STABLE ISOTOPE ANALYSIS OF LATE CRETACEOUS (MAASTRICHTIAN) SHARK TEETH (*SERRATOLAMNA SERRATA*; *CARCHARIAS HOLMDELENSIS*) FROM THE WESTERN INTERIOR SEAWAY

by

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Title: Stable Isotope Analysis of Late Cretaceous (Maastrichtian) Shark Teeth
(*Serratolamna serrata*; *Carcharias holmdelensis*) from the Western Interior Seaway

Approved: *Edward Davis, Ph.D.*
Primary Thesis Advisor

The Western Interior Seaway was a Late Cretaceous (100.5-66 Mya) inland sea that, at its largest, stretched north to south from the modern-day Arctic Ocean to the Gulf of Mexico. Research concerning this seaway has revealed that there was likely a significant temperature gradient present, with cooler temperate waters to the north and warmer subtropical waters to the south. I sampled fossilized teeth from two species of sharks (*Serratolamna serrata*; *Carcharias holmdelensis*) collected from an Arkansas site located in the Late Maastrichtian of the Western Interior Seaway. I used laser ablation techniques to do stable isotope analysis on 10 teeth from *S. serrata* and 8 teeth from *C. holmdelensis*. The mean δ^{18}O (VSMOW) isotopic value for *S. serrata* (22.2‰) and *C. holmdelensis* (22.3‰) indicate no significant difference in primary habitat. The mean reconstructed paleotemperature was 19.5 °C, putting this locality at within the upper parameters of a warm temperate climate. The mean δ^{13}C (VBDP) isotopic value for *S. serrata* (-7.23‰) and *C. holmdelensis* (-9.58‰) indicate a difference in dietary habits or preferences. I hypothesize that these differences are attributed to significant size differences between *S.* serrata and *C. holmdelensis.* These size differences would have enabled them to fill slightly different ecological niches which would result in somewhat differing prey sources. Future research is needed to expand upon the paleoecology of Late Cretaceous sharks and the Maastrichtian Western Interior Seaway.

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I would first and foremost like to thank my thesis committee: Professor Edward Davis (Primary Thesis Advisor), Professor Lisa Munger (CHC Representative), and Kellum Tate-Jones (2nd Reader) for leading me through this process and providing support whenever needed. I'd like to thank Professor Samantha Hopkins, Dana Reuter, and the rest of the UO vertebrate paleontology lab for teaching me, supporting me, and always providing useful insights into my research that I would've been lost without. I'd like to thank Professor Scott Blumenthal and Jensen Wainwright from the UO stable isotope lab for guiding me through my research, teaching me about the laser ablation process, and dedicating hours of their time to ensuring that I was able to receive the results for my thesis. I'd also like to thank Professor Martin Becker from William Patterson University for providing much-needed knowledge on Cretaceous shark tooth identification.

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Chapter 1: Introduction

Lasting from roughly the **Late Cretaceous** (100.5-66 Mya; Figure 1) to the early **Paleogene** (~66-55 Mya), the Western Interior Seaway (WIS) was an **epicontinental** shallow inland sea. At its largest, the seaway served as a connector between the cold, **boreal** waters up north and the warmer, subtropical waters in the south. In modern times, this seaway would have stretched from the present-day Arctic Ocean to the Gulf of Mexico (Nicholls & Russell, 1990).

