The Evolution of Shark Teeth in Relation to Prey Specialization

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Introduction

Modern sharks first appeared in the fossil record nearly 100 million years ago and they haven't evolved much since they first appeared (Mojetta, 1997). One major evolutionary advancement found in modern sharks are their jaws. Today's sharks have a jaw that is comprised of several working parts. The jaws float in the skull, attached by strong tendons and muscles (Skomal, 2016). The floating jaw structure, known as a hyostylic jaw, allows for sharks to extend their jaws out and down for the greatest mobility and flexibility while capturing prey (Mojetta, 1997; Skomal, 2016). Modern sharks also have several rows of teeth that are constantly worked and shed. The front row, or "working teeth," are the largest teeth in the jaw, with each tooth behind it becoming progressively smaller (Stevens, 1997). For sharks to rapidly replace their teeth when shed, the teeth cannot be embedded in the jaw. Instead they are connected with soft tissues. These soft tissues allow for new teeth to shift forward like a conveyer belt, replacing the lost tooth within just a few days (Skomal, 2016). Most modern sharks lose and replace one tooth at a time. However, there are some species like the cookie cutter shark (*Isistius brasiliensis*) that will replace an entire row at a time (Parker, 2008). Modern sharks will typically lose 20,000 teeth in their lifetime (Parker, 2008).

Sharks are mostly known in the fossil record from their teeth, calcified vertebrae, as their skeletons are made of cartilage which does not fossilize as well as bone (Whitenack & Motta, 2010). There are very few well-preserved specimens available for paleontologists to study ancient sharks (Whitenack & Motta, 2010). In 1896 the Louis Henry Sullivan, an American architect, stated, "Form ever follows function" (Sullivan, 1896). While this may be true in architecture, in a truly Darwinian understanding of evolution, form proceeds function. Through the study of the shark fossil record, observations of modern shark feeding behaviors, and modern shark teeth biomechanics, it is possible to reconstruct the world of the ancient sharks, what they fed on, and examine their predator-prey relationships (Whitenack & Motta, 2010; Whitenack et al., 2011).

Fossil Sharks

Ancient sharks first made an appearance in the fossil record around 390 million years ago in the Devonian period (Mojetta, 1997). Ancient sharks displayed a great range of diversity, across 45 families, with many morphologies no longer found in extant sharks (Cuny, Suteethorn, Kamha, & Buffetaut, 2008). The cladodont sharks are the first sharks known to science. These sharks appeared around 391 million years ago in the early Devonian period (Whitenack et al., 2011). The cladodonts are almost exclusively known from their teeth. Their teeth had a single large cusp in the center with several smaller cusplets laterally, and a flattened, disk-like base (Case & Cappetta, 2004) (Appendix, Figure 1). The upper jaw of the cladodonts were ventrally fused to the brain case which limited the movement of the upper jaws. The lower jaws were supported by cartilage but also became fixed at the rear. This type of structure is known a amphistylic jaw (Mojetta, 1997). Damage on a fossil Viséan branchiopod, a class of crustaceans, *Delepinea destinezi*, suggests the cladodonts fed on hard-bodied prey (Elliott & Brew, 1988).

During the age of the cladodonts, the ability to replace worn teeth evolved (Ginter & Hansen, 2010). This is an advantageous evolutionary step for sharks for both health and defense. It allows for sharks to reject an unhealthy tooth, avoiding potential infections that afflict humans and other animals. It also means that if prey struggles the tooth can easily detach, saving the shark from further jaw damage (Skomal, 2016). The Denaea family provides evidence of base tooth attachment with no change to the general function of the tooth (Ginter & Hansen, 2010). They had very small teeth, approximately 1 mm in maximum dimension, and had a large central cusp and 5 to 7 slender lateral cusps. However, *Denaea saltsmani* and *Denaea meccaensis* displayed differences in tooth attachment. The formation of secondary openings of the basal canal coupled with a loss of the button, or the point of articulation on the oral-lingual side of the base (Appendix, Figure 1), marks an increase in the role of soft tissue attachment (Ginter & Hansen, 2010). *D.saltsmani* shows no clear button, only a vague bump, suggesting that *D.saltsmani* may have had the ability to replace worn teeth, while *D.meccaensis* represents a more primitive tooth attachment (Appendix, Figure 2).

