Reconstructed Dentition of the Rare Lamnoid Shark
Parotodus benedeni (le Hon) from the Yorktown Formation
(Early Pliocene) at Lee Creek Mine, North Carolina

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ABSTRACT — An assemblage of 114 teeth of the extinct lamnoid shark Parotodus benedeni (le Hon) collected from the basal Yorktown Formation is described. Available evidence supports the interpretation of this assemblage as the remains of an originally intact dentition. The dentition reconstructed from this assemblage exhibits moderate denticulate and disjunct monognathis heterodonty with surprisingly large lateral and posterior teeth.

Introduction

The extinct lamnoid shark Parotodus benedeni is presently known only from its large, robust teeth. Typically these teeth are found as isolated specimens, although three assemblages of P. benedeni teeth have been previously reported — one from the Oligocene of New Zealand (Davis, 1888), one from the Miocene of Australia (illustrated without discussion in the popular work by Alston, et al., 1986), and one from the Miocene of Japan (Osawa, et al., 1978). The first two assemblages are relatively small, each having twenty or fewer teeth. The Japanese assemblage is somewhat larger (about 44 teeth) and has associated dermal denticles.

In overall form, the teeth of P. benedeni superficially resemble those of mako sharks in the genus Isurus (= Oxyrhina), to which this species was originally assigned (as O. benedeni). However, the teeth of this species are sufficiently distinctive that Cappetta (1980) placed them in a new monotypic genus, Parotodus. Kuga (1985) independently concluded that this species did not belong in Isurus and erected the genus Uyenoa (now a junior synonym of Parotodus). The teeth of Parotodus differ from those of Isurus in being remarkably massive, with short stout crowns and corpulent roots. Parotodus also differs from Isurus in a number of fine details of tooth morphology, leading Cappetta (1980) and Kuga (1985) to ally Parotodus with the genera Otolus Agassiz, 1843b and Carcharocles Jordan and Hannibal, 1923a (Lamniformes, Otodontidae).

P. benedeni has been previously reported in temperate zone fossil beds from the early Oligocene into the early Pliocene of Europe, West and South Africa, Australia, New Zealand, Japan, and North America (Davis, 1888; Davies, 1964; Osawa, et al., 1978; Kuga, 1985; Alston, et al., 1986; Cappetta, 1987). Although widespread, this species is typically rare.

This paper has two purposes. First, to describe an assemblage of 114 P. benedeni teeth collected from a small, restricted site in the lower Yorktown Formation in the Lee Creek Mine, Aurora, North Carolina, U.S.A. This assemblage is more than twice as large as any other known for P. benedeni, and is the first for this species reported from either the Atlantic Ocean or the Pliocene. Second, to reconstruct the appearance of an intact Parotodus dentition from the assemblage and compare this reconstruction with the dentitions of other lamnoids.

Collection

The assemblage described here was collected from a spoil pile in Lee Creek Mine, on the south shore of the Pamlico River, near Aurora, Beaufort County, North Carolina, U.S.A. Although these redeposited sediments lack precise stratigraphic controls, the excavation method used at the mine causes specific strata to be deposited in localized regions within the spoil piles (Gibson, 1987). Further, the teeth were confined to a relatively restricted site on one face of a single spoil pile. A total of ten P. benedeni teeth were collected on the sediment surface of the site during three different trips to the site in the early autumn of 1992. This relatively large number of teeth from a small area suggested that an assemblage could be present. Consequently, the site was excavated with a water pump. Sixty-eight whole and broken teeth were collected from an excavation roughly 0.9 m long, 0.7 m wide and 0.5 m deep (Figure 1; excavation a). During a second trip an additional ten teeth and fragments were collected with the aid of a water pump from an excavation 0.5 m long x 0.4 wide x 0.5 m deep located about 1.5 m northwest of the original excavation (Figure 1; excavation b). Four of the collected fragments matched broken teeth collected during the
first hydraulic excavation. The area around these two excavations was washed and screened with the water pump, ultimately enlarging the excavated portion of the site to 3.6 x 2.4 x 0.8 m (Figure 1: excavation c).

Figure 1. Overview of the Parotodus benedeni tooth assemblage site, Lee Creek Mine, on the south shore of the Pamlico River, near Aurora, Beaufort County, North Carolina. Sectional view of main site shown at lower left; see text for details.

