

## Speculations on the Size and Morphology of the Extinct Lamnoid Shark, *Parotodus benedeni* (le Hon)

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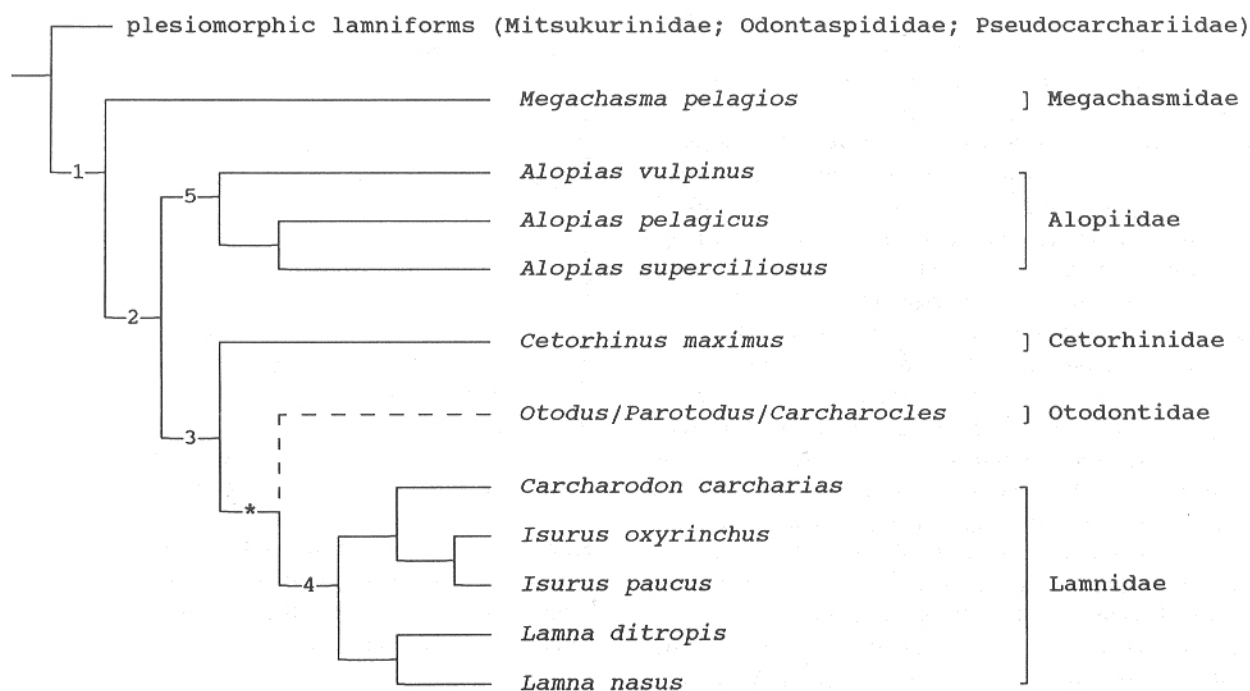
**ABSTRACT** — The body length, weight and appearance are reconstructed for the extinct lamnoid shark, *Parotodus benedeni* (le Hon). Disparate body length estimates based on tooth height and upper jaw perimeter suggest a fundamentally different set of scaling relationships than those in the similarly-sized extant species, *Carcharodon carcharias*. Body form was probably conservative, and similar to that of living lamnids. Implications of decoupled scaling functions on length estimates of the larger otodontid, *Carcharocles megalodon*, are also discussed.

### Introduction

The extinct lamnoid shark *Parotodus benedeni* (Lamniformes, Otodontidae) is a rare and, until recently, poorly known Cenozoic species. The recent description of a reconstructed dentition of this species (Kent and Powell, this volume) now allows a more detailed assessment of the size and, ultimately, paleobiology of this species. Body size, or more specifically body weight, is one of the most important attributes to be elucidated during paleobiological reconstructions of extinct species. Body weight is correlated with a number of ecological and physiological factors, such as, population density, diet, community structure, metabolism, thermoregulation and growth

rates (Damuth, 1981; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Damuth and MacFadden, 1990). Mammalian paleobiologists have been particularly active in the various aspects of size estimation, ranging from the comparisons of methodologies to the analysis of functional morphology and the evaluation of paleoecological inferences.

