deposits worldwide (Cappetta, 1987; Siverson, 1992, 1996). Its body form, body size, and life style could have resembled extant *Carcharodon carcharias* (Shimada, 1997b, 1997c, 1997d; Shimada and Hooks, 2004; Shimada and Everhart, 2004). However, many of its anatomical features remain unknown, so *C. mantelli* is excluded from the analysis until the phylogenetic relationships of living lamniforms are elucidated. Such an exclusion is justified because an excess number of problematic character-state entries (coded as "?") can interfere with the computer algorithm used in the phylogenetic analysis (Grande and Bemis, 1998).

Phylogenetic relationships of extant taxa.—My analysis produced three equally most parsimonious trees. Their consensus tree is shown in Figure 3-1. The exact relationship among the outgroup (*Scyliorhinus*), *Mitsukurina owstoni*, and a clade uniting all other examined taxa is not clear, as demonstrated by a trichotomy. The trichotomy suggests that *Mitsukurina owstoni* could lie outside Lamniformes; however, as in most other studies (e.g., Figures 2-1, 2-2), *M. owstoni* is the most basal species if one assumes the species to be a lamniform. My analysis also supports the view that *Cetorhinus* is sister to the lamnid species, indicating the independent acquisition of filter-feeding in *Cetorhinus* and *Megachasma*. However, interrelationships among several taxa toward the tree base (*Carcharias*, *Odontaspis*, *Pseudocarcharias*, and *Megachasma*) are unclear. Thus, the sister relationship between *Pseudocarcharias* and *Megachasma* as well as the *Carcharias*-*Odontaspis* paraphyly cannot be confirmed.

My study supports the monophyly of *Alopias*, and it is sister to the clade uniting *Cetorhinus* and lamnids (Figure 3-1). This systematic position agrees with other morphology-based analyses, but not with molecular-based studies (Figure 2).

Lamnid monophyly is also supported (Figure 3-1). The exact relationships among *Carcharodon* and the two *Isurus* species are uncertain, but they constitute a monophyletic group. The group is sister to the clade uniting the two *Lamna* species, and this sister relationship is consistent with Compagno (1990; Figure 2-1) and Naylor and others' (1997; Figure 2-3) studies, but not with Long and Waggoner's (1996) analysis.

Systematic position of Cretoxyrhina mantelli.—

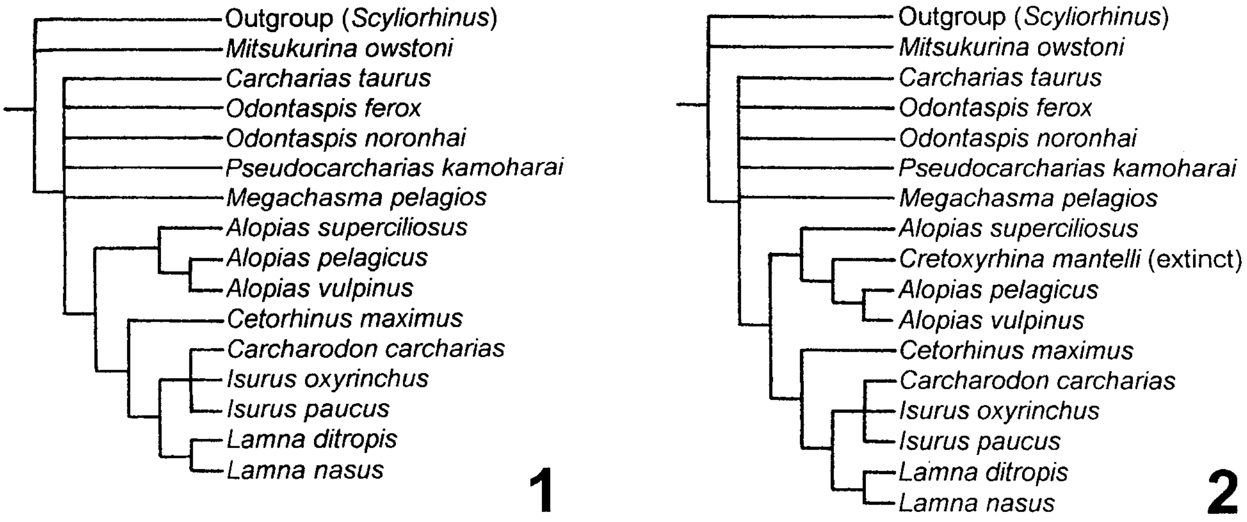

Figure 3. Consensus trees showing phylogenetic relationships of lamniform species based on 42 morphological characters. **1**, 15 extant species alone (tree length = 89, CI = 0.52, RI = 0.69); **2**, 15 extant species plus one extinct species, *Cretoxyrhina mantelli* (tree length = 89, CI = 0.52, RI = 0.70).

Shimada (1997c) suggested that *Cretoxyrhina mantelli* might be closely related to Pseudocarchariidae or Alopiidae. Based on published skeletal and dental data (Shimada, 1997a, 1997c, 2002a), inferences regarding the phylogenetic position of *C. mantelli* are made here cladistically. A character matrix for the fossil taxon was added to the matrix for the 15 extant lamniform species and their outgroup (the first 42 characters in Table 2). It must be noted that the polarity for 28 (of 42) characters could not be determined for *C. mantelli* because of missing data and polymorphism.

The analysis gave 13 equally most parsimonious trees. Their consensus tree places *Cretoxyrhina mantelli* within the *Alopias* clade, and as sister to the clade uniting *A. pelagicus* and *A. vulpinus* (Figure 3-2). This tree differs little from the cladogram based only on extant lamniforms (Figure 3-1). Thus, there is a possibility that the fossil taxon may not merit its own genus (*Cretoxyrhina* Glickman, 1958) or family (Cretoxyrhinidae Glickman, 1958), and could be congeneric with *Alopias*. However, this result is still premature and might only be an artifact because of many characters with uncertain coding for *C. mantelli*. Therefore, it is recommended here that the taxon should be kept within the Cretoxyrhinidae.

Contribution of dental characters

General background and plan

Many extinct sharks, including lamniforms, are represented almost exclusively by their teeth. Thus, most hypotheses about phylogeny of extinct sharks rely heavily on dental morphology (e.g., Janvier and Welcomme, 1969; Goto, 1994; Applegate and Espinosa-Arrubarrena, 1996). However, one may ask: what contribution do dental characters make to elucidating phylogenetic relationships of sharks? The same question was recently addressed by Poyato-Ariza (2003) using extinct osteichthyan fishes, pycnodonts, and his study suggested that dental morphology in pycnodonts appears to produce considerable "phylogenetic noise" over "phylogenetic signal."

Long and Waggoner (1996) conducted a cladistic analysis of extant lamniforms based solely on 23 dental characters. Except for the topology within the lamnid clade and for the position of two microphagous forms (*Megachasma* and *Cetorhinus*), their cladogram broadly agreed with that of Compagno (1990; Figure 2-1). However, their study is problematic because of uncertainty in how they identified homologous teeth across lamniform taxa (vs. repeatable homology identification method outlined by Shimada, 2002a). Most of their characters depended on the identification of tooth types (their Characters 3–5, 8–22), but they did not describe their homology criteria. This homology issue (e.g., Shimada, 2002a) is particularly critical for characters dealing with the number of rows of each tooth type and the size of teeth in each tooth type (e.g., Long and Waggoner's Characters 13–19). To note, a similar problem (i.e., the practice of not considering the homology issue critically) is found in the phylogenetic study of squaliform sharks by Adnet and Cappetta (2001), but the study may be justified because squaliforms generally have a lesser degree of heterodonty in their dentition compared to lamniforms.

