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Functional Tooth Morphology and Chondrichthyan Vulnerability During the Ocean Anoxia Event 2

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FUNCTIONAL TOOTH MORPHOLOGY AND CHONDRICHTHYAN VULNERABILITY DURING THE OCEAN ANOXIA EVENT 2

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in

EARTH AND PLANETARY SCIENCES

by

Melanie A. Gagucas

August 2025

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Table of Contents

List of Figures

Abstract

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by

Melanie A. Gagucas

Functional tooth morphology is a useful proxy in determining the ecological roles of chondrichthyans in marine systems past, present, and future. As the oceans continue to change due to anthropogenic processes, it is increasingly important to understand the potential impacts of stressors such as warming, acidification, and anoxia on marine ecosystems. Chondrichthyans have a 400-million-year evolutionary history, during which they have survived multiple extinction events. This study uses functional tooth morphology to infer the ecological response of chondrichthyans to low-oxygen conditions, such as those in the mid-Cretaceous Ocean Anoxia Event 2 (OAE2). We compiled over 10,000 Cretaceous chondrichthyan genus-level occurrences from the Paleobiology Database and categorized each into one of four functional morphotypes: crushing, cutting, clutching, or piercing–grasping. Genera exhibiting crushing and clutching dentition tend to have a benthic, slow-moving lifestyle, whereas those with cutting and piercing-grasping morphotypes are typically open-ocean predators, living an active lifestyle. These ecological tendencies associated with habitat depth and metabolic demand may play a role in determining the sensitivity of chondrichthyans to low-oxygen areas. Accordingly, the extinction intensity of each morphotype was then calculated across the OAE2 boundary using the boundary-crosser extinction method. All morphotypes showed elevated extinction intensity, especially crushing and clutching teeth, indicating that, despite the various ecological roles linked to dentition type, chondrichthyans were broadly vulnerable to the environmental conditions associated with widespread anoxia.

Acknowledgments

I want to thank my advisor, Matthew Clapham, for his endless patience and guidance throughout this project, and for showing me what it means to be a kind, supportive, and principled academic. I would also like to extend my thanks to my graduate cohort, who made me feel welcomed and heard, and ensured I never felt alone during my graduate studies. Finally, I wish to thank my friends and family, who never quite understood what I was doing, but supported me all the same. Thank you.

1 Introduction

1.1 History of Chondrichthyan Evolution and Extinction

Chondrichthyans are one of the oldest extant taxa of vertebrates, originating more than 400 million years ago and surviving ecological changes, environmental shifts, and extinction events (da Silva Rodrigues Filho & de Luna Sales, 2017). This group, which includes more than 1400 extant species of sharks, skates, rays, and chimaeras (Carrier et al., 2022), can be differentiated from their closest bony vertebrate relatives, Osteichthyes, by their cartilaginous skeleton (Hedges & Kumar, 2009). They are distributed across the world's oceans, inhabiting environments from coastal shores to the open ocean, and occupy the water column from the surface to depths of approximately 3,000 meters (Camhi et al., 2009). Chondrichthyans are divided into two subclasses, Elasmobranchii and Holocephali (Klimley, 2013). Elasmobranchs are characterized by the multiple gills on either side of their head, whereas Holocephalans have a single gill slit on either side (Klimley, 2013).

Sharks, skates, and rays fall under Elasmobranchii, while chimaeras are categorized under Holocephali (Klimley, 2013). Sharks tend to have that characteristic torpedo-shaped body, but some benthic sharks and all batoids (skates and rays) have a more dorsoventrally flattened shape (Hedges & Kumar, 2009; Klimley, 2013). Chimaeras have a large, round head, large eyes, protruding teeth, a flexible body, and a long tail (Klimley, 2013). The cartilaginous make-up of chondrichthyans has about the same strength as bone, but is much lighter and more flexible, and enables these fish to accelerate, rapidly change directions, and successfully capture their prey. To understand how chondrichthyans have persisted over millions of years, it is important to examine the traits that have enabled their survival through past environmental stress and assess their resilience across evolutionary history.

Throughout their long evolutionary history, these vertebrates have diversified to occupy numerous ecological niches, ranging from open-ocean predators to bottom-dwelling shell-crushing species and freshwater species (Carrier et al., 2022). Early elasmobranchs differed significantly from modern sharks, and much of this can be inferred from their teeth, which are the most common chondrichthyan fossil due to poor preservation of the cartilaginous skeleton and their polyphyodont dentition, meaning their teeth are continuously shed throughout their lifetime (Carrier et al., 2022). Composed primarily of fluorapatite with less than 5% organic matter, shark teeth are incredibly durable compared to mammalian teeth made of hydroxyapatite (Enax et al., 2012; Carrier et al., 2022). Teeth made of fluorapatite result in a rich fossil record that reveals the evolutionary history of chondrichthyans.

Studies suggest that the origin of chondrichthyans occurred during the Ordovician (485-443.8) or the Silurian (443.8-419 Ma) period based on dermal denticles found in sediments that are 440 to 450 million years old (Carrier et al., 2022). However, the oldest chondrichthyan teeth date back to the lower Devonian (~420 to 410 Ma), a period of rapid diversification for fishes (Carrier et al., 2012). While the Devonian, known as the “Age of Fishes,” resulted in the evolution of various groups, such as armored jawed, stem jawed, and jawless fishes, it was during the Carboniferous (358-299 Ma) and Permian (299-252 Ma) that stem chondrichthyes experienced rapid evolutionary expansion as exemplified by the wide array of fossils that have been discovered in a diversity of environments, including freshwater rivers, lacustrine, estuarine, coastal, and pelagic settings, suggesting a similar range of habitats compared to modern chondrichthyans (Carrier et al., 2022).

The anatomical innovations of early sharks allowed them to better adapt to their marine environment and diversify into many niches by the Cretaceous (Klimley, 2013). Besides the development of a cartilaginous skeleton, another key physical trait was their multiple rows of teeth (Klimley, 2013). The outer teeth of modern sharks tend to fall out after a week's use and are replaced by a tooth from the row behind (Klimley, 2013). Oftentimes, the teeth shed from modern sharks remain sharp as they have not been worn down from use (Klimley, 2013). In contrast, earlier shark teeth show signs of wear and abrasion, suggesting that their outer teeth were replaced more slowly, possibly due to fewer rows of teeth (Klimley, 2013). Regardless of the replacement speed, this multi-rowed dentition likely gave early sharks a competitive advantage over other jawed fishes of the Paleozoic, which typically possessed only a single row of teeth (Klimley, 2013). Multiple rows of teeth would have enabled sharks to maintain sharp, functional dentition throughout their lives, unlike a single row, which, if broken or worn, could have compromised feeding efficiency.

Another key morphological innovation that contributed to the success of early sharks as dominant predators was their streamlined, torpedo-shaped body, which was propelled by a homocercal (two, equal sized lobes) caudal fin at the posterior end

(Klimley, 2013). Elasmobranchs also had paired dorsal and anal fins that helped stabilize the body and reduce lateral sway, as well as horizontal pectoral and pelvic fins that provided lift and prevented unwanted rolling during swimming (Klimley, 2013). These features, which contributed to their success, allowed chondrichthyans to endure cataclysmic extinction events and establish themselves as one of the most successful aquatic vertebrates in terms of historical endurance (Klimley, 2013).

Despite surviving multiple mass extinctions, such as the end-Permian and end-Cretaceous, today Chondrichthyes are faced with an unprecedented threat: humans. Worldwide, unsustainable fishing practices that also destroy their habitats have drastically decreased the population of sharks and rays (da Silva Rodrigues Filho & de Luna Sales, 2017). In addition to the threat of overexploitation, chondrichthyans face the consequences of human-driven climate change. As atmospheric carbon increases due to anthropogenic processes, there will be detrimental changes to the global environment. The ocean will experience increased temperatures, acidification, circulation changes, water column stratification, and deoxygenation (Carrier et al., 2022; Doney et al., 2012). The combined effects of global warming and other human impacts, such as intensive fertilizer use, habitat destruction, and overfishing, will ultimately threaten marine organisms and cause large-scale changes to their surrounding ecosystem (Doney et al., 2012; Cahill et al., 2013).

Past extinction events in Earth's history were often driven by the same environmental stressors that occur in modern ecosystems, making them valuable analogues for investigating patterns of ecological selectivity and survival. The Permian extinction has received increasing attention due to its noticeable parallels with the modern environmental crises driven by climate change. During the end-Permian extinction, rapid, cataclysmic CO_2 outgassing from the Siberia Traps large igneous province resulted in the extinction of nine out of ten marine animals (Mayhew et al., 2008). However, active chondrichthyans did not experience elevated extinctions in the end-Permian (Vázquez & Clapham, 2017). Several Paleozoic chondrichthyan lineages crossed the Permian-Triassic boundary, likely because of their substantial energy reserves and ability to inhabit diverse environments (Guinot et al., 2013; Vázquez & Clapham, 2017).

The Cretaceous-Paleogene event had a significantly larger impact on elasmobranch diversity, eliminating 62.6% of species (Guinot & Condamine, 2023). However, the extinction was not ecologically uniform. Taxa that displayed durophagous dentition had higher extinction rates than non-durophagous taxa. In contrast, generalist, non-durophagous shark genera did not show a marked extinction, suggesting they were less selected for in the extinction event (Guinot & Condamine, 2023). Extinctions among sharks and batoids were severe, with the majority of batoid species lost. Furthermore, similar extinction levels were observed in selachians and bottom-dwelling chondrichyans inhabiting continental shelves and shallow regions, except for benthopelagic and deep-sea taxa, which remained largely unaffected (Kriwet & Benton, 2004). Most of the taxa that disappeared by the end of the Cretaceous were medium to large apex predators that inhabited epipelagic and shelf zones and had a generalist diet. Ecological factors, such as habitat depth and trophic roles, may have influenced the extinction risk of chondrichthyans during the end-Cretaceous period. Benthic chondrichthyans, such as Orectolobiformes, which are bottom-dwelling and possess durophagous dentition, may have been especially vulnerable due to their habitat in expanded oxygen minimum zones. In these low-oxygen regions, the invertebrate prey that durophagous taxa feed on are also at risk of going extinct, thereby subjecting chondrichthyans with specialized tooth morphology to extinction.

Following the K-Pg event, Bazzi et al. (2018) observed a decline in Lamniformes with low-profile triangular teeth, while Carcharhiniformes with similar dentition proliferated. Concurrently, there was a decrease in cephalopods and pelagic amniotes, and a significant increase in teleost fishes. It is suggested that changes in prey availability reshaped the trophic web in a way that favored Carcharhiniformes (Bazzi et al., 2018).

Both the end-Permian and end-Cretaceous events demonstrate the resilience of active chondrichthyes, but also reveal a level of vulnerability, particularly in those with specialized tooth morphology. Given the relationship between extinction selectivity and functional morphology of teeth, the various types of dentition across chondrichthyan taxa may give insight into how chondrichthyes will react to other global stressors. One of the lesser-known episodes, particularly the Ocean Anoxic Event 2 at the Cenomanian-Turonian boundary, provides a scenario where the primary stressor is widespread anoxia.

Ocean Anoxia Event 2 is one interval in a series of oceanic anoxic events in the mid-Cretaceous (Elewa & Abdelhady, 2020). Schlanger & Jenkyns (1976) were among the first to recognize the phenomena of both mid-Cretaceous ocean anoxia events, the Aptian-Albian (OAE1) and the Cenomanian-Turonian (OAE2) (Fig.1). From a series of drilled cores, Schlanger & Jenkyns (1976) found the presence of carbonaceous sediments and minerals such as siderite and pyrite, indicative of reducing conditions. The Cenomanian-Turonian (C-T) boundary can be characterized by the widespread deposition of carbonaceous sediments beyond local basins (Schlanger & Jenkyns, 1976). Record of an ocean anoxia event during the OAE2 was found in multiple settings, including plateaus and broad rises in the open Pacific, the Tethyan continental margins, and the northeastern European shallow shelf (Schlanger & Jenkyns, 1976).