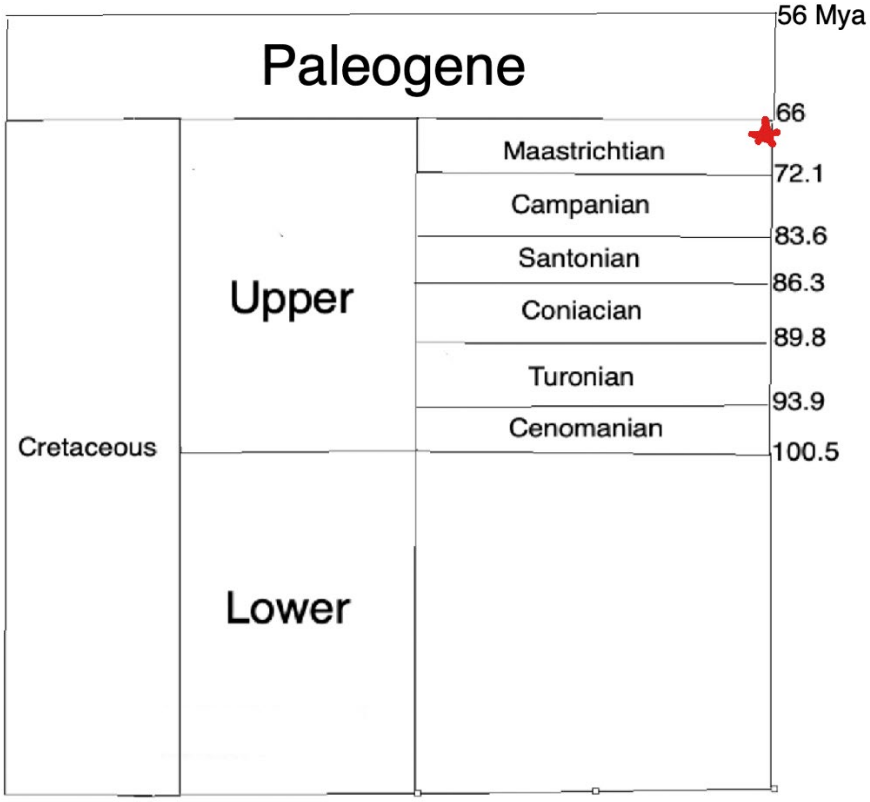


Figure 1: Geologic Time Scale of the Upper (Late) Cretaceous

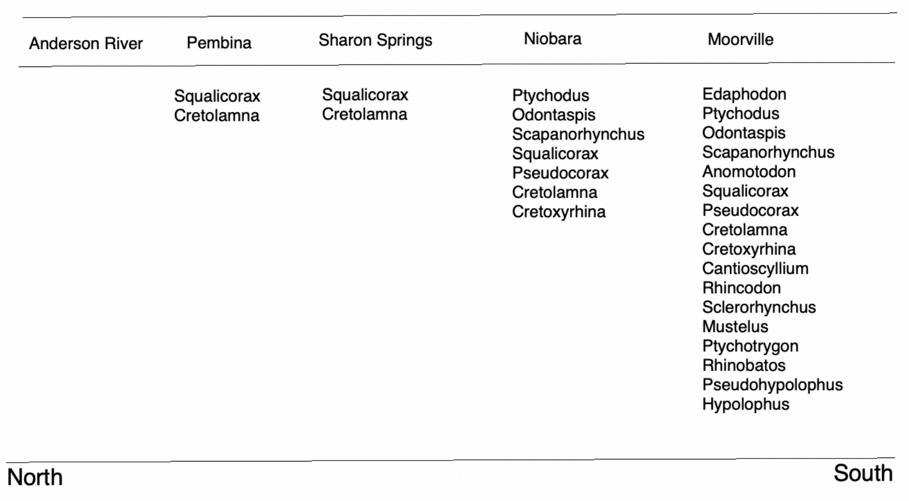
Red star refers to age of fossil shark teeth

Paleobiogeography of the Western Interior Seaway

In the **Maastrichtian** (72.1-66 Mya), the seaway first experienced a prolonged **third order regression**, causing a sea level drop of 50-150 ft, followed by a short period of **transgression** as the sea level rose again (Hay et al., 1993). Because of these relatively frequent transgressive-regressive cycles, the shoreline of the WIS can be drawn differently depending on the moment in geologic time. During the Maastrichtian, the shoreline of the seaway stretched far enough east to reach the middle of modern-day Arkansas (Kauffman, 1984; Nicholls & Russell, 1990).

Researchers have attempted to divide up the seaway into **paleogeographical** and **paleobiogeographical** provinces based on differing types of criteria. One researcher studying **cephalopods** identified the northern part of the seaway as the "North American Boreal Province" but did not name the southern part as they felt that the faunal changes from north to south were too gradational to merit a distinction between provinces (Jeletzky, 1968; Jeletzky, 1971). Another researcher studying **gastropods**, as well as a separate team of researchers studying **molluscan** groups, did identify two separate northern and southern interior provinces (Sohl, 1967; Sohl, 1971; Scott & Taylor, 1977). Most notably, Kauffman (1973; 1977; 1984) explored multiple ways of dividing the seaway before ultimately using a variety of invertebrate groups and **foraminifera** to identify four provinces: Northern Interior Subprovince, Central Interior Subprovince, Gulf and Atlantic Subprovince, and the Western Interior Endemic Center which overlaps onto the other three (Kauffman, 1973; Kauffman, 1977; Kauffman, 1984). All studies mentioned above used temperature zonation to divide the seaway, with cool and mild temperate temperatures in the northern provinces and warmer temperate and subtropical temperatures in the southern provinces. These different province boundaries have significant overlap in placement (Jeletzky, 1971; Kauffman, 1984; Sohl, 1971; Nicholls & Russell, 1990).

In a synthesis study of publications examining the WIS **faunal assemblages**, Nicholls & Russell (1990) report a distinct north-south gradient in faunal assemblages throughout the seaway (Russell, 1970; Martin & Stewart, 1982; Meyer, 1974; Nicholls, 1987a; Nicholls, 1989). They then propose their own set of provinces based on the distribution of fauna found in different localities throughout the Lower **Campanian** of the seaway. They separate the seaway into two provinces based on faunal gradients: the Northern Interior Province and the Southern Interior Province. The Northern Interior Province is characterized by a high abundance of **plesiosaurs** with low overall diversity in other vertebrate groups, particularly **chondrichthyans** (primarily sharks) and turtles. In contrast, the Southern Interior Province is characterized by rare appearances of plesiosaurs and a very high abundance of sharks and turtles (Figure 2; Nicholls & Russell, 1990). The boundary between these provinces is gradational rather than abrupt due to the **cosmopolitan** nature of marine vertebrates, in that they are unconstrained by specific habitats and can travel long distances.



