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Tooth Cusp Radius of Curvature as a Dietary Correlate in Primates

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Tooth Cusp Radius of Curvature as a Dietary Correlate in Primates

A Dissertation Presented

by

MICHAEL A. BERTHAUME

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

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September 2013

Mechanical Engineering
Tooth Cusp Radius of Curvature as a Dietary Correlate in Primates

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Michael A. Berthaume

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To my amazing family,

Mom, Dad, Andy, Maria, Angie, there is no way I could be where I am today without your amazing love and support, whether it be taking me in, helping me move, listening to me drone on about teeth and FEA of biological systems, or making me crack up at one of our three hour long family dinners.

Together, we make the craziest, happiest, and most powerful and loving group of people I know.

Thank you.

*Insanity runs in my family. It practically gallops.*

-Cary Grant
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ABSTRACT

TOOTH CUSP RADIUS OF CURVATURE AS A DIETARY CORRELATE IN PRIMATES

SEPTEMBER 2013

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Tooth cusp radius of curvature (RoC) has been hypothesized to play an important role in food item breakdown, but has remained largely unstudied due to difficulties in measuring and modeling RoC in multicusped teeth. We tested these hypotheses using a parametric model of a four cusped, maxillary, bunodont molar in conjunction with finite element analysis. When our data failed to support existing hypotheses, we put forth and tested the Complex Cusp Hypothesis which states that, during brittle food items breakdown, an optimally shaped molar would be maximizing stresses in the food item while minimizing stresses in the enamel. After gaining support for this hypothesis, we tested the effects of relative food item size on optimal molar morphology and found that the optimal set of RoCs changed as relative food item size changed. However, all optimal morphologies were similar, having one dull cusp that produced high stresses in the food item and three cusps that acted to stabilize the food item.

We then set out to measure tooth cusp RoC in several species of extant apes to determine if any of the predicted optimal morphologies existed in nature and whether
tooth cusp RoC was correlated with diet. While the optimal morphologies were not found in apes, we did find that tooth cusp RoC was correlated with diet and folivores had duller cusps while frugivores had sharper cusps. We hypothesize that, because of wear patterns, tooth cusp RoC is not providing a mechanical advantage during food item breakdown but is instead causing the tooth to wear in a beneficial fashion. Next, we investigate two possible relationships between tooth cusp RoC and enamel thickness, as enamel thickness plays a significant role in the way a tooth wears, using CT scans from hundreds of unworn cusps. There was no relationship between the two variables, indicating that selection may be acting on both variables independently to create an optimally shaped tooth. Finally, we put forth a framework for testing the functional optimality in teeth that takes into account tooth strength, food item breakdown efficiency, and trapability (the ability to trap and stabilize a food item).
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CHAPTER 1

GENERAL INTRODUCTION

1.1 Overview

Teeth are among the most common biological structures represented in the fossil record, largely due to their primarily inorganic composition (Crowell et al., 1934). Teeth also contain an immense amount of information: from a single mammalian molar, researchers can determine an animal’s age (Smith et al., 2010), dental ecology (Cuozzo and Sauther, 2012), and diet. Diet is frequently inferred from metrics that encompass aspects of tooth morphology and are either correlated to quantitative aspects of diet, such as food item material properties (Lucas et al., 2001; Lucas, 2004; Vogel et al., 2008; Wright et al., 2008), or qualitative aspects of diet, such as dietary categories (Evans et al., 2007; Santana et al., 2011).

Some of the first metrics that correlated tooth morphology to diet were presented in Kay (1975), where Kay analyzed six tooth measurements of primate upper and lower second molars, including tooth length, length of the cristid obliqua and the projective crown height. Ultimately, Kay used these measurements to devise a metric he referred to as the shearing quotient (SQ), which was found to be highly correlated to dietary categories within given clades (Kay, 1975). The shearing quotient is defined as

\[
SQ = \frac{(S_o - S_E) \times 100}{S_E}
\]  

(1.1)
where $S_o$ is the observed summed shearing blade length and $S_E$ is the expected summed shearing blade length for the second molar (Kay and Simons, 1980). It was observed that frugivores have poor shearing, crushing and grinding features, and therefore have a small shearing quotient, while folivores and insectivores tend to have more prominent crests, and therefore have a larger shearing quotient.

There were some drawbacks to this method, however. First, there is a level of discrepancy in the SQ values for some taxa. A well-known example of this is *Lepilemur*, a recognized folivore, was being classified as a frugivore (Kirk and Simons, 2001; Boyer, 2008; Godfrey et al., 2012). Second, the accuracy of the shearing quotient measurement decreases with tooth wear, so teeth that are heavily worn can provide drastically different SQ values than unworn teeth from the same species. This led to a series of techniques to be developed that fell into the general category of dental topography.

Dental topography involves taking 2.5D surface scans of teeth and analyzing functional aspects of tooth shape with Geographic Information Systems (GIS) software (Zuccotti et al., 1998). One of the first metrics developed using dental topography techniques was the relief index (RFI), which can be thought of as a 3D version of the shearing quotient (M'Kirera and Ungar, 2003). The relief index is the same as occlusal relief, and is measured by taking the 3D surface area of the tooth and dividing it by its 2D cross-sectional area. Originally, it was introduced as a way of distinguishing between two closely related species: *Pan troglodytes* and *Gorilla gorilla*. Later, Boyer (2008) expanded the study to include extant euarchontan mammals and measured the RFI of scandentians (tree shrews), dermopterans (flying lemurs) and prosimians (strepsirrhines and tarsiers). He discovered that, although the relief index was efficient at distinguishing
frugivores/gummivores from omnivores and folivores/insectivores for all species, it could only efficiently differentiate between folivores and insectivores if the study were to be limited to primates. A number of other metrics for inferring diet from tooth shape were also developed, including dental complexity, which is measured through OPC, TPC, OPD and TPD (orientation and topographic patch count and diversity), and/or OIC and TIC (image compression ratio of surface maps) (Evans et al., 2007; Santana et al., 2011), Dirichlet normal surface energy (DNE) (Bunn et al., 2011; Godfrey et al., 2012), and angularity (Ungar and M’kirera, 2003; Peter, 2004) (see Evans, 2013) for a review).

One metric of tooth shape that has gone largely unstudied over the past several decades is tooth cusp sharpness, measured by radius of curvature (RoC). Unlike the metrics listed above which take into account the entire occlusal surface of the tooth, tooth cusp RoC is location specific, and a single tooth will have multiple measurements (Evans and Sanson, 1998; Berthaume et al., 2013; Frunza and Suciu, 2013). Competing hypotheses, namely the Blunt, Strong, and Pointed Cusp Hypotheses, have been generated about the biomechanical role tooth cusp RoC plays in brittle food item breakdown efficiency. Dull cusps are hypothesized to be more efficient under the Blunt and Strong Cusp Hypotheses because they reduce the force/energy absorbed by the food item and the principal stresses in the enamel, while sharp cusps are hypothesized to be more efficient under the Pointed Cusp Hypothesis because they increase principal stresses in the food item (Kay, 1981; Luke and Lucas, 1983; Evans and Sanson, 1998; Evans and Sanson, 2003; Lucas et al., 2008; Lawn et al., 2009; Berthaume et al., 2010). These were initially put forth and tested on hominin teeth in Berthaume et al. (2010), but no concrete conclusions were drawn.
Given the uncertainty surrounding the biomechanical significance of tooth cusp RoC, this dissertation sets out to address the biomechanical significance of tooth cusp RoC for understanding primate diets. This will be done using finite element (FE) models of teeth to test the Blunt, Pointed, and Strong Cusp Hypotheses in new ways. Next, tooth cusp RoC will be measured in a number of apes, and finally the correlation between tooth cusp RoC and another variable which affects stresses in the enamel, enamel thickness, will be analyzed in macaques. Finally, the information learned concerning the biomechanics of tooth cusp RoC will be combined with information learned about the biomechanics of teeth to provide a framework to be used in the future for analyzing tooth function.

1.2 Organization of the Document

This document is organized into six chapters. Chapter 1 provides a brief background and motivation to the problem at hand. Chapter 2 sets out to pick up where Berthaume et al. (2010) left off, and uses a parametric finite element (FE) model to retest the Blunt, Strong, and Pointed Cusp Hypotheses for a four cusp, bunodont molar where RoC is allowed to vary independently for each cusp in both the buccolingual and mesiodistal directions. In Chapter 2, we also put forth and test the Complex Cusp Hypothesis, which states that selection may be acting to maximize the maximum principal stresses in the food item, promoting food item breakdown, while minimizing the maximum tensile stresses in the enamel, preserving enamel integrity, during brittle food item fracture. We then use the complex Cusp Hypothesis to determine what an optimal set for tooth cusp RoCs would be for a bunodont molar during brittle food item fracture.
This chapter is based on the following our recently published paper (Berthamaume et al. 2013).

Most studies of tooth shape frequently begin with the assumption that teeth are optimal for the function, and assume that the function is to breakdown food items with certain sets of material properties or belonging to certain dietary categories. This leads to researchers ignoring the effect of relative food item size on optimal tooth shape. Chapter 3 uses the parametric FE model to test the effects of relative food item size on optimal tooth cusp RoC. This chapter investigates whether the set of optimal tooth cusp RoCs stay constant or changes as relative food item size changes, and whether not the importance of tooth cusp RoC changes with relative food item size. Chapter 4 takes the knowledge gained in Chapters 2 and 3 and measures tooth cusp RoC on 6 species and subspecies of apes to see if folivorous apes could be differentiated from frugivorous apes on the basis of tooth cusp RoC alone. This chapter yielded some interesting and unexpected results that indicate tooth cusp RoC may not be conferring a biomechanical advantage during food item breakdown, but may instead be causing the tooth to wear in a way that is efficient for frugivores and folivores. This led to Chapter 5, where we investigated the relationship between tooth cusp RoC and enamel thickness at the tip of the cusp in macaques.

Finally, Chapter 6 takes all the information learned during this dissertation concerning tooth form and function, and provides a framework for comparing morphological and biologically diverse teeth. This framework is unique in that it takes into account multiple aspects of tooth function, namely tooth strength, food breakdown efficiency, and trapability (the ability to trap and stabilize a food item), and provides
researchers with a way to take all three variables into account when analyzing tooth shape.
CHAPTER 2

HOW DOES TOOTH CUSP RADIUS OF CURVATURE AFFECT BRITTLE FOOD ITEM PROCESSING?

2.1 Abstract

Tooth cusp sharpness, measured by Radius of Curvature (RoC), has been predicted to play a significant role in brittle/hard food item fracture. Here, we set out to test three existing hypotheses about this relationship; namely the Blunt and Strong Cusp hypotheses, which predict that dull cusps will be most efficient at brittle food item fracture, and the Pointed Cusp Hypothesis, which predicts that sharp cusps will be most efficient at brittle food item fracture using a four cusp bunodont molar. We also put forth and test the newly constructed Complex Cusp Hypothesis, which predicts that a mixture of dull and sharp cusps will be most efficient at brittle food item fracture. We tested the four hypotheses using finite element (FE) models of four cusped, bunodont molars. When testing the three existing hypotheses, we assumed all cusps had the same level of sharpness (RoC), and gained partial support for the Blunt Cusp Hypotheses. We found no support for the Pointed Cusp or Strong Cusp Hypotheses. We used the Taguchi sampling method to test the Complex Cusps Hypothesis with a morphospace created by independently varying the radii of curvature of the four cusps in the buccolingual and mesiodistal directions. The optimal occlusal morphology for fracturing brittle food items consists of a combination of sharp and dull cusps, which creates high stress concentrations in the food item while stabilizing the food item and keeping the stress
concentrations in the enamel low. This model performed better than the Blunt Cusp Hypothesis, suggesting a role for optimality in the evolution of cusp form.

2.2 Introduction

There are two different approaches to reconstructing the diets of extinct animals based on their tooth morphology. The first is comparative and uses extant animals as a model for inferring diet from dental morphology and tooth wear (Ungar and Sponheimer, 2011; Wood and Schroer, 2012; Strait et al., 2013). In mammals, this has led to the development of many useful metrics for quantifying the occlusal surface of teeth, including: the shearing quotient (SQ) (Kay, 1975; Kay and Simons, 1980; Kay, 1981), the relief index (RFI) (M'Kirera and Ungar, 2003; Boyer, 2008), orientation patch counts (OPC) (Evans et al., 2007; Santana et al., 2011), relative enamel thickness and enamel decussating (Dumont, 1995; Stefen, 1999; Lee et al., 2009; Constantino et al., 2011) and Dirichlet Normal Energy (DNE) (Bunn et al., 2011; Godfrey et al., 2012).

The second approach is to use engineering principles to quantify complex sets of interactions surrounding the tooth-food interaction. Given its complexity, this approach requires both assumptions and simplifications. One common simplification is to model a single tooth cusp in contact with a food item prior to and during the process of fracturing the food item (Abler, 1992; Evans and Sanson, 1998; Freeman and Lemen, 2007). For example, Evans and Sanson (1998) proved that punches with sharper cusps and tips require less force and energy to fracture beetles than punches with duller cusps and tips. This is because sharper cusps and tips reduce the contact area between the punch and the food item, reducing the force needed to obtain the principal stresses needed to fracture
the exoskeleton. This is one of the reasons why tooth cusp sharpness, measured by Radius of Curvature (RoC) (teeth with higher RoCs are duller and teeth with lower RoCs are sharper), has become a metric of interest in recent years (Evans and Sanson, 1998; Yamashita, 1998; Evans and Sanson, 2003; Lucas, 2004; Hartstone-Rose and Wahl, 2008; Berthaume et al., 2010). The assumption that cusps act independently to fracture food items has been a necessary and useful simplification. In this study we propose to investigate how the multiple cusps of mammalian molars contribute to the process of fracturing food items.

Modeling the material properties of food items is a critical first step in investigating how they fracture. Many of the metrics mentioned above focus on how tooth morphologies reflect the extent to which the foods that an animal eats are mechanically challenging. Mechanically challenging foods are generally broken into two categories: tough, or displacement limited, and hard, or stress limited (Lucas, 2004). Traditionally, hard food items have also been classified as brittle (Agrawal et al., 1997; Lucas et al., 2000; Yamashita, 2003; Dominy et al., 2008; Yamashita, 2008; Norconk et al., 2009; Yamashita et al., 2009). However, this classification system may not always be useful, as some tough food items are brittle and some hard food items are not. Moreover, it does not describe how food items fail. Here we suggest two categories for mechanically challenging food items taken from materials science: brittle and ductile. Brittle items exhibit little to no plastic deformation prior to failure, while ductile items absorb a large
Tension tests allow the user to calculate both the stress and strain of the material at any given point in time up to fracture (denoted by the red X). A stress-strain plot can be obtained by plotting strain on the x-axis and stress on the y-axis. This plot is used to calculate several material properties of the specimen being tested. For example, the slope of the stress-strain curve in the linear, elastic region is Young’s modulus. The elastic region of the stress-strain curve ends at the yielding point, which usually occurs after .2% strain. Brittle materials tend to fracture soon after the yielding point while ductile materials continue to deform in the plastic region until fracture occurs.

Brittle materials can have either high (i.e. cast iron) or low (i.e. porcelain, leaves, rock salt) moduli of elasticity (Young’s Modulus), but they exhibit little to no yielding on a stress-strain curve prior to fracture (Fig. 2.1). Brittle materials tend to deform strictly in the elastic region of the stress-strain curve and fracture at or soon after the yield stress is reached, while ductile materials continue to experience high levels of strain and deformation (with little increase in stress) prior to fracture. In contrast to brittle materials, ductile materials leave the elastic region and have a large plastic region on their stress-strain...
strain curves prior to fracture. They also tend to absorb high levels of strain energy per unit volume (defined as the area under the stress-strain curve) and have high toughness values (as defined by Callister (2004)). The concept of toughness in feeding biomechanics differs from the concept of toughness in materials science. Toughness in feeding biomechanics has units of Joules/meter$^2$, while toughness in materials science has units of Joules/meter$^3$. The concept of toughness used in feeding mechanics is identical to the engineering concept of work of crack propagation per area of crack (G).

Studies of enamel fracture have drawn from concepts in fracture mechanics. Fracture mechanics is based on the idea that all materials have inherent flaws and microcracks, and, once a certain amount of energy has been absorbed by the material through the application of tensile stresses, these cracks will propagate through the materials (Wang, 1996). One metric for a material’s resistance to crack propagation that has been used in recent studies of enamel chipping is fracture toughness (e.g. (Bechtle et al., 2010; Constantino et al., 2012)). Fracture toughness is not the same as toughness (mentioned above) and has units of Pascals*√meters.

Here we test three existing, sometimes contradictory, hypotheses, and one novel hypothesis concerning the relationship between brittle food items and optimal occlusal morphology of mammalian upper molars (Berthaume et al., 2010). The first is the Blunt Cusp Hypothesis, which encompasses two predictions. First, it predicts that teeth comprised entirely of dull cusps can fracture brittle food items with lower force or energy than teeth comprised entirely of sharp cusps. Second, it predicts that teeth comprised entirely of dull cusps can fracture brittle food items with lower force or energy than teeth
comprised of a mixture of sharp and dull cusps (Peter, 2004; Berthaume et al., 2010). This hypothesis is based on the observation that mammals that consume hard (brittle) food items tend to have teeth with dull cusps (Kay, 1981; Luke and Lucas, 1983). This hypothesis would be supported if strain energy absorbed by a brittle food item is negatively correlated with RoC (Fig. 2.2).

The second hypothesis is the Pointed Cusp Hypothesis, which contradicts the Blunt Cusp Hypothesis and states that teeth with sharp cusps are the most efficient at fracturing brittle food items. The rationale behind this hypothesis is that sharper cusps can apply a given force over a smaller contact area, creating high stress concentrations in a food item (Evans and Sanson, 2003; Berthaume et al., 2010). Indeed, sharp, man-made tools (with low RoCs) such as knives and blades require less force to fracture/deform thin
surfaces than do blunt tools (Evans and Sanson, 1998; Xie and Hawthorne, 2002; Freeman and Lemen, 2006). (Note, however, that these are “single cusped” tools, meaning that the total contact area between the tool and the surface is a function of RoC. This relationship may or may not hold true for “multiple cusped” tools, such as mammalian molars.) The Pointed Cusp Hypothesis predicts that the contact area between a food item and a tooth is positively correlated with RoC and that stresses in the food item are negatively correlated with RoC (Fig. 2.2).

The third hypothesis is the Strong Cusp Hypothesis, which, similarly to the Blunt Cusp Hypothesis, states that dull cusps are most efficient at fracturing brittle food items. However, the Strong Cusp Hypothesis states that dull cusps are more efficient because they prevent high stresses from forming in the enamel. This prevents microcracks, which can ultimately lead to enamel fracture, from forming in the enamel (Lucas et al., 2008; Lawn and Lee, 2009; Lee et al., 2009; Berthaume et al., 2010). This hypothesis predicts that tensile stresses in the enamel should be negatively correlated with RoC (Fig. 2.2).

There is a significant body of evidence demonstrating that a considerable number of microcracks form at the enamel dentin junction (EDJ) over the useful life of human molars (Keown et al., 2012), any of which could cause enamel chipping to occur. Here we assume that microcracks are randomly distributed along the EDJ. Because crack propagation requires tensile stresses, we assume that higher tensile stresses increase the likelihood of a crack of random size and orientation resulting in an energy release rate greater than the critical energy release rate, thus increasing the probability of crack propagation.
We also test the novel Complex Cusp Hypothesis. This hypothesis embraces both the Strong and Pointed Cusp Hypotheses, and incorporates the idea that it may be advantageous to simultaneously preserve enamel integrity and maximize the efficiency of processing brittle food items. The Complex Cusp Hypothesis predicts that the optimal tooth morphology for fracturing brittle food items exhibits a mixture of both dull and sharp cusps; the dull cusps act to minimize stress in the enamel while the sharp cusps serve to maximize stress in the food item. We define the optimality criterion by the function

\[
\text{Optimality Criterion} = \max \left( \frac{\text{maximum tensile stresses in the food item}}{\text{maximum tensile stresses in the enamel}} \right)
\]  

(2.1)

Unlike the other hypotheses, this hypothesis does not predict a relationship between RoC and any single measure of performance in either the tooth or food item. Rather it predicts that the optimal tooth morphology will exhibit a combination of sharp and dull cusps (i.e., low and high RoCs).

Both the Blunt and Pointed Cusps Hypotheses deal strictly with the function of breaking down food items (minimizing strain energy or maximizing stresses in the food item), making them applicable to all mammals. Conversely, the Strong Cusp Hypothesis and the Complex Cusp Hypotheses place high value on conserving enamel. Therefore, the latter two hypotheses may not apply to all mammalian teeth as some animals are affected less by enamel fracture than others.
2.3 Materials and Methods

2.3.1 Finite Element Analysis and Model Construction

We used ANSYS APDL 13.0 finite element program (Canonsburg, PA) to test our hypotheses because it supports non-linear elastic contact simulations and parametric modeling through the ANSYS Parametric Design Language (APDL). We wrote an APDL code (see Appendix A) to automatically construct a parametric model of a tooth, a brittle food item, and to execute simulated interactions between them. We assigned 19 parameters to the model, including the heights of the cusps (4 parameters), the distances between the cusps in the mesiodistal and the buccolingual directions (2 parameters), the heights of the valleys in between the cusps (4 parameters), the RoCs of the cusps in the mesiodistal direction (4 parameters), the RoCs of the cusps in the buccolingual direction (4 parameters), and enamel thickness (1 parameter) (Fig. 2.3). We held enamel thickness constant over the entire occlusal surface of the tooth at 1 mm. We set the heights of the cusps and valleys at 5 mm and 3 mm, respectively. The distance between the cusps in the buccolingual direction was held at 15.4 mm and the distance between the cusps in the mesiodistal direction was held at 15.7 mm. Distances between cusps are based on the average width and length of a male gorilla tooth (Gingerich et al., 1982). The eight RoCs were the only variables allowed to vary from model to model.

To begin constructing the tooth model, we created four cross-sections of the tooth, each of which traversed two cusp tips and modeled enamel and dentin separately. This defined the tooth in two mesiodistal and two buccolingual planes. We then used splines to create an outline of the bottom of the tooth, again keeping enamel distinct from dentin. We used Coons patches (patches that are fitted between four arbitrary curves) to create
the occlusal surface of the tooth, the EDJ and the bottom of the tooth crown. The Coons patches were used to construct the dentin and the enamel cap volumes. These volumes were meshed separately with 10-noded brick elements, which are quadratic elements with nodes at the 4 vertices and on the mid-side of the 6 edges of the element. The use of the mid-side nodes allows the elements to properly mimic the curved geometry of the tooth (Fig. 2.4), as well as enable the stress and strain fields to vary linearly within the element.

We assigned isotropic material properties to the enamel cap (Young’s modulus = 84,100 MPa, Poisson’s ratio = 0.3) and the dentine (Young’s modulus = 8,600 MPa Poisson’s ratio = 0.31) (Benazzi et al., 2011). Following Berthaume et al. (2010) we constructed a hemispherical model of a brittle food item (diameter = 28.2 mm) with a Young’s modulus of 2,000 MPa and a Poisson’s ratio of 0.4.

The food item was centered over the occlusal surface of the tooth, and constraints were applied to the bottom of the tooth and the food item. The tooth had constraints
Figure 2.4: One of the completed models, where all RoCs of the tooth are being held constant at 5 mm.

applied to bottom of the crown, preventing translation in the buccolingual and mesiodistal directions. It also had a 3 mm displacement applied to the bottom of the crown in the vertical direction, which moved the tooth towards the food item to simulate biting. Constraints were applied to the bottom of the food item preventing translation in the vertical direction and rotation around an imaginary axis running through the center of the food item in the vertical direction. The rotational constraints stabilized the food item while allowing it to translate in the buccolingual and mesiodistal directions, thus allowing it the food item to settle into the position of lowest potential energy during the simulations (Berthaume et al., 2010).

The simulations were solved in ten substeps, and results (displacement, reaction force, contact area and tensile stresses for the enamel and food item) were extracted at each substep. Quadratic equations of the displacement of the food item in the vertical direction vs. reaction force and were used to interpolate the displacement that resulted in
a 2 kN reaction force. Quadratic equations were also used to relate displacement to reaction force, strain energy, and contact area, while cubic equations were used to relate displacement to tensile stresses. The equation relating displacement to reaction force was used to determine displacement corresponding to a 2 kN force (the maximum bite force of an orangutan (Lucas et al., 1994)), and the subsequent equations were used to calculate the strain energy, contact area and tensile stresses at the calculated displacement. Linear regression analyses testing the Blunt, Pointed, and Strong Cusp Hypotheses were carried out using R (www.r-project.org, (Ihaka and Gentleman, 1997)).

2.3.2 Failure Criterion

Although a compressive force was applied to the tooth and the food item during mastication, it is tensile stresses (i.e., maximum principal stresses) and not compressive stresses that cause failure in these structures (Rudas et al., 2005; Chai et al., 2009b). Tensile stresses along the EDJ are of concern for the enamel because failure tends to initiate at microcracks along the EDJ, which is where tensile stresses are the highest in both experimental studies (Chai et al., 2009b; Lee et al., 2009; Lawn et al., 2010) and our models. For the food items, fracture was initiated on the inner surface of the hemisphere where tensile stresses are the highest, and then propagated to the outer surface.

We tested the Blunt, Pointed and Strong Cusp hypotheses by assuming that the RoC for all the cusps was equal, and then varied the RoCs from 2.5 mm to 7.6 mm in 0.25 mm increments (2.5, 2.75, 3.0…7.25, 7.5 and 7.6, see Fig. 2.5). Based on the correlations predicted in Fig. 2.2, both the Blunt and Strong Cusp hypotheses would be supported if a tooth comprised entirely of dull cusps performed best. Similarly, the
Pointed Cusp Hypothesis would be supported if a tooth comprised entirely of sharp cusps performed best.

To test the Complex Cusps Hypothesis, that the optimal tooth morphology for fracturing brittle food items exhibits some combination of both dull and sharp cusps, we created a morphospace by altering the mesiodistal and buccolingual RoCs of the tooth cusps and mapped the optimality function (equation 1) onto that space. If each of the eight RoCs were allowed to have three discrete values (dull (7 mm), medium (5 mm) or sharp (3 mm)), a full factorial set of simulations would require 6561 simulations to construct the morphospace. Instead we used the more efficient Taguchi method to run a partial factorial set of simulations to define the morphospace and capture the main effects (Taguchi, 1987; Dar et al., 2002; Lee and Zhang, 2005; Lin et al., 2007). The Taguchi method utilizes orthogonal arrays (in this case, an L18 orthogonal array, see Table 2.1) to examine the morphospace. After generating the basic morphospace, we ran additional simulations to define the most optimal area of the morphospace in more detail.
Table 2.1: RoC of each of the cusps (sharp, medium or dull). T1-T18 represent the 18 teeth produced using the Taguchi method (i.e. T1=first tooth produced using Taguchi method), and Optimum is the optimal tooth morphology. The subscripts next to RoC tell which cusp is being described (cusps a, b c and d) and the direction in which the RoC is being described (1=mesiodistal plane and 2= buccolingual plane).

