Project Summary

Teeth are an important aspect of vertebrate anatomy: they lie directly at the interface of the animal and its environment and are therefore an ideal tool to explore the biomechanics and ecology diversity of extinct organisms. Dental structures in vertebrates come in a wide range of shapes and sizes and are abundant in the fossil record. Tooth form, even in extinct animals, offers a direct link to whatever the animal is capable of feeding upon and how feeding was performed, i.e. their *functional ecology*. Furthermore, teeth have the potential to be a model system for comparisons of function and ecology across clades and through time as the mechanical processes involved in food mastication can be explored through the paradigm of universal physical laws and applied to any vertebrate group. The objective of this project was to quantify the biomechanical/ecological diversity of vertebrate dental structures over time and explore the role that evolutionary convergence plays in shaping the pattern of functional and ecological change. There were two main goals to this project: 1) *Quantify the relationship between tooth shape, complexity, and function* and then use the data from the first part 2) *To quantify changes in the patterns and diversity of tooth design across taxa and through time.*

Tooth biomechanics

The relationship between tooth morphology and function is highly complex and heavily influenced by the material properties of the food being eaten. Physical cutting experiments performed using a specially-designed guillotine testing device show that variation in tooth shape can have drastic effects on the energy required to fracture food. However, this is heavily influenced by the properties of the food, whether they are soft and deformable (meat) or stiff and more fibrous (vegetables)[1]. Parallel work on beak shape in African seedcrackers shows that this is true of non-dental feeding structures as well. The types of food being chewed can also have a great impact on the types of stress and potential damage seen in teeth. Using finite element models (FEM) I tested the effects of different stresses on teeth created by different types of food. I isolated specific structures, such as a ring of enamel around the base of some mammal teeth called a cingulum, and found that the cingulum is particularly useful in reducing strains caused by chewing soft, tough foods such as gum or caramel[2]. These results are of particular interest to dentists, who have long noted specific types of tooth damage (called abfraction), which occurs precisely in the region where a cingulum would be in human teeth.

In order to further explore the relationship between tooth form and food properties, I have pursued ways of integrating physical fracture experiments and FE models. Fully validated FE models based on physical experiments show that the relationship between food and tooth is an energetic one[3]. Animals feed to gain energy; however, it takes energy to chew and break down food. My results show that certain tooth forms can reduce the energy required to break down food by reducing the amount of energy expended during chewing. This means that the food is being processed more efficiently at less cost to the animal.

Adding to the complexity of this system is the question of how complex teeth are. In this case, complexity simply means how many bumps and edges does the tooth have. A metric developed by one of my collaborators actually measures complexity of teeth by counting the number of features. In partnership with him and other colleagues, I have compared the complexity of a tooth with a variety of different functional features[4]. Highly complex teeth generally repeat the same basic features over and over again, creating a complex, but very homogenous tooth surface. Less complex teeth have more room to include a larger number of different kinds of shapes (bumps, edges and so forth). This further influences tooth function as the highly complex teeth are better at reducing tough materials, but are potentially more specialized than less complex teeth. This research is ongoing and has the potential to allow us to relate tooth form and even development to feeding function.

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[1] Anderson, PSL 2009. *Journal of Experimental Biology*, **212**: 3627-3632.

[2] Anderson, PSL, PG Gill, & EJ Rayfield, 2011. *Journal of Morphology*, **272**: 50-65.

[3] In Revision

[4] In Prep

Functional diversity of teeth and jaws.

The second half of this project focused on what these aspects of tooth function can tell us about the evolution of feeding diversity through time. I focused initially on the earliest radiation of jawed vertebrates. More than 99% of modern vertebrates (animals with a backbone, including humans) have jaws, yet 420 million years ago, jawless, toothless, armour-plated fishes dominated the seas, lakes, and rivers. There were no vertebrates yet on land, and the recently evolved jawed fishes were minor players in this alien world, some sporting unusual jaw and tooth shapes that bear little physical resemblance to modern animals. However, 80 million years later, jawed vertebrates sporting a wide variety of dental structures were dominant in the marine realm and had already invaded land. What happened during this intervening time span (the Devonian period)? I along with colleagues in the UK and The Netherlands performed the first analysis of functional diversity amongst the earliest vertebrates with jaws and teeth[5]. Analyses of functional disparity based on biomechanical jaw and tooth traits across all Devonian jawed vertebrate groups reveal that these early forms reach peaks in functional disparity by the Early Devonian, well before the taxonomic diversification seen later in the period. Furthermore, the results indicate that long-held assumptions concerning the replacement of jawless fishes by newly evolved jawed forms are likely wrong. The variety of feeding mechanism s in early jawed animals appears to have had little to no affect on the diversity of jawless fishes, which shared ecological space with the jawed fishes for at least 30 million years before beginning to notably decline. When the jawless fishes do decline, we see no indication that their jawed cousins took up new functional roles, calling into question old ideas of ecological replacement.

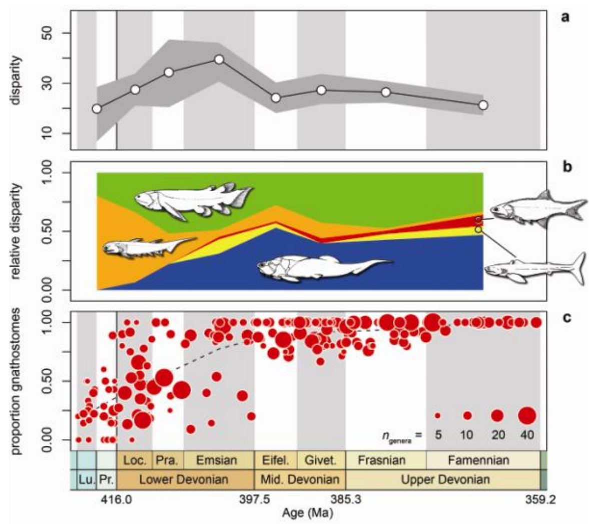

Figure 1: Figure from Anderson et al. 2011 (*Nature*) showing the functional disparity among Silurian/Devonian gnathostomes. a, Disparity across eight time bins. Light grey region denotes 95% confidence intervals. b, Relative contributions (partial disparity) of major gnathostome groups to overall functional disparity. c, Faunal composition data for the late Silurian and Devonian. Discs represent individual vertebrate assemblages plotted as a function of time and proportion of gnathostomes ,which comprise those faunas.

However, the functional evolution of teeth did not stop at the end of the Devonian 360 million years ago. If anything, teeth have gotten more and more varied and complex. I have recently completed work involving describing the range of tooth form in a large clade of modern coral reef fishes (the labrids). Results indicate variation in evolutionary rates between clades based on diet, further illustrating the connection between morphology and function[6]. In an effort to draw comparisons between tooth structures in an even wider variety of taxa, my colleagues and I have been developing functional morphological methods for quantifying the biomechanical profile in tooth forms. The schema focuses on aspects of occlusion (how teeth fit together) and dental tool shape (cusps and blades) to identify both convergences in dental forms between disparate clades as well as traits that lead to massive diversifications. This method will be applicable to any features used to break down food (ie. beaks, invertebrate feeding structures) and will give insights into palaeoecological patterns through time. Once in place, this scheme will allow for trends in functional diversity to be mapped and compared with other trends such as climate change, extinction events and similar large-scale geological trends. We will then have a method for exploring the effects of extinction events on ecological biodiversity, offering new insights into how mass loss of taxa can affect ecosystems.

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[5] Anderson, PSL, M Friedman, MD Brazeau & EJ Rayfield, 2011. *Nature*, **476**: 206-209.

[6] In Prep