Anderson River	Pembina	Sharon Springs	Niobara	Moorville
	Squalicorax	Squalicorax	Ptychodus	Edaphodon
	Cretolamna	Cretolamna	Odontaspis	Ptychodus
			Scapanorhynchus	Odontaspis
			Squalicorax	Scapanorhynchus
			Pseudocorax	Anomotodon
			Cretolamna	Squalicorax
			Cretoxyrhina	Pseudocorax
				Cretolamna
				Cretoxyrhina
				Cantioscyllium
				Rhincodon
				Sclerorhynchus
				Mustelus
				Ptychotrygon
				Rhinobatos
				Pseudohypolophus
				Hypolophus

North South

Figure 2: A list of chondrichthyan genera recorded from WIS localities from the Lower Campanian

Adapted from Nicholls & Russell (1990). The localities are ordered north to south from left to right. This list drew from the sources: Russell, 1976c; Nicholls, 1989; Russell, 1988; Meyer, 1974; Applegate, 1970.

Geologic Setting

The Arkadelphia Formation is located in Southwest Arkansas, and is primarily exposed in outcrops by the Red, Little Missouri, and Ouachita Rivers and their tributaries (Becker et al., 2006). At the outcrops along the Ouachita River where the fossil material for this thesis was collected the formation consists of **marl** and **marly clay** (Becker et al., 2006). The geological age of the Arkadelphia Formation has been determined to be late Maastrichtian in age based on **magnetostratigraphic** interpretations made by Liddicoat et al. (1981) as well as **ostracod** assemblages analyzed by Pitakpaivan & Hazel (1994).

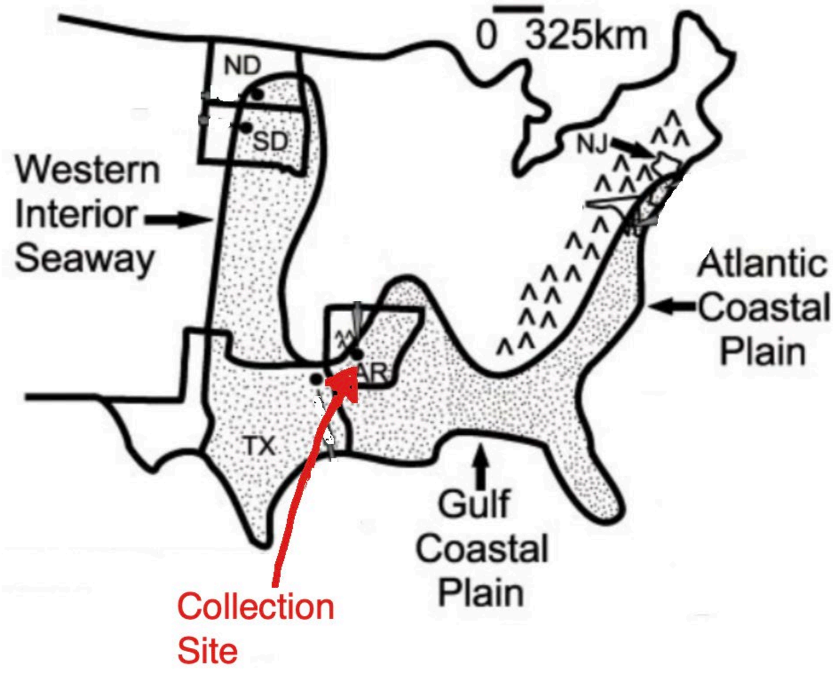


Figure 3: Map of the Maastrichtian Western Interior Seaway with Arkadelphia Formation Collection Site

Adapted from Becker, 2006. The collection site where the teeth mentioned in this paper were collected is indicated by the red arrow.

Stable Isotopes

The elements analyzed in this study were carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$). The $\delta^{13}C$ values provide insight into the eating habits of these shark species and reveal notable differences in their diets (DeNiro & Epstein, 1978). $\delta^{18}O$ values are useful for determining the physical range that the organisms occupied. Different oxygen isotopic values would have indicated that these shark species were occupying different physical habitats or spaces that were different enough in temperature, salinity, and oxygen composition to warrant a noticeable difference in isotope values (Drago et al., 2020).

Methods

I aimed to answer the question: What types of inferences can be made about shark ecology from fossil shark teeth and how does this relate to the paleoecology of the Western Interior Seaway?

The material for this thesis was collected in May of 2017 by K. Tate-Jones. 111 complete and incomplete fossils, all tooth material, were collected. 37 were identified to the species level as *Serratolamna serrata*, 64 as *Carcharias holmdelensis*, 1 as *Cretoxyrhina mantelli*, 1 as *Squalicorax kaupi*, and 1 as *Squalicorax falcatus*. One was identified to belong to the **genus** *Palaeogaleus* and another to the genus *Cretodus*. The final 5 could not be identified beyond **Class** Lamniformes.