Paleobiologists have made few size estimates for fossil sharks. This paucity of published studies is more a reflection of the nature of the available evidence, than a lack of interest on the part of researchers. Although sharks have probably the most extensive fossil record of any vertebrate (Maisey, 1984), it consists almost exclusively of isolated teeth. Estimating the body length and weight from isolated teeth requires extrapolation from



**Figure 1.** Cladistic analysis of advanced lamniform whole body morphology (redrawn from Compagno, 1990). See text for details of numbered ancestral nodes. The inferred position of the otodontids in the cladogram is based on the hypothesized origin of both otodontids and lamnids from *Cretolamna* (Casier, 1960; Cappetta, 1987). Position of the ancestral *Cretolamna* is indicated by an asterisk (\*).

a very restricted portion of the body. Potentially more accurate measurements, such as skull length or total body length are almost never available. Randall (1973) published data on the body length of the extant great white shark, *Carcharodon carcharias* (Lamniformes, Lamnidae), with respect to (1) the enamel height of the largest upper anterior tooth, (2) the perimeter of the upper jaw, and (3) the body weight. This data is unique in that it can be used for size estimates (both length and weight) of extinct lamnoid sharks. Randall uses this data to estimate the maximum length of the extinct giant white shark, *Carcharocles megalodon* (Lamniformes, Otodontidae) at about 13 m. Most other estimates of size for fossil sharks (e.g., Hansen, 1978) have relied on more tenuous assumptions.

*Parotodus benedeni*, although rare, is widely distributed in fossil beds in temperate regions worldwide (Kent and Powell, this volume). However, other than descriptions of individual *P. benedeni* teeth, relatively little is known of this species. The dual purpose of this paper is to (1) describe and evaluate estimates for the body length and body weight of *P. benedeni*, and (2) use cladistic techniques to reconstruct a plausible whole-body morphology for *P. benedeni*.

## Methods

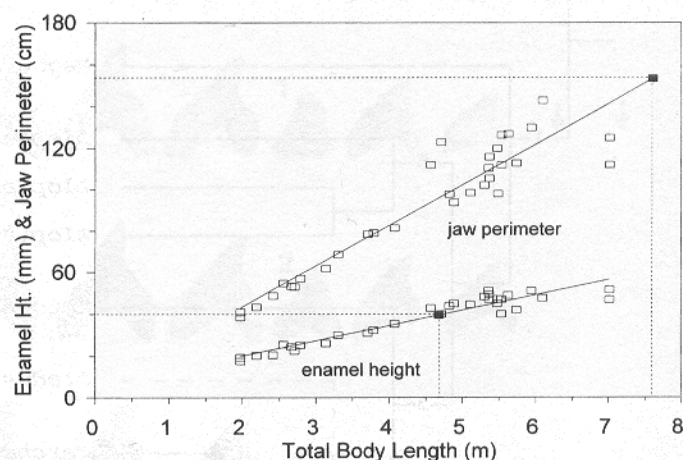
The body length of *Parotodus benedeni* was estimated by utilizing two different correlations (data in Mollet, et al., 1996) for *C. carcharias*; (1) the enamel height of upper anterior teeth, and (2) the perimeter of the upper jaw. The obvious advantage of having two separate estimates is that they are independent, mutually supportive, appraisals of body size. However, there is a second, and perhaps more important, benefit. In *C. carcharias* there are distinct interrelationships between tooth size, dentition length and body length that have been evolutionarily derived. If independent estimates of body length in *P. benedeni* provide similar values, this implies a similar set of scaling relationships within this species, as well. But, if the independent estimates of size are markedly dissimilar, this suggests fundamental scaling differences between living and extant species that may have important ecological ramifications (Van Valkenburgh, 1990).