Although cladistics assumes that every signal is phylogenetic, it is true that different data sets usually give different tree topologies (e.g., Cavin, 2001), suggesting that certain characters are often phylogenetically more informative than others. I used Poyato-Ariza's (2003) approach in investigating the phylogenetic role of teeth in lamniform sharks. Three experimental cladograms were constructed to examine the extent of the contribution of dental characters for the elucidation of lamniform phylogeny: 1) a consensus tree based on non-dental and dental characters combined, 2) that based solely on non-dental characters, and 3) that based solely on dental characters. I compared the topological congruency among the cladograms that resulted from the three different data sets.

To obtain the three experimental cladograms, additional dental characters were necessary, because Character 42 was the only dental character in the original data set. However, tooth homologies are uncertain for non-lamniform elasmobranchs, including *Scyliorhinus*, and this situation did not allow me to make polarity decisions. Therefore, for the purpose of this analysis, I removed *Scyliorhinus* from the data matrix and used *Mitsukurina* as an outgroup instead (which is now justified as a basal taxon within the initial ingroup taxa; Figure 3). I also removed *Megachasma* and *Cetorhinus* from the data set, because tooth homologies are also uncertain in these two microphagous forms (see Shimada, 2002a). For the purpose of this analysis, Shimada's (2002a) tooth type identification (Figure 4) was assumed to be correct, and dental measurements (described below) were taken accordingly. Such modifications and assumptions permitted an addition of 19 dental characters (Characters 43–61) to the data matrix (Table 2; see Appendix 3 for definition). In Appendix 3, dental characters without the specification of tooth types (Characters 47, 48, and 50) are based on teeth in A1-L8 and in a1-l7 (Figure 4). Dental characters of lateral teeth, but without the specification of certain tooth rows (Characters 49 and 60), are based on teeth in L2-L8 and/or l1-l7 (Figure 4).

As a result of switching the outgroup from *Scyliorhinus* to *Mitsukurina* and omitting *Megachasma* and *Cetorhinus*, some changes also took place within the first 42 characters (Table 2). First, by assigning *Mitsukurina* as an outgroup, the polarity of 12 non-dental characters (Characters 1, 8, 10, 13, 16, 17, 20, 23, 25, 27, 33, and 36) became reversed, so they were omitted for the new analysis. Second, Character 5 became binary from multistate. Third, the only dental character in the original data set, Character 42, became uninformative, because *Megachasma* and *Cetorhinus* were the only taxa with a derived character state; thus, this character was omitted for the new analyses.

In summary, the taxa in the new data matrix consisted of 12 ingroup species: *Carcharias taurus*, *Odontaspis ferox*, *O. noronhai*, *Pseudocarcharias kamoharai*, *Alopias pelagicus*, *A. superciliosus*, *A. vulpinus*, *Carcharodon carcharias*, *Isurus oxyrinchus*, *I. paucus*, *Lamna ditropis*, and *L. nasus*. There were 29 non-dental characters (Characters 2–7, 9, 11–12, 14–15, 18–19, 21–22, 24, 26, 28–32, 34–35, 37–41) and 19 dental characters (Characters 43–61). The examination of root morphology was difficult because teeth were still attached to the jaw cartilage (often with the covering of soft tissues) in specimens I examined. Therefore, my dental characters do not include root characters. I should also note that many dental characters were based on quantitative data, which were of a continuous nature (Appendices 4–7). However, along with a goal to obtain a large number of dental characters, such quantitative data were necessary to accommodate tooth variation known to occur in various lamniforms (e.g., Hubbell, 1996). Because of the continuous nature, the division between separate character states for each of such characters presented in Appendix 3 should be considered as working hypotheses.

Dental measurements

The following jaw and tooth measurements (Figure 5) were taken from each non-embryonic specimen (cf. Shimada, 2002b) with known total length ("Measured specimens" in Appendix 1): basal crown width (BCW: maximum crown width), crown height (CH: maximum vertical enameloid height), distal crown edge length (DCL: straight line between the crown tip and distalmost point of the crown), lower jaw length (LJL: length of the Meckel's cartilage from the symphysis to the center of the lateral quadratomandibular joint contouring the occlusal jaw rim), mesial crown edge length (MCL: straight line between the crown tip and mesialmost point of the crown), mid-crown width (MCW: crown width at the half of the CH), tooth position (TP: distance between the symphysis and at the half of BCW for each tooth contouring the occlusal jaw rim), and upper jaw length (UJL: length of the palatoquadrate from the symphysis to the center of the lateral quadratomandibular joint contouring the occlusal jaw rim). Raw measurements (i.e., archived in Shimada, 1999) are then used to obtain the following

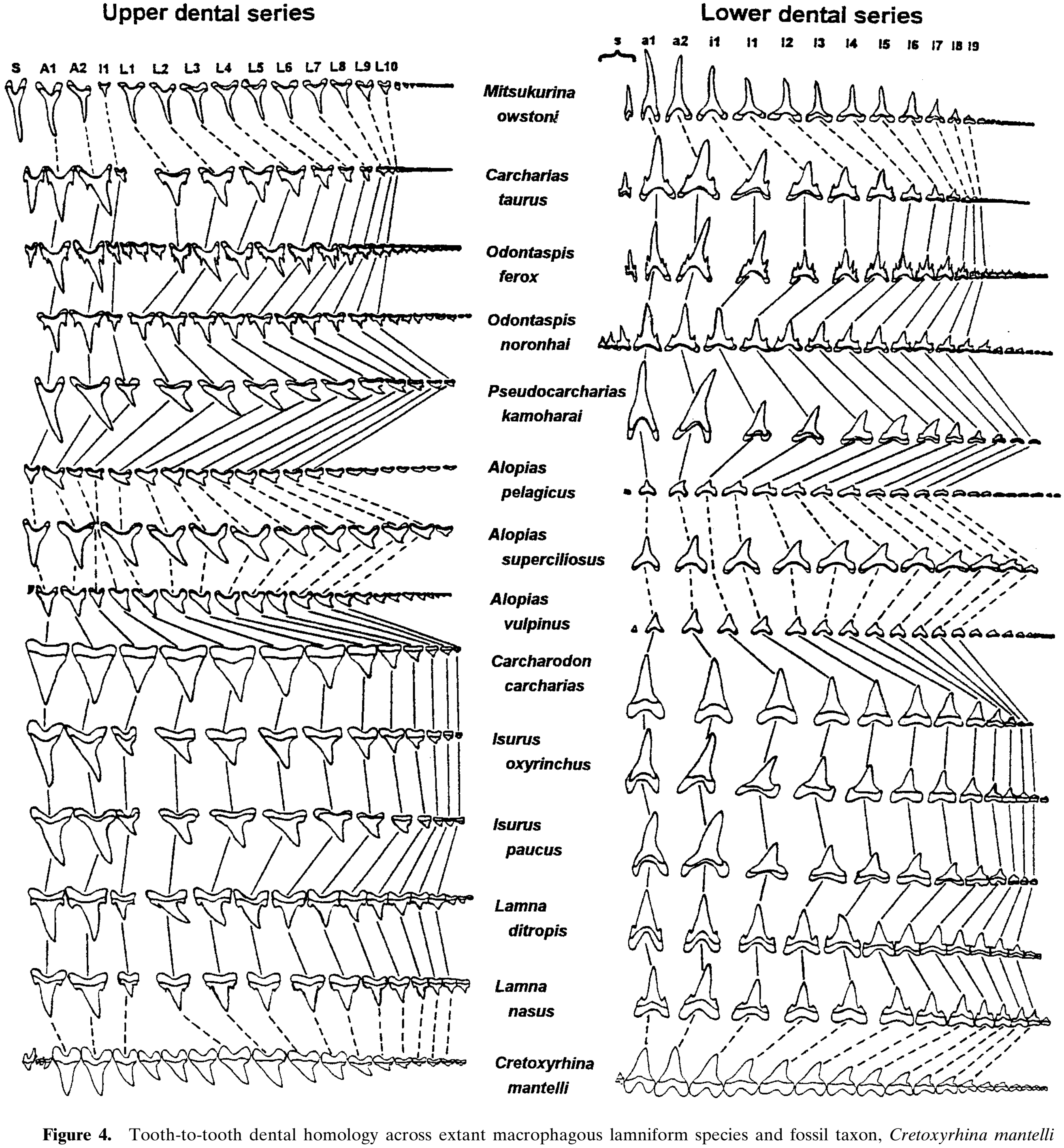

Figure 4. Tooth-to-tooth dental homology across extant macrophagous lamniform species and fossil taxon, *Cretoxyrhina mantelli* (mesial to the left; labial view; broken line = tentative homology identification; not to scale: for detail, see Shimada, 2002a). Tooth types: A or a, anterior tooth; I or i, intermediate tooth; L or l, lateral tooth; S or s, symphysial tooth; upper case = upper teeth; lower case = lower teeth.

