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Mosasaur Feeding Ecology from the Campanian Bearpaw Formation, Alberta, Canada: A Preliminary Multi-Proxy Approach

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Abstract: Mosasaur taxa recovered from the Bearpaw Formation, Alberta, Canada, generally show exceptional preservation after rapid burial. Since the mosasaur community consisted of two dominant taxa, *Mosasaurus missourensis Prognathodon overtoni*, and three less prevalent taxa *Tylosaurus proriger*, *Mosasaurus conodon*, and *Plioplatecarpus primaevus*, some form of habitat or dietary niche partitioning is to be expected. To test this, several approaches are tried. Two-dimensional microwear analysis is used as an exploratory method to quantify tooth abrasion by food items. The good preservation of skull material reveals complete tooth rows of the upper and lower jaws for *Mosasaurus missouriensis* and *Prognathodon overtoni,* as well as isolated teeth for all taxa. The teeth are also measured for tooth bending strength to test stress regarding usage of teeth per taxon. Energy-dispersive X-ray spectroscopy (EDX) measurements show trace elements which may be a preliminary test for relative trophic level positioning. Some mosasaurs have their stomach contents preserved, providing direct and unambiguous evidence of diet. The results show a relatively clear separation of two-dimensional microwear counts between *Mosasaurus*, *Prognathodon*, and *Plioplatecarpus*, which, to some extent, is reflected in the EDX analyses, too. Tooth bending strength measurements show a clear difference between the latter three mosasaurs but no difference between the lower and upper jaws in *Mosasaurus* or *Prognathodon*. The combination of these three techniques maps a clear dietary niche differentiation of Bearpaw mosasaurs, which lays the groundwork for future analytical or chemical palaeoecological studies.

Keywords: Mosasauridae; Bearpaw Formation; dental microwear; feeding ecology; Cretaceous; geochemical analysis

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1. Introduction

The Campanian Bearpaw Formation of Southern Alberta, Canada, represents one of the northernmost extensions of the Western Interior Seaway [1,2]. In Southern Alberta, it consists of marine shale with nodular concretions [3]. Ammolite mining, a precious stone derived from fossilized ammonites [4,5] at the city of Lethbridge, as well as other excavations, have yielded a considerable amount of vertebrate and invertebrate marine fossils, representing a Campanian marine ecosystem (74.1 Ma) with average bathymetry of

~40 m (MM pers. obs.) Prominently and consistently present are mosasaurs (Reptilia: Squamata) [6]. During the Campanian, mosasaurs already showed a worldwide distribution [7]. Although the southern exposures of the Western Interior Seaway (e.g., Kansas, Alabama, and New Jersey, all present in the USA) show higher mosasaur diversity [8], the northern edge of the Western Interior Seaway in Alberta preserves a mosasaur community consisting of four to five taxa: *Mosasaurus missouriensis*, potentially *Mosasaurus conodon* (Amelia Zietlow, pers. comm.), *Prognathodon overtoni*, *Plioplatecarpus primaevus*, and *Tylosaurus* sp., likely *Tylosaurus proriger* (Amelia Zietlow, pers. comm. and pers. obs). *Mosasaurus missouriensis* and *Prognathodon overtoni* are found to be the most common taxa. Specimens from the ammolite mines around Lethbridge are especially well preserved, although mosasaur material is also found at Manyberries, Alberta [9]. The local mosasaur taxonomy has been extensively researched in previous studies [9,10]. The excellent preservation after the rapid burial of some of these specimens also revealed soft tissue and stomach contents, thus directly elucidating the animal's diet [10]. The latter study already hypothesized ecological niche differentiation between the most common mosasaurs *Prognathodon* and *Mosasaurus*, citing differences in tooth morphology and dental mesowear. Here, we continue with this mosasaur research and present a study on the feeding ecology of all Southern Alberta mosasaurs to map the highest levels of the Bearpaw foodweb.

Previous research already demonstrated the applicability of two-dimensional dental microwear and three-dimensional surface texture microwear to elucidate mosasaur feeding behavior [11,12]. Microwear is defined as microscopic damage to teeth, usually on wear facets, by tooth–tooth and tooth–food abrasion [13]. However, the preliminary results of these previous mosasaur microwear studies clearly show the need for additional lines of evidence beyond microwear to be explored, as microwear only indicates the use of the animal's teeth in the final weeks to months before its death. For isolated teeth, only the size, shape, and type of animal can be ascertained, but the well-preserved Bearpaw Fm specimens can provide information on differences in tooth morphology on the toothrow, bite force, skull kinetics, and size of the animal to reveal the trophic level. Finally, geochemical analysis can be employed on the well-preserved dental remains. Strontium concentration in relation to Calcium and Barium ratios in teeth has been successfully shown to indicate relative trophic position, following from studies conducted on extinct mammals [14,15]. In recent years, Strontium, Calcium, and Barium have been proven to function as dietary niche proxies in extinct marine as well as terrestrial organisms [16].

Here, a number of Bearpaw Fm. mosasaur remains, both isolated teeth and crania, are studied in order to determine a first trophic-level framework. Two-dimensional microwear, tooth bending strength, and Sr/Ba and Ca/Ba ratios via EDX analysis are all measured in order to provide a multi-proxy approach to determine local Bearpaw Fm feeding ecology.

2. Materials and Methods

2.1. Microwear

Isolated mosasaur teeth from the collections of the Royal Tyrrell Museum of Palaeontology (RTMP) collections were used as is; however, teeth from tooth-bearing bones were cast from direct molds using Moldstar 20T parts A and B mixed equally. See Table 1 for provenance and number of teeth used.

Table 1. Materials and number of teeth used for each analysis, including localities.

Taxon	***Mosasaurus***	***Prognathodon***	***Tylosaurus***	***Plioplatecarpus***	**Elasmosaur**	**Sawfish**	**Shark**
Type	Skull and teeth	Skull and teeth	Teeth	Teeth	Teeth	Teeth	Teeth
Locality	Lethbridge	Lethbridge	Manyberries	Lethbridge	DPP	Iddlesleigh	Iddlesleigh
Formation	Bearpaw	Bearpaw	Bearpaw	Bearpaw	Bearpaw	Bearpaw	Bearpaw
Microwear	10	5	2	3	-	-	-
EDX	16	16	9	7	5	4	15
Bending Strength	30	28	-	5	-	-	-

Two-dimensional microwear was measured using a Hitachi tabletop TM-1000 Scanning Electron Microscope (Hitachi High-Tech Canada Inc., Toronto, ON, Canada). Specimens were mounted on putty, and the apex was focused on, as this is usually where the bulk of the microwear is visible on the wear facet of the tooth [11]. Magnifications ranged between 200× to 400×. Four to six images of each tooth were taken, and all microwear visible in each image was counted (see Supplementary Information for microwear counts).

