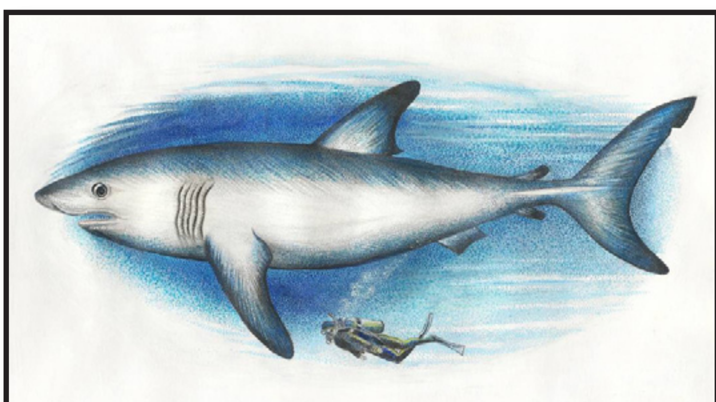
I ❤ *Parotodus benedeni*

by Nando Musmarra
translated by Wendell Ricketts

Parotodus benedeniiiiiiiiiiiiiiiii!!!!!



The body shape and size of *P. benedeni* as drawn by paleoartist Loana Riboli.

Parotodus benedeniiiiiiiiiiiiiiiiiiii!!!!!!

My ecstatic shout breaks through the dull heat of a late-May North Carolina morning. There it is, halfway up the slope. This time I'm not dreaming, though I give myself a pinch just to make sure.

The frogs quit their croaking; even the Canadian geese stop honking and stare at one another in consternation, wondering, perhaps, why the quarry has been invaded by this howling Tarzan. The only other sound is the whisper of the wings of a Great Blue Heron, motionless at the edge of a pond until a moment ago, as it flies off in fright.

10 minutes before—The Premonition

This is what I call "The Feeling." It's about to happen again, I'm sure of it! I'm about to find a really terrific fossil … that's the way it almost always happens, though I still don't know exactly where "the feeling" comes from.

12 hours before—Reading

The day has been a lot of fun, but exhaustion is starting to take its toll. I've been awake since dawn, and tomorrow I'm going to have to do it all over again. There's no hiding the fact that I'm as excited as a greenhorn by the opportunity to collect at the Lee Creek Mine. My eyelids are heavy, and I'm not sure I have the energy to stay awake long enough to take a look at Bretton W. Kent and George Powell's study, "Reconstructed Dentition of the Rare Lamnoid *Parotodus benedeni* from the Early Pliocene at Lee Creek Mine, North Carolina." On the night stand, the *Parotodus benedeni* tooth that I bought at the auction today keeps me company.

18 hours before—Sold!

At the auction, Lot 104 finally comes up for bids. It's an "historic" *Parotodus benedeni* tooth collected long ago in the famous New Bern Quarry, which has been closed for years. The tooth is in excellent condition, though the crown shows some minor evidence of prep work. I can't keep my hand down and, after beating back a couple of higher bidders, I manage to win the magnificent tooth for $70. On the back of the small box that holds the fossil there's an old-fashioned label written with a fountain pen. It seems an additional confirmation of the specimen's age.

24 hours before—George Powell, Jr.

The fair is glorious again this year and the atmosphere is friendly. I wander around among the tables where paleontologists from the Smithsonian sit, displaying publications, reconstructions, and real fossils.

The scientists, headed by Bob Purdy, bend over backwards to identify the teeth that many fossil enthusiasts, especially children, are vying to show them. I can't help but think how much good this kind of coöperation between professional paleontologists and ordinary fossil fans does for the field. It's the author himself, George Powell, Jr., who presents me with a copy of *The Mosasaur* that contains a series of scientific papers on *P. benedeni.* I'll spend the night avidly reading this wonderful gift.

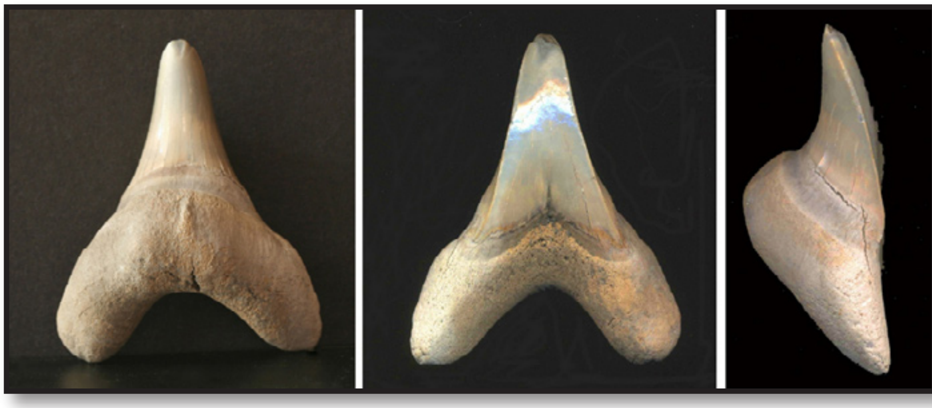
I know George from "vertebra day." I'd never seen so many vertebrae together in one place: sharks, whales, porpoises, dolphins, tuna, and other inhabits of the ocean depths. That day, it seemed as though vertebrae were the only way they'd ever been fossilized. A handful of shark teeth, a few whale tympanic bones, some beautiful volutids and perfectly conserved *Pecten*—and then vertebrae, more vertebrae, and still more vertebrae.