Around 248 million years ago, in the Triassic period, a new shark morphology became dominant: the hybodonts (Schaeffer, 1967). While these sharks were present in the early Devonian period, their numbers remained low until after likely environmental changes led to the extinction of the cladodonts at the end of the Pennsylvanian period. The hybodonts were first described for science from isolated teeth in 1837 (Maisey, 1982). They were characterized by teeth that were either multi-cusped, though less dramatically than the cladodonts, or molar-like (Cappetta, 1987) (Appendix, Figure 3). The hybodonts typically had the sharp multi-cusped teeth in the front of their jaws with the molar-like teeth in the back (Mojetta, 1997).

Along with changes in tooth structure, the hybodonts also evolved more flexible jaw structures. Though the amphistylic jaw structure remained, the jaw became more flexible and mobile than the cladodonts (Mojetta, 1997). The length of the mouth also reduced, and became more sub-terminal than terminal as in the cladodonts. These evolutionary steps allowed for the hybodonts to catch prey more easily, and therefore allowed them to be more generalized predators, than their predecessors (Mojetta, 1997). These changes likely coincided with a change in diet from hard-bodied prey to soft-bodied prey, such as invertebrates and early bony fishes (Cappetta, 1987). Based on these evolutionary adaptations, the hybodonts represent a halfway stage between the cladodonts and modern sharks.

Modern Sharks

Modern sharks first appeared in the fossil record around 100 million years ago. Modern sharks are characterized by a series of anatomical changes related to swimming and diet. Modern sharks sport calcified vertebrae and a ventrally fused pelvic girdle that aids in swimming dynamics (Mojetta, 1997). The jaws of modern sharks changed from amphistylic to hyostylic, allowing for a far greater range of motion in their jaws than ancient sharks. These changes coincide with the spread of teleosts, or bony ray-finned fishes, which would become the main source of nutrients for most modern sharks (Stevens, 1997). The hybodonts and early modern sharks shared the seas for nearly 40 million years. However, competition between the two eventually led to the disappearance of the hybodonts at the end of the Jurassic period 65 million year ago (Rees & Underwood, 2008; Whitenack & Motta, 2010).

Modern sharks display a great variety of teeth including flattened pavement teeth, non-serrated teeth, broad triangular serrated teeth, and even extremely tiny teeth (Whitenack et al., 2011). These teeth morphologies have been ascribed functions that correlate with hunting methods of preferred prey items, such as crushing, piercing, and tearing (Whitenack et al., 2011). Studies have demonstrated that each tooth morphology performs differently when puncturing different prey items (Whitenack & Motta, 2010; Whitenack et al., 2011).

Crushing teeth are typical of sharks that spend most of their lives on the seafloor feeding on hard prey items like mollusks and crustaceans, like the bamboo shark (*Chiloscyllium plagiosum*) (Appendix, Figure 4). These sharks have developed specialized plate-like teeth that work to crush the hard shells of their prey much like a nut cracker (Parker, 2008). Often these sharks capture prey with a large, sudden intake of water that sucks their prey into their mouths and over the crushing pavement teeth (Parker, 2008; Skomal, 2016).

Non-serrated, smooth edged teeth are associated with fish feeding species. In 1988, Frazzetta was the first to address the relation of shark tooth morphology and biomechanics. He found that smooth, slender teeth performed best while puncturing and piercing slippery, soft-bodied prey like fishes (Frazzetta, 1988). These teeth are typical of sharks like the makos (*Isurus*), goblin shark (*Mitsukurina owstoni*), and sand tiger shark (*Carcharias taurus*) (Whitenack & Motta, 2010) (Appendix, Figure 5). These long, needle-like cusps act as fishing hooks, piercing into the slippery fish and pulling it into the shark's mouth to be swallowed whole (Parker, 2008).