Heavy rains during the winter of 1992-93 eroded the site and washed teeth downslope, redepositing them in two large gullies and a delta in a temporary pond at the base of the site. Sediment in the gullies and delta were carefully washed and screened with a water pump during the spring and autumn of 1993.

During this prolonged collecting period three additional P. benedeni teeth were obtained from the sediment surface of the site by fossil collectors not affiliated with the main excavation. These specimens were subsequently obtained by the authors.

The surrounding sediment was an apparently pure sample of basal Yorktown Formation material with essentially no intrusion of sediments from the underlying Pungo River Formation or overlying higher levels of the Yorktown Formation. The sediment was a blue, silty sand with numerous black phosphate nodules of small to moderate size. Characteristic basal Yorktown species, such as the scallops Placopeten clintonius clintonius and Chesapetic jeffersonius jeffersonius, were abundant at the site. Barnacles, shark teeth and cetacean bone fragments were also common. The lithology and associated fauna of the site suggest that the tooth assemblage was originally deposited in either the upper portion of unit 1 or the lower portion of unit 2 of the Yorktown Formation, with estimated water depths of 80 to 100 m (Gibson, 1983, 1987).

The minimum age for the assemblage is 4.4 ± 0.2 million years, based on K/Ar date for glauconite from sediments immediately above the correlated Placopeten horizon along the James River in Virginia (Blackwelder and Ward, 1976). Correlations between microfossils and radiometric dates suggest the maximum age for the assemblage (i.e., the base of the Placopeten horizon in Lee Creek Mine) is about 4.8 million years (Hazel, 1983).

The junior author has deposited the tooth assemblage in the Smithsonian Institution, United States National Museum of Natural History (USNM 489114).

Analysis

The P. benedeni teeth in the assemblage exhibit the full range of morphologies and relative sizes that would be expected for a typical lamniform dentition (Plates 1-4; Bigelow and Schroeder, 1948; Cappetta, 1987, p. 13). The largest specimens have tall, prominent crowns that are indicative of anterior teeth. The upper anterior teeth, as is typical of many lamniforms, have crowns that are broad and distally inclined, with a flat or slightly concave labial face. Lower anterior teeth are narrower, more nearly erect, and have a convex labial face. The roots of the lower anterior teeth are also thicker and more massive than those of the upper anterior teeth. Specimens of intermediate size have lower crowns, but otherwise resemble anterior teeth in that the crowns have narrow, erect, and more robust roots. Posterior teeth are all comparable in form, with low strongly oblique crowns and large roots.

Several sets of pathological teeth occur in the assemblage. While most of the distortions are minor, four teeth are exceptionally deformed (Plate 4, teeth 1-4). The crowns of these teeth are very small and claw-like. Two of these teeth have labially-directed crowns, the third has the crown bent lingually, and the fourth has a fractured crown. The roots of all four specimens are compact and globular with labially-directed root lobes. These teeth are also of graded size, with linear size increasing 5-10% between specimens. Strongly pathological teeth of similar form have been previously described from P. benedeni (Lawley, 1881; Oxyrhina fossils, plate 4, figures 4 and 4a).

Several lines of circumstantial evidence suggest that this assemblage of teeth represents the remains of a dentition. First, P. benedeni is a rare shark in the general study area. The senior author has made an extensive stratigraphically-controlled collection of makos shark (Isurus) teeth at Lee Creek Mine, currently numbering slightly more than 1,900 specimens. Yet despite the overall similarity in tooth size and shape between Isurus and Parotodus, only one P. benedeni tooth has been collected. The junior author has more than 17,000 teeth from Lee Creek Mine, but only six from P. benedeni (prior to the collection of the assemblage described here). The rarity of this species in Lee Creek Mine (as elsewhere; Cappetta, 1987) makes it extremely unlikely that more than 100 unrelated teeth would be found in such a restricted area.

Second, the teeth represent a full range of morphologies in graded sizes, from presumed upper and lower anteriors, laterals and posteriors from both the left and right sides of the jaw. These obvious relationships between size and shape support the interpretation of this assemblage as the remnants of a dentition, rather than assembled by postmortem winnowing and redeposition.
Third, the presence of several sets of pathological teeth of similar morphology and graded size suggests the presence of a partial dentition. The unique shapes of these teeth indicate that each set probably represents successive tooth generations in a single tooth file.