Two weeks before

Dr. Cliff Jeremiah, a shark expert (in addition to his

Ardea herodias, the Great Blue Heron. Birds have been visiting the area of the current Lee Creek Mine since time immemorial. Purdy's 2001 study identified 112 species of bird (including grebes, plovers, albatrosses, pelicans, ducks, and swans) in the Yorktown Fm. The fact that these avian fossils so closely resemble the bones of living birds indicates that many species never went extinct.

Scene from the auction



At first this specimen appeared to be a symphyseal tooth, but Bretton Kent (personal communication) identified it definitively as a third anterior of the mandible. Height: 5 cm.

personal passion for shark teeth, he's a dentist by profession), has reconstructed the jaws of Tertiary sharks and donated them to the Florida Museum of Natural History in Gainesville. The fossil teeth, which come from a number of different specimens, are authentic, while the jaws that contain them are made of fiberglass and modeled to resemble those of living sharks. I'm here to photograph the reconstruction of the jaws of *Parotodus benedeni*. The hall is very dark and the reconstructions are protected behind thick glass. The lack of light and the reflections in the glass make it clear that photography won't be easy. Since I can't use the tripod, I decide to try the flash and I manage to salvage a handful of decent shots, more or less free of glare. In the afternoon, I receive an email asking me whether I would be available to lend a hand during the upcoming fossil auction, which will be held in Aurora, North Carolina in a few weeks. The proceeds benefit the local natural history museum, and they need volunteers because they're expecting an enormous crowd. I respond immediately: I'll be there! (I wouldn't miss the event for anything in the world, even if it meant swimming from Italy. I know they aren't really going to need me, though: folks are going to rush to help, and there'll be many more volunteers than they can use. That's an important consideration, because it means I'll be free to participate in the auction as a buyer and not as a gofer.

A shark tooth for sale at the auction

George Powell, Jr. (right)

Five months before—Geology and Paleontology of the Lee Creek Mine

The mail carrier delivers my copy of the third volume of Geology and Paleontology of the Lee Creek Mine, North Carolina, a four-volume work published in 2001 by the Smithsonian Institution. In a section dedicated to fish, Robert W. Purdy identifies 104 species and fifty-two families of cartilaginous fish and Osteichthyes in the Pungo River Formation (Burdigalian) and the Yorktown Formation (Zanclean). Among the book's many clarifications regarding the taxonomy of sharks, *Parotodus benedeni* is assigned definitively to the family Lamnidae.

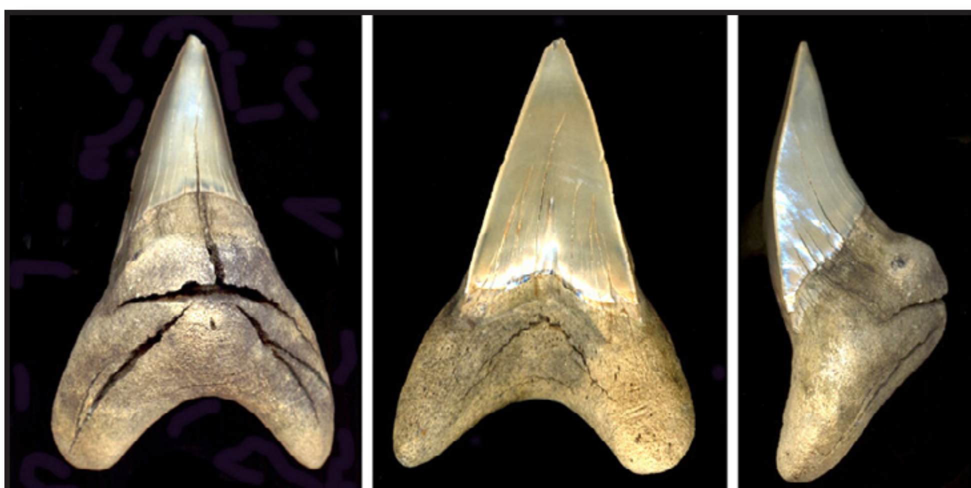
<u>*6 months before—Pat Young*</u>

Specimens of *P. benedeni* aren't easy to find as one makes the rounds of natural history museums. Other than the museums in North Carolina, I've also had the pleasure of admiring some splendid *P. benedeni* teeth in a display case at the Museum of Natural History of the Accademia dei Fisiocritici in Siena, Italy. My direct experience, unfortunately, ends there. I've hunted for *P. benedeni* teeth in Belgium and in North Carolina, but I've never been lucky enough to find one nor have I ever been present to witness someone else's discovery of a specimen of one of this mysterious shark's impressive teeth. I'd like to know more, but I have neither photos nor publications at hand, other than Bretton W. Kent's excellent 1994 book, <u>Fossil Sharks of the Chesapeake Bay Region</u>. The cover bears two photographs: a *Carcharocles megalodon* tooth, and, to the right of it, a tooth belonging to *Parotodus benedeni*.

