Importance of being organized: the effects of changing tooth arrangement on durophagous predation

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Blinks NSF REU Beacon Internship

Summer 2014

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Introduction

The literature on paleontology and functional morphology both include many studies on the feeding mechanics of organisms. In extinct organisms, physiological data must be inferred from bone structure, or muscles scars, even in the most exceptionally preserved specimens (Benton, 2010). However even reconstruction and analysis of muscle scars in fossils rely heavily on assumptions (Rieppel, 2002).

Given the resilient nature of enamel, teeth are often the most commonly found remains of extinct organisms, and in some cases they are only known remains (Adnet et al., 2009; Pol, 2012). Enamel is highly calcified and so, unlike other softer portions of an organism's anatomy, is readily preserved (Lucas et al., 2008). Fortunately, there is a close relationship between tooth form and function, which allows researchers to infer the ecology of the extinct organisms. Slender, pointed teeth, are ideal for puncturing, and bladed teeth are best suited for tearing and cutting prey, whereas more rounded and blunt teeth are thought to function better in crushing prey (Massare, 1987), a feeding strategy termed durophagy. Durophagous predators typically have robust jaw bones in addition to their distinctive and molariform teeth on the premaxilla, maxilla, dentary or the pharyngeal (Norton, 1988, Wilga and Motta, 2000). It is thought that this molariform tooth morphology, as well as tooth arrangement, may serve to increase tooth surface area, thus reducing the stress applied to teeth (Ramsay and Wilga, 2007) when crushing.

Studies on the functional ability and structure of durophagous teeth have focused on a range of both extinct and extant organisms, including borophagines canids, early hominoids, and elasmobranchs (Lee et al., 2011; Lucas et al., 2008; Tseng ZJ and Wang X, 2010). For these groups, tooth form dictates diet and, by extension, habitat selection and population ecology. From there it is possible to study large-scale evolutionary patterns, co-evolutions, and trophic interactions (Lauten 2013).

To understand the relationship between form and function in the teeth of extinct organisms, physical models can be constructed to test the limitations of these structures either through fossil re-creation or inference from testing on extant relatives. Single cusped mammalian teeth (Lee et al., 2011), flat surfaces of the labially compressed bamboo shark teeth (Shimada et al., 2009), and teeth with varying concavities representative of eels (Crofts and Summers, 2014), have all been created and tested on an individual basis. These studies found that a single concave tooth required more force to fracture prey than a convex tooth, and Lee et al. (2011) found that a domed tooth surface works well to strengthen the overall tooth structure. However, Ramseys and Wilga (2007) posit that many teeth contacting prey simultaneously could be vital for durophagy, since multiple contact points will serve to spread bite force over a larger surface area. Most modelling studies, to date, focus on the functional morphology of a single tooth, not the effects of multiple teeth on a prey item.

While there are a number of durophagous lineages, all specialized on the same hard-prey consuming life-style, the arrangement of teeth varies between species. For example, ancient durophagous elasmobranchs such as *Ptychodus occidentalis* exhibit cusped teeth of the dentary premaxilla and maxilla in rows similar to modern carnivorous sharks (Shimada et al., 2009). In contrast, *Megapiranah paranensis*, an extinct Serrasalmid, has a staggered, zig-zag dentition on the oral jaws (Grubich et al., 2012). Some durophagous teleost fishes have completely skipped the oral jaws and use flattened pharyngeal tooth plates for crushing (Hernandez and Motta, 1997). Similarly the extinct marine Sauropterygians, the Placodonts, also evolved tooth plates, but on completely different bones. Those goals of this study are: (i) to determine how tooth arrangement affects the ability to crush a simplified prey item, (ii) to test if and how the effects of tooth arrangement vary with tooth occlusal morphology, and (iii) to determine if crushing idealized prey items is a feasible proxy for natural prey items.

Materials and Methods

Tooth Plate Morphology

To test how well different tooth arrangements were able to crush prey items and to determine if there is an interaction between tooth shape and tooth arrangement, we modelled plate patterns and concavities after arrangements seen occurring naturally (Fig. 1). The linear arrangement (Fig 1A) mirrors the linear arrangement or most oral teeth, the zig zag pattern (Fig. 1B) represents the proposed transitional dentition of *Megapiranah paranensis*, the quad (Fig 1C) is representative of the packed together teeth seen on most tooth plates, and the modified quad (Fig 1D) is similar to the palatal dentition seen in placodonts. In these models, the size of each individual tooth (measured by radius around the body of the tooth) is 5mm, except in the modified quad arrangement. In more derived placodonts, the caudal-most palatal teeth are enlarged relative to the other palatal teeth, which we mimicked by increasing the diameter of the two posterior teeth so that they have a diameter of 7 mm greater the anterior teeth. In addition, we created multiple models of each of the four tooth plates, each with a tooth morphology that varied from concave to convex (Figure 2).