Microwear was counted by hand by one single observer (FH) to avoid inter-observer bias [11,17]. Microwear was categorized into gouges (large scratches), thin scratches, and pits, as in [11]. See Figure 1 for microwear types. After confirming that assumptions for parametric tests were met, data were analyzed using *t*-tests for comparisons between two groups using or ANOVAs for comparisons among more than two groups. We tested for interspecific differences in microwear on teeth from all jaw locations combined, for intraspecific differences between teeth from different jaw locations, and for interspecific differences between teeth from the same jaw location. Significant ANOVAs were performed, followed by a post hoc Tukey HSD test. All statistics were run in R version 4.3.1 [18] and are included in our Supplementary File S1. Due to the relative scarcity of isolated teeth of all taxa, both worn as well as new teeth were used for each analysis. Only teeth from skulls with an 'open mouth' where the dentition was readily available for casting were used, limiting the number of complete toothrows useful for this study. A study on differences between casts of teeth (using different casting and molding agents) and actual teeth in terms of microwear quality is in preparation by FH and Dr. Lorna O'Brien, former chief technician at the RTMP, and is therefore intended as a follow-up to this current study.

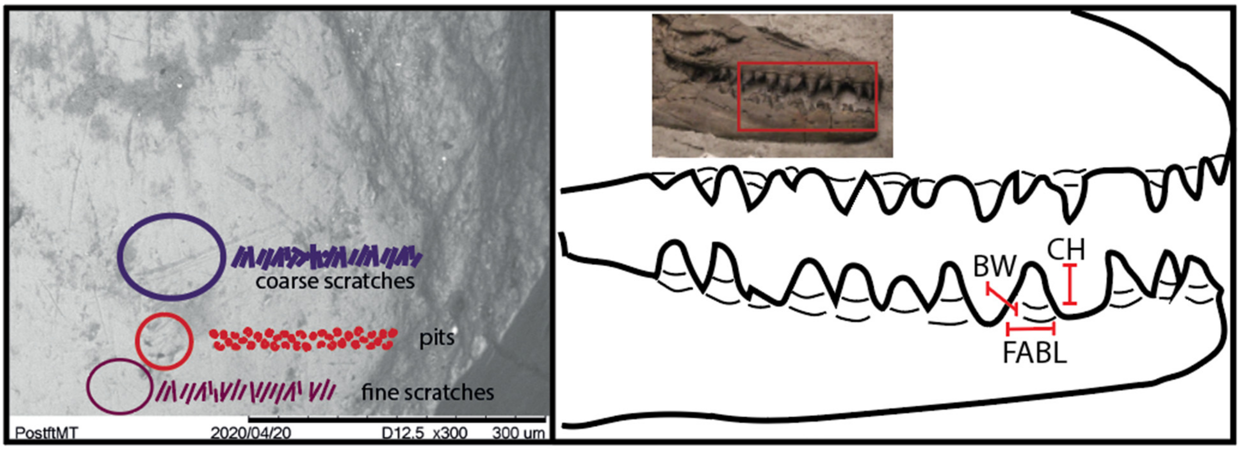

Figure 1. Selection of types of microwear and schematic of mosasaur tooth bending strength measurements.

2.2. EDX

Energy-dispersive X-ray spectroscopy (EDX) was used for elemental analysis. The Hitachi tabletop TM-1000 used for SEM at the Royal Tyrrell Museum of Palaeontology has a simplified EDX system which was used in this exploratory study. Measurements are displayed as discrete counts, which have been converted into ratios. Diagenetic noise was ruled out by checking for sulfur (S) spikes [19]. If no peak was found, the tooth could be measured for Sr, Ba, and Ca.

All trace elements are stored in bioapatite via food and water intake, but Ca is preferentially stored over Sr and Ba. This means that in every step up the food chain, Sr and Ba decrease until these are finally the lowest in terrestrial hypercarnivores. In a marine setting, Sr, Ba, and Ca are proven to distinguish different trophic levels as well. Therefore, all mosasaur taxa, the indeterminate elasmosaurs, and sawfish and shark teeth have been measured for these trace elements. Sr/Ca and Ba/Ca ratios were statistically tested using Anova and inverse log ratios displayed in a principal component analysis.

2.3. Tooth Bending Strength

Tooth bending strength, or the amount of stress a tooth can structurally withstandwhen in use, was calculated using the formula used in [20] for tooth measurements in theropods. The tooth crown height (CH) and foreaft (mesiodistal) basal length (FABL) and basal (anteroposterior) width (BW) at the base were measured in mm. The tooth bending strength formula is expressed as follows (see Figure 1):

Bending strength of anteroposterior side:

$$(\mathrm{AP}) = (((\pi \times 0.5 \times \mathrm{FABL}) \times ((0.5 \times \mathrm{BW})^2))/4)/(\mathrm{CH} \times (0.5 \times \mathrm{FABL})))$$

Bending strength of mediolateral side:

$$(\mathrm{ML}) = (((\pi \times (0.5 \times \mathrm{FABL}) \times ((0.5 \times \mathrm{BW})^3))/4)/(\mathrm{CH} \times (0.5 \times \mathrm{BW})))$$

The Log_{10} value of the crown height (Log_{10} CH) is plotted against the Log_{10} value of the anteroposterior bending strength and mediolateral bending strength in scatter plots. See [20] for the rationale behind the calculation.

3. Results

3.1. Microwear

The two-dimensional microwear counts are shown in the overview graph in Figure 2. Though the data quality differed between teeth and molds, some intraspecific patterns could be discerned. All mosasaurs have significant high numbers of pits dominated by *Prognathodon* and *Plioplatecarpus*. The latter taxon also has the highest number of fine scratches on average, followed by *Mosasaurus*. These two are the only taxa with higher numbers of fine scratches than gouges and pits in this dataset. *Prognathodon* and Tylosaurus, in contrast, display a higher number of pits than gouges and fine scratches in their microwear. *Tylosaurus* has more fine scratches than gouges, whereas *Prognathodon* has the lowest number of fine scratches compared to its gouges and pits. Intraspecific differences were found to be statistically significant by an ANOVA for several taxa and for all microwear types (fine scratches, gouges, and pits). For all microwear types, significant differences between *Plioplatecarpus* and *Mosasaurus* were found, as well as between *Prognathodon* and *Plioplatecarpus* (see Statistics Section in Supplementary File S1).