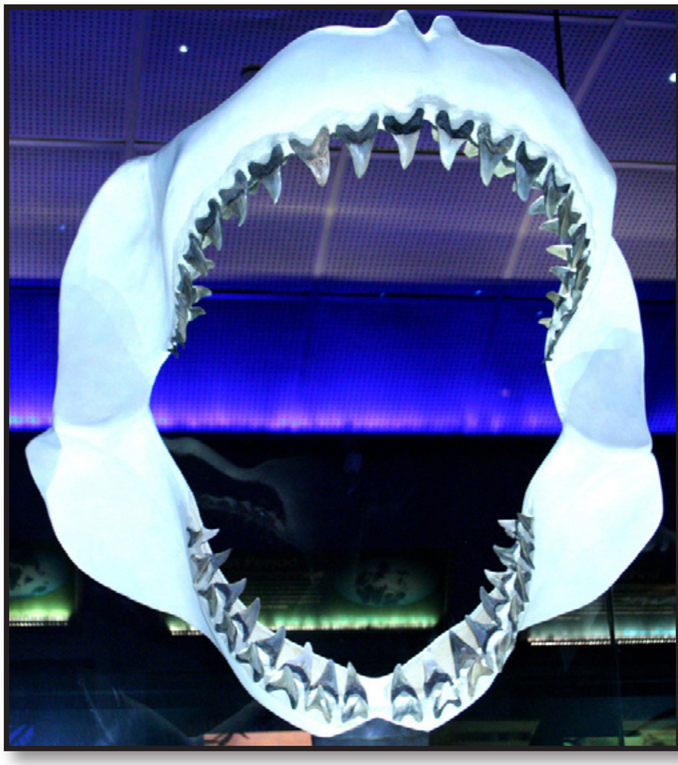
Calling all shark tooth lovers ... follow the blue sign!!!

The lower jaw of *P. benedeni* as reconstructed at the Florida Museum of Natural History, Gainesville, Florida

But thinking about *P. benedeni* teeth has become a torment. I've even started dreaming about them! I suddenly recall a conversation I had with Patricia and Kenneth Young, who had mentioned finding *Parotodus* teeth in North Carolina. Fortunately, at this hour of the night, they're still not asleep on the other side of the Atlantic… I decide to send an email asking them to send me a picture of a *P. benedeni* tooth. I write to various other friends as well, "fishing for" whatever they have on this elusive shark.



Note the thickness of the root on this *P. benedeni* tooth. Height: 5.7 cm. Collected and photographed by Pat & Ken Young.



The complete reconstruction of the jaws of *P. benedeni* by Cliff Jeremiah, on display at the Florida Museum of Natural History, Gainesville.

Pat Young

The responses are all but instantaneous. Less than an hour has passed when a photograph of three beautiful Pliocene teeth arrives via email, along with a fourth tooth, more unusual still, from the Miocene. I love technology. The photos are perfect; I'd even call them scientific: they show labial, lingual, and lateral views for each tooth. I've finally got something solid to go on.

6 months and 10 minutes before—Parotodus benedeni —The Dream

I've just found a *Parotodus benedeni* tooth and someone is trying to take it away from me. I defend my tooth with all my might, but he yanks it from my hand. I lurch awake, sweating…it was just a terrible nightmare….

Parotodus benedeni, the Unknown Shark

The first documented specimens of *Parotodus benedeni* are a number of fossil teeth found during the excavations carried out for the fortification of the city of Antwerp, Belgium. Henri Le Hon described the teeth in 1871: "Species with an enormous thickness resembling the Cretaceous *Oxyrhina crassidens* of Dixon… The crown is more or less inclined and the curved or hooked teeth, having the same characteristics, appear to belong to the same animal." Le Hon also noted that the deposits in which the fossils were found belonged to Pliocene beds.