10 complete teeth from *Serratolamna serrata* and 8 complete teeth from *Carcharias holmdelensis* were sampled in this study. Shark teeth analyzed in this study were prepared for isotopic analysis by following pretreatment protocols used by previous laser ablation studies of fossil teeth (Kimura et al., 2013). Teeth were treated using 0.1 M buffered acetic acid solution for 30 minutes to remove any potential contaminating **secondary carbonates**. The carbon and oxygen isotope composition of tooth enamel was measured using **laser ablation-gas chromatography-isotope** ratio mass spectrometry (LA-GC-IRMS) using a custom designed laser system housed in the University of Oregon Stable Isotope Laboratory. Teeth were loaded onto a stage in a glass chamber that is purged with helium for at least 12 hours to remove residual or outgassing CO2 from sample surfaces. Tooth enamel was ablated using a New Wave Research MIR-10 CO2 infrared laser and liberated CO2 gas was concentrated, purified, and analyzed using a Nu Horizon 2 IRMS. Laser power, number of shots, and position

of shots on shark teeth were optimized to generate enough CO2 gas for adequate signal (> 10 nA) while maintaining the integrity of each tooth. The resulting data were then corrected using calcite and tooth enamel internal laboratory reference materials calibrated to the primary reference material IAEA-603 for the **Vienna Pee Dee Belemnite** (VPBD) scale.

Tooth enamel was sampled over **dentine** or other dental tissues because it is less susceptible to **diagenesis** than other tooth tissues.

To convert the oxygen isotope values from VPDB to **Vienna Standard Mean Ocean Water** (VSMOW), the following equation from van Baal et al. (2013) and Friedman & O'Neil (1977) was used:

$$\delta^{18}O_{VSMOW} = 1.03086 * \delta^{18}O_{VPDB} + 30.86$$

Tooth enamel has three oxygen-containing components: phosphate, carbonate, and hydroxyl. The laser ablation system provides bulk oxygen from the enamel sampled. However, the equation used to estimate paleotemperature requires just the phosphate component of tooth enamel. Phosphate makes up ~90% of the oxygen-containing components of tooth enamel. To correct for this, the approach from Cullen et al. (2019) was used. 1‰ was subtracted from each $\delta^{18}O$ (VSMOW) value to convert from laser $\delta^{18}O$ to phosphate equivalent $\delta^{18}O$.

To reconstruct the paleotemperature (Table 2), the following equation from Pucéat et al. (2010) was used:

$$T = 124.6 - 4.52 * (\delta^{18}O_p - \delta^{18}O_w)$$

T refers to the reconstructed paleotemperature in degrees Celsius, $\delta^{18}O_p$ refers to the oxygen isotope of the sampled tooth enamel, and $\delta^{18}O_w$ refers to the oxygen isotope value of the Maastrichtian ocean (specific VSMOW). The VSMOW used for this equation is -1‰ (Shackleton & Kennett, 1975; van Baal et al., 2013).

Box plots highlighting the differences between genera were constructed on RStudio for both $\delta^{18}O$ and $\delta^{13}C$ values. T-tests between *S. serrata* and *C. holmdelensis* were done for both $\delta^{18}O$ and $\delta^{13}C$ values in Microsoft Excel.

Chapter 2: Results

Systematic Paleontology

Class Lamniformes (Berg, 1958)

Family Serratolamnidae (Landemaine, 1991)

Genus Serratolamna (Landemaine, 1991)

Serratolamna serrata (Agassiz, 1843)

Materials - 37 complete teeth from UO 5201 Arkadelphia Formation, Arkansas from F-81301, F-81302, F-81303, F-81304, F-81305, F-81306, F-81307, F-81308, F-81309, F-81310, F-81311, F-81312, F-81313, F-81314, F-81315, F-81316, F-81317, F-81318, F-81319, F-81320, F-81321, F-81322, F-81323, F-81324, F-81325, F-81326, F-81327, F-81328, F-81329, F-81330, F-81331, F-81332, F-81333, F-81334, F-81335, F-81336, F-81337. The 18 teeth sampled are: F-81332, F-81322, F-81334, F-81324, F-81318, F-81320, F-81325, F-81327, F-81317, F-81319, F-81336, F-81331, F-81315, F-81329, F-81313, F-81311, F-81326, F-81321 (see Figure 4 for example photo).

Description - **Root** is **bilobate**, broad, and has a small **nutrient groove**. **Crown** is triangular and broad-based. **Cusp** is smooth and slightly curving. Two **cusplets** are present, both triangular, angled away from the crown, one on each side.

Discussion - Teeth belonging to *Serratolamna* display multiple diverging cusplets, asymmetry, a short nutrient groove, and smooth crown faces (Landemaine, 1991).