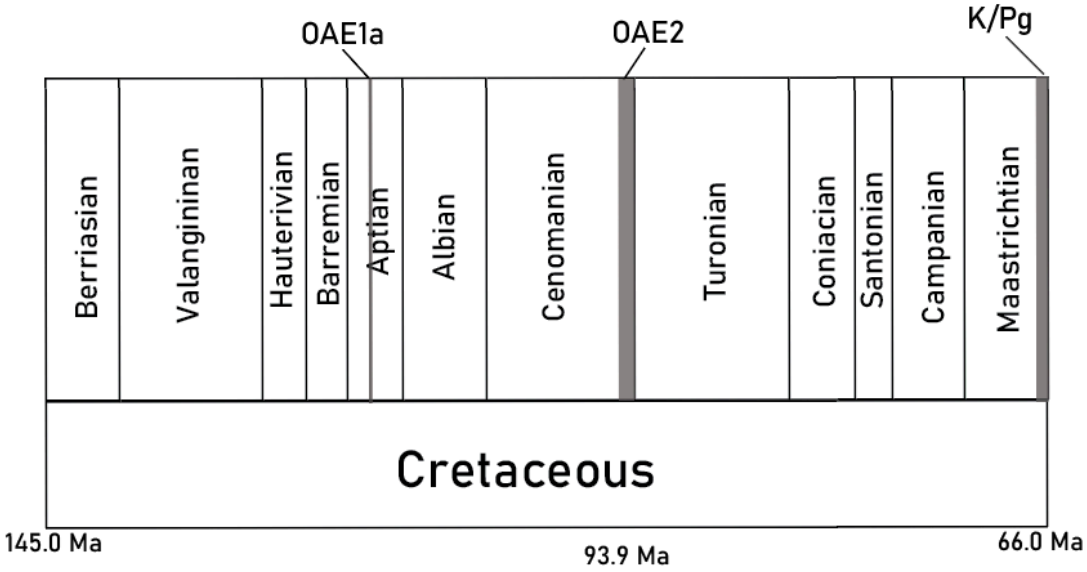

Figure 1. Geological time scale of the Cretaceous. The solid gray bars show the timing of the OAEs and the K/Pg mass extinction.

OAE2 was caused by intense volcanic activity that disrupted atmospheric and oceanic processes (Schlanger & Jenkyns, 1976). Leading up to the OAE2 were large igneous provinces that developed at the Caribbean plateau and Madagascar traps, which increased hydrothermal marine activity and released considerable amounts of greenhouse gases into the atmosphere (Monteiro et al., 2012). Reconstructions of atmospheric carbon dioxide during this time suggest levels between 500 – 3300 ppmv (Bice et al., 2006). The difference in CO_2 content led to warmer temperatures and intensified continental weathering, causing a large influx of nutrients into the ocean through fluvial inputs. The result is increased biological productivity from which organic matter originated and was subsequently respired, leading to an uptake of oxygen (Monteiro et al., 2012). Alongside marine productivity, oxygen solubility in the ocean decreased with rising temperatures and salinity, lowering the oxygen content of the surface ocean. Moreover, with warmer temperatures, the ocean's overturning circulation slowed down significantly (Monteiro et al., 2012; Arthur et al., 1987). In some regions characterized by humid climates and heavy influx of freshwater discharge, sea-level rise led to episodic development of salinity-stratified water masses with subsequent oxygen deficiency in the lower part of the water column (Arthur et al., 1987). In summary, various feedback mechanisms led to widespread marine deoxygenation, resulting in one of Earth's most severe biotic crises.

About 8% of marine families and 26% of genera are estimated to have gone extinct (Elewa & Abdelhady, 2020). During this time of intensified oxygen deficiency, primarily in intermediate to shallow-intermediate water masses, benthic faunas were absent or scarce due to the poorly oxygenated environment (Arthur et al., 1987). Species-level extinction was high for most macroinvertebrates; those especially vulnerable in the C-T transgression had large morphologies and were geographically restricted to low and middle latitudes (Elewa, 2008). While benthic macroinvertebrates experienced severe losses during this interval, widespread anoxia also impacted the more mobile, marine vertebrates such as elasmobranchs.

Guinot (2013), in his analysis of patterns in late Cretaceous selachian diversity, reported a notable drop in Carcharhiniform (ground sharks) and Orectolobiform (carpet sharks) genera and species during the middle to late

Cenomanian in the Anglo-Paris Basin and northwestern Europe. In the Turonian, diversity in these same orders, and Rajiformes, increased, while Lamniform diversity declined. In contrast, the Western Interior Seaway exhibited a decrease in Carcharhiniformes prior to the Campanian, though batoids still maintained high genus-level richness (Guinot, 2013). While Guinot (2013) provides valuable insight into regional trends among late Cretaceous selachians, the results may be limited by regional sampling biases, as well as broad temporal resolutions used in the study that hinder the ability to detect short-term ecological responses. To build on the findings centering on chondrichthyans of the OAE2, more recent studies have shifted their focus towards functional attributes and morphological changes connected to environmental stress.

Following the OAE2, tooth shape disparity increased with trends toward larger tooth sizes. Carchariids, small-bodied Lamniformes, exhibited a rise in morphological disparity relative to earlier periods, while anacoracids, medium to large-bodied Lamniformes, developed larger teeth (Bazzi et al., 2022). Trends in tooth morphology after the OAE2 seemed to be influenced by habitat differences, specifically differences between epicontinental seas and neritic shelf environments. Tooth disparity was observed to be higher in neritic settings, whereas epicontinental seas reduced disparity (Bazzi et al., 2022). Bazzi et al. (2022)'s study sheds light on morphological trends that occur post-OAE2, showing how tooth disparity varies with habitat among Lamniform sharks. However, their findings mainly focus on

Lamniformes, which constrain our understanding of the broader selachian diversity and extinction patterns during the OAE2.

My project aims to address the knowledge gaps left by Guinot (2013) and Bazzi et al. (2022) by analyzing the functional attributes and morphological traits of various chondrichthyan teeth at a genus level, across finer substage intervals, and categorizing them based on detailed morphological features.

As seen throughout their evolutionary history, chondrichthyans have great ecological breadth, but they still experience vulnerability to environmental stressors such as widespread anoxia. The C-T boundary represents a minor extinction scenario that allows for the assessment of whether functional tooth morphology influenced chondrichthyan survival. Since tooth shape can be linked to specific ecological roles, functional morphology offers a valuable proxy for understanding extinction selectivity.

1.2 Functional Tooth Morphology

Henri Cappetta, an ichthyologist specializing in the paleontology of chondrichthyes, has extensively researched the dentition of these cartilaginous fishes. Cappetta helped lay the groundwork for categorizing the various types of chondrichthyan teeth into distinct morphotypes, which could then reflect the trophic adaptation of the species (Cappetta, 1987). However, this did not come without difficulty; a natural character of chondrichthyan teeth is that different shapes and sizes can be present along a single row of dentition, also known as heterodonty. Furthermore, heterodonty can be monognathic, different morphotypes along a single jaw, or dignathic, different morphotypes between the upper and lower jaw (Cappetta, 1987). In some instances, such as in the Hexanchidae family, monognathic and dignathic heterodonty can co-occur (Cappetta, 1987). There is also ontogenic heterodonty, morphological differences in teeth with age, and sexual dimorphism, tooth differences between the two sexes of the same species (Cappetta, 1987). In particular species of the family Scyliorhinidae, the young will display more lateral cusplets on the anterior files and a more folded enameloid (Cappetta, 1987). In *Dasyatis* and *Raja*, notable batoids, females will have more rounded crowns, while males will have a sharper crown (Cappetta, 1987). These various types of heterodonty often result in an abundance of fossil species that are, in reality, teeth in different positions of the same species (Cappetta, 1987). However, given comparative material from extant species and an extensive series of fossils from various localities, it is possible to achieve a reliable phylogenetic systematics of fossil and living taxa (Cappetta, 1987). Although there is a considerable amount of morphological diversity in chondrichthyan teeth, there is still a relatively small number of dental types that coincide with feeding specializations (Cappetta, 1987).

There are five main categories of functional morphotypes as described by Cappetta: tearing, clutching, cutting, crushing, and grinding. While grinding teeth represents a specialized form of durophagy, they also perform a crushing function and will be combined with the crushing category in this study (Britto et al., 2024; Guinot & Condamine, 2023). The tearing category has often been described in more recent papers as having piercing and grasping mechanisms, and to better reflect those functional interpretations, this study will refer to this morphotype as "piercing-grasping." The general outline of a piercing-grasping tooth is a cusp that is narrow, elongated, sometimes recurved, and smooth with a sharpened point (Ciampaglio et al., 2005; Whitenack & Motta, 2010; Cappetta, 1987). Additionally, in a paper on shark teeth as proxies for functional traits by Cooper et al. (2023), it is suggested that the piercing longitudinal outline of a tooth with one or more pairs of lateral cusplets is associated with a grasping mechanism. The most representative taxa of this piercing-grasping dentition are Mitsukurinidae sharks of the order Lamniformes (Fig.2) (Cappetta, 1987). This dental type is best suited for puncturing and wrenching its prey (Ciampaglio et al., 2005; Whitenack & Motta, 2010). The primary prey of *Mitsukurina owstoni,* a Lamniform shark that possesses this tooth type, are teleosts (Yano et al., 2007). However, they also feed on various types of prey, including crustaceans, cephalopods, and other fish besides teleosts, implying that these sharks may forage at both benthic and pelagic regions of the ocean (Diggers III et al., 2014). This also suggests that chondrichthyan genera with these teeth are capable of feeding on hard-shelled prey and tend to be generalists when searching for food.

Figure 2. Teeth exhibiting the piercing-grasping outline from the order Lamniformes, scale bar: 10 mm. C: *Clerolamna umovae* with lingual (C1) and labial (C2) view. D: *Clerolamna umovae* with lingual (D1) and labial (D2) views. Reproduced from: Popov, E. V., Lopyrev, V. A., Panteleev, A. V., Birlukov, A. V., and Timirchev, F. K. "Chondrichthyan Fishes from the Middle Eocene Osinovaya Formation of Rostov Region, Russia." *Historical Biology* 37, no. 1 (2023): 126–152. © 2023, reprinted by permission of Informa UK Limited, trading as Taylor & Francis Group, https://www.tandfonline.com.

The cutting dentition of sharks is split into two subtypes. The first subtype is the cutting-type and is described as a labio-lingually flattened cusp with a crown that widens towards the base (Fig. 3) (Cappetta, 1987; Whitenack & Motta, 2010). Some genera, such as *Carcharodon* of the order Lamniformes, will possess a cutting-type tooth with a straight, tall, and thin cusp. In contrast, other genera, such as *Squalicorax*, also of the order Lamniformes, and *Galeocerdo* of the order Carcharhiniformes, will have a cusp slanted towards the rear (Cappetta, 1987). The presence of serrations along the edge of the cusp enhances the cutting performance of the tooth but makes it more prone to trapping material between the serrations and ripping tissue of the prey (Ciampaglio et al., 2005; Whitenack & Motta, 2010; Cappetta, 1987). This subtype mainly has monognathic and dignathic homodonty

(Cappetta, 1987). *Carcharodon carcharias*, commonly known as the great white shark, exhibits this morphotype and mainly feeds on pinnipeds, but will also eat cetaceans and large fish like tuna (Jaime-Rivera et al., 2014). Similar to the great white shark, other chondrichthyans with this tooth type may indicate a preference for larger marine vertebrates found in offshore and nearshore environments (Jaime-Rivera et al., 2014; Cooper et al., 2023).