As persuasive as this circumstantial evidence may be, it does not provide unambiguous evidence for the presence of a dentition. More definitive statistical tests are required to fully support this interpretation. Specifically, if the *P. benedeni* assemblage originated from a single individual, it should be statistically distinct from an unassociated, time-averaged sample derived from numerous individuals of dissimilar sizes, ages and genders. Ideally, this assemblage should be compared to a time-averaged sample of teeth from *P. benedeni*. Unfortunately, the rarity of *P. benedeni* precludes obtaining such a stratigraphically-controlled, time-averaged sample of this species. Instead, a time-averaged sample of 110 *Isurus hastalis* teeth from units 1 and 2 of the Yorktown Formation in Lee Creek Mine was used for comparison. This common species has teeth of comparable size and shape to those of *P. benedeni*. Further, the statistical properties of this time-averaged tooth sample of *I. hastalis* is representative of a wide range of shark species from Lee Creek Mine (Kent, unpubl. data).

The *P. benedeni* assemblage has a very distinctive size-frequency distribution with a preponderance of large teeth and progressively fewer smaller specimens (Figure 2A). This differs markedly from the slightly skewed, weakly lognormal size-frequency distribution for unassociated teeth of the lamnoid *Isurus hastalis*. The difference between these two distributions is readily apparent and highly significant (Kolmogorov-Smirnov test, $D = 0.33, P < 0.01$).

This assemblage also displays a high degree of correlation between tooth height and the orthogonal metrics, tooth width ($r = 0.90$) and tooth thickness ($r = 0.95$), and the non-orthogonal metric of coronal angle ($r = 0.67$; Figure 2B). By comparison, the unassociated *I. hastalis* teeth have consistently lower correlation coefficients ($r = 0.80, 0.87$, and $0.24$, respectively). These lower correlation coefficients are again typical for unassociated shark teeth from Lee Creek Mine (Kent, unpubl. data), and undoubtedly reflect the combination of both within- and between-individual variation in time-averaged samples.

A dentition for *P. benedeni* was reconstructed, based on the teeth in this assemblage. The initial problem in constructing such a dentition is to determine the probable number of tooth files in each jaw. Glückman (1964) suggests that there are ten to twelve files on each side of the jaw for members of the family Otodontidae. However, he provides no supporting data and this estimate appears to be based on the dentitions of living lamnids. The recently reconstructed *Carcharocles megalodon* dentition at the U.S. National Museum of Natural History (Washington, DC) uses slightly higher numbers of files (thirteen upper and twelve lower files; R. Purdy, pers. comm.). Since *Parotodus* and *Carcharocles* are apparently sister groups (Cappetta, 1987), the initial attempts at reconstruction assumed that there were about twelve files in each half jaw.

Position-dependent changes in tooth form along the jaw are more difficult to assess without using the dentitions of living sharks as models. Dentitions of six species of extant lamniforms

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**Figure 2.** Statistical description of the *Parotodus benedeni* tooth assemblage. A. size-frequency distribution for the *Parotodus benedeni* assemblage (filled bars) and a time-averaged sample of *Isurus hastalis* (hatched bars). B. linear regressions of tooth height with other tooth metrics for the *Parotodus benedeni* assemblage, tooth width ($\square; r = 0.91$), tooth thickness ($\blacksquare; r = 0.95$) and coronal angle ($\ast; r = 0.64$).
were used to survey trends in tooth morphology along tooth rows. Four of these species are lamnids, and are presumably the closest living relatives of Parotodus — the shortfin mako (Isurus oxyrinchus), the longfin mako (I. paucus), the porbeagle (Lamna nasus) and the great white (Carcharodon carcharias). The other two extant species studied were aleopids — the common thresher (Alopias vulpinus) and the bigeye thresher (A. superciliosus). While not as closely allied to Parotodus as the lamnids, they have teeth that superficially resemble those of Parotodus.

These extant sharks not only exhibit markedly different dentitions, but also wide variation in tooth size. Cappetta (1987) lists maximum heights as 1.5 cm in Alopias, 2 cm in Lamna, 6 cm in Carcharodon and 7 cm in Isurus. Consequently, only the latter two genera have teeth of comparable size to the approximately 6 cm teeth in the P. benedeni tooth assemblage.