Since the extinct otodontids (*Otodus*, *Parotodus* and *Carcharocles*) are lamniforms that are most closely allied to the extant lamnids (Cappetta, 1987), a plausible whole body morphology of *P. benedeni* can be reconstructed by evaluating the distribution of synapomorphic traits among lamniform sharks. The most detailed cladistic analysis of the lamniform sharks was produced by Compagno (1990; Figure 1). Also of interest, for understanding the thermal biology of *P. benedeni*, is the ability to maintain elevated body core temperatures (= gigantothermy; Paladino, et al., 1990) among lamniform sharks, since this phenomenon is known in the genera *Alopias*, *Carcharodon*, *Lamna* and *Isurus* (Carey and Teal, 1969; Carey, et al., 1981, 1982, 1985).

## Results

Using *C. carcharias* data (Mollet, et al., 1996) and measurements from the dentition described by Kent and Powell (this volume), two different estimates of *P. benedeni* body length were obtained (Figure 2). The first estimate was based on the enamel height of the largest upper anterior tooth in the dentition (= 39.5 mm), and was slightly less than 4.7 m. The second estimate used the upper jaw perimeter of the dentition. Unfortunately, the upper jaw perimeter cannot be measured directly, since it consists of the upper tooth row lengths plus the tooth-free spaces between the posterior teeth and the jaw articulation. Using tooth spacings comparable to those of extant lamnids, the upper jaw tooth rows measured a total of 131 cm. Measurements on an extant *C. carcharias* jaw (USNM 232642) indicate that the tooth-free space increases the total jaw perimeter by about 17%. For the *P. benedeni* dentition, this yields an upper jaw perimeter of 153 cm and an estimated body length of about 7.6 m. The substantial difference between the enamel height and jaw perimeter estimates of *P. benedeni* body length (4.7 vs. 7.6 m) is not solely due to the estimated tooth-free gape. Using the upper jaw tooth rows alone still produces an estimated body length of 6.5 m.

Published length-weight regressions for lamnid sharks yield widely divergent predictions of body weight in *P. benedeni* (Table 1). The estimated weights based on the enamel height derived body length of 4.7 m ranges from 928 to 1066 kg, while the longer body length estimate of 7.6 m produced from the upper jaw perimeter yields weights of 4118 to 4822 kg.



**Figure 2.** Estimated total body length for the *Parotodus benedeni* with the dentition described by Kent and Powell (this volume). Estimates based on published data for *Carcharodon carcharias* (Mollet, et al., 1996).

**Table 1.** Estimated body weight (kg) of *Parotodus benedeni* based on published data for total length (m) and body weight (kg) of extant lamnids, with fork length correction for Casey and Kohler (1992).

Extant Species (Reference)	Body Length Range (Sample Size)	Regression Equation	<i>Parotodus</i> Est. Wt. based on Enamel Height	<i>Parotodus</i> Est. Wt. based on Upper Jaw Perimeter
<i>C. carcharias</i> (Mollet & Cailliet, 1996)	0.96-4.65 (327)	$W = 7.914 TL^{3.096}$	953	4221
<i>C. carcharias</i> (Compagno, 1984)	1.27-5.54 (98)	$W = 8.27 TL^{3.14}$	1066	4822
<i>I. oxyrinchus</i> (Stevens, 1983)	0.58-3.43 (80)	$W = 7.658 TL^{3.10}$	928	4118
<i>C. carcharias</i> (Gottfried, et al., 1996)	Not specified (175)	$W = 7.332 TL^{3.174}$	996	4581
<i>I. oxyrinchus</i> (Casey & Kohler, 1992)	Not specified (2081)	$W = 9.933 FL^{3.155}$ ( $FL = 0.929 TL - 0.017$ )	1024	4687

Lamnid external morphology is relatively conservative (Compagno, 1990). Since the otodontids, including *P. benedeni*, appear to be more closely related to lamnids than any other extant group (Casier, 1960; Cappetta, 1987), they probably resembled them in many respects. Probable advanced lamniform synapomorphies found in *P. benedeni*, would include (Figure 1; ancestral node and familial distribution listed in parentheses):