The second subtype is cutting-clutching dentition (Fig. 4), which is a condition within jaws typically characterized by dignathic heterodonty. In addition to the cutting-clutching subtype being a common form of dignathic heterodonty, it is also expressed differently in various families (Cappetta, 1987). On one jaw, teeth become progressively wider and flatter in the lingual-labial direction, while on the opposing jaw, the cusps remain tall and narrow (Cappetta, 1987). In the families Carcharhinidae and Hemigaleidae, the wide, flat teeth often appear on the upper jaw, but in Squalidae and Hexanchidae, they appear on the lower jaw. In terms of tooth morphology, the clutching part of this subtype, which is not to be confused with the original category of clutching dentition, can be described as being lingually-labially flattened, but with multiple cuspids along the crown. A taxon representative of this type of tooth occurs commonly in Hexanchiformes (cow and frilled sharks) (Fig. 4) (Cappetta, 1987). Cappetta (1987) suggests that this subtype is an upgrade from the first subtype of just cutting teeth. The clutching dentition within the jaw helps the predator hold the prey, while the regular, cutting teeth help cut the prey like a trimmer (Cappetta, 1987). Cow and frilled sharks, much like the great white shark, are of a large size, high trophic level, and can be considered opportunistic feeders. All species of Hexanchiformes are considered demersal, inhabiting areas such as continental shelves, estuaries, and shallow bays (Barnett et al., 2012). Much of the prey that has been found in their stomachs indicates that they forage deep in the water column, as well as in shallow coastal areas. Several stomachs of these individuals have contained teleosts, deep-water sharks, squids, whale carrion, and the occasional crustacean (Barnett et al., 2012).

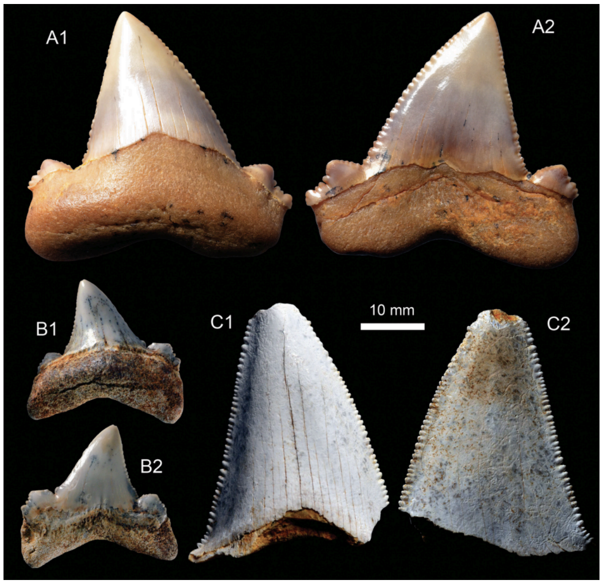

Figure 3. Teeth of the Lamniform order showcasing the cutting-type morphotype. A: *Otodus auriculata* with lingual (A1) and labial (A2) views. B: *Otodus auriculatus* with lingual (B1) and labial (B2) views. C: *Otodus sokolovi* with lingual (C1) and labial (C2) view. Scale bar: 10 mm. Reproduced from: Popov, E. V., Lopyrev, V. A., Panteleev, A. V., Birlukov, A. V., and Timirchev, F. K. "Chondrichthyan Fishes from the Middle Eocene Osinovaya Formation of Rostov Region, Russia." *Historical Biology* 37, no. 1 (2023): 126–152. © 2023, reprinted by permission of Informa UK Limited, trading as Taylor & Francis Group, https://www.tandfonline.com.

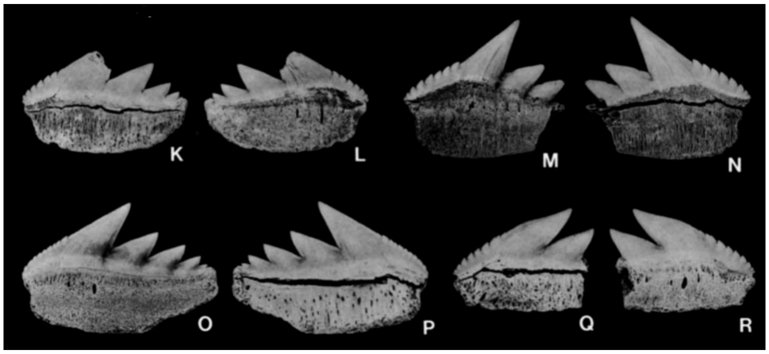

Figure 4. Teeth from *Notorynchus apiensis* of the Hexanchiformes order exhibiting the cutting-clutching dentition. K-L: lower left anterolateral tooth, labial and lingual views, 10.7 mm wide. M-N: lower right anterolateral teeth, labial and lingual views, 10.9 mm wide. O-P: lower right anterolateral tooth, labial and lingual views, 9.4 mm wide. Q-R: lower left anterolateral tooth, labial and lingual views, 9.4 mm wide. Reproduced from: Siverson, M. "Sharks from the Mid-Cretaceous Gearle Siltstone, Southern Carnarvon Basin, Western Australia." *Journal of Vertebrate Paleontology* 17, no. 3 (1997): 453–465. © 1997, reprinted by permission of Informa UK Limited, trading as Taylor & Francis Group, https://www.tandfonline.com.

A clutching tooth is a dental type associated with a low, pointed cusp profile that is broad and robust, typically with the presence of small cusplets that make it easier to hold prey (Fig. 5) (Cappetta, 1987). Moreover, they often have enameloid folded on their lingual and labial faces to serve as crown reinforcement (Ciampaglio et al., 2005; Cappetta, 1987). Clutching type dentition is used to clutch soft-bodied prey, while also carrying the structural integrity to crush hard-shelled prey (Ramsay & Wilga, 2007). This dentition is primarily present in smaller sharks that live near or on the bottom of the ocean (Cappetta, 1987). It is also present within some batoids, such as the males of the Rajidae and Dasyatidae families (Cappetta, 1987). Common families of chondrichthyans found with these teeth are Orectolobidae, Ginglymostomatidae, Squantidae, and Scyliorhinidae (Whitenack & Motta, 2010; Ramsay & Wilga, 2007). Wobbegong sharks, *Orectolobus ornatus* of the Orectolobiform order, are considered to be demersal sharks, typically sitting on the substratum. Consequently, their diet consists of demersal prey species of bony fish, chondrichthyans, and cephalopods (Huveneers et al., 2007).

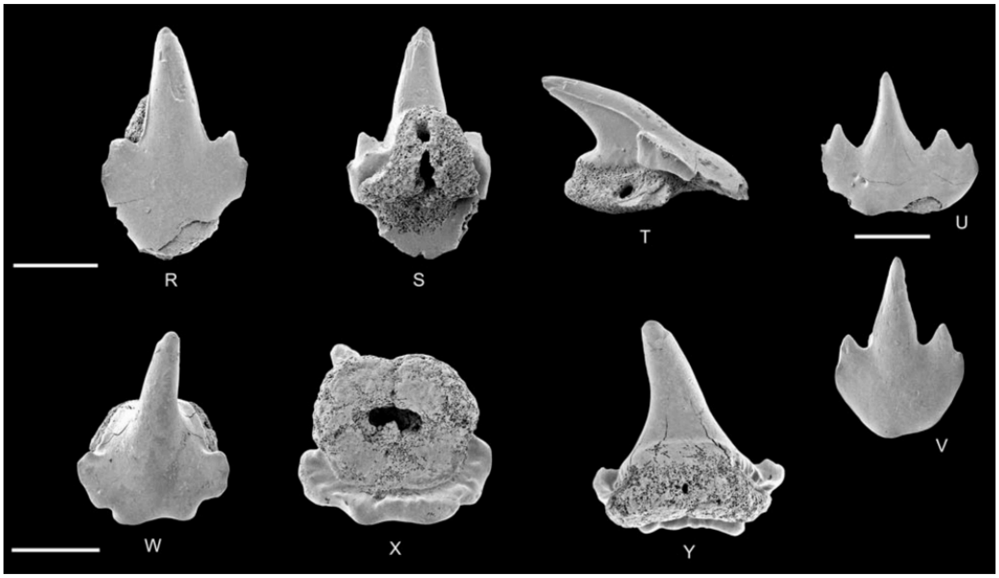

Figure 5. Orectolobiform teeth exhibit the clutching type dentition. R-V, Orectolobiformes *incertidae sedis* 1; W-Y, Orectolobiformes incertae sedis 2; scale bars: 500 µm. Reproduced from: Underwood, C. J., H. Cappetta, G. Guinot, et al. "Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK." *Journal of Systematic Palaeontology* 11, no. 5 (2013): 589–671. © 2013, reprinted by permission of Informa UK Limited, trading as Taylor & Francis Group, https://www.tandfonline.com.

The crushing dentition of chondrichthyes is characterized by a crown with no cutting edges and lacking a piercing longitudinal outline (Fig. 6). In selachians, a crushing-type tooth has a bulging crown that is transversely streamlined and is either smooth or has pitted enameloid (Ciampaglio et al., 2005; Cappetta, 1987). These teeth represent cartilaginous vertebrates that live near the bottom and are most often correlated with durophagous groups, predators that consume prey with hard exoskeletons such as molluscs and crustaceans, as well as shellfish, small fishes, and cephalopods (Guinot & Condamine, 2023; Cappetta, 1987). This morphotype can be found among Rajiformes, Dasyatidae, and Carcharhiniformes (Cappetta, 1987). Grinding teeth, another tooth representative of durophagy, also appear in fish with a benthic way of life. These teeth possess a high crown with a polygonal outline. They overlap and form a dental plate that results in a nearly plane surface (Cappetta, 1987). Taxa with this tooth type are mainly Myliobatiformes, with *Aetobatus* being the most derived form. A dietary assessment on Myliobatidae, a suborder of Myliobatiformes, revealed that they mostly foraged for decapod crustaceans, molluscs, and teleosts (Jacobsen & Bennett, 2013). Dietary evidence from Myliobatidae hints at a preference for benthic and benthopelagic hard-shelled prey, indicating their geographic distribution to be near coastal regions.

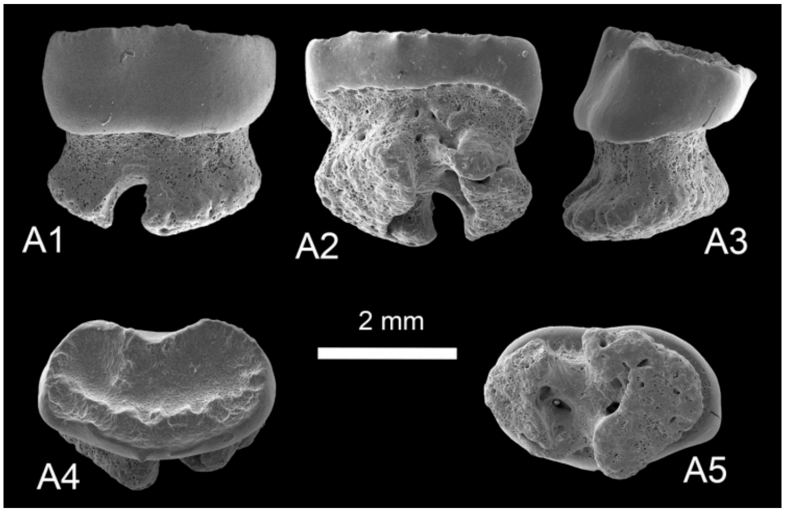

Figure 6. ***Coupatezia woutersi*** **of the Myliobatiform order, representing a crushing morphotype; scale bar: 2mm.** Reproduced from: Popov, E. V., Lopyrev, V. A., Panteleev, A. V., Birlukov, A. V., and Timirchev, F. K. "Chondrichthyan Fishes from the Middle Eocene Osinovaya Formation of Rostov Region, Russia." *Historical Biology* 37, no. 1 (2023): 126–152. © 2023, reprinted by permission of Informa UK Limited, trading as Taylor & Francis Group, https://www.tandfonline.com.

These tooth morphologies and their corresponding functional traits can help illuminate the ecological roles chondrichthyans played in marine systems in the distant past. However, a common idea is that many chondrichthyans are opportunistic feeders. There is an overlap in prey preferences across tooth morphologies, primarily between clutching, cutting, and piercing-grasping teeth (Cooper et al., 2023). While this is true, several picky eaters are specialized to feed within a smaller range of prey items (Compagno et al., 2005). Sharks on a quaternary trophic level that consume larger organisms like high vertebrates generally consume a wide range of prey (Cooper et al., 2023; Klimley, 2013**)**. Sharks and rays that fall into the tertiary consumer level tend to feed on small fishes, cephalopods, and mollusks (Cooper et al., 2023). However, among the four established morphotypes by Cappetta (1987), there is a clear distinction between durophagous feeders with crushing dentition and non-durophagous feeders that display the remaining three morphotypes. Many of the taxa with crushing teeth are benthic inhabitants that tend to have a prey preference for invertebrates (Cappetta, 1987; Cooper et al., 2023). Due to their benthic lifestyle, bottom water anoxia might affect these cartilaginous fish with crushing teeth. Chondrichthyes with the clutching morphotype could also be affected by deoxygenation in the deep water column, as this dentition is prevalent among bottom-dwelling taxa. Although they have the presence of pointed cusps that will give the fish a wider range of prey they can consume, clutching taxa will likely be impacted to a lesser degree compared to the fish with crushing dentition.