The published dentitions of two extinct cretoxyrhinids, Cretoxyrhina mantelli and Paraisurus compressus (Welton and Farish, 1993; Shimada, 1997) were also examined. The cretoxyrhinids are an extinct lamnoid family that apparently gave rise to both the lamnids and otoconids (Cappetta, 1987). Maximum tooth size for these genera is 4 cm for Paraisurus and 6 cm for Cretoxyrhina (Cappetta, 1987).

In evaluating these dentitions, no effort was made to fit the Parotodus tooth assemblage to the dental pattern of any particular species. Instead, positional changes in tooth configuration along the jaws in extant species were documented and these general patterns of position-dependent shape change then used to infer positions for individual Parotodus teeth.

Ultimately, position assignments in the Parotodus dentition were based on several factors. First, the absolute size of each tooth (measured by vertical height, maximum width and maximum thickness) was used to indicate of its approximate position, with anterior teeth being generally larger than teeth more posterior in the jaw. Angular measurements were also useful. Both the coronal angle (angle of the apex with respect to the basal margin of the root lobes) and the root lobe angle (angle between the two root lobes) were used for two different purposes, to distinguish between upper and lower teeth of similar size and to distinguish position along the jaw. Upper teeth had smaller coronal angles and larger root lobe angles than lower teeth of similar size. Within a jaw, posterior teeth consistently had smaller coronal angles and larger root lobe angles than more anterior teeth.

Second, relative sizes (e.g., relative width = width/height and relative thickness = thickness/height) were used to distinguish between upper and lower teeth. Upper teeth were consistently broader and thinner than lower teeth of equivalent vertical height.

Third, root lobe cross-sectional shape was found to be highly indicative of tooth position. Anterior teeth have root lobes that are nearly circular in cross-section. Lateral and posterior teeth have root lobes that become progressively more compressed.

Finally, mirror reflections of equivalent teeth from opposite sides of the jaw were used to determine the presence of gaps in the tooth row. This technique proved to be surprisingly sensitive in detecting the subtle differences in size and morphology between teeth in adjacent and collateral files.

The P. benedeni dentition, as reconstructed here, consists of fourteen files in each upper ramus and thirteen files in each lower ramus (Figure 3). Since there is no clear demarcation between lateral and posterior teeth, any dental formula is somewhat arbitrary, but A 2/3, I 1/0, L 7/6, P 4/4, or in expanded form,

<table>
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<tr>
<th>A2</th>
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<th>L7</th>
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<td>A3</td>
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seems the most parsimonious. As is the case in most extant lamnids, the first upper anterior tooth (A1) in each ramus has been evolutionarily repressed, so that only A2 and A3 remain (Applegate, 1963). This is then followed by a reduced tooth, the upper intermediate (I), that is only known to occur in lamniforms. Likewise, as in extant lamnids, the distinctive tooth in the lower third file is identified as A3.

The reconstructed dentition has statistical attributes independent of those for the unsorted tooth assemblage shown in Figure 2. Collectively, these attributes suggest that the
arrangement of teeth in the reconstructed dentition reflects a partial dentition (Plates 1-4). First, the distribution of teeth remaining in individual files of the reconstructed dentition is consistent with random loss from a dentition of 54 total files (Poisson distribution; Kolmogorov-Smirnov test, D = 0.11, P > 0.10). Second, the distribution of teeth by position from the symphysis is not significantly different from expected values for a dentition with fourteen files per upper ramus and thirteen files per lower ramus (Kolmogorov-Smirnov test, D = 0.10, P > 0.10). Finally, the total numbers of mesial teeth (= anterior + intermediate) and total numbers of distal teeth (= lateral + posterior) are not significantly different from that expected for random tooth loss from an A 2/3, I 1/0, L 7/6, P 4/4 dentition (chi-squared goodness of fit test, $\chi^2 = 1.95$, P > 0.10).

Comparisons with Other Lamnoid Dentitions

Despite the singularly robust morphology of individual P. benedeni teeth, the disposition of teeth within the dentition is fairly typical for a lamnoid. With respect to changes in tooth size along the jaw, the reconstructed dentition most closely resembles that of the lamnids L. nasus (Figure 4A) in having a modestly-sized upper intermediate tooth and relatively large posterior teeth. L. nasus and P. benedeni also have similar numbers of teeth in each ramus, with the fourteen upper and thirteen lower teeth of the latter species well within the range of 12-16 uppers and 11-13 lowers for the former species (Castro, 1983).

