Sharks, With a Focus on Shark Teeth: Tooth Composition, Structure, and Properties, with a Comparative Analysis to Other Fish

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ABSTRACT: Shark teeth are everywhere in society's imagination. From *Jaws* to *Sharknado*, pop culture is obsessed with the haunting grins of sharks, especially the great white. Despite the shark-craze in pop culture, shark studies were relatively few and far between, but are now gaining in popularity. There is still much that is unknown about sharks, and some species even remain mysteries. New techniques in the world of biomineralization, and science in general, have led to an increased understanding of these colossal ocean titans. The purpose of this paper is to shed light on sharks, specifically on the biomineralization of shark teeth, how different shark teeth function, and how they can be compared to each other and other types of toothed fish.

INTRODUCTION

Sharks belong to the same family as skates and rays but are distinctly different in a common ancestor. There are over four hundred shark species and twelve orders of sharks, four of which have gone extinct (including the megalodon, although the order of the megalodon is debated).[1] Sharks are easily recognizable by their dorsal and pectoral fins, as well as their gills and large jaws. Some sharks, such as hammerheads, whale sharks, and bull sharks have distinct characteristics that make identification simple, whereas other sharks are not as easy to characterize.

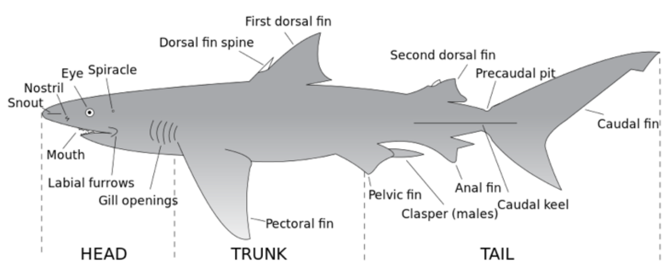


Figure 1. General anatomy of a shark.[1]

Different sharks have very unique behaviors, diets, and lifestyles. For example, the diet of a whale shark, a filter feeder, is very different from the aggressive, predatory tiger shark. Sharks also live in diverse areas of the sea. From nurse sharks in warm, shallow waters to terrifying goblin sharks in the ocean's depths, sharks inhabit nearly all waters in the world. This has led to incredible amounts of biodiversity in the species.

This paper will investigate biodiversity in sharks through their teeth, with particular emphasis on what shark teeth are made of and how different teeth are used for different hunting methods. Sharks have multiple rows of teeth, some of which have different structures depending on whether they are posterior or anterior teeth.

This paper will also investigate several studies that highlight the methods that science has uncovered the mysteries of shark teeth. From the first application of the electron microscope on shark teeth to today's modern computational and scientific methods, this paper will analyze how this fascinating creature utilizes biomineralization in the genesis of its teeth.

CHARACTERIZATION (Methods and Results)

Shark teeth come in a large variety of different forms. Often, the type of tooth a shark has is determined by environmental factors, such as diet. The teeth of whale sharks, who largely eat krill through filter feeding, are very different from the jagged, horrifying beauty of the great white. In the following sections, three major topics will be discussed of shark teeth: their composition (chemical), structure (physical), and their physical properties (how the chemical structure is useful for the purpose of consuming prey). A larger emphasis will be put on the diversification of shark teeth than on one particular species. Later in the paper, shark teeth in general will be compared to the chemical structure and function of other toothed fish, such as parrotfish, sheepsheads, and piranhas.

Composition

Much like teeth in mammals, teeth in sharks contain some essential compounds necessary for formation, structure, and maintenance of form. The exact composition of shark teeth was well debated for over a century, before more accurate methods of measurement were introduced to figure out the exact composition of biomineralized substances.[13]

Initially, it was debated whether or not fish, and sharks in particular, had bone in their teeth, or just a cartilage derivative. For biologists, the presence of bone would not make evolutional sense; it would indicate that the lack of bone in fish and sharks was not due to osteogenic (bone-creating) viability in sharks, but that more localized factors resulted in the use of cartilage over bone.[13]

In one early anatomic study of sharks by Columbia University in 1970, the jaw of a mature sand shark (*squalus acanthias*) was analyzed for evidence of traditional bone, like the bone found in mammals.[13]