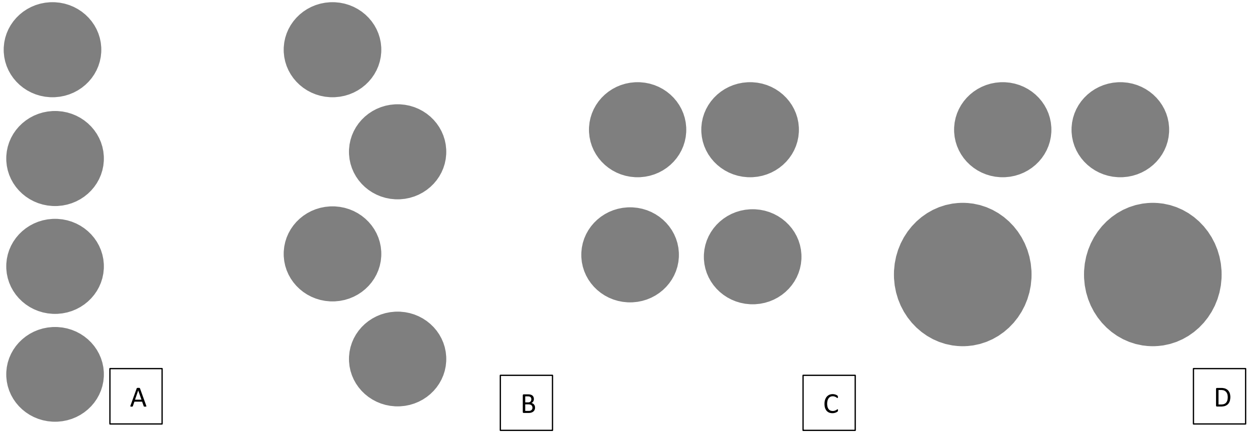

Fig. 1. (A) Linear Arrangement (B) staggered Arragnement (C) Quad Arrangement (D) Modified Quad Arrangmemt

Fig. 2. From left to right, each radius of curvature from concave to convex is represented. These morphologies were modeled for final tooth plates.

Tooth plates were designed in 123D Design (Autodesk Inc, 2014) and following Crofts & Summers (2014), we used Sprutcam7.0 to generate milling tool paths. These tool paths were upload to a Tormach CNC 4-axis mill, and teeth were milled from aluminum stock (6061 T6) using a 0.254 ballnose carbide drill and a 0.082 round carbide end mill. Final tooth plates varied between 2.5 – 5 cm in length, 2.2 – 2.6 cm in width, and 2.5 – 2.8 in height depending on tooth arrangement and occlusal convexity (Fig. 3).

Fig 3. Final tooth plates exhibiting the flat tooth morphology.

Prey Morphology

To measure the force required by each model to break a shelled prey item, we needed a standardized prey item to rule out the variability and wear of natural history found in live organisms. Therefore, we used ceramic filter tubes (Fluval ceramic filter media, Quebec) as idealized prey items; similar artificial prey items have previously been used to measure the bite force of *Mylopharyngodon piceus* (Gidmark et al., 2013). Since Fluval tubes are made from the same material and are of approximately the same shape, we were able to reduce the variance in load to failure due to differences in prey material properties due to life history. However, the Fluval tubes do not have completely identical morphologies, so we measured the volume of each tube in order to standardize the load to failure across all test. For each tooth plate/tooth morphology combination we tested 40 Fluval tubes, for a total of 800 tests in all.