The fundamental difference between L. nasus and P. benedeni is that the latter species has larger teeth (compared to the anteriors) in L$^1$ through P$^3$ (positions 4 through 13 from the symphysis) than the former species. This is particularly noticeable in L$^1$ through L$^4$ (positions 4 through 7), where the teeth are essentially identical to the anterior teeth in relative height.

The reconstructed P. benedeni dentition shows fewer similarities to the dentitions of C. carcharias and I. oxyrinchus (Figure 4B). As in L. nasus and P. benedeni there is an incremental size increase in the lateral teeth immediately following the intermediate tooth. However, in these species there is a precipitous decline in relative tooth size in the posterior half of the jaw, such that the teeth become tiny near the corners of the jaws. A third extant lamnid, I. paucus, is not shown in Figure 4, but follows the basic pattern of reduced upper third teeth followed by two or three files of incrementally larger teeth and tiny posterior teeth. P. benedeni also differs from these species in having higher tooth counts — 13 upper and 11-12 lowers in C. carcharias, 12-13 in each jaw of I. oxyrinchus, and 12-13 uppers and 11-13 lowers in I. paucus (Castro, 1983). Since Carcharodon and Isurus are sister groups that are collectively more distantly related to Lamna (Compagno, 1990; Martin et al., 1992), the tiny posteriors and reduced number of tooth files in these two genera are probably synapomorphies that would not be expected in the still more distantly related odontids, such as Parotodus.

The reconstructed dentition has few parallels with those of the Cretaceous lamnoids, P. compressus and C. mantelli, published by Welton and Farish (1993, Figure 5A). The

![Figure 4. Relative tooth size for upper teeth of the reconstructed Parotodus benedeni dentition (x, based on mean heights at each position), compared to representative dentitions of the lamnids (A) Lamna nasus (■), and (B) Carcharodon carcharias (■) and Isurus oxyrinchus (■). Relative tooth size for any position 1 was calculated as logH$^*$ - logH$^*$_1, where H$^*$ = the height of tooth in position i and H$^*$_1 = the height of tooth in position 1. To simplify comparisons, the relative tooth sizes of extant species shown here are based on dentitions illustrated in Bigelow and Schroeder (1948) — Lamna nasus (fig. 16), Carcharodon carcharias (fig. 20) and Isurus oxyrinchus (fig. 19). Lower tooth rows are not shown, but follow a similar pattern with P. benedeni most closely resembling L. nasus.](image-url)
dentition of *P. compressus* is very unusual, exhibiting a high degree of homodonty and completely lacking a reduced intermediate tooth. The *C. mantelli* dentition is even more bizarre, with wildly variable tooth sizes in the anterior third of the jaw. Recent work by Shimada (1997), on a nearly intact *C. mantelli* dentition, has produced a more plausible reconstruction for this species. The Shimada reconstruction has both a higher number of tooth files (19-21) and less extreme tooth size variation along the jaw than the Welton-Farish reconstruction. Neither of these reconstructions is comparable to that of *P. benedeni* in overall form.

The extant alopids are still more distantly allied to the otodontids than the lamnids, having diverged from a common ancestral stock (the cetoxyrhinids?) in the Albion (Cappetta, 1987; Martin, et al., 1992). Alopid dentitions are also highly derived and very different from that of *P. benedeni*. In *A. vulpinus*, a typical upper intermediate tooth is present, but the number of teeth in each ramus is much higher than in lamnids (20 in the upper rami and 21 in the lower; Castro, 1983). The tooth count in the dentition of *A. superciliosus* has been secondarily reduced to 11-12 in the upper rami and 10-12 in the lower rami (Castro, 1983; Compagno, 1990). *A. superciliosus* has also lost the upper intermediate tooth. Consequently, tooth size declines along the jaw (Figure 5B) in a manner analogous to that of the cetoxyrhinid, *P. compressus*.

The reconstructed dentition of *P. benedeni* also differs from the illustrated lamniform dentitions in having a first upper tooth (A²) that is slightly smaller than the second upper (A³). However, this appears to be due to individual variation, since some specimens of *C. carcharias* also have this pattern (e.g., Bigelow and Schroeder, 1948; p. 136).