Benthic inhabitants have a dorsoventrally compressed body with a color pattern that matches the surrounding environment, which is helpful for their mode of predation (Klimley, 2013). They are ambush predators with a tactic that requires them to lie motionless at the bottom of the water column, waiting for prey (Klimley, 2013). A deoxygenated environment, such as one proposed by the OAE2, might threaten their ability to hunt and compromise their food source at the ocean bottom. In contrast, fish that display piercing-grasping and cutting dentition, such as Lamniformes and Carcharhiniformes, may represent taxa less affected by the OAE2 due to their more pelagic nature and generalist diet. By analyzing the functional morphology of teeth, it may be possible to infer the ecological responses of chondrichthyans to the widespread anoxic conditions of the OAE2.

2 Methods

When categorizing the various genera into their functional types, a certain degree of subjectivity is undoubtedly involved when analyzing tooth morphology. To ensure consistency and objectivity, several studies created a well-defined list of functional attributes that can be used to classify chondrichthyan teeth into functional groups. This study follows the established categories of teeth outlined in works by Henri Cappetta and more recent morphological studies on shark teeth (Cappetta, 1987; Ciampaglio et al., 2005; Cooper et al., 2023; Whitenack & Motta, 2010) . The dataset includes 437 marine chondrichthyan genera (sharks, skates, rays, chimaeras) compiled from the Paleobiology database.

Teeth from each genus were visually assessed through detailed photographs and diagrams in the literature collected through the database and sorted into their corresponding functional morphotype. Visible traits such as cusp shape, presence or absence of serrations, and/or cusplets, were used to distinguish between functional types. For instance, teeth with narrow, pointed cusps and no serrations were categorized as piercing-grasping, while wider teeth with low, flattened crown surfaces were assigned to the crushing category. Tooth position within the jaw was not considered when classified, as many fossil specimens are isolated and lack enough contextual information to determine their original placement. Instead, the basis of classification depends on overall morphology.

A scoring system was used to help determine which functional trait best reflected the general morphology of the tooth. A score from 0 to 2 was assigned for each potential functional category based on how strongly the tooth morphology aligned with the characteristics of that category. A score of 0 meant no resemblance, 1 indicated partial or moderate resemblance, and 2 showed a strong likeness with the category. For example, a tooth with a bulging crown, no piercing longitudinal outline, and no cutting edges would have a 2 under the “crushing” category and 0 for piercing-grasping, clutching, and cutting. These rankings were put into R and processed through a function that randomly assigns a single tooth morphotype to each genus 100 times, with probabilities weighted according to the assigned scores. This approach accounted for uncertainty in cases where multiple categories were possible. If a tooth displayed various traits that made it fall into more than one category, such as a wide, serrated tooth indicative of a cutting mechanism, but also including cusplets (traits associated with piercing-grasping), it would have a score of 2 under both cutting and piercing-grasping. In such cases, each category with a score of 2 had equal probability of being selected, and over 100 repetitions, each would be assigned as the morphotype about 50 times. When a single category received a score of 2, and others received a 1 or 0, the highest score (2) was prioritized in the weighted sampling. Therefore, that category would be the most frequently assigned morphotype during the sampling. This allowed both the dominant and secondary traits to be accounted for when assigned a morphotype, while prioritizing each tooth's most defining characteristic. Of the 437 marine chondrichthyan genera collected, 336 were able to be ranked accordingly. The remaining 101 genera did not have sufficient enough information to be included in the morphotype-based analysis.

For each morphotype, a function calculates how it fared across the time intervals using the boundary-crosser extinction equation E = -log (N_bt / N_b) (Foote, 2000). N_bt represents the number of genera belonging to that morphotype that crossed the bottom and top boundaries of the stratigraphic interval, N_bL is the number of genera that crossed only the bottom boundary and last appeared within the interval, and N_b denotes all genera that crossed the bottom boundary (N_b = N_bt + N_bL). These extinction rates were calculated at a substage level (e.g., early, middle, and late subdivisions of stages such as Cenomanian, Turonian, etc.) to improve temporal resolution, and to account for the varying number of samples across different intervals, stages with less than 10 taxa were removed. With 100 replicates of this, we can analyze the average extinction rate of each morphotype per time interval, using the tenth and ninetieth percentiles to gain an idea of the spread or uncertainty around the extinction values.

3 Results

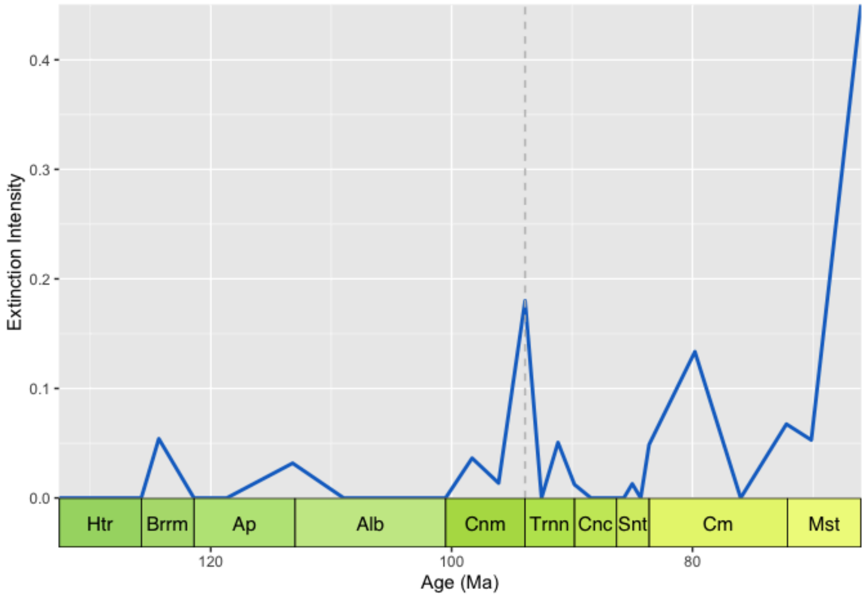

Figure 7. Boundary-Crosser extinction rates for chondrichthyes. The dashed line represents the C-T boundary at 93.9 Ma. Cretaceous geological ages: Htr–Hauterivian, Brrm–Barremian, Ap–Aptian, Alb–Albian, Cnm–Cenomanian, Trnn–Turonian, Cnc–Coniacian, Snt–Santonian, Cm–Campanian, Mst–Masstrichtian

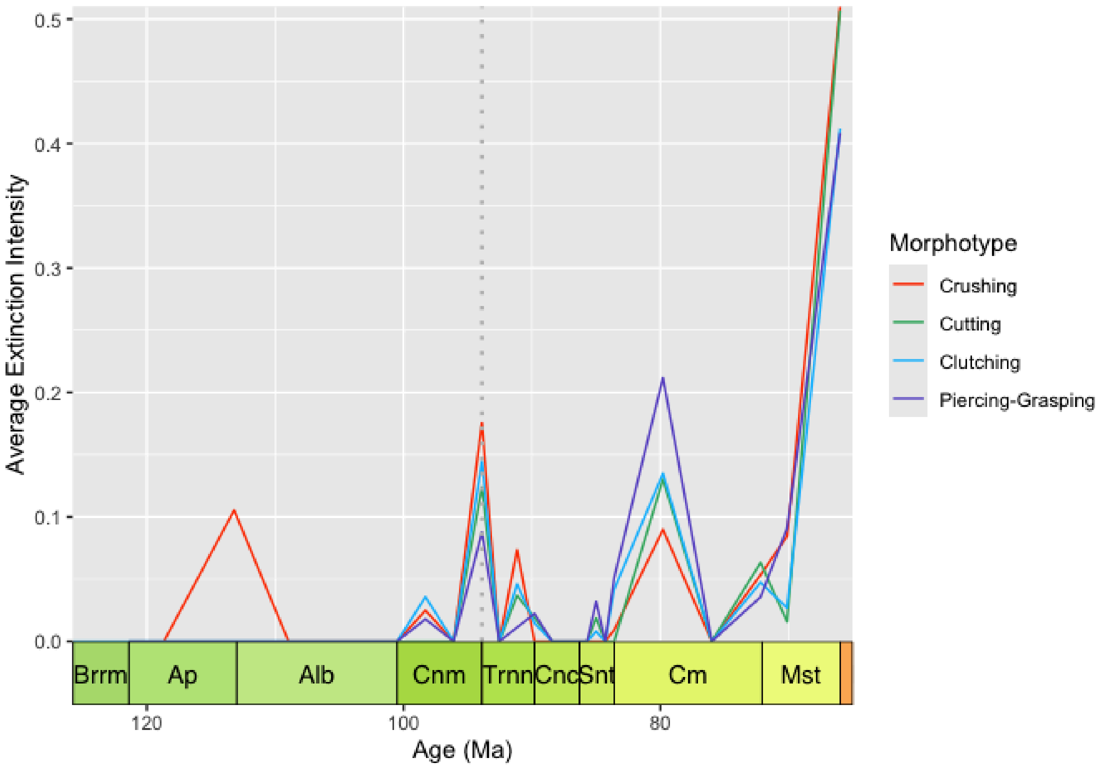

Figure 8. Average extinction intensity of chondrichthyes (sharks, skates, rays, chimaeras) based on their morphotypes from the Valanginian to the Maastrichtian. The dashed line represents the C-T boundary.

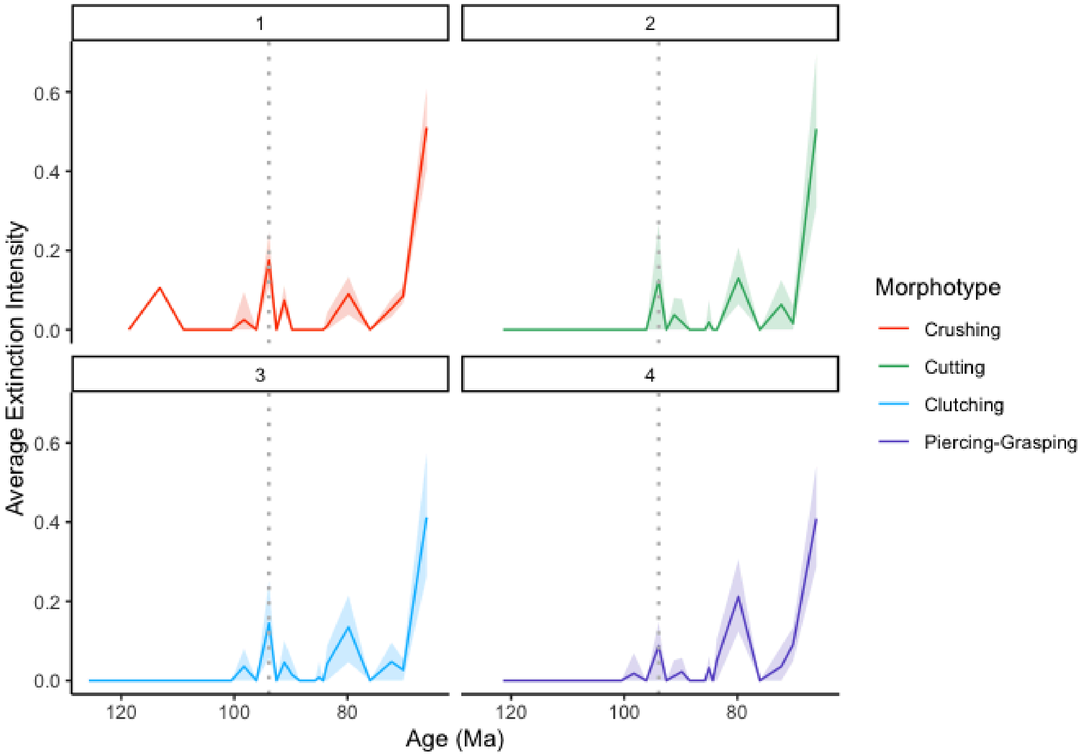

Figure 9. Extinction rate of each morphotype with confidence intervals (lower limit: 10%, upper limit: 90%). 1) Crushing, 2) Cutting, 3) Clutching, 4) Piercing-grasping.