<table>
<thead>
<tr>
<th>Tooth</th>
<th>RoC(a1)</th>
<th>RoC(b1)</th>
<th>RoC(c1)</th>
<th>RoC(d1)</th>
<th>RoC(a2)</th>
<th>RoC(b2)</th>
<th>RoC(c2)</th>
<th>RoC(d2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>T1</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
<td>sharp</td>
</tr>
<tr>
<td>T2</td>
<td>sharp</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T3</td>
<td>sharp</td>
<td>sharp</td>
<td>dull</td>
<td>dull</td>
<td>dull</td>
<td>dull</td>
<td>dull</td>
<td>dull</td>
</tr>
<tr>
<td>T4</td>
<td>sharp</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>dull</td>
</tr>
<tr>
<td>T5</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>dull</td>
<td>sharp</td>
<td>sharp</td>
</tr>
<tr>
<td>T6</td>
<td>sharp</td>
<td>medium</td>
<td>dull</td>
<td>dull</td>
<td>sharp</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T7</td>
<td>sharp</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>dull</td>
</tr>
<tr>
<td>T8</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>dull</td>
<td>medium</td>
<td>sharp</td>
<td>dull</td>
<td>sharp</td>
</tr>
<tr>
<td>T9</td>
<td>sharp</td>
<td>dull</td>
<td>dull</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
</tr>
<tr>
<td>T10</td>
<td>medium</td>
<td>sharp</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>medium</td>
<td>sharp</td>
<td>dull</td>
</tr>
<tr>
<td>T11</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
<td>sharp</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T12</td>
<td>medium</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>medium</td>
<td>sharp</td>
<td>sharp</td>
<td>dull</td>
</tr>
<tr>
<td>T13</td>
<td>medium</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T14</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
</tr>
<tr>
<td>T15</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
</tr>
<tr>
<td>T16</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T17</td>
<td>medium</td>
<td>dull</td>
<td>medium</td>
<td>sharp</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>medium</td>
</tr>
<tr>
<td>T18</td>
<td>medium</td>
<td>dull</td>
<td>medium</td>
<td>sharp</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
</tr>
<tr>
<td>Optimum</td>
<td>sharp</td>
<td>dull</td>
<td>sharp</td>
<td>dull</td>
<td>sharp</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
</tr>
<tr>
<td>SubOpt1</td>
<td>sharp</td>
<td>dull</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>sharp</td>
<td></td>
</tr>
<tr>
<td>SubOpt2</td>
<td>medium</td>
<td>dull</td>
<td>dull</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>sharp</td>
<td></td>
</tr>
<tr>
<td>SubOpt3</td>
<td>medium</td>
<td>dull</td>
<td>medium</td>
<td>medium</td>
<td>dull</td>
<td>sharp</td>
<td>sharp</td>
<td></td>
</tr>
</tbody>
</table>

2.3.3 Model Validation

No experimentation was carried out to validate the FE models. However, we felt the models were valid for a number of reasons. First, when there is symmetry in the tooth, as is the case in testing the Blunt, Pointed, and Strong Cusp Hypotheses, one would expect there to be symmetry in the stress distributions in both the food item and enamel cap, and there was. In addition, when there is asymmetry in the tooth, as is the case when testing the Complex Cusp Hypothesis, one would expect there to be asymmetry in the stress distributions in both the food item and enamel cap, and there was.
Second, results from this model are only being compared to other results gained from the model, so if there is any error all models should be equally affected. This implies that the results need to be consistent and resolute, but not necessarily accurate. We tested the resolution of the model by conducting a mesh quality test, increasing the number of nodes in the model from about 150,000 to over 1,500,000. The largest models took up to two weeks to run, an increase in time of over 8,000%, and resulted in less than a 3% change in the optimality ratio. This leads us to have high confidence in both the resolution of our model and in our comparative results. We do not have high confidence in the magnitudes of our results, since numerous assumptions went into the construction of the model (i.e. force applied, constraints, material properties, and geometry).

Third, the proxy food item used in this model is identical to the one used in Berthaume et al. (2010), which was partially validated through physical experimentation. In addition, we performed a sensitivity study on the model for the 2010 paper where geometry, constraints, material properties, and mesh size were altered.

2.4 Results

As predicted by the Blunt Cusp Hypothesis, there was a significant, negative relationship between RoC and strain energy when all RoCs are assumed to be equal (p < 0.01, y=-3.74*x+380.12, r = 0.812; Fig. 2.6). However, there was no evidence that teeth composed entirely of dull cusps performed any worse (exhibited higher strain energy) than teeth with both sharp and dull cusps (Table 2.2). In addition, the magnitude of the strain energy varied over a relatively small range (353 - 379 Joules) relative to the range of values seen in the Taguchi simulations (362-554 Joules; Table 2.2).
The Pointed Cusp Hypothesis predicted a positive correlation between contact area and RoC and, as a consequence, a negative correlation between RoC and tensile stresses in the food item (Fig. 2.2). We did find a significant positive correlation between contact area and RoC (p < 0.01, y=0.31*x+33.91, r = 0.872). (Note that this correlation is not higher because contact area calculations are dependent on element sizes, which are finite.) However, we found a positive relationship between tensile stresses in the food item and RoC (p < 0.01, y=0.53*x+64.10, r = 0.859) (Fig. 2.6). This is likely because of the complex interactions occurring between the tooth and the food item, where forces are being transferred from the tooth to the food item at a variety of angles.
Under the Strong Cusp Hypothesis, we predicted a negative correlation between tensile stresses in the enamel and RoC. We did not find a correlation between these two variables (Fig. 2.6), but the lowest tensile stresses in the enamel did occur when the cusps were as dull as possible.

As predicted under the Complex Cusps Hypothesis, the optimal tooth exhibits a combination of sharp and dull cusps (Fig. 2.7). The four most optimal teeth (Optimum, SubOpt1, SubOpt2 and Subopt3) have very high optimality ratios compared to the least optimal tooth (T1; Table 2.2). In general, for the four most optimal teeth, there is one dull cusp which acts to create high stresses in the food item while decreasing the stresses in the enamel, while the other cusps are acting to stabilize the food item.
Table 2.2: Results of the Taguchi simulations. Teeth are arranged from most optimal (top) to least optimal (bottom). SubOpt1 and SubOpt2 are suboptimal teeth that had optimality ratios extremely close to the optimal tooth’s optimality ratio.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Reaction Force (kN)</th>
<th>Contact Area (mm²)</th>
<th>Food Item</th>
<th>Maximum Tensile Stress (MPa)</th>
<th>Strain Energy (J)</th>
<th>Enamel Maximum Tensile Stress (MPa)</th>
<th>Optimality Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Optimum</td>
<td>2</td>
<td>30.61</td>
<td>150</td>
<td>495</td>
<td>91</td>
<td>1.640</td>
<td></td>
</tr>
<tr>
<td>SubOpt1</td>
<td>2</td>
<td>30.33</td>
<td>149</td>
<td>489</td>
<td>94</td>
<td>1.594</td>
<td></td>
</tr>
<tr>
<td>SubOpt2</td>
<td>2</td>
<td>31.38</td>
<td>136</td>
<td>490</td>
<td>87</td>
<td>1.570</td>
<td></td>
</tr>
<tr>
<td>SubOpt3</td>
<td>2</td>
<td>31.80</td>
<td>140</td>
<td>492</td>
<td>89</td>
<td>1.570</td>
<td></td>
</tr>
<tr>
<td>T5</td>
<td>2</td>
<td>32.01</td>
<td>140</td>
<td>554</td>
<td>96</td>
<td>1.469</td>
<td></td>
</tr>
<tr>
<td>T18</td>
<td>2</td>
<td>32.23</td>
<td>128</td>
<td>414</td>
<td>96</td>
<td>1.336</td>
<td></td>
</tr>
<tr>
<td>T8</td>
<td>2</td>
<td>33.27</td>
<td>99</td>
<td>399</td>
<td>75</td>
<td>1.320</td>
<td></td>
</tr>
<tr>
<td>T10</td>
<td>2</td>
<td>34.29</td>
<td>122</td>
<td>394</td>
<td>93</td>
<td>1.315</td>
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2.5 Discussion

Our results support the Complex Cusp Hypothesis and portions of the Blunt and Pointed Cusp Hypotheses, but fail to support the Strong Cusp Hypothesis. There was a significant negative correlation between RoC and strain energy as predicted by the Blunt Cusp Hypothesis, although strain energy differed by only 26 Joules between the sharpest
and dullest tooth models we tested (which raises the question whether the difference in performance between a tooth comprised of all-dull and a tooth composed of all-sharp cusps is biologically significant). However, when we inspected the optimality morphospace, in which RoCs among cusps were varied independently, we found that several teeth comprised primarily of sharp cusps caused less strain energy in the food item than teeth comprised entirely of dull cusps (SubOpt2 and SubOpt3 models in Table 2.2). This fails to support the second part of the Blunt Cusp Hypothesis, which predicts that given equal bite forces, a tooth composed of a combination of dull and sharp cusps will cause a food item to absorb lower strain energy than a tooth containing primarily of sharp cusps. We also found that the optimality score of a tooth comprised entirely of dull cusps was lower (model All Dull, Table 2.2) that the optimality ratio in teeth that contained both sharp and dull cusps (i.e. models T17, 1.047, and SubOpt2, 1.570; Table 2.2). Within the confines of this study, teeth comprised of both sharp and dull cusps have an advantage over teeth composed entirely of dull cusps.

In terms of optimality of the tooth shapes spanned by the model morphospace, the tooth composed of entirely sharp cusps has the worst optimality ratio; stresses were higher in the enamel than in the food item (T1, Table 2.2). In contrast, the optimal tooth was composed of a mixture of dull, medium and sharp cusps (model Optimum, Table 2.2); here the food item experienced much higher tensile stresses than the enamel. To visualize the difference between the most and least optimal teeth, it is useful to examine the distributions of tensile stress in the food item and along the EDJ of Optimum, SubOpt1, SubOpt2, SubOpt3 and T1 (Fig. 2.8). The least optimal tooth morphology (T1) was comprised of four equally sharp cusps and produced four, low stress concentrations.
Figure 2.8: Tensile stress distributions for the most optimal (upper left), least optimal (upper right), and suboptimal (bottom) teeth. The top contour plots are the tensile stress distributions on the underside of the food item, and the bottom are the tensile stress distributions along the EDJ. These illustrate the stress distributions at the load step closest to a 2 kN bite force.
in the food item and four areas of higher tensile stress in the enamel at the EDJ. This is the stress distribution predicted for crushing via uniform compression.

The optimal tooth morphology (Fig. 2.7, Tables 2.1 and 2.2) produced a single, extremely high stress concentration in the food item, which should promote crack initiation and propagation, and only two areas of high tensile stress along the EDJ, both of which are lower than the stress concentrations in the food item (Fig. 2.8). This is because the morphologies of the two cusps on the mesial side of the tooth act to deform the food item in the distal direction. At the same time, the combined morphology of the cusps on the distal side prevents the food item from deforming too far in the distal direction and effectively stabilizes the food item. This forces the food item to remain in contact with cusps the cusps on the mesial side of the tooth. The area of high stress in the food item, surprisingly, does not come from the food item interacting with any of the sharp cusps, but from the food item interacting with the cusp comprised entirely of dull RoCs.

The stress concentrations in the enamel along the EDJ in the most optimal tooth morphologies are restricted to the valleys between the cusps, while the stress concentrations in the least optimal tooth are closer to the tips of the cusps. It is interesting that the stress concentrations in the optimal tooth models correspond to where enamel tends to be thicker, harder and stronger in some mammals (i.e. the great apes and modern humans), while the stress concentrations in the least optimal tooth correspond to where enamel tends to be thinner, more compliant and weaker in primates (e.g., (Kono et al., 2002; Constantino et al., 2011)).
There are a number of factors researchers have used to measure effective brittle food item fracture (e.g. strain energy, stresses in the food item, stresses in the enamel). From the perspective of inducing high stresses in a food item, the food item experienced the highest stresses when the RoCs were varied independently. However, the level of strain energy in the food item and the tensile stresses in the enamel tend to be lowest in teeth in which the RoCs were modeled as equal, and higher in teeth in which the RoCs were allowed to vary independently. If minimizing strain energy in the food item or minimizing the maximum tensile stresses in the enamel were more important than producing high stresses in the food item, then having a tooth where all the RoCs are equal would be beneficial. However, if producing high stresses in the food item were more important, having a tooth comprised of both sharp and dull cusps would be beneficial.

2.6 Conclusions

We were unable to support the Strong Cusp hypothesis. The results did support the first part of the Blunt and Pointed Cusp Hypotheses, but not the second part. Our exploration of optimal designs supports the Complex Cusps Hypothesis: a combination of sharp and dull cusps is the most efficient morphology for fracturing brittle, hemispherical food item because it produces high stress concentrations in the food item while minimizing stresses in the enamel. However, if the function of a tooth is to minimize strain energy absorbed by the food item or to preserve the integrity of the enamel (and not fracture a brittle food item), having a tooth that is composed of cusps with equal RoCs in all directions is optimal.
Our results show that optimally shaped teeth have a combination of sharp and dull cusps, where some cusps are acting to initiate fracture while others are acting to stabilize the food item. This indicates that the mechanics of biting a food item sufficiently large enough to be contacted by multiple cusps cannot be addressed by considering only single cusp/food item interaction. For large food items, the morphology of the entire occlusal surface becomes important, and the mechanical relationship between the occlusal surface and the food item becomes complex. This may explain, in part, while the molars of most mammals have cusps with different radii of curvature.

It is not uncommon to use FEA to understand how aspects of tooth morphology affect function (Thresher and Saito, 1973; Berthaume et al., 2010; Anderson et al., 2011; Benazzi et al., 2011; Wood et al., 2011). However, these models tend to be simplistic, dealing with small, calculable aspects of tooth morphology or represent a small sample of possible tooth morphology, making it difficult, if not impossible to fully understand the complexity of tooth/food item interactions. As demonstrated in this study, the combination of FEA and parametric modeling allows for multiple parameters to be analyzed at once and for a large sample size to be generated. Results of such a study can lead to a better understanding the complex role of tooth/food item interactions.
CHAPTER 3

THE EFFECTS OF RELATIVE FOOD ITEM SIZE ON OPTIMAL TOOTH CUSP SHARPNESS DURING BRITTLE FOOD ITEM PROCESSING

3.1 Abstract

Teeth are assumed to be optimal for their function; this allows researchers to derive dietary signatures from teeth with different shapes. During these analyses it is common to normalize for size, effectively masking the effects of relative food item size. Here, we investigate how relative food item size affects optimal tooth cusp radius of curvature (RoC) during brittle food item fracture. We used a finite element (FE) model of a four cusped, parametric, bunodont molar where tooth cusp RoCs could be varied independently in both the buccolingual and mesiodistal direction to determine the optimal set of tooth cusp RoCs at a 2kN bite force for four different food item sizes: small, medium, large, and x-large. The optimal set of tooth cusp RoCs maximize tensile stresses in the food item, promoting fracture, while minimizing tensile stresses in the enamel, preserving enamel integrity (Berthaume et al., 2013). Optimal combinations of tooth cusp RoCs were determined for each food item size by using morphospaces constructed by varying tooth cusp RoCs. The effects of changes in tooth cusp RoC on variations in metrics of tooth performance were also investigated to determine if changes in tooth cusp RoC affected variations in performance variables equally across food item
sizes. We found that, as food items increase in size, they go from interacting primarily with the valleys between the cusps to interacting primarily with the cusps themselves, changing the interactions between the tooth and the food item, changing the optimal set of RoCs. However, all optimal morphologies were fairly similar, having one dull cusp that promoted food item failure and three cusps that acted to stabilize the food item. There was also a positive correlation between food item size and variation in maximum tensile stresses in the food item, and a negative correlation between food item size and variation in maximum tensile stresses in the enamel, suggesting that changes in tooth cusp RoC will have a larger effect on tensile stresses in the food item when the food item is large, and a larger effect on tensile stresses in the enamel when the food item is smaller.

3.2 Introduction

One way that mammals are unique is that they chew their food prior to swallowing. This is one of the factors that has led to a functional difference between the anterior and posterior teeth during mastication, where anterior teeth are used primarily to parse food into smaller pieces and posterior teeth are used primarily to grind food up prior to digestion (Lucas, 2004). This has led to a number of metrics to quantify posterior tooth shape (i.e. orientation patch count (Evans et al., 2007; Santana et al., 2011), the relief index (M'Kirera and Ungar, 2003; Boyer, 2008), angularity (Ungar and M'kirera, 2003; Peter, 2004), and Dirichlet normal surface energy (Bunn et al., 2011; Godfrey et al., 2012)) where shape is used to infer function (see (Evans, 2013) for a review). While
distinct, these metrics share two common assumptions. First, teeth are optimally shaped for their function. If they were not optimally shaped for their function, mammalian teeth would not be able to be differentiated on the basis of diet. Second, none of the metrics take food item shape or size into account; rather, they relate metrics of tooth shape to broad dietary categories and/or food item material properties.

One metric that has been used to quantify tooth shape is tooth cusp sharpness (Yamashita, 1998; Hartstone-Rose and Wahl, 2008; Berthaume et al., 2013). Tooth cusp sharpness is commonly measured by radius of curvature (RoC), where cusps with higher RoCs are duller and cusps with lower RoCs are sharper. For single cusp-food item interactions, sharper teeth reduce the contact area between the tooth and the food item, leading to a reduction in energy and reaction force during food item fracture and increasing food breakdown efficiency (Evans and Sanson, 1998; Evans and Sanson, 2003; Lucas, 2004; Freeman and Lemen, 2007). This increase in efficiency, however, comes at a cost. The reduction in contact area between the tooth and the food item also causes the stresses in the tooth to increase, increasing the probability of enamel fracture (Lawn et al., 2009). Unfortunately, as more complicated occlusal morphologies are considered (i.e. multicusped teeth), these relationships begin to fall apart (Berthaume et al., 2013).

In multicusped teeth, RoC can be measured in terms of blade or cusp sharpness (Popowics and Fortelius, 1997; Yamashita, 1998; Evans et al., 2005; Berthaume et al., 2013; Frunza and Suciu, 2013). While similar, blade and cusp sharpness are distinct, mostly in that they are affected by tooth wear in different ways. Worn cusps tend to get duller with wear (up until they are worn down to the dentin) while worn blades can get
duller or sharper, depending on the level of attrition (tooth-tooth wear) that is occurring (Greaves, 1973; Luke and Lucas, 1983; Popowics and Fortelius, 1997; Evans and Sanson, 2005; Evans et al., 2005; Evans et al., 2005). Therefore, wear will decrease a cusp’s efficiency at food item breakdown but can increase a blade’s efficiency at food item breakdown by keeping the blades sharp (Teaford and Walker, 1983; Popowics and Fortelius, 1997).

Since blade and cusp sharpness are correlated to food item breakdown efficiency in multicusped teeth, the question then becomes, “Does relative food item size matter?” Studies on allometric scaling of blade sharpness in mammals have led to puzzling results: it appears that there is no allometric scaling with blade sharpness and body size (Evans et al., 2005), although some animals with identical diets have duller teeth if they are larger (i.e. *Bison bison*) and sharper teeth if they are smaller (i.e. *Alcelaphus buselaphus*). And if blade sharpness is truly a correlate, these differences in blade sharpness suggest there is an allometric relationship (Popowics and Fortelius, 1997). However, it is more likely than not that blade sharpness is correlated to some other factors (e.g. bite force, enamel thickness, tooth size) that are roughly correlated with body size (Evans et al., 2005). To date, no such study has been conducted concerning cusp sharpness (but see Chapter 4).

Regardless of whether or not an allometric relationship exists, it may not be practical to normalize for size when investigating size relationships of functional parameters (blade and cusp sharpness), since function may be masked by the animal’s size. For example, Patas monkeys (*Erythrocebus patas*), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla, Gorilla beringei*) are all known to predate on ants (Isbell et al., 2013) but vary greatly in tooth size (Gingerich et al., 1982; Lucas et al., 1986).
Therefore, ants are larger relative to tooth size for *Erythrocebus* than for either *Pan* or *Gorilla*. This will lead to a very different functional interaction between the food item and the tooth (see Fig. 3.1) where the *Erythrocebus* tooth will cut and crush the ant into smaller pieces while the *Gorilla* tooth will crush and grind the ant (Luke and Lucas, 1983). While allometric scaling is a necessary sacrifice for functional parameters in the absence of information concerning the external environment, it may not always be an acceptable one.

In addition, single cusped teeth that are sharp, regardless of tooth size, experience higher stresses than single cusped teeth that are dull, and are consequently more likely to fracture at lower loads. (Again, the exact relationship between sharpness and probability of fracture in complex, multicusped teeth, is unknown.) Therefore, normalizing for body size could be masking size-dependent effects on the tooth’s shape (Evans et al., 2005).

Here, we test the relationship between relative food item size and optimal tooth cusp RoCs against two null hypotheses. The first null hypothesis states that relative food item size does not affect optimal tooth cusp sharpness during brittle food item fracture. As established under the Complex Cusp hypothesis (Berthaume et al., 2013), an optimal morphology for brittle food item fracture is one that maximizes tensile stresses in the food item (causing the brittle food item to fracture (Callister, 2004; Berthaume et al., 2013)) while minimizing tensile stresses in the enamel (preventing enamel fracture (Lucas et al., 2008; Lawn and Lee, 2009; Lee et al., 2009; Constantino et al., 2012)). Optimality is judged using the following criterion:

\[
Optimality\ Criteria = \max \left( \frac{\text{maximum tensile stresses in the food item}}{\text{maximum tensile stresses in the enamel}} \right)
\]  

(3.1)
For the null hypothesis to hold, the optimal morphology will remain constant for a food item with a given shape and set of material properties, as the food item is isometrically scaled.

The second null hypothesis states that tooth cusp sharpness is equally important during brittle food item fracture, regardless of relative food item size. For mammals that regularly consume relatively large food items, changes in tooth cusp sharpness may affect the efficiency of food item breakdown differently for mammals that regularly consume relatively small food items or a mixture of relatively large and relatively small food items (Fig. 3.1). Food item breakdown efficiency for brittle food items has been measured using a number of performance metrics. Here, we will examine four, namely maximizing the optimality criterion (Complex Cusp Hypothesis, (Berthaume et al., 2013)), maximizing tensile stresses in the food item (Pointed Cusp Hypothesis, (Freeman and Weins, 1997; Evans and Sanson, 1998; Evans and Sanson, 2003; Berthaume et al., 2010)), minimizing tensile stresses in the enamel (Strong Cusp Hypothesis, (Lucas et al., 2008; Lawn and Lee, 2009; Lee et al., 2009; Berthaume et al., 2010)), and minimizing
energy absorbed by the food item (Blunt Cusp Hypothesis, (Kay, 1981; Luke and Lucas, 1983)). This hypothesis states that variation in performance metrics, when averaged over a given set of tooth shapes, will not vary as the food item is isometrically scaled.

Variation in performance metrics will be measured using the coefficient of variation. The coefficient of variation provides a unitless measure that captures the level of variation present in these metrics without having size effects. Some of the measurements of food breakdown efficiency are highly dependent on absolute size (i.e. tensile stresses are higher in the enamel and the food item at a given bite force when the food item is smaller). The coefficient of variation enables us to measure variation in performance metrics as tooth cusp RoC changes independent of absolute size effects, allowing us to compare variability in performance metrics across different food item sizes. If the coefficient of variation changes with relative food item size, this would support our assumption that, when measuring RoC, one should not normalize for size.

### 3.3 Materials and Methods

We used a parametric finite element (FE) model of a four cusped, maxillary bunodont molar in ANSYS APDL 13.0 to test our null hypotheses. Details concerning the construction of the model are discussed in Berthaume et al. (2013). Briefly, there are a number of parameters that can be varied in this model (cusp height, valley height, cusp sharpness, enamel thickness, and distance between the cusps), but for this study, all parameters other than tooth cusp sharpness were held constant at the following values: cusp height=5mm, valley height=3mm, enamel thickness=1mm, distance between the
cusps in the mesiodistal direction=15.7mm, distance between the cusps in the buccolingual direction=15.4mm. Distances between cusps are based on the average width and length of a male gorilla tooth (Gingerich et al., 1982). Cusps were allowed have one of three values for sharpness: sharp (RoC=3mm), medium (RoC=5mm), or dull (RoC=7mm). Since tooth cusp sharpnesses are allowed to vary independently in both the buccolingual and mesiodistal directions, this gave us a total of eight variables that could be varied (Frunza and Suciu, 2013), Chapter 4.

Food items were modeled as hollow hemispheres (Berthaume et al., 2010; Berthaume et al., 2013), which were isometrically scaled to be small, medium, large and x-large (outer radii=5.9, 10.0, 14.1 and 18.2mm, inner radii=4.82, 8.16, 11.5, and 14.84mm respectively, see Fig. 3.2). We know from experimentation and finite element analysis that the hollow hemispheres fracture because of high tensile stresses that build up along the inner surface (Berthaume et al., 2010; Berthaume et al., 2013) and that, when interacting with a large food item, tensile stresses along the enamel dentin junction (EDJ) cause enamel to fail (Chai et al., 2009b; Lawn et al., 2009; Barani et al., 2011; Keown et al., 2012; Berthaume et al., 2013). Therefore, maximum tensile stresses in the food item and enamel were used in calculating the optimality criterion.

The food item was centered over the occlusal surface of the tooth and constraints were placed on the bottom of the food item, preventing it from translating away from the occlusal surface of the tooth and from rotating around an imaginary axis that ran through the apex of the food item. These constraints allowed the food item to settle into the position of minimum potential energy along the occlusal surface of the tooth during the simulations (Berthaume et al., 2010). Constraints were also placed on the bottom of the
Figure 3.2: Four hollow, hemispherical food items. From left to right, outer radii=5.9mm, 10.0mm, 14.1mm, and 18.2mm, inner radii=4.82mm, 7.4mm, 11.5mm, and 14.84mm.

tooth to prevent it from translating in the mesiodistal and buccolingual directions, and a displacement of 3mm was placed on the bottom of the tooth, translating it into the food item to simulate biting.

Finally, contact elements were placed on the outside of the food item and target elements were placed on the surface of the tooth. These elements allow ANSYS to detect when the tooth is intersecting the food item during the simulation, as there was initially a gap between the food item and the tooth. Contact simulations were solved in a minimum of 10 substeps to maximize accuracy. Results were exported at each substep and equations were constructed of reaction force vs. displacement, and displacement vs. stresses and energy, so the displacement, energy, and stresses at a 2 kN reaction force could be calculated (Lucas et al., 1994; Berthaume et al., 2013).

To test the first null hypothesis, optimal combinations of RoCs for each food item size were determined. This was done by creating four morphospaces (one morphospace per food item size) using an L18 orthogonal array with the Taguchi sampling method.
The Taguchi method is a statistical, partial factorial sampling method which allows users to run the minimum number of simulations necessary to construct a multivariable morphospace (Taguchi, 1987; Lee and Zhang, 2005; Lin et al., 2007). Optimal sections of the morphospaces were continually sampled until the optimal set of RoCs were obtained for each morphospace, resulting in an additional 25-40 simulations being run per morphospace (Berthaume et al., 2013). To gain support for the first null hypothesis, the four optimal combinations of RoCs from each morphospace would need to be the same.

The Taguchi method allows for an unbiased sampling of design variables, and provides 18, distinct tooth morphologies that represent an equal sampling of tooth morphologies over a given morphospace. The results from these 18 morphologies, when run against a small, medium, large and x-large food items, were used to test the second null hypothesis (see Table 2.1). As stated above, food item breakdown efficiency and tooth preservation are measured in a variety of manners, including reducing work/energy to fracture, minimizing reaction forces at fracture and promoting high stresses in the food item (e.g. (Abler, 1992; Freeman and Weins, 1997; Evans and Sanson, 1998; Freeman and Lemen, 2006; Freeman and Lemen, 2007; Freeman and Lemen, 2007; Lucas et al., 2008; Anderson, 2009; Berthaume et al., 2010; Whitenack and Motta, 2010; Anderson and Rayfield, 2012; Berthaume et al., 2013)). While all these variables are size dependent, some are dependent on absolute size and some are dependent on relative size (Lucas et al., 2008).

We chose to look at four measures of performance, namely the optimality criterion, maximum tensile stress in the food item, maximum tensile stress in the enamel,
and energy absorbed by the food item. The first three criterion are of particular importance during brittle food item fracture, while the fourth more important during ductile food item fracture. The coefficients of variation (standard deviation/mean) were calculated for these variables for a given food item size across all 18 tooth shapes. Since the coefficients of variation have no variation for a given food item size, it is impossible to test significant differences in coefficients of variation using an ANOVA. Statistically significant differences were tested using linear regressions, where the second null hypothesis would be rejected if a statistically significant linear relationship existed between food item size and the coefficients of variation for the performance variable.