four derived measurements for each tooth: 1) tooth inclination (the proportion of MCL to DCL: assumed symmetrical where MCL/DCL = 1; mesially inclined where MCL/DCL < 1; and distally inclined where MCL/DCL > 1); 2) standardized crown height (CH of each tooth divided by the UJL); 3) standardized tooth position (each TP of the upper teeth divided by the UJL and that of the lower teeth by the LJL), and 4) crown acuteness (a ratio obtained by dividing one half of each CH by its MCW provided a measure of the

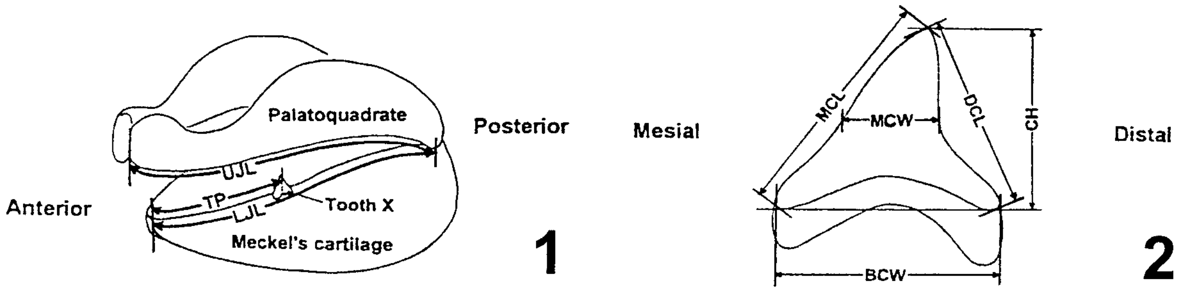

Figure 5. Jaw (**1**) and tooth (**2**) measurements taken for this study (see text for detail; abbreviations: BCW, basal crown width; CH, crown height; DCL, distal crown edge length; LJL, lower jaw length; MCL, mesial crown edge length; MCW, mid-crown width; TP, tooth position; UJL, upper jaw length). Illustrations not to scale.

shape of each crown at its apical half; the crown width at its apical half was measured instead of the whole crown width because a cusp of a crown could be narrow or broad regardless of its BCW). The average value for each tooth for each derived measurement used in this study can be found in Appendices 4–7.

Results and discussion

When the 48 (dental + non-dental) characters were analyzed, six equally most parsimonious trees were produced. Their consensus tree (Figure 6-1) supported the *Alopias* monophyly as well as the lamnid monophyly, although topological arrangements within each of these two clades differ from those in the analysis based on 15 ingroup species (Figure 3-1). Intriguingly, the topological resolution of other ingroup species (*Carcharias*, *Odontaspis*, and *Pseudocarcharias*) showed an improvement (Figure 6-1; cf. Figure 3), approaching Compagno's (1990; Figure 2-1) cladogram with the paraphyletic Odontaspididae. As a side note, the following consensus tree was obtained from 24 equally most parsimonious trees when the fossil taxon, *Cretoxyrhina mantelli*, was included in the analysis: [*Mitsukurina owstoni* + *Carcharias taurus* + [*O. ferox* + *O. noronhai* + [*P. kamoharai* + [*A. vulpinus* + *Cretoxyrhina mantelli* + [*A. pelagicus* + *A. superciliosus*] + [*Isurus oxyrinchus* + *I. paucus* + [*Carcharodon carcharias* + [*Lamna ditropis* + *L. nasus*]]]]]]] (tree length = 91, CI = 0.59, RI = 0.73).

When non-dental characters were processed alone, three equally most parsimonious trees were produced. Their consensus tree (Figure 6-2) showed an identical topological arrangement to that based on 48 characters (Figure 6-1) except for the difference in the relationships among lamnid species, i.e., [*Lamna* + [*Carcharodon* + *Isurus* spp.]] (note: the closer relationship between *Carcharodon* and *Isurus* with respect to *Lamna* agrees with Compagno [1990; Figure 2-1] and Naylor *et al.* [1997; Figure 2-3]). On the other hand, when dental characters are processed alone, the topology of the consensus tree (Figure 6-3) from two equally most parsimonious trees was quite different from that of the other trees (Figures 2, 3, 6-1, 6-2).

The notable topological discrepancies between the tooth-based tree and all the other trees suggest that dental characters generate considerable phylogenetic noise. This interpretation can be supported by the fact that the tree statistics (i.e., tree length as well as CI and RI values) for the cladogram based solely on non-dental characters (Figure 6-2) are better than those for the cladogram based on the combination of dental and non-dental characters (Figure 6-1). Nevertheless, some taxonomic congruence (sensu Kluge, 1989) among all the consensus trees does exist. For example, all cladograms show *Alopias* monophyly. Also, *Odontaspis* and *Carcharias* occur near the base of each cladogram. These patterns suggest that dental characters provide at least some phylogenetic signal.

Evolutionary trends in lamniform dentition

General plan

I examined evolutionary trends of selected dental features through lamniform phylogeny. This was achieved by mapping some of my quantitative dental data on my cladogram based exclusively on non-dental characters in extant macrophagous lamniforms (Figure 6-2: i.e., the mapped data were independent of characters used to generate the cladogram). The mapped data were: tooth row counts (Appendix 2), average standardized crown height (Appendix 5), and average crown acuteness (Appendix 7).

Tooth row count

Among the macrophagous lamniforms, *Mitsukurina owstoni* has the largest total tooth row count, primar-