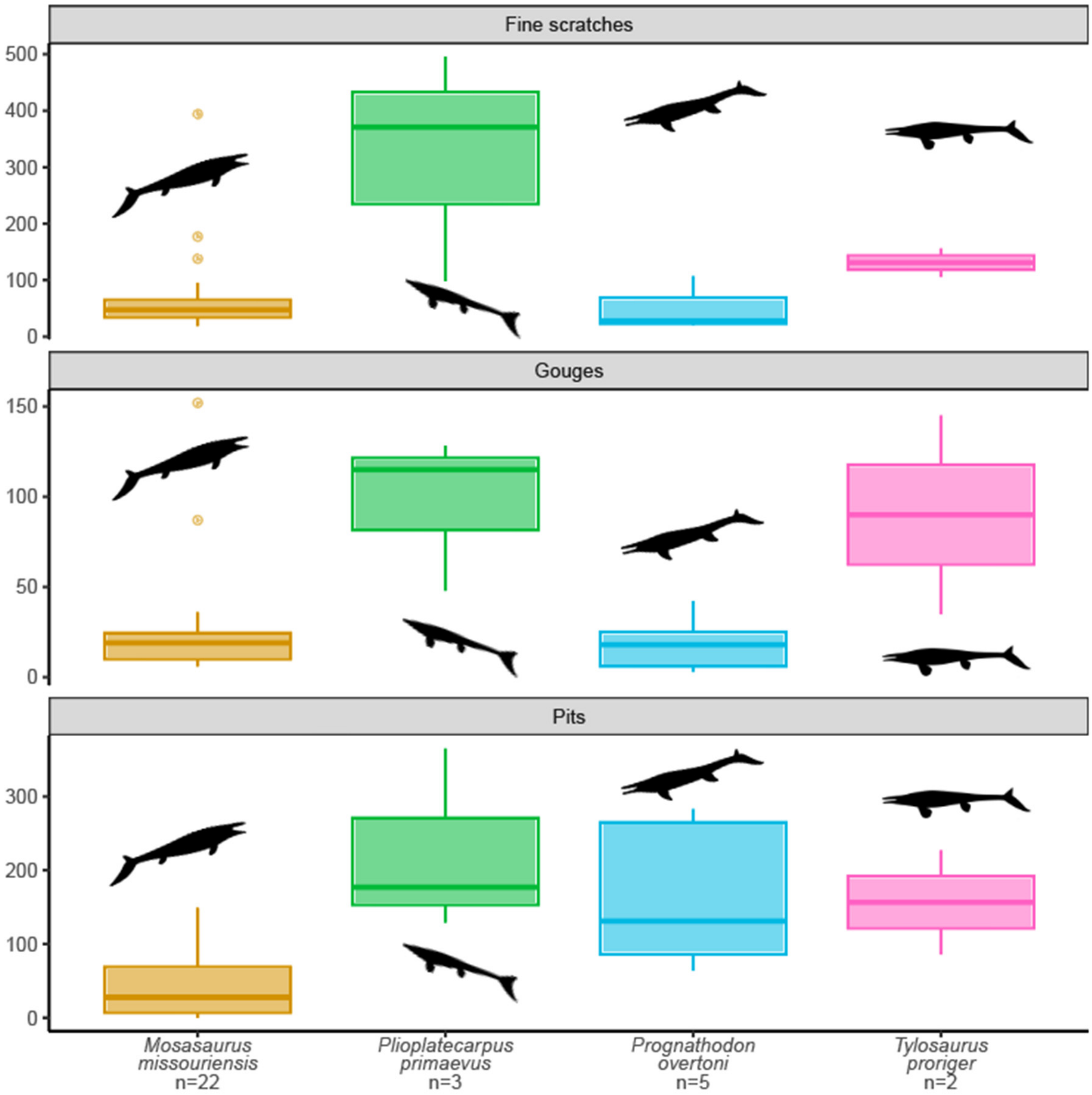

Figure 2. Microwear between all mosasaur taxa. Mosasaur silhouettes from Phylopic; see Data Availability Statement for all creators and CC licenses.

When looking at differences between premaxillary, maxillary, and dentary microwear counts (only between *Mosasaurus* and *Prognathodon* of which complete skulls and measurable dentition were available), some patterns in the counts are visible (see Figure 3). *Mosasaurus* has high counts of fine scratches and pits in its dentary, compared to lower counts of scratches in both the maxilla and premaxilla. The premaxilla has higher counts of pits than the maxilla. For *Prognathodon*, the maxilla displays high counts of pits and fine scratches, with much less microwear displayed in the dentary and premaxilla, hinting at the most tooth–tooth or tooth–food abrasion occuring in the lower jaws.

Between the larger and smaller *Mosasaurus* specimens, there are some differences as well. The large *Mosasaurus missouriensis* TMP 2012.010.0001 shows high counts of fine scratches both in the premaxilla and the maxilla, as well as a high number of pits in the premaxilla. The smaller *Mosasaurus missouriensis* TMP 2008.036.0001 shows the highest numbers of fine scratches and pits in the dentary, as well as a high number of fine scratches in the maxilla. This shows that there is a similar microwear pattern for fine scratches in the maxillae of both larger and smaller *Mosasaurus missouriensis* and, therefore, tooth–tooth or tooth–food abrasion, as well as high individual or ontogenetic variation. However, when tested with an ANOVA for statistically significant microwear differences between jaw locations between *Mosasaurus* and *Prognathodon*, no significance was found (see Statistics Section in Supplementary File S1). Similarly, interspecific microwear differences between jaw locations were not statistically significant for *Prognathodon* nor for *Mosasaurus*.