3.4 Results

Numerical results from the simulations conducted to construct the four morphospaces, along with the results from the simulations with the optimal tooth morphologies, can be found in Table 3.1. There is a decrease in the optimality criterion, maximum tensile stresses in the food item, maximum tensile stresses in the enamel, and energy absorbed by the food item as the food item increases in size. As the food item increases in size isometrically, the thickness of the hemisphere increases, changing the effective stiffness of the system and allowing the smaller, thinner walled food items to deform more than the larger, thicker walled food items. This in turn causes an increase in strains and consequently, an increase in stresses in the smaller food items, causing them to absorb a larger amount of energy at a given bite force. The smaller food items also cause a decrease in contact area between the tooth and the food item, causing an
increase in the tensile stresses in the enamel. Because the maximum tensile stresses decrease at a faster rate in the food item than in enamel as the food item increased in size, the optimality criterion decreased as the food item increased in size.

Three distinct optimal tooth shapes were derived from the four morphospaces: one for the small food item, one for both the medium and large food item, and one for the x-large food item (Fig. 3.3, Table 3.1). The optimal morphologies are similar, consisting of one mesiolingual cusp that is dull in both the buccolinguinal and mesiodistal directions, one mesiobuccal cusp that is sharp in the buccolinguinal direction and dull in the mesiodistal direction, and two distal cusps that are sharp in the mesiodistal direction. The differences between the teeth lie in the distal cusps, which are dull, sharp, or a mixture of dull, medium and/or sharp in the buccolinguinal direction.
Table 3.1: Results of the Taguchi simulations. T1–T18 are the 18 tooth shapes constructed using the Taguchi method. Small, Med/Large, and X-Large are the optimally-shaped teeth for the small, medium, large, and x-large food items. Because the food item was more flexible and given the ability to deform more, the smaller food items, making them more flexible and giving them the ability to deform more. The causes them to have higher strains, and consequently, stresses than the larger food items, and allows them to absorb more energy. This also causes

<table>
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<th>T2</th>
<th>T3</th>
<th>T4</th>
<th>T5</th>
<th>T6</th>
<th>T7</th>
<th>T8</th>
<th>T9</th>
<th>T10</th>
<th>T11</th>
</tr>
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<td>2.107</td>
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<td>1.32</td>
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<td>1.296</td>
</tr>
<tr>
<td>X-Large</td>
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Table 3.2: Coefficients of variation for the performance metrics, calculated for each food item size across the 18 tooth morphologies created using the Taguchi method.

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<th>Maximum tensile stress, enamel</th>
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The coefficients of variation for the performance variables at each food item size are presented in Table 3.2. There is a statistically significant linear relationship between both the coefficients of variation for maximum tensile stresses in the food item ($r=0.92$, $p=0.04$) and the coefficients of variation for maximum tensile stresses in the enamel ($r=-0.92$, $p=0.04$) and food item size. The linear relationships between the coefficients of variation for the optimality criterion and food item size ($r=0.8647$, $p=0.0701$) as well as strain energy absorbed by the food item ($r=-0.6244$, $p=0.2098$) and food item size were not statistically significant.

### 3.5 Discussion

As food item size changed, so did the optimal tooth morphology, leading us to reject our first null hypothesis, that optimal tooth shape is independent of relative food item size. For all optimal teeth, the duller (mesiolingual) cusp consistently promoted high stresses in the food item while resisting high stresses in the enamel. It did this by interacting with the food item more than the other cusps, effectively transferring more of the 2kN force to the food item and causing a high stress concentration along the inner surface of the food item while dissipating the stresses in the enamel, assuming the food
item is placed centrally. The other three cusps acted primarily to stabilize the food item and force it to interact with the dull cusp. All optimal teeth also minimized the number of stress concentrations in the food item to two, while the most non-optimal teeth had up to four stress concentrations in the food item, causing more of an isostress condition.

All optimal teeth have similar morphologies; the only difference between them is the RoC in the buccolingual direction on the two distal cusps. This change occurred because, as the food item increased in size, the fundamental interactions between the tooth and the food item changed. The small food item interacted primarily with the valleys between the cusps while the medium and large food items interacted nearly equally with the valleys between the cusps and the cusps themselves, and the x-large food item interacted primarily with the cusps themselves (see Fig. 3.2).

The changes in the distal cusps of the optimal morphologies for the small, and medium/large food items reflects changes necessary for food item stabilization. When the food item was small, it fit in the valleys between the cusps. However, there was some extra space, so the distal cusps needed to be duller (and larger) in order to minimize the number of unconstrained degrees of freedom and stabilize the food item. As the food item increased in size (i.e. medium and large food items), it still mostly fit in the valleys between the cusps, but only when the distal cusps got sharper in order to increase the size of the valleys. Finally, when the food item became too large (i.e. x-large) to fit in the valleys, food item stabilization could only be done by the cusps themselves. This made the distal cusps duller. While this is happening, the mesiobuccal cusp remains sharp in the buccolingual direction to allow the food item to have enough space to interact
primarily with the mesiolingual cusp and dull in the mesiodistal direction to form a wall
that prevents the food item from drifting too far in the buccal direction.

Each cusp serves a distinct purpose; either to promote high stresses in the food
item or to stabilize the food item and cause it to interact in an efficient way with the cusp
that is promoting high stresses. Because the fundamental interactions between the tooth
and the food item change as the food item changes in size, the cusps that cause
stabilization must change in order to properly stabilize the food item. The cusp that
promotes high stresses, however, does not need to change.

The coefficients of variation change as the food item changes in size, leading us
to reject our second null hypothesis. In particular, there is a statistically significant
correlation between stresses in the food item and stresses in the enamel and food item
size. This implies that changes in tooth cusp sharpness will lead to a larger change in
stresses in the food item when the food item is large compared to when it is small.
Therefore, if creating stresses in the food item is important, there may be a larger
selective pressure for tooth cusp sharpness during brittle food item processing when the
food item is large compared to the tooth. The correlation between stress in the enamel
and food item size predict the exact opposite: the negative correlation between the
variables predicts that there may be a larger selective pressure for tooth cusp sharpness (if
reducing stresses in the enamel is being selected for) when the food item is small
compared to the tooth.

In terms of comparative biology, this means that if an animal regularly consumes
brittle food items that are relatively large and there is a large coefficient of variation in
tooth cusp sharpness measurements, this would imply that having predictable stresses in the food item is not as important as having predictable stresses in the enamel. If there is a small coefficient of variation in tooth cusp sharpness measurements, this would imply that having predictable stresses in the enamel is not as important as having predictable stresses in the food item. The opposite is true for small food items.

Data sets for tooth cusp sharpness are rare, and most focus on a subset of tooth cusp RoC dimensions (i.e. just the buccolingual RoCs, (Yamashita, 1998; Vinyard et al., 2011)), making it difficult to test these predictions. Furthermore, while data on food item size and material properties are sometimes collected, the level of brittleness/ductility is often not tested (e.g. (Dominy et al., 2008; Vogel et al., 2009)) because food items are assumed to be perfectly brittle (Lucas, 2004). This makes it difficult to test the predictions made in this paper with data that currently exist in the literature.

Finally, it has been assumed that food item material properties and not food item size drives changes in optimal tooth shape (Lucas, 2004); this is an invalid assumption. Food item size, along with food item related properties such as food item material properties, affect optimal tooth shape.

3.6 Conclusion

As brittle, hemispherical food items increase in size, their fundamental interactions with the occlusal surface of the tooth change, going from interacting primarily with the valleys between the cusps to interacting primarily with the cusps themselves. This causes the optimal set of tooth cusps RoCs to change with relative food
item size, invalidating the assumption that food item size does not impact optimal tooth shape. Furthermore, variation in tooth cusp RoC affects some metrics for functionality during food item breakdown (i.e. stresses in the food item and enamel) more than others (i.e. energy and optimality criterion). This supports the idea that, when measuring tooth cusp RoC, it should not be normalized for by tooth size. Instead, if the information is available, RoC should be normalized with relative food item size, or not at all, and the data should just be phylogenetically corrected.

Further investigations into the effect relative food item size and shape have on other tooth shape metrics (e.g. relief (M'Kirera and Ungar, 2003; Boyer, 2008; Godfrey et al., 2012; Evans, 2013)), after we have accounted for food material properties, may reveal correlations between these metrics and food item shapes and sizes. Finally, by extending this type of analysis to the micro scale, we may begin to have some insight into the effects of internal tooth structure (i.e. enamel decussation (Chai et al., 2009b), enamel thickness distribution (Kono et al., 2002; Shimizu, 2002)) on food item breakdown and be able to further expand our understanding of the biomechanics of microwear (Lucas et al., 2013).
4.1 Abstract

Mammalian molars have undergone heavy scrutiny to determine correlates between aspects of occlusal morphology and diet. Here, we examine the relationship between one aspect of occlusal morphology, tooth cusp radius of curvature (RoC), and two broad dietary categories, folivory and frugivory, in apes. We hypothesize that there is a relationship between tooth cusp RoC and diet, and that folivores had sharper teeth than frugivores. We further test the correlation between tooth cusp RoC and tooth cusp size. Eight measures of tooth cusp RoC were taken from 53 M2s (two RoC measurements per cusp, one in the buccolingual plane and one in the mesiodistal direction) from four species and subspecies of frugivorous apes (Pongo pygmaeus, Pan troglodytes troglodytes, Pan troglodytes schweinfurthii, and Gorilla gorilla gorilla) and two subspecies of folivorous apes (Gorilla beringei beringei, and Gorilla beringei graueri). Phylogenetically corrected ANOVAs were run on the full dataset and several subsets of the full dataset, revealing that, when buccolingual RoCs are taken into account, tooth cusp RoCs could statistically differentiate between folivorous and frugivorous apes, and PCAs revealed that folivores had duller teeth and frugivores had sharper teeth. In addition, a weak, but statistically significant positive correlation exists between tooth cusp size and tooth cusp RoC. We hypothesize differences in tooth cusp RoC are
correlated with wear rates, where, per vertical unit of wear, duller teeth will have a longer length of exposed enamel ridge than sharper teeth. Finally, more data needs to be gathered to determine if the correlation between tooth cusp RoC and tooth cusp size holds true when small primates are considered, or if the relationship falls apart as it does with blade sharpness and body size (Evans et al., 2005).

4.2 Introduction

The relationship between diet and post-canine morphology has been successfully established in a number of mammals (e.g. lemurs (Godfrey et al., 2012), carnivorans, rodents (Evans et al., 2007), and bats (Dumont, 1995; Santana et al., 2011). A number of aspects of tooth morphology have been identified as being important in food item breakdown, e.g. radius of curvature, rake angle, notch angle, and shearing crest length (Evans and Sanson, 2003; Lucas, 2004). Some of these morphologies have been well studied and linked to diet—for example, shearing crest length has been linked to food breakdown efficiency in folivorous primates (Sheine and Kay, 1982; Ungar and Williamson, 2000; Shimizu, 2002; Lucas, 2004; King et al., 2005), while some aspects of tooth morphology have been less well studied and not as well correlated with diet. One example is tooth cusp sharpness measured by Radius of Curvature (RoC) (Yamashita, 1998; Evans and Sanson, 2005; Berthaume et al., 2010).

RoC is quantified by fitting a circle to the profile of a tooth cusp and measuring the radius of the circle, leading sharper cusps to have smaller RoCs and duller cusps to have larger RoCs. During single cusp food item interactions, teeth with smaller RoC (i.e. sharper teeth) have been shown to reduce the energy and force necessary to breakdown
food items (Evans and Sanson, 1998; Song et al., 2011). This is believed to be the reason behind differences in incisor RoC in tamarins and marmosets (Vinyard et al., 2011). When multiple cusps interact with the food item, the relationship becomes more complex because the bite force is not distributed evenly between all cusps (Berthaume et al., 2013). This has led to limited success in correlating molar RoC with diet in multicusp molars (Yamashita, 1998; Hartstone-Rose and Wahl, 2008; Berthaume et al., 2010).

RoC of multicusp teeth is commonly measured solely in the buccolingual direction (Yamashita, 1998; Berthaume et al., 2010). This is the functional aspect of tooth sharpness in blades, which have an “infinite” RoC in the mesiodistal direction (Popowics and Fortelius, 1997; Lucas, 2004; Evans et al., 2005). Unlike blades, tooth cusps have a finite RoC in the mesiodistal direction and could therefore play a role in food item breakdown. Although datasets comparing buccolingual to mesiodistal RoC in molars are rare, difference between mesiodistal and buccolingual RoCs has been documented in human mandibular third molars, which could be linked to functional differences in mesiodistal and buccolingual cusp RoCs (Frunza and Suciu, 2013).

Other measures of tooth morphology, correlated with tooth sharpness, have shown a significant difference between folivorous or frugivorous primate molars, where folivores have sharper teeth than frugivores. For example, Kay has shown that primates with folivorous and insectivorous diets tend to have longer, sharper crests compared to frugivorous primates (Kay, 1977; Kay and Simons, 1980; Kay and Covert, 1984; Teaford and Ungar, 2000). Boyer (2008) further supported this conclusion by showing that folivorous prosimians (e.g. *Indri indri*) have higher relief indices than frugivorous prosimians (e.g. *Daubentonia madagascariensis*) (Boyer, 2008). No such study has yet
been done to determine if differences in tooth cusp RoC exists between folivorous and frugivorous primates or mammals. Here, we investigate whether RoC is correlated to diet in extant great apes.

We test the null hypothesis that there is no correlation between tooth cusp RoC and diet in great apes, with an alternative hypothesis that folivorous great apes will have sharper cusps than frugivorous great apes.

In studies concerning functional morphology, it is common to normalize for size. While no information exists concerning allometric relationships between tooth cusp sharpness and body size, two studies have been done concerning the relationship between blade sharpness and body size. Popowics and Fortelius (1998) determined that there was a correlation between blade sharpness and body size, but when the study was expanded to include bats in Evans et al. (2005), the correlation disappeared. Regardless of whether a strong correlations exist between blade RoC and body size, it is obvious that medium and large-bodied mammals (e.g. bison and giraffes) have duller teeth than small-bodied mammals (e.g. bats) (Popowics and Fortelius, 1997; Evans et al., 2005). If a relationship exists between tooth cusp sharpness and size, we predict that it will exist between tooth cusp sharpness and tooth cusp size (i.e. RoC of the protocone in the buccolingual direction would be correlated with the width of the protocone, and RoC of the protocone in the mesiodistal direction would be correlated with the length of the protocone) and not body size.

The question then becomes, when looking at the correlation between tooth cusp RoC and diet, should RoC be normalized using tooth cusp size? From an efficiency viewpoint, the answer is no since a sharper tooth will be more efficient than a duller tooth.
at breaking down a food item, regardless of the size of the tooth, just like a sharp, small pair of scissors will be more efficient at cutting than a dull, large pair of scissors. Therefore, we predict that correlations between tooth cusp sharpness and diet should not be affected by body size in apes.

In this study, the folivorous apes are represented by two subspecies of eastern gorillas: *Gorilla beringei beringei* and *Gorilla beringei graueri*. While it is generally accepted that *G.b.beringei* is folivorous (e.g. (Elgart-Berry, 2004; Robbins, 2007; Rothman et al., 2007; Taylor et al., 2008)), the categorization of *G.b.graueri* as a folivore is not as well accepted. This is because *G.b.graueri* is less folivorous than *G.b.beringei*, prefers ripe fruit when available, and fruit is frequently found in their fecal samples (Yamagiwa et al., 1992; Yamagiwa et al., 1994; Yamagiwa et al., 1996; Robbins, 2007; Constantino et al., 2009). However, studies where fecal samples are collected and analyzed consistently show that *G.b.graueri* consumes more plant matter than fruit. Furthermore, a recent 9 year study showed that folivorous matter made up 70% of *G.b.graueri’s* diet (Yamagiwa et al., 1992; Yamagiwa et al., 2005). This has led us to classify *G.b.graueri* as a folivore.

The frugivorous apes are represented by western gorillas (*Gorilla gorilla gorilla*), two subspecies of chimpanzees (*Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*) and orangutans (*Pongo pygmaeus*). *G.g.gorilla* and *P.t.troglodytes* are sympatric species in western Africa that are frugivorous with largely overlapping diets, preferring ripe fruit to unripe fruit (Rogers et al., 1990; Williamson et al., 1990; Wrangham et al., 1998; Head et al., 2011), but falling back on different resources(M'Kirera and Ungar, 2003; Ungar and M'kirera, 2003; Peter, 2004).
Table 4.1: Teeth analyzed for this experiment. NMNH=National Museum of Natural History, MRAC=Royal Museum for Central Africa, AMNH=American Museum of Natural History, SAPM=Staatssammlung für Anthropologie und Paläoanatomie München (State Museum of Anthropology and Paleontology in Munich).

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample Size</th>
<th>Museums</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gorilla beringei beringei</em></td>
<td>8</td>
<td>NMNH</td>
</tr>
<tr>
<td><em>Gorilla beringei graueri</em></td>
<td>7</td>
<td>MRAC</td>
</tr>
<tr>
<td><em>Gorilla gorilla gorilla</em></td>
<td>10</td>
<td>AMNH, CMNH</td>
</tr>
<tr>
<td><em>Pan troglodytes schweinfurthii</em></td>
<td>11</td>
<td>AMNH, MRAC</td>
</tr>
<tr>
<td><em>Pan troglodytes troglodytes</em></td>
<td>9</td>
<td>CMNH</td>
</tr>
<tr>
<td><em>Pongo pygmaeus</em></td>
<td>8</td>
<td>SAPM</td>
</tr>
</tbody>
</table>

*P.t.schweinfurthii* is sympatric with *G.b.graueri* but has a more frugivorous diet. *P.t.schweinfurthii* regularly consumes figs throughout the year and expands its foraging range during fallback episodes (Yamagiwa et al., 1996). Finally *P.pygmaeus* is generally categorized as being highly frugivorous, although it is known to exhibit a high level of granivory (seed predation) and tends to fall back on more mechanically challenging food items than the other apes (Conklin-Brittain et al., 2001; Vogel et al., 2009). While we recognize the benefits of differentiating between frugivory and granivory because of differences in mechanical properties and nutritional value that exist between the skin, flesh, and seed of the fruit, it is not uncommon in the literature concerning *P.pygmaeus*’s diet to have the general category of frugivory encompass granivory. Furthermore, studies that differentiate between granivory and frugivory classify *P.pygmaeus*’s diet as more frugivorous than granivorous (Conklin-Brittain et al., 2001).

### 4.3 Materials and Methods

RoC was measured in both the buccolingual and mesiodistal direction for the four maxillary cusps of M2 for the six species and subspecies of apes were analyzed (Table
4.1). M\textsuperscript{2} were chosen because M\textsuperscript{1} was generally too worn for analysis and M\textsuperscript{3} was not always present.

Tooth cusp RoC is highly sensitive to tooth wear and cannot be measured if the tooth’s cusp is not present. Therefore, the least worn teeth from the Paleoanthropology Laboratory at the University of Arkansas (courtesy of Peter Ungar) were chosen for analysis. Detailed descriptions of how casts were obtained and molds were created can be found in the more detail in the published literature (M'Kirera and Ungar, 2003; Peter, 2004; Klukkert et al., 2012). Briefly, high resolution casts of posterior tooth rows of museum specimens were manufactured for dental topographic analysis. The casts are made of a translucent epoxy mixed with a pale pink pigment, and were coated with a thin layer of Magnaflux Spotcheck SKD-S2 Developer to aid the XSM multi-sensor scanner (Xystrum Corp., Turino, Italy) in picking up the surface of the tooth (Peter, 2004). Prior to scanning, teeth were oriented in anatomically correct position such that the y-axis ran in the mesiodistal direction and the x-axis ran in the buccolingual direction, with the most distal molar placed closest to the origin. Scans were taken at a resolution of 50\textmu m, resulting in 400 data points per square millimeter.

4.3.1 Measuring RoC

There are three published methods for measuring sharpness using RoC. The first is to take a cross-section of the tooth in the buccolingual direction, fit a circle to the tip of cusp, and measure the radius of the circle (Arcona and Dow, 1996; Popowics and Fortelius, 1997; Yamashita, 1998; Vinyard et al., 2011). While efficient, this method is prone to have a high degree of human error. The second is to fit a polynomial function to the cross-section of the tooth and the polynomial is used to calculate RoC (Evans and
While less prone to human error, the polynomial function is affected by the order of the function, resolution of the scans and how much of the cusp is used to create the polynomial function. Finally, the third is to fit a paraboloid to the surface of the cusp tip and use the equation of the paraboloid to calculate the RoC (Frunza andSuciu, 2013). Unfortunately, Frunza and Suciu (2013) did not test this method's feasibility, and we found that it was impossible to consistently fit a paraboloid to the surface of a cusp. This was because particularly sharp cusps with irregular geometries caused singularities that were impossible to capture with a second or third order surface functions. Given the level of human error in the first method and the infeasibility of the third method, we chose to use the second method and fit a third order polynomial function to the tooth cusp to measure RoC.

There are two ways to define the geometry of the tooth cusp, by outlining the profile of the cusp (Evans and Sanson, 1998; Yamashita, 1998) and by extracting a cross-section of the cusp through physical or digital sectioning (Popowics and Fortelius, 1997; Evans et al., 2005; Vinyard et al., 2011). It was determined that, when measuring RoC through viewing the profile of the cusp, RoC was larger than when measuring RoC through sectioning. Since sectioning gives a more accurate representation of the geometry of the cusp, we chose to digitally section the teeth.

To measure RoC, CloudCompare, an open source 3D point cloud and mesh processing program (http://www.danielgm.net/cc/), and ToothCuspRoC, an in house program written in Matlab (http://www.mathworks.com/ ) were used. CloudCompare was used to extract the x, y, and z coordinates for five points per cusp: the apex of the cusp, and the limits of the cusp tip in the mesial, distal, buccal, and lingual directions. This information was
then used by ToothCuspRoC to extract cusp cross-sections from the point cloud data that passed through the apex of the cusp in the buccolingual and mesiodistal directions. ToothCuspRoC then fit third order polynomials to the profiles of the cusps using the least squares method (Dai and Newman, 1998; Dai et al., 2007), and the coefficient of determination was determined. If the coefficient of determination was 0.975 or higher, the polynomial equation was considered a good fit for the cross-section of the cusp. If the coefficient of determination was less than 0.975, the polynomial was considered to be a bad fit, the portions of the cross-sections with the lowest z-coordinates were rejected, and a new polynomial equation was fit to the new cross-section (see Fig. 4.1). This process was repeated until a coefficient of determination of 0.975 or higher was reached or there were less than 11 data points left representing the cross-section of the cusp, in which case the cusps were reconstructed.

Once a third order polynomial was obtained, the second derivative was taken, since RoC is equal to the inverse of the second derivative.

\[ z = Ax^3 + Bx^2 + Cx + D \quad (4.1) \]
\[ \frac{dz}{dx} = 3Ax^2 + 2Bx + C \quad (4.2) \]
\[
\frac{d^2z}{dx^2} = 6Ax + 2B \\
RoC = \left| \frac{1}{6Ax + 2B} \right|
\] (4.3) (4.4)

In the equations above, A, B, C, and D are constants defined by the polynomial function, \(z\) is the height of the cusp, and \(x\) is the distance being traveled along the cross-section. Since \(x\) is a continuous variable, having it in equation (4.4) was problematic. To measure tooth cusp RoC, the \(x\) variable that corresponded with the location of the tip of the cusp, (aka the local maximum of the polynomial function) needed to be calculated. This was done by taking the first derivative (equation (4.2)), setting it equal to zero and solving for \(x\) using the quadratic equation.

\[
0 = 3Ax^2 + 2Bx + C \\
x = \frac{-2B \pm \sqrt{4B^2 - 4(3A)C}}{2(3A)} \\
x = \frac{-2B \pm \sqrt{4B^2 - 12AC}}{6A} \\
x = \frac{-B \pm \sqrt{B^2 - 3AC}}{3A}
\] (4.5)

The \(x\)-value from equation (4.5) gives a negative value for \(\frac{d^2z}{dx^2}\) when substituted into equation (4.3) is the \(x\)-value that corresponds with the location of the cusp tip.
In total, each cusp had 8 RoC measurements; four in the buccolingual direction and four in the mesiodistal direction.

4.3.2 Cusp Reconstruction

If a cusp was worn, damaged, or had a cross-section that never had a high enough coefficient of determination, the original cross-sections of the cusps were exported from ToothCuspRoC and brought into Excel. If the cusp was worn or damaged, the worn or damaged portion of the cusp was removed and a third order polynomial was fit to the undamaged portions of the cusp (Fig. 4.2). The cusp was then centered so the z-axis ran through the tip of the polynomial function representing the cusp and the coefficients for the third order polynomial equation were recorded and used to calculate the RoC. Centering the cusp minimized any round-off error that may have been present in calculating the coefficients of the third order polynomials in Excel.

If the cusp was not worn/damaged and a coefficient of determination of 0.975 was never reached, the cross-section was edited in Excel until a third order function was obtained that visually mimicked the geometry of the tooth (Fig. 4.2). As with worn or damaged cusps, the function was centered around the z-axis and the coefficients of the
third order polynomial were used to calculate the RoC. Nearly all RoCs taken from reconstructions fell in the range or tooth cusp RoCs calculated using ToothCuspRoC.

4.3.3 Relationship between Tooth Cusp Sharpness and Tooth Cusp Size

After RoC measurements were calculated, CloudCompare was used to measure the maximum cusp width and length for each cusp. If a relationship exists between tooth cusp sharpness and tooth cusp size, it should exist regardless of which cusp is being analyzed. Therefore, we combined the data for all the cusps and ran a linear regression using R statistical package (www.r-project.org, (Ihaka and Gentleman, 1997)) between all tooth cusp sizes and tooth cusp RoCs.

4.3.4 Data Analysis

The full dataset of 8 RoCs per tooth and three subsets of that data were analyzed to determine if there was a correlation between tooth cusp RoC and diet. The first subset of data consisted of the four buccolingual RoCs to determine if the buccolingual RoCs could be used by themselves to determine diet since this has been done in the past (Yamashita, 1998; Vinyard et al., 2011). The second subset consisted of the four mesiodistal RoCs to determine if the mesiodistal RoCs were correlated with diet or if they could be ignored as this has been done in the past (Yamashita, 1998). Finally, the third subset was the buccolingual RoCs of just the paracone and metacone, since just the buccolingual RoC on the buccal side of the tooth when measuring blade sharpness (Popowics and Fortelius, 1997; Evans et al., 2005).

The importance of controlling for phylogeny when inferring diet from molar morphology is well documented (e.g. (Kay and Ungar, 1997; Peter, 2004)). We believe that if there is a biomechanical signal for diet, it should tease out from the dataset once
the dataset has been phylogenetically corrected, regardless of how closely related the species are.

To correct for phylogenetic signals, we ran a phylogenetically corrected ANOVA with a Bonferroni correction to determine if there was a correlation between diet and tooth cusp sharpness. The geiger package in R (Harmon et al., 2008) was used with a recent primate phylogeny what was created using a supermatrix to differentiate between our species (G.gorilla, G.beringei, P.troglodytes and P.pygmaeus) (Springer et al., 2012). The tree we used put the divergence time between Pongo and Hominidae at 15.6277 mya, Gorilla and Pan at 7.2877 mya, P.troglodytes and P.paniscus at 2.1921 mya, and G.beringei and G.gorilla at 2.183 mya. As no data exists concerning the divergence between G.bgraueri and G.b.beringei (Thalmann et al., 2007) and the data concerning the divergence of the subspecies of chimpanzees are inconsistent (Won and Hey, 2005; Caswell et al., 2008), we created four possible trees to cover the extreme cases of divergence (Fig. 4.3).