What the lab discovered is that the "usual" odontoblastic cytodifferentiation did not occur in the teeth of the shark. They noted that shark teeth form in the opposite way that mammal teeth do. The formation of the basal plate, for example, precedes the formation of the mass of dentin in the undifferentiated tissue. It is only when the tooth matures that dentine forms within the pulpal cavity (the inner tooth cavity), constricting that space down to a size that depends on the tooth morphology.[13]

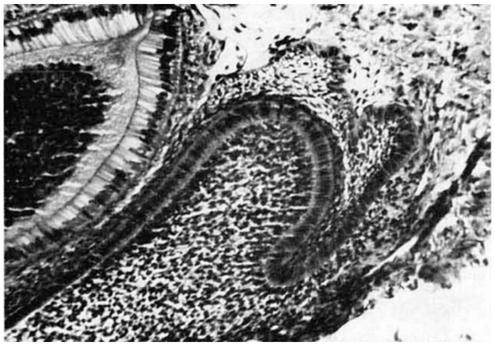


Figure 2. “Amelogenesis [formation of enamel in teeth] in *squalus acanthias.* The dental lamina and the first stage of odontogenesis are fully illustrated, as is a portion of the second stage.” [13]

Another study done in 1970, the first shark study done with electron microscopy, on nurse sharks (*ginglymostoma cirratum*) discovered that dentine was produced in the early formation of shark teeth. The study also remarked that the formation of shark teeth differs greatly from mammal tooth generation in that the matrix of the tooth cap is the first to be formed in sharks, whereas it is the last in mammals.[8] However, at this point, it was still unknown to science whether or not shark teeth were comprised of enamel, like mammals.

It was also discovered that shark teeth lack the collagen that mammal teeth have. In mammals, biomineralization of bone tissue occurs along fibrous strands of collagen. This lab noted that shark teeth lack the amino acids present in collagen, but still form an enamel complex on the outside of the teeth with a different protein. They proposed that “true” enamel, or what humans consider enamel, could be seen in mammals, but not sharks. This was theorized because of hydration issues, as the enamel in mammals needs to be able to survive contact with air, whereas sharks do not have this issue.[8] Despite this proposal, it would be years before the properties of shark teeth were properly analyzed.

These results were later discussed in a study of the blackspot shark (*carcharhinus menisorrah*). The researchers of this study discovered with an electron microscope that there were pockets of mineralization, called palisades, with “elongate enamel crystals coursing in paths within which the crystals were parallel.” The enameline matrix was materializing in hollow fibrils, to be called enameline fibrils. It was discovered that sharks do contain an enamel cap with crystals, like mammals, but inner components of the tooth were formed of soft tissue and nerves.[10] It also isn’t made of the same substance as mammal enamel is, so there was some debate whether or not this matrix qualified as true enamel or not.

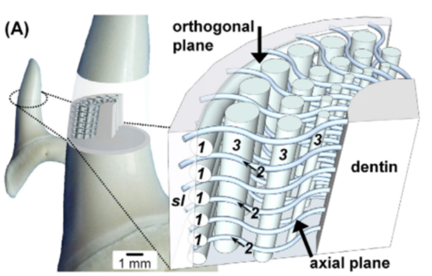


Figure 3. Inner machinations of shark teeth, depicting the fibrous nature of the tooth filaments.[7]

Shark teeth, then, are distinctly non-collagenous, though the enameline fibrils do mimic the function of collagen. Shark enameline shares the same pattern of crystal development that mammals have, in that the pattern of crystal development occurs within the interior of these tubules. In addition to this, it was observed in the lab that biomineralization in shark teeth is hexagonal and behaved more like fluorapatite than hydroxyapatite.[3] The lab also proposed that adding fluoride to the environment of the shark could affect the shape of crystal growth. Another proposed possibility is that shark teeth are free to grow unilaterally (due to the difference in tubules) as opposed to mammalian teeth, which are compressed by dentin and/or enamel.[10]

Figure 4. Lateral view of a block of jaw from *carcharhinus menisorrah*, showing a single set of eight teeth. The first two teeth are recently formed, the third has begun to calcify around the tip, the fourth is more calcified, and the remaining four are heavily calcified.[10]

In 2010, it was found that this enameloid was indeed composed mostly of hydroxyapatite crystallites, that forms a layer 0.2–0.9 mm thick. These crystals form bundles that arrange depending on the direction of the tooth.[14] These hydroxyapatite crystals are the reason that shark teeth have razor-sharp and jagged edges.