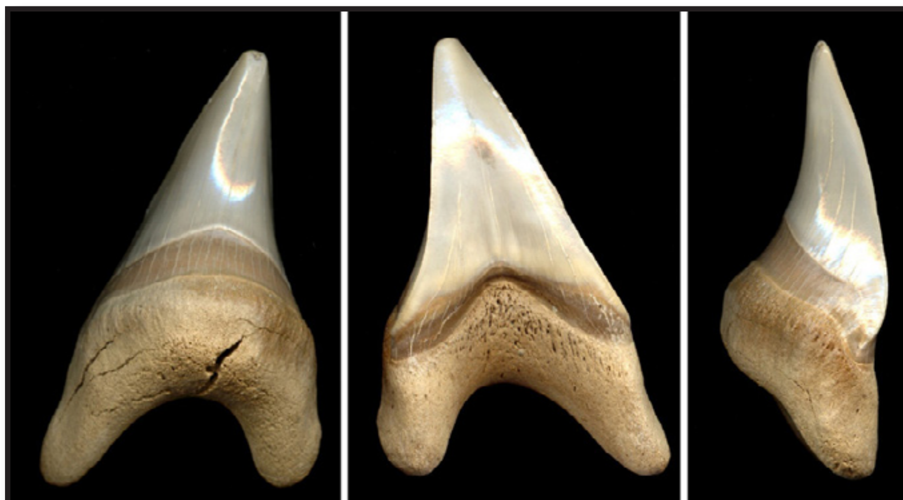
During the early 1880s, Pliocene specimens were also noted by Robert Lawley from Italy and by A.S. Woodward from England. In 1888, James W. Davis described an assemblage of some twenty *Oxyrhina vonhaastii* teeth (later identified as *P. benedeni)* from the Oligocene of New Zealand; and, in 1910, Maurice Leriche reported *Parotodus* from the early Oligocene (Rupelian) of Belgium. Leriche's teeth included two specimens of *Lamna rupeliensis*, which he identified as *Oxyrhina benedenii (Oxyrhina=Isurus)*. Leriche also noted that the teeth he studied were much smaller than those Le Hon had identified forty years earlier. Later finds of isolated teeth in Miocene deposits in Italy, Malta, Switzerland, and Portugal, along with still others in Belgium, demonstrated that *P. benedeni* was a notably long-lived shark. Before going extinct, in addition, the species had swum the oceans during a span of time that extended from the early Oligocene to the Pliocene—a voyage of more than twenty million years.

Because of the resemblance of *P. benedeni* teeth to those of another shark, *Isurus (Oxyrhina), P. benedeni* was originally assigned to *Isurus (Oxyrhina) benedenii.* As late as 1970, Portuguese researchers Miguel Telles Antunes and S. Jonet continued to maintain that existing specimens of *P. benedeni* teeth were nothing other than the symphyseal teeth of *Isurus hastalis.*

Splendid specimens of *P. benedeni* collected by George Powell, Jr.

In 1974, the description of a new species of shark appeared from the Miocene of Japan; the specimens on which the species was based—all teeth identical to *P. benedeni*—were assigned to *Isurus moniwaensis.*

The confusion persisted until 1980, when Henri Cappetta correctly argued that these teeth, because of their highly diverse root shapes, represented a variety of positions within the shark's jaw and, thus, that they could not be the symphyseal teeth of *Isurus hastalis*. The thickness of the roots, in addition, was proportionally much greater than corresponding *Isurus* teeth. Their unusual shape, meanwhile—the distinctive root lobes, the thick crown, and the "D"-shaped cross-section—led Cappetta to align the specimens with Agassiz's *Otodus* and to erect a new genus, *Parotodus*, which he assigned to Order Lamniformes.



Lower *P. benedeni tooth*. Height: 4.5 cm. Collected and photographed by Pat & Ken Young

The creation of a new genus was reflected in common speech as well, and *P. benedeni* has been known ever since as the "false mako" (mako=*Isurus*).

Matters seemed to have been clarified. In 1985, however, in a study that seemed not to take Cappetta's previous work into consideration, Naoyuki Kuga reshuffled the deck, erecting a new genus, *Uyenoa benedeni*, which he placed in the Lamnidae rather than in the Otodontidae as Cappetta had done (*Uyenoa*, however, remains as a junior synonym for *Parotodus*.)

Hi ho, hi ho, it's off to work we go!!!

The four pathological teeth. Aurora Fossil Museum, Aurora, N.C.

In 1988, French oceanographers Patrick Geistdoerfer and M. Roux reported *P. benedeni* teeth associated with *C. megalodon* in ocean-bottom Pleistocene deposits in New Caledonia. Given the impossibility of conducting stratigraphic studies of the deposits where the specimens where found, however, discussion regarding the new discoveries remained (in keeping with our theme) in deep water (!). In all likelihood, however, Roux and Geistdoerfer's teeth came from redeposited Miocene or Pliocene strata.

In addition to confirming that *Parotodus benedeni* belonged to the Lamnidae, in 1991 Noel Kemp described an exceptional assemblage of thirty associated teeth from the Miocene Batesford Formation of Australia. An unusual feature of the find was the presence of two symphyseal teeth, which had been absent from all the other assemblages studied up to that time. The thirty Australian teeth were mentioned, in fact, in a popular guide to sharks by Alice Alston in 1986, but without scientific description.

This beautiful tooth has just been found by a lucky fossil-hunter. For several dozen fantastic *C. megalodon* specimens collected, however, only one *P. benedeni* comes to light.

In 2001, the Smithsonian published a significant study by Robert W. Purdy and five co-authors on the fossil fauna of the North Carolina's Lee Creek Mine. The richness of the Lee Creek fauna made it possible to clarify a number of issues with regard to shark taxonomy and, most importantly, to assign *Parotodus benedeni* to the Lamnidae once and for all.