Tree1 assumes that the divergence between G.b.beringei and G.b.graueri occurred only 10,000 years after the divergence between G.beringei and G.gorilla, and the divergence between P.t.troglodytes and P.t.schweinfurthii happened only 10,000 years after the divergence between P.troglodytes and P.paniscus. Tree2 assumes that the divergence between G.b.beringei and G.b.graueri occurred only 10,000 years ago and the divergence between P.t.troglodytes and P.t.schweinfurthii occurred only 10,000 years after the split between P.troglodytes and P.paniscus. Tree3 assumes that the divergence between G.b.beringei and G.b.graueri occurred only 10,000 years after the divergence between G.beringei and G.gorilla, and the divergence between P.t.troglodytes and
Figure 4.3: Four possible phylogenies.

*P.t.schweinfurthii* happened only 10,000 years ago. Finally, Tree4 assumes that the divergence between *G.b.beringei* and *G.b.graueri*, and between *P.t.troglodytes* and *P.t.schweinfurthii* occurred only 10,000 years ago.

All datasets of data were run through the phylogenetically corrected using all four trees. If the p-values from the ANOVA analyses for all four trees was statistically significant (p<0.05), we considered the set of data to be both sufficient and robust for determining diet for tooth cusp RoC. Finally, PCAs were run on the datasets that were statistically significant to determine which morphological characteristics differentiated folivores from frugivores.
Table 4.2: Averages and standard deviations for cusp tip sharpnesses (RoC) in the mesiodistal (MD) and buccolingual (BL) directions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Protocone</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MD</td>
<td>BL</td>
<td>MD</td>
<td>BL</td>
<td>MD</td>
<td>BL</td>
<td>MD</td>
</tr>
<tr>
<td>G.b.beringei</td>
<td>2.543</td>
<td>1.14</td>
<td>2.175</td>
<td>0.695</td>
<td>2.041</td>
<td>0.44</td>
<td>1.558</td>
</tr>
<tr>
<td></td>
<td>(1.14)</td>
<td>(0.695)</td>
<td>(0.44)</td>
<td>(0.41)</td>
<td>(0.442)</td>
<td>(0.334)</td>
<td>(0.171)</td>
</tr>
<tr>
<td>G.b.graueri</td>
<td>2.216</td>
<td>0.461</td>
<td>2.098</td>
<td>0.663</td>
<td>2.145</td>
<td>0.542</td>
<td>1.27</td>
</tr>
<tr>
<td></td>
<td>(1.282)</td>
<td>(0.461)</td>
<td>(0.663)</td>
<td>(0.542)</td>
<td>(1.056)</td>
<td>(0.312)</td>
<td>(0.416)</td>
</tr>
<tr>
<td>G.g.gorilla</td>
<td>2.063</td>
<td>0.693</td>
<td>1.529</td>
<td>0.48</td>
<td>1.165</td>
<td>0.393</td>
<td>0.808</td>
</tr>
<tr>
<td></td>
<td>(0.693)</td>
<td>(0.48)</td>
<td>(0.258)</td>
<td>(0.393)</td>
<td>(0.349)</td>
<td>(0.199)</td>
<td>(0.268)</td>
</tr>
<tr>
<td>P.t.schweinfurthii</td>
<td>1.394</td>
<td>0.719</td>
<td>1.003</td>
<td>0.419</td>
<td>1.138</td>
<td>0.54</td>
<td>0.859</td>
</tr>
<tr>
<td></td>
<td>(0.719)</td>
<td>(0.419)</td>
<td>(0.54)</td>
<td>(0.405)</td>
<td>(0.473)</td>
<td>(0.153)</td>
<td>(0.301)</td>
</tr>
<tr>
<td>P.t.troglodytes</td>
<td>2.175</td>
<td>0.556</td>
<td>1.642</td>
<td>0.655</td>
<td>1.038</td>
<td>0.456</td>
<td>0.832</td>
</tr>
<tr>
<td></td>
<td>(0.733)</td>
<td>(0.556)</td>
<td>(0.655)</td>
<td>(0.456)</td>
<td>(0.335)</td>
<td>(0.199)</td>
<td>(0.207)</td>
</tr>
<tr>
<td>P.pygmaeus</td>
<td>2.419</td>
<td>0.755</td>
<td>1.793</td>
<td>0.964</td>
<td>1.45</td>
<td>0.605</td>
<td>1.49</td>
</tr>
<tr>
<td></td>
<td>(1.36)</td>
<td>(0.755)</td>
<td>(0.964)</td>
<td>(0.605)</td>
<td>(1.029)</td>
<td>(0.179)</td>
<td>(0.945)</td>
</tr>
</tbody>
</table>

4.4 Results

Averages and standard deviations for the eight measures of RoCs and the widths and lengths of each cusp for each species can be found in Table 4.2 and Table 4.3. A total of 38.2% of the cusps needed to be reconstructed, mostly due to tooth wear or damage. 18.6% of the G.b.beringei, 50% of the G.b.graueri, 55.7% of the P.t.schweinfurthii, 22.5% of the G.g.gorilla, 39.1% of the P.pygmaeus, and 36.1% of the P.t.troglodytes cusps needed to be reconstructed.

A linear regression analysis revealed a weak but statistically significant correlation between tooth cusp size and RoC (Fig. 4.4). Although statistically significant, the low coefficient of determination makes it difficult to use this correlation to predict tooth cusp RoC from tooth cusp size. For example, P.t.troglodytes has similar RoC measurements to G.g.gorilla, but G.g.gorilla has larger cusps. In addition G.b.beringei, G.b.graueri, and G.g.gorilla have similarly sized cusps but very different RoCs.
Table 4.3: Averages and standard deviations for cusp widths and lengths. Mesiodistal dimensions correspond to lengths and buccolingual dimensions correspond to widths.

### Cusp Widths and Lengths (mm)

<table>
<thead>
<tr>
<th></th>
<th>Protocone</th>
<th>Hypocone</th>
<th>Paracone</th>
<th>Metacone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MD</td>
<td>BL</td>
<td>MD</td>
<td>BL</td>
</tr>
<tr>
<td><strong>G.b.beringei</strong></td>
<td>9.925</td>
<td>8.644</td>
<td>7.113</td>
<td>7.675</td>
</tr>
<tr>
<td></td>
<td>(0.994)</td>
<td>(0.993)</td>
<td>(0.684)</td>
<td>(0.819)</td>
</tr>
<tr>
<td></td>
<td>(0.52)</td>
<td>(0.766)</td>
<td>(0.817)</td>
<td>(0.925)</td>
</tr>
<tr>
<td><strong>G.g.gorilla</strong></td>
<td>8.934</td>
<td>8.125</td>
<td>6.12</td>
<td>7.425</td>
</tr>
<tr>
<td></td>
<td>(0.798)</td>
<td>(0.739)</td>
<td>(0.382)</td>
<td>(0.536)</td>
</tr>
<tr>
<td><strong>P.t.schweinfurthii</strong></td>
<td>5.818</td>
<td>6.027</td>
<td>4.459</td>
<td>5.086</td>
</tr>
<tr>
<td></td>
<td>(0.653)</td>
<td>(0.851)</td>
<td>(0.589)</td>
<td>(0.869)</td>
</tr>
<tr>
<td><strong>P.t.troglodytes</strong></td>
<td>5.522</td>
<td>5.872</td>
<td>4.4</td>
<td>5.344</td>
</tr>
<tr>
<td></td>
<td>(0.346)</td>
<td>(0.658)</td>
<td>(0.706)</td>
<td>(0.621)</td>
</tr>
<tr>
<td><strong>P.pygmaeus</strong></td>
<td>7.213</td>
<td>7.025</td>
<td>4.975</td>
<td>5.869</td>
</tr>
<tr>
<td></td>
<td>(0.91)</td>
<td>(0.594)</td>
<td>(1.132)</td>
<td>(0.781)</td>
</tr>
</tbody>
</table>

Figure 4.4: Linear regression between tooth cusp size and tooth cusp RoC.
Table 4.4: P-values for the phylogenetically corrected ANOVA analyses with Bonferroni corrections using four possible phylogenetic trees, covering the extreme ranges for the split between the subspecies of *G. beringei* and *P. troglodytes* (Fig. 4.3). P-values less than .05 are statistically significant.

<table>
<thead>
<tr>
<th></th>
<th>Full dataset (all RoCs)</th>
<th>First Subset (BL RoCs)</th>
<th>Second Subset (MD RoCs)</th>
<th>Third Subset (BL RoCs for Paracone and Metacone)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree1</td>
<td>0.001</td>
<td>0.003</td>
<td>0.155</td>
<td>0.010</td>
</tr>
<tr>
<td>Tree2</td>
<td>0.002</td>
<td>0.007</td>
<td>0.173</td>
<td>0.020</td>
</tr>
<tr>
<td>Tree3</td>
<td>0.001</td>
<td>0.001</td>
<td>0.138</td>
<td>0.001</td>
</tr>
<tr>
<td>Tree4</td>
<td>0.001</td>
<td>0.001</td>
<td>0.090</td>
<td>0.001</td>
</tr>
</tbody>
</table>

The phylogenetically corrected ANOVAs revealed a statistically significant difference between folivores and frugivores for three of the four datasets (see Table 4.4). When considering all 8 RoC measurements, just the buccolingual RoC measurements, and just the buccolingual RoC measurements for the paracone and the metacone, folivores separated from frugivores with a Bonferroni corrected p-value less than 0.05, for all four trees. When just the mesiodistal RoC measurements were used, folivores and frugivores did not separate out from one another, regardless of which tree was used (p>0.05).

PCA revealed that, in all cases where folivores separate out from frugivores, folivores had duller cusps (see Fig. 4.5). In the case of the third PCA, where only the buccolingual RoCs for the paracone and metacone were taken into account, the paracone did a better job at separating the folivores from the frugivores than the metacone.
c)

Figure 4.5: Biplot from a PCA, for the three datasets that separated out folivores from frugivores (Pr=protocone, Hy=hypocone, Pa=paracone, Me=metacone, MD=mesiodistal, BL=buccolingual), where the vectors depict the direction of increasing RoC. There are three sets of data: a) contains the full dataset, b) contains only the buccolingual RoC measurements, and c) contains the buccolingual RoC measurements of the buccal side of the tooth. In the first two cases, folivores had duller cusps, and in the third case the paracone was duller for folivores. Frugivores have red symbols and polygons while folivores have black symbols and polygons.

In general, gorillas and chimpanzees have about the same level of variation within for RoC measurements, with gorillas having coefficients of variation between 10.2 - 57.8% and chimpanzees having coefficients of variation between 14.1-51.5%. Orangutans, however, have a larger level of variation for RoC measurements, with coefficients of variation between 23.7-75.4%, resulting in a much larger area being covered by orangutans when a PCA scores are plotted (see Fig. 4.5).
4.5 Discussion

Tooth Cusp RoC measurements of M2s can successfully differentiate frugivorous apes from folivorous apes in three of the four datasets analyzed, leading us to reject our null hypothesis. Our results indicate that folivorous apes tend to have duller cusps while frugivorous apes tend to have sharper cusps, which is the opposite of what was predicted under our alternative hypothesis. As mentioned previously, teeth with little to no wear were analyzed in this study because it would be impossible to measure tooth cusp RoC in teeth that have any significant level of wear. However, it is difficult to find teeth with no wear in nature (Teaford and Walker, 1983; Teaford and Oyen, 1989; Zuccotti et al., 1998; Ungar and Williamson, 2000; Lucas, 2004; Peter, 2004; King et al., 2005; Godfrey et al., 2012; Lucas and Omar, 2012). How could tooth cusp RoC confer a functional advantage to frugivores or folivores if it disappears fairly easily and early on in an individual’s life?

We postulate that the differences in tooth cusp RoC may not convey a functional advantage in terms of increasing or decreasing contact area between the tooth and the food item, but may in fact cause ape teeth to wear in a way that is functionally advantageous. It is common to measure tooth wear in terms of factors such as percent of dentin exposed (Elgart, 2010). While effective, this does not convey how much height the cusp has lost due to wear. Here we discuss tooth wear in terms of vertical wear, where vertical wear defines the change in height of the enamel of the tooth cusp relative to an unworn version of the cusp.

As a dull cusp wears, it exposes a longer effective cutting surface per unit of vertical wear than a sharp cusp. Imagine two theoretical cusps, one dull (RoC=0.84mm) and one sharp (RoC=0.33mm), with widths of 1.5mm and perfectly circular cross-
sectional areas (Fig. 4.6), that are worn at a rate of 0.2mm per frame in . As the cusps wear, shearing crests are formed by the exposed enamel ridges, which form shearing crests and play an integral role in food item breakdown efficiency (King et al., 2005). The length of the exposed enamel ridges can be quantified by measuring the length of exposed enamel-dentin junction (EDJ) (Elgart, 2010). For a given level of vertical wear, a duller cusp will have a larger region of exposed EDJ and therefore have a longer shearing crest than a sharper cusp (Fig. 4.7). Having long enamel ridges is important to folivores, since it provides more cutting surfaces for fibrous foods to be processed on (King et al., 2005; Bunn and Ungar, 2009). Therefore, it would be advantageous for folivores to have duller teeth since this would increase the length of shearing crests exposed per unit of vertical tooth wear.

There is a statistically significant correlation between tooth cusp RoC and tooth cusp size, though the correlation is not strong. Before any definite conclusions can be drawn considering the relationship between tooth cusp RoC and tooth cusp size, more data, particularly concerning small primates, should be added to the dataset. This is because Evans et al. (2005) showed how a correlation between blade sharpness and body size, which can be present in medium and large bodied mammals (Popowics and Fortelius, 1997), can disappear when small mammals are included in the analysis. If, when the dataset is expanded, the correlation still exists, tooth cusp RoC should still not be normalized for by size since this could mask function (larger, duller scissors are less efficient than smaller, sharper ones). If RoC were normalized by some aspect of size, it should be normalized by bite force, since dull teeth with a large bite force may perform
Figure 4.6: Cross section of two theoretical cusps that are the same size (1.5 mm wide) but different RoCs: the cusp on the left has a RoC of 0.84 mm and the cusp on the right has a RoC of 0.33 mm. Each successive version of the cusp (top down) has had 0.02 mm of the tooth removed from the tip of the cusp, and a dotted red line is drawn in to show how much dentin would be exposed. The length of the dotted red line was then measured, and, assuming the cusp has a perfectly circular cross-sectional area, the circumference of this circle is equal to the length of the EDJ exposed. Vertical wear vs. length of EDJ exposed is graphed in Fig. 4.7.

just as well as sharp teeth with a small bite force. While bite force data currently exists for orangutans, no such data exists for chimpanzees and gorillas (Lucas et al., 1994).
Tooth cusp RoC was successful at separating folivorous from frugivorous apes when taking into account all 8 RoCs, just the buccolingual RoCs, and just the buccolingual RoCs of the paracone and metacone, but not when taking into account just the mesiodistal RoCs. If this pattern hold true across all primates and mammals, this supports the use of just buccolingual RoC measurements when inferring broad categories of diet (Popowics and Fortelius, 1997; Yamashita, 1998; Evans et al., 2005). Furthermore, it demonstrates that, while mesiodistal RoC measurements can be used in conjunction with buccolingual RoC measurements to infer diet, they cannot be used by themselves and may not serve a functional purpose during food item breakdown. Given this information, it appears mesiodistal RoCs do not need to be taken into account when inferring diet in apes.

PCA analyses revealed a large level of variation in *P. pygmaeus* and a smaller level of variation in *Gorilla* and *Pan*: this could be due to differences in enamel thickness and the high level of crenulations on orangutan teeth. *Gorilla* and *Pan* have relatively
thin enamel while *Pongo* is characterized as having medium to thick enamel (Smith et al., 2005; Vogel et al., 2008). This may prevent the cusps from wearing down and forming enamel ridges quick enough to be advantageous. In addition, the high level of crenulations present on the teeth of *P. pygmaeus*, particularly compared to the other species and subspecies looked at in this study, could be performing the same function as the enamel ridges would, causing tooth cusp RoC and the necessity of wearing teeth to produce the enamel ridges to be less important.

Finally, it should be noted that RoC is not the only way that tooth sharpness can be measured. Power equations (y=ax^b) can be fitted to the cross-sections of the cusps, where sharper teeth have higher power coefficients (b), providing a measurement for tooth cusp sharpness similar to RoC (Freeman and Lemen, 2007). Angularity, which can be measured using dental topographic techniques on both worn and unworn teeth, can also be used to measure tooth sharpness (Ungar and M'kirera, 2003; Bunn and Ungar, 2009; Klukkert et al., 2012). This is particularly useful when unworn teeth cannot be obtained, such as when analyzing certain parts of the fossil-record (Peter, 2004; Ungar and Scott, 2009). However, it provides a different type of information as it calculates the sharpness of the entire tooth, opposed to just the cusps. This, in turn, gives no information regarding the location of where the tooth is sharp and where the tooth is dull, potentially masking vital information about the occlusal morphology of the tooth (Shimizu, 2002; Evans and Sanson, 2003; Evans and Sanson, 2006; Benazzi et al., 2011; Berthaume et al., 2013)
4.6 Conclusion

Tooth cusp RoC can efficiently differentiate between folivores and frugivores when considering unworn, ape M2s. Surprisingly, folivores had duller teeth than frugivores: this could be because tooth cusp RoC does not directly impose functional advantages in food item breakdown (i.e. sharper cusps impose higher stresses in the food item (Berthaume et al., 2013)) but instead, may enable the tooth to wear in a certain manner that increases the amount of exposed enamel ridges per unit of vertical wear, giving folivores more cutting surfaces per unit of wear.

Diet is not the only factor that influences tooth cusp RoC: tooth cusp size also affects tooth cusp RoC. However, when inferring diet from tooth cusp RoC, it should not be normalized for by tooth cusp size since a cusp with a high RoC will perform the same way regardless of how big the cusp is. If some correlate of body size were to affect tooth cusp RoC, it should be bite force. However, the lack of bite force data for great apes prevents this hypothesis from being tested here. Furthermore, the correlation between tooth cusp RoC and diet may break down when primates of a wide range of body sizes are considered. Finally, when data is phylogenetically corrected, any correlations between morphology, such as tooth cusp RoC, and diet should come through.
CHAPTER 5
INFERRING FUNCTION FROM MOLARS: IS INTERNAL STRUCTURE OR SHAPE ALONE ENOUGH?

5.1 Abstract

Enamel thickness and tooth cusp sharpness (measured by radius of curvature, RoC) have been used as dietary indicators in mammals and are important factors in resisting enamel fracture and influencing tooth wear. Here, we investigate the presence of a relationship and/or trade-off between tooth cusp RoC and enamel thickness at the tip of the cusp and the implications that such a relationship would have on potential morphologies that could exist in nature. Tooth cusp RoC and enamel thickness were measured on digitally sectioned CT scans of unerupted and mostly unworn molars from three species of macaques (Macaca fascicularis, M. fuscata, and M. mulatta). No trade-off existed, but a weak, statistically significant linear trend existed only when outliers were removed from the data set ($r^2=0.0546$, $p<0.01$). However, this relationship had significant scatter, making it difficult to use enamel thickness to predict RoC. The lack of a strong correlation and trade-off implies that tooth cusp RoC and enamel thickness may be independent adaptations related to enamel fracture and influencing tooth wear. Furthermore, a range of cusp morphologies with varying abilities at resisting enamel fracture and influencing wear can exist in nature. These morphologies could be advantageous for different diets, and by taking only one variable into account, the dietary signal could be distorted due to commutations between the variables. These could be
present because of weak selective forces, homoplasies, and/or homologies. By taking both shape factors and internal architecture factors into account when deriving diet from teeth, it may be possible to tease out dietary signals, even when commutations are present.

5.2 Introduction

Thick enamel and dull cusps have been hypothesized to be dietary adaptations for consumption of mechanically challenging food items in mammals. While both characteristics have independently been correlated to diet, no studies have incorporated both characteristics into their analyses (Kay, 1981; Luke and Lucas, 1983; Dumont, 1995; Yamashita, 1998), automatically dismissing any type of multivariate relationships that may be occurring between enamel thickness and tooth cusp sharpness (measured through radius of curvature, RoC). Seeing as these variables are adaptations for the same selective forces (resisting enamel fracture and influencing tooth wear), multivariate relationships between enamel thickness and tooth cusp RoC could be significant and have significant influences on diet.

Thick enamel and dull cusps both play the same role in resisting enamel fracture, but influence tooth wear differently. Thick enamel reduces the stresses in the enamel along the EDJ, decreasing the probability of enamel fracture and allows a larger volume of enamel to be removed before the dentin is exposed compared to thin enamel (see Fig. 5.1 and Fig. 5.2) (Dumont, 1995; Lucas et al., 2008; Vogel et al., 2008; Smith et al., 2012; Lucas et al., 2013; Pampush et al., 2013). During single cusp/food item
interactions, dull cusps with high RoCs reduce the stresses in the enamel along the EDJ and expose a larger amount of EDJ per unit of vertical wear (after the cusp has been worn down to the dentin) than sharp cusps with low RoCs. The increase in EDJ exposure increases the length of shearing crest available, which is advantageous for food item processing in some primates (King et al., 2005) (see Fig. 5.1 and Fig. 5.2) (Lawn and Lee, 2009; Berthaume et al., 2010; Berthaume et al., 2013), Chapter 5. This may lead to two cusps that are equally efficient at resisting enamel fracture (sharp, thick enameled and dull, thin enameled) but wear in very different ways: the sharp, thick enameled cusp would resist wear longer but the dull, thin enameled cusp would wear in a manner that exposes a larger amount of EDJ per unit of vertical wear.
Figure 5.2: Length of exposed EDJ as a function of vertical wear for four cusps of identical widths with varying levels of tooth cusp RoC and enamel thickness. Duller cusps have a higher rate of length of EDJ per unit of vertical wear than sharper cusps, but ultimately the two will have the same length of exposed EDJ. Thin enameled teeth will have a longer length of exposed EDJ than thick enameled teeth.

Influences of both tooth shape and tooth internal structure, such as RoC and enamel thickness, on selective forces, such as enamel fracture and tooth wear, are often ignored or assumed to be negligible (but see (Luke and Lucas, 1983; Kay, 1985)). This assumption is valid if the variables are highly correlated so that one can be used to predict the other or if one of the variables has a relatively small influence on the selective force compared to the other variable and is therefore negligible (see Appendix C). Otherwise, the two variables will be interacting in such a way a commutation will be occurring (e.g. thickening enamel and not dulling cusps to resist enamel fracture) that could obscure the dietary signature hidden in the tooth. If a commutation is occurring, understanding why it is occurring (e.g. constraints, homoplasy, homology, weak selective force etc.) will provide significant insights as to why the combinations of tooth shape and internal structure present exist as they do.
No study to date has tested if enamel thickness and tooth cusp RoC are correlated, although studies have concluded that both variables affect enamel fracture and tooth wear (Lucas et al., 2008; Constantino et al., 2011; Berthaume et al., 2013). If the variables are correlated, this would prevent sharp, thick enameled cusps and dull, thin enameled cusps from existing. If the variables are uncorrelated, this could lead to teeth with dull cusps and thin enamel (e.g. possibly *Gorilla beringei beringei* (Martin, 1985; Smith et al., 2005), Chapter 5) or teeth with sharp cusps and thick enamel (e.g. possibly *Pongo pygmaeus* (Vogel et al., 2008; Smith et al., 2012), Chapter 6). These combinations of enamel thicknesses and tooth cusp RoCs could lead to teeth which experience an intermediate level of stress in the enamel along the EDJ that either maximize or minimize the rate at which EDJ is exposed, relative to vertical tooth wear (Fig. 1, Fig. 2).

A potential trade-off between enamel thickness and RoC has been hypothesized by Evans (2005): when a tooth has not yet worn down to the dentin, RoC cannot be greater than one-half the enamel thickness (RoC ≤ 0.5*enamel thickness). This trade-off implies that both enamel thickness and RoC need to be taken into account in order to infer diet from teeth. Trade-offs are common in nature (e.g. (Alexander, 1996; Dumont, 2010; Rivera and Stayton, 2011)), and always end up limiting the morphospace which can be occupied by a species, usually because of some type of constraint. In this case, they would prevent dull, thin enameled cusps from forming, a morphology that could be advantageous for animals which are trying to wear down their cusps quickly and expose long lengths of EDJ (Shimizu, 2002; King et al., 2005).

Here, we set out to test two null hypotheses. First, we test the null hypothesis that RoC and enamel thickness are uncorrelated. If they are correlated, then either enamel
thickness or RoC can be used to predict diet and the other can be ignored. If not, RoC and/or thick enamel may not be good enough to predict diet by themselves. Second, we test the null hypothesis that tooth cusp RoC is limited by enamel thickness (RoC ≤0.5*Enamel Thickness) (Evans et al., 2005). If enamel thickness limits RoC, it could prevent dull, thin enameled cusps from forming.

5.3 Materials and Methods

High resolution CT scans were taken of maxillary and mandibular tooth rows from juvenile *Macaca fascicularis* (22), *Macaca fuscata* (11) and *Macaca mulatta* (18). First, second and third molars were considered, but only unerupted or just erupted molars were used to ensure the teeth were either entirely or nearly unworn. Teeth were digitally sectioned along the coronal plane through the mesial cusps (Martin, 1985; Dumont, 1995; Smith et al., 2012) using methods presented in Smith et al., 2010. One molar was also sectioned through the distal cusps. Two RoC and enamel thickness measurements were taken per tooth section, one for the mesial and one for the distal cusp, giving us a total of 332 RoC and enamel thickness measurements.

Digital sections were imported into ImageJ (http://rsbweb.nih.gov/ij/) and oriented so the tips of the pulp horns created a horizontal line (see Fig. 3). While ape teeth in a previous study were oriented differently (anatomically correct position), we did not CT scan the ape teeth and therefore could not orient them using the internal structure of the tooth, which could be a useful method for orienting scans of teeth that have wear and/or were not scanned in anatomically correct position. We did find that orienting the
digital sections with respect to the pulp horns generally oriented the teeth in anatomically correct position. Some teeth had previously dried out and cracked, in which case segments of the cracked tooth were digitally repositioned in order to eliminate the crack, and if necessary, the tooth was reoriented again.

Digital sections were thresholded, converted to binary images, and the profile of the molar and the enamel dentin junction (EDJ) were isolated. Profiles of the molar and the EDJ were saved as separate text image files, giving each pixel a value of 255 if it was black or 0 if it was white, and converted to *.csv files using Microsoft Excel, 2007. The *.csv files were imported into a Matlab program which refined the profile of the molar and the EDJ by assigning an (x,y) coordinate to each pixel (x-coordinate=column number, y-coordinate=number of rows-row number). It then determined the y-coordinate...
of the highest black pixel for each column that contained black pixels, giving a maximum
of one y-coordinate per x-coordinate, which allowed a function to be fit to the profile of
the molar and the EDJ. The profile of the molar and the EDJ were then plotted to ensure
accuracy. Although enamel thickness varies spatially along the enamel crown (Kono et
al., 2002; Shimizu, 2002), we chose to measure enamel thickness at the tip of the cusp
because this is where it is most likely to be related to tooth cusp RoC.

Mathematically, RoC for a function f(x) is defined as the inverse of the curvature
of a function, which is given as the absolute value of the second derivative with respect to
x. To calculate RoC, a third order cubic polynomial, y, was fit to the top two rows of
pixels that made up the tip of the cusp using the least squares method (Dai and Newman,
1998; Dai et al., 2007) Chapter 5, and the absolute value of the inverse of the second
derivative was taken (see equations in chapter 4). Having a continuous variable (x) in the
RoC measurement is problematic. The x-coordinate that corresponds with the tip of the
cusp, where the first derivative goes from being negative to positive, and can be
calculated by setting the first derivative (equation (4.2)) equal to zero and solving for x.
The x-value from equation (4.5) that gives a negative value for \( \frac{d^2y}{dx^2} \) when plugged into
equation (4.3) corresponds with a local maximum in equation (4.1) and is the tip of the
cusp. The coefficient of determination for the function was then calculated to determine
how accurately the function represented the tip of the cusp.