Cutting teeth are characterized by broad, flattened bases with a large single cusp that has a serrated cutting edge. These teeth are typical of the Carcharhinidae family, which is comprised of requiem sharks (Whitenack & Motta, 2010). In his study, Frazzetta found that serrated teeth were better suited for slicing and cutting (Frazzetta, 1988). These teeth trap tissues within the serrations, tearing through soft tissues as the teeth withdraw from the prey source (Abler, 1992). However, the serrated blades do not perform as well on the puncture of prey as non-serrated teeth, placing more stress on the cutting edges in order to puncture (Whitenack & Motta, 2010; Whitenack et al., 2011). The broad serrations of the great white shark (*Carcharodon carcharias*) (Appendix, Figure 6), for example, exhibits high initial pressure when puncturing the common grunt (*Haemulon plumierii*), compared to the low pressure needed from the shortfin mako (*I. oxyrinchus*) (Whitenack & Motta, 2010). Sharks like the great white (*C. carcharias*) that have these broad serrated teeth tend to feed more commonly on marine mammals and large oceanic fishes (Parker, 2008). These sharks tear away large chunks of flesh from their prey as opposed to swallowing their prey whole (Stevens, 1997).

Not all modern sharks are active hunters that require crushing, tearing, or cutting teeth. There are only three known species of filter feeders: the megamouth shark (*Megachasma pelagios*), the basking shark (*Cetorhinus maximus*) and the whale shark (*Rhincodon typus*) (Skomal, 2016). These sharks swim with their large mouths wide open collecting tiny, microscopic planktonic organisms. But these sharks still have teeth. Filter feeders have nearly 200 incredibly tiny teeth per row which line the upper and lower jaws (Martin, 2007). These velcro-like teeth are considered by ichthyologists to be vestigial structures and are not used to feed. Instead, filter feeders use gill rakers to feed (Martin, 2007; Parker, 2008). The gill rakers are specialized screens located inside the gills that catch the plankton and funnel it directly to the shark's stomach. The rakers can be seen through the gill slits from behind the shark (Appendix, Figure 7). It is speculated that filter feeders use their teeth in social interactions such as mating; however, no mating behaviors have ever been observed in any species of filter feeder (Martin, 2007; Sims & Quayle, 1998).

Conclusion

Through the study of the shark fossil record, which consists mostly of teeth, calcified spines, and a handful of well-preserved specimens, it is possible to reconstruct the world of the ancient sharks. The first sharks present in the fossil record around 390 million years ago were the cladodonts. These sharks had amphistylic jaws and multi-cusped teeth and likely fed on early invertebrates. While these sharks were successful for approximately 150 million years, likely changes in hard bodied prey availability led to their extinction. The hybodonts then became the dominate shark morphology, thriving in their prehistoric environment. Their jaws became more flexible, and their teeth featured molar-like crushing teeth in the rear of the jaw and sharp multi-cusped teeth in the front. After approximately another 150 million years, the modern sharks made their first appearance in the fossil record. Likely competition between the modern sharks and the hybodonts led to the extinction of the hybodonts after 40 million years of coexistence.

Modern sharks are characterized by their hyostylic jaws and teeth of varying morphology. Some species feed exclusively on benthic prey items and have hard, pavement like crushing teeth suited for hard bodied prey like crustaceans. Some species feature teeth with large, broad serrations that tear away flesh in chunks from large oceanic fishes and marine mammals. Still other species have long, needle-like teeth that pierce and hold slippery fishes. And some sharks have evolved to feed without teeth, instead filtering water and microscopic prey items through large gill rakers. Though modern sharks are vastly different than ancient sharks, observations of modern shark feeding behaviors and teeth biomechanics helps to create a clearer picture of the evolutionary arms race between ancient predator and prey.