The extinction intensity for all chondrichthyes during the C-T is elevated compared to background events from the Barremian to the Albian (Fig. 7). Furthermore, all functional morphotypes of chondrichthyans experienced a considerable rise in extinctions across the Cenomanian-Turonian boundary (Fig. 8). On average, there does not appear to be a significant difference in extinction intensity between the various types of dentition, crushing, cutting, clutching, and piercing-grasping, indicating that no single functional morphotype was disproportionately affected during this time interval. However, subtle patterns are present: the crushing morphotype had a higher extinction intensity in the Early and Late Cenomanian, as well as the Late Turonian, compared to cutting and piercing-grasping dentition (Fig. 9). Clutching also exhibited an elevated extinction intensity relative to cutting and piercing-grasping, though the difference is less pronounced than that observed for crushing. The cutting dentition shows no apparent losses from the Albian to the middle Cenomanian, followed by a rise in extinction intensity during the late Cenomanian and middle to late Turonian (Fig. 8). The piercing-grasping morphotypes generally showed a low extinction intensity throughout the Cenomanian and Turonian. However, the Campanian has the highest intensity, while crushing displays the lowest (Fig. 8).

The confidence intervals (CI) (Fig. 9) for all morphotypes are relatively moderate across most substages, including the Cenomanian-Turonian (C-T) boundary. The crushing morphotype (Fig. 9.1) shows a narrow CI during the Barremian and Aptian, but widens during the C-T and again in the Campanian. The more narrow CI in the Barremian and Aptian reflects the presence of more diagnostically clear crushing-type dentition (Fig. 9.1), which makes their assignment of functional morphotypes more consistent across the repetitions. In contrast, other intervals might have genera with more ambiguous tooth assignments, resulting in greater variability. The cutting morphotype (Fig. 9.2) has slightly wider CIs than crushing, particularly during the C-T, Turonian, Campanian, and Maastrichtian. The CI for clutching teeth (Fig. 9.3) is broader than crushing, with ranges similar to cutting. Finally, the piercing-grasping teeth (Fig. 9.4) also exhibit broader intervals compared to crushing teeth, and have a similar CI range to both cutting and clutching teeth.

Sampling varies throughout the various substages (Fig. 10), which is reflected in the extinction intensities for each morphotype. For instance, the Campanian is seemingly well-sampled, which may explain the significant jump in extinction intensity during the Early Campanian (Fig. 7, 8). It should be noted that the number of taxa within some categories is relatively small, mainly when the data is divided into substages, which limits statistical power and the ability to detect subtle trends. Other sources of noise that may stem from uneven sampling or local environmental disturbances may also obscure any signals in extinction selectivity. As a result, these patterns should be interpreted cautiously.

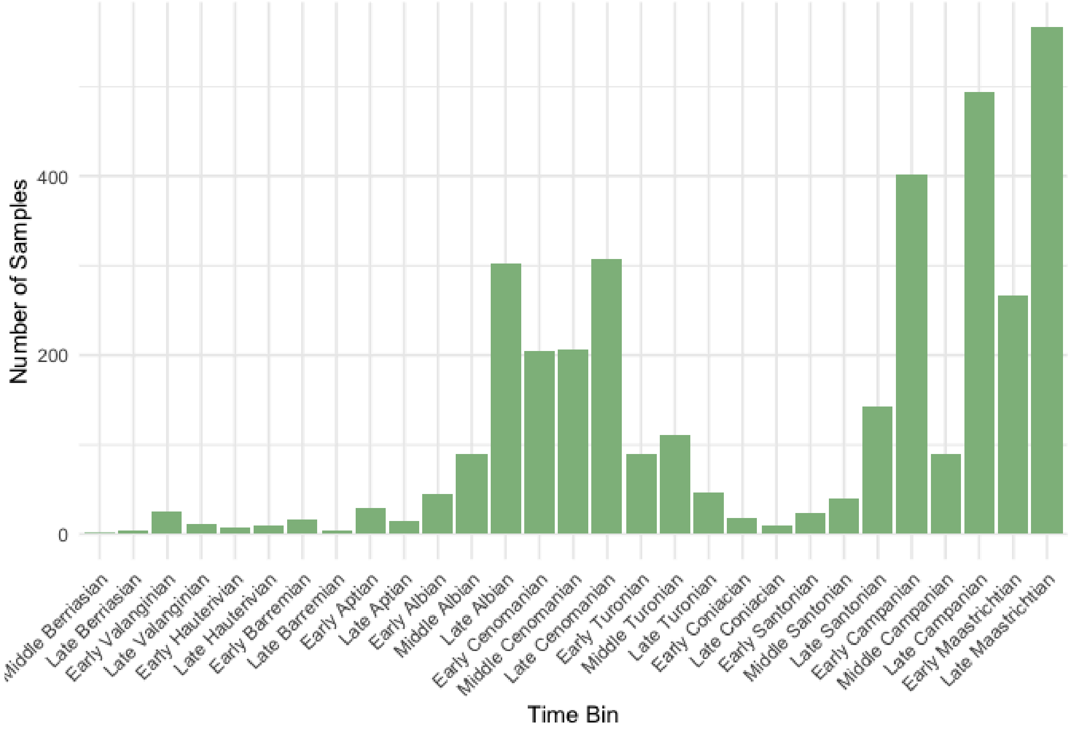

Figure 10. The number of occurrences per substage from the Middle Berriasian to the Late Maastrichtian.

4 Discussion

The elevated extinction event across all morphotypes during the C-T boundary (Fig. 8) suggests that most chondrichthyans, regardless of functional tooth morphotype, are vulnerable to widespread ocean anoxia. Although this extinction event occurs at an intensity much less than the End-Cretaceous event, the OAE2 still resulted in a non-selective extinction of several genera of chondrichthyes. The apparent rise in extinction intensity at the C–T boundary highlights the need to consider potential sampling biases, as uneven preservation or recovery may inflate the magnitude of the OAE 2.

The data collection mainly includes coastal samples; therefore, it may not be a good representation of pelagic sharks. Additionally, some Late Cenomanian samples came from the Lagerstätten quarries of Lebanon, where fauna included soft-bodied preservation. These occurrences were removed to check for limited geographic representation, skewed morphotype distribution, or potential bias in extinction intensity, such as a local extinction event instead of a global one. The outcome showed no significant differences in overall extinction intensity (Fig. 11) and average extinction intensity between the functional morphotypes, strengthening the reliability of the original findings. The patterns reflected in the dataset do not seem overly sensitive to regional overrepresentation or sampling anomalies. However, there may be limitations to the method that must also be considered.

Functional morphology often involves subjectivity in categorizing teeth into functional groups, especially when teeth display traits that overlap multiple morphotypes. This is reflected in the moderately broad error bars shown in Figure 9, exhibiting a relatively high degree of variability and uncertainty. Despite this level of subjectivity, given the size and scope of the dataset, the results may still be considered robust and unlikely to change substantially even if some tooth type assignments are inaccurate. The probabilistic method, in which an R function is used to randomly assign morphotypes to each genus, allowed the analysis to incorporate the ambiguity in categorization. The 100 repetitions of weighted randomization help mitigate the effects of occasional misassignments by preventing any single misclassification from disproportionately influencing the extinction rate of a given morphotype. Nonetheless, the significant challenge of heterodonty in chondrichthyans complicates ecological interpretations, where individual species may exhibit multiple functional types.

There are various morphologies across life stages or sexes and taxonomic ambiguity, all of which reduce the reliability of assigning ecological roles to fossil specimens. However, Cooper et al. (2023) found that tooth position was not an indicator of functional traits, suggesting that heterodonty has limited effects on the relationship between dental morphology and functional characteristics in isolated teeth. Rather, their study maintains that the overall longitudinal outline of a tooth is the most common and useful proxy for feeding mechanisms in extinct sharks. Cooper et al. (2023)'s paper also highlights the reliability of tooth morphology as a proxy for prey preference, with crown size and cutting edge as the most common representatives for prey selection. Conversely, Whitenack & Motta (2010)'s paper on the biomechanical findings of shark tooth performance demonstrates that morphology alone cannot reliably predict function. For instance, in puncture tests, broad triangular teeth were less efficient at puncturing prey compared to the more narrow, cusped teeth, but these differences are heavily influenced by prey type and tissue composition (Whitenack & Motta, 2010). In the same study, draw performance showed that features typically associated with enhanced cutting efficiency, such as serrations and notching, did not significantly improve cutting ability (Whitenack & Motta, 2010). Tooth function may also rely on tooth overlap, collagenous attachment, and size differences within morphotypes. Furthermore, shark teeth serve multiple roles, including prey capture and mating, which may complicate the correlation between form and function (Whitenack & Motta, 2010). Therefore, relying solely on tooth morphology may oversimplify the complexity of ecological roles, as it captures only a tiny facet of an organism's overall biology and environmental interactions. While it might be a valuable proxy to reveal the general trends in feeding adaptations and potential shifts in ecological niches over time, caution should be used when applying functional tooth morphology to infer environmental responses.

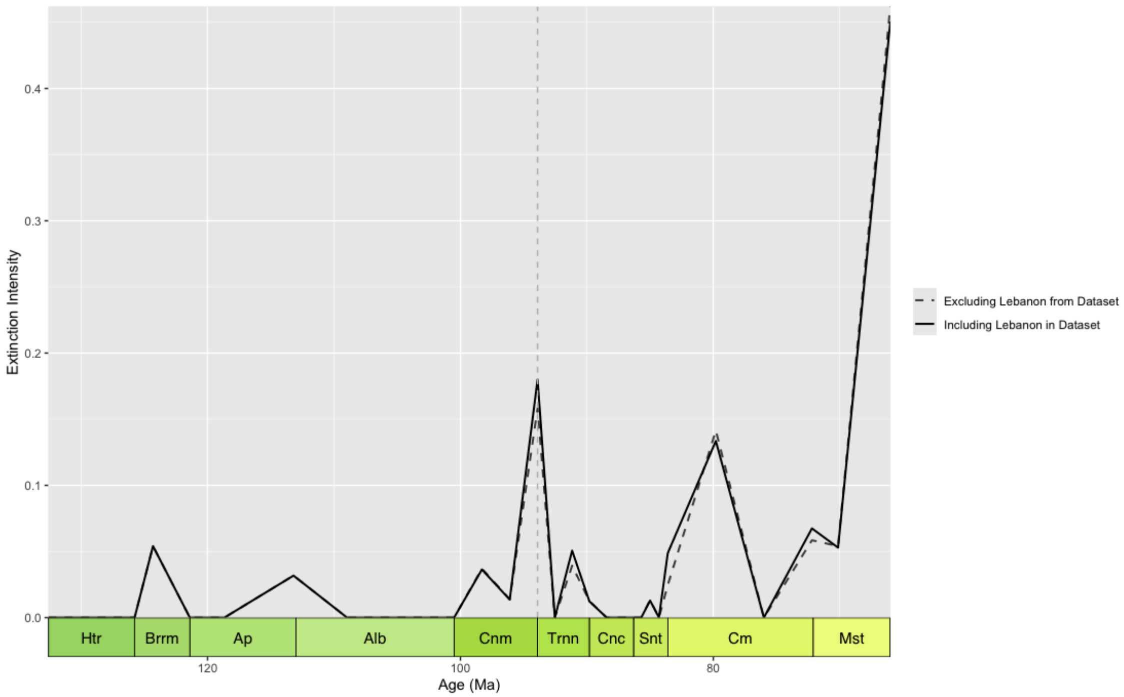

Figure 11. Overall extinction comparison between the dataset includes occurrences from the Lagerstätten Quarry of Lebanon, and the dataset excludes those occurrences.