This process was iterated several times, each iteration taking into account an
additional row of pixels, allowing the cubic equation to be fitted to a larger portion of the
cusp each iteration until the entire cusp was used. RoC is sensitive to amount of the data
being used to approximate the tooth cusp (Evans and Sanson, 1998), Chapter 5, and it is sometimes difficult to determine how much of the cusp should be used. The coefficient of determination can be used to remedy this problem, since it can be used to determine when the cubic function most accurately mimics the profile of the cusp, and therefore produces the most accurate RoC measurement. In a previous study on ape teeth where the resolution of the scans was 50 micrometers, an $r^2$ value of 0.975 or higher produced cubic equations that effectively mimicked the profile of the tooth. Therefore, in this study, the RoC measurement was based on the largest portion of the cusp fitted by a cubic equation with an $r^2$ value of 0.975 or higher. Exceptions included when the $r^2$ value never reached at least 0.975 and when there was a significant drop in the $r^2$ values between iterations. In the first situation, the RoC at the iteration with the highest $r^2$ value was used. In the second situation, the RoC measurement that corresponded at the iteration before the large drop in the $r^2$ value was used.

Two statistical analyses were carried out on both the full dataset and a partial dataset (when outliers were removed) using R statistical package (www.r-project.org, (Ihaka and Gentleman, 1997)). Because the RoC measurements did not follow a normal distribution, outliers were determined using quartiles ($> (Q3+1.5*\text{IQR})$ or $< (Q1-1.5*\text{IQR})$). To test the first null hypothesis, a linear regression was run between enamel thickness and tooth cusp RoC to determine if RoC is dependent on enamel thickness. To test the second null hypothesis, a linear regression was run on the upper bounds of the enamel thickness vs. RoC bivariate plot. The upper bound was determined by binning the enamel thicknesses and determining the maximum RoC for each bin, following protocol from Blackburn et al. (1992). It is recommended that between 6 and 15 bins
exist per dataset, so data was binned at 0.1mm intervals. If linear regressions on the upper bound were statistically significant, the slopes and intercepts were tested to see if they were significantly different from 0.5 and 0, respectively, using the SMATR package in R (Warton et al., 2006).

5.4 Results

Analysis of the full dataset (N=332) revealed no linear relationship between RoC and enamel thickness (y=0.0167*x+0.2595, $r^2=0.0004$, p=0.726, Fig. 5.4). When the outliers were removed (n=309), a weak but statistically significant linear relationship was detected between the two variables (y=0.14096*x+0.16783, $r^2=0.0546$, p=3.329e-05, Fig. 5.4). When the data was binned in order to test for an upper limit in the data set, none was revealed for either the full data set (y=-0.4657*x+1.0276, $r^2=0.1523$, p=0.1444) or when the outliers were removed (y=0.0167*x+0.4235, $r^2=0.0032$, p=0.8341). Because of this, the upper bounds were not tested to see if their slopes and intercepts differed significantly from 0.5 and 0, respectively.

Some of the extreme cases concerning the relationship between tooth cusp RoC and enamel thickness (dull cusp with thin enamel, dull cusp with thick enamel, sharp cusp with thin enamel, sharp cusp with thick enamel) are depicted in Fig. 5.5.
Figure 5.4: Scatter plot of the full dataset (left) and without outliers (right). The solid black line is the linear regression between enamel thickness and RoC and the dotted gray line is the limit predicted by Evans et al. (2005). According to the predicted limit, all data should fall below the dotted gray line.

Figure 5.5: Examples of sharp and dull cusps with thick and thin enamel. From top left to bottom right: *M.fascicularis* (M2), *M.fascicularis* (M1), *M.fuscata* (M3), and *M.mulatta* (M3).
5.5 Discussion

Our results lead us to gain support for the first null hypothesis and reject the second. We feel confident supporting the first null hypothesis (Ho=enamel thickness and tooth cusp RoC are uncorrelated) because, although a statistically significant linear relationship was observed between enamel thickness and RoC when the outliers were removed, the absence of a strong correlation ($r^2=0.0546$) and considerable scatter in Fig. 5.4 makes it difficult to use enamel thickness to predict RoC. In addition, the linear relationship does not exist when the full dataset is considered. We rejected the second null hypothesis because no statistically significant upper limit could be found which would indicate that enamel thickness limits RoC. An immense amount of data also crossed the predicted threshold both when outliers were included and excluded (see dotted gray line, Fig. 5.4). Furthermore, Fig. 5.5 shows how four different combinations of enamel thickness and RoC can exist in macaque cusps, each having varying levels of efficiency at resisting enamel fracture and will wear in different manners.

A large range of cusp morphologies with varying enamel thicknesses and RoCs can exist, and looking at just one variable could provide a narrow window into the dietary signature concealed by the cusp’s morphology. Several techniques have been developed that analyze the entire occlusal surface of the tooth in order to give a more holistic view of how the tooth is functioning in an effort to look through a wider window (e.g. (M'Kirera and Ungar, 2003; Ungar and M'kirera, 2003; King et al., 2005; Evans et al., 2007; Boyer, 2008; Bunn et al., 2011; Godfrey et al., 2012), see (Evans, 2013) for a review). However, these techniques tend to focus on the shape of the tooth and ignore
the tooth’s internal structure and microstructure. Furthermore, they tend to ignore gross wear patterns (but see (King et al., 2005)).

Relating information about tooth wear back to factors that affect tooth wear is critical, particularly in view of adaptations of these variables. Recent work on enamel thickness in primates has shown that relative enamel thickness (RET) is correlated with both durophagy and phytolod (the percentage of high-phytolith content plants in an animal’s total diet), a proxy for tooth wear (but see (Lucas et al., 2013)) (Rabenold and Pearson, 2011; Pampush et al., 2013). This led Pampush et al. (2013) to conclude that thick enamel is a homoplasy in primates, and that it is not be possible to differentiate teeth that have evolved to resist enamel fracture from those that have evolved to resist wear solely through RET. Including tooth shape factors that play a role in tooth wear with enamel thickness data could aid in the differentiation between these two groups once phylogenetic signatures have been corrected for.

Since a metric of tooth cusp shape was analyzed in this study, a measure of enamel thickness at the tip of the cusp was appropriate. When using measures of enamel thickness that take into account the entire tooth (i.e. RET or average enamel thickness, AET), more comprehensive measures of tooth sharpness (e.g. shearing quotient (Kay, 1975), relief index (M’Kirera and Ungar, 2003; Boyer, 2008), or angularity (Ungar and M’kirera, 2003; Peter, 2004)) should be used.

Similarly, including factors that describe the internal structure of the tooth in tooth shape studies can lead to the same sets of problems. This idea has been touched upon by researchers (e.g. (Kay, 1985; Lucas et al., 2008), where information about tooth
shape and enamel thickness are used to infer diet. However, as mentioned above, these studies tend not to focus on using these factors to predict how a tooth will wear, and whether the way in which the tooth will wear is going to be advantageous or detrimental to the organism. Although much progress has been made in understanding how teeth function, much more remains to be done where a more holistic view of how the tooth functions is considered. Although this could not be done in the past because of technological constraints, developments and applications of new methods such as finite element analysis (FEA) are making it possible for much more complex analysis concerning tooth function to be carried out (Benazzi et al., 2011; Benazzi et al., 2013).

5.6 Conclusion

Enamel thickness and tooth cusp RoC are uncorrelated variables and do not limit one another. If they are both adaptations for consumption of mechanically challenging food items, this implies that they are independent adaptations. They can also produce morphologies that wear in a wide variety of manners with varying degrees of ability to resisting high stresses in the enamel along the EDJ. This brings about the importance of having a holistic view of the tooth and including aspects of both tooth shape and the internal structure when analyzing it for dietary adaptations, as just one metric can provide false information due to homoplasies, homologies and/or trade-offs (Godfrey et al., 2012; Pampush et al., 2013). Furthermore, the presence of commutations in nature stresses the need for taking multiple lines of evidence when inferring diet from teeth.
CHAPTER 6

TESTING FUNCTIONAL OPTIMALITY IN TEETH

6.1 Abstract

Comparative studies of mammalian teeth often begin with the assumption that teeth are optimal for their function. Function, however, is highly dependent on developmental, phylogenetic, and ecological constraints and factors, which makes it difficult to use one test for function across a variety of taxa with varying diets (Luke and Lucas, 1983). Here, we present a model for testing function in teeth, where function can be broken into three categories: tooth strength, food item breakdown efficiency, and trapability (the ability to trap/stabilize a food item). When plotted using area coordinates, these variables create a morphospace which makes it possible to understand how teeth with vastly different functions can all be optimal. In addition, it allows these teeth to be directly comparable to one another, and gives researchers the ability to track how the optimal function of teeth can change with wear, and over evolutionary time within a clade.

6.2 Mammalian Tooth Function

Mammalian teeth come in a variety of unique shapes and sizes which are related to the animal’s development, phylogeny and ecology (Cuozzo and Sauther, 2012; Evans, 2013). To analyze tooth morphology, researchers generally begin with the assumption
that teeth are optimally shaped for their function; this enables them to tease out adaptive and dietary signatures (Lucas, 2004). Usually, this means picking a metric for a performance function and using it to test a sample of teeth. However, defining tooth function during mastication can be difficult, as function changes with respect to physical demands imposed on the tooth such as the composition of the animal’s diet (e.g. folivore, frugivore, insectivore), the position of the tooth in the animal’s mouth (i.e. anterior vs. posterior), and the role of the tooth plays in mastication (e.g. shearing, grinding). This could lead to the wrong functional test being chosen and, consequently, to optimally shaped teeth receiving low functional and optimality scores.

Here, we argue for a multivariate test for optimization that takes into account the primary aspects of tooth function during mastication. We argue that the primary all aspects of tooth function can be divided into three general categories: tooth strength, food item breakdown efficiency and trapability. By taking all three aspects of function into account, it is possible to determine what function the tooth is optimal for and to explain how two teeth with vastly different functional scores for one test can both be optimal for their own, respective functions.

6.2.1 Tooth Strength

Tooth strength is the ability of a tooth to resist destructive forces, such as fracture and wear. Metrics for tooth strength are dependent on the way in which a tooth is loaded, relative food item size, the material properties of the food items being consumed, material properties of the tooth, and the geometry/shape of the (Yamashita, 1998; Chai et al., 2009b; Keown et al., 2012).
In mammals, anterior teeth are generally used to parse foods into smaller pieces, graze, and browse, which induce bending and/or compressive loads on the teeth. Canines, in particular, are hypothesized to be particularly efficient at resisting bending loads (Valkenburgh and Ruff, 1987; Plavcan and Ruff, 2008). Posterior teeth, however, are used to breakdown food items into small pieces in preparation for digestion, which induce compressive and/or shearing loads on the teeth (Lucas, 2004; Deane, 2012). The difference in loading conditions could produce selective forces that would lead to teeth that are optimal for resisting masticatory loads, but look very different from one another. In addition, as the food item is masticated, food item size changes relative to tooth size. This would lead anterior teeth to regularly encounter food items that are relatively larger than the posterior teeth. This difference in relative food item size could also act to promote differentiation in optimal shape between anterior and posterior teeth and between small and large bodied mammals, see Chapter 3.

Material properties of food items are correlated with certain aspects of tooth morphology that deal with resisting fracture (Yamashita, 1998). In engineering, principal stresses are defined as force per perpendicular unit area. Hard, brittle, mechanically challenging food items tend to require a larger bite force to breakdown, and therefore impart larger reaction forces on teeth during mastication than compliant ones. This can create larger stress concentrations in the enamel. This has led to series of paper where enamel strength and its resistance to cracking and chipping during hard food item consumption has been analyzed (e.g. (Lucas et al., 2008; Constantino et al., 2009; Lawn et al., 2009; Lee et al., 2009; Lawn et al., 2010; Barani et al., 2011; Constantino et al., 2011; Keown et al., 2012)). The Strong Cusp Hypothesis was then formulated, based on
the idea dull teeth have been selected for in animal’s that consume hard, brittle food items as a way of reducing these stress concentrations, protecting the enamel’s integrity (Berthaume et al., 2010; Berthaume et al., 2013). While this set of hypotheses holds true for single-cusp contact mechanics problems (e.g. a canine penetrating a hide (Freeman and Lemen, 2007)), it does not hold true for more complicated contact mechanics problems (e.g. multi-cusp/food item interactions), where the bite force is not equally spread between all the cusps and the food item (Berthaume et al., 2013). Although much more information needs to be gathered to understand how food item material properties affect teeth during multi-cusp/food item interactions, it is clear that food item material properties have significant effect on optimal tooth morphologies (Freeman, 1979; Freeman, 1992; Vogel et al., 2008).

Finally, factors that are correlated with the internal structure of teeth and external shape factors greatly affect tooth strength. Material properties of enamel are known to vary, not only from tooth to tooth but within a tooth (Harrison et al., 1979; Cuy et al., 2002; Lee et al., 2010), where enamel with a high Young’s modulus would be stronger and resist wear more efficiently than enamel with a low Young’s modulus. In addition, enamel prism orientation is known to greatly influence tooth strength and tooth wear, where decussated prisms are efficient at resisting crack propagation and prisms that are perpendicular to the surface of the enamel are efficient at resisting wear (Martin, 1985; Chai et al., 2009b). Finally, enamel thickness is correlated with tooth fracture and tooth wear, where thicker enamel decreases the stresses along enamel dentin junction (EDJ), reducing the probability of enamel fracture and allows a larger volume of enamel to be
removed before the dentin is exposed (Dumont, 1995; Smith et al., 2012; Smith et al., 2012).

These variables, in addition with tooth shape factors, have implications in terms of enamel cracking and chipping (Chai and Lawn, 2007; Chai et al., 2009a; Constantino et al., 2010). For example, tooth cusp sharpness (measured through radius of curvature, RoC) reduces the stresses along the EDJ during single-cusp/food item interactions, increasing the tooth’s strength (Hartstone-Rose and Wahl, 2008; Lawn et al., 2009; Berthaume et al., 2013). Blade sharpness is also related to tooth strength, where sharper blades are not as strong as dull blades (Popowics and Fortelius, 1997; Evans et al., 2005). There are certainly other parameters of tooth shape that are correlated with tooth shape (e.g. occlusal relief (M'Kirera and Ungar, 2003; Boyer, 2008), angularity (Ungar and M'kirera, 2003)) but studies have yet to corroborate the relationship between these variables and stresses in the enamel. Furthermore, there are certainly interactions occurring between internal structure and tooth shape, such that by measuring tooth strength through just one of the variables could lead to skewed results, see Chapter 5.

Tooth strength can be measured physically or through computer simulation techniques. Enamel material properties, such modulus of elasticity and fracture toughness, have been calculated using Instron machines and indenters and been used to create equations to predict tooth failure (Cuy et al., 2002; Xie and Hawthorne, 2002; Lucas et al., 2008; Lawn et al., 2009; Lee et al., 2010; Barani et al., 2011). A common method used for predicting stresses, which can then be used as a metric for tooth strength, is finite element analysis (FEA). FEA is a powerful tool developed by engineers to find approximate solutions to continuum-mechanics problems using computer simulations. It
has the ability to take multiple factors into account, such as internal tooth structure and occlusal shape. Starting in the mid 1970s, researchers began using FEA to construct simplistic models of teeth, originally to understand the effects of tooth restoration (Farah and Craig, 1974; Yettram et al., 1976), calculating principal and shear stresses in the tooth as a way of measuring tooth strength. While simplistic models can still be used to answer complicated questions (e.g. (Anderson et al., 2011; Anderson and Rayfield, 2012; Barani et al., 2012)), advances have been made that enable researchers to construct much more complicated models that can be assigned complex sets of material properties and undergo complex loading conditions (Benazzi et al., 2011; Benazzi et al., 2013; Berthaume et al., 2013). Furthermore, FEA can be used in conjunction with other methods (i.e. Occlusal Fingerprint Analysis, OFA) to produce even more accurate models (Kullmer et al., 2009; Benazzi et al., 2011; Benazzi et al., 2013).

6.2.2 Food Item Breakdown Efficiency

Functionally, the primary role of mammalian teeth is to breakdown food items into smaller pieces, making food item breakdown efficiency critical in tooth shape studies. Because different food items break down in different manners, quantifying food item break down efficiency tends to difficult, particularly when being done across different species with different diets. Quantification of food item breakdown efficiency has been quantified in more ways than can be summarized in a few short paragraphs: here, we will describe a few of those methods.

The ability to break down food items into smaller pieces (i.e. chewing efficiency) is fairly easy to measure experimentally. Humans are frequently used as test subjects because extraneous variables (e.g. number of chews, side of the mouth chewing is
occurring on) can be controlled and subjects can be told to spit out the food so correlates of chewing efficiency (e.g. bolus and food particle size) can be easily measured (Lucas and Luke, 1983; Van der Bilt et al., 1993; Laird and Pontzer, 2013). Enough data has been gathered on humans that chewing efficiency can now be predicted with mathematical formulae (e.g. (Van der Bilt et al., 1987; Baragar et al., 1996; Prinz and Lucas, 1997), see Lucas 2004 for a review). One conclusion that can be drawn from these experiments and models is that, in humans, tooth size is highly correlated with chewing efficiency: a small reduction in tooth size can lead to a dramatic reduction in food item breakdown efficiency. It is inherently difficult to gather data on chewing efficiency in nonhuman mammals and consequently difficult to create mathematical models. However, factors such as food particle size can be measured in fecal matter and used as a measure for chewing efficiency, although caution should be taken when dealing with ruminants and animals with fermentation chambers (Pérez-‐Barbería and Gordon, 1998; Fritz et al., 2009). Recent work by Laird and Pontzer (2013) has begun to identify links between tooth shape and chewing efficiency, but more work needs to be done, particularly with nonhuman mammals.

Models that quantify food item breakdown efficiency fall into two categories: modeling through physical experimentation and with computers. Physical experiments usually involve loading either real or theoretical teeth into an Instron machine and using the teeth to fracture real or theoretical food items. Instron machines record vertical displacement via crosshead position (u) and reaction forces (F) caused by the tooth/food item interaction: this information can be used to calculate energy (E) absorbed by the system up to and at the point of fracture (Abler, 1992; Evans and Sanson, 1998; Freeman
and Lemen, 2006; Anderson and LaBarbera, 2008; Patel et al., 2008; Anderson, 2009; Berthaume et al., 2010; Whitenack and Motta, 2010; Anderson and Rayfield, 2012).

\[ E = \int F * du \]  \hspace{1cm} (6.1)

The experiments are often used to determine how efficient a tooth or shape is at breaking down a food item, where efficiency is determined by minimizing energy and/or force necessary for fracture (e.g. (Abler, 1992; Freeman and Lemen, 2007; Anderson and Rayfield, 2012)). These experiments and optimization analyses are particularly useful when attempting to analyze the effect of a discrete characteristic of a tooth, such as notch angle (Anderson, 2009; Anderson and Rayfield, 2012) or cusp tip sharpness (Evans and Sanson, 1998; Freeman and Lemen, 2006; Berthaume et al., 2010), but have severe limitations, particularly if the teeth being tested have not been selected to minimize energy and/or force necessary to fracture.

Computer models range in their level of complexity and, like with physical models, can be of either real or theoretical teeth. As with tooth strength, FEA can answer many questions concerning food item breakdown efficiency, namely the magnitudes and distributions of stresses and strains in the food item, along with forces and energy being absorbed by the food item. FE models which aim to understand the effect of tooth shape on food item breakdown efficiency can be fairly simplistic and employ 2.5D surface models of teeth (e.g. (Patel et al., 2008; Patel, 2009; Berthaume et al., 2010)). More complex metrics of food item breakdown efficiency (i.e. energy release rate) can also be measured with FEA, but requires intricate knowledge of the food item being modeled.

Food item material properties are also used in conjunction with aspects of tooth shape to infer food item breakdown efficiency (Strait and Vincent, 1998). This can be
done in two ways. First, hypotheses are made concerning differences in diet material properties tooth morphology in extant species (Yamashita, 1998; Taylor et al., 2008; Vogel et al., 2008; Yamashita, 2008; Yamashita et al., 2009) and then diet material properties are collected for those species (Elgart-Berry, 2004; Lucas, 2004; Wright et al., 2008; Vogel et al., 2009; Wright et al., 2009). If the differences in morphology are correlated with differences in material properties, the same measurements can be taken on teeth of other, sometimes extinct, animals and be used to predict food item breakdown efficiency (Wood and Schroer, 2012; Strait et al., 2013). Second, experiments can be run on using simple, theoretical teeth to breakdown foods with varying material properties. The results can be used to hypothesize what shaped tooth would be most efficient at processing what types of food items, and teeth with similar shapes found in nature can be deemed highly efficient at breaking down those food items (Freeman and Lemen, 2007; Anderson and LaBarbera, 2008).

This same method is also used with broad dietary categories and metrics of tooth shape (e.g. (Dennis et al., 2004; Boyer, 2008; Bunn et al., 2011; Croft et al., 2011; Godfrey et al., 2012)). Metrics of tooth shape can either take into account the entire occlusal shape of the tooth (e.g. Dirichlet normal energy (Bunn et al., 2011; Godfrey et al., 2012), dental complexity (Evans et al., 2007; Santana et al., 2011), and dental topography: relief index (M'Kirera and Ungar, 2003; Boyer, 2008), and angularity (Ungar and M'kirera, 2003; Peter, 2004; Ungar et al., 2008)), or portions of the occlusal surface of the tooth (e.g. shearing quotient (Kay, 1975; Kay, 1977; Kay, 1981), shearing crest length (King et al., 2005; Evans, 2013) and tooth cusp sharpness, see Chapter 5). It is assumed that teeth with certain values for certain metrics are efficient at breaking down
certain types of food items (e.g. molars with high relief are efficient at breaking down folivorous foods). This information can then be used as a measure for food item breakdown efficiency.

Finally, food item breakdown efficiency can be affected by the size of the food item and extrinsic materials attached to the food item. As food item size changes, the fundamental interactions between the food item and tooth change (i.e. small food items are more likely to interact with the occlusal basins and the cusps, while large food items are more likely to interact solely with the cusps), changing food item breakdown efficiency, see Chapter 3. Extrinsic materials, such as quartz grit, can also remove enamel from the tooth during mastication, changing the enamel’s shape. This can make the tooth less efficient as mastication and reduce food item breakdown efficiency (Lucas et al., 2013).

6.2.3 Trapability

Trapability is the ability for a mammal to trap and stabilize a food item, an action that is critical during mastication (Evans and Sanson, 2003). The concept of trapability is not as well studied as tooth strength and food item breakdown efficiency, but some aspects of tooth shape have been related to an animal’s ability to trap a food item, such as the angle of the notches between cusps (Anderson and LaBarbera, 2008; Anderson, 2009; Hartstone - Rose, 2011), cusp basin size (Yamashita, 1998), serration on the edge of the tooth (Abler, 1992), crenulations on cusps (Martin et al., 2003; Smith et al., 2005; Vogel et al., 2008) and the number of blade edges present (Evans and Sanson, 2003). Particle clearance during mastication is also an important part of trapability. For example, if
trapability is measured in terms of cusp basin size where larger basins have higher trapability, clearing the food out of the basin between chewing cycles is critical.

To increase stability of a rigid body in a 3D space at the beginning of the chewing cycle, the number of unconstrained degrees of freedom must be minimized. In total, there are six degrees of freedom, three along the principal axes (translation) and three around principal axes (rotation). Therefore, trapability is not only affected by the shape of the tooth but also by the direction loading is taking place and the location of the food item within the mouth. After the food item has initially been stabilized and the chewing cycle continues, the material properties of the food item then play a role in the importance of trapability. If a material is highly extensible (i.e. has a high Poisson’s ratio and/or is ductile), then it is important to minimize the number of unconstrained degrees of freedom (i.e. for the tooth to have a high trapability) because highly extensible foods tend to deform large amounts prior to fracture, and if the food item is partially unconstrained it will deform in those directions (Evans and Sanson, 2003). Consequently, if the food item is not able to deform in any direction because the food item is over constrained (i.e. high trapability) then the food item will be broken down faster. However, this can lead to an increase in the efficiency of the system (Anderson, 2009). Finally, if the material is not highly extensible (i.e. has a low Poisson’s ratio and/or is brittle) then trapability is not as important past initial stabilization of the food item (Lucas, 2004; Anderson, 2009).

The ability to trap and stabilize food is not as important when considering food items which are large compared to the oral cavity, since the food item can be stabilized through external forces and manipulation (i.e. hands, paws). This is why anterior teeth,
especially mammalian canines, can have low levels of trapability but still remain optimal for their function. This is not necessarily true for posterior teeth, which are used primarily for grinding food items and as such need to be able to stabilize the food items (Luke and Lucas, 1983; Evans and Sanson, 2003; Lucas, 2004).

### 6.3 Trade-Offs

Theoretically, an optimal tooth would maximize tooth strength, food breakdown efficiency, and trapability. This is not possible. The interdependence of these variables prevents them all from being maximized at the same time: an increase in one variable will lead to a decrease in one or both of the other variables. In design optimization, these trade-offs can be plotted between two variables using Pareto curves. These curves can then be used to predict the optimal combination of variables for a given design. For example, a strong canine tooth would be robust and have a dull tip to prevent fracture. In order to maximize food breakdown efficiency, sharpness should be maximized by minimizing tooth cusp RoC (i.e. minimize force and energy to fracture) (Freeman and Lemen, 2007). This comes at cost to the tooth’s strength: sharp, single-cusped teeth are more susceptible to fracture than dull teeth. All the while the tooth has had extremely low trapability, as it is difficult to stabilize a food item at the tip of a single-cusped tooth. In order to increase trapability, the number of contact points between the tooth and the food item should be increased through making the tooth serrated (Abler, 1992).
Figure 6.1: Optimization space showing the transition from a dull to sharp canine, then to a stronger canine which has a more elliptical cross-sectional area and is slightly duller, to a final shape where the canine is serrated.

6.4 Modeling Optimization

This series of events described above can be visualized in 2D morphospace and be used to track the changes in tooth morphology (Fig. 6.1). In this optimization space, the closer the tooth is to each of the vertices the more optimally the tooth is designed for that function. The tooth described above starts off dull, in the bottom right hand corner of the morphospace. It then increases in efficiency and decreases its strength and moves to the top of the morphospace. Then, by making the tooth serrated, the efficiency decreases (there is an increase in the contact area between the tooth and the food item) and trapability increases. Meanwhile, strength remains low because each serration is weak and prone to fracture. If these three teeth came from three separate species, it would be easy to explain how each tooth is optimal for its function even if each has radically different performance metrics using this morphospace.
Another example of how this morphospace can be used can be found in Fig. 6.2, where the contour plot is used to depict changes in trapability. The dashed black arrow shows how tradeoffs can be occurring between efficiency and strength while not affecting trapability, and the white arrow shows a path that would increase trapability while maintaining the same level of tradeoff between efficiency and strength. The teeth in this example show how three teeth with the same cross-sectional area can occupy the three corners of the morphospace. The tooth in the lower right corner (maximum strength) is short and has a rounded tip, making it strong. The tooth in the top corner has a single, extremely sharp cusp which is very efficient at fracturing food items, and the tooth in the lower left hand corner is extremely efficient at trapping and stabilizing the food item.
Assuming the morphospace has a unit area, data can be plotted on the morphospace using area coordinates (Coxeter 1969; see Fig. 6.3).

\[ A_{\text{strength}} + A_{\text{efficiency}} + A_{\text{trapability}} = 1 \]  

(6.2)

where the area coordinates are calculated using the following equations

\[
\text{Strength}_{\text{tooth}} = \frac{\text{Measured strength of the tooth}}{\text{maximum strength of all the teeth}}
\]

\[
\text{Efficiency}_{\text{tooth}} = \frac{\text{Measured efficiency of the tooth}}{\text{maximum efficiency of all the teeth}}
\]

\[
\text{Trapability}_{\text{tooth}} = \frac{\text{Measured trapability of the tooth}}{\text{maximum trapability of all the teeth}}
\]

\[
A_{\text{strength}} = \frac{\text{Strength}_{\text{tooth}}}{\text{Strength}_{\text{tooth}} + \text{Efficiency}_{\text{tooth}} + \text{Trapability}_{\text{tooth}}}
\]

\[
A_{\text{efficiency}} = \frac{\text{Efficiency}_{\text{tooth}}}{\text{Strength}_{\text{tooth}} + \text{Efficiency}_{\text{tooth}} + \text{Trapability}_{\text{tooth}}}
\]

\[
A_{\text{trapability}} = \frac{\text{Trapability}_{\text{tooth}}}{\text{Strength}_{\text{tooth}} + \text{Efficiency}_{\text{tooth}} + \text{Trapability}_{\text{tooth}}}
\]

If one of the metrics has not been measured (e.g. trapability) the tradeoff that is occurring between the other two variables can still be quantified and analyzed (Fig. 6.2).