**Discussion**

Since the teeth described here were collected from disturbed sediments their interpretation as the disassociated dentition of a single individual must be treated with appropriate caution. Despite the exceptional size and quality of the described assemblage, the absence of strict stratigraphic controls means that some doubt must always remain about their interrelationships. However, even given these difficulties, all available evidence supports the interpretation of this assemblage being derived from a single individual.

The most striking feature of the reconstructed dentition is the surprisingly large and uniform size of teeth in most tooth positions. While the anteriors and upper intermediate tooth are entirely comparable in relative size to that of extant lamnids, the lateral and posterior teeth are consistently larger than teeth in the same position of extant lamnids. Even *L. nasus*, which exhibits the greatest similarity to *P. benedeni*, has lateral and posterior teeth that are markedly smaller in relative size than those of *P. benedeni*.

The reconstruction shown here is different in two respects from an earlier reconstruction based on the same tooth assemblage (Kent, 1994; figure B.13). First, the most distal lower posterior tooth in the earlier reconstruction (P₃ in Figure 3) was still comparatively large. An examination of extant

![Figure 5. Relative tooth size for upper teeth of the reconstructed Parotodus benedeni dentition (A; based on mean heights at each position), compared to representative dentitions of (A) the cetoxyrhinids Cetoxyrhina mantelli (Ⅲ) and Parasilurus compressus (Ⅳ), and (B) the alopid Alopias superciliosus (Ⅳ). Relative tooth size for any position i was calculated as logHᵢ - logHᵢ₋₁, where Hᵢ = the height of tooth in position i and Hᵢ₋₁ = the height of tooth in position i - 1. To simplify comparisons, the relative tooth sizes of species shown here are based on dentitions illustrated in Welton and Farish (1993; C. mantelli, p. 102 and P. compressus, p. 109), and Bigelow and Schroeder (1948; A. superciliosus, fig. 26). Lower tooth rows are not shown, but follow a similar pattern, except in C. mantelli, where there is much less variation in tooth size in positions 1 through 5.](image-url)
lamnid dentitions indicated that the last lower posterior tooth was almost always as small, or smaller, than the last upper posterior. This suggested that a thirteenth, unrepresented file was likely present in each lower ramus. Figure 3 includes an additional lower posterior tooth of appropriate size and shape (Pa), based on examinations of other lamniform dentitions.

Second, in the earlier reconstruction, a coronal fragment (Plate 3, tooth 2) was ignored during analysis, having been tentatively identified as an upper anterior tooth of the mako shark, Isurus desori. Subsequent, more detailed, statistical analyses indicated that this coronal fragment was attributable to *P. benedeni*. Given the general rarity *P. benedeni*, it seemed unlikely that a tooth from a second *P. benedeni* individual would be present within the assemblage. The fragment was far more likely to be a component of the assemblage itself. However, it was noticeably smaller and more gracile than any other specimen in the assemblage.

The morphology of this coronal fragment is also unusual. It was relatively narrow and erect, as is typical of *P. benedeni* anterior teeth, but compressed to a degree generally seen in *P. benedeni* lateral teeth. The small size of this crown, combined with the curious mixture of anterior and lateral characteristics, suggested that it may represent an upper intermediate tooth. This fragment was compared with a number of other, unassociated *P. benedeni* teeth to determine the most likely shape of the original tooth. Measurements of both the fragment and teeth of similar shape were then used to estimate the size of the intact tooth. Estimates ranged from 30-40 mm, with the majority at about 35 mm. The shape and estimated size of this tooth were consistent with the upper intermediate teeth of extant lamnid dentitions and this specimen was placed in that position (I; Figure 3) of the reconstruction. In general, lamnoid sharks have a dentition characterized by dognathic and disjunct monognathic heterodonty (Cappetta, 1987; Welton and Farish, 1993). Each upper ramus contains two enlarged anteriors, and a reduced upper intermediate tooth followed by two or more files of lateral teeth that are of transitional size between the intermediate tooth and the largest lateral tooth. The lower dental rows of lamnoids are similar to the upper rows, but lack a reduced intermediate tooth. The adaptational function of this dental pattern in lamnoids is unclear. Based on analogy with the sand tiger *Carcharias taurus* (Lamniformes, Odontaspididae) the small intermediate tooth of a disjunct dentition serves to spatially separate two groups of functionally different teeth (Applegate, 1965; Espinosa-Arrubarrena, 1987). The enlarged anterior teeth are used for grasping and holding prey, while the more blade-like laterals cut the prey into smaller pieces for swallowing.