In addition to the enameloid, it was discovered that two types of dentin occur in shark teeth. Osteodentine functions like spongy bone does in mammals and orthodentine forms the base layer of all shark teeth. Depending on the structure of the shark teeth, the teeth are separated into two groups;[14] this will be discussed later in the Structure section.

Structure

This section will focus on the macrostructure of shark teeth. Macrostructure is a direct result of the microstructure of shark teeth, but for this section, different shapes of shark teeth will be discussed, as well as differences among species. As previously mentioned in the last section, shark teeth largely have a lot of the same components, but they form different shapes due to environmental factors.

Shark teeth come in a few general structural variants. There are osteodont teeth (teeth without a cavity in them) and orthodont teeth (with cavity).[14]

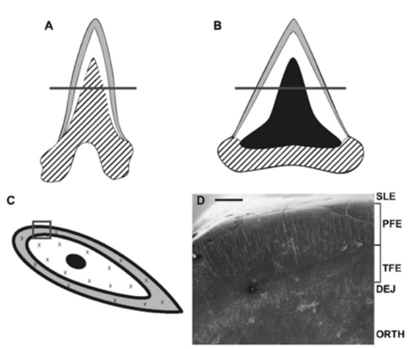


Figure 5 (previous). (a) A typical osteodont tooth (e.x. the sand tiger shark, *carcharias taurus*). (b) A typical orthodont tooth (e.x. the bonnethead shark, *sphyrna tiburo*). White is orthodentine, grey is the enameloid layer, black is the pulp cavity, and hatched is osteodentine. (c) A horizontal cross-section of tooth. (d) Scanning tunneling micrograph of sand tiger enameloid.[14]

From these two varieties, many different subsets of shark teeth exist. Osteodont and orthodont teeth only define whether or not there are is a cavity within the tooth, not the metastructure of the tooth or what the function of the tooth is.[14]

The extant morphology of shark teeth can manifest in many different forms. From triangular serrated cusps, oblique serrated and non-serrated cusps, notched serrated, non-serrated recurved cusps, and many others, there are nearly as many morphologies as there are sharks.[15] Even after differentiation, there are many factors that influence the morphology of shark teeth, such as hardness, diet, and utility.

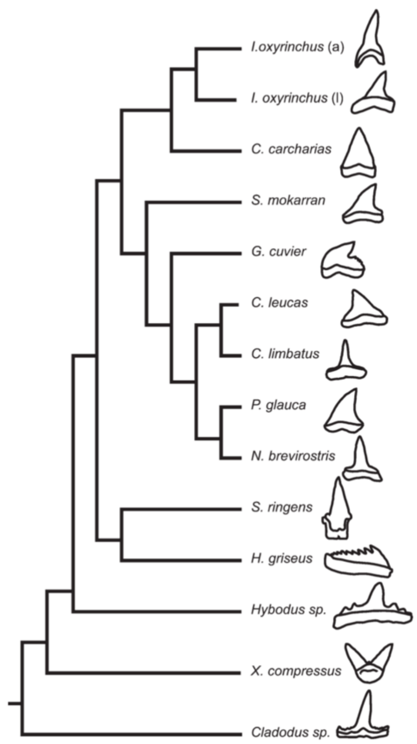


Figure 6. Composite phylogenic tree of species from a conducted study of extant shark teeth. Drawings show the tooth used for the study; each shark has several teeth of different structure, so only one was used for comparison.[15]

As seen from the diagram, there are many diverse teeth morphologies for many different species of shark. The lower teeth of the bluntnose sixgill shark (*hexanchus griseus*), for example, are very different from the great white's (*carcharodon carcharias*) powerful, pointed jaws.[15]

Of those two examples, however, the great white's cone-shaped teeth are more characteristic of traditionally aggressive predatory sharks. To contrast the great white, consider the bluntnose sixgill, which is a decomposer. When whale carcasses hit the ocean floor, the sixgill takes large chunks from the carcass, and is more worried about retaining food in its mouth than hunting live prey, which is why the lower teeth are angled backward and feature many small, rigid edges.[5] The great white's teeth, in comparison, are cone-like, and perfectly suited for impaling prey.