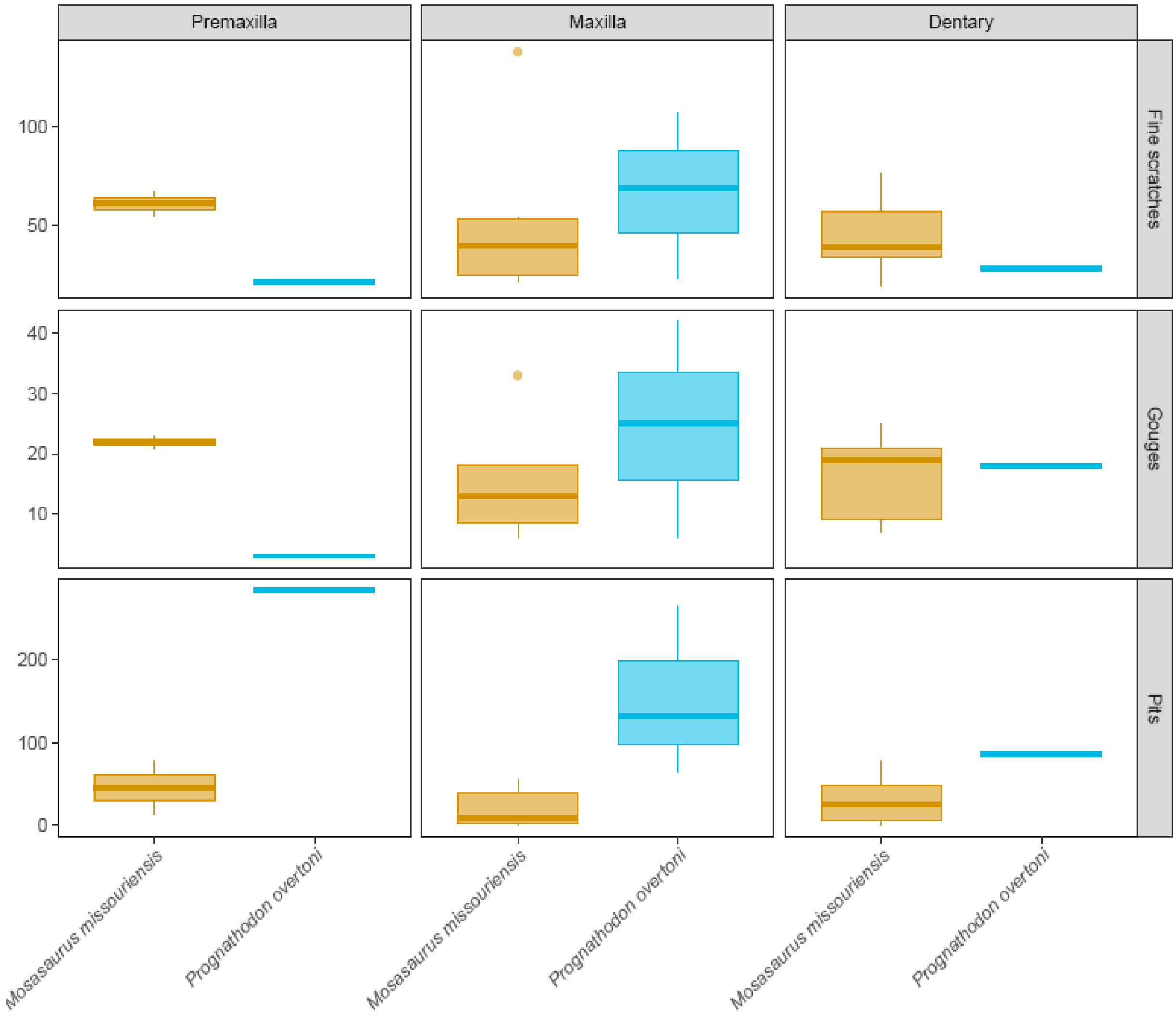

Figure 3. Microwear counts between upper and lower jaws between *Mosasaurus* and *Prognathodon*.

3.2. EDX Analysis

The lowest rates of Sr/Ca are seen in *Prognathodon* (and sawfish), followed closely by *Mosasaurus*; see Figure 4. Whilst the range for *Mosasaurus missouriensis* in terms of Sr/Ca is quite high, the rates of Sr/Ca are the highest in Tylosaurus and the indeterminate elasmosaur teeth. Finally, the hybodont shark teeth show a high variation in their Sr/Ca ratio. *Plioplatecarpus* has the most intermediate Sr/Ca ratio.

Prognathodon and *Mosasaurus missouriensis* have a similarly large range for their Ba/Ca ratio; see Figure 5. However, *Prognathodon* and *Plioplatecarpus* have the lowest Ba/Ca rates, with *Mosasaurus missouriensis*, possibly *Mosasaurus conodon*, and hybodont sharks following with an intermediate level of Ba/Ca. *Tylosaurus*, the indeterminate elasmosaurs, and sawfish have the highest average Ba/Ca ratios, with the elasmosaurs displaying the narrowest range. While both Sr/Ca and Ba/Ca rates meet the assumptions for ANOVA (normality, homoscedasticity, and independence), only the Sr/Ca ratio showed significant differences between taxa, whereas the Ba/Ca ratio did not. However, the Ba/Ca ratio showed a p value on the lower side, indicating that with more data, the p value might be statistically significant.