6.5 Applications and Future Directions

Modeling tooth optimization in this manner will be particularly useful in interspecies comparisons of tooth morphologies (e.g. (Peter, 2004; Boyer, 2008; Godfrey et al., 2012; Smith et al., 2012; Evans, 2013)). It also has applications in analyzing extinct species, some of which are represented by little more than their teeth, and it can be used to understand evolutionary changes within a species through time. Furthermore, it affords researchers the opportunities to compare multiple metrics of tooth function to
each other simultaneously, giving researchers the opportunity to have a more holistic view of the tooth’s function.

This optimality space only has the ability for analyzing one performance metric at a time per functional variable. For example, if tooth strength is being measured through tooth cusp RoC, variations in tooth material properties are assumed to have negligible effects on tooth strength (Korostoff et al., 1975; Staines et al., 1981; Cuy et al., 2002; Jantarat et al., 2002; Imbeni et al., 2005; Chai et al., 2009b). If both tooth cusp RoC and tooth material properties play a critical role in terms of tooth strength, a more holistic measurement of tooth strength (e.g. stresses measured in a finite element model) should be performed.

While useful for interspecies comparisons of tooth shape of extant species, this morphospace can also be used to analyze the effects of tooth wear on optimal tooth shape for a given individual. There are two common types of wear: attrition and abrasion. Attrition (tooth-tooth wear) helps maintain tooth function throughout its life while abrasion (tooth-food item wear) is potentially dangerous, since it removes enamel without reshaping the tooth to help maintain function (Kay and Covert, 1983; Popowics and Fortelius, 1997; Daegling and Grine, 1999; Evans and Sanson, 2005; Evans et al., 2005; Lucas et al., 2013). In the case of attrition, the tooth would not be expected to move around on the optimality morphospace since the tooth will always be efficient at breaking down food items. In the case of abrasion, the tooth could be becoming weaker due to loss of enamel and could also be becoming more or less efficient, depending on how it is affecting the length of the shearing crest (King et al., 2005; Elgart, 2010). In addition,
trapability would be increasing as more EDJ becomes exposed because it is increasing friction between the food items and the tooth (Lucas, 2004).

6.6 Conclusion

It is common in tooth studies for researchers to assume that teeth are optimally shaped for their function, and for this assumption not to be tested. Furthermore when this assumption is tested, researchers often end up with such a large range of potential optimality that there is no way for the tooth to fall out of that range. Or if the tooth is not optimal, it is common for the researcher to assert that their experiment was flawed. Neither path is conducive to advancing the field.

We propose that the primary aspects of tooth function can be categorized as either metrics for tooth strength, food breakdown efficiency or trapability. By using these three categories and plotting them on an optimality morphospace using area coordinates, it is possible to test what the tooth is optimal for. Furthermore, this holistic view gives researchers a framework for addressing differences in tooth shape and structure that takes into account multiple aspects of tooth function instead of just one.
CHAPTER 7

CONCLUDING THOUGHTS

7.1 Overview

Tooth cusp radius of curvature (RoC) has been hypothesized to be functionally important during brittle food item fracture. Until now, this assumption has remained largely untested. In this dissertation, I first tested existing hypotheses concerning the role of tooth cusp RoC in brittle food item fracture using a parametric model of a bunodont molar (Chapter 2). After all existing hypotheses were rejected, I put forth and tested my own novel hypothesis, aptly named the Complex Cusp Hypothesis. After gaining support for the Complex Cusp Hypothesis, I tested the effects of relative food item size on the optimal set of RoCs during brittle food item fracture (Chapter 3), and found that relative food item size can have a significant effect on the optimal set of RoCs and that the importance of tooth cusp RoC changes with relative food item size.

Next, I examined tooth cusp RoC from several species and subspecies of great apes to see if any of the predicted optimal morphologies put forth in Chapters 2 and 3 existed in nature. Although I did not find any of the optimal sets of RoCs I was looking for in nature, I was able to differentiate folivorous apes from frugivorous apes based on tooth cusp RoC alone and discovered that folivorous apes had duller teeth than frugivorous ones. I then put forth a hypothesis that tooth cusp RoC is not providing a functional advantage in the traditional sense (i.e. minimizing contact area between the
tooth and the food item) but is causing the tooth to wear in a manner that is functionally advantageous (Chapter 4).

If this hypothesis gains further support, it would then become important to understand if tooth cusp RoC is correlated to other factors that affect the way the tooth wears. Therefore, in Chapter 5 the possible relationships between tooth cusp RoC and enamel thickness was investigated. However, no such relationship was found. Finally, in Chapter 6, we put forth a multi-function model of teeth, in which tooth function can be divided into three categories: tooth strength, food item breakdown efficiency, and trapability (the ability to trap/stabilize a food item). Although this model remains untested, we propose that it will give researchers a more holistic view of tooth function and give them the ability to effectively compare teeth that are very functionally different (e.g. felid canines and ape molars).

### 7.2 Possible Problems

Several assumptions were made in the parametric model of the bunodont molar. For example, a uniform enamel thickness was assigned to the entire model, the most buccal, lingual, mesial, and distal sides of the model were horizontal walls, the distance between the protocone and paracone equaled the distance between the hypocone and metacone, the distance between the protocone and hypocone equaled the distance between the paracone and metacone, and the angles between the tips of any three cusps was held constant to 90°. In addition, when testing the Blunt, Pointed, Sharp, and Complex Cusp Hypotheses in Chapter 2, we assumed that tooth cusp height and valley height were held constant. It is also impossible to model crenulations with our model,
and, as stated in Chapter 2, the model was never validated with physical experimentation. However, we believe our model is valid for reasons stated in Chapter 2, and believe that, even if our model mimicked teeth found in nature more accurately, the Blunt, Pointed, and Strong Cusp Hypotheses would still remain rejected and the Complex Cusp Hypothesis would still have gained support.

In addition, the reconstruction method used in Chapter 4 is not perfect. However, because full datasets of completely unworn ape teeth do not exist, we must make do with what we have. And in the case of measuring tooth cusp RoC, this means reconstructing the cusps of partially worn teeth.

### 7.2 Future Directions

There are several future directions that can be taken from this dissertation. First, a more comprehensive set of tooth cusp RoCs that include smaller primates should be collected to see if the correlation between tooth cusp RoC and diet holds up. The hypothesis that dull cusps wear in a way that is advantageous for folivores must also be further tested, and possible relationships between tooth cusp RoC and other factors that affect the way teeth wear should be investigated.

Finally, the method for testing tooth function proposed in Chapter 6 should be rigorously tested across multiple species of mammals. Once this all has been done, if any correlations between tooth shape and diet still exist, they should be used to investigate the fossil record and be used to generate hypotheses about the diets of these extinct animals.
APPENDIX A

CODE FOR CONSTRUCTING A PARAMETRIC MODEL OF A BUNODONT MOLAR IN ANSYS 13.0

!Parametric model of the tooth
!Cusp a is the metacone cusp, b is the hypocone, c is the paracone and d is the protocone

!___________________________________
!!!!!!!!!!!!!!!!!!Code!!!!!!!!!!!!!!!
!___________________________________

finish
/clear

raa=3 !radius of cusp a in XY plane
rba=3 !radius of cusp b in XY plane
rca=3 !radius of cusp c in XY plane
rda=3 !radius of cusp d in XY plane

rab=3 !radius of cusp a in YZ plane
rbb=3 !radius of cusp b in YZ plane
rcb=3 !radius of cusp c in YZ plane
rdb=3 !radius of cusp d in YZ plane

ha=5 !height of cusp a
hb=5 !height of cusp b
hc=5 !Height of cusp c
hd=5 !Height of cusp d

hdab=3 !height of the depth between cusps a and b
hdcd=3 !height of the depth between cusps c and d
hdac=3 !height of the depth between cusps a and c
hdbd=3 !height of the depth between cusps b and d

wab=15.7 !width between cusps a and b
dac=15.4 !distance between the metacone and paracone cusps
wcd=wab !Setting the distance between the para and proto equal to that between the meta and hypo
dbd=dac !Setting the distance between the hypo and proto equal to that between the meta and para
108

\[ e = 1 \]

! *ask, e, What is the enamel thickness?, 1

*if, e + 0.000001, GT, raa, THEN
*ask, raa, Reenter a value for the radius of curvature for cusp a \{raa\}, e + 0.1
*endif

*if, e + 0.000001, GT, rba, THEN
*ask, rba, Reenter a value for the radius of curvature for cusp b \{rba\}, e + 0.1
*endif

*if, e + 0.000001, GT, rca, THEN
*ask, rca, Reenter a value for the radius of curvature for cusp c \{rca\}, e + 0.1
*endif

*if, e + 0.000001, GT, rda, THEN
*ask, rda, Reenter a value for the radius of curvature for cusp d \{rda\}, e + 0.1
*endif

*if, e + 0.000001, GT, rab, THEN
*ask, rab, Reenter a value for the radius of curvature for cusp a \{rab\}, e + 0.1
*endif

*if, e + 0.000001, GT, rbb, THEN
*ask, rbb, Reenter a value for the radius of curvature for cusp b \{rbb\}, e + 0.1
*endif

*if, e + 0.000001, GT, rcb, THEN
*ask, rcb, Reenter a value for the radius of curvature for cusp c \{rcb\}, e + 0.1
*endif

*if, e + 0.000001, GT, rdb, THEN
*ask, rdb, Reenter a value for the radius of curvature for cusp d \{rdb\}, e + 0.1
*endif

*if, rba + raa + 0.000001, GT, wab, THEN
*ask, wab, The cusps are too close remember raa + rba < wab, raa + rba + 0.1
*endif

*if, rca + rda + 0.000001, GT, wab, THEN
*ask, wcd, The cusps are too close remember rca + rda < wcd, rca + rda + 0.1
*endif

*if, rab + rbb + 0.000001, GT, dac, THEN
*ask, dac, The cusps are too close remember rab + rbb < dac, rab + rbb + 0.1
*endif

*if,rcb+rdb+0.000001,GT,dac,THEN
*ask,dbd,The cusps are too close remember rcb+rdb<dbd  ,rcb+rdb+0.1
*endif

*if,wcd,GT,wab,THEN
wab=wcd
*ELSE
wcd=wab
*endif

*if,dbd,GT,dac,THEN
dac=dbd
*ELSE
dbd=dac
*endif

!___________________________________________
/prep7

PI=acos(-1)

k,1,0,ha-raa,0
k,2,wab,hb-rba,0

cyl4.0,ha-raa,raa-e,0,raa,180
cyl4,wab,hb-rba,rba-e,0,rba,180

xpa=(wab-raa-rba)/2+raa
hdabe=hdab-e
k,11,xpa,hdab,0                      !Creates keypoint between cusps
k,12,xpa,hdabe,0                      !Creates keypoint between cusps

HHa=hdab-ha+raa
OPa=sqrt((xpa)*(xpa)+(HHa)*(HHa))
betaa=asin(HHa/OPa)               !tangent, top of cusp a
alphaa=acos(raa/OPa)
thetaa=alphaa+betaa
xaa=raa*cos(thetaa)
yaa=raa*sin(thetaa)+ha-raa

k,13,xaa,yaa,0
L,11,13
\[ HH_b = h_b - r_b - h_d a_b \]
\[ OP_b = \sqrt{((x_{p a} - w_{a b})^2 + (x_{p a} - w_{a b})^2 + HH_b^2} \]
\[ \text{betab} = \arcsin(HH_b/OP_b) \]  
\[ \text{alphab} = \arccos(r_b/OP_b) \]
\[ \text{thetab} = \text{alphab} - \text{betab} \]
\[ x_{b b} = r_b \cos(\pi - \text{thetab}) + w_{a b} \]
\[ y_{b b} = r_b \sin(\text{thetab}) + h_b - r_b \]

\[ k, 14, x_{b b}, y_{b b}, 0 \]
\[ \text{L, 11, 14} \]

\[ HH_{a e} = h_{d a b} - h_a + r_{a e} \]
\[ OP_{a e} = \sqrt{HH_{a e}^2 + x_{p a}^2} \]
\[ \text{betaae} = \arcsin(HH_{a e}/OP_{a e}) \]  
\[ \text{alphaae} = \arccos((r_{a e} - e)/OP_{a e}) \]
\[ \text{thetaae} = \text{alphaae} + \text{betaae} \]
\[ x_{a a e} = (r_{a e} - e) \cos(\text{thetae}) \]
\[ y_{a a e} = (r_{a e} - e) \sin(\text{thetae}) + h_a - r_{a e} \]

\[ HH_{b e} = h_b - r_b - h_d a_b \]
\[ OP_{b e} = \sqrt{((x_{p a} - w_{a b})^2 + (x_{p a} - w_{a b})^2 + HH_{b e}^2} \]
\[ \text{betabe} = \arcsin(HH_{b e}/OP_{b e}) \]  
\[ \text{alphabe} = \arccos((r_b - e)/OP_{b e}) \]
\[ \text{thetab} = \text{alphabe} - \text{betabe} \]
\[ x_{b b e} = (r_b - e) \cos(\pi - \text{thetab}) + w_{a b} \]
\[ y_{b b e} = (r_b - e) \sin(\text{thetab}) + h_b - r_b \]

\[ \text{Next bit of code creates enamel layer between cusps} \]
\[ m = (y_{a a e} - h_d a_b)/(x_{a a e} - x_{p a}) \]
\[ k, 15, w_{a b}, m*(w_{a b} - x_{a a e}) + y_{a a e}, 0 \]
\[ k, 16, x_{a a e}, y_{a a e}, 0 \]
\[ 1, 15, 16 \]

\[ mm = (y_{b b e} - h_d a_b)/(x_{b b e} - x_{p a}) \]
\[ k, 17, 0, y_{b b e} - mm, x_{b b e}, 0 \]
\[ k, 18, x_{b b e}, y_{b b e}, 0 \]
\[ 1, 17, 18 \]

\[ \text{lsbl, 11, 12} \]
\[ \text{idele, 13} \]
\[ \text{kdele, 12} \]
\[ \text{kdele, 15} \]
\[ k, 18, x_{b b e}, y_{b b e}, 0 \]
\[ 1, 18, 19 \]

\[ \text{*GET, filab1, line, 9, leng} \]
*GET,filab2,line,10,leng
*GET,filab3,line,11,leng
*GET,filab4,line,14,leng

*IF,filab1,LE,filab2,AND,filab1,LE,filab3,THEN
  *IF,filab1,LE,filab4,THEN
  filab=filab1-filab1/10
  *ENDIF
*ENDIF

*IF,filab2,LE,filab1,AND,filab2,LE,filab3,THEN
  *IF,filab2,LE,filab4,THEN
  filab=filab2-filab2/10
  *ENDIF
*ENDIF

*IF,filab3,LE,filab1,AND,filab3,LE,filab2,THEN
  *IF,filab3,LE,filab4,THEN
  filab=filab3-filab3/10
  *ENDIF
*ENDIF

*IF,filab4,LE,filab1,AND,filab4,LE,filab2,THEN
  *IF,filab4,LE,filab3,THEN
  filab=filab4-filab4/10
  *ENDIF
*ENDIF

LFILLT,9,10,filab/2, , !Creates a rounded corner in the area
LFILLT,14,11,filab/2+e, , !between the cusps of the teeth

adele,all !cleaning up unnecessary geometry
larc,4,13,1,raa
larc,5,16,1,raa-e
ldele,3
ldele,1
larc,14,7,2,rba
larc,18,10,2,rba-e
ldele,4,8
kdele,3
kdele,6
kdele,8,9
kdele,11
kdele,19
bottom=(ha+hb+hc+hd+raa+rba+rca+rda)/6

k,3,wab+rba,-bottom,0
k,6,wab+rba-e,-bottom,0
k,8,-raa,-bottom,0
k,9,-raa+e,-bottom,0

idele.2

1,8,9
1,9,6
1,3,6
1,4,8
1,5,9
1,10,6
1,7,3
1,12,17

AL,2,6,7,16,15,9,14,18  !makes enamel region
AL,18,12,13,10,11,1,3,8,17,5  !makes dentin region
AL,4,7,16,14,13,11,3,8
aadd,2,1

!________________________________________________________________
!making cusps c and d 2D
!________________________________________________________________

k,11,0,hc-rca,dac
k,19,wcd,hd-nda,dbd
cyl4,0,hc-rca,rca-e,0,rca,180,dac
cyl4,wcd,hd-nda,rda-e,0,rda,180,dbd

vdele,all
adele,11,14
adele,5,9
adele,1
idele,18,21
idele,26,33
idele,38,41
kdele,21,24
kdele,29,32

xpc=(wcd-rca-rda)/2+rca
hdcde=hdcd-e
k,21,xpc,hdcd,(dac+dbd)/2
\[ k,22, \text{xpc}, \text{hdcde}, (\text{dac}+\text{dbd})/2 \]

\[ \text{HHc} = \text{hdcde} - \text{hc} + \text{rca} \]
\[ \text{OPc} = \sqrt{((\text{xpc})^2 + (\text{HHc})^2)} \]
\[ \text{betac} = \arcsin(\text{HHc}/\text{OPc}) \quad \text{!tangent, top of cusp c} \]
\[ \text{alphac} = \arccos(\text{rca}/\text{OPc}) \]
\[ \text{thetac} = \text{alphac} + \text{betac} \]
\[ \text{xcc} = \text{rca} \cdot \cos(\text{thetac}) \]
\[ \text{ycc} = \text{rca} \cdot \sin(\text{thetac}) + \text{hc} - \text{rca} \]

\[ k,23, \text{xcc}, \text{ycc}, (\text{dac}+\text{dbd})/2 \]
\[ \text{L}, 21, 23 \]

\[ \text{HHd} = \text{hd} - \text{rda} - \text{hdcde} \]
\[ \text{OPd} = \sqrt{((\text{xpc})^2 - \text{wcd})^2 + (\text{HHd})^2} \]
\[ \text{betad} = \arcsin(\text{HHd}/\text{OPd}) \quad \text{!tangent, top of cusp d} \]
\[ \text{alphad} = \arccos(\text{rda}/\text{OPd}) \]
\[ \text{thetad} = \text{alphad} - \text{betad} \]
\[ \text{xdd} = \text{rda} \cdot \cos(\pi - \text{thetad}) + \text{wcd} \]
\[ \text{ydd} = \text{rda} \cdot \sin(\text{thetad}) + \text{hd} - \text{rda} \]

\[ k,24, \text{xDD}, \text{yDD}, (\text{dac}+\text{dbd})/2 \]
\[ \text{L}, 21, 24 \]

\[ \text{HHce} = \text{hdcde} - \text{hc} + \text{rca} \]
\[ \text{OPce} = \sqrt{(\text{HHce}^2 + \text{xpc}^2)} \]
\[ \text{betace} = \arcsin(\text{HHce}/\text{OPce}) \quad \text{!tangent, dentine of cusp c} \]
\[ \text{alphace} = \arccos((\text{rca} - \text{e})/\text{OPce}) \]
\[ \text{thetace} = \text{alphace} + \text{betace} \]
\[ \text{xcce} = (\text{rca} - \text{e}) \cdot \cos(\text{thetace}) \]
\[ \text{ycce} = (\text{rca} - \text{e}) \cdot \sin(\text{thetace}) + \text{hc} - \text{rca} \]

\[ \text{HHde} = \text{hd} - \text{rda} - \text{hdcde} \]
\[ \text{OPde} = \sqrt{((\text{xpc})^2 - \text{wcd})^2 + (\text{HHde})^2} \]
\[ \text{betade} = \arcsin(\text{HHde}/\text{OPde}) \quad \text{!tangent, dentine of cusp d} \]
\[ \text{alphade} = \arccos((\text{rda} - \text{e})/\text{OPde}) \]
\[ \text{thetad} = \text{alphade} - \text{betade} \]
\[ \text{xdde} = (\text{rda} - \text{e}) \cdot \cos(\pi - \text{thetad}) + \text{wcd} \]
\[ \text{ydde} = (\text{rda} - \text{e}) \cdot \sin(\text{thetad}) + \text{hd} - \text{rda} \]

\[ \text{mmm} = (\text{ycc} - \text{hdcde})/(\text{xcc} - \text{xpc}) \quad \text{!Next bit of code creates} \]

enamel layer between cusps c & d
\[ k,29, \text{wcd}, \text{mmm} \cdot ((\text{wcd} - \text{xcce}) + \text{ycce}, (\text{dac}+\text{dbd})/2 \]
\[ k,30, \text{xcce}, \text{ycc}, (\text{dac}+\text{dbd})/2 \]
\[ 1, 29, 30 \]
\[ \text{mmmm} = \frac{\text{ydd-hdcd}}{\text{xdd-xpc}} \]

\[ k,31,0,\text{ydde} - \text{mmmm} \times \text{xdde} \times \frac{(\text{dac}+\text{dbd})}{2} \]

\[ k,32,\text{xdde} \times \text{ydde} \times (\text{dac}+\text{dbd})/2 \]

\[ 1,31,32 \]

\[ \text{lsbl,20,21} \]

\[ \text{ldele,26} \]

\[ \text{kdele,29} \]

\[ k,22,\text{xdde} \times \text{ydde} \times (\text{dac}+\text{dbd})/2 \]

\[ 1,22,37 \]

*GET,\text{filcd1},line,18,leng
*GET,\text{filcd2},line,19,leng
*GET,\text{filcd3},line,20,leng
*GET,\text{filcd4},line,27,leng

*IF,\text{filcd1},LE,\text{filcd2},AND,\text{filcd1},LE,\text{filcd3},THEN
  *IF,\text{filcd1},LE,\text{filcd4},THEN
    \text{filcd} = \text{filcd1} - \text{filcd1}/10
  *ENDIF
*ENDIF

*IF,\text{filcd2},LE,\text{filcd1},AND,\text{filcd2},LE,\text{filcd3},THEN
  *IF,\text{filcd2},LE,\text{filcd4},THEN
    \text{filcd} = \text{filcd2} - \text{filcd2}/10
  *ENDIF
*ENDIF

*IF,\text{filcd3},LE,\text{filcd1},AND,\text{filcd3},LE,\text{filcd2},THEN
  *IF,\text{filcd3},LE,\text{filcd4},THEN
    \text{filcd} = \text{filcd3} - \text{filcd3}/10
  *ENDIF
*ENDIF

*IF,\text{filcd4},LE,\text{filcd1},AND,\text{filcd4},LE,\text{filcd2},THEN
  *IF,\text{filcd4},LE,\text{filcd3},THEN
    \text{filcd} = \text{filcd4} - \text{filcd4}/10
  *ENDIF
*ENDIF

\[ \text{lfillt,18,19,filcd/2, }, \]
\[ \text{lfillt,20,27,filcd/2+e, }, \]

\[ \text{adele,10} \]

\[ \text{adele,2} \]
larc,23,26,11,rca
larc,27,30,11,rca-e
ldele,22,25
larc,24,33,19,rda
larc,22,36,19,rda-e
ldele,34,37
kdele,28
kdele,25
kdele,34,35
kdele,37
kdele,21

k,21,wcd+rda,-bottom,(dac+dbd)/2
k,25,wcd+rda-e,-bottom,(dac+dbd)/2
k,28,-rca,-bottom,(dac+dbd)/2
k,34,-rca+e,-bottom,(dac+dbd)/2

1,26,28
1,27,34
1,34,28
1,36,25
1,33,21
1,25,21
1,34,25
1,31,32

Al,24,28,18,21,35,26,27,29,25,30
Al,35,19,22,32,33,31,23,20
Al,34,25,29,26,27,20,23,31
aadd,1,2

!__________________________________________________________________
!making cusps a and c 2D
!__________________________________________________________________

k,41,0,ha-rab,rab-e !Keypoints to make cusp a 3-D in plane b
k,42,0,ha-rab,rab
k,43,0,ha-rab,-rab+e
k,44,0,ha-rab,-rab
k,45,0,ha-e,0
k,46,0,ha,0

Larc,43,41,45,rab-e
Larc,44,42,46,rab
keypoints to make cusp c 3D in plane b
k,52,0,hc-rcb,dac+rcb
k,53,0,hc-rcb,dac-rcb+e
k,54,0,hc-rcb,dac-rcb
k,55,0,hc-e,dac
k,56,0,hc,dac
k,57,0,hc-rcb+(rcb-e)*sin(PI/4),dac+(rcb-e)*sin(PI/4)  
   !for some reason it wont make the dentin layer like it did before, so I have to put in extra keypoints
k,58,0,hc-rcb+(rcb-e)*sin(PI/4),dac+(rcb-e)*sin(PI/4)
Larc,53,55,57,
Larc,51,55,58,
Larc,54,52,56,rcb
Lcomb,37,38,0
dele,57,58

xpac=(dac-rab-rcb)/2+rab
hdace=hdac-e
k,55,0,hdace,xpac
k,37,0,hdace,xpac

HHac=hdac-ha+rab
OPac=sqrt(xpac*xpac+HHac*HHac)
betaac=asin(HHac/OPac)
alpaca=acos(rcb/OPac)
thetaac=alphaac+betaac
zac=rab*cos(thetaac)
yac=rab*sin(thetaac)+ha-rab

k,39,0,yac,zac
l,35,39

HHca=hdac-hc+rcb
OPca=sqrt((xpac-dac)*(xpac-dac)+HHca*HHca)
betaca=asin(HHca/OPca)
alphaca=acos(rcb/OPca)
thetaa=alphaca+betaca
zca=-rcb*cos(thetaa)+dac
yca=rcb*sin(thetaa)+hc-rcb

k,40,0,yca,zca
l,35,40
HHace=hdace-ha+rab
OPace=sqrt(xpac*xpac+HHace*HHace)
betace=asin(HHace/OPace)
alpahaace=acos((rab-e)/OPace)
thetaace=alphace+betace
zace=(rab-e)*cos(thetaace)
yace=(rab-e)*sin(thetaace)+ha-rab

HHcae=hdace-hc+rcb
OPcae=sqrt((xpac-dac)*(xpac-dac)+HHcae*HHcae)
betacae=asin(HHcae/OPcae)
alpahaace=acos((rcb-e)/OPcae)
thetaace=alphace+betace
zcae=(rcb-e)*cos(theta)+dac
yae=(rcb-e)*sin(theta)+hc-rcb

mac=(yac-hd)/(zac-xpac)
k,47,0,mac*(dac-zac)+yace,dac
k,48,0,yace,zace
1.47,48

mca=(yca-hd)/(zca-xpac)
k,49,0,yca-mca*zcae,0
k,50,0,ycae,zcae
1.49,50

lsbl,41,42
ldele,43
kdele,37
kdele,47
k,50,0,yca,zca
1.55,50

*GET,filac1,line,38,leng
*GET,filac2,line,40,leng
*GET,filac3,line,41,leng
*GET,filac4,line,44,leng

*IF,filac1,LE,filac2,AND,filac1,LE,filac3,THEN
  *IF,filac1,LE,filac4,THEN
    filac=filac1-filac1/10
  *ENDIF
*ENDIF

!This part of the code was acting weird...cant find
!the problem so I used thetacae instead of thetaace
!Same angle, dunno why I was going thru all this
!complex geometry before every time...