In fact, the cone-shape of shark teeth was studied in 2016 for its amazing bite-to-dentation ratio, in a study on the physics of puncture mechanics. Dentation (and similarly, the Young's modulus) of bone is of great interest to science, as the strain put on a material can be a direct result of the chemical structure of a substance. From this shark teeth are incredibly powerful. They are resistant to dentition yet can deliver devastating bite force on prey.[2]

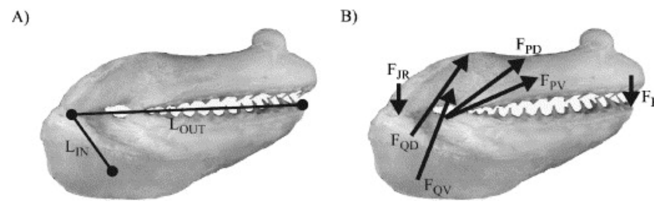
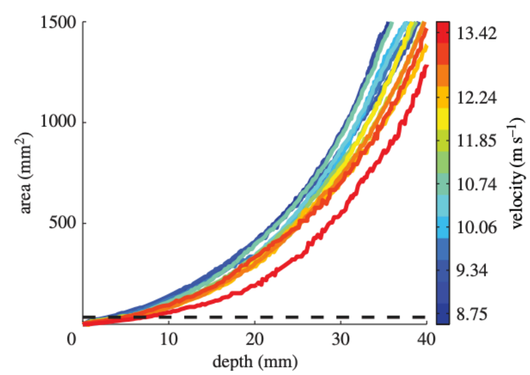


Figure 7. A force diagram of the bite of a blacktip shark (*carcharhinus limbatus*) demonstrating how shark teeth puncture prey.[9]

The study compared two variables in puncture: mass of the puncture tool and velocity of the tool. It was discovered that as animals get larger, the biological necessity of larger velocity is favorable, because teeth have less mass. The animal needs to maintain a certain ratio between speed and mass to achieve a given depth of puncture.[2]



Graph 1. Graph of data from the lab demonstrating the correlation between area and velocity on the depth of puncture.[2]

This is applicable to shark teeth, because shark teeth have incredible weight and power, in addition to incredibly fast biting mechanisms. Sharks can bite at a high velocity, and large predatory sharks such as the great white have large, mass-heavy teeth. In particular, the great white's teeth are suited for taking one gigantic bite to puncture the skin of its prey, then the great white retreats to allow its prey to undergo shock or die from hemorrhaging. This tactic is only viable because of the incredible weight of the teeth, as well as a biting stress of over 600 MPA.[4] The conclusion is that the combination of shape, as well as the speed and mass of the teeth, is what results in the largely effective bite of a shark.[2]

Properties

Teeth all have the same general function: mechanically digesting prey for the benefit of the shark, before chemical digestion begins. However, different types of sharks seek out different prey, and the structure of a shark's teeth is directly influenced by the shark's diet, and how best to digest its prey.

When considering how the structure of each type of shark tooth impacts the tooth's function, it is pivotal to interrogate the Young's modulus (ability to withstand changes in length under compression) and hardness of the teeth. A study from 2010 was the first to investigate the mechanical properties of shark teeth. In this lab, teeth from an orthodentine shark, the bonnethead (*sphyrna tiburo*), and from an osteodentine shark, the sand tiger shark (*carcharias taurus*) were collected and tested for their physical properties.[14]

Five teeth were collected from one individual of each species. The five teeth from the sand tiger shark were freshly shed, then acquired from a tank at Walt Disney World's Epcot center. The five bonnethead teeth were acquired from a recently euthanized laboratory specimen from the Mote Marine Laboratory in Florida. The teeth were then prepared for cutting by halving them vertically and flatting the base so the teeth would lie flat.[14]

The specimens were tested with a nanoindenter, equipped with a Berkovich diamond tip. The lab then measured the indentations for hardness and the Young's modulus through a series of calculations. An interesting note is that the Poisson's ratio (a ratio measure of the increase in stretch as something decreases in width) was unknown for shank enameloid and dentine, so values were substituted with values for mammal enamel and dentine. The lab states that this substitution is not unreasonable, however, because many biominerals have Poisson values that are very similar.[14]

Species	**Mean hardness of enameloid (GPa)**	**Mean Young's modulus of enameloid (GPa)**
s. tiburo	3.53 +/- 0.30	68.88 +/- 1.50
c. taurus	3.20 +/- 0.20	72.61 +/- 4.73

Table 1. Table of the discovered values for mean hardness and mean Young's modulus for enameloid.[14]

	Mean hardness for type of dentine (GPa)	**Mean Young's modulus for type of dentine (GPa)**
s. tiburo (ortho)	0.97 +/- 0.07	22.49 +/- 1.72
c. taurus (osteo)	1.21 +/- 0.16	28.44 +/- 2.21