Previously, species that belong to *Serratolamna* were classified into the genus *Cretolamna* by Gluckman, 1958 (Kent, 1994; Becker et al., 2006). However, the diagnostic features of *Serratolamna* are not noted to be shared by members of *Cretolamna* (Welton & Farish, 1993; Becker et al., 2006). *Serratolamna serrata* is most well-known from the Maastrichtian in Africa, Europe, the Atlantic, the Gulf Coastal Plains, and, as is the case for these teeth, the Western Interior Seaway (Becker et al., 2006; Welton & Farish, 1993; Kent, 1994; Case, 1995; Hoganson et al., 1996; Case & Capetta, 1997; Hartstein et al., 1999; Hoganson & Murphy, 2002; Becker et al., 2004; Robb, 2004; Arambourg, 2005; Capetta, 1987).

Figure 4: Photo of *Serratolamna serrata* tooth with scale bar

Taken with DinoLite

Class Lamniformes (Berg, 1958)

Family Odontaspididae Muller & Henle, 1837)

Genus Carcharias (Rafinesque, 1810)

Carcharias holmdelensis (Cappetta & Case, 1975a)

Materials - 64 complete teeth from UO 5201 Arkadelphia Formation, Arkansas from F-81338, F-81339, F-81340, F-81341, F-81342, F-81343, F-81344, F-81345, F-81346, F-81347, F-81348, F-81349, F-81350, F-81351, F-81352, F-81353, F-81354, F-81355, F-81356, F-81357, F-81358, F-81359, F-81360, F-81361, F-81362, F-81363, F-81364, F-81365, F-81366, F-81367, F-81368, F-81369, F-81370, F-81371, F-81372, F-81373, F-81374, F-81375, F-81376, F-81377, F-81378, F-81379, F-81380, F-81381, F-81382, F-81383, F-81384, F-81385, F-81386, F-81387, F-81388, F-81389, F-81390, F-81391, F-81392, F-81393, F-81394, F-81395, F-81396, F-81397, F-81398, F-81399, F-81400, F-81401. The 10 teeth sampled are: F-81350, F-81397, F-81339, F-81377, F-81366, F-81347, F-81371, F-81351, F-81381, F-81379. (see Figure 5 for example photo)

Description - Root is bilobate, broad, and has a raised, deep nutrient groove. Crown is triangular, narrow, and elongated. The **labial** face is smooth, whereas the **lingual** face is **striated**. Cusp is slightly curved lingually but is otherwise symmetrical. At the base of the tooth crown is a defined **dental band**. One small cusplet lies on each shoulder of the tooth.

Discussion - *Carcharias holmdelensis*, originally categorized as *Odontaspis* *holmdelensis* by Cappetta & Case (1975a), is set apart from *Carcharias samhammeri* by the presence or lack of striations on the lingual crown face (Becker, 2006; Kent, 1994). Whereas *C. samhammeri* do not possess lingual striations, *C. holmdelensis* has been described to have striations on the lingual crown face (Becker, 2006). *C. holmdelensis* is known from the Campanian and Maastrichtian, where materials have been documented from the Atlantic Coastal Plain as well as Texas and Arkansas (Becker, 2006; Cappetta & Case, 1975a; Kent, 1994; Hartstein et al., 1999; Case & Cappetta, 1997).

Figure 5: Photo of *Carcharias holmdelensis* tooth with scale bar

Taken with DinoLite

Isotopic Results

Sample ID	Genus	$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VSMOW)
F-81332	Serratolamna	-7.0	22.4
F-81322	Serratolamna	-6.2	22.0

F-81334	Serratolamna	-3.0	22.2
F-81324	Serratolamna	-7.0	22.4
F-81318	Serratolamna	-6.4	21.0
F-81320	Serratolamna	-8.0	22.6
F-81325	Serratolamna	-5.6	23.8
F-81327	Serratolamna	-7.5	21.9
F-81317	Serratolamna	-12.3	24.6
F-81350	Carcharias	-10.8	22.6
F-81319	Serratolamna	-6.6	22.3
F-81397	Carcharias	-12.8	19.4
F-81339	Carcharias	-5.4	21.9
F-81377	Carcharias	-11.5	23.9
F-81366	Carcharias	-7.9	23.3
F-81336	Serratolamna	-5.0	22.0
F-81331	Serratolamna	-5.4	21.4
F-81315	Serratolamna	-9.6	23.0
F-81329	Serratolamna	-6.2	22.2
F-81347	Carcharias	-7.7	21.5
F-81313	Serratolamna	-9.5	22.1
F-81311	Serratolamna	-6.3	21.3
F-81326	Serratolamna	-9.5	21.4
F-81371	Carcharias	-9.7	22.9

F-81321	Serratolamna	-9.3	21.9
F-81351	Carcharias	-7.9	22.0
F-81381	Carcharias	-12.7	23.1
F-81379	Carcharias	-9.3	22.1

Table 1: Corrected isotopic data

Carbon data is represented in VPDB and oxygen data is represented in VSMOW

Genus	Average δ^{18}O (VSMOW)	Paleotemperature Estimate (°C)
Serratolamna	22.2	19.7
Carcharias	22.3	19.3

Table 2: Average δ^{18}O value per genera and paleotemperature estimate

Serratolamna serrata had a less negative δ^{13}C value (x=-7.2) than *Carcharias holmdelensis* (x=-9.6) based on a two-tailed t-test (t=2.65, df=26, p<0.01).