*GET,filac1,line,38,leng
*GET,filac2,line,40,leng
*GET,filac3,line,41,leng
*GET,filac4,line,44,leng

*IF,filac1,LE,filac2,AND,filac1,LE,filac3,THEN
  *IF,filac1,LE,filac4,THEN
    filac=filac1-filac1/10
  *ENDIF
*ENDIF
*IF, filac2, LE, filac1, AND, filac2, LE, filac3, THEN
  *IF, filac2, LE, filac4, THEN
    filac = filac2 - filac2/10
  *ENDIF
*ENDIF

*IF, filac3, LE, filac1, AND, filac3, LE, filac2, THEN
  *IF, filac3, LE, filac4, THEN
    filac = filac3 - filac3/10
  *ENDIF
*ENDIF

*IF, filac4, LE, filac1, AND, filac4, LE, filac2, THEN
  *IF, filac4, LE, filac3, THEN
    filac = filac4 - filac4/10
  *ENDIF
*ENDIF

lfillt, 38, 40, filac/2, ,
lfillt, 41, 44, filac/2+e, ,
kdele, 55
kdele, 35

larc, 43, 48, 1, rab-e
larc, 44, 39, 1, rab
ldele, 35, 36
larc, 50, 51, 11, rcb-e
larc, 40, 52, 11, rcb
ldele, 37
ldele, 39
kdele, 53, 54
kdele, 41, 42

k, 35, 0, -bottom, -rab,
k, 41, 0, -bottom, -rab+e,
k, 42, 0, -bottom, dac+rcb,
k, 53, 0, -bottom, dac+rcb-e,

1, 43, 41
1, 41, 35
1, 35, 44
1, 41, 53
1, 51, 53
1, 53, 42
1, 42, 52
Making cusps b and d 2-D

Keypoints to make cusp b 3-D

Keypoints to make cusp d 3-D

Lcomb,55,56,0
kdele,77,78

xpbd=(dbd-rbb-rdb)/2+rbb
hdbde=hdbd-e
k,54,(wab+wcd)/2,hdbd,xpbd
k,55,(wab+wcd)/2,hdbde,xpbd

HHbd=hdbd-hb+rbb
\[
\begin{align*}
\text{OPbd} &= \sqrt{\text{xpb}d \cdot \text{xpb}d + \text{HHbd} \cdot \text{HHbd}} \\
\text{betabd} &= \sin(\text{HHbd} / \text{OPbd}) \\
\text{alphabd} &= \cos(\text{rbb} / \text{OPbd}) \\
\text{thetabd} &= \text{alphabd} + \text{betabd} \\
\text{zbd} &= \text{rbb} \cdot \cos(\text{thetabd}) \\
\text{ybd} &= \text{rbb} \cdot \sin(\text{thetabd}) + \text{hb} - \text{rbb} \\
\end{align*}
\]

\[
\begin{align*}
\text{k,58,wab,ybd,zbd} \\
\text{l,54,58} \\
\end{align*}
\]

\[
\begin{align*}
\text{HHdb} &= \text{hdbd} - \text{hd} + \text{rdb} \\
\text{OPdb} &= \sqrt{(\text{xpb}d \cdot \text{dbd}) \cdot (\text{xpb}d - \text{dbd}) + \text{HHdb} \cdot \text{HHdb}} \\
\text{betadb} &= \sin(\text{HHdb} / \text{OPdb}) \\
\text{alphadb} &= \cos(\text{rdb} / \text{OPdb}) \\
\text{thetadb} &= \text{alphadb} + \text{betadb} \\
\text{zdb} &= \text{rdb} \cdot \cos(\text{thetadb}) + \text{dbd} \\
\text{ydb} &= \text{rdb} \cdot \sin(\text{thetadb}) + \text{hd} - \text{rdb} \\
\end{align*}
\]

\[
\begin{align*}
\text{k,59,wcd,ydb,zdb} \\
\text{l,54,59} \\
\end{align*}
\]

\[
\begin{align*}
\text{HHbde} &= \text{hdbde} - \text{hb} + \text{rbb} \\
\text{OPbde} &= \sqrt{(\text{xpb}d \cdot \text{dbd}) \cdot (\text{xpb}d - \text{dbd}) + \text{HHbde} \cdot \text{HHbde}} \\
\text{betabde} &= \sin(\text{HHbde} / \text{OPbde}) \\
\text{alphabde} &= \cos(\text{rbb} / \text{OPbde}) \\
\text{thetabde} &= \text{alphabde} + \text{betabde} \\
\text{zbde} &= (\text{rbb} - \text{e}) \cdot \cos(\text{thetabde}) \\
\text{ybde} &= (\text{rbb} - \text{e}) \cdot \sin(\text{thetabde}) + \text{hb} - \text{rbb} \\
\end{align*}
\]

\[
\begin{align*}
\text{HHdbe} &= \text{hdbde} - \text{hd} + \text{rdb} \\
\text{OPdbe} &= \sqrt{(\text{xpb}d \cdot \text{dbd}) \cdot (\text{xpb}d - \text{dbd}) + \text{HHdbe} \cdot \text{HHdbe}} \\
\text{betadbe} &= \sin(\text{HHdbe} / \text{OPdbe}) \\
\text{alphadbe} &= \cos(\text{rdb} / \text{OPdbe}) \\
\text{thetadbe} &= \text{alphadbe} + \text{betadbe} \\
\text{zdbe} &= -(\text{rdb} - \text{e}) \cdot \cos(\text{thetadbe}) + \text{dbd} \\
\text{ydbe} &= -(\text{rdb} - \text{e}) \cdot \sin(\text{thetadbe}) + \text{hd} - \text{rdb} \\
\end{align*}
\]

\[
\begin{align*}
\text{k,67,wcd,ydbe,zdbe} \\
\text{l,68,60} \\
\end{align*}
\]

\[
\begin{align*}
\text{mdb} &= (\text{ybd} - \text{hdbd}) / (\text{zbd} - \text{xpb}d) \\
\text{k,68,wab,mdb} &= (\text{dbd} - \text{zbde}) + \text{ybd}, \text{dbd} \\
\text{k,60,wab,ydbe,zbde} \\
\text{l,68,60} \\
\end{align*}
\]

\[
\begin{align*}
\text{mdb} &= (\text{ybd} - \text{hdbd}) / (\text{zdb} - \text{xpb}d) \\
\text{k,69,wcd,ydbe-mdb} &= \text{zbde}, 0 \\
\end{align*}
\]
k,67,wcd,ydbe,zdbe
1,67,69

lsbl,58,59
ldele,61
kdele,68
kdele,55
k,55,wcd,ydbe,zdbe
1,55,70

*GET,filbd1,line,56,leng
*GET,filbd2,line,57,leng
*GET,filbd3,line,58,leng
*GET,filbd4,line,60,leng

*IF,filbd1,LE,filbd2,AND,filbd1,LE,filbd3,THEN
  *IF,filbd1,LE,filbd4,THEN
    filbd=filbd1-filbd1/10
  *ENDIF
*ENDIF

*IF,filbd2,LE,filbd1,AND,filbd2,LE,filbd3,THEN
  *IF,filbd2,LE,filbd4,THEN
    filbd=filbd2-filbd2/10
  *ENDIF
*ENDIF

*IF,filbd3,LE,filbd1,AND,filbd3,LE,filbd2,THEN
  *IF,filbd3,LE,filbd4,THEN
    filbd=filbd3-filbd3/10
  *ENDIF
*ENDIF

*IF,filbd4,LE,filbd1,AND,filbd4,LE,filbd2,THEN
  *IF,filbd4,LE,filbd3,THEN
    filbd=filbd4-filbd4/10
  *ENDIF
*ENDIF

lfillt,56,57,filbd/2, , 
lfillt,58,60,filbd/2+e, , 
kdele,54
kdele,70

larc,72,59,19,rdb
larc,71,55,19,rdb-e
ldel,54,55
kdele,73,74
larc,58,64,2,rbb
larc,60,63,2,rbb-e
ldel,52,53
kdele,61,62

k,61,wab,-bottom,-rbb
k,62,wab,-bottom,-rbb+e
k,73,wcd,-bottom,dbd+rdb
k,74,wcd,-bottom,dbd+rdb-e

1,61,64
1,62,63
1,61,62
1,62,74
1,74,71
1,74,73
1,73,72
1,67,75

AL,57,58,59,61,62,63,66,67,68,69
AL,52,53,54,55,56,60,64,69
Al,53,55,58,60,61,63,65,66
aadd,1,2

!Making areas to cover the areas I created, aka making the tooth 3D
!

FLST,3,9,3 !creates a bottom spline for the tooth (enamel layer)
FITEM,3,28
FITEM,3,8
FITEM,3,35
FITEM,3,61
FITEM,3,3
FITEM,3,21
FITEM,3,73
FITEM,3,42
FITEM,3,28
BSPLIN, ,P51X

ldiv,69,0.01, ,2,0 !divides the bottom spline into 8 distinct regions
lsbl,70,6
!Starts dividing the existing lines into distinct regions and grouping appropriate lines

!Combines all the segments of lines so each section has 3 or 4 lines defining it
NUMMRG,ALL,(e-e/10), , ,LOW

Merges all keypoints that may or may not already be merged

VA,all

creates a volume containing the enamel and dentine

Now the dentine section will be created

FLST,3,9,3
creates a bottom spline for the tooth (enamel layer)

FITEM,3,62
FITEM,3,6
FITEM,3,25
FITEM,3,74
FITEM,3,53
FITEM,3,34
FITEM,3,9
FITEM,3,41
FITEM,3,62
BSPLIN, ,P51X

ldiv,10,0.01, ,2,0
divides the bottom spline into 8 distinct regions

lsbl,12,8
lsbl,21,31
lsbl,22,66
lsbl,28,49
lsbl,22,25
lcomb,19,10
lsbl,38,7
lsbl,22,37

lsbl,3,55
Starts dividing the existing lines into distinct regions and grouping appropriate lines

lsbl,23,63
lsbl,45,16
lsbl,35,29
!Combines all the segments of lines so each section has 3 or 4 lines defining it

NUMMRG, ALL, (e-e/10), , , LOW

asel, u,, 1,50
VA,all

! Creates a volume containing JUST the dentine

allsel,all

ASBA,18,28
vdele,1
adele,3,10
adele,18
asel,u,,,28

VA,all

! Creates a volume that is solely the enamel

!_____________________________________________________________________

!Meshing the tooth

ET,1,solid186

MPTEMP,,,,,,
MPTEMP,1,0
MPDATA,EX,1,,84100
MPDATA,PRXY,1,,0.3

vsel,s,,,1
aslv,s
AESIZE,all,wab/20,

MSHAPE,1,3D
MSHKEY,0
!* CM,_Y,VOLU
VSEL,,,1
CM,_Y1,VOLU
CHKMSH,'VOLU'
CMSEL,S_,_Y
VMESH,_Y1
CMDELE,_Y
CMDELE,_Y1
CMDELE,_Y2
/UI,MESH,OFF

MPTEMP,,,,,,
MPTEMP,1,0
MPDATA,EX,2,,18600
MPDATA,PRXY,2,,0.31

!Enamel Material Properties

!Dentine material properties
mat,2

vsel.s,,2
aslvs
aesize,all,wab/10

CM_,Y,VOLU
VSEL,,2
CM_,Y1,VOLU
CHKMSH,'VOLU'
CMSEL,S_,Y
VMESH_,Y1
CMDELE_,Y
CMDELE_,Y1
CMDELE_,Y2
/UI,MESH,OFF

!Meshes the dentine

vsel,s,,1
!/COLOR,ELEM,BLUE,all
allsel,all

Foodor=14.1
Foodir=11.5
Height=50

SPH4,0,Height,Foodor,Foodir
!creates the geometry of the food item
AL,27,20,29,22,14,26,25,13
vdele,3
adele,3
adele,5
va,4,6,7

mptemp,,,,,
!material properties of the food item
mptemp,1,0
mpdata,ex,3,,2000
mpdata,prxy,3,,0.4
mat,3
vsel,s,,3
aslvs
aesize,all,Foodor/10
Vmesh,3

esel,s,cent,y,Height-foodor,Height-foodor/2
erfine,all,,,1,0,1,1
allsel,all

!____________________________________________________________________
!Creates contact pair
!____________________________________________________________________

/COM, CONTACT PAIR CREATION - START
CM,_NODECM,NODE
CM,_ELEMCM,ELEM
CM,_KPCM,KP
CM,_LINECM,LINE
CM,_AREACM,AREA
CM,_VOLUCM,VOLU
/GSAV,cwz,gsav,,temp
MP,MU,1,
MAT,1
R,3
REAL,3
ET,2,170
ET,3,174
KEYOPT,3,9,0
KEYOPT,3,10,2
R,3,
RMORE,
RMORE,0
RMORE,0
! Generate the target surface
ASEL,S,,,1
ASEL,A,,,2
ASEL,A,,,11
ASEL,A,,,12
ASEL,A,,,13
ASEL,A,,,14
ASEL,A,,,15
ASEL,A,,,16
ASEL,A,,,17
CM,_TARGET,AREA
TYPE,2
NSLA,S,1
ESLN,S,0
ESLL,U
ESEL,U,ENAME,,188,189
NSLE,A,CT2
ESURF
CMSEL,S,_ELEMCM
! Generate the contact surface
ASEL,S,,,4
CM_,CONTACT,AREA
TYPE,3
NSLA,S,1
ESLN,S,0
NSLE,A,CT2 ! CZMESH patch (fsk qt-40109 8/2008)
ESURF
ALLSEL
ESEL,ALL
ESEL,S,TYPE,,2
ESEL,A,TYPE,,3
ESEL,R,REAL,,3
/PSYMB,ESYS,1
/PNUM,TYPE,1
/NUM,1
EPLT
ESEL,ALL
ESEL,S,TYPE,,2
ESEL,A,TYPE,,3
ESEL,R,REAL,,3
CMSEL,A,_NODECM
CMDEL,_NODECM
CMSEL,A,_ELEMCM
CMDEL,_ELEMCM
CMSEL,S,_KPCM
CMDEL,_KPCM
CMSEL,S,_LINECM
CMDEL,_LINECM
CMSEL,S,_AREACM
CMDEL,_AREACM
CMSEL,S,_VOLUCM
CMDEL,_VOLUCM
/GRES,cwz,gsav
CMDEL,_TARGET
CMDEL,_CONTACT
/COM, CONTACT PAIR CREATION - END
/MREP,EPLT

VGEN, ,3, , ,wab/2,-33,dac/2, , ,1 !moves volume
!________________________________________________________
!Creating constraints
!________________________________________________________

!Note, move the food item into position FIRST!

kbetw,17,20,0,rati,0.5

cskp,11,1,22,17,16,1,1,
csys,11
asel,s,,7
nsla,s
nrotat,all
asel,s,,7
nsla,s
finish

/solu
def,all,,0,,,,uy,uz,,,,
finish

/prepare7
csys,0
nrotat,all
finish

/solu
asel,s,,28
asel,a,,29
nsla,s
def,all,,0,,,,ux,uz,,,,
def,all,,3,,,,uy

!_________________________________________________________
!Analysis type
!_________________________________________________________
NSUBST,10,1000,10
OUTRES,ERASE
OUTRES,ALL,ALL
AUTOTS,1

!_________________________________________________________
!Solve and Post process
!_________________________________________________________
allsel,all
APPENDIX B

NUMERICAL RESULTS USED TO TEST THE BLUNT, POINTED, AND STRONG CUSP HYPOTHESES

Table B.1: Numerical results of what is depicted in Fig. 2.6.

<table>
<thead>
<tr>
<th>Radius of Curvature</th>
<th>Reaction Force (kN)</th>
<th>Contact Area (mm²)</th>
<th>Food Item</th>
<th>Enamel</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Maximum Tensile Stress (MPa)</td>
<td>Maximum Tensile Stress (MPa)</td>
</tr>
<tr>
<td>2.25</td>
<td>2</td>
<td>34.18</td>
<td>64.57</td>
<td>379</td>
</tr>
<tr>
<td>2.5</td>
<td>2</td>
<td>34.23</td>
<td>65.80</td>
<td>372</td>
</tr>
<tr>
<td>2.75</td>
<td>2</td>
<td>34.57</td>
<td>65.01</td>
<td>368</td>
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<tr>
<td>3</td>
<td>2</td>
<td>35.10</td>
<td>65.09</td>
<td>372</td>
</tr>
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<td>2</td>
<td>35.22</td>
<td>65.21</td>
<td>374</td>
</tr>
<tr>
<td>3.5</td>
<td>2</td>
<td>34.89</td>
<td>65.68</td>
<td>369</td>
</tr>
<tr>
<td>3.75</td>
<td>2</td>
<td>35.62</td>
<td>66.99</td>
<td>366</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>35.40</td>
<td>67.32</td>
<td>365</td>
</tr>
<tr>
<td>4.25</td>
<td>2</td>
<td>35.20</td>
<td>66.27</td>
<td>360</td>
</tr>
<tr>
<td>4.5</td>
<td>2</td>
<td>35.18</td>
<td>66.64</td>
<td>360</td>
</tr>
<tr>
<td>4.75</td>
<td>2</td>
<td>35.13</td>
<td>66.81</td>
<td>358</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>35.47</td>
<td>67.07</td>
<td>357</td>
</tr>
<tr>
<td>5.25</td>
<td>2</td>
<td>35.81</td>
<td>67.20</td>
<td>356</td>
</tr>
<tr>
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<td>2</td>
<td>35.71</td>
<td>67.40</td>
<td>355</td>
</tr>
<tr>
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<td>35.46</td>
<td>67.43</td>
<td>355</td>
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<td>354</td>
</tr>
<tr>
<td>6.25</td>
<td>2</td>
<td>36.51</td>
<td>67.13</td>
<td>353</td>
</tr>
<tr>
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<td>2</td>
<td>36.00</td>
<td>68.12</td>
<td>353</td>
</tr>
<tr>
<td>6.75</td>
<td>2</td>
<td>35.75</td>
<td>68.06</td>
<td>357</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>35.82</td>
<td>67.92</td>
<td>363</td>
</tr>
<tr>
<td>7.25</td>
<td>2</td>
<td>36.13</td>
<td>67.86</td>
<td>353</td>
</tr>
<tr>
<td>7.5</td>
<td>2</td>
<td>35.93</td>
<td>67.22</td>
<td>353</td>
</tr>
<tr>
<td>7.6</td>
<td>2</td>
<td>36.13</td>
<td>67.31</td>
<td>362</td>
</tr>
</tbody>
</table>

Range         ---         2.33  3.55  26    4.51  0.058
APPENDIX C
INTERVARIABLE INTERACTIONS

If two independent variables, x and y, are used to predict a dependent variable, z, with a second order polynomial and are correlated (eqn. 1), then substitutions can be made to (x for y or y for x) allowing the intervariable interactions between x and y to be ignored.

\[ z = Ax^2 + By^2 + Cxy + Dx + Ey \]  
\[ x = 0.5y \]

\[ z = A(0.5y)^2 + By^2 + C(0.5y)y + D(0.5y) + Ey \]
\[ z = (0.25A + B + 0.5C)y^2 + (0.5D + E)y \]  

Furthermore, if one of the independent variables (x or y) has comparatively little influence on the dependent variable, z, it can be ignored.
APPENDIX D

ANSYS CODE FOR EXPORTING PARAMETRIC MODEL RESULTS

!\\\\\\\\\\\\\\\FIRST STEP\\\\\\\\\\\\\\

!This selects the food item and the contact elements attached to the food item, plots a
!contour plot of displacement in the y-direction, changes the font size, creates a table
!for the strain energy and lists the reaction forces in the y-direction

esel,s,mat,,3
nsle,s
esln,s
/POST1
AVPRIN,0, ,
ETABLE, ,SENE,

! /DEV,FONT,LEGEND,MENU
/dev,font,1,Courier*New,400,0,-16,0,0,,

/EFACET,1
PLNSOL, U,Y, 0,1.0

PRRSOL,FY
/replo
!\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\}
esel,s,etable,contpene,0.000001,20,,0
etable,contarea,volu
ssum
APPENDIX E

TOOTHCUSPROC CODE FOR MATLAB

clear
cle

scans=csvread('NMNH545032cp.csv');
limits=csvread('PointsNMNH545032.csv');

% for these scans, the BL direction is in the y-direction and the MD direction is in the x-direction
% The numbers below indicate the points in list limits, i.e. %1 is the first point in limits

% This dictates the location of the cusp
xdmax=limits(1,2); %1
xumax=limits(2,2); %2
yrmin=limits(3,3); %3
yavg=limits(5,3); %5
yrmx=limits(7,3); %7
xdavg=limits(8,2); %8
xuavg=limits(9,2); %9
yrmin=limits(10,3); %10
ylavg=limits(12,3); %12
ylrmx=limits(14,3); %14
xdmin=limits(15,2); %15
xumin=limits(16,2); %16

% This is the coordinates of the cusp tips
uprightx=limits(6,2); %6
uprighty=limits(6,3); %6
downrightx=limits(4,2); %4
downrighty=limits(4,3); %4
upleftx=limits(13,2); %13
uplefty=limits(13,3); %13
downleftx=limits(11,2); %11
downlefty=limits(11,3); %11

% Make sure to set the resolution to the resolution of the scans and accuracy to the R^2 value you would like to use
resolution=.05;
accuracy=.975;

% Now the work can begin. Lets extract the coordinates of all the points for each cusp
i=1; j=1; k=1; l=1;

for n=1:length(scans)
    if scans(n,1)<(max(xumax,xdmax)) & scans(n,1)>(min(xdmin,xumin)) &
        scans(n,2)>(min(ylmin,yrmin)) & scans(n,2)<(max(ylmax,yrmax))
        if scans(n,1)>xuavg & scans(n,1)<xumax & scans(n,2)>yravg & scans(n,2)<yrmax
            Upright(i,1)=scans(n,1);
            Upright(i,2)=scans(n,2);
            Upright(i,3)=scans(n,3);
            i=i+1;
        elseif scans(n,1)>xdavg & scans(n,1)<xdmax & scans(n,2)>yravg &
            scans(n,2)<yrmin
            Downright(j,1)=scans(n,1);
            Downright(j,2)=scans(n,2);
            Downright(j,3)=scans(n,3);
            j=j+1;
        elseif scans(n,1)<xuavg & scans(n,1)>xumin & scans(n,2)>ylavg &
            scans(n,2)<ylmax
            Upleft(k,1)=scans(n,1);
            Upleft(k,2)=scans(n,2);
            Upleft(k,3)=scans(n,3);
            k=k+1;
        elseif scans(n,1)<xdavg & scans(n,1)>xdmin & scans(n,2)>ylavg &
            scans(n,2)<ylmin
            Downleft(l,1)=scans(n,1);
            Downleft(l,2)=scans(n,2);
            Downleft(l,3)=scans(n,3);
            l=l+1;
        end
    end
end

%Export profiles of Upright, Downright, Upleft, and Downleft
i=1; j=1;
for n=1:length(Upright)
    if Upright(n,1)>(uprightx-resolution*.2) & Upright(n,1)<(uprightx+resolution*.2)
        MDupright(i,1)=Upright(n,1);
        MDupright(i,2)=Upright(n,2);
        MDupright(i,3)=Upright(n,3);
        i=i+1;
    end
    if Upright(n,2)>(uprighty-resolution*.2) & Upright(n,2)<(uprighty+resolution*.2)
        BLupright(j,1)=Upright(n,1);
        BLupright(j,2)=Upright(n,2);
        BLupright(j,3)=Upright(n,3);
        j=j+1;
    end
end
end
end
i=1;
j=1;
for n=1:length(Downright)
    if Downright(n,1)>(downrightx-resolution*.2) &
        Downright(n,1)<(downrightx+resolution*.2)
        MDdownright(i,1)=Downright(n,1);
        MDdownright(i,2)=Downright(n,2);
        MDdownright(i,3)=Downright(n,3);
        i=i+1;
    end
    if Downright(n,2)>(downrighty-resolution*.2) &
        Downright(n,2)<(downrighty+resolution*.2)
        BLdownright(j,1)=Downright(n,1);
        BLdownright(j,2)=Downright(n,2);
        BLdownright(j,3)=Downright(n,3);
        j=j+1;
    end
end
i=1;
j=1;
for n=1:length(Upleft)
    if Upleft(n,1)>(upleftx-resolution*.2) &
        Upleft(n,1)<(upleftx+resolution*.2)
        MDupleft(i,1)=Upleft(n,1);
        MDupleft(i,2)=Upleft(n,2);
        MDupleft(i,3)=Upleft(n,3);
        i=i+1;
    end
    if Upleft(n,2)>(uplefty-resolution*.2) &
        Upleft(n,2)<(uplefty+resolution*.2)
        BLupleft(j,1)=Upleft(n,1);
        BLupleft(j,2)=Upleft(n,2);
        BLupleft(j,3)=Upleft(n,3);
        j=j+1;
    end
end
i=1;
j=1;
for n=1:length(Downleft)
    if Downleft(n,1)>(downleftx-resolution*.2) &
        Downleft(n,1)<(downleftx+resolution*.2)
        MDdownleft(i,1)=Downleft(n,1);
        MDdownleft(i,2)=Downleft(n,2);
        MDdownleft(i,3)=Downleft(n,3);
        i=i+1;
    end
if Downleft(n,2)>(downlefty-resolution*.2) & Downleft(n,2)<(downlefty+resolution*.2)
    BLdownleft(j,1)=Downleft(n,1);
    BLdownleft(j,2)=Downleft(n,2);
    BLdownleft(j,3)=Downleft(n,3);
    j=j+1;
end
end

%Sorts the profile so we can reject what we don't want as time goes on
MDupright=sortrows(MDupright,3);
MDupright2=MDupright;
i=1;
while i==1
    avg=0;
    for m=1:length(MDupright)
        %This creates the function that defines the profile
        Aoour(m,1)=1;
        Aoour(m,2)=MDupright(m,2);
        Aoour(m,3)=MDupright(m,2)^2;
        Aoour(m,4)=MDupright(m,2)^3;
        Your(m,1)=MDupright(m,3);
        avg=MDupright(m,3)+avg;
    end
    coeff=Aoour\Your;
    %Determines the coefficients for the best fit function
    Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);
    yur=MDupright(:,2);
    zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
    avg=avg/(length(MDupright));
    SSerryur=0;SStotyur=0;
    %This determines the R^2 value for the curve given the data
    for m=1:length(Aoour)
        SSerryur=(MDupright(m,3)-zur(m))^2+SSerryur;
        SStotyur=(MDupright(m,3)-avg)^2+SStotyur;
    end
    %This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of the cusp and tries again
    Rsquauredyur=1-SSerryur/SStotyur;
    if Rsquaaredyur>=accuracy
        i=10000;
    else
        for l=1:length(MDupright)-2
            for p=1:3
                if Downleft(n,2)>(downlefty-resolution*.2) & Downleft(n,2)<(downlefty+resolution*.2)
                    BLdownleft(j,1)=Downleft(n,1);
                    BLdownleft(j,2)=Downleft(n,2);
                    BLdownleft(j,3)=Downleft(n,3);
                    j=j+1;
                end
            end
        end
    end
    %Sorts the profile so we can reject what we don't want as time goes on
    MDupright=sortrows(MDupright,3);
    MDupright2=MDupright;
    i=1;
    while i==1
        avg=0;
        for m=1:length(MDupright)
            %This creates the function that defines the profile
            Aoour(m,1)=1;
            Aoour(m,2)=MDupright(m,2);
            Aoour(m,3)=MDupright(m,2)^2;
            Aoour(m,4)=MDupright(m,2)^3;
            Your(m,1)=MDupright(m,3);
            avg=MDupright(m,3)+avg;
        end
        coeff=Aoour\Your;
        %Determines the coefficients for the best fit function
        Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);
        yur=MDupright(:,2);
        zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
        avg=avg/(length(MDupright));
        SSerryur=0;SStotyur=0;
        %This determines the R^2 value for the curve given the data
        for m=1:length(Aoour)
            SSerryur=(MDupright(m,3)-zur(m))^2+SSerryur;
            SStotyur=(MDupright(m,3)-avg)^2+SStotyur;
        end
        %This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of the cusp and tries again
        Rsquaaredyur=1-SSerryur/SStotyur;
        if Rsquaaredyur>=accuracy
            i=10000;
        else
            for l=1:length(MDupright)-2
                for p=1:3
                    if Downleft(n,2)>(downlefty-resolution*.2) & Downleft(n,2)<(downlefty+resolution*.2)
                        BLdownleft(j,1)=Downleft(n,1);
                        BLdownleft(j,2)=Downleft(n,2);
                        BLdownleft(j,3)=Downleft(n,3);
                        j=j+1;
                    end
                end
            end
        end
    end
y(l, p) = MDupright(l+2, p);
end
end
clear('MDupright');
MDupright = y;
clear('Aoour'); clear('Your'); clear('avg'); clear('coeff'); clear('Aour'); clear('Bour'); clear('Cour'); clear('Dour'); clear('yur'); clear('zur'); clear('SSerryur'); clear('SStotyur'); clear('Rsquaredyur'); clear('y');
end
if length(MDupright) < 11
i = 10000;
Aour = 5000; Bour = 5000; Cour = 0; Dour = 500;
clear('MDupright');
MDupright = MDupright2;
end
end
% if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2 - 12*Aour*Cour) < 0;
    Xour = (-2*Bour + sqrt(4*Bour^2 - 12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2 - 12*Aour*Cour) > 0;
    Xour = (-2*Bour - sqrt(4*Bour^2 - 12*Aour*Cour))/(6*Aour);
end
RoCMDupright = abs(1/(6*Aour*Xour + 2*Bour))
clear('Aoour'); clear('Your'); clear('avg'); clear('coeff'); clear('Aour'); clear('Bour'); clear('Cour'); clear('Dour'); clear('yur'); clear('zur'); clear('SSerryur'); clear('SStotyur'); clear('Rsquaredyur');