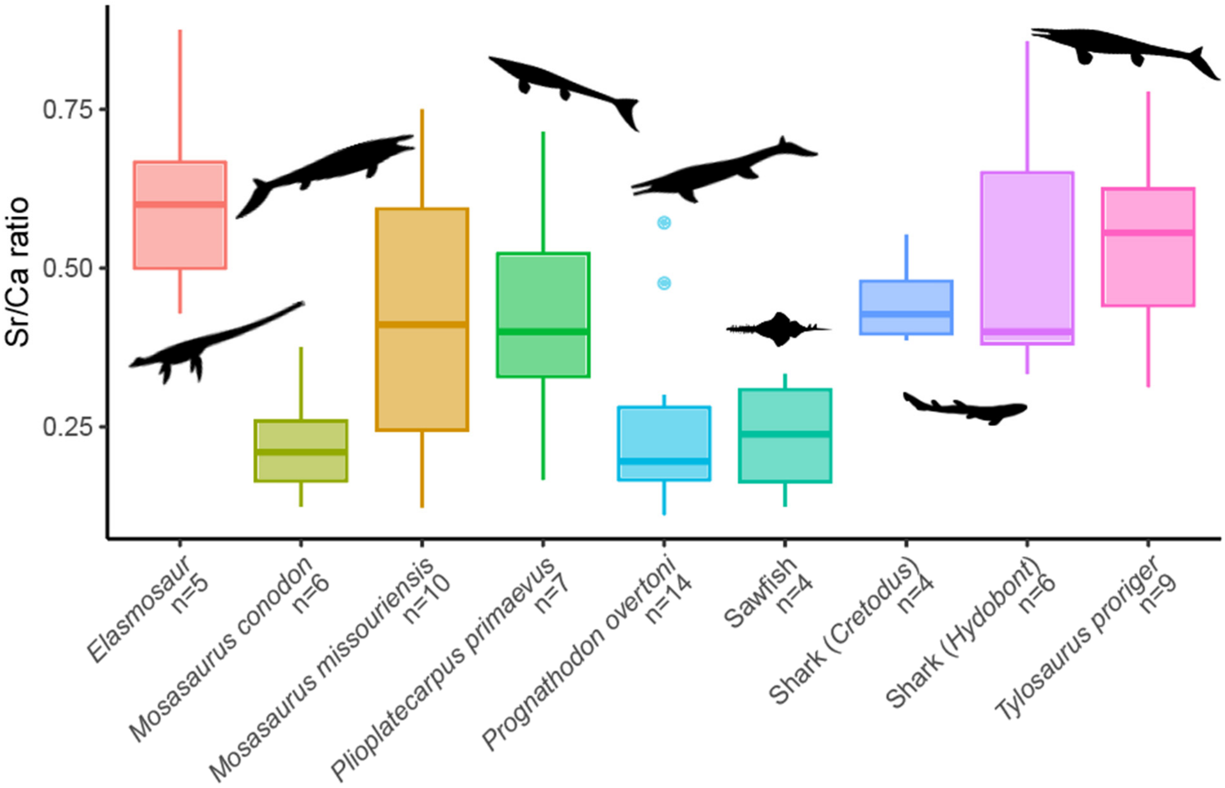

Figure 4. Sr/Ca ratios between Bearpaw sea vertebrates.

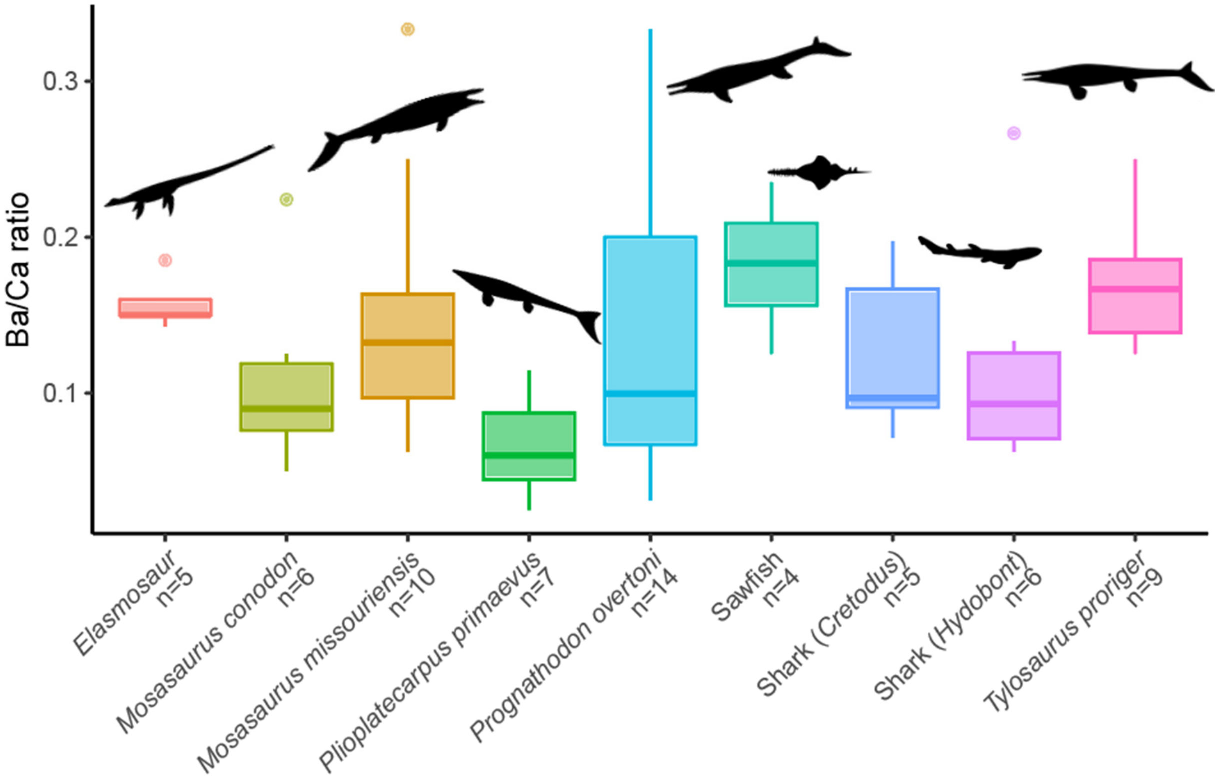

Figure 5. Ba/Ca ratios for all Bearpaw vertebrates.

3.3. Tooth Bending Strength

Following [20], a Log_{10} value of the bending strength of the anteroposterior side (AP, x-axis) is plotted against the Log_{10} value of the bending strength of the mediolateral side (ML, y-axis). The resulting scatterplot (Figure 6) roughly follows the trend seen in [20] for the tooth bending strength of several theropods, extant and extinct felids, and extant and extinct canids. Indeterminate mosasaurs were also plotted. Therefore, the general trend of the scatterplot is perhaps not surprising (Figure 6). However, there are differences between the mosasaurs measured here: *Mosasaurus missouriensis* scatters with lower bending strength ranges, *Prognathodon overtoni* scores the higher/highest bending strength, and *Plioplatecarpus* takes an intermediate position, though it is still higher than *Mosasaurus* on average. There is not much of a difference between the larger and smaller *Mosasaurus* specimens in terms of the overall bending strength; however, there is a difference between the upper and lower jaws in larger specimens overall. The tooth bending strength meets the assumptions for ANOVA.