The C-T presented marine conditions where regions along the bottom of the ocean are anoxic, effectively decreasing the availability of habitats for bottom-dwellers, as well as vertically compressing pelagic habitats for the more open ocean chondrichthyans (Waller et al., 2024; Abraham et al., 2023). The change in salinity, temperature, and oxygen content in the late Cenomanian also likely caused physiological stress in prey species, leading to population declines and reducing food availability for most chondrichthyans (Arthur et al., 1987). Additionally, chondrichthyans require energy costs and maneuvers that might be unsustainable in widespread anoxic conditions. The combination of habitat loss, prey decline, and energy requirements may have made all cartilaginous fishes vulnerable to their surroundings, with some variation among functional morphtoypes.

Chondrichthyans are considered generalists in their diet, preying on marine mammals, birds, and bait left on fishing hooks (Carrier et al., 2012). Pelagic or semi-pelagic sharks have a diet that mainly consists of teleosts, cephalopods, and other elasmobranchs, while more demersal sharks, rays, and skates prefer to feed on benthic invertebrates, smaller fish, and cephalopods (Camhi et al., 2009; Carrier et al., 2012). Given that the wide dietary range of Chondrichthyes mostly consists of prey inhabiting neritic zones and that the fossilized shark teeth analyzed in this study are typically associated with coastal environments, it can be inferred that the expansion of oxygen minimum zones during the OAE2 likely impacted the foraging capabilities of sharks across the varying tooth morphotypes, particularly those genera with crushing and clutching dentition that live and feed on or near the substrate.

Common prey capture behavior and feeding mechanisms utilized by chondrichthyan taxa that feed on or near the bottom might require energetic costs and movement patterns that would be insupportable in regions of anoxia. For instance, skates and rays, which tend to have crushing dentition that can eat armored invertebrates, dig up buried prey, or feed on pieces of sessile invertebrates (Carrier et al., 2012). In the wild, rays have been observed flapping their wings to disturb the sand at the seafloor and uncover their prey. Laboratory observations show rays near the substrate opening and closing their jaws repeatedly in 2.4 to 2.9-second cycles. This creates a ventrally directed flow of water that overturns both the sand and prey, allowing the food and sand to be separated, so that the ray can feed more efficiently (Carrier et al., 2012). Other bottom-feeding chondrichthyans, usually in possession of clutching teeth, will utilize prey capture behavior that involves suctioning their prey from the sand (Carrier et al., 2012). For instance, *Triakis semifasciata* (leopard shark) uses suction to remove worms from their burrows. *Hemiscyllium ocellatum* (epaulette shark) and *Chiloscyllium plagiosum* (white spotted bamboo shark) will sometimes plunge their head up to their first gill into the sediment and use suction to capture benthic worms and crabs (Carrier et al., 2012). While their clutching dentition may make it easier to grasp and hold on to these prey, these foraging strategies may be physiologically taxing in an oxygen-depleted environment, particularly for taxa that feed continuously, like rays, compared to sharks, which tend to feed intermittently (Carrier et al., 2012). While the overall extinction intensity was largely non-selective, the heightened extinction intensity of crushing and clutching teeth relative to cutting and piercing-grasping (Fig. 8) may reflect subtle ecological differences, such as greater exposure to anoxic environments. However, it was not only the bottom feeders with crushing and clutching tooth morphologies that were affected. More pelagic, actively swimming chondrichthyans, represented by cutting and piercing-grasping morphotypes, also experienced losses during OAE2.

Predators with the cutting morphtypes displayed a slightly lower extinction intensity compared to chondrichthyans with the crushing and clutching morphology (Fig.8), which may be explained by their opportunistic feeding strategies. If prey along the substrate is unavailable, they may go in search of food higher in the water column, but this may not always be the case. Hammerhead sharks have been observed using their cephalofoil to pin rays against the substrate before delivering a bite. Grey reef sharks, another example of the cutting tooth type, primarily feed on benthic-associated teleosts and invertebrates (Carrier et al., 2012). Obligate ram-ventilating sharks, which in most cases are active, tertiary chondrichthyans with cutting dentition, foraging near the bottom may be subject to anoxic regions, adversely affecting their physiological health. In response to low oxygen, ram-ventilating sharks increase their swimming speed to obtain sufficient oxygen (Carrier et al., 2012). However, this behavioral response may be costly regarding their metabolism, increasing oxygen demand when it is already limited, heightening their vulnerability (Waller et al., 2024; Carrier et al., 2012).

Body size may also play a role in determining energetic requirements and oxygen limitations. Generally, active large-bodied individuals, such as sharks of the Lamnidae family, tend to have higher oxygen demands due to large gill surface area, greater heart mass, and regional endothermy (Waller et al., 2024). These traits allow them to swim continuously and expand thermal niches, but they also make them less tolerant in hypoxic regions because of higher oxygen requirements (Waller et al., 2024). Less active, small-bodied elasmobranchs, possess behavioral compensations that help suppress activity and metabolism to survive in low-oxygen areas in the short-term (Waller et al., 2024). However, small species with a demersal lifestyle, are at greater risk during prolonged hypoxia events with their limited mobility. For example, the spotted dogfish (*Scyliorhinus canicula*) and the Florida smoothhound

(*Mustelus norrisi*) rely on buccal pumping, metabolic rate, and decreased activity in a low dissolved oxygen environment. Decreased activity conserves energy while enhancing increased water flow over the gills, but it may also constrain foraging ability (Carrier et al., 2012).

Both pelagic and benthic chondrichthyans are potentially affected by anoxia. During the OAE2, both groups may have faced a decrease in food supply, a decline in habitat availability, or environmental changes that would have negatively affected their physiological health. Chondrichthyans of the crushing and clutching morphotype, however, are especially affected by anoxic conditions, as they tend to inhabit regions where low oxygen levels are more prevalent. It is also important to remember that this dataset mainly comprises coastal occurrences, suggesting that these interpretations mostly apply to the inshore taxa rather than the open ocean taxa. In the modern ocean, there may be instances where pelagic chondrichthyes are vulnerable to low oxygen levels, especially set against the backdrop of overexploitation and habitat destruction, which together can further threaten their survival.

5 Conclusion

This study uses functional tooth morphology to infer the ecological response of chondrichthyes to widespread anoxia during the OAE2. By closely analyzing the physical attributes of fossilized chondrichthyan teeth, the genera used in this study were placed into categories of functional morphotypes: crushing, cutting, clutching, and piercing-grasping. The extinction intensity of each morphotype was then calculated using the boundary-crosser extinction equation. All functional morphotypes experienced an increase in extinction intensity during the C-T boundary, suggesting that most chondrichthyans, particularly benthic taxa with crushing and clutching morphotypes, were vulnerable to anoxic environments such as the one posed in the OAE2. Noticeable decreases in chondrichthyan genera during the C-T may stem from a lack of food sources, changes to their physiological ability to hunt food, and/or habitat loss. Although there are caveats to using functional tooth morphology to understand the response of past chondrichthyans to extinction events, it provides valuable insight into their ecological sensitivity and highlights the broader implications of environmental stressors for present-day chondrichthyans.

Bibliography

Abraham, M. A. F., Naafs, B. D. A., Lauretano, V., Sgouridis, F., & Pancost, R. D. (2023). Warming drove the expansion of marine anoxia in the equatorial Atlantic during the Cenomanian leading up to Oceanic Anoxic Event 2. *European Geosciences Union*, *19*(12), 2569-2580. https://cp.copernicus.org/articles/19/2569/2023/cp-19-2569-2023.html

Adnet, S., & Cappetta, H. (2007). A palaeontological and phylogenetical analysis of squaliform sharks (Chondrichthyes: Squaliformes) based on dental characters. *Lethaia*, *34*(3), 234-248. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1502-3931.2001.tb00052.x?casa_token=ED9EHQYylxMAAAAA%3AZ-lq1GBb2_4lXcFToSKBSUOriEAAayGVGBZ0R80Tn1d6p-3gSR1JFnS24UrcyjiEs9e2ct3HZJ_I

Arthur, M.A., Schlanger, S.O., & Jenkyns, H.C. (1987, 1 1). The Cenomanian-Turonian Oceanic Anoxic Event, II. Palaeoceanographic controls on organic-matter production and preservation. *Geological Society, London, Special Publications*, *26*(1), 401-420. https://doi.org/10.1144/gsl.sp.1987.026.01.25

Barnett, A., Braccini, J.M., Awruch, C.A., & Ebert, D.A. (2012, April 12). An overview on the role of Hexanchiformes in marine ecosystems: biology, ecology and conservation status of a primitive order of modern sharks. *Journal of Fish Biology*, *80*(5), 966-990. https://doi.org/10.1111/j.1095-8649.2012.03242.x

Bazzi, M., Kear, B. P., Blom, H., Ahlberg, P. E., & Campione, N. E. (2018). Static Dental Disparity and Morphological Turnover in Sharks across the End-Cretaceous Mass Extinction. *Current Biology*, *28*, 2607-2615. https://pdf.sciencedirectassets.com/272099/1-s2.0-S0960982217X00171/1-s2.0-S0960982218307632/main.pdf?X-Amz-Security-Token=IQoJb3JpZ2luX2VjEJL%2F%2F%2F%2F%2F%2F%2F%2F%2F%2FwEaCXVzLWVhc3QtMSJIMEYCIQD0BUUoHx6Ifj020toPqBmLQsHV4geXzAlmfj1eQiIkvwIhAKY6n056%2F4C

Bazzi, M., Kear, B. P., & Siversson, M. (2022). Southern higher-latitude lamniform sharks track mid-Cretaceous environmental change. *Gondwana Research*, *103*, 362-370. https://www.sciencedirect.com/science/article/pii/S1342937X21003063

Bice, K. L., Birgel, D., Meyers, P. A., Dahl, K. A., Hinrichs, K.-U., & Norris, R. D. (2006, April 8). A multiple proxy and model study of Cretaceous upper ocean temperatures and atmospheric CO2 concentrations. *Paleoceanography*, *21*(2). 10.1029/2005PA001203

Britto, T., Rosa, M. A., Medeiros, S., Oddone, M. C., & Dentzien-Dias, P. (2024). Quaternary fossil diversity of stingrays (Chondrichthyes: Myliobatiformes) from the eastern coast of South America, Brazil, southwestern Atlantic. *Journal of South American Earth Sciences*, *140*(104929). https://www.sciencedirect.com/science/article/pii/S0895981124001512?via%3Dihub

Cahill, A. E., Aiello-Lamens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Walkdron, J. B., Warsi, O., & Wiens, J. J. (2013, January 7). How does climate change cause extinction. *Proceedings of The Royal Society B*, *280*(1750). https://doi.org/10.1098/rspb.2012.1890

Camhi, M. D., Pikitch, E. K., & Babcock, E. A. (Eds.). (2009). *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Wiley.

Cappetta, H. (1987). *Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii*. F. Pfeil Verlag.

Carrier, J. C., Musick, J. A., & Heithaus, M. R. (Eds.). (2012). *Biology of Sharks and Their Relatives*. Taylor & Francis Group.

Carrier, J. C., Simpfendorfer, C. A., Heithaus, M. R., & Yopak, K. E. (Eds.). (2022). *Biology of Sharks and Their Relatives*. CRC Press.

Ciampaglio, C. N., Wray, G. A., & Corliss, B. H. (2005, December 1). A Toothy Tale of Evolution: Convergence in Tooth Morphology among Marine Mesozoic -- Cenozoic sharks, Reptiles, and Mammals. *The Sedimentary Record*, *3*(4), 4-8. https://doi.org/10.2110/sedred.2005.4.4

Compagno, L. J. V., Dando, M., & Fowler, S. L. (2005). *A field guide to the sharks of the world*. Collins.