Test and Analysis

To test each arrangement, tooth plate models were attached to the moving crosshead of a materials testing system (Synergie 100, MTS systems corporation) equipped with a 500 N load cell. Tubes were placed on a platform situated directly beneath the model, and a rubber pad was set on the platform to ensure there were no unwanted stress concentrations at the point where the tube connected the platform. Tubes were centered under the tooth platforms so that the different morphologies had at least half of the four teeth contacting the ring at any one point Fig 4. The tooth plate model was lowered towards the shell at a constant rate of 2.7 mm/s until fracture occurred and the tube failed. The point of failure was determined, as in a previous study (Crofts & Summers, 2014), to be the point at which the applied load dropped by 60% indicating a break. Since the Fluval tubes varied in morphology, we normalized the force at failure by the volume of the tube tested to determine force of failure per volume F/V; N/m^{-3}). We analyzed these data analyzed using two-way ANOVA and Tukey tests.

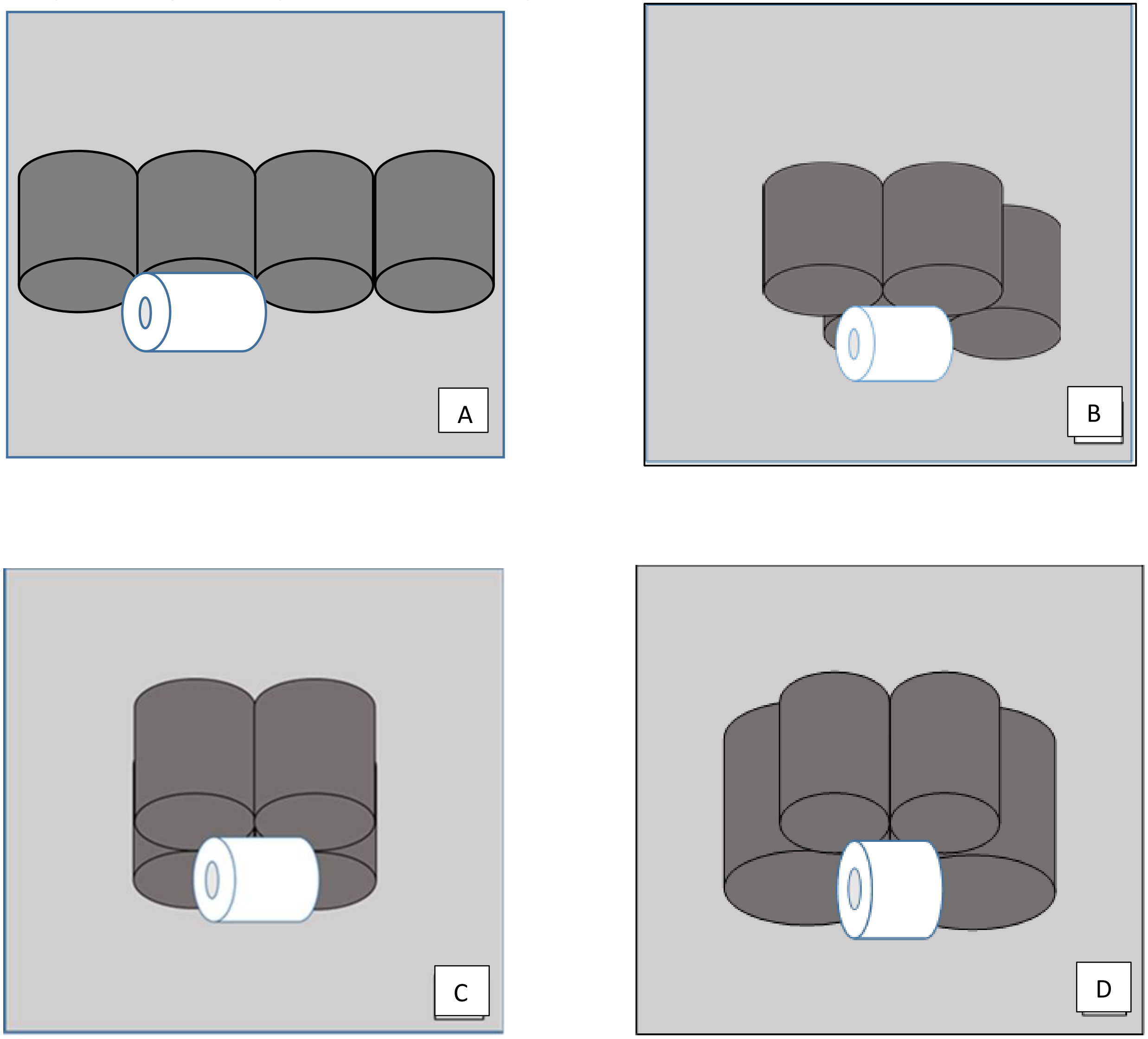

Fig.4 . Representation of tubes placed on tooth plate model (A) Linear model with ceramic tube (B) Staggered model with ceramic tube (C) Quad model with ceramic tube (D) Modified Quad model with ceramic tube