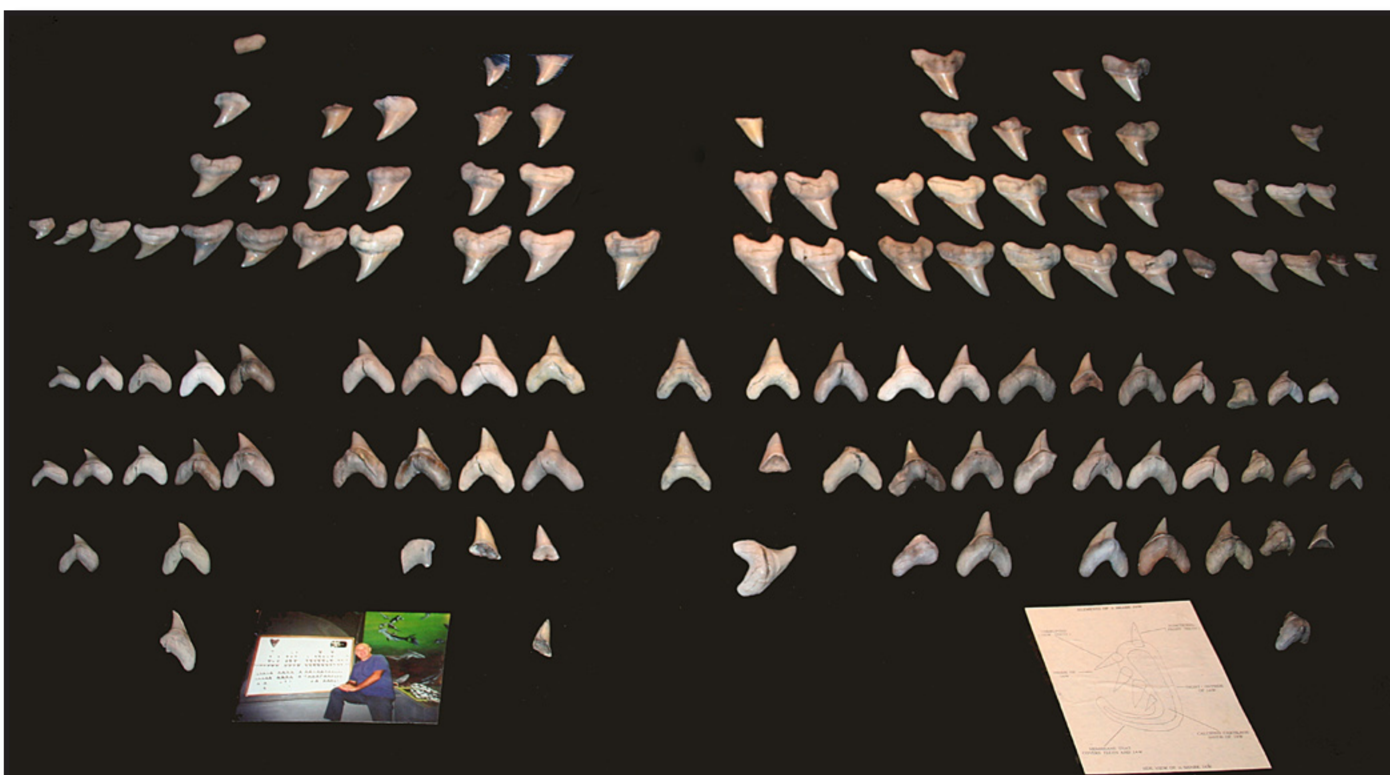
In addition, Purdy noted the discovery by amateur paleontologists at the Lee Creek Mine of a notable assemblage of more than one hundred *Parotodus benedeni* teeth. The Lee Creek assemblage constituted a giant leap forward in knowledge about the mysterious *P. benedeni* because investigations at the mine allowed paleontologists to recover a great deal of data regarding the paleoenvironment in which *Parotodus benedeni* had lived (or, at least, in which it had died). Significantly, the assemblages previously discovered—in New Zealand in the late 1800s and a hundred years later in Australia—had been made up of teeth alone, although a tooth-set reported from the Miocene of Japan in 1978 contained dermal denticles in addition to forty-four teeth.

An Exceptional Find

It all began when George Powell, Jr. and Clyde Swindell identified ten *P. benedeni* teeth in a small plot of ground no more than a meter square. Such a high concentration of highly unusual teeth in such a small area obviously deserved more careful study. The excavation was enlarged to approximately ten meters square and the sediments were washed to the depth of one meter using a pressure hose. After an additional sixty-eight teeth were recovered using this method, work was forced to a halt by the torrential rains of the winter of 1993. When access to the site once again became possible and the excavation continued, Powell found other teeth, some of them in the runnels created by the cascades of rainwater. In the end, the number of specimens climbed to the considerable number of 114 teeth (actually, four had been obtained from other collectors who had found them, in the meantime, at the same locality).

How many paleontologists could an extinct shark eat in one bite? The jaws of *C. megalodon* as reconstructed at the Smithsonian's Museum of Natural History.