Table 2. Table of the discovered values for mean hardness and mean Young's modulus for each type of dentine (orthodentine and osteodentine, respectively).[14]

From the data above, the lab concluded that there were no significant differences in the material and physical properties for enameloid in each of the shark species. However, the lab did conclude that there was a significant difference in the hardness and Young's modulus between the two types of dentine; osteodentine was harder than orthodentine. The enameloid also proved to be much harder than the dentine, which makes sense biologically, as the enameloid comes into direct contact with the shark's prey and environment.[14]

Another physical property to note is size (mass) of different shark teeth. Though few-to-no studies have been done comparing the mass of shark teeth, it is easy to qualitatively notice the difference in the mass of shark teeth. This contrast is best seen in the differences between the great white shark (*carcharodon carcharias*) and the basking shark (*cetorhinus maximus*). Though the basking shark is the second largest living shark species on earth, it feeds solely on zooplankton, and has incredibly tiny teeth.[11] Great whites, on the other hand, grow to be, at their largest, only half the size of the basking shark; yet great whites are known for their large, powerful, and fear-inducing teeth. Over a hundred basking shark teeth can fit in a human palm, but just one large great white tooth can span the entire horizontal distance of a human hand.

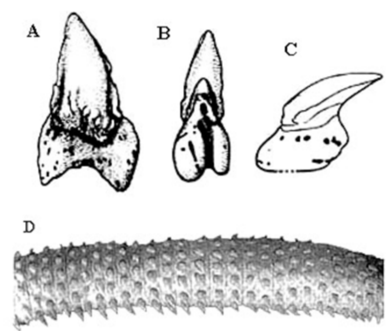


Figure 8. (A) Labial, (B) basal, and (C) lateral views of basking shark teeth. (D) Enlarged view of a portion of the jaw of a basking shark.[11] The teeth are small and offset, for the purpose of retaining zooplankton.

COMPARATIVE ANALYSIS (More Methods and Results)

Sharks are not the only fish to have evolved teeth; several other species of marine life have evolved analogous structures. In this section, structural differences in teeth between different species of fish will be analyzed, to the extent of what the teeth are made of and how they differ from other species.

Piranhas

Piranhas (*serrasalmus manueli*) are carnivorous fish, famous for their aggression and fearsome jaws. However, despite their popularity in the horror genre and in pop culture, the mechanical properties of piranha teeth were not investigated until 2011. The study also investigated the properties of great white shark teeth (carcharadon carcharias), a useful comparison when considering differences between analogous structures.[4]

Piranha teeth have two components: the outer layer is the enameloid layer (to reiterate, the enamel layer is comprised of rod-shaped hydroxyapatite crystals) and the inner layer is the dentin layer. The external edges are covered in jagged, mineralized serrations, which the piranha uses to convert some dragging force into puncture force. Interestingly, the inner layer of dentin in piranha teeth is mineralized around collagen, though the lab did not draw parallels to human teeth here.[4]

By using nanoindentation, it was discovered that the enameloid of piranha teeth has a mean reduced Young's modulus of 86.5 +/- 15.9 GPa and a mean hardness of 4.1 +/- 0.9 GPa, whereas the dentin had a mean reduced Young's modulus of 23.0 +/- 6.0 GPa and a hardness of 0.8 +/- 0.3 GPa. An interesting distinction that the lab made is that when the teeth were hydrated, the values for hardness and Young's modulus were lower than those under dry conditions. Especially noteworthy is that the values for hydrated dentin plummeted, indicating a sharp decline in the firmness of piranha dentin when hydrated.[4]

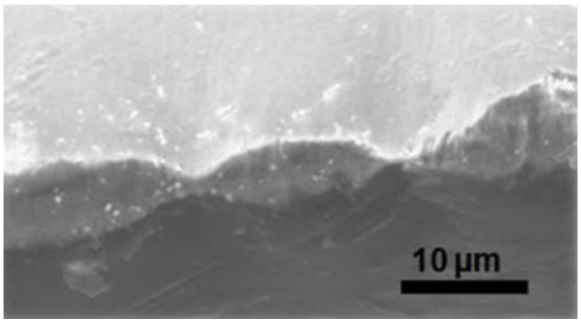


Figure 9. Details in the serrations of piranha teeth.[4]