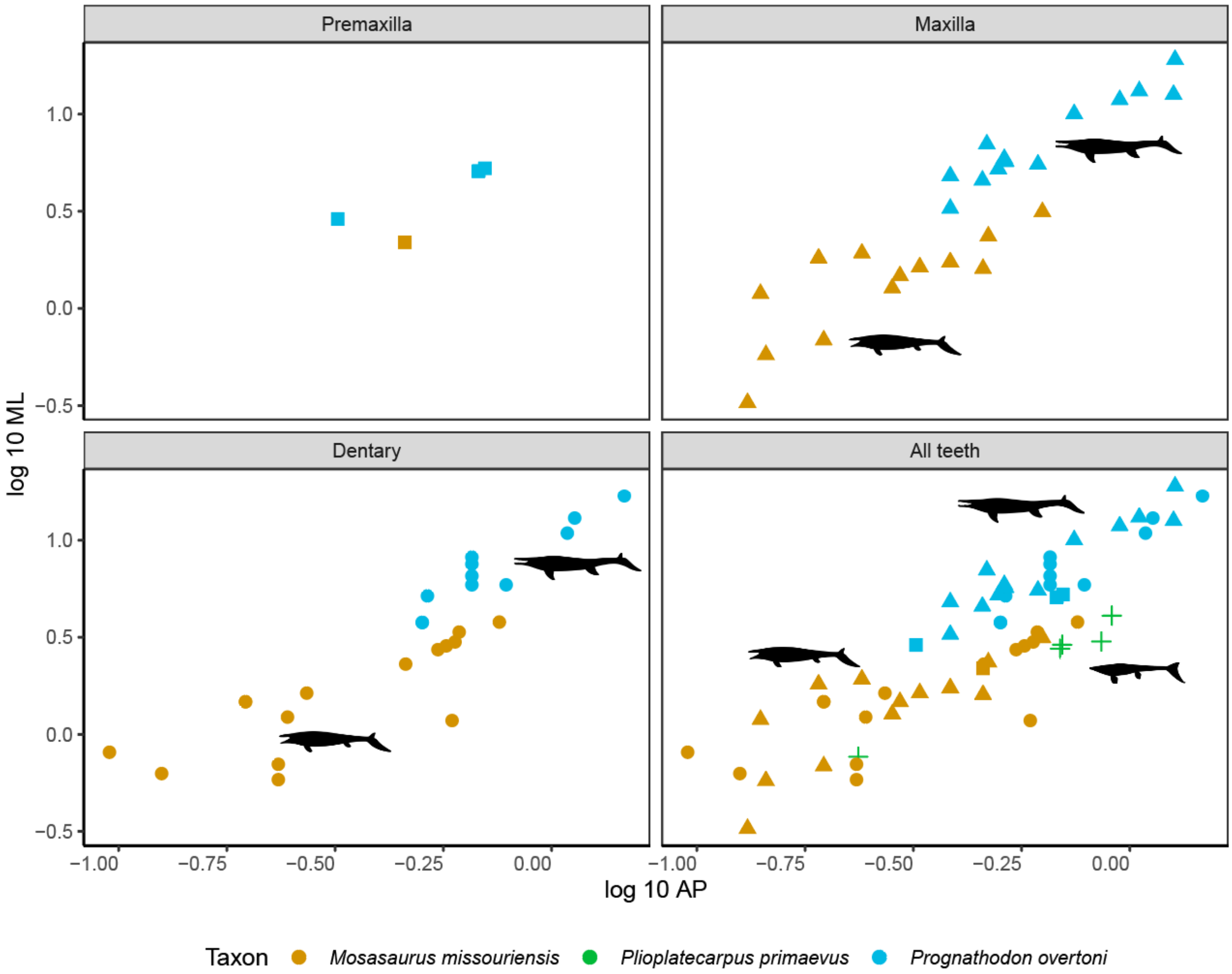

Figure 6. Tooth bending strength for *Mosasaurus* (orange), *Prognathodon* (blue), and *Plioplatecarpus* (green).

4. Discussion

4.1. EDX-Based Sr/Ca and Ba/Ca Differences

A PCA of the EDX measurements is shown in Figure 7.

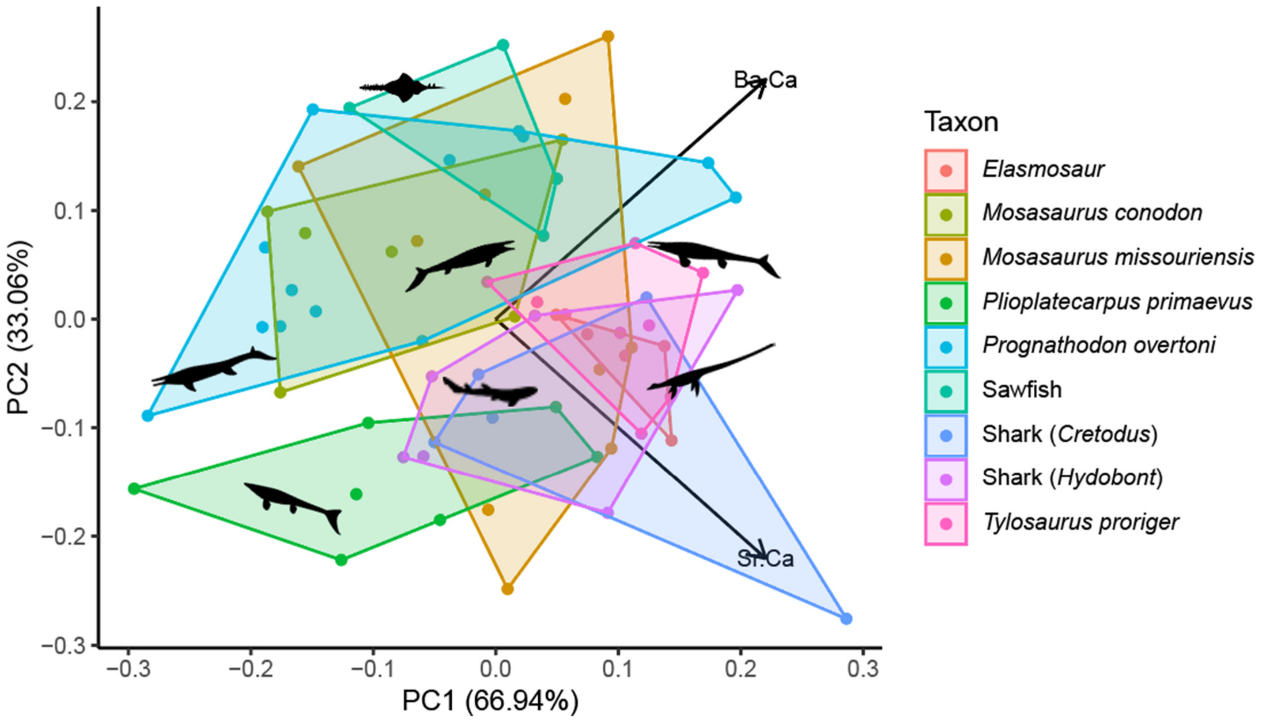

Figure 7. PCA of all Bearpaw vertebrates' Sr/Ca and Ba/Ca ratios.