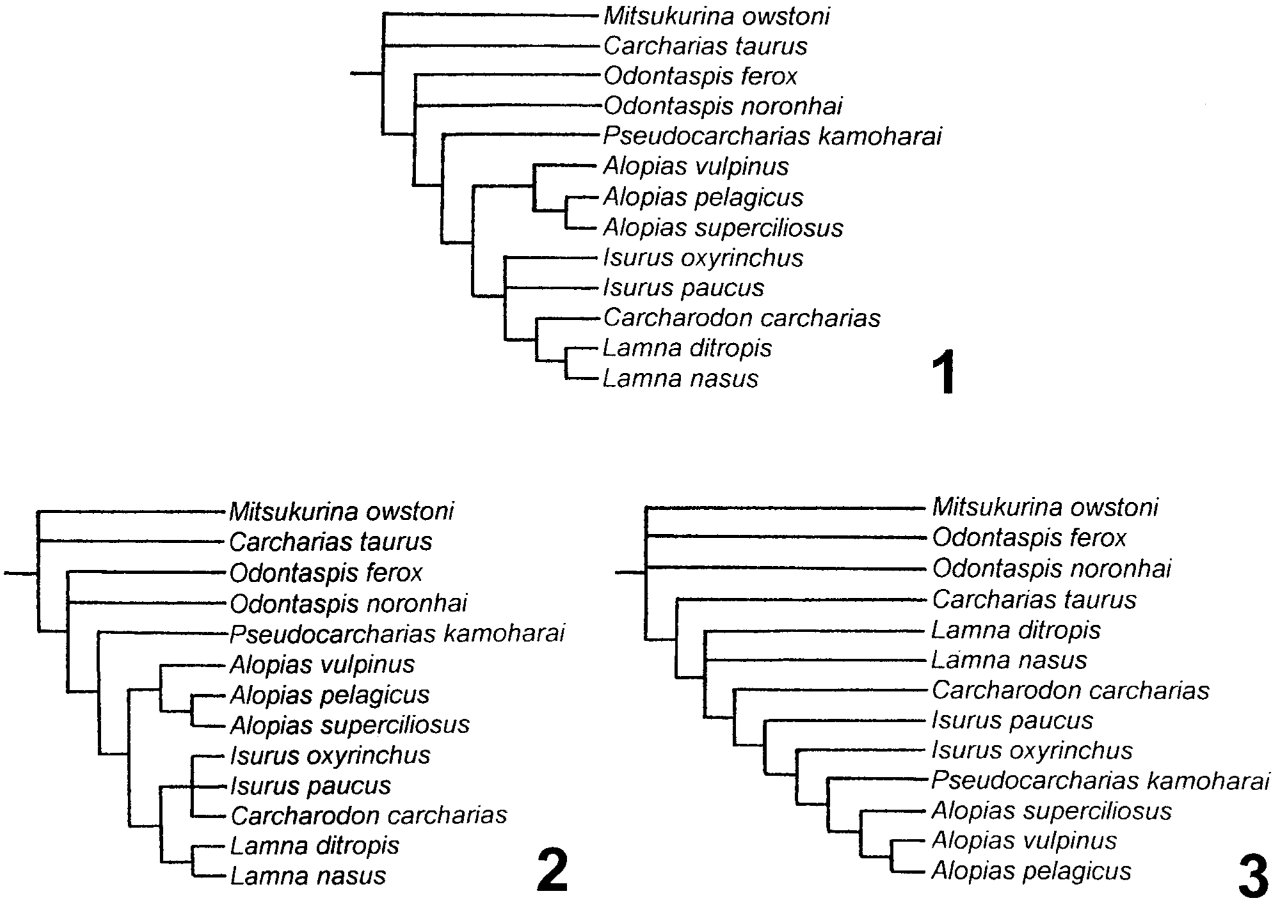

Figure 6. Consensus trees based on experimental analyses using *Mitsukurina owstoni* as an outgroup and removing *Megachasma* and *Cetorhinus*. **1**, tree based on dental and non-dental characters combined (48 characters; tree length = 82, CI = 0.65, RI = 0.78); **2**, tree based on non-dental characters alone (29 characters; tree length = 43, CI = 0.76, RI = 0.87); **3**, tree based on dental characters alone (19 characters; tree length = 33, CI = 0.63, RI = 0.76).

ily influenced by the number of lateral tooth rows (Appendix 2). Lamnid species show low tooth row counts compared to other lamniforms. Low tooth row counts also occur sporadically in non-lamnid taxa, such as *Pseudocarcharias kamoharai* and *Alopias superciliosus* (note that disproportionately large tooth row counts also occur sporadically in lamniform phylogeny: i.e., *Megachasma* and *Cetorhinus* in Figure 3). However, tooth row counts in macrophagous lamniform taxa other than *M. owstoni* and lamnids generally range between those of *M. owstoni* and lamnids. Thus, although *A. vulpinus* and *A. pelagicus* retain moderately high counts, tooth row counts appear to decrease through lamniform phylogeny.

Another possible evolutionary trend among macrophagous lamniforms is the loss of symphysial teeth in more derived taxa. For example, *Mitsukurina owstoni*, *Carcharias taurus*, and *Odontaspis* spp. usually possess one or more rows of symphysial teeth, whereas lamnids in particular rarely possess any rows of symphysial teeth (Appendix 2).

Standardized crown height

Among macrophagous lamniforms, mesially located teeth (particularly the lower ones) in the three monophyletic *Alopias* species (Figure 6-2) have smaller average standardized crown height values compared to those in the other species (Appendix 5; see also Character 61 in Appendix 3). *Alopias* spp. have diets similar to other extant macrophagous lamniforms (e.g., Compagno, 1984). However, *Alopias* spp. differ from other macrophagous lamniforms in their feeding habit in that they use their elongated tail (Figure 1) as a stunning device to assist in prey capture (e.g., Gubanov, 1972; Stillwell and Casey, 1976; Kitadani and Nishida, 1996). Like the two microphagous lamniforms, *Megachasma* and *Cetorhinus*, which have minute teeth (= low crown heights), teeth may be less important for food acquisition in *Alopias* compared to other macrophagous lamniform. If so, one can argue that, in lamniforms, standardized crown heights may reflect food types or feeding habits.

Crown acuteness

Average crown acuteness values (Appendix 7) mapped onto the cladogram (Figure 6-2) suggest that *Mitsukurina owstoni* generally has the narrowest crowns (i.e., high crown acuteness values) among extant macrophagous lamniform species. Within the lamnids, *Lamna* usually has narrower crowns than *Carcharodon* and *Isurus*, particularly in the lateral tooth rows. *Carcharias*, *Odontaspis*, and *Pseudocarcharias*, that are placed topologically between *Mitsukurina* and lamnids (Figure 6-2), tend to have crowns narrower than lamnids and broader than *Mitsukurina*. Crown acuteness in *Alopias* spp. is overall as broad as in *Carcharodon* and *Isurus*. These mapping results appear to suggest that the narrower crowns are plesiomorphic in lamniforms. Narrow crowns are efficient in grasping food, whereas broad crowns are generally associated with a well-developed cutting edge along the mesial and distal crown margins. Thus, "cutting teeth" are a derived feature within lamniforms.

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Appendix 1. List of examined specimens of extant, non-embryonic modern lamniforms. Total length (TL) and sex data are provided for specimens of which dental measurements were taken (''Measured specimens''; not applicable for microphagous forms due to uncertain dental homologies). ''Other examined samples'' are those of which only the tooth row counts were taken. Complete citation of specimens from literature (''Number of specimens from literature''), which offered tooth row counts (Appendix 2), can be found in Shimada (1999).

Mitsukurina owstoni (goblin shark). Measured specimens: CAS 113888, 120 cm TL, female; MCZ 1279, 110 cm TL, female; NMNH 50972, 335 cm TL, female; TU-Mistu1-01, 208 cm TL, male. Other examined specimens: none. Number of specimens from literature: at least 18 specimens.

Carcharias taurus (sandtiger shark). Measured specimens: AMNH 079962SD, 241 cm TL, male; LACM 39334-2, 273 cm TL, female; LACM 39335-1, 112 cm TL, male; LACM 39336-1, 113 cm TL, female; LACM 39336-2, 118 cm TL, male; LACM 39336-3, 140 cm TL, female; LACM 39336-4, 148 cm TL, male; LACM 39455-2, 120 cm TL, female; GH-Eug-01, 251 cm TL, female; GH-Eug-02, 271 cm TL, female. Other examined specimens: AMNH 053033SD, 059008SW, CAS 33487 (2 specimens); FMNH 16136, 51193A, 51193B; LACM 38116-46, 38290-11, 39334-3, 39336-5, 39336-6; NMNH 110888 (2 specimens), 110933, GH-Eug1-uncat (62 specimens). Number of specimens from literature: at least 683 specimens.