The fossils were not collected from a single stratigraphic succession, but rather from Yorktown For-



The complete assemblage of 114 teeth collected by George Powell, Jr. and reconstructed by Bretton Kent. Aurora Fossil Museum, Aurora, N.C.

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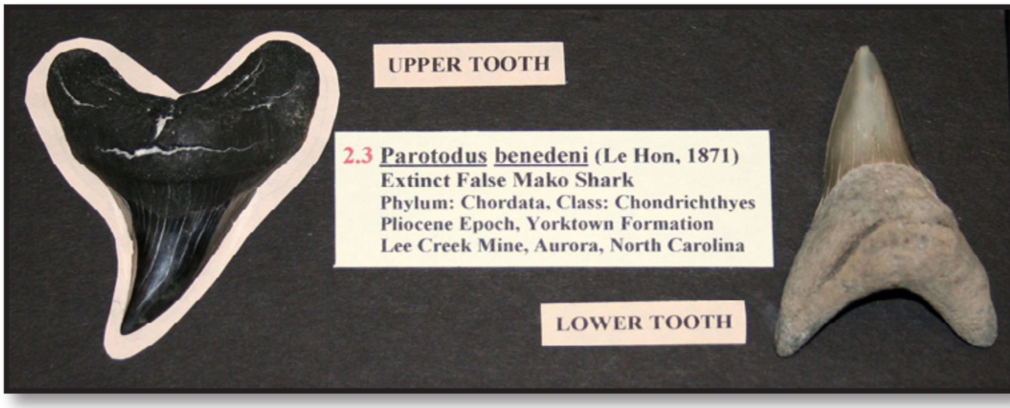


Examples of upper and lower *P. benedeni* teeth

mation deposits that had been significantly "disturbed" by enormous earth movers searching for phosphate. As a result, once the specimens had arrived at the Smithsonian (Powell had generously arranged to donate them), Bretton Kent approached the interpretation of the find with due caution. That such a large number of teeth—from a shark as unusual as *P. benedeni* and recovered in such a restricted area—could only have come from a single individual was nonetheless strikingly obvious. (Powell told me that, in the years before the discovery of the 114-tooth assemblage, only six *P. benedeni* teeth had been recovered among some 17,000 *Isurus* teeth collected at the Lee Creek Mine.)

Lateral tooth of *P. benedeni,* Pliocene. Height: 3.5 cm.
Collected and photographed by Pat & Ken Young.

Additional evidence for the hypothesis that the teeth had come from the same shark was the presence of four pathological teeth (a relatively common occurrence in *P. benedeni*, as Lawley had already noted in 1881), all with similar deformations: very small, hook-shaped crowns and roots that were compressed rather than globose. The gradually decreasing size of these pathological teeth led to the supposition that the largest belonged to the functional row while the others belonged to successively smaller replacement rows.

Because it would have been impossible to confront the Lee Creek specimens with other assemblages belonging to the same species, a comparative study was made of the 114 *P. benedeni* teeth, arranged in rows of decreasing size and according to their shape, with 114 *Isurus* teeth collected from the same deposits. Unlike the *P. benedeni* teeth, the 114 *Isurus* teeth could not be arranged in the same way—both because of the presence of numerous duplicates and because of marked differences in size and shape among the *Isurus* teeth. Indeed, such a low correlation coefficient is typical of surface collecting of shark teeth at the Lee Creek Mine (Kent, 1999a).

The uniformity in the size of the *P. benedeni* teeth, the difference in root shape, and the diversity apparent in the shape and functioning of the teeth themselves made it very plausible that the assemblage represented a complete *P. benedeni* dentition and not simply a post-mortem scattering of single teeth from various individuals.

"Oh, the shark has pretty teeth, dear,
And he shows them pearly white…."

The lyrics from "Mack the Knife" must have popped into Bretton Kent's head more than once as he set about studying the exceptional Lee Creek assemblage. His first task was to attempt to understand how many teeth he needed to reconstruct the functional rows of *P. benedeni's* jaws, an effort that began with Cappetta's assertion in 1987 that *Parotodus* and *Carcharocles* belonged to tightly homologous clades. This meant that the jaws of *P. benedeni* should contain thirteen teeth per hemi-arch, as does the famous reconstruction of the jaws of a *megalodon* at the Smithsonian's Museum of Natural History in Washington, D.C.

Kent also considered Purdy's suggestion that the functional row of the upper jaw should contain thirteen teeth in each hemi-arch, with twelve teeth in each hemi-arch of the lower. In addition, Kent analyzed the dentition of four species of living Lamnidae, presumably close relatives of *P. benedeni: Isurus oxyrinchus* (the shortfin mako), *I. paucus* (the longfin mako), *Lamna nasus* (the porbeagle), and *Carcharodon carcharias* (the great white shark), along with two thresher sharks *(Alopias vulpinus* and *Alopias superciliosus)*—not because the teeth of these latter sharks were similar to *P. benedeni*, but because their teeth, although much smaller, resembled *P. benedeni* at least superficially. As a standard of comparison, the reconstructed jaws of *Cretoxyrhina mantelli* and *Paraisurus compressus*, two Cretaceous members of the Cretoxyrhinidae (extinct sharks that are believed to have given rise to the Lamnidae and Otodontidae families), were also examined.