High Ba values are observed in marine fauna feeding near the base of the marine foodweb, which is then reflected in high Ba levels in higher trophic levels. The highest Ba/Ca ratio is found in plants and invertebrates that bio-accumulate it in high doses; higher trophic level feeders that directly feed from this source will have higher rates of Ba/Ca. This is observed in conodonts (but the Ba-rich food source in question remains elusive) [16]. In fish, Ba is seen as indicative of diet, as Sr remains constant in fish [21]. That said, Ba/Ca ratios in fish are highly variable, whilst the Sr/Ca ratio is conservative, so if a mosasaur is mostly piscivorous, their dentition should indicate variable Ba/Ca ratios as well. We indeed see higher Ba/Ca ratios in presumably piscivorous elasmosaurs, but not the highest levels of this sample of marine vertebrates. *Tylosaurus* seems to closely follow the ranges of Sr/Ca and Ba/Ca of elasmosaurs, only with slightly lower values of Sr (likely confirming a higher trophic level) and slightly wider-ranging Ba levels (likely confirming a wider array of diet than elasmosaurs, the latter which seem to be specialized into feeding/predation on one category). Tylosaurs from the Campanian of Alabama are thought to have occupied shallower, near-shore waters [22], and in the Bearpaw sea, they might have occupied a similar niche as elasmosaurs. However, as *Tylosaurus saskatchewanensis* from the Bearpaw sea of Saskatchewan (more into the northern middle section of the Western Interior Seaway) and *Tylosaurus proriger* from the Niobrara Fm of Kansas (the southern section of the Western Interior Seaway) have small mosasaurs and elasmosaurs in their stomach content, respectively, it is also not impossible for the EDX analysis to reveal a direct predator–prey relationship [23]. Elasmosaurs show a narrow range in Sr, with the highest Sr values of this marine vertebrate assemblage, and a very narrow range in Ba values. This places them at a lower trophic level than the mosasaurs, with the aforementioned narrow Ba range indicating a specific food source, likely fish and/or squid. Elasmosaurs from elsewhere are known to have benthic diets as well as more sarcophagous diets [24,25]. However, the Bearpaw elasmosaurs seem to have been more restrictive and specialized in their dietary niche, which is also observed in Western Interior Seaway elasmosaurs from the Pierre Shale as well as Upper Cretaceous plesiosaurs from South Australia [26,27].

Hybodont sharks from Cretaceous of Thailand [28] have a diverse diet, interpreted as opportunist feeding, with potentially some shell-crushing durophagy of hybodontiform sharks with low cusped teeth similar to some Bearpaw sharks. In other hybodont sharks, direct evidence of predation on ammonites is shown [29,30]. Both predation on shellfish and ammonites, as filterfeeding organisms of plankton, would account for high rates of Ba/Ca in the upper ranges of *Prognathodon*, *Mosasaurus*, and hybodont sharks. Furthermore, similarly to mosasaurs, hybodontid and cretodid sharks have 'clutching or piercing' dentitions, thought to make them active predators of large prey (such as fish, other sharks, and other marine vertebrates) [31]. Therefore, some overlap in Sr/Ca and Ba/Ca ratios, especially with the more piscivorous mosasaurs, is explained here.

4.2. Inferred Diet and Niche Partitioning

See Table 2 for an overview of the inferred diets of the mosasaurs in this study. The authors of [9] already hypothesized about ecological niche differentiation for the Alberta Bearpaw *Mosasaurus* and *Prognathodon* based on differences in tooth morphology and differences observed in dental mesowear. Together with the two other less common mosasaurs from the area, this study confirms the above hypothesis. The authors of [10] placed *Mosasaurus missouriensis* firmly in the 'cut' guild sensu [32] based on their recurved teeth, no exposed horizontal wear facets, and—perhaps most compellingly—mostly fish-based contents, as well as squid, in the gut. This is different in the Bearpaw *Prognathodon overtoni* TMP 2007.034.0001, which was found not only with turtle remains in its stomach, but also with large horizontal wear facets on its dentition. The authors of [33] demonstrated that the dental spalling or large, oval, longitudinal wear facets on the metriorhynchid *Dakosaurus* points to macrophagy or eating large prey by shearing them in pieces before consumption. The authors of [33] observed this type of spalling in indeterminate mosasaurs from the American Museum of Natural History. Both *Tylosaurus* and *Plioplatecarpus* were also placed in this macrophagous group of mosasaurs by the authors of [10]. Although this study did not find significant spalling as mesowear and used microwear instead, the two-dimensional microwear largely confirms the *Mosasaurus*-*Prognathodon* niche differentiation hypothesis. Empirically, both intraspecific and interspecific differences between the upper and lower toothrows in terms of microwear were also found. The statistical analysis did not find these differences to be significant, though. It is possible that more data would be needed to explore this further, as the authors of [34] found intraspecific microwear differences along the toothrows of crocodylians and varanids, both of whom could be argued to be extant equivalents of extinct marine reptiles. Moreover, the highly kinetic skulls of mosasaurs would infer a similar outcome, as with skull kinesis, different parts of the dentition would be expected to generate different microwear.

Coupling back to the EDX, although there is some overlap between *Prognathodon* and *Mosasaurus*, there is a stark difference between both types provided by the Sr/Ca and Ba/Ca ratios. *Mosasaurus* seems to be an 'all-rounder', overlapping with almost all other groups. Indeed, a Dental Microwear Texture Analysis (DMTA) of type-Maastrichtian *Mosasaurus hoffmanni* displays a generalist diet for this large taxon [12]. Though not as large as *M. hoffmanni*, *M. missouriensis* was definitely on the larger side of the Bearpaw mosasaur spectrum (reaching up to 8 m in length). Its two-dimensional microwear shows a general high distribution of fine scratches, as well as pits, indeed confirming usage of its teeth for both softer and harder food items. Finally, the tooth bending strength between the two taxa clearly separates *Mosasaurus* from *Prognathodon*, with the latter showing higher tooth bending strength and therefore teeth that could withstand higher stresses, which concurs with the microwear and EDX.