Appendix

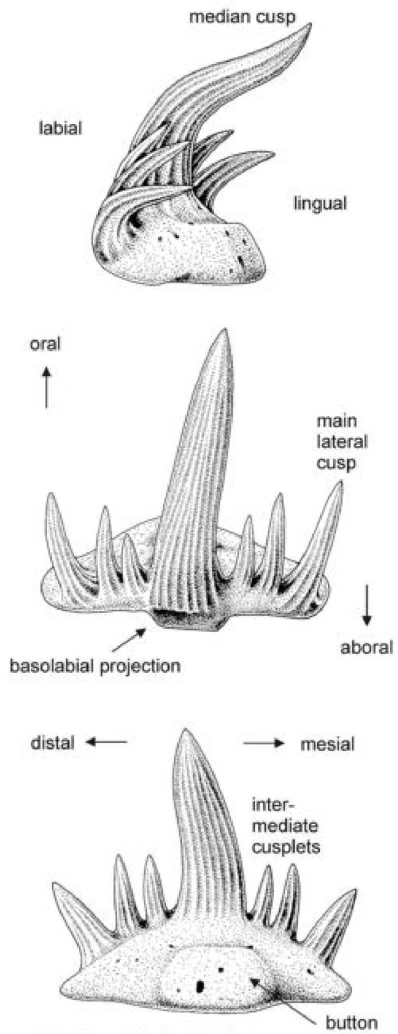

Figure 1. Morphology of a Cladodont shark tooth: a large central cusp with small lateral cusps on each side. This sharks likely fed on soft bodied prey items like early invertebrates (Figure 1, Ginter & Hansen, 2010).

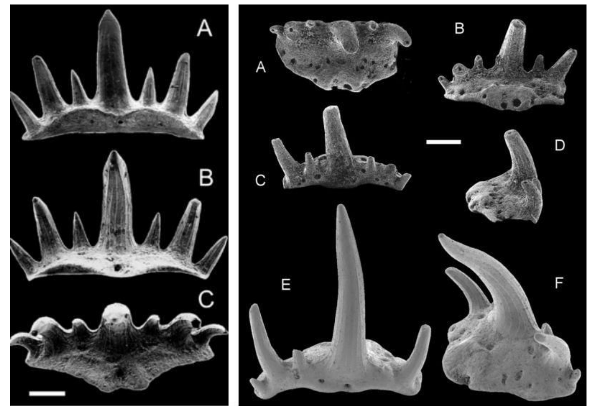

Figure 2. **Right**: *Denaea meccaensis* tooth features a primitive attachment mechanism, suggesting the teeth were fixed in the jaw (Figure 7, Ginter and Hansen, 2010). **Left**: *Denaea saltsmani* tooth features a more modern attachment mechanism without changes in tooth function. This suggests that soft tissues were becoming more important in tooth attachment (Figure 2, Giner and Hansen, 2010).

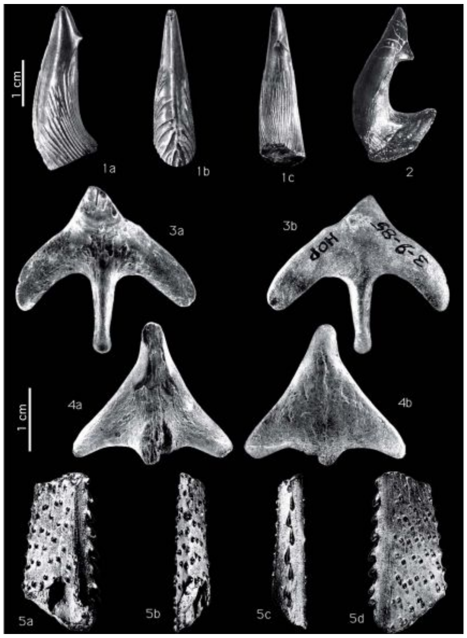

Figure 3. Morphology of teeth from hybodont shark, *Hybodus novojerseyensis*. The pavement-like morphology suggests a change in prey specialization from soft bodied prey to hard bodied prey, like crustaceans (Case & Cappetta, 2004).