Ultimately, Kent concluded that the dental apparatus of *P. benedeni* consisted of a functional row of fifty-four teeth, with fourteen in each hemi-arch of the upper jaw and thirteen in each hemi-arch of the mandible. Despite the exceptionally robust structure of the teeth, their arrangement in the jaws appeared fairly typical for a lamnid, and the reconstruction of the complete dentition-set offered numerous analogies with *Lamna nasus*. Similarities to *C. carcharias* and *I. oxyrinchus*, meanwhile, were few and fewer still in comparison to *Cretoxyrhina mantelli* and *Paraisurus compressus*.

Sedimentary Analyses

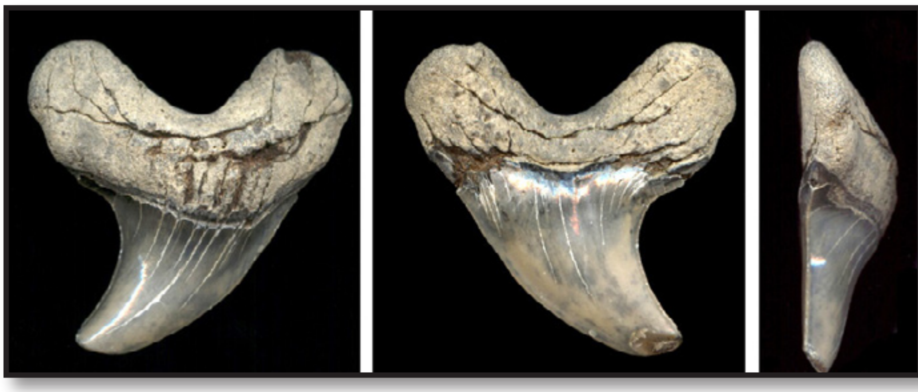
In his "Speculations on the Size and Morphology of the Extinct Lamnoid Shark, *Parotodus benedeni*," Kent (1999a) advanced an hypothesis regarding the body shape and overall proportions of *Parotodus*. In specific, he approached the problem by first attempting to establish the age of the deposits where the 114 teeth had been found through an analysis of the planktonic species present in the Yorktown Formation. Based on this analysis and on radiometric dating of phosphate nodules and glauconitic zones, Kent concluded that the deposits were between 4.4 and 4.8 million years in age.

Typical surface-collecting conditions. An *I. hastalis* tooth at the Lee Creek Mine.

Water temperatures must have been temperate at the time, because the majority of the marine fossils recovered from the Yorktown derived from warm-water fish species (the presence of some cold-water species was attributed more to significant intrusions from cold, deep-ocean springs than to an overall decrease in water temperatures). The other macrofossils present *(Placopecten clintonius, Chesapecten jeffersonius*, cirripedes, the teeth of other sharks, and cetacean bone fragments) along with the general lithology (small and medium-sized phosphate nodules, sand and silt zones) pointed to an ocean depth of between 80 and 100 meters.

Parotodus benedeni: Hypotheses Regarding its Appearance and Behavior

Who was this shark? What were its habits? What role did it play in an ecosystem dominated by the gigantic *C. megalodon?* Above all, why is the *P. benedeni* fossil evidence, which is recorded from virtually the entire world, restricted to the occasional discovery of isolated teeth (with the obvious exception of the assemblages mentioned above)?



Rare Miocene specimen from the Pungo River Fm.
Collected and photographed by Pat & Ken Young.

This is despite the fact, of course, that *P. benedeni* was a very long-lived species with an extensive evolutionary span from the Oligocene to the Pliocene.

Cappetta had already attempted to respond to these questions in 1980. He attributed the lack of fossil evidence to the fact that *P. benedeni* was a pelagic species accustomed to inhabiting deep ocean environments, only occasionally approaching coastal waters. Most of the Neogene fossil strata that we're concerned with here, of course, were formed from just such relatively shallow waters. In addition, returning to some of Leriche's earlier observations (Leriche had noted that *P. benedeni* teeth from the Oligocene were considerably smaller than those from the Pliocene), Cappetta maintained, in his 1987 study, that *P. benedeni* had lived during a series of major marine transgressions characterized by a marked diversification of cetacean species and by a general increase in the size of those species.

Our shark very likely adapted to the increase in the dimensions of its prey, improving the power and effectiveness of its bite by increasing the size and robustness of its teeth. The jaw reconstructed by Kent and Powell showed long, massive front teeth as well. Surprisingly, the teeth grew in size as they moved in the direction of the lateral teeth, making clear *P. benedeni's* distinctly heterodont dentition (a gradual change in the size of teeth along the arcade of the same jaw).