The δ^{13}C values of *C. holmdelensis* ranged from -12.7‰ to -5.4‰, with a difference of -7.3‰. These were different from the δ^{13}C values of *S. serrata* which ranged from -12.3‰ to -3‰ with a difference of -9.3‰.

Serratolamna serrata had an almost equal δ^{18}O value (x=22.2) as *Carcharias holmdelensis* (x=22.3) based on a two-tailed t-test (t=-0.06, df=26, p<0.95).

The δ^{18}O values of *C. holmdelensis* ranged from 19.4‰ to 23.9‰, with a difference of 4.5‰. These were significantly similar to the δ^{18}O values of *S. serrata* which ranged from 20.9‰ to 24.6‰ with a difference of 3.7‰.

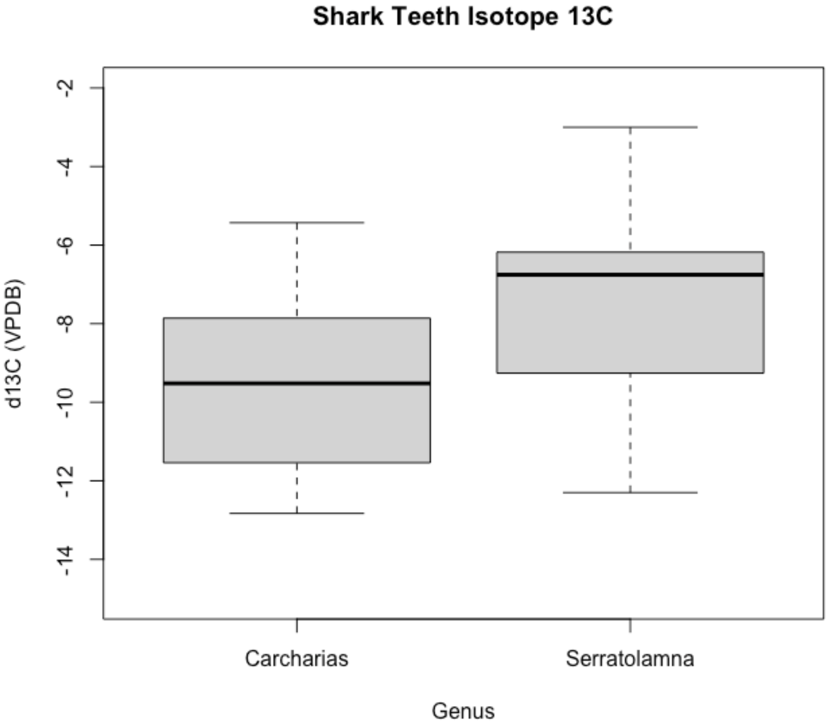


Figure 6: Boxplot showing the differences in isotopic carbon values between genera

Overall, teeth from *Carcharias* tend to have a more negative carbon value, with the mean at -9.6‰. In contrast, although *Serratolamna* has more range, the overall trend shows less negative values than *Carcharias*, and the mean is -7.2‰.

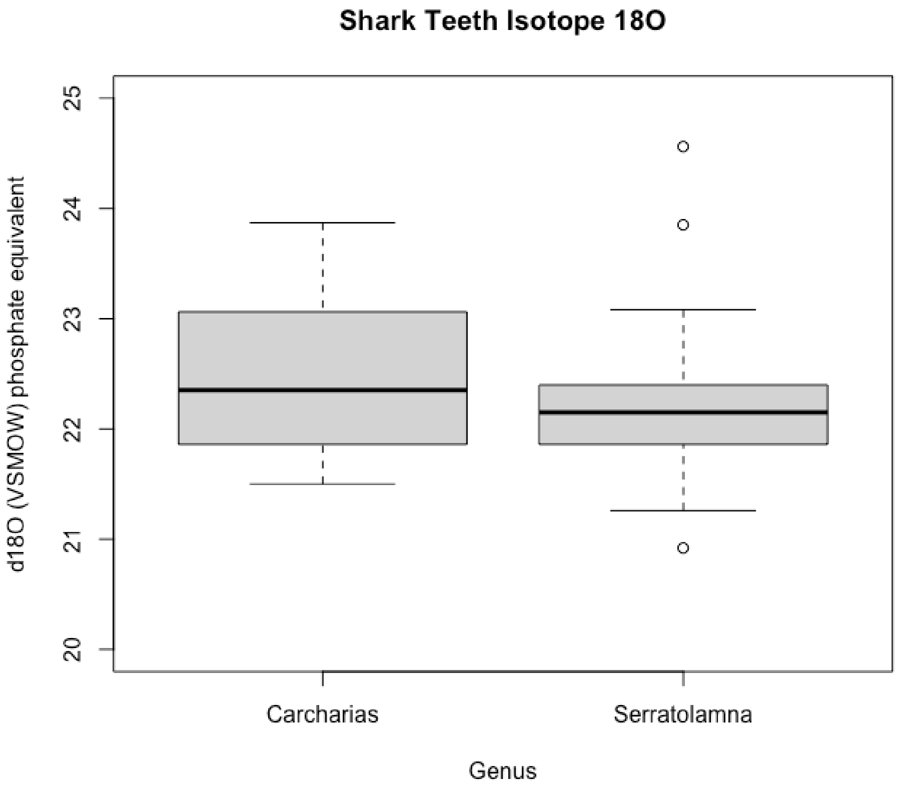


Figure 7: Boxplot showing the differences in isotopic oxygen values between genera