This adaptive explanation for upper intermediate teeth is less applicable to species, such as *C. carcharias*, where the dentition is of the disjunct form, but the anterior, intermediate and lateral teeth are all comparatively large. In this species, these large blade-like teeth are used to gouge chunks of flesh from large prey (Compagno, 1984).

The reconstructed *P. benedeni* dentition parallels that of *C. carcharias* in having anterior and lateral teeth that are similar in size and shape. However, due to differences in tooth morphology between these two species, their dentitions were undoubtedly used in different ways. *C. carcharias* has a dentition composed of highly compressed, serrated teeth adapted for slicing flesh (Frazzetta, 1988), while the sturdy, smooth-edged teeth in the *P. benedeni* dentition are poorly suited to this function. Instead, *P. benedeni* teeth are adapted for piercing and rending fibrous, compliant tissues (Sibbing, 1991), such as the skin and muscles of vertebrate prey.

The teeth of *P. benedeni* are comparatively small in early Oligocene representatives, but during the Neogene become markedly larger and more robust (Cappetta, 1987). This change in tooth size and morphology occurred during a series of major marine transgressive events that are correlated with increased primary productivity, the diversification of marine mammals, and the evolutionary escalation of marine communities (Lips and Mitchell, 1976; Vermeij, 1987). By the early Pliocene, when the tooth assemblage was deposited, the teeth of *P. benedeni* were large, but had stout, comparatively short crowns and massive roots. With a dentition containing substantial numbers of these teeth, Pliocene *P. benedeni* were unquestionably formidable carnivores. But the ecological role of *P. benedeni* in complex Neogene paleocommunities that were dominated by the giant white shark, *C. megalodon*, is, at present, speculative. Functionally, the teeth and dentition of *P. benedeni* more closely resemble those of the extant mosasaurs and the extant killer whales, than those of other sharks. With a piercing-lacerating dentition of large, robust teeth attached to equally robust jaws, *P. benedeni* could have produced gaping wounds and massive soft tissue trauma in their prey. The nature of the prey for which these teeth evolved is still poorly known and the focus of ongoing research.

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Literature Cited


Plate 1. *Parotodus benedeni* teeth (USNM 489114) from the upper left jaw ramus (lingual view, symphysis at right edge of photograph). Files A2, I, and L3 (indicated by arrows) are missing. Teeth within each file are arranged from the smallest in the bottom row to the largest in the top row. Teeth labeled with an asterisk (*) in the upper left corner could not be assigned to a specific file. Scale bar is 2 cm.

Plate 2. *Parotodus benedeni* teeth (USNM 489114) from the lower left jaw ramus (lingual view, symphysis at right edge of photograph). Files A2, L4, and P4 (indicated by arrows) are missing. Teeth within each file are arranged from the smallest in the top row to the largest in the bottom row. Teeth labeled with an asterisk (*) in the lower right corner could not be assigned to a specific file. Scale bar is 2 cm.
Plate 3. Parotodus benedeni teeth (USNM 489114) from the upper right jaw ramus (lingual view, symphysis at left edge photograph). File P² (indicated by an arrow) is missing. Teeth within each file are arranged from the smallest in the bottom row to the largest in the top row. Teeth labeled with an asterisk (*) in the upper right corner could not be assigned to a specific file. Tooth (USNM 489115) was purportedly obtained from the tooth assemblage site by an amateur collector (and subsequently traded with other collectors), but is not comparable to the teeth in the dentition. This tooth apparently came from a different individual, and probably different site, within the mine. Tooth 2 is the upper intermediate tooth fragment discussed in the text. Scale bar is 2 cm.

Plate 4. Parotodus benedeni teeth (USNM 489114) from the lower right jaw ramus (lingual view, symphysis at left edge of photograph). Files P₃ and P₄ (indicated by arrows) are missing. Teeth within each file are arranged from the smallest in the top row to the largest in the bottom row. Tooth labeled with an asterisk (*) in the lower left corner could not be assigned to a specific file. Teeth 1-4 are pathological specimens discussed in the text. Scale bar is 2 cm.