Cooper, J. A., Griffin, J. N., Kindlimann, R., & Pimiento, C. (2023, January 14). Are shark teeth proxies for functional traits? A framework to infer ecology from the fossil record. *Journal of Fish Biology*, *103*, 789-814.

da Silva Rodrigues Filho, L. F., & de Luna Sales, J. B. (Eds.). (2017). *Chondrichthyes: Multidisciplinary Approach*. InTech. https://mts.intechopen.com/storage/books/5895/authors_book/authors_book.pdf

Diggers III, W. B., Davis, K. S., Moore, C., & Carlson, J. K. (2014). New record of a goblin shark Mitsukurina owstoni (Lamniformes: Mitsukurinidae) in the western North Atlantic Ocean. *Marine Biodiversity Records*, *7*(e96). https://www.cambridge.org/core/journals/marine-biodiversity-records/article/new-record-of-a-goblin-shark-mitsukurina-owstoni-lamniformes-mitsukurinidae-in-the-western-north-atlantic-ocean/D17A2F84AED9B441E00F68AC6D92331E

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science*, *4*, 11-37. 10.1146/annurev-marine-041911-111611

Elewa, A. M.T. (Ed.). (2008). *Mass Extinction*. Springer Berlin Heidelberg.

Elewa, A. M.T., & Abdelhady, A. A. (2020, February). Past, Present, and Future mass extinctions. *Journal of African Earth Sciences*, *162*. https://doi.org/10.1016/j.jafrearsci.2019.103678

Enax, J., Prymak, O., Raabe, D., & Epple, M. (2012). Structure, composition, and mechanical properties of shark teeth. *Journal of Structural Biology*, *178*(3), 290-299. https://www.sciencedirect.com/science/article/pii/S1047847712001025

Guinot, G. (2013). Regional to global patterns in Late Cretaceous selachian (Chondrichthyes, Euselachii) diversity. *Journal of Vertebrate Paleontology*, *33*(3), 521-531. https://www.tandfonline.com/doi/abs/10.1080/02724634.2013.740116?casa_token=NTpsGm5OKH8AAAAA:utxRfYx6MYiaeeqetzgFkbi4Ij3oqP0wKdNsYrLugD7FJeTLmVfQQAyrmhMW6vHyrO5CwLrn6w

Guinot, G., Adnet, S., & Cappetta, H. (2012). An Analytical Approach for Estimating Fossil Record and Diversification Events in Sharks, Skates and Rays. *PLOS One*, *7*(9), e44632. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0044632

Guinot, G., Adnet, S., Cavin, L., & Cappetta, H. (2013). Cretaceous stem chondrichthyans survived the end-Permian mass extinction. *Nature Communications*, *4*(1). https://www.nature.com/articles/ncomms3669

Guinot, G., & Condamine, F. L. (2023). Global impact and selectivity of the Cretaceous-Paleogene mass extinction among sharks, skates, and rays. *Science*, *379*(6634), 802-806. https://www.science.org/doi/full/10.1126/science.abn2080

Guinot, G., Underwood, C. J., Cappetta, H., & Ward, D. J. (2013, May 10). Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK.

Journal of Systematic Paleontology, *11*(6), 589-671. https://doi.org/10.1080/14772019.2013.767286

Hedges, S. B., & Kumar, S. (Eds.). (2009). *The Timetree of Life*. OUP Oxford.

Huveneers, C., Otway, N. M., Gibbs, S. E., & Harcourt, R. G. (2007, July 21). Quantitative diet assessment of wobbegong sharks (genus Orectolobus) in New South Wales, Australia. *ICES Journal of Marine Science*, *64*(6), 1272-1281. https://academic.oup.com/icesjms/article/64/6/1272/616342

Jacobsen, I. P., & Bennett, M. B. (2013, August 1). A Comparative Analysis of Feeding and Trophic Level Ecology in Stingrays (Rajiformes; Myliobatoidei) and Electric Rays (Rajiformes: Torpedinoidei). *PLOS One*, *8*(e71348). https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0071348

Jaime-Rivera, M., Caraveo-Patiño, J., Hoyos-Padilla, M., & Galván-Magaña, F. (2014, June). Feeding and migration habits of white shark Carcharodon carcharias (Lamniformes: Lamnidae) from Isla Guadalupe inferred by analysis of stable isotopes δ15N and δ13C. *Revista de Biologia Tropical*, *62*(2). https://www.scielo.sa.cr/scielo.php?pid=S0034-77442014000100019&script=sci_arttext&tlng=en

Klimley, A. P. (2013). *The Biology of Sharks and Rays*. University of Chicago Press.

Kriwet, J., & Benton, M. J. (2004, November 18). Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous–Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *214*(3), 181-194. https://www.sciencedirect.com/science/article/abs/pii/S0031018204004201

Mayhew, P. J., Jenkins, G. B., & Benton, T. G. (2008, October 24). A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. *Proceedings of the Royal Society B Biological Sciences*, *275*, 47-53. 10.1098/rspb.2007.1302

Monteiro, F. M., Pancost, R. D., Ridgwell, A., & Donnadieu, Y. (2012, December 15). Nutrients as the dominant control on the spread of anoxia and euxinia across the Cenomanian-Turonian oceanic anoxic event (OAE2): Model-data comparison. *Paleoceanography*, *27*(4). https://doi.org/10.1029/2012PA002351

Popov, E. V., Lopyrev, V. A., & Panteleev, A. V. (2024, January 11). Chondrichthyan fishes from the Middle Eocene Osinovaya Formation of Rostov Region, Russia. *An international Journal of Paleobiology*, *37*(1), 126-152. https://doi.org/10.1080/08912963.2023.2291774

Popov, E. V., Lopyrev, V. A., Panteleev, A. V., Birlukov, A. V., & Timirchev, F. K. (2023, December 3). Chondrichthyan fishes from the Middle Eocene Osinovaya Formation of Rostov Region, Russia. *Historical Biology*, *37*(1), 126-152. https://www.tandfonline.com/doi/epdf/10.1080/08912963.2023.2291774?needAccess=true

Ramsay, J. B., & Wilga, C. D. (2007, April 25). Morphology and mechanics of the teeth and jaws of white-spotted bamboo sharks (Chiloscyllium plagiosum). *Journal of Morphology*, *268*(8), 664-682. https://doi.org/10.1002/jmor.10530

Schlanger, S.O., & Jenkyns, H.C. (1976). Cretaceous Oceanic Anoxic Events: Causes and Consequences. *Geologie en Mijnbouw*, *55*(3-4), 179-184. https://ora.ox.ac.uk/objects/uuid:0921605b-4793-43df-889d-7b896790de62/files/m06799ee531ed600a7ef8bc4fe33dccb7

Serena, F., Abella, A.J., Bargnesi, F., Barone, M., Colloca, F., Ferretti, F., Fiorentino, F., Jenretta, J., & Moro, S. (2020). Species diversity, taxonomy and distribution of Chondrichthyes in the Mediterranean and Black Sea. *The European Zoological Journal*, *87*(1), 497-536. https://www.tandfonline.com/doi/epdf/10.1080/24750263.2020.1805518?needAccess=true

Siverson, M. (1997, August 24). Sharks from the mid-Cretaceous Gearle Siltstone, Southern Carnarvon Basin, Western Australia. *Journal of Vertebrate Paleontology*, *17*(3), 453-465. https://doi.org/10.1080/02724634.1997.10010995

Vázquez, P., & Clapham, M. E. (2017). Extinction selectivity among marine fishes during multistressor global change in the end-Permian and end-Triassic crises. *Geology*, *45*(5), 395-398. https://pubs.geoscienceworld.org/gsa/geology/article-abstract/45/5/395/207898/Extinction-selectivity-among-marine-fishes-during?redirectedFrom=PDF

Waller, M. J., Humphries, N. E., Womersley, F. C., Loveridge, A., Jeffries, A. L., Watanabe, Y., Payne, N., Semmens, J., Queiroz, N., Southall, E. J., & Sims, D. W. (2024, May 20). The vulnerability of sharks, skates, and rays to oceandeoxygenation: Physiological mechanisms, behavioralresponses, and ecological impacts. *Journal of Fish Biology*, *105*, 482-511. https://onlinelibrary.wiley.com/doi/epdf/10.1111/jfb.15830

Watson, A. J., Lenton, T. M., & Mills, B. J.W. (2017, June 21). Ocean deoxygenation, the global phosphorus cycle and the possibility of human-caused large-scale ocean anoxia. *Philosophical Transactions A*, *375*. https://royalsocietypublishing.org/doi/full/10.1098/rsta.2016.0318

Whitenack, L. B., & Motta, P. J. (2010, May 19). Performance of shark teeth during puncture and draw: implications for the mechanics of cutting. *Biological Journal of the Linnean Society*, *100*(2), 271-286. https://academic.oup.com/biolinnean/article/100/2/271/2450530

Yano, K., Aizawa, M., & Noichi, T. (2007, November 26). Some aspects of the biology of the goblin shark, Mitsukurina owstoni, collected from the Tokyo Submarine Canyon and adjacent waters, Japan. *Ichthyological Research*, *54*, 388-398. https://link.springer.com/article/10.1007/s10228-007-0414-2

Appendix

Table of chondrichthyan genera used in the study. This table includes all genera in the dataset categorized by functional tooth morphology.

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Abdounia	0	2	1	1
Physogaleus	0	2	1	1
Carcharhinus	0	2	0	0
Triaenodon	0	2	1	1
Physodon				
Negaprion	0	1	0	2
Prionace				
Rhizoprionodon	0	2	0	1
Glyphis				
Aprionodon				
Scoliodon	0	1	0	2
Hypoprion				
Misrichthys	0	2	0	1
Isogomphodon	0	1	0	2
Alopiopsis				
Danogaleus	0	1	1	2
Eogaleus	0	2	2	1
Pseudabdounia	0	2	2	2
Archaeogaleus	0	1	1	1
Florenceodon	0	1	1	2
Galeocerdo	0	2	1	1
Hemipristis	0	2	0	1
Paragaleus	0	2	2	1
Chaenogaleus	0	2	2	0
Moerigaleus	0	2	2	1
Leptocharias	1	0	1	2
Platyrhizodon	1	0	0	2
Corysodon	2	1	2	1
Diprosopovenator	0	1	1	2
Pseudoscyliorhinus	0	0	1	2
Scyliorhinus	0	1	2	1
Pteroscyllium	0	1	1	2
Premontreia	0	1	1	2
Megascyliorhinus	0	1	0	2
Galeus	0	2	2	1
Microscyliorhinus	0	1	0	2
Casieria	0	1	1	2

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Foumtizia	0	1	1	2
Premontreia (Oxyscyllium)	0	1	2	1
Scyllium				
Pachyscyllium	0	0	2	1
Bythaelurus	0	2	1	1
Crassescyliorhinus	0	0	2	1
Porodermoides	0	1	1	2
Premontreia (Premontreia)	0	2	2	1
Protoscyliorhinus	1	0	2	0
Scyliorhinotheca				
Cretascyliorhinus	0	2	2	1
Parasymbolus	0	1	2	1
Sigmoscyllium	1	0	1	2
Prohaploblepharus	0	0	2	1
Palaeoscyllium	0	0	1	2
Thiesus	0	0	1	2
Cadiera	0	0	1	2
Stenoscyllium	0	0	0	2
Sphyrna	0	2	0	1
Zygaena				
Pachygaleus	0	2	1	0
Galeorhinus	0	2	1	1
Mustelus	2	0	0	0
Triakis	1	1	2	1
Palaeogaleus	1	0	2	1
Squatigaleus	2	1	1	1
Archaeotriakis	2	0	2	1
Paratriakis	0	1	1	2
Meridiogaleus	1	1	2	1
Kallodentis	1	1	2	1
Pseudocorax	0	2	0	0
Khouribgaleus	1	2	1	1
Callorhinchus	2	0	0	0
Ischyodus	2	0	0	0
Elasmodus	2	0	0	0
Callorhynchus				
Ptyktoptychion	2	0	0	0