At the same time, the substantial size and functional morphology of *P. benedeni's* teeth made them very different from those of other large sharks living at the time. The teeth of *P. benedeni,* for example, bear neither the lateral cusplets that are typical of teeth adapted for seizing prey (although Cappetta noted residual cusplets in the Oligocene forms) nor the compressed shape and serrations that serve to shear off large pieces of meat such as are found in *Carcharodon carcharias* and *Carcharocles megalodon.*

Indeed, *P. benedeni's* dental apparatus probably resembled the jaws of living killer whales and extinct mosasaurs more closely than it did that of other sharks. Such powerful teeth, likely associated with a jaw force that was no less impressive, would have made *P. benedeni* a formidable carnivore, capable of using its front teeth to bite, hold, and tear even tough, fibrous muscle tissue, which could then be sliced into smaller pieces with its lateral teeth and swallowed.

Although numerous studies have attempted to reconstruct the appearance and size of fossil mammals, very few such estimates have been made for extinct sharks—precisely because fossil shark remains other than teeth and vertebrae are exceedingly rare. During Kent's attempts to reconstruct *P. benedeni* (1999b), he had no easy time creating a workable hypothesis regarding its body shape and overall dimensions. Body weight,

In this reconstruction by Bretton Kent and George Powell, Jr., note the change in size of the teeth along the same hemi-arch of each jaw. Aurora Fossil Museum, Aurora, N.C.

which is correlated with a large number of variables including population density, the quality and quantity of food available, community structures, metabolism, thermoregulation, and growth rate, just to name a few, was particularly difficult to establish.

As a point of departure, Kent used previous studies of the weight and dimensions of the modern great white shark *(Carcharodon carcharias)* and the *P. benedeni* jaw measurements that Kent and Powell had estimated from the 114 Lee Creek teeth. These data led to two very different estimates regarding the hypothetical body length of *P. benedeni* (if anything, these estimates may well have been on the low side; *P. benedeni* teeth have been recovered from the Pliocene that are even larger than the Lee Creek specimens).

The first hypothesis, based solely upon the height of the crown (39.5 mm) of the largest anterior tooth of the upper jaw, suggested a body length for *P. benedeni* of 4.7 meters (approx. 15.4 feet). The second estimate, considered much more reliable, was based upon the entire length of the dentition-set of the reconstructed upper jaw, and resulted in a body length that well exceeded seven meters (approx. 23 feet). Considering this figure in light of the proportions of living Lamniformes (e.g. *C. carcharias*), Kent produced a weight estimate for *P. benedeni* of between 4,118 and 4,822 kg (approx. 9,078-10,630 lbs).

In order to establish *P. benedeni's* body shape and design, Kent followed Compagno (1990), who maintained that the evolution in the body shape of the Lamniformes had changed little over the millennia and that Paleogene Lamnidae and Otodontidae, including *P. benedeni,* were much more similar to modern Lamniformes than to any other living group.

Armed with these propositions, and taking into account the fact that *P. benedeni* was distributed in the warm waters of the entire planet, that it was a pelagic species, and, finally, that *P. benedeni* fossils had been found in association with manganese nodules typical of deep-ocean environments, Kent determined a body shape and design for *P. benedeni* with the following characteristics: *P. benedeni*, like modern, open-ocean sharks *(Alopias superciliosus*, the bigeye thresher; *Isurus paucus*, the longfin mako; *Carcharinus longimanus*, the oceanic whitetip; and *Prionace glauca*, the blue shark) would have evolved very large, wing-shaped "oceanic" pectoral fins that allowed it to swim slowly and approach its prey stealthily; in addition, its ability to regulate its body temperature through structures known as the retia mirabilia would have maintained its internal body temperature even in the coldest seas, just as occurs in *Alopias, Carcharodon, Lamna,* and *Isurus*, thus maximizing energy consumption as it propelled its mass through the water (a phenomenon known as "gigantothermy"; see Paladino et al., 1990).

To sum up, here is a profile of *Parotodus benedeni:*

1) long pectoral fins, as in the Megachasmidae (megamouth sharks), the Alopiidae (thresher sharks), the Cetorhinidae (basking sharks), and the Lamnidae (makos and white sharks),
2) very tall dorsal fin, as in the Alopiidae, Cetorhinidae, and Lamnidae.
3) streamlined body shape, crescent-shaped tail, jaw not markedly prominent, very wide branchial

apertures, and reduced caudal peduncle, as in the Cetorhinidae and Lamnidae
4) posterior dorsal fin and anal fin reduced, as in the Alopiidae and the Lamnidae.

Based upon what is currently known about *P. benedeni,* scientists have been able to hypothesize its appearance, size, and weight; reconstruct the environment in which it lived; and speculate about the way its teeth were used and the strength of its bite. On the other hand, its behavior and diet remain unknowns, as does the biggest puzzle of all: the ecological role *P. benedeni* played in Neogene marine paleocommunities dominated by *C. carcharias* and *C. megalodon*. Such mysteries will remain unsolved until someone, perhaps even a collector reading this article, discovers a complete, fossilized *P. benedeni* specimen and allows us to fill in the gaps in our understanding of this mighty and fascinating shark.

All photos by Nando Musmarra except as noted

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