Table 2. Sr/Ca and Ba/Ca ranges of all mosasaurs from this study, with dominant microwear and inferred prey.

Taxon	*Mosasaurus*	*Prognathodon*	*Tylosaurus*	*Plioplatecarpus*
Sr/Ca range	0.2–0.73	0.11–0.57	0.31–0.77	0.17–0.71
Ba/Ca range	0.06–0.33	0.03–0.33	0.13–0.21	0.03–0.11
Dominant microwear	Fine scratches	Pits	Gouges	Fine scratches
Inferred prey	Large range of vertebrate prey items Large range of invertebrate prey items	Harder vertebrate prey items (turtles and large fish) Harder invertebrate prey items (shellfish and ammonites)	Fish and larger vertebrates	Softer prey items (squid and fish) Harder prey items (large fish and ammonites)

Prognathodon is represented at one end of the spectrum (Figure 7), closer to sawfish than sharks, and is clearly separated from *Plioplatecarpus*. Dental microwear texture analysis of type-Maastrichtian mosasaurs revealed that prognathodons surprisingly not only foraged for harder prey items, but softer invertebrates as well, likely displaying foraging behavior on benthic invertebrates [12]. Modern sawfish show a propensity to bottom-feeding durophagy, which is another link to the microwear in this current study, the DMTA [12], and the *Prognathodon* stomach content of TMP 2007.034.0001 and its mesowear. Finally, a partial lobster was recovered as putative stomach content of Bearpaw *Prognathodon* TMP 2007.034.0001, but this was never confirmed as the position of the lobster was not as undeniable as stomach content as the turtle and fish were [9]. If it was stomach content, this would again confirm both *Prognathodon*'s position in the PCA diagram as overlapping with bottom-feeding sawfish, as well as being a consumer of both harder prey and invertebrates. The tooth bending strength shows higher levels for *Prognathodon* compared to the other measured mosasaurs (Figure 6). *Prognathodon* teeth are higher in FABL and BW than *Mosasaurus* and *Plioplatecarpus*. This emphasizes the fact that *Prognathodon*'s teeth were suitable to process much harder prey. Together with a high overall count of pits, especially compared to fine scratches and gouges, this shows a handling of prey items through more oral food processing than *Mosasaurus*.

Plioplatecarpus also occupies a distinct position in the Sr/Ca Ba/Ca spectrum with little overlap with sharks and elasmosaurs. Traditionally, plioplatecarpids, by virtue of their presumed piscivorous tooth morphology, are placed in the piscivorous 'cut' end of the guild sensu [32]. However, type-Maastrichtian *Plioplatecarpus marshi* displays a surprising tendency for harder invertebrate consumption [12]. Two-dimensional microwear counts from the Bearpaw *Plioplatecarpus primaevus* equally show microwear pointing to harder prey items besides fine scratches pointing to softer prey. The authors of [22] already questioned plioplatecarpids exclusively feeding on softer prey items such as belemnites, and with its EDX results showing an offset from the other Bearpaw mosasaurs, away from sharks and piscivorous elasmosaurs, this smaller type of mosasaur presents the most enigmatic feeding ecology. A clue, perhaps, comes from another Bearpaw *Plioplatecarpus*: TMP 2022.043.0001 [35]. This particular specimen has very large orbits, which, according to [35] indicates visual foraging at the deepest reaches of the photic zone. The large parietal is similarly proposed by the authors of [35] to have been of use for fast movement and chasing agile prey, as well as dodging larger predators (such as *Prognathodon* and *Mosasaurus*). This hypothesis would suit an existence in a different feeding niche from the other Bearpaw mosasaurs, as indicated by the EDX results, and to a lesser extent, the microwear of this study. Another clue could come from a unique basicranial circulation pattern discovered by the authors of [36]. Here, the type of circulation to the cranium that plioplatecarpines display is likened to those of arboreal snakes and helps with being upside down whilst hunting for prey. Perhaps *Plioplatecarpus* dove for prey out of reach of other mosasaurs. This does not, however, answer the question of why *Plioplatecarpus* demonstrates such 'rough' microwear. Even with this limited sample, *Plioplatecarpus* shows an intermediate to high tooth bending strength (Figure 6). Harder prey such as large fish with hard ganoid scales or ammonites, could have been on the *Plioplatecarpus* menu, but there is no unequivocal evidence of this [37–39]. Moreover, an isotopic analysis of *Plioplatecarpus* dentition from the type Maastrichtian does not support a deep diving lifestyle [40].

An additional future line of evidence to answer some of these standing questions would involve using DMTA on these Bearpaw mosasaurs as well as an isotope analysis of dental enamel. Both are currently in preparation for future studies. What seems to become more clear, however, is that Cretaceous marine ecosystems were high in productivity, supporting rich fauna, and were able to support multiple predators, as seen in [12,40,41].

5. Conclusions

A combination of two-dimensional microwear analysis, EDX analysis using Sr/Ca and Ba/Ca ratios, and calculated tooth bending strengths for the Alberta Bearpaw mosasaurs *Mosasaurus missouriensis*, *Prognathodon overtoni*, *Plioplatecarpus primaevus*, *Tylosaurus proriger*, and possibly *Mosasaurus conodon*, shows a distinct niche differentiation pattern. There is a clear separation between *Mosasaurus* and *Prognathodon*, with the former showing generalist dietary preferences and the latter showing a tendency to feed on harder prey items and a possible tendency for macrophagy. *Plioplatecarpus* remains an enigmatic smaller mosasaur in terms of dietary preferences, although it also shows a distinct dietary area according to EDX and the tooth bending strength analysis, with a mainly piscivorous note from its microwear, and additional foraging on harder prey that is still unidentified. *Tylosaurus* seems to follow a similar diet to the Bearpaw elasmosaurs or even predated on them. Future DMTA and isotopic studies will further clarify the dietary niches of the Bearpaw mosasaurs.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17030205/s1, Supplementary File S1, and at Figshare. https://doi.org/10.6084/m9.figshare.28009238.v1.

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