The means for both *Carcharias* and *Serratolamna* are almost the same, 22.3‰ and 22.2‰ respectively. There are some notable outliers for both genera, but overall, the ranges for both species are almost identical.

Chapter 3: Discussion

The $\delta^{18}O$ values for both species are markedly similar (Figure 7). Similar oxygen values are to be expected given that the shark tooth fossils were recovered from the same site the likelihood that these sharks lived in Nicholl and Russell's (1990) Southern Interior Province. The striking similarity of $\delta^{18}O$ values between these two genera of sharks indicates that they did inhabit the same physical habitat. The $\delta^{18}O$ ranges are overall constrained to range no larger than 4.5‰, but there are multiple outliers in both species. This is not unexpected, as these sharks were able to swim long distances and stray outside of their preferred habitat, which would contribute to a more varied and unique isotopic signal. Oxygen isotopic studies on modern-day shark species are significantly different than the $\delta^{18}O$ values from these fossil sharks. In one study, $\delta^{18}O$ values of modern-day sharks averaged about 31‰ in comparison to the 22.2‰ and 22.3‰ means from *S. serrata* and *C. holmdelensis* respectively (Vennemann et al., 2001).

$\delta^{18}O$ values, aside from being indicative of how consistent the shark species were in remaining within their specific habitat, are also useful for interpreting paleotemperatures of the water that they lived in (Pucéat et al., 2010). A separate paleotemperature reconstruction was calculated for each genus sampled (Table 2). The average reconstructed paleotemperature is 19.5 °C. The reconstructed paleotemperature would have to lie within the range of 15-27 °C to fulfill the requirements of being warm temperate to subtropical, as multiple researchers have determined the southern half of the WIS in the Campanian and Maastrichtian to have been (Jeletzky, 1968; Jeletzky, 1971; Sohl, 1967; Sohl, 1971; Scott & Taylor, 1977; Kauffman, 1973; Kauffman, 1977;

Kauffman, 1984). Lying 2.5 °C below the maximum boundary for temperate ocean water temperatures according to Köppen (1884), the average paleotemperature reconstructed in this study indicates that these sharks were living in a habitat that was about three fourths down the seaway from the north. This is supported by the southwestern Arkansas locality (Figure 3), as it lies south of the midline of the Maastrichtian WIS but is not at the farthest southern end. This paleotemperature is similar to sea temperatures along the modern-day Southern California coast in the summer (~20°C).

The $\delta^{13}C$ values (Figure 6) differ significantly between the two genera as compared to the similarity of their $\delta^{18}O$ values. Their ranges overlap, but there is a difference in means of 2.4‰. This indicates that there is some difference in prey source or diet. I hypothesize that this is likely related to differences in their overall body size and in their functional dental morphology.

The smaller teeth of *Serratolamna serrata* have been interpreted as an indicator of a relatively small shark (body size) in comparison to other sharks that were active during the same time period. The dental morphology of *S. serrata* suggests that it likely did not reach longer than 1.5m in length and is indicative of a tearing-type of dentition associated with scavenging (Cappetta, 1987; Underwood & Mitchell, 2000). Likely, *S. serrata* was more successful as a scavenger than as an active predator. However, *S. serrata* might have also preyed upon smaller fishes.

Carcharias holmdelensis, on the other hand, was likely larger than *S. serrata* at around 2-3m body length on average based on the extant species *Carcharias taurus* (Retzler et al., 2013). Few studies explore the feeding habits of *C. holmdelensis* but based on the data from Figure 6, it is highly likely that this species was eating prey that differed from *S. serrata.* An explanation for the difference in their isotopic values could be that since *C. holmdelensis* was a little larger, it might have engaged in more active predation rather than sticking to scavenging. *C. holmdelensis* also had narrower teeth with smoother and rounder edges, indicating a preference for biting and clamping rather than tearing flesh. Since these sharks lived in the same basic habitat, indicated by $\delta^{18}O$ values and their occurrence in the same faunal assemblage, it is unclear whether they would have preferred to eat different prey. *C. holmdelensis* could have had a wider range of prey to choose from as an active predator, altering its carbon isotopic composition, whereas *S. serrata* was more constrained by smaller prey and what food it could find to scavenge.