Odontaspis ferox (smalltooth sandtiger). Measured specimens: SIO 80-255, 214 cm TL, sex unknown; GH-Odont1-01, 314 cm TL, male; GH-Odont1-02, 275 cm TL, sex unknown. Other examined specimens: LACM uncat; GH-Odont1-uncat (3 specimens). Number of specimens from literature: at least 37 specimens.

Odontaspis noronhai (bigeye sandtiger). Measured specimens: GH-Odont2-01, TL unknown, sex unknown. Other examined specimens: none. Number of specimens from literature: 7 specimens.

Pseudocarcharias kamoharai (crocodile shark). Measured specimens: CAS 58069, 96 cm TL, female; GH-Pseud1-01, 103 cm TL, male; GH-Pseud1-02, 97 cm TL, female; GH-Pseud1-03, 99 cm TL, male; GH-Pseud1-04, 80 cm TL, male; GH-Pseud1-05, 51 cm TL, male. Other examined specimens: LACM 42155-1, 45857-1; NMNH 303206, 303207. Number of specimens from literature: at least 38(?) specimens.

Megachasma pelagios (megamouth shark). Measured specimens: none (not applicable). Other examined specimens: LACM 43745-1. Number of specimens from literature: 3 specimens.

Alopias pelagicus (Pelagic thresher). Measured specimens: LACM 38116-40, 170 cm TL, male; LACM 38116-39, 179 cm TL, female; LACM 38116-39, 241 cm TL, female. Other examined specimens: NMNH 196038; GH-Alop3-uncat (2 specimens). Number of specimens from literature: at least 13 specimens.

Alopias superciliosus (bigeye thresher). Measured specimens: CAS 76134, 372 cm TL, male; GH-Alop1-01, 325 cm TL, male; GH-Alop1-02, 386 cm TL, female; GH-Alop1-03, 386 cm TL, female; GH-Alop1-04, 404 cm TL, female; GH-Alop1-05, 320 cm TL, female; GH-Alop1-06, 356 cm TL, female; GH-Alop1-07, 343 cm TL, male; GH-Alop1-08, 312 cm TL, female; GH-Alop1-10, 339 cm TL, male; GH-Alop1-11, 291 cm TL, male; GH-Alop1-13, 305 cm TL, male. Other examined specimens: AMNH 79396SW; LACM 39320-1, 39321-1, 39571-1; MCZ 36215; SIO 81-132; GH-Alop1-12, GH-Alop1-uncat (5 specimens). Number of specimens from literature: at least 49 specimens.

Alopias vulpinus (common thresher). Measured specimens: CAS 65976, 155 cm TL, female; LACM 39325-1, 356 cm TL, sex unknown; LACM 39342-1, 131 cm TL, male; LACM uncatalogued (VP collection) 161 cm TL, female; MCZ 36089, 397 cm TL, sex unknown; GH-Alop2-01, 397 cm TL, sex unknown; GH-Alop2-02, 315 cm TL, male; GH-Alop2-03, 275 cm TL, sex unknown. Other examined specimens: CAS 5581, 20453, 52992; LACM 10, 35592-1, 36360-1, 36964-1, 36964-2, 36964-4, 36999-2 (11 specimens), 37000-1 (13 specimens), 37001-1 (2 specimens), 38453-1, 39319-1, 39323-1, 39324-1, 39327-1, 39328-1, 39329-1; NMNH 16203; GH-Alop2-04. Number of specimens from literature: at least 65 specimens.

Cetorhinus maximus (basking shark). Measured specimens: none (not applicable). Other examined specimens: CAS 2224, 25873; LACM 35876-1, 39461-1. Number of specimens from literature: 22 specimens.

Carcharodon carcharias (great white shark). Measured specimens: LACM 39474-1, 165 cm TL, male; SIO 55-95g, 181 cm TL, female; GH-Car1-01, 272 cm TL, male; GH-Car1-02, 170 cm TL, male; GH-Car1-06, 125 cm TL, male; GH-Car1-08, 523 cm TL, female; GH-Car1-09, 282 cm TL, female; GH-Car1-11, 474 cm TL, male; GH-Car1-13, 379 cm TL, male; GH-Car1-14, 554 cm TL, female; GH-Car1-15, 554 cm TL, female; GH-Car1-19, 594 cm TL, female. Other examined specimens: CAS 26245, 26378, 26694, 26781, 48413, 55467, 72090; LACM 37513-1, 38194-1, 39341-1, 39431-1, 42728-1, 43805-1; SIO 88-105; GH-Car1-03, GH-Car1-04, GH-Car1-05, GH-Car1-07, GH-Car1-10, GH-Car1-12, GH-Car1-16, GH-Car1-17, GH-Car1-18, GH-Car1-20, GH-Car1-21, GH-Car1-uncat (7 specimens). Number of specimens from literature: at least 95 specimens.

Isurus oxyrinchus (shortfin mako). Measured specimens: LACM 32667-1, 351 cm TL, female; LACM 39338-1, 121 cm TL, male; GH-Isur1-05, 198 cm TL, male; GH-Isur1-06, 254 cm TL, male; GH-Isur1-07, 320 cm TL, female; GH-Isur1-08, 264 cm TL, male; GH-Isur1-12, 274 cm TL, female; GH-Isur1-14, 183 cm TL, female; GH-Isur1-15, 304 cm TL, female; GH-Isur1-17, 277 cm TL, male; GH-Isur1-18, 76 cm TL, male. Other examined specimens: CAS 53202, 81629, 112678; FMNH 35587, 51196, 83731; LACM 3336, 30353-1, 39276-17, 39276-18, 39276-76, 39337-1, 39338-1 (another specimen), 39411-1, 39468-1, 39469-1, 39470-1, 39471-1, 39473-3, 39473-5, uncat (2 specimens); SIO 54-140, 54-149; GH-Isur1-01, GH-Isur1-02, GH-Isur1-03, GH-Isur1-04, GH-Isur1-09, GH-Isur1-10, GH-Isur1-11, GH-Isur1-13, GH-Isur1-16, GH-Isur1-18, GH-Isur1-uncat (39 specimens). Number of specimens from literature: at least 253 specimens.

Isurus paucus (longfin mako). Measured specimens: GH-Isur2-01, 224 cm TL, male; GH-Isur2-02, 263 cm TL, female; GH-Isur2-03, 427 cm TL, female; GH-Isur2-04, 240 cm TL, male; GH-Isur2-05, 286 cm TL, female; GH-Isur2-06, 254 cm TL, male; GH-Isur2-07, 385 cm TL, female; GH-Isur2-08, 206 cm TL, male; GH-Isur2-09, 414 cm TL, female; GH-Isur2-10, 284 cm TL, female; GH-Isur2-16, 229 cm TL, male; GH-Isur2-20, 221 cm TL, male. Other examined specimens: GH-Isur2-11, GH-Isur2-12, GH-Isur2-13, GH-Isur2-14, GH-Isur2-15, GH-Isur2-17, GH-Isur2-18, GH-Isur2-19, GH-Isur2-uncat (3 specimens). Number of specimens from literature: at least 24(?) specimens.

Lamna ditropis (salmon shark). Measured specimens: CAS 26683, 207 cm TL, male; CAS 112656, 92 cm TL, male; GH-Lamn2-01, 214 cm TL, male. Other examined specimens: CAS 55476, 55496; KS-Lamn2-uncat (discarded). Number of specimens from literature: at least 23 specimens.