Figure 4. Bamboo shark (*Chiloscyllium plagiosum*) crushing teeth. These teeth are specialized for crushing hard bodied prey, like crustaceans, similar to hybodont sharks (Tobze, 2010).

Figure 5. Sand tiger shark (*Carcharias taurus*) with non-serrated, gripping, piercing teeth. These teeth are best suited for holding slippery prey items like bony fishes (Sand tiger teeth, n.d.).

Figure 6. Great white shark (*C.carcharias*) serrated tooth. The large serrations are adapted to tearing away flesh from large marine prey items, like marine mammals and turtles (Buried Treasures Fossils, n.d.).

Figure 7. Whale shark (*Rhincodon typus*) teeth and gill rakers. These sharks do not use their teeth in feeding, but rely on gill rakers to filter out microscopic planktonic organisms. The teeth are likely vestigial structures (Feeding whale shark, n.d.; Whale shark teeth, n.d.; shark gills, n.d.).

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SHARK TEETH

The Evolution of Shark Teeth Specialization

Fossil shark teeth first appear in the fossil record 391 million years ago

Cladodont

The earliest fossil shark teeth, the Cladodonts, date back to the Middle Devionian (391 million years ago) [1]. The Cladondonts are characterized by a large central cusp with several lateral cusps on either side [2]. Most Cladodont sharks did not shed their teeth l²⁻ⁿ modern sharks, but retained them th. ,hout their lives. Replaceable teeth probably evolved during this time in the Denaea family [3]. These sharks likely fed on soft invertebrates such as early cephalopds [4].

Hybodont

The Hybodont teeth became the dominant morphology beginning in the Triassic (248 million years ago) through the Jurassic (206 million years ago) [5]. The Hybodont teeth featured either multicusped teeth - though less dramatic than the Cladodonts- or molar like teeth [6¹ These sharks likely fed on invertebrates , soft bodied fishes [7]. Despite being the dominant group during this time with 45 families, the hybodants went extinct at the end of the Jurassic period [8].

Modern shark teeth first appear in the fossil record 150 million years ago

Serrated

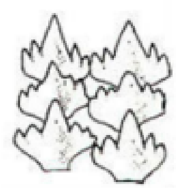
The large serrated teeth of the great white shark (Carcharodon carcharias) are made for piercing, cutting, and tearing away flesh from large marine mammals [9]. These teeth act as a steak knife cutting away large chunks of flesh from prey items. The serrations trap material between the serrations, ripping away tissues as they are carried by the teeth [10].

Smooth

These long, needle-like teeth are ideal for piercing and gripping slippery prey items like bony fishes [9]. Sharks like the shortfin mako (*Isurus oxyrinchus*) and the sand tiger shark (Carcharias taurus) are perfect examples of species with these smooth edge teeth. These teeth out perform the serrated teeth when puncturing prey, placing less stress on the cusp than the broader serrated teeth [1,2].

Filtering

There are three species of known filter feeders: the whale shark (Rhincodon typus), the basking shark (Cetorhinus maximus), and the megamouth shark (Megachasma pelagios) [11]. These sharks have hundreds of rows of tiny, velcro-like teeth. These teeth are not used in feeding [12]. These sharks swim with their mouths wide open to filter out food using their gill rakers. It is thought these teeth are used in social interactions between sharks, such as mating [12].



Crushing

These flat, plate-like teeth are typically found in benthic sharks that prey on crustaceans and bivalves [11]. These teeth are ideal for crushing hard shells, much like a nut cracker. Some species, like the horn (*Heterodontus francisci*) and port jackson sharks (Heterodontus portusjacksoni) feature clutching teeth in the anterior part of the jaw and crushing teeth posteriorly [2]. Hence their genus name Heterodontus, "hetero" meaning different and "dontus" meaning teeth [11]

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