Overall, the lab concluded that the biominerals in piranha teeth, and other mineralized fish, are essential for survival. Specifically, in piranhas and great whites, it is critical that teeth have these properties due to the intense strain the teeth undergo during puncture.[4]

It is also important to note that these biominerals have formed analogously in these fish, indicating similar evolutionary mechanics in a few differentiated, isolated cases. Another important note was that hydrating the dentin greatly reduced the mechanical properties of dentin, but not enameloid; therefore, enameloid functions like a type of shield, protecting the dentin from exposure to hydration.[4]

Sheepshead

Archosargus probatocephalus, also known as sheepshead, are strange-looking toothed fish that feed on oysters, clams, and other bivalves. They're infamous for their awkward, human-like teeth. In this 2017 study of the mechanical properties of sheepshead teeth, researchers examined the chemical and physical properties of the teeth.[6]

The lab investigated the composition and structure of sheepshead teeth through X-Ray Energy Dispersive Spectroscopy (EDS). Teeth were extracted from a specimen from the Mississippi Gulf Coast, polished, then inspected with a nanoindenter. They then tested the chemical composition of the teeth, with particular focus on the percent of calcium, phosphorus, and fluoride.[6]

From the nanoindentation tests, the lab found that the dentin in the sheepshead teeth had a hardness of 0.89 +/- 0.21 GPa and a Young's modulus of 23.29 +/- 5.30 GPa. The enameloid measured mush harder, at a hardness of 4.36 +/- 0.44 GPa and a Young's modulus of 98.14 +/- 6.91 GPa.[6]

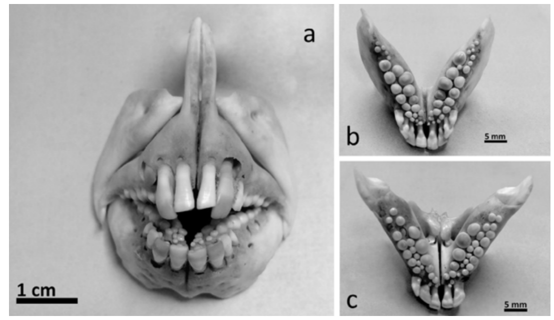
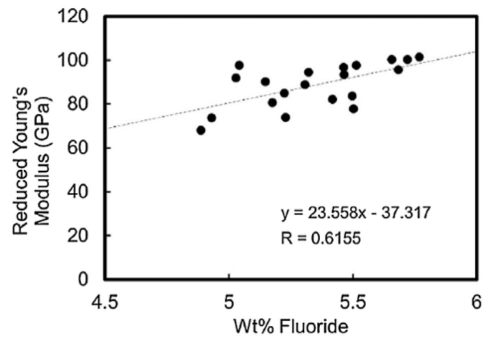
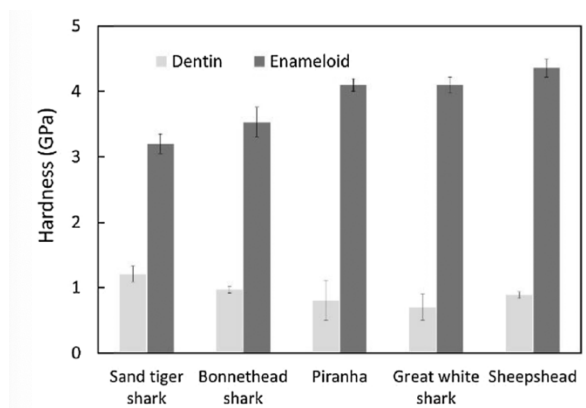


Figure 10. Sheepshead teeth used in the study.[6]



Graph 2. Graph of Young's modulus as fluorine concentration increases in sheepshead teeth. As more fluorine is present in the teeth, the teeth become less stiff and more susceptible to change.[6]

Compared to the values of hardness of previously mentioned shark teeth (sand tiger and bonnethead), sheepshead dentin is less stiff and has a higher Young's modulus, but sheepshead enamel is more firm and more durable than shark teeth.[6]



Graph 3. A comparison of hardness between sand tiger, bonnethead, and great white sharks with piranhas and sheepsheads.[6]

Parrotfish

Parrotfish (*scaridae*) are similar to sheepsheads, but feed on stony corals for their polyps and symbionts. Parrotfish have a significant impact on the health of natural coral reefs, as without a diversity of parrotfish, differentiated corals cannot grow.[12]