Lamna nasus (porbeagle). Measured specimens: GH-Lamn1-03, 234 cm TL, female; GH-Lamn1-04, 229 cm TL, male; GH-Lamn1-10, 234 cm TL, male; GH-Lamn1-11, 229 cm TL, female; GH-Lamn1-12, 231 cm TL, female; GH-Lamn1-20, 224 cm TL, male; GH-Lamn1-21, 224 cm TL, female; GH-Lamn1-28, 152 cm TL, female; GH-Lamn1-34, 208 cm TL, female; GH-Lamn1-39, 204 cm TL, male; GH-Lamn1-43, 222 cm TL, male; GH-Lamn1-44, 104 cm TL, male. Other examined specimens: FMNH 51197; LACM 38174-1; MCZ 36251, 36252, 36253, 36254, 36258; GH-Lamn1-01, GH-Lamn1-02, GH-Lamn1-05, GH-Lamn1-06, GH-Lamn1-07, GH-Lamn1-08, GH-Lamn1-09, GH-Lamn1-13, GH-Lamn1-14, GH-Lamn1-15, GH-Lamn1-16, GH-Lamn1-17, GH-Lamn1-18, GH-Lamn1-19, GH-Lamn1-22, GH-Lamn1-23, GH-Lamn1-24, GH-Lamn1-25, GH-Lamn1-26, GH-Lamn1-27, GH-Lamn1-29, GH-Lamn1-30, GH-Lamn1-31, GH-Lamn1-32, GH-Lamn1-33, GH-Lamn1-35, GH-Lamn1-36, GH-Lamn1-37, GH-Lamn1-38, GH-Lamn1-40, GH-Lamn1-41, GH-Lamn1-42, GH-Lamn1-uncat (7 specimens). Number of specimens from literature: at least 54 specimens.

Appendix 2. Row count of each tooth type and total tooth row count in each extant lamniform species (for sample sizes, see Appendix 1; a complete list of tooth row counts in each sample as well as corrections of errors in published data can be found in Shimada, 1999). Abbreviations of species: Ap, *Alopias pelagicus*; As, *A. superciliosus*; Av, *A. vulpinus*; Cc, *Carcharodon carcharias*; Cm, *Cetorhinus maximus*; Ct, *Carcharias taurus*; Io, *Isurus oxyrinchus*; Ip, *I. paucus*; Ld, *Lamna ditropis*; Ln, *L. nasus*; Mo, *Mitsukurina owstoni*; Mp, *Megachasma pelagios*; Of, *Odontaspis ferox*; On, *O. noronhai*; Pk, *Pseudocarcharias kamoharai*. Abbreviations of tooth types, as for Figure 4. Most common row count (= modal count) followed by the minimum and maximum row counts as a range in parenthesis; asterisk = exclude *Megachasma pelagios* and *Cetorhinus maximus*.

Species	Row count based on tooth types				Total count
Upper dental series					
	S	A	I	L	
Mo	1(1–1)	2(2–2)	0(0–1)	23(19–28?)	26(22–32?)
Ct	1(1–2)	2(2–2)	1(0–5)	16(13–27)	20(16–36)
Of	1(0–2)	2(2–2)	4(2–6)	18(15–20)	25(19–30)
On	0(0–1)	2(2–2)	1(1–1)	17(14–18)	20(17–22)
Pk	0(0–0)	2(2–2)	1(0–2)	10(10–13)	13(12–17)
Mp	–	–	–	–	?(42–56)
Ap	0(0–2)	2(2–2)	1(1–2)	18(16–22)	21(19–28)
Ap	0(0–0)	2(2–2)	0(0–1?)	10(9–11)	12(11–14?)
Av	0(0–2)	2(2–2)	1(0–2)	20(16–26)	23(18–32)
Cm	–	–	–	–	?(100?–131)
Cc	0(0–0)	2(2–2)	1(1–1)	10(8?–11)	13(11?–14)
Io	0(0–0)	2(2–2)	1(0?–1)	10(8?–11)	13(10?–14)
Ip	0(0–0)	2(2–2)	1(1–1)	10(8–11)	13(11–14)
Ld	0(0–0)	2(2–2)	1(1–1)	12(9–13?)	15(12?–16?)
Ln	0(0–0)	2(2–2)	1(0–1)	11(10–13)	14(12–16)
Total Range	(0–2)	(2–2)	(0–6)	(8–28?)	(11–36)*
Lower dental series					
	s	a	i	l	
Mo	1(1–1)	2(2–2)	1(1–1)	21(19–26)	25(23–30)
Ct	1(1–1)	2(2–2)	1(1–1)	14(11–22)	18(15–26)
Of	1(1–2?)	2(2–2)	1(1–1)	18(13–20)	22(17–25?)
On	3(1–4)	2(2–2)	1(1–1)	16(13–17?)	22(17–24?)
Pk	0(0–0)	2(2–2)	1(1–1)	9(6?–11)	12(8–14)
Mp	–	–	–	–	?(43?–69)
Ap	1(0–1)	2(2–2)	1(1–1)	17(15–19)	21(19–23)
As	0(0–1)	2(2–2)	0(0–0)	9(8–10)	11(10–13)
Av	1(0–2?)	2(2–2)	1(1–1)	15(13–22)	19(16–27?)
Cm	–	–	–	–	?(100?–139)
Cc	0(0–0)	2(2–2)	1(1–1)	8(8–11)	11(11–14)
Io	0(0–0)	2(2–2)	1(1–1)	10(7–11)	13(10–14)
Ip	0(0–0)	2(2–2)	1(1–1)	9(8–10)	12(11–13)
Ld	0(0–1)	2(2–2)	1(1–1)	11(10–12?)	14(13–16?)
Ln	0(0–0)	2(2–2)	1(1–1)	10(8–13)	13(11–16)
Total Range	(0–4)	(2–2)	(0–1)	(6?–26)	(8–30)*

Appendix 3. Characters used in the cladistic analysis. Literature sources for extant forms: Characters 5–24, 26–27, and 34, based on data or illustrations in Compagno, 1988, 1990; Characters 8, 11, 14, and 15, inferred for *Odontaspis noronhai* from Sadowsky *et al.*, 1984, figure 3; Characters 36–41, based on illustrations in Compagno, 1984; additional information and sources, if any, are noted with each character description. Information on *Cretoxyrhina mantelli* is based on Shimada (1997a, 1997c, 2002a).

1. Dental bullae: [0] absent, [1] present (note: see Shimada, 2002a).
2. "Orbital process" (sensu Compagno, 1990) of palatoquadrate: [0] present, [1] absent (note: the orbital process is assumed to be fused with the upper dental bulla in *Pseudocarcharias kamoharai* [Compagno, 1990]).