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Chimaera				
Elasmodectes				
Canadodus				
Edaphodon	2	0	0	0
Amylodon				
Harriotta				
Wodnika				
Echinorhinus	0	2	1	1
Heterodontus	1	0	2	0
Strongyliscus				
Paracestracion	1	0	2	1
Chlamydoselachus	0	0	1	2
Rolfodon	0	1	1	2
Dykeius				
Pachyhexanchus	0	2	2	0
Hexanchus	0	2	2	0
Notorhynchus	0	2	2	0
Notidanodon	0	2	1	1
Heptranchias	0	1	1	2
Notidanus				
Notorynchus	0	2	2	1
Gladioserratus	0	2	2	1
Xampylodon				
Protoheptranchias				
Komoksodon				
Weltonia	0	2	2	1
Welcommia	0	2	2	1
Strophodus	2	0	0	0
Asteracanthus	0	0	2	0
Acrodus				
Distobatus				
Glickmanodus				
Aegyptobatus				
Hybodus	1	1	2	1
Meristodonoides	1	2	1	1
Miosynechodus				
Planohybodus	0	2	2	1

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Tribodus	2	0	1	0
Egertonodus	0	1	1	2
Heteroptychodus	2	0	1	0
Lonchidion	2	1	1	0
Parvodus	2	1	1	1
Isanodus	2	0	0	0
Diabodus	2	0	1	0
Hylaeobatis				
Lissodus	2	0	0	0
Polyacrodus	2	1	1	1
Ptychodus	2	0	0	0
Paranomotodon	0	0	0	2
Alopias	0	0	0	2
Squalicorax	0	2	0	1
Nanocorax	0	2	0	0
Microcorax				
Galeocorax	0	2	0	0
Scindocorax	0	2	0	0
Cretomanta				
Aquilolamna				
Archaeolamna	0	1	1	2
Telodontaspis				
Carcharias	0	1	1	2
Dwardius	0	1	1	2
Cardabiodon	0	2	1	1
Cetorhinus	0	0	0	0
Keasius	0	0	0	0
Caucasochasma				
Cretoxyrhina	0	2	1	1
Plicatolamna	0	1	1	2
Dallasiella	0	1	1	2
Acrolamna				
Leptostyrax	0	1	1	2
Eoptolamna	0	1	1	2
Haimirichia	0	2	1	1
Roulletia	0	1	1	2
Lamna	0	1	1	2

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Isurolamna	0	1	1	2
Isurus	0	2	1	1
Carcharodon	0	2	0	1
Macrorhizodus	0	2	1	1
Carcharoides	0	1	1	2
Cosmopolitodus	0	2	0	0
Alopecias				
Megachasma	0	0	0	0
Scapanorhynchus	0	0	1	2
Anomotodon	0	1	1	2
Striatolamia	0	0	1	2
Mitsukurina	0	1	0	2
Clerolamna	0	0	1	2
Woellsteinia				
Carchariolamna				
Acutalamna	0	0	0	1
Odontaspis	0	1	1	2
Hypotodus	0	1	1	2
Palaeohypotodus	0	0	1	2
Jaekelotodus	0	2	1	1
Brachycarcharias	0	1	1	2
Araloselachus	0	1	1	2
Microcarcharias	0	0	1	2
Eostriatolamia	0	0	0	2
Pseudodontaspis	0	1	1	2
Synodontaspis				
Hispidaspis	0	0	0	0
Cenocarcharias	0	1	1	2
Sylvestrilamia				
Tethylamna	0	1	1	2
Johnlongia	0	0	1	2
Pseudomegachasma				
Mennerotodus	0	1	1	2
Pueblocarcharias	0	2	1	1
Cretolamna	0	2	1	1
Carcharocles	0	2	0	0
Otodus	0	2	1	1

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Palaeocarcharodon				
Parotodus	0	2	0	1
Megalolamna				
Megaselachus	0	2	0	0
Otodus (Otodus)	0	2	1	0
Kenolamna				
Paraisurus				
Pseudocarcharias				
Pseudocorax	0	2	0	0
Cretodus	0	1	1	2
Protolamna	0	1	1	2
Pseudoscapanorhynchus	0	0	0	2
Serratolamna	0	1	1	2
Aetobatus	2	0	0	0
Dasyatis	2	0	0	0
Glikmania	2	0	0	0
Viperecucullus	2	0	0	0
Hypolophites	2	0	0	0
Hypolophus	2	0	0	0
Palaeodasyatis				
Taeniura	2	0	0	0
Neotrygon	2	0	0	0
Pastinachus	2	0	0	0
Taeniurops	2	0	0	0
Mecotrygon	2	0	0	0
Subathunura	2	0	0	0
Gymnura	2	0	0	0
Ouledia	2	0	0	0
Himantura	2	0	0	0
Burnhamia	2	0	0	0
Myliobatis	2	0	0	0
Brachyrhizodus	2	0	0	0
Aetomylaeus	2	0	0	0
Archaeomanta	0	0	0	0
Manta	2	0	0	0
Meridiania	2	0	0	0
Plinthicus	2	0	0	0

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Igdabatis	2	0	0	0
Pteromylaeus	2	0	0	0
Mobula	2	0	1	0
Leidybatis	2	0	0	0
Eomobula	2	0	0	0
Lophobatis	2	0	0	0
Pseudaetobatus	2	0	0	0
Amamriabatis	2	0	0	0
Coupatezia	2	0	0	0
Texabatis				
Hypolophodon	2	0	0	0
Merabatis	1	0	2	1
Arechia	2	0	0	0
Promyliobatis				
Aturobatis	2	0	0	0
Ixobatis				
Heterobatis	2	0	0	0
Ishaquia				
Heterotorpedo	2	0	1	0
Dasyrhombodus				
Prosopodon				
Delpitia	2	0	1	0
Myliodasyatis	2	0	0	0
Lessiniabatis				
Potamotrygon				
Rhinoptera	2	0	0	0
Garabatis	2	0	0	0
Eorhinoptera				
Pucabatis	2	0	0	0
Rhombodus	2	0	0	0
Urolophus	2	0	2	0
Gyrace				
Pseudogaleus				
Odontorhytis	0	0	0	2
Machichnus				
Nanocetorhinus	0	0	0	0
Enantiobatis				

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Cheirostephanus				
Pliotrema				
Protospinax	2	0	0	0
Plesiozanobatus				
Galeolamna				
Oxyrhina				
Anotodus	0	2	0	1
Lamiostoma				
Xiphodolamia	0	2	0	1
Eostegostoma	0	1	2	1
Brachaelurus	1	0	2	1
Nebrius	0	0	2	1
Ginglymostoma	0	1	2	1
Plicatoscyllium	1	0	2	1
Cantioscyllium	1	1	2	1
Protoginglymostoma	0	0	2	1
Ganntouria	0	1	2	1
Pseudoginglymostoma	0	1	2	0
Delpitoscyllium	1	0	2	1
Hologinglymostoma	1	0	2	1
Chiloscyllium	1	0	2	1
Hemiscyllium	1	0	2	1
Almascyllium	1	0	2	1
Adnetoscyllium	1	0	2	1
Pseudospinax	1	0	2	1
Palaeobrachaelurus	1	0	2	1
Mesiteia	1	0	2	1
Acanthoscyllium				
Parasquatina	1	0	2	0
Annea	1	0	2	1
Ornatoscyllium	1	0	2	1
Garrigascyllium	1	0	2	1
Magistrauia	1	0	2	1
Parahemiscyllium	1	0	2	1
Columbusia	1	0	2	0
Restesia				
Cretorectolobus	1	0	2	1

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Gryphodobatis				
Squatiscyllium	1	0	2	1
Cederstroemia	1	0	2	1
Orectoloboides				
Orectolobus	1	0	2	1
Eometlaouia	1	1	2	1
Pararhincodon	1	0	2	0
Rhincodon	0	0	0	0
Palaeorhincodon	1	0	2	0
Stegostoma	0	0	2	0
Glossodus				
Rhaibodus				
Pristiophorus	1	0	1	1
Ikamauius	0	1	0	2
Pseudohypolophus	2	0	0	0
Squatirhina	2	0	0	0
Protoplatyrhina	2	0	0	0
Hamrabatis	2	0	0	0
Tomewingia				
Turoniabatis	2	0	0	0
Sechmetia				
Urobatis	2	0	0	0
Ostarriraja	2	0	0	0
Archingeayia	2	0	0	0
Engolismaia	1	0	2	0
Mafdetia	2	0	1	0
Vascobatis				
Ataktobatis	2	0	0	0
Tanoutia				
Erguitaia	2	0	0	0
Parapalaeobates	2	0	0	0
Platyrhina				
Tingitanius				
Cretaplatyrhinoidis				
Platyrhinoidis	2	0	0	0
Pseudoplatyrhina	2	0	0	0
Eoplatyrhina				

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Ptychotrygon	2	0	0	0
Texatrygon	2	0	1	0
Ptychotrygonoides	2	0	1	0
Asflapristis				
Raja	2	0	2	1
Pararaja	2	0	2	1
Beringraja				
Dipturus	2	0	2	1
Walteraja	2	0	2	1
Actinobatis				
Nebriimimus	2	0	2	1
Rhinobatos	2	0	0	0
Myledaphus	2	0	0	0
Rhinobatus				
Spathobatis	2	0	0	0
Zapteryx				
Paratrygonorrhina	2	0	0	0
Belemnobatis	2	0	0	0
Pseudorhinobatos	2	0	0	0
Rhombopterygia	2	0	0	0
Eorhinobatos	2	0	0	0
Isidobatus				
Pucapristis	2	0	2	1
Ischyrhiza	2	0	1	1
Marckgrafia	2	0	1	1
Sclerorhynchus	2	0	2	1
Ganopristis	2	0	2	1
Onchopristis	2	0	1	2
Ctenopristis	2	0	2	0
Schizorhiza	2	0	2	1
Dalpiazia	2	0	2	1
Ankistrorhynchus	2	0	2	1
Onchosaurus	2	0	2	1
Celtipristis	2	0	2	0
Libanopristis	2	0	2	1
Micropristis	2	0	1	0
Agaleorhynchus	2	0	2	1

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Baharipristis	1	1	2	0
Biropristis	2	0	0	0
Renpetia				
Borodinopristis	2	0	0	0
Tlalocbatos				
Pristis	2	0	0	0
Peyeria	2	0	1	1
Anoxypristis	1	0	1	2
Propristis	2	0	0	0
Aktaua	2	0	0	0
Oxypristis				
Rhynchobatus	2	0	0	0
Youssoubatis	2	0	0	0
Hypsobatis				
Xenodolamia				
Cyclobatis	2	0	0	0
Centrophorus	0	2	0	0
Deania	0	2	0	0
Centrodeania				
Isistius	1	2	1	1
Dalatias	0	2	0	0
Squaliodalatias	1	2	1	1
Angoumeius				
Squaliolus	1	2	1	1
Eosqualiolus	1	2	1	1
Oligodalatias	1	2	0	0
Hessinodon				
Eoetmopterus	1	2	2	1
Paraetmopterus	1	2	2	1
Etmopterus	1	2	2	1
Trigonognathus				
Orthechinorhinus	0	0	0	2
Proetmopterus	1	2	2	1
Incognitorapax				
Fredipristis	1	2	2	1
Scymnorhinus	0	2	2	1
Cretascymnus	1	2	1	1

Genus	Crushing	Cutting	Clutching	Piercing/Grasping
Centroscymnus	1	2	1	1
Rhinoscymnus	0	2	0	1
Somniosus	0	2	0	1
Scymnodalatias				
Protoxynotus	1	2	1	1
Squalus	1	2	1	0
Centrosqualus				
Centrophoroides	1	2	1	0
Protosqualus	1	2	1	0
Scymnodon				
Zameus				
Spinax				
Protocentrophorus	1	2	1	0
Microetmopterus	1	2	1	1
Megasqualus	1	2	1	0
Pseudorhina	1	1	2	1
Squatina	1	0	2	0
Squatina (Cretascyllium)	1	1	2	1
Squatina (Squatina)	1	1	2	0
Cretasquatina				
Danaea	0	1	1	2
Sphenodus	0	0	0	2
Occitanodus	0	0	0	2
Synechodus	1	0	2	0
Antrigoulia	1	0	2	1
Paraorthacodus	0	1	2	1
Narcine	2	0	2	0
Titanonarke	2	0	2	0
Eotorpedo	0	0	0	2
Torpedo	2	0	2	0