Parrotfish have two sets of teeth: a beak for biting into corals, and a pharyngeal mill for mechanically breaking down the coral into digestible parts. The following study, conducted in 2017, was done on the biting beak to discover the mechanical properties under stress. To do this, the lab investigated the chemical structure and the nano- and micro-structures of the steephead parrotfish (*chlorurus mircorhinus*).[12]

The lab first measured the mechanical properties of polished sections from a sample steephead parrotfish jaw. Parrotfish jaws contain two rows of upper dental plates and two lower ones, each containing around fifteen rows of teeth. The teeth begin growth around a soft tissue at the bottom of the jaw, then gradually become more mineralized and rigid as they move closer and closer to the tip of the beak.[12]

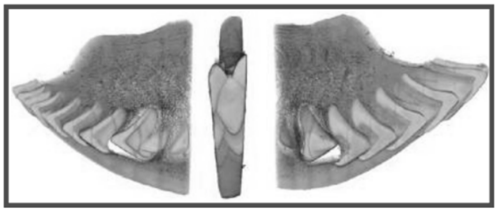
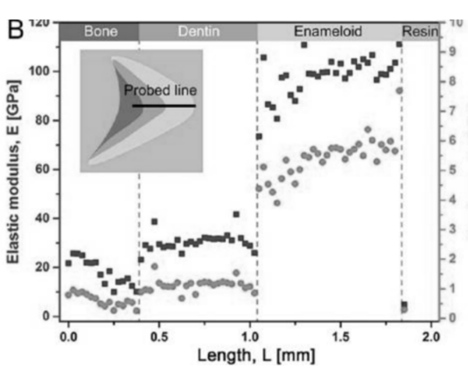


Figure 11. 3D volume rendering of one-fourth of a parrotfish beak specimen. Denser enamel is represented in the lighter tooth sections. Dentin and surrounding bone have similar densities.[12]

The lab performed nanoindentation on the sections of polished jaw with both blunt and sharp contact geometries, to measure the mechanical properties of the teeth. Then, chemical and structural analyses were correlated via a scanning electron microscope.[12]

From this analysis, it was discovered that stiffness ratio of enameloid in parrotfish matched the basal and prismatic values for single crystals of fluorapatite, which had been predicted from a computer program. The parrotfish enameloid (along the biting direction) was found to be stiffer than almost any other comparable biomineral, and is comparable to chiton teeth, sea urchin teeth (another stony-coral feeder), and shark tooth enameloid. The hardness, which reaches 7.3 +/- 0.4 GPa near the biting tip, is greater than moth other biting fish, including great white shark teeth and piranha teeth (but not teeth from other shark species). Another similarity between shark and parrotfish teeth is that SEM indicates a change from hydroxyapatite to fluorapatite from dentin to enameloid, a change which had been previously recorded in shark teeth. Similarities continue in the fibrous nature of the enameloid, but sharks have much more defined fibrous layers in their tooth biomineralization.[12]



Graph 4. Elasticity and hardness of enameloid, dentin, and bone in the steephead parrotfish. Enameloid is the hardest and most elastic material, followed by dentin, then bone.[12]

At the conclusion of the paper, the researchers stated that the properties discovered in parrotfish teeth result in highly stiff teeth that are resistant to abrasion from stony corals. It is theorized that these properties arise from the crystal orientation in the tooth biomineralization, the spacial variations, and the residual compressive strains. Overall, the lab concluded that the incredibly complicated and intricate structure of parrotfish teeth is what results in such incredible hardness and durability.[12]

CONCLUSION

In conclusion, this investigation of the biomineralization of shark teeth has been a valuable insight on different methods of biomineralization in non-human species. It is important to understand many different methods of biomineralization, especially when considering the different conditions that crystals form under in different species. In the case of marine life, understanding how crystals form in such an aqueous environment is critical, and it is fascinating to see how these boneless species still biomineralize for the purpose of survival.

The data provided and the processes examined can offer powerful insights into several scientific fields. Most obviously are the fields of ecology and dentistry; for ecologists, the study of analogous structures (such as teeth) can offer insights into evolutionarily viable structures, whereas in the field of dentistry, understanding variable tooth formations and different methods of biomineralization in teeth could lead to new scientific breakthroughs. Though those may be two more obvious applications, there are plenty of other ways that the study of teeth can be applied to science, such as material science, bioinformatics, genetics, and other fields. Regardless of the purpose, it is critical that humanity continues to learn about natural life, one tooth at a time.

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