1. elongate pectoral fins (node 1; Megachasmidae, Alopiidae, Cetorhinidae, Lamnidae),
2. elevated 1st dorsal fin (node 2; Alopiidae, Cetorhinidae, Lamnidae),
3. stiff, fusiform body; lunate tail; restricted jaw protrusion; enlarged gill slits; depressed caudal peduncle; caudal keels (node 3; Cetorhinidae, Lamnidae), and
4. reduced second dorsal and anal fins with pivoting bases; gigantothermy (nodes 4 and 5; Alopiidae, Lamnidae).

Compagno (1990) suggests that the second dorsal and anal fins of the alopiids and lamnids evolved independently (nodes 4 and 5), but an earlier appearance (node 2) and subsequent loss in the cetorhinids is equally likely (Abbott, et al., 1985). Similarity, the appearance of gigantothermy in the lamnoids could have followed either of these evolutionary trajectories. Gigantothermy in fishes allows efficient foraging in colder waters (Block, et al., 1993) and is consistent with the temperate distribution of *P. benedeni* (Kent and Powell, this volume).

## Discussion

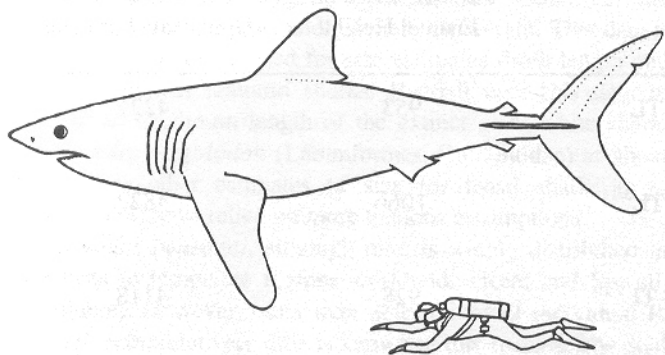
The widely disparate *P. benedeni* body length estimates based on anterior tooth enamel height and upper jaw perimeter suggest a fundamental divergence from the *C. carcharias* paradigm. Such differences are not surprising since *P. benedeni*

has anterior teeth with short, robust crowns, rather than the tall, blade-like crowns of *C. carcharias*. Of the two estimates, that based on the jaw perimeter is probably the more reliable. The short crowns of *P. benedeni* would lead to a substantial underestimate of body length, producing a relatively short shark with absurdly large jaws. Further, studies on size estimation of fossil mammals suggest that, in general, the larger the body component studied, the more reliable the estimate of overall body size (e.g., various papers in Damuth and MacFadden, 1990). On general principles alone, we would expect the jaw perimeter to provide a more reasonable estimate than that obtained from a single tooth.

The weight estimates for *P. benedeni* are more difficult to assess, since weight varies more drastically through time than length, in response to the health and nutritional state of the individual. Further, even slight differences in body length can lead to substantial differences in weight because weight approximates a cubic function of length (Schmidt-Nielsen, 1984). Despite the disparate origins of the data in Table 1, the estimates are not that dissimilar. For the more likely body length estimated from the jaw perimeter, all three produce reasonably consistent weight estimates of about 4100 to 4800 kg.

Individual species also evolve autapomorphic traits that are specific to their life style. Kuga (1985) and Cappetta (1987) concluded that *P. benedeni* was an offshore, pelagic species, based in its wide distribution, association with midocean manganese nodules, and general rarity in neritic fossil beds. Extant open-ocean sharks (*Alopias superciliosus*, *Isurus paucus*, *Carcharhinus longimanus*, *Prionace glauca*) have independently evolved wing-like "oceanic" pectoral fins that allow them to swim very slowly when stalking prey (Compagno, 1988). Given the known geographic and bathymetric distribution

of *P. benedeni*, such fins are a plausible autapomorphy in this species, as well. Taking the estimates of size derived from the described *P. benedeni* dentition and the probable whole body morphology of this species, it is possible to reconstruct this species as it might appear if it were alive today (Figure 3).