% Sorts the profile so we can reject what we don't want as time goes on
BLupright = sortrows(BLupright, 3);
i = 1;
BLupright2 = BLupright;
while i == 1
    avg = 0;
    for m = 1:length(BLupright)
% This creates the function that defines the profile
        Aoour(m, 1) = 1;
        Aoour(m, 2) = BLupright(m, 1);
        Aoour(m, 3) = BLupright(m, 1)^2;
        Aoour(m, 4) = BLupright(m, 1)^3;
        Your(m, 1) = BLupright(m, 3);
        avg = BLupright(m, 3) + avg;
    end
end
coeff=Aouri;Your; %Determines the coefficients for the best fit function
Aouri=coeff(4);Bouri=coeff(3);Couri=coeff(2);Douri=coeff(1);

yur=BLupright(:,1);
zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
avg=avg/(length(BLupright));
SSerryur=0;SStotyur=0;

%This determines the R^2 value for the curve given the data
for m=1:length(Aouri)
    SSerryur=(BLupright(m,3)-zur(m))^2+SSerryur;
    SStotyur=(BLupright(m,3)-avg)^2+SStotyur;
end

%This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of
the cusp and tries again
Rsquaredyur=1-SSerryur/SStotyur;
if Rsquaredyur>=accuracy
    i=10000;
else
    for l=1:length(BLupright)-2
        for p=1:3
            y(l,p)=BLupright(l+2,p);
        end
    end
    clear('BLupright');
    BLupright=y;
end
if length(BLupright)<11
    i=10000;
    Aouri=5000;Bouri=5000;Couri=0;Douri=500;
    clear('BLupright');
    BLupright=BLupright2;
end
end
%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bouri^2-12*Aouri*Couri)<0;
    Xouri=(-2*Bouri+sqrt(4*Bouri^2-12*Aouri*Couri))/(6*Aouri);
elseif sqrt(4*Bouri^2-12*Aouri*Couri)>0;
    Xouri=(-2*Bouri-sqrt(4*Bouri^2-12*Aouri*Couri))/(6*Aouri);
end
RoCBLupright = \frac{1}{6} \left| \frac{1}{Aour \cdot Xour + 2 \cdot Bour} \right|

clear('Aour'); clear('Your'); clear('avg'); clear('coeff'); clear('Aour'); clear('Bour'); clear('Cour'); clear('Dour'); clear('yur'); clear('zur'); clear('SSerryur'); clear('SStotyur'); clear('Rsquaredyur');

% Sorts the profile so we can reject what we don't want as time goes on
MDdownright = sortrows(MDdownright, 3);
MDdownright2 = MDdownright;
i = 1;
while i == 1
    avg = 0;
    for m = 1:length(MDdownright)  % This creates the function that defines the profile
        Aour(m, 1) = 1;
        Aour(m, 2) = MDdownright(m, 2);
        Aour(m, 3) = MDdownright(m, 2)^2;
        Aour(m, 4) = MDdownright(m, 2)^3;
        Your(m, 1) = MDdownright(m, 3);
        avg = MDdownright(m, 3) + avg;
    end
% Determines the coefficients for the best fit function
coeff = Aour \backslash Your;
Aour = coeff(4); Bour = coeff(3); Cour = coeff(2); Dour = coeff(1);
yur = MDdownright(:, 2);
zur = coeff(1) + coeff(2) * yur + coeff(3) * yur.^2 + coeff(4) * yur.^3;
avg = avg / (length(MDdownright));
SSerryur = 0; SStotyur = 0;

% This determines the R^2 value for the curve given the data
for m = 1:length(Aour)
    SSerryur = (MDdownright(m, 3) - zur(m))^2 + SSerryur;
    SStotyur = (MDdownright(m, 3) - avg)^2 + SStotyur;
end
% This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of
% the cusp and tries again
Rsquaredyur = 1 - SSerryur/SStotyur;
if Rsquaredyur >= accuracy
    i = 10000;
else
    i = 1:
    for m = 1:(length(MDdownright)-2)
        for p = 1:3
            y(l, p) = MDdownright(l+2, p);
        end
    end
end
end
clear('MDdownright');

MDdownright=y;

clear('Aour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('Serryur');clear('SStotyur');clear('Rsquaredyur');clear('y');

end

if length(MDdownright)<1
i=10000;
Aour=5000;Bour=5000;Cour=0;Dour=500;
clear('MDdownright');
MDdownright=MDdownright2;
end
end

%if the second derivative is positive, use one of the solutions of setting the first derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end

RoCMDdownright=abs(1/(6*Aour*Xour+2*Bour))
clear('Aour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('Serryur');clear('SStotyur');clear('Rsquaredyur');
toc

%Sorts the profile so we can reject what we don't want as time goes on
BLdownright=sortrows(BLdownright,3);
BLdownright2=BLdownright;
i=1;
while i==1
avg=0;
for m=1:length(BLdownright)  
%This creates the function that defines the profile
  Aour(m,1)=1;
  Aour(m,2)=BLdownright(m,1);
  Aour(m,3)=BLdownright(m,1)^2;
  Aour(m,4)=BLdownright(m,1)^3;
  Your(m,1)=BLdownright(m,3);
  avg=BLdownright(m,3)+avg;
end

coeff=Aour\Your;  
%Determines the coefficients for the best fit function
Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);
yur=BLdownright(:,1);
zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
avg=avg/(length(BLdownright));
SSerryur=0;SStotyur=0;
%This determines the R^2 value for the curve given the data
for m=1:length(Aoour)
    SSerryur=(BLdownright(m,3)-zur(m))^2+SSerryur;
    SStotyur=(BLdownright(m,3)-avg)^2+SStotyur;
end
%This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of
the cusp and tries again
Rsquaredyur=1-SSerryur/SStotyur;
if Rsquaredyur>=accuracy
    i=10000;
else
    for l=1:length(BLdownright)-2
        for p=1:3
            y(l,p)=BLdownright(l+2,p);
        end
    end
    clear('BLdownright');
    BLdownright=y;
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('SSerryur';clear('SStotyur';clear('Rsquaredyur');clear('y');
end
if length(BLdownright)<11
    i=10000;
    Aour=5000;Bour=5000;Cour=0;Dour=500;
    clear('BLdownright');
    BLdownright=BLdownright2;
end
end
%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
    Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
    Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end
RoCBLdownright=abs(1/(6*Aour*Xour+2*Bour))
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('SSerryur');clear('SStotyur');clear('Rsquaredyur');

MDupleft=sortrows(MDupleft,3);                    %Sorts the profile so we can reject what we don't want as time goes on
MDupleft2=MDupleft;
i=1;

while i==1
    avg=0;
    for m=1:length(MDupleft)                         %This creates the function that defines the profile
        Aoour(m,1)=1;
        Aoour(m,2)=MDupleft(m,2);
        Aoour(m,3)=MDupleft(m,2)^2;
        Aoour(m,4)=MDupleft(m,2)^3;
        Your(m,1)=MDupleft(m,3);
        avg=MDupleft(m,3)+avg;
    end
    coeff=Aoour\Your;                       %Determines the coefficients for the best fit function
    Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);
    yur=MDupleft(:,2);
    zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
    avg=avg/(length(MDupleft));
    SSerryur=0;SStotyur=0;

    %This determines the R^2 value for the curve given the data
    for m=1:length(Aoour)
        SSerryur=(MDupleft(m,3)-zur(m))^2+SSerryur;
        SStotyur=(MDupleft(m,3)-avg)^2+SStotyur;
    end

    %This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of the cusp and tries again
    Rsquauredyur=1-SSerryur/SStotyur;
    if Rsquauredyur>=accuracy
        i=10000;
    else
        for l=1:length(MDupleft)-2
            for p=1:3
                y(l,p)=MDupleft(l+2,p);
            end
        end
    end
clear('MDupleft');
MDupleft=y;
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('SSerruyr');clear('SStotyur');clear('Rsquaredyur');clear('y');
end
if length(MDupleft)<11
i=10000;
Aour=5000;Bour=5000;Cour=0;Dour=500;
end
end
end
%if the second derivative is positive, use one of the solutions of setting the first
%derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end
RoCMDupleft=abs(1/(6*Aour*Xour+2*Bour))
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('SSerruyr');clear('SStotyur');clear('Rsquaredyur');
toc
%Sorts the profile so we can reject what we don't want as time goes on
BLupleft=sortrows(BLupleft,3);
BLupleft2=BLupleft;
i=1;
while i==1
avg=0;
for m=1:length(BLupleft)        %This creates the function that defines the profile
    Aoour(m,1)=1;
    Aoour(m,2)=BLupleft(m,1);
    Aoour(m,3)=BLupleft(m,1)^2;
    Aoour(m,4)=BLupleft(m,1)^3;
    Your(m,1)=BLupleft(m,3);
    avg=BLupleft(m,3)+avg;
end
coeff=Aoour\Your;                  %Determines the coefficients for the best fit function
Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);

yur=BLupleft(:,1);
zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
avg=avg/(length(BLupleft));
SSerryur=0;SStotyur=0;

%This determines the R^2 value for the curve given the data
for m=1:length(Aoour)
    SSerryur=(BLupleft(m,3)-zur(m))^2+SSerryur;
    SStotyur=(BLupleft(m,3)-avg)^2+SStotyur;
end

%This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of
%the cusp and tries again
Rsqauredyur=1-SSerryur/SStotyur;
if Rsqauredyur>=accuracy
    i=10000;
else
    for l=1:length(BLupleft)-2
        for p=1:3
            y(l,p)=BLupleft(l+2,p);
        end
    end
    clear('BLupleft');
    BLupleft=y;
end

if length(BLupleft)<11
    i=10000;
    Aour=5000;Bour=5000;Cour=0;Dour=500;
    clear('BLupleft');
    BLupleft=BLupleft2;
end
end

%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
    Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
    Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end

RoCBLupleft=abs(1/(6*Aour*Xour+2*Bour))
clear('Aoour'); clear('Your'); clear('avg'); clear('coeff'); clear('Aour'); clear('Bour'); clear('Cour'); clear('Dour'); clear('yur'); clear('zur'); clear('SSerryur'); clear('SStotyur'); clear('Rsquaredyur');

% Sorts the profile so we can reject what we don't want as time goes on
MDdownleft = sortrows(MDdownleft,3);
MDdownleft2 = MDdownleft;
i = 1;

while i == 1
    avg = 0;
    for m = 1:length(MDdownleft) % This creates the function that defines the profile
        Aoour(m,1) = 1;
        Aoour(m,2) = MDdownleft(m,2);
        Aoour(m,3) = MDdownleft(m,2)^2;
        Aoour(m,4) = MDdownleft(m,2)^3;
        Your(m,1) = MDdownleft(m,3);
        avg = MDdownleft(m,3) + avg;
    end
    coeff = Aoour\Your; % Determines the coefficients for the best fit function
    Aour = coeff(4); Bour = coeff(3); Cour = coeff(2); Dour = coeff(1);
    yur = MDdownleft(:,2);
    zur = coeff(1) + coeff(2) * yur + coeff(3) * yur.^2 + coeff(4) * yur.^3;
    avg = avg / (length(MDdownleft));
    SSSerryur = 0; SStotyur = 0;

    % This determines the R^2 value for the curve given the data
    for m = 1:length(Aoour)
        SSSerryur = (MDdownleft(m,3) - zur(m))^2 + SSSerryur;
        SStotyur = (MDdownleft(m,3) - avg)^2 + SStotyur;
    end

    % This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of the cusp and tries again
    Rsqsquaredyur = 1 - SSSerryur / SStotyur;
    if Rsqsquaredyur >= accuracy
        i = 10000;
    else
        for l = 1:length(MDdownleft) - 2
            for p = 1:3
                y(l,p) = MDdownleft(l + 2, p);
            end
        end
        clear('MDdownleft');
    end
MDdownleft=y;
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('COUR');clear('Dour');clear('yur');clear('zur');clear('SSerryur');clear('SSotyur');clear('Rsquaredyur');clear('y');
end
if length(MDdownleft)<11
    i=10000;
    Aour=5000;Bour=5000;Cour=0;Dour=500;
clear('MDdownleft');
    MDdownleft=MDdownleft2;
end
end
% if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
    Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
    Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end
RoCMDdownleft=abs(1/(6*Aour*Xour+2*Bour))
clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('COUR');clear('Dour');clear('yur');clear('zur');clear('SSerryur');clear('SSotyur');clear('Rsquaredyur');
toc

% Sorts the profile so we can reject what we don't want as time goes on
BLdownleft=sortrows(BLdownleft,3);
BLdownleft2=BLdownleft;
i=1;
while i==1
    avg=0;
    for m=1:length(BLdownleft) % This creates the function that defines the profile
        Aoour(m,1)=1;
        Aoour(m,2)=BLdownleft(m,1);
        Aoour(m,3)=BLdownleft(m,1)^2;
        Aoour(m,4)=BLdownleft(m,1)^3;
        Your(m,1)=BLdownleft(m,3);
        avg=BLdownleft(m,3)+avg;
    end
    coeff=Aoour\Your; % Determines the coefficients for the best fit function
    Aour=coeff(4);Bour=coeff(3);Cour=coeff(2);Dour=coeff(1);
yur=BLdownleft(:,1);
zur=coeff(1)+coeff(2)*yur+coeff(3)*yur.^2+coeff(4)*yur.^3;
avg=avg/(length(BLdownleft));
SSerryur=0;SStotyur=0;
%This determines the R^2 value for the curve given the data
for m=1:length(Aoour)
    SSerryur=(BLdownleft(m,3)-zur(m))^2+SSerryur;
    SStotyur=(BLdownleft(m,3)-avg)^2+SStotyur;
end
%This tests if the R^2 value is high enough. If it is not, it cuts off part of the bottom of
the cusp and tries again
Rsquaredyur=1-SSerryur/SStotyur;
if Rsquaredyur>=accuracy
    i=10000;
else
    for l=1:length(BLdownleft)-2
        for p=1:3
            y(l,p)=BLdownleft(l+2,p);
        end
    end
    clear('BLdownleft');
    BLdownleft=y;
    clear('Aoour');clear('Your');clear('avg');clear('coeff');clear('Aour');clear('Bour');clear('Cour');clear('Dour');clear('yur');clear('zur');clear('SSerryur');clear('SStotyur');clear('Rsquaredyur');clear('y');
end
if length(BLdownleft)<11
    i=10000;
    Aour=5000;Bour=5000;Cour=0;Dour=500;
    clear('BLdownleft');
    BLdownleft=BLdownleft2;
end
end
%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*Bour^2-12*Aour*Cour)<0;
    Xour=(-2*Bour+sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
elseif sqrt(4*Bour^2-12*Aour*Cour)>0;
    Xour=(-2*Bour-sqrt(4*Bour^2-12*Aour*Cour))/(6*Aour);
end
RoCBLdownleft=abs(1/(6*Aour*Xour+2*Bour))
clear('Aoour'); clear('Your'); clear('avg'); clear('coeff'); clear('Aour'); clear('Bour'); clear('Cour'); clear('Dour'); clear('yur'); clear('zur'); clear('SSerryur'); clear('SStotyur'); clear('Rsquaredyur');

final(1) = RoCMDupright;
final(2) = RoCBLupright;
final(3) = RoCMDdownright;
final(4) = RoCBLdownright;
final(5) = RoCMDupleft;
final(6) = RoCBLupleft;
final(7) = RoCMDdownleft;
final(8) = RoCBLdownleft;

final
%This code is to take enamel and dentin profiles out of binary images and calculates the RoC and enamel thickness. See Chapter 6

clear
clc

enamel=csvread('CPC 39259_LLM2 tooth_1_enamel.csv');
dentin=csvread('CPC 39259_LLM2 tooth_1_dentin2.csv');
accuracy=.975;      %R^2 value
cuspmid=511;        %make sure to figure out the midpoint between the 2 cusp and update this number for every image

[rows,cols]=size(enamel);
[rows2,cols2]=size(dentin);
kid=1;

%This takes the pixel information for the enamel profile and makes it into "Point Cloud" information
for m=1:rows
    for n=1:cols
        if enamel(m,n)>0
            PCenamel(kid,1)=n;            %PC stands for Point Cloud
            PCenamel(kid,2)=rows-m;
            kid=kid+1;
        end
    end
end

kid=1;
%This takes the pixel information for the dentin profile and makes it into "Point Cloud" information
for m=1:rows2
    for n=1:cols2
        if dentin(m,n)>0
            PCdentin(kid,1)=n;
            PCdentin(kid,2)=rows2-m;
            kid=kid+1;
        end
    end
end

start=min(PCenamel(:,1));
start2=min(PCdentin(:,1));

% makes the mesiodistal profile
for m=1:length(PCenamel)
    topenamel(m,(PCenamel(m,1)-start+1))=PCenamel(m,2);
end
for m=1:length(PCdentin)
    topdentin(m,(PCdentin(m,1)-start2+1))=PCdentin(m,2);
end

% Extracts the top of the MD profile
topenamel=max(topenamel);
topenamel=topenamel';
topdentin=max(topdentin);
topdentin=topdentin';

for m=1:length(topenamel)
    TOPenamel(m,2)=topenamel(m);
    TOPenamel(m,1)=(start+m-1);
end
for m=1:length(topdentin)
    TOPdentin(m,2)=topdentin(m);
    TOPdentin(m,1)=(start2+m-1);
end

TOPenamel2=TOPenamel;
kid=length(TOPenamel2)+1;
pop=length(TOPenamel2);

% This fills in the holes in the profile so I can measure the enamel thicknesses
for m=1:(length(TOPenamel2)-1)
    if (TOPenamel2(m,2)-TOPenamel2(m+1,2))>2
        Sam=TOPenamel2(m,2);
        for n=1:((TOPenamel2(m,2)-TOPenamel2(m+1,2))/2-1)
            TOPenamel2(kid,1)=TOPenamel2(m,1);
            TOPenamel2(kid,2)=Sam-2;
            Sam=TOPenamel2(kid,2);
            kid=kid+1;
        end
    end
end

if (TOPenamel2(pop,2)-TOPenamel2(1,2))>2
    Sam=TOPenamel2(pop,2);
    for m=1:((TOPenamel2(pop,2)-TOPenamel2(1,2))/2-1)
        TOPenamel2(kid,1)=TOPenamel2(pop,1);
        TOPenamel2(kid,2)=Sam-2;
        kid=kid+1;
    end
end
Sam=TOPenamel2(kid,2);
kid=kid+1;
end
end

TOPdentin2=TOPdentin;
kid=length(TOPdentin2)+1;
pop=length(TOPdentin2);

%Fills in the holes in the dentin
for m=1:(length(TOPdentin2)-1)
    if (TOPdentin2(m,2)-TOPdentin2(m+1,2))>2
        Sam=TOPdentin2(m,2);
        for n=1:((TOPdentin2(m,2)-TOPdentin2(m+1,2))/2-1)
            TOPdentin2(kid,1)=TOPdentin2(m,1);
            TOPdentin2(kid,2)=Sam-2;
            Sam=TOPdentin2(kid,2);
            kid=kid+1;
        end
    end
end

if (TOPdentin2(pop,2)-TOPdentin2(1,2))>2
    Sam=TOPdentin2(pop,2);
    for m=1:(TOPdentin2(pop,2)-TOPdentin2(1,2))/2-1)
        TOPdentin2(kid,1)=TOPdentin2(pop,1);
        TOPdentin2(kid,2)=Sam-2;
        Sam=TOPdentin2(kid,2);
        kid=kid+1;
    end
end

%finds enamel thickness for a given location on the enamel by determining the minimum
distance between the enamel location and the EDJ
for n=1:length(TOPdentin2)
    for m=1:length(TOPenamel2)
        euclidean(n,1)=sqrt((TOPenamel2(m,1)-TOPdentin2(n,1))^2+(TOPenamel2(m,2)-
            TOPdentin2(n,2))^2);
    end
    [xi,yi]=find(euclidean==min(euclidean(:)));
    euclidean2(m,2)=euclidean(xi(1),1);
end

%finds the enamel thickness for a given location on the EDJ
for n=1:length(TOPdentin2)
    for m=1:length(TOPenamel2)
euclidean3(n,1)=sqrt((TOPdentin2(m,1)-TOPenamel2(n,1))^2+(TOPdentin2(m,2)-TOPenamel2(n,2))^2);
end
[xi2,yi2]=find(euclidean3==min(euclidean3(:)));
euclidean4(m,1)=euclidean3(xi2(1),1);
end

%Now to find the RoC of each cusp

kid=1;
child=1;
for m=1:length(TOPenamel2) %breaks up data into left and right cusp
    if TOPenamel2(m,1)<=cuspmid
        LTOPenamel2(kid,1)=TOPenamel2(m,1);
        LTOPenamel2(kid,2)=TOPenamel2(m,2);
        kid=kid+1;
    else
        RTOPenamel2(child,1)=TOPenamel2(m,1);
        RTOPenamel2(child,2)=TOPenamel2(m,2);
        child=child+1;
    end
end

%start with the cusp on the left

height=max(LTOPenamel2(:,2));
valley=min(LTOPenamel2(:,2));
range=height-
for k=2:(range-1)
    kid=1;
    for l=1:length(LTOPenamel2)
        if LTOPenamel2(l,2)>(height-k)
            newLTOPenamel2(kid,1)=LTOPenamel2(l,1);
            newLTOPenamel2(kid,2)=LTOPenamel2(l,2);
            kid=kid+1;
        end
    end
end

x=newLTOPenamel2(:,1);
y=newLTOPenamel2(:,2);
avg=0;
%This creates the function that defines the profile
for m=1:length(newLTOPenamel2)
    A0(m,1)=1;
    A0(m,2)=newLTOPenamel2(m,1);
Ao(m,3)=newLTOPenamel2(m,1)^2;
Ao(m,4)=newLTOPenamel2(m,1)^3;
Y(m,1)=newLTOPenamel2(m,2);
end

avg=sum(newLTOPenamel2(:,2));

coeff=Ao\Y;                               %Determines the coefficients for the best fit function
A=coeff(4);B=coeff(3);C=coeff(2);D=coeff(1);

yy=coeff(1)+coeff(2)*x+coeff(3)*x.^2+coeff(4)*x.^3;
avg=avg/(length(newLTOPenamel2));
SSerr=0;SStot=0;

%This determines the R^2 value for the curve given the data
for m=1:size(Ao,1)
    SSerr=(newLTOPenamel2(m,2)-yy(m))^2+SSerr;
    SStot=(newLTOPenamel2(m,2)-avg)^2+SStot;
end

Rsqaured=1-SSerr/SStot;

%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*B^2-12*A*C)<0;
    Xo=(-2*B+sqrt(4*B^2-12*A*C))/(6*A);
elseif sqrt(4*B^2-12*A*C)>0;
    Xo=(-2*B-sqrt(4*B^2-12*A*C))/(6*A);
end

RoC=abs(1/(6*A*Xo+2*B));
Matrix(k,1)=Rsqaured;
Matrix(k,2)=RoC;
clear RoC
end

for m=1:length(Matrix)-1;
    matrix(m,1)=Matrix(m+1,1);
    matrix(m,2)=Matrix(m+1,2);
end

i=1;
height2=max(RTOPenamel2(:,2));
valley2=min(RTOPenamel2(:,2));
range2=height2-valley2;
for k=2:(range2-1)
kid=1;
for l=1:length(RTOPenamel2)
    if RTOPenamel2(l,2)>(height2-k)
        newRTOPenamel2(kid,1)=RTOPenamel2(l,1);
        newRTOPenamel2(kid,2)=RTOPenamel2(l,2);
        kid=kid+1;
    end
end
%This creates the function that defines the profile
x2=newRTOPenamel2(:,1);
y2=newRTOPenamel2(:,2);
avg2=0;
for m=1:length(newRTOPenamel2)
    Ao2(m,1)=1;
    Ao2(m,2)=newRTOPenamel2(m,1);
    Ao2(m,3)=newRTOPenamel2(m,1)^2;
    Ao2(m,4)=newRTOPenamel2(m,1)^3;
    Y2(m,1)=newRTOPenamel2(m,2);
end
avg2=sum(newRTOPenamel2(:,2));
%Determines the coefficients for the best fit function
coeff2=Ao2\Y2;
A2=coeff2(4);B2=coeff2(3);C2=coeff2(2);D2=coeff2(1);

yy2=coeff2(1)+coeff2(2)*x2+coeff2(3)*x2.^2+coeff2(4)*x2.^3;
avg2=avg2/(length(newRTOPenamel2));
SSerr2=0;SStot2=0;
%This determines the R^2 value for the curve given the data
for m=1:length(Ao2)
    SSerr2=(newRTOPenamel2(m,2)-yy2(m))^2+SSerr2;
    SStot2=(newRTOPenamel2(m,2)-avg2)^2+SStot2;
end
Rsquaured2=1-SSerr2/SStot2;
%if the second derivative is positive, use one of the solutions of setting the first
derivative equal to zero, if the second derivative is negative, use the other
if sqrt(4*B2^2-12*A2*C2)<0;
    Xo2=(-2*B2+sqrt(4*B2^2-12*A2*C2))/(6*A2);
elseif sqrt(4*B2^2-12*A2*C2)>0;
    Xo2=(-2*B2-sqrt(4*B2^2-12*A2*C2))/(6*A2);
end
RoC2=abs(1/(6*A2*Xo2+B2));

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Matrix2(k,1)=Rsquaured2;
Matrix2(k,2)=RoC2;
end

for m=1:length(Matrix2)-1;
    matrix2(m,1)=Matrix2(m+1,1);
    matrix2(m,2)=Matrix2(m+1,2);
end
i=1;

hold on
scatter(TOPenamel2(:,1),TOPenamel2(:,2))
scatter(TOPdentin2(:,1),TOPdentin2(:,2))
scatter(TOPenamel2(:,1),euclidean2(:,2))
scatter(TOPdentin2(:,1),euclidean4(:,1))

%These matrices hold the results. TOPenamel2 and TOPdentin2 hold the enamel and
dentin profiles, and euclidean 2 and euclidean4 have the enamel thicknesses at the
various locations along the cusp and the EDJ. matrix and matrix2 hold the information
containing the R^2 and RoC values for the left and right cusps, respectively. This
program does not take into account the resolution of the image, so the final results should
be multiplied by the pixel size afterwards to get the proper RoC and enamel thicknesses.

TOPenamel2
euclidean2
TOPdentin2
euclidean4
matrix
matrix2


Patel ND. 2009. Efficient prediction of bite fracture force for hard food items. MS thesis, Department of Mechanical Engineering, University of Massachusetts, Amherst, MA.