3. Mesial process of palatoquadrate: [0] absent, [1] present (note: character for Clade 11b of Compagno, 1990).
4. Notch on dorsal side of palatoquadrate immediately lateral to upper dental bulla: [0] absent or shallow, [1] deep.
5. Rostral node of cranium: [0] absent, [1] present without vertical fenestra, [2] present with vertical fenestra.
6. Rostral appendices of cranium: [0] absent, [1] present.
7. Medial rostral cartilage of cranium: [0] narrow, [1] broad.
8. Rostral length anterior to nasal capsule compared to total cranial length: [0] short (proportion < 0.20), [1] long (proportion ≥ 0.20).
9. Separation between base of lateral rostral cartilages and nasal capsules: [0] absent, [1] present (note: character for Clade 12b of Compagno, 1990).
10. Lateral rostral cartilages form part of anterior fontanelle of cranium: [0] no, [1] yes.
11. Length of nasal capsules compared to cranial length behind rostrum: [0] long (proportion ≥ 0.30), [1] short (proportion < 0.30).
12. Ventral level of nasal capsules: [0] elevated above, or approximately equal to, level of basal plate, [1] depressed below level of basal plate.
13. Interruption of subethmoid fossa between right and left nasal capsules: [0] absent, [1] present.
14. Cranial width at preorbital processes compared to that at nasal capsules: [0] equal or narrower, [1] much wider.
15. Cranial width at postorbital processes compared to that at preorbital processes: [0] approximately equal or narrower, [1] much wider.
16. Orbital diameter compared to cranial length behind nasal capsules: [0] large (proportion ≥ 0.55), [1] small (proportion $<$ 0.55).
17. Dorsal extent of cranial roof: [0] approximately equal level to dorsal edge of orbit [1] arched far above dorsal edge of orbit (note: inferred for *Odontaspis noronhai* from Humphreys *et al.*, 1989, figure 1).
18. Cranial height (excluding rostral cartilages and nasal capsules) compared to cranial length behind nasal capsules: [0] low (proportion < 0.60) [1] moderate (proportion 0.60–0.70), [2] high (proportion > 0.70).
19. Cranial width at preorbital processes compared to cranial length behind level of preorbital processes: [0] approximately equal or greater ("short cranial roof"), [1] much lesser ("long cranial roof").
20. Overall outline of posterior edge of cranium when viewed dorsoventrally: [0] convex, [1] straight.
21. Prominent lateral wing (including "ectethmoid processes" of Compagno, 1990) of suborbital shelf of cranium: [0] absent, [1] present (note: modified from Character 12 of Shirai, 1996).
22. Stapedial foramina of cranium: [0] small, [1] medium, [2] large.
23. Secondary calcification of vertebrae with endochordal radii radiating from notochordal sheath: [0] absent, [1] present (note: modified from Character 76 of Shirai, 1996).
24. Total vertebral count: [0] ≤ 200, [1] >200 (note: additional data from Springer and Garrick, 1964; Compagno, 1988, 1990; Last and Stevens, 1994).
25. Nictitating lower eyelid (modified from Character 43 of Shirai, 1996): [0] present, [1] absent (note: additional data from Humphreys *et al.*, 1989).
26. Labial furrows: [0] present, [1] absent (note: additional data from Maul, 1955; Last and Stevens, 1994).
27. Intestinal valve type: [0] spiral, [1] ring (note: see Compagno, 1988, 1990; Carvalho, 1996; Shirai, 1996).
28. Number of turns of valvular intestine: [0] ≤ 32, [1] >32 (note: modified from character for Clade 7b of Compagno, 1990).
29. "Nuchal groove" on each side of head above gills: [0] absent, [1] present (note: character for Clade 9b of Compagno, 1990).
30. Precaudal pit at origin of upper caudal lobe: [0] absent, [1] present (note: character for Clade 2b of Compagno, 1990; see also Character 103 of Shirai, 1996).
31. Precaudal keel: [0] absent, [1] present (note: modified from Character 104 of Shirai, 1996; additional data from Compagno, 1990).
32. Secondary caudal keel: [0] absent, [1] present (note: character for Clade 12b of Compagno, 1990).
33. Pectoral fin origin: [0] under, or anterior to, fourth gill opening, [1] behind fourth gill opening (note: data based on Compagno, 1984, 1990).
34. Pectoral fin radials: [0] aplesodic, [1] plesodic (note: Character 66 of Shirai, 1996).
35. First dorsal fin radials: [0] aplesodic, [1] semiplesodic (note: modified from Character 83 of Shirai, 1996; see also character for Clade 7b of Compagno, 1990).
36. Position of first dorsal fin: [0] directly above or posterior to level of pelvic fins, [1] anterior to level of pelvic fins.
37. Height of second dorsal fin compared to first dorsal fin: [0] approximately equal, [1] approximately 1/2, [2] very low.
38. Size of pelvic fins compared to that of first dorsal fin: [0] approximately equal or larger, [1] much smaller.
39. Height of anal fin compared to that of first dorsal fin: [0] approximately equal or larger, [1] approximately 1/2, [2] much smaller.
40. Length of upper caudal fin lobe compared to precaudal body length: [0] much shorter, [1] approximately equal.
41. Length of lower caudal fin lobe compared to that of upper caudal fin lobe: [0] much shorter, [1] approximately equal.
42. Total number of tooth rows on each jaw (Appendix 2): [0] ≤ 40, [1] >40 (note: additional data from Compagno, 1988).
43. Upper symphysial teeth (Appendix 2): [0] present, [1] absent.
44. Lower symphysial teeth (Appendix 2): [0] present, [1] absent.
45. Upper extrabullar intermediate teeth (sensu Shimada, 2002a; Appendix 2): [0] absent, [1] present.
46. Modal row count of upper and lower lateral teeth (Appendix 2): [0] ≥ 13, [1] <13.
47. Long, fine vertical grooves on lingual surface of central cusp: [0] present, [1] absent.
48. Distal lateral cusplet(s) in adults: [0] present, [1] absent (note: presence of "mesial lateral cusplet(s)" is polymorphic in *Mitsukurina owstoni*).
49. Blade-like distal heel on lateral teeth: [0] absent, [1] present (note: modified from Character 20 of Long and Waggoner, 1996).
50. Shape of nutritive foramen on lingual protuberance of root: [0] long groove, [1] short groove or pit.
51. Distal inclination of central cusp of first upper anterior tooth (A1; Appendix 4): [0] vertical or weakly inclined (mean value ≤ 1.10), [1] strongly inclined (mean value > 1.10).
52. Distal inclination of central cusp of second upper anterior tooth (A2; Appendix 4): [0] vertical or weakly inclined (mean value ≤ 1.10), [1] strongly inclined (mean value > 1.10).
53. Mesial inclination of central cusp of first lower anterior tooth (a1; Appendix 4): [0] vertical or weakly inclined (mean value > 0.95), [1] strongly inclined (mean value ≥ 0.95).
54. Distal inclination of central cusp of second lower anterior tooth (a2; Appendix 4): [0] vertical or weakly inclined (mean value ≤ 1.10), [1] strongly inclined (mean value > 1.10).
55. Distal inclination of central cusp of first lower lateral tooth (l1;

Appendix 4): [0] vertical or weakly inclined (mean value ≤ 1.10), [1] strongly inclined (mean value > 1.10) (note: cf. Character 10 of Long and Waggoner, 1996).

56. Average standardized crown height (Appendix 5) of first lower anterior tooth (a1) compared to that of first upper anterior tooth (A1): [0] taller, [1] equal, [2] shorter.
57. Average standardized crown height (Appendix 5) of second lower anterior tooth (a2) compared to that of second upper anterior tooth (A2): [0] taller, [1] equal, [2] shorter.
58. Average tooth position of first lower lateral tooth (l1; Appendix 6): [0] value > 0.25, [1] value ≤ 0.25 (note: this character reflects the distal extent of lower dental bulla; see Shimada, 2002a).
59. Average crown acuteness of upper anterior teeth (Appendix 7): [0] narrow crown (value > 2.3), [1] broad crown (value ≤ 2.3).
60. Average crown acuteness of upper lateral teeth (Appendix 7): [0] narrow crown (value > 2.3), [1] broad crown (value ≤ 2.3).
61. "Size heterodonty" (differences in size of teeth within a dentition; Shimada, 2001) measured by average standardized crown height (Appendix 5) of lower anterior teeth: [0] strong (value of >0.5), [1] weak (value of ≤0.5) (note: the taller the anterior teeth are, the greater the size differences to distally located teeth).

Appendix 4. Average tooth inclination of selected teeth in each extant macrophagous lamniform species (see Appendix 1 for measured specimens). Abbreviation of species, as for Appendix 2; abbreviation of tooth rows, as for Figure 4.