**Figure 3.** Reconstructed appearance of *Parotodus benedeni* compared to a human diver.

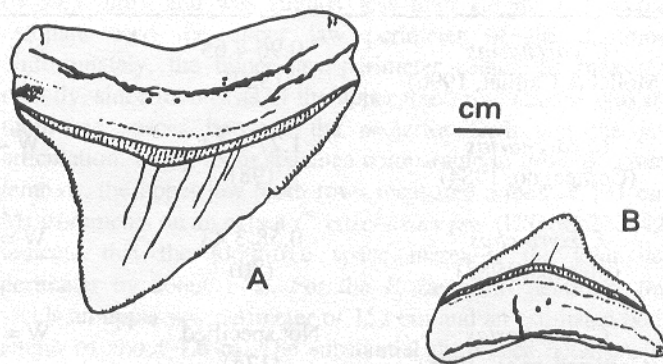
The estimated size of *P. benedeni* reported here probably does not reflect the maximum for this species. Cappetta (1987) lists the largest teeth for this species as having a vertical height of about 6 cm, comparable to the largest teeth in the dentition used in this study. However, several larger, unassociated teeth of *P. benedeni* (largest = 7.2 cm) are known from private collections. These teeth suggest that the largest *P. benedeni* could reach body lengths perhaps 20% longer than that reported here.

The decoupled scaling of anterior tooth size with upper jaw perimeter in the *P. benedeni* dentition also suggests that present body length estimates for an even larger otodontid, the giant white shark (*C. megalodon*), must be reevaluated. Specifically, if scaling of body length with the dentition is similar in *C. megalodon* and *P. benedeni*, the use of upper anterior tooth size could substantially underestimate body length in either species.

The two most carefully documented estimates of body length in *C. megalodon* are about 13 m (Randall, 1973; based on the enamel height of upper anterior teeth) and at least 16 m (Gottfried, et al., 1996; based on the total midline height of upper anterior teeth). Both estimates implicitly assume that *C. megalodon* had coupled scaling functions like those of *C. carcharias*.

There is some circumstantial evidence that *C. megalodon* scaling functions more closely resemble those of *P. benedeni*. Like the latter species, *C. megalodon* has low, broad posterior teeth (Figure 4) that differ from the somewhat narrower posterior teeth of extant lamnids. Tooth 4A has a height of 6.0 cm and a width of 7.1 cm, while tooth 4B is 3.1 cm tall and 4.9 cm wide. Using *P. benedeni* scaling functions (e.g., for upper teeth see Figure 4 in Kent and Powell, this volume), the largest anterior tooth corresponding to tooth 4A would be between 9.3 and 10.1 cm tall and for tooth 4B, between 8.3 and 9.3 cm in height. But when *C. carcharias* tooth scaling is used (e.g., Figure 4B in

Kent and Powell, this volume), the minimum height estimate for the anterior teeth corresponding to these posterior teeth is 23-25 cm. This is a remarkable 6-8 cm greater than the largest, reliably measured *C. megalodon* tooth (R. Purdy, pers. comm.). Further, the specimens shown in Figure 4 are not exceptional. Even larger posterior *C. megalodon* teeth are known from private collections.



**Figure 4.** Posterior *Carcharocles megalodon* teeth from the basal Yorktown Formation (Lee Creek Mine, Aurora, North Carolina) in the author's collection at the University of Maryland. A, left P<sup>1</sup> tooth (UMLS 12047); B, right P<sub>3</sub> tooth (UMLSP 11207).

While the presence of large posterior teeth suggests that current *C. megalodon* body length assessments may have underestimated the size of this species, the magnitude of this error is unclear. Of the available estimates, that of at least 16 m by Gottfried, et al. (1996) seems the most tenable. Unfortunately, the reliability of this estimate is uncertain, since the degree of decoupling, associated with the deeper, more acutely angled roots of *C. megalodon* anterior teeth, has yet to be rigorously evaluated.

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