Results

We tested forty shells per tooth model (N=800, n=40) and measured initial load to failure for each test. Load to failure was characterized by a drop in the recorded measured force and the associated breaking of the tube . In most case cracks could be seen occurring and propagating simultaneously across the longitudinal axis of the tube and the latitudinal axis of the tube at the point of failure. This resulted in four broken pieces of the original structure that were approximately equal in size Fig 5A. In other cases breaks occurred either along the axis perpendicular to the load Fig 5B or the axis parallel to the load Fig 5C.

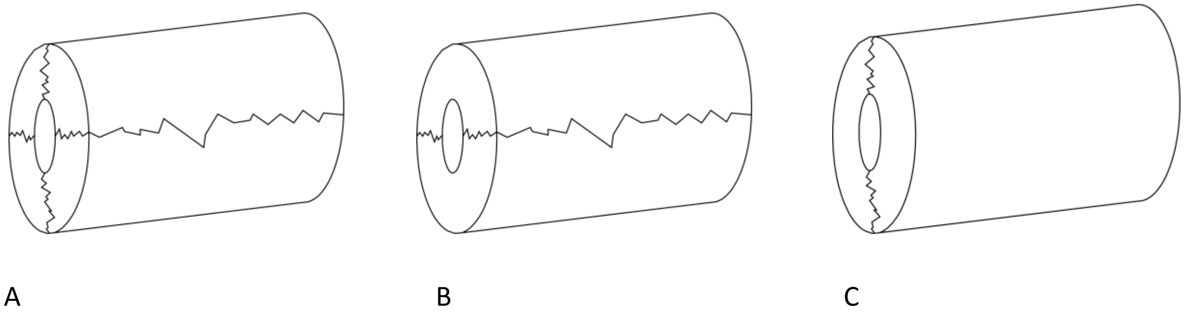

Fig 5. Depiction of most observed break (A) Less observed longitudinal break (B) Less observed latitudinal break (C)

Tooth Plate	Shape	Radius of Curvature (mm)	F/V (N m^{-3})
Linear	Convex 1	10	305.383
	Convex 2	6	302.051
	Flat	∞	305.989
	Concave 1	-6	280.471
	Concave 2	-10	286.497
Staggered	Convex 1	10	386.536
	Convex 2	6	251.132
	Flat	∞	312.799
	Concave 1	-6	283.607
	Concave 2	-10	287.293
Quad	Convex 1	10	305.383
	Convex 2	6	302.051
	Flat	∞	305.989
	Concave 1	-6	280.471
	Concave 2	-10	286.497
Modified Quad	Convex 1	10	354.113
	Convex 2	6	343.868
	Flat	∞	324.871
	Concave 1	-6	272.068
	Concave 2	-10	268.758

Table 1. Mean data for each modelled tooth plate. Includes Radius of curvature measurements and force to failure scaled by tube volumes. Outliers still present in data.