Conclusion

The fossil teeth from both *S. serrata* and *C. holmdelensis* have $\delta^{18}O$ values that are within 0.1‰ of each other, providing evidence that suggests these species coexisted in the same consistent habitat. The $\delta^{13}C$ values display a noticeable and significant difference between the two species. They displayed a mean difference of -2.4‰ and some range overlap. These differences in both mean and overall range indicate that the species had differing dietary habits. *S. serrata*, based on tooth morphology and predicted body size, was likely a scavenger and an active predator of small fish. This reconstructed ecology indicates that *S. serrata*'s choice of prey was constrained to what can easily be scavenged from active predators (other sharks, bigger fish, marine reptiles, etc) and what they can easily prey upon. *C. holmdelensis* on the other hand, has a larger predicted body size. This, paired with the differences in $\delta^{13}C$ values, indicates active predation upon a range of fishes as well as larger marine organisms (other sharks, marine reptiles, etc).

Paleotemperature estimates demonstrate an upper threshold for warm temperate water temperature, corroborating previous research that has separated the seaway into provinces based on temperature gradients in which the southern provinces varied from warm temperate to subtropical (Jeletzky, 1968; Jeletzky, 1971; Sohl, 1967; Sohl, 1971; Scott & Taylor, 1977; Kauffman, 1973; Kauffman, 1977; Kauffman, 1984).

The results from this study suggests that future research could be done on the specific dietary habits of Late Cretaceous sharks, predicting their behavior and feeding habits through functional morphology and paleoecological geochemical research.

Glossary

Bilobate – having, or consisting of, two lobes

Boreal – relating to, or located in, Northern regions

Campanian – the second to last stage of the Cretaceous that lasted from 83.6-72.1 million years ago

Cephalopods – a marine animal, such as a squid or octopus, that is characterized by a set of arms or tentacles, bilateral symmetry, and a prominent head

Chondrichthyans – a class containing the cartilaginous fish, including sharks and rays

Class – a taxonomic category that is below phylum but above order

Cosmopolitan – found all over the world

Crown (of tooth) – often the visible part of the tooth, that is covered in enamel

Cusp (of tooth) – an elevated part of a tooth (ex. The raised surfaces on molars)

Cusplets – a small cusp

Dental band – a defined line that runs along the boundary between the root and the crown of a tooth

Dentine – one of the main supporting components of a tooth and the second hardest component, second to enamel

Diagenesis – physical and chemical changes brought on by interactions with water, microbes, and rock that can alter structures such as tooth enamel and dentine

Epicontinental – areas of a sea or ocean overlying a continental shelf (a portion of a continent that is submerged under relatively shallow water)

Faunal assemblage – the complete collection of fossil animals found at a specific site at a specific locality

Foraminifera – single-celled marine organisms that are often found as micro-fossils, often used as indicators of temperature and salinity through isotopic studies

Gas Chromatography – a type of chromatography that separates different gasses and other materials from each other

Gastropods – a type of animal, including snails and slugs

Genus – a taxonomic category that is below family but above species

Isotope – two or more forms of the same element that have the same number of protons but differing numbers of neutrons, thus changing the atomic weight of the element without altering the chemical properties

Labial – relating to, or on the side toward, the lips

Late Cretaceous – the second half of the Cretaceous period which lasted from 100.5-66 million years ago. It is often thought of as the last "Age of the Dinosaurs", since the transition out of the Cretaceous also marked the extinction of the dinosaurs.

Lingual – relating to, or on the side toward, the tongue

Paleobiogeographical – paleobiogeography is the study of biological geography in the geologic past

Paleogene – the period that marked the end of the Cretaceous period and the Mesozoic epoch and lasted from 66-23.1 million years ago.

Paleogeographical – paleogeography is the study of physical geography in the geologic past

Plesiosaurs – a clade of extinct marine reptiles from the Mesozoic that appeared 215 million years ago and went extinct with the dinosaurs 66 million years ago

Maastrichtian – the last stage of the Cretaceous that lasted from 72.1-66 million years ago

Magnetostratigraphic – a branch of stratigraphy that makes stratigraphic divisions based on magnetic signals

Marl – an earthy material that is rich in carbonate minerals, clays, and silt that can eventually harden into marlstone

Marly clay – a marlstone/mudstone that contains a high amount of clay as opposed to silt and other carbonate minerals

Molluscan – a class of primarily marine or freshwater invertebrate animals, such as clams or squid, that contains roughly 85,000 different species

Nutrient groove – a small groove that often serves to supply veins or arteries that supply the bone (tooth)

Ostracod – a group of crustaceans, typically small (~1mm) in size, also known as seed shrimp

Root (of tooth) – the part of the tooth below the gums

Secondary carbonates – refers (in this case) to contaminates on the surface of the teeth that accumulated while the teeth were still in the ground, that would influence experiment results if allowed to remain

Striated – marked with long and thin parallel streaks

Third order regression/transgression – a type of cyclical sea level change that is large enough to shift sea level by 50-150 ft. Regression refers to a fall in sea level whereas transgression refers to a rise in sea level.

VPDB – Vienna Pee Dee Belemnite is a global isotopic standard

VSMOW – Vienna Standard Mean Ocean Water is a global isotopic standard for water

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