Species (Sample size)	A1	A2	a1	a2	l1
Mo (4)	1.03	1.06	1.00	1.02	1.01
Ct (10)	1.08	1.11	1.02	1.07	1.09
Of (3)	0.97	1.09	1.02	1.08	0.99
On (1)	1.01	1.07	0.97	1.03	0.96
Pk (6)	1.14	1.19	1.03	1.12	1.21
Ap (3)	0.99	1.23	0.91	1.31	1.29
As (12)	1.00	1.11	1.05	1.16	1.31
Av (8)	0.91	1.09	1.07	1.08	1.11
Cc (12)	1.06	1.06	0.94	1.03	1.02
Io (11)	1.20	1.28	1.06	1.15	1.17
Ip (12)	1.12	1.18	1.00	1.08	1.15
Ld (3)	0.98	1.14	0.98	1.06	1.06
Ln (12)	1.04	1.24	0.97	1.08	1.04

Appendix 5. Average standardized crown height of each homologous tooth in upper and lower dental series of each extant macrophagous lamniform species. Sample sizes, abbreviations of tooth types and species, and other specifications, as for Appendix 4.

Row	Mo	Ct	Of	On	Pk	Ap	As	Av	Cc	Io	Ip	Ld	Ln
Upper													
A1	0.8	0.9	0.8	0.5	1.1	0.3	0.7	0.4	0.8	0.8	0.9	0.6	0.7
A2	0.6	0.8	0.8	0.6	1.0	0.3	0.7	0.4	0.8	0.8	0.9	0.5	0.6
I1	0.2	0.3	0.3	0.4	0.5	0.2	–	0.2	0.6	0.4	0.4	0.3	0.3
L1	0.5	0.6	0.5	0.4	0.6	0.3	–	0.4	0.7	0.5	0.6	0.4	0.5
L2	0.6	0.6	0.6	0.4	0.6	0.3	0.6	0.4	0.7	0.6	0.6	0.4	0.5
L3	0.6	0.6	0.6	0.4	0.6	0.3	0.6	0.3	0.7	0.6	0.6	0.4	0.5
L4	0.5	0.5	0.5	0.4	0.5	0.2	0.6	0.3	0.5	0.5	0.5	0.4	0.5
L5	0.5	0.4	0.5	0.4	0.4	0.2	0.5	0.3	0.4	0.4	0.4	0.4	0.4
L6	0.5	0.3	0.4	0.3	0.3	0.2	0.4	0.3	0.2	0.3	0.3	0.4	0.4
L7	0.4	0.2	0.3	0.3	0.2	0.2	0.4	0.3	0.2	0.2	0.2	0.3	0.3
L8	0.4	0.2	0.3	0.3	0.2	0.2	0.3	0.3	0.1	0.2	0.1	0.3	0.2
Lower													
a1	1.0	1.1	1.0	0.7	1.5	0.2	0.5	0.3	0.7	0.9	0.9	0.6	0.7
a2	1.0	1.1	1.0	0.7	1.3	0.3	0.5	0.4	0.7	0.9	1.0	0.6	0.7
i1	0.8	0.9	0.8	0.6	0.7	0.3	–	0.3	0.6	0.6	0.7	0.5	0.6
l1	0.6	0.6	0.6	0.6	0.6	0.2	0.5	0.3	0.5	0.5	0.6	0.5	0.5
l2	0.6	0.6	0.6	0.5	0.6	0.2	0.5	0.3	0.5	0.5	0.6	0.4	0.5
l3	0.6	0.5	0.5	0.5	0.5	0.2	0.4	0.3	0.4	0.4	0.4	0.4	0.5
l4	0.5	0.4	0.5	0.4	0.4	0.2	0.4	0.3	0.3	0.4	0.4	0.4	0.4
l5	0.5	0.3	0.4	0.4	0.3	0.2	0.4	0.2	0.2	0.3	0.3	0.4	0.4
l6	0.4	0.2	0.4	0.4	0.3	0.2	0.3	0.2	0.1	0.2	0.2	0.3	0.3
l7	0.3	0.2	0.3	0.3	0.2	0.1	0.2	0.2	0.1	0.2	0.1	0.3	0.2

Appendix 6. Average standardized tooth position of first lower lateral tooth row (l1) in each extant macrophagous lamniform species. Sample sizes, abbreviations of tooth types and species, and other specifications, as for Appendix 4. A value of zero indicates a position at the symphysis, and that of 1 at the jaw joint. Complete list of average standardized tooth position values can be found in Shimada (2002a, table 3).

Row	Mo	Ct	Of	On	Pk	Ap	As	Av	Cc	Io	Ip	Ld	Ln
l1	.30	.31	.29	.24	.36	.20	.20	.24	.36	.36	.35	.33	.32

Appendix 7. Average crown acuteness of each homologous tooth in upper and lower dental series of each extant macrophagous lamniform species. Sample sizes, abbreviations of tooth types and species, and other specifications, as for Appendix 4.

Row	Mo	Ct	Of	On	Pk	Ap	As	Av	Cc	Io	Ip	Ld	Ln
Upper													
A1	4.5	2.7	2.5	2.8	3.3	1.5	1.5	1.3	1.1	1.9	1.7	2.0	1.7
A2	4.3	2.5	2.5	2.7	2.5	1.2	1.4	1.1	1.1	1.5	1.5	1.9	1.5
I1	1.6	1.8	2.7	2.4	1.9	0.7	–	1.0	0.9	0.9	1.1	1.3	1.1
L1	3.6	2.0	2.2	2.3	1.6	0.7	–	1.1	1.0	1.0	1.1	1.5	1.3
L2	3.5	1.9	2.0	2.3	1.5	0.7	1.2	1.0	1.0	1.1	1.1	1.7	1.6
L3	3.3	1.8	1.9	2.3	1.3	0.7	1.0	0.9	1.0	1.1	1.1	1.5	1.4
L4	3.1	1.7	1.7	2.2	1.1	0.7	1.0	0.9	0.9	1.1	1.1	1.3	1.3
L5	3.0	1.5	1.7	2.0	1.0	0.7	0.9	0.9	0.9	1.0	1.0	1.6	1.3
L6	2.9	1.2	1.8	1.9	0.9	0.7	0.8	0.9	0.9	0.9	0.9	1.5	1.3
L7	2.6	1.1	1.8	1.7	0.8	0.6	0.7	0.8	0.7	0.8	0.8	1.4	1.2
L8	2.4	0.8	1.8	1.9	0.7	0.6	0.6	0.8	0.7	0.7	0.6	1.2	1.2
Lower													
a1	5.0	3.2	3.0	2.8	4.2	1.1	1.3	1.2	1.7	2.5	2.1	2.5	2.1
a2	5.1	3.0	2.8	3.1	3.4	1.0	1.2	1.2	1.5	2.2	1.8	2.2	1.9
i1	4.7	2.6	2.7	2.8	2.6	0.9	–	1.1	1.4	1.4	1.4	2.0	1.8
l1	4.2	2.3	2.4	3.1	2.3	0.8	1.1	1.0	1.4	1.2	1.3	1.9	1.8
l2	4.2	2.2	2.4	2.8	2.1	0.8	1.0	0.9	1.3	1.2	1.2	1.9	1.8
l3	4.1	2.1	2.4	2.7	1.9	0.7	0.9	0.9	1.3	1.2	1.2	1.8	1.7
l4	3.8	1.9	2.3	2.7	1.5	0.7	0.8	0.9	1.2	1.1	1.1	1.7	1.7
l5	3.8	1.4	2.2	2.6	1.3	0.6	0.7	0.8	1.1	1.0	1.0	1.6	1.7
l6	3.4	1.0	2.4	2.7	1.0	0.5	0.6	0.7	0.9	0.9	0.8	1.6	1.6
l7	2.9	0.8	2.2	2.0	0.8	0.5	0.5	0.6	0.6	0.8	0.6	1.6	1.3