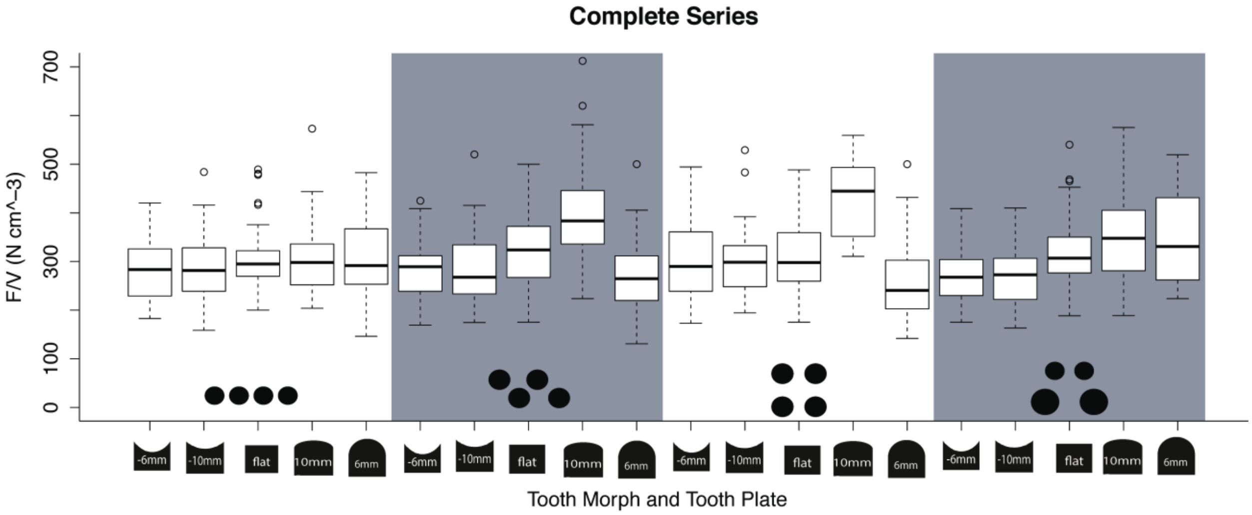

Fig. 6. Complete data set. Morphologies are organized across arrangements and arrangements are ordered linear, staggered, quad, and modified quad.

When tooth morphology data were pooled and only tooth arrangement was compared, the F/V generated by the linear arrangement and the quad arrangement were the only significantly different groups (two-way ANOVA: $p <<0.005$), with the linear tooth plate requiring less F/V to break the Fluval tubes than the quad morphology. Overall, there was a general trend wherein the linear tooth plate required less F/V than all other tooth plates, including the staggered (Fig. 6; $p =0.07$) and the modified quad ($p =0.12$) plates.

When looking at the F/V of different tooth morphologies, with tooth plate data pooled, there were also statistically significant differences (two-way ANOVA: $p << 0.005$). Both concave tooth morphologies showed significant differences between the flat morphology as well as the 10 mm convex morphology (two-way ANOVA: $p <0.05$). The 10 mm convex morphology also differed significantly from the 6mm convex flat tooth morphologies (two-way ANOVA $p << 0.005$).

The effects of adding morphology together with tooth plate arrangement are less straight forward. For the linear tooth arrangement there was no significant difference between any of the tooth morphologies (two-way ANOVA: $p >0.05$). Within the staggered arrangement the 10 mm convex morphology differed significantly from all other morphologies (two-way ANOVA: $p <0.05$) and required more force to break the Fluval tubes. Similarly, the 10 mm convex morphology required a significantly greater F/V to fracture than the other morphologies for the quad arrangement (two-way ANOVA: $p <0.001$). In the modified quad series there was no statistical difference between the 10 mm convex morphology and the 6mm convex morphology (two-way ANOVA: $p >0.05$) and these two morphologies required significantly greater F/V to fracture the Fluval tubes than the other morphologies within the same arrangement (two-way

ANOVA: *p* <0.001). Comparing the F/V needed across all tooth arrangements by the 10 mm convex tooth morphology (Fig 7), since this was the tooth morphology that varied the most, the linear tooth arrangement still required the least F/V, and the modified quad appears to require less F/V to fracture than either the quad arrangement (two-way ANOVA: *p* <0.001) or the staggered arrangement (two-way ANOVA: *p* =0.3).

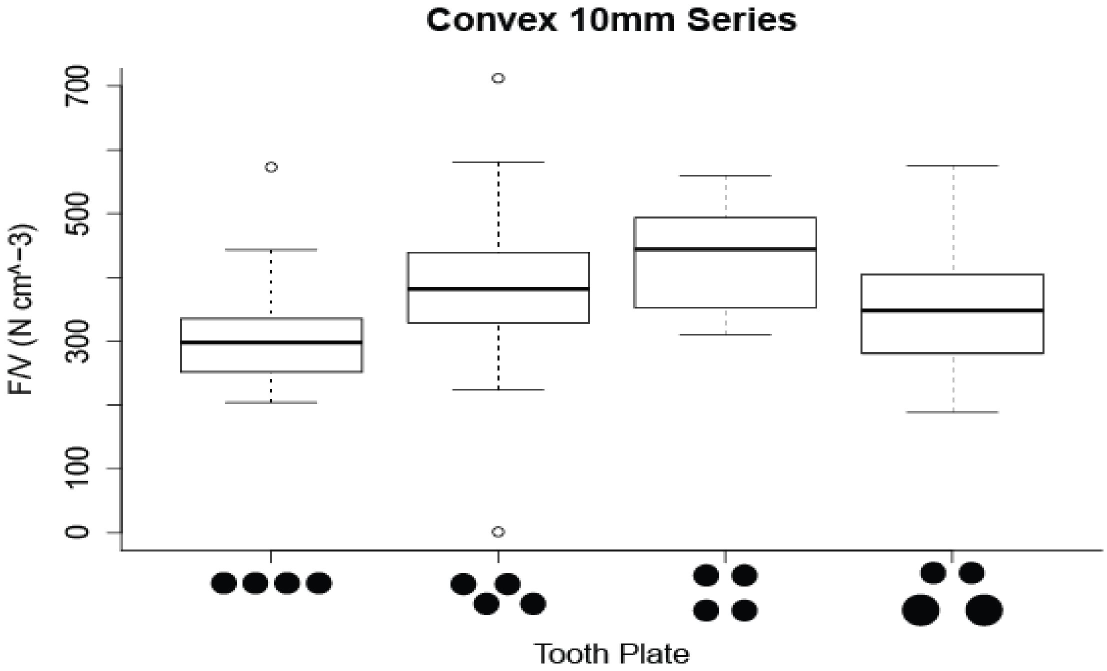

Fig. 7. F/V to failure for convex 10 mm morphology across all tooth arrangements.

Discussion

By testing different model tooth arrangements, based on real morphologies, we have found that there is a limited effect of tooth arrangement on the ability to crush idealized hard prey items. A linear tooth arrangement performs significantly better than the quad tooth arrangement, and there is a general trend indicating that a linear tooth arrangement may also outperform the staggered and modified quad morphologies as well. This is contrary to our initial predictions that tooth plate morphologies would spread bite force and break prey items more easily.

There also appears to be an interaction between tooth morphology and tooth arrangement. In general, all arrangements of concave and flat teeth required less force to fracture prey items than convex teeth. Within the convex teeth the 10mm convex tooth, the least convex morphology, required significantly more force to break the prey item in the non-linear tooth arrangements, except in the modified quad arrangement, where both convex morphologies performed at about the same level. These findings disagree with previous studies, which have shown that when working as a single unit, convex teeth require less F/V to break prey items than concave teeth (Crofts & Summers, 2014).

To explain this disparity, it may be important to address what portion of the plate is touching the prey. Since the addition of a cusp concentrates the force being applied to the prey (Crofts and Summers 2014), then the number of teeth or tooth cusps interacting with the prey item should increase the areas of stress concentration on the prey item. Therefore, one would predict that the convex tooth morphologies in the quad or modified quad series would provide the ideal arrangement. However this is not the case. It may be that for a tooth plate with concave teeth, the edges of abutting teeth are instead more intensely concentrating force and increasing the applied stress. Effectively, these edges may be functioning as even narrower cusps than we modeled in the convex morphologies. This would mean that while they would apply just as much force, the application would be over a smaller surface area, increasing the applied stress.

In our tests, the flat morphologies performed as well as the concave models. While this could be a result of the prey morphology (Crofts& Summers, 2014), it runs contrary to our predictions for the behavior of multiple teeth. One reason for this pattern could be the way the different tooth morphologies load the prey item. When applying force with a flat tooth, forces are directed vertically. However, applying a load with cusped teeth will cause portions of total force to interact with the prey item horizontally (Wess, 1993). This redistribution of forces may cause the tooth morphologies to preferentially load certain areas of the prey item, while neglecting others (Rapp 1954). By providing the localized vertical forces, the flat teeth may be able to use the applied forces more efficiently than other morphologies. This more efficient use of applied forces to overcome the specific energy of the prey item, could explain the occurrence of flat teeth in natural systems.

Changes in tooth arrangement, from linear to quad, do not decrease the force required to break a prey item. In fact, for our artificial prey item, this change in tooth arrangement may have increased the force required to fracture. Since there is no apparent benefit to breaking efficiency, why do hard-prey crushing organisms modify their tooth arrangement with such regularity? There may be an increase in resistance to tooth failure that comes from how teeth are arranged. For example, individually, concave teeth appear to be better able to handle high forces, since they tend to have lower strain concentrations than their convex counter parts (Crofts – *in prep*). When multiple teeth interact, this durability may be multiplied as the teeth could serve to strengthen neighboring teeth at the base. This is of note because Crofts (*in prep*) found that concave teeth shifted higher loads to rings around the periphery